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Systematics within the Zopheridae Complex (Coleoptera: Tenebrionoidea).

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SYSTEMATICS WITHIN THE ZOPHERID COMPLEX (COLEOPTERA: TENEBRIONOIDEA)

by

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DISSERTATION

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DEDICATION

I dedicate this work to my grandmother, Marjorie Heidt, who always encouraged me to follow my passions. Thank you, Grandma. You were the best.

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ABSTRACT

The Ironclad Beetles, Cylindrical Bark Beetles, and Monommatid Beetles are a cosmopolitan family with over 1,700 species worldwide. Now constituting members from three previous families (Zopheridae, Monommatidae, Colydiidae), Zopheridae represent a wide array of morphological diversity and variability. Larvae of most members are fungivores/detritovores, while some are suspected of boring into sound wood. Adults are predaceous or fungivores, and some zopherids have been linked to the spread of fungal disease. Morphologically, adults are hard to separate from other tenebrionoid families. Zopherids can be distinguished by 9-11 segmented antennae with a usually abrupt, 1-3 segmented club, antennal insertions concealed from above, closed mesocoxal cavities, 4-4-4 or 5-5-4 tarsal formula, heteromeroid trochanters, and a tenebrionoid aedeagus. Systematically, the constitution and classification of Zopheridae is not yet settled, and the monophyly of the group with respect to other members of the Tenebrionoidea is in question. The research that follows attemps to rectify the classification of this

taxonomically challenging group by investigating the relationships within and among zopherid members, as well as provide useful tools for the identification of these difficult little brown beetles.

In Chapter 1, I present IroncladID: A Tool for Diagnosing Ironclad and Cylindrical Bark Beetles (Coleoptera: Zopheridae) of North America north of Mexico. This is an interactive electronic key designed to aid in the identification of adult Ironclad and Cylindrical Bark Beetles. A web interface was constructed to house a number of resources for the diagonsis of zopherid beetles including a specially-built Lucid interactive key (available from http://coleopterasystematics.com/ironcladid/index.html). Appendices A–F are located in the Appendices section of this document. Appendix F contains the USDA Announcement for IroncladID and is available as a supplementary file via LoboVault. See PDF titled “Appendix_F_USDA_Announcement”.

In Chapter 2, I present an Illustrated Catalogue and Type Designations of the New Zealand Zopheridae (Coleoptera: Tenebrionoidea). This comprehensive catalogue to the New Zealand members of the family Zopheridae was produced in an effort to stabilize the nomenclature preceding extensive revisionary taxonomy within the group. A checklist of the 17 New Zealand zopherid genera and an account for each of the 189 species (by current combination) is provided. Appendix G contains the figures 1–421 for Chapter 2 and is available as a supplementary file via LoboVault. See PDF titled “Appendix_G_Figures_Chapter2”.

In Chapter 3, I present a Phylogenetic Analysis of the Ironclad and Cylindrical Bark Beetles of the World (Coleoptera: Tenebrionoidea: Zopheridae). I inferred the first molecular phylogenetic hypothesis for Zopheridae. Portions of three genes (28S rDNA, cytochrome c oxidase I and histone III) were analyzed. One hundred eighty three zopherid species were included, representing 2/2 subfamilies, 15/15 tribes, and more than half of the currently recognized genera. Twelve outgroup taxa from eight other families of Tenebrionoidea were included. Parsimony and partitioned Bayesian analyses were performed on the combined data set. In both phylogenetic analyses, Zopheridae was not recovered as monophyletic. The subfamily Zopherinae was not recovered as monophyletic in both analyses, and the subfamily Corticariinae was recovered as monophyletic only in the Bayesian analysis. Appendix H contains the figures 1a–2d for Chapter 3 and is available as a supplementary file via LoboVault. See PDF titled "Appendix_H_Figures_Chapter3".

In Chapter 4, I present Novel Microscopy Techniques Reveal Multiple Evolutionary Origins of Metal Incorporation into Mandibles of the Megadiverse Beetles (Coleoptera). A broad survey of presence/absence of mandibular metals across the order Coleoptera was conducted. To test for phylogenetic signal and evolutionary correlation between presence/absence of metals and adult mandibular use, we constructed a phylogeny under a Bayesian framework from a subsampling of a pre-existing dataset (Hunt *et al.* 2007), performed discrete statistical analyses on character evolution via *BayesTraits Discrete* (Pagel *et al.* 2004), and performed ancestral state reconstructions under both Parsimony and Bayesian frameworks via *Mesquite* (Maddison and Maddison 2011) and *BayesTraits Multistate* (Pagel *et al.* 2004). Resultant patterns of metal incorporation were strongly correlated with adult mandibular use and appear to have originated several times throughout Coleoptera. Additionally, the location and types of cuticular metals are demonstrated to be potentially valuable characters for taxonomic diagnoses. Appendix I contains the figures 1–17 for Chapter 4 and is available as a supplementary file via LoboVault. See PDF titled "Appendix_I_Figures_Chapter4". Appendix J contains the supplementary ESEM-EDS mandibular scans and is available as a supplementary file via LoboVault. See PDF titled "Appendix_J_EDS_Chapter4".

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INTRODUCTION

Zopheridae are a worldwide group of small, litter-dwelling or subcortical beetles that exhibit tremendous morphological diversity. Members of the Zopheridae are thought to include both economically beneficial *and* harmful insects, as several genera (*Colydium*, *Aulonium*, *Nematidium*) are predaceous as both larvae and adults of destructive wood-boring insects, while others have been documented to transmit crop-destroying fungi (Ivie 2002a, b, c; Ślipiński and Lawrence 1997). Thus, studies of the taxonomy and natural history of the group is of economic relevance. Before the economic impact of these beetles can be adequately assessed, however, several major problems persist. As proposed by Ślipiński and Lawrence (1999), Zopheridae (*sensu novo*) contains three previously separate families: the ironclad beetles (Zopheridae=Zopherinae *s.n.*), the monommatid beetles (Monommatidae=Zopherinae *s.n.*), and the cylindrical bark beetles (Colydiidae=Colydiinae *s.n.*) (for classification history of the groups, see Ślipiński and Ivie, 1990: 2–4). As currently constituted, Zopheridae contains nearly 180 genera, 15 tribes, and over 1,700 species (Ślipiński and Lawrence 2010). Despite their relative diversity and decent amounts of taxonomic attention by previous workers, the monophyly of the family is still strongly questioned. Seemingly few characters unite the groups included in Zopheridae, often making identification of its members quite difficult. In reference to the identification of North American Coleoptera, Ivie (2002a: 445) states: "However if it has 4-4-4 tarsi and doesn't fit somewhere else, try this family." Only two comprehensive catalogues to these groups exist: Hetschko (1930) and Ivie and Ślipiński (1990). Hetschko's catalogue validated the assertion of the group as a "wastebasket taxon" (Lawrence 1980: 305), as his concept of the family was later shown to contain members from ~85 genera across 14 other families of Coleoptera *not* currently recognized as Zopheridae (Ivie and Ślipiński 1990: 16-18). Ivie and Ślipiński's catalogue rectified many issues on the generic level, but higher-level groups remained problematic.

In order to address some of the persistent issues revolving around this family, I conducted several independent studies to 1) aid in positive identification of the North American Zopheridae, 2) stabilize the nomenclature of an important New Zealand subset Zopheridae, and 3) construct the first molecular phylogeny of the group in an effort to eludicade relationships between and among members of Zopheridae and other tenebrionoid families. Additionally, a fourth study of a more general scope was conducted on the presence/absence of mandibular metals in beetles.

Chapter 1 introduces IroncladID, an interactive key to the genera and species of North American Zopheridae. A web interface was constructed to house a number of resources for the diagonsis of zopherid beetles including a specially-built Lucid interactive key (available from http://coleopterasystematics.com/ironcladid/index.html). Taxonomic coverage includes 37 genera and 112 species of North American zopherids, representing all known members from the region. The purpose of this tool is to assist non-experts in the identification of a difficult but oft-encountered little brown beetle group. This work was funded by the Center for Plant Health Science and Technology (CPHST), Animal and Plant Health Inspection Service (APHIS), and the U.S. Department of Food and Agriculture (USDA).

Chapter 2 introduces an illustrated catalogue to the New Zealand Zopheridae. A checklist of the 17 New Zealand zopherid genera and an account for each of the 189 species (by current combination) is provided. Type material for nearly all species was examined, and type specimens are designated herein (89 confirmed holotypes, 103 lectotypes, 283 paralectotypes). Images of all primary type specimens and labels examined are provided. *Pycnomerus sulcatissimus* Sharp, 1886 is a junior synonym and secondary homonym of *Pycnomerus sulcatissimus* (Reitter, 1880). One replacement name is proposed, *Chorasus beckae* **nom. nov.**, for *Chorasus subcaecus* (Broun), and 24 new combinations are given.

Chapter 3 introduces the first molecular phylogenetic analyses of the family. Portions of three genes (28S rDNA, cytochrome c oxidase I and histone III) were analyzed. One hundred eighty three zopherid species were included, representing 2/2 subfamilies, 15/15 tribes, and more than half of the currently recognized genera. Twelve outgroup taxa from eight other families of Tenebrionoidea were included. Parsimony and partitioned Bayesian analyses were performed on the combined data set. In both phylogenetic analyses, Zopheridae was not recovered as monophyletic. The subfamily Zopherinae was not recovered as monophyletic in both analyses, and the subfamily Corticariinae was recovered as monophyletic only in the Bayesian analysis.

Chapter 4 introduces a broad study of metal incorporation in beetle mandibles across the order, correlated with a known phlogeny and mandibular use. Using a novel combination of microscopy instrumentation and analytical techniques, we demonstrate the ability to rapidly and inexpensively visualize and analyze elemental incorporation and composition. Utilizing these techniques, we investigated metal incorporation within the mandibles of 117 taxa across the megadiverse order Coleoptera. Several lineages were found to incorporate zinc or manganese into various locations on the mandibular surface. To test for phylogenetic signal and evolutionary correlation between presence/absence of metals and adult mandibular use, we constructed a phylogeny under a Bayesian framework from a subsampling of a pre-existing dataset (Hunt *et al.* 2007), performed discrete statistical analyses on character evolution via *BayesTraits Discrete* (Pagel *et al.* 2004), and performed ancestral state reconstructions under both Parsimony and Bayesian frameworks via *Mesquite* (Maddison and Maddison 2011) and *BayesTraits Multistate* (Pagel *et al.* 2004). Resultant patterns of metal incorporation were strongly correlated with adult mandibular use and appear to have originated several times throughout Coleoptera.

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CHAPTER 1

IroncladID: A Tool for Diagnosing Ironclad and Cylindrical Bark Beetles (Coleoptera: Zopheridae) of North America north of Mexico.

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Appendices A–F are located in the Appendices section of this document. Appendix F contains the USDA Announcement for IroncladID and is available as a supplementary file via LoboVault. See PDF titled “Appendix_F_USDA_Announcement”.

Abstract

IroncladID, an interactive tool for the identification of Ironclad and Cylindrical Bark Beetles of North America north of Mexico is presented herein. Ironclad ID is an interactive electronic key designed to aid in the identification of adult Ironclad and Cylindrical Bark Beetles, a large, worldwide group of diverse, subcortical beetles thought to include both harmful and beneficial species. A web interface was constructed to house a number of resources for the diagonsis of zopherid beetles including a specially-built Lucid interactive key (available from http://coleopterasystematics.com/ironcladid/index.html). Taxonomic coverage includes 37 genera and 112 species of North American zopherids, representing all known members from the region. The purpose of this tool is to assist non-experts in the

identification of a difficult but oft-encountered little brown beetle group. This work was funded by the Center for Plant Health Science and Technology (CPHST), Animal and Plant Health Inspection Service (APHIS), and the U.S. Department of Food and Agriculture (USDA).

Introduction

The beetle family Zopheridae is a cosmopolitan group consisting of two subfamilies (Zopherinae and Colydiinae), 190 genera, and ~1,700 species. The current family is composed of members of 3 separate, previously recognized families: Colydiidae, Zopheridae, and Monommatidae. Members of Zopheridae previously resided within the family Tenebrionidae, but were raised to family rank by Böving and Craighead (1931). The bulk of the diversity lies within the subfamily Colydiinae (1,000+ species), where the generic and tribal concepts are still in a state of flux (Ślipiński and Lawrence 2010). The only major family-level analyses were conducted by Lawrence (1994) and Ślipiński and Lawrence (1999). Much work is needed to solidify the higher level classifications within the family, as well as the specific placement of Zopherinae and sister-group relationships within the Tenebrionoidea.

Biology: Ironclad and Cylindrical Bark Beetles are usually found under bark of dead or dying trees or in the surrounding litter. Some members are strictly found on conifers, others on hardwoods, and a number on both. Many of these beetles are cylindrical in shape and are frequently found in the holes or passages bored by other insects. Members of the Zopheridae are thought to include both economically harmful and beneficial insects.

Risk Taxa: Several zopherid groups may also be destructive, with members frequently associated with particular fungi known to harm or kill valuable hardwood trees. It is speculated that these beetles may play a critical role in the spread of these fungal diseases. *Colobicus parilus* is frequently found on stored roots and fruits and is suspected to transmit Diplodia (Coelomycetes) to yams, sweet potatoes, cassava and citrus. This species is imported in commercial shipments of stored goods (Hinton 1945). *Phloeodalis reitteri* has been recorded as the carrier of *Fusarium moniliforme* var. *subglutinans*, the fungal species causing pineapple gum disease. It has been shown that pineapple crop losses are unusually high when large numbers of the beetle are present, and, when artificially infested with adults, fruits in the flowerings stage rotted in 100% of cases. Several genera (*Bitoma*, *Synchita*, *Microsicus*, *Paha*) are frequently found on dead or dying trees associated with *Hypoxylon*, a fungus that kills many valuable hardwood trees throughout the US. It is possible these beetles play a role in the introduction or transportation of the fungus, although this needs further examination (Stephan 1989). The larvae of several other zopherid groups (Usechini, *Phellopsis*) bore into soft wood in search of fungus. The genera *Phloeodes* and *Zopherus* (Zopherini) also have anatomical modifications as both larvae and adults that suggest the ability to bore into sound wood, many having been collected on or under the bark or roots of *Populus*, *Morus*, *Cayra*, *Pinus*, *Juniperus*, and*Quercus*. These beetles may pose a potential hazard to lumber products. Due to the subcortical, saprophagous/mycophagous nature of these beetles, it is very possible the introduction and subsequent establishment of foreign taxa will be a common occurrence.

Beneficial Taxa: Several genera (*Colydium*, *Aulonium*, *Nematidium*, *Lasconotus*) are frequently encountered in the bored tunnels of platypodine and scolytine ambrosia beetles (*Scolytus*, *Ips*, *Dendroctonus* spp.). These genera (and no doubt numerous others) are thought to be predaceous as both larvae and adults on these destructive beetle pests, serving as potential biological control agents (Ivie 2002a; Ślipiński and Lawrence 2010; Stephan 1989).

Geographic Distribution: Ironclad and Cylindrical Bark beetles are distributed worldwide, with highest diversity in the Neotropics and Australasia. In North America, 37 genera and ~112 species are known to occur. In the United States, zopherids are found in every state. In Canada, zopherids occur in all provinces and territories except for Yukon, Nunavut, Nova Scotia, Prince Edward Island, and Labrador (Newfoundland) (Ivie 2002).

Accurate identification of zopherid species or even genera is often difficult due to the lack of available resources. This tool was constructed as an attempt to remedy this issue. IroncladID includes an interactive Key to Genera & Species, Genus Fact Sheets, species diagnoses, and hundreds of images to aid in the identification of Ironclad and Cylindrical Bark Beetles found in North America north of Mexico. Upon completion, the tool was peer reviewed by a number of taxonomic experts and then released for distribution. This tool is currently included in the larger USDA Wood Boring Beetle Resource, a comprehensive resource of identification and screening tools for wood boring beetles of the world (available from: http://wbbresource.org/).

Materials and Methods

Web-Based Interface

Web Site: A web site was constructed to serve as the web-based interface for IroncladID. Individual pages contain general information on Zopheridae including biological information, diagnostic features of zopherid subfamilies and tribes, geographic distribution, and taxonomy. The website also includes access to the Lucid key, explanations of how to run the key, feature/state definitions, genus fact sheets, an extensive gallery, a morphological atlas, a glossary, complete references, and supplemental material. The website is available from the following address (last updated 05 June, 2011): http://coleopterasystematics.com/ironcladid/ All web design and code was written by EHN.

Lucid Key: A Lucid key to the genera and species of North American Zopheridae was constructed in LucidBuilder v.3.5. Potential morphological characters suitable for key construction were taken from the literature and improved upon via specimen study. In an attempt to account for morphological variability within and between genera and species, roughly 1,000 specimens were loaned from the United States National Museum (USNM – Washington, D.C., USA) and the Florida State Collection of Arthropods (FSCA – Gainesville, FL, USA). Exclusively external morphology was used, as an important feature of the Lucid framework is the selection and construction of characters, terminology, and keys as to optimize utility and ease-of-use to a broad audience of non-specialists. The external morphology was scored for nearly all species according to the key features and states. Species not available for study were scored from the literature. The LucidBuilder matrix is available upon request. Before you start the key, please visit the Ironclads and Cylindrical Bark Beetles page. Also, the key assumes that you have access to a dissecting microscope with strong lighting. This is needed in order to see the morphological details such as the antennal club, elytral ornamentation, etc.

Fact Sheets: Fact sheets were created for each genus. A fact sheet includes a diagnosic description, similar genera, known distribution within North America north of Mexico, biology/natural history (if known), relative abundance, a list of North American species, species diagnoses and distributions (if more than one species present), discussion, potential problems with identification, and selected references. Information for the fact sheets was compiled from the literature, specimens, specimen label data, and personal observations and collection by NPL.

Gallery / Imaging: Color habitus images were captured using a Visionary Digital™ Passport and BK Plus imaging systems equipped with a Canon 40D and/or 7D DSLR camera. Image stacks were montaged in Zerene Stacker v.1.04 (Zerene Systems LLC, Richland, WA, USA). Images were edited in Adobe Photoshop CS5 v.12.0.4. Dorsal habitus images were taken for all genera and nearly all species of North American Zopheridae and are displayed in a gallery arranged by genus. An images of each species is also linked on the genus fact sheets, as well as the Lucid key entities (viewable during key operation).

Morphological Atlas / Illustrations: Line drawings were digitally rendered in Adobe Illustrator CS5, v.15.0.2 (Adobe Systems, Inc., San Jose, CA, USA). A morphological atlas was constructed to aid in the identification and recognition of major morphological structures of a typical zopherid utilized in the key (*Zopherus* illustrated).

Lucid3 System Requirements

The interactive key to the ironclad and cylindrical bark beetles is a Lucid3 Java Applet. Lucid3 (Lucid version 3) is software for creating and using interactive identification keys. Lucid was developed by the QAAFI Biological Information Technology at the University of Queensland in Australia. Visit the Lucidcentral website for more information on Lucid and Lucid3.

HTML pages in Ironclad ID outside of the Lucid3 interactive key are viewable without the Lucid3 Applet Player. Please check the Lucid3 system requirements below if you would like to use the interactive key.

Operating System: Windows 2000 (SP3)/XP/Vista, Mac OSX 10.4 or greater, Linux (that supports J2RE), Solaris 7-10. (The key will run on Windows 98/ME/NT4 but these platforms are no longer supported.)

System Memory: 256MB RAM (512MB or greater recommended).

Web browser: Java-enabled web browser such as Internet Explorer, Firefox, Chrome, or Safari. Note: You may need to adjust your browser settings to allow pop-ups *and* active content (this particularly applies to Internet Explorer) when viewing the key as a Java applet.

Hard Drive Space: 150MB if running tool from hard drive (excluding space required for Java Runtime Environment and web browser).

Software: The Lucid3 interactive keys will run embedded within a web browser as a Java applet Player. Java Runtime Environment (JRE) version 1.4.2 (1.5 or greater recommended) must be installed on your computer for the Lucid3 Applet Player to run successfully.

How to Use This Key

<u>Structure and format:</u> The Lucid interactive key is a Java applet embedded in an HTML page. For information about Java and other computer settings required in order to use the key, see the <u>System Requirements</u> page.

The Lucid key has four panels. Each feature in the Features Available panel is listed above two or more of its states (also referred to as feature states). For example, "straight or nearly so" and "at least slightly curved" are two states of the feature "Antennomere III shape." Depending on the viewing mode, each state is shown alongside or under a state illustration or icon. State illustrations are indicated by icons, thumbnails, or gallery view, depending on the display options you choose under Features > Display. Once a state has been chosen, it will appear in the lower left Features Chosen panel. The taxa that match the chosen features are displayed in the upper right Entities Remaining panel, while those that do not will be moved to the Entities Discarded panel in the lower right corner.

Each genus in Entities Remaining (possible genera) is linked to an HTML fact sheet page containing informational text and images. This page is indicated by a grey icon to the right of the image or image icon. Each genus is also linked directly to a lateral view image of that entity. Images for each genus are indicated by icons or thumbnails, depending on the display options you choose.

NOTE: web pages such as fact sheets attached to items in Lucid v 3.4 interactive key matrices may be considered pop-ups by certain browsers (such as Internet Explorer [IE]) when clicked on by users. If your browser blocks these pop-ups, in your browser's Internet settings you should change the settings to allow pop-ups for this Lucid tool.

Additionally, Internet Explorer may block "active content" on web pages or interactive keys. To allow active content: in Internet Explorer under Tools, Internet Options, Advanced tab, Security category, the box next to the setting "Allow active content to run in files on My Computer" should be checked. Additionally, certain settings under Tools, Internet Options, Security, Custom level, ActiveX controls and plug-ins, may need to be changed depending on your computer settings.

Clicking on an image thumbnail or icon (or, if in state gallery view, on the small corner square within the gallery thumbnail) opens an image window. This image window provides access to all images linked to that taxon or state, as well as to images linked to other taxa or states, via arrows and indices in the image window toolbar.

Making an identification: recommendations for using the interactive key: The first suggested step to take is to go to the Ironclads > Diagnostic Features page. Using simple characters, this page shows how to confirm your specimen is an ironclad and not something similar. Once you know that your specimen is an ironclad, you can proceed to the key.

A good way of proceeding into the key is to select what you believe is a strong character in your subject. You may also choose to use Lucid's "Best" mode, which will take you to the feature that will most effectively reduce the number of entities remaining. For this, go to "Features" and select "Best" from the menu, or select the "magic wand" icon in the menu bar. The features are organized (top to bottom) by body, head, thorax, elytra, wings, legs, and abdomen.

For convenience, technical terms used in this tool are defined in the glossary;

however, users may find it worthwhile to familiarize themselves with general morphological features such as antennal club, elytra, pronotal disc, and so on, prior to starting the key. Understanding these terms will allow the user to navigate more effortlessly though the identification of a specimen. Note: this page adapted from Bark Beetle Genera of the United States.

“Best” mode: In order to allow for the fastest identification possible, it is strongly encouraged the user make use of the "Best" feature in the Lucid3 player. This button (located on the top tool bar, represented as a magic wand) automatically selects the "best" character for you to use. Once selected, the key will automatically jump to the next "best" character, re-calibrated due to your previous selections.

Limitations of the Key: This key has been constructed for identifying all genera and species of Ironclad and Cylindrical Bark Beetles known to occur in North America north of Mexico. This key does not include taxa known to occur in Mexico. It is very possible (and likely) additional zopherid taxa have been and will be introduced into or discovered within North America. If you believe you have a specimen that does not properly key to a listed entity, please contact the key author.

Feature / State Explanations

Occasionally, a character is presented that may be too difficult, may not be visible, or perhaps may not be known for a given specimen (e.g., the head has fallen off, or there is no locality data, or it is a "male" character and you are unsure of the sex). In these situations, it is advisable to select the "Next best" button and skip to the next best feature remaining. This course of action is preferred over guessing at the states of features if you are unsure. Given below are definitions and explanations for the features and states that may be interpreted differently and/or sometimes appear ambiguously.

GEOGRAPHIC OCCURRENCE

Regional occurrence: this is based on an observation by Karl Stephan (1989) that while many of the genera are widely distributed throughout North America, the vast majority of the species either occur on the eastern or western side of the 100th meridian. This is a very useful distributional character. The 100th meridian passes through more or less the center of North Dakota and South Dakota, the western 1/3 of Nebraska and Kansas, the handle of Oklahoma, and the western 1/3 of Texas (see image).

State occurrence: this character is only scored for the taxa where occurrence in a particular state or states within the United States aids in identification. This scoring is by no means comprehensive and should not necessarily be used to completely eliminate taxa, as new distributions will undoubtedly be discovered.

BODY

General Shape: *Elongate, cylindrical* is defined as the length being several times the width of the beetle, and there is little question of the cylindrical nature (e.g. *Nematidium, Eudesma, Lobogestoria, Antilissus*).

Flattened or sub-depressed is defined as the body not distinctly elongate and cylindrical, but not dorsally and ventrally convex. This is the standard state for most of the Zopheridae of this region, and encompasses a variety of forms.

Oval, dorsally and ventrally convex is defined as distinctly oval or elliptical in shape with the lateral margins nearly evenly curved throughout, and both dorsal and ventral surfaces exhibiting some degree of convexity. This is found within the Monommatini (*Hyporhagus*, *Spinhyporhagus*, and *Aspathines*).

HEAD

Antennae

Antennal club – Number of segments: The antennal club is here defined as beginning with the antennomere that is a departure in size or shape from the previous antennomeres. While the club segments may be indistinct in some (*Rhagodera*), usually the 9th, 10th, or 11th antennomere is greatly enlarged or of a different shape than the preceding segments. In some taxa (e.g. *Eucicones*), the terminal segment bears an annulation in which the apical half is densely setose. This setose portion may be mistaken for a distinct segment, but should not be scored as such. To define seperate segments, there should be a very clear line separating antennomeres from one another, and generally a difference in size of the club segments, with the connecting margins not completely flush (e.g. *Lobogestoria*, *Endeitoma*).

Antennal club – structure: *Loose* is defined as the club segments not completely abutting one another, with the connecting margins not completely flush. The segments may be very loose (e.g. *Rhagodera*) to slightly loose (e.g. *Coxelus*). All taxa with a 1-

segmented club were scored as "compact."

Compact is defined as the club segments completely abut one another, the connecting margins being completely flush (e.g. *Acolobicus*). If one antennomere is distinctly smaller than the other but flush with the preceding (e.g. *Endeitoma*), this was scored as "compact."

Mouthparts

Labial palpi insertion – separation: *Approximate* is defined by the insertions of the labial palpi being nearly approximate, with little discernable space between each palpus that the base. This is the most common state for the group (e.g. *Nematidium*).

Moderately to widely separated is defined by the bases of the labial palpi being distinctly separated from one another (e.g. *Phloeodes*).

Head Capsule

Antennal groove beneath eye – Presence: *Antennal groove absent* is defined as lack of a clear, well-delimited groove or channel below the eye in which the antennae rests when retracted. Several taxa (e.g. *Coxelus*) have a raised subgenal brace and a clearly protruding eye, but the space between the eye and subgenal brace is wide and slightly depressed. This is not considered an antennal groove because it is not delimited. Other taxa have a clearly delimited antennal groove/cavity on the prothoracic hypomeron, but no distinct groove on the head capsule itself (e.g. *Usechus, Usechimorpha, Zopherus*). In this case, the antenna rests across the eye and then fits into the hypomeral antennal groove.

Antennal groove present is defined as the presence of a clear, well-delimited groove or channel below the eye in which the antennae rests when retracted. This groove may be short or long, extending to hind margin of eye or beyond (e.g. *Eucicones*, *Acolobicus*), straight or curved. In some, the antennal groove is simply a clearly depressed (but defined) area near the antennal insertion.

Eyes

Eye facets: *Eye facets fine* is defined as the individual eye facet not distinctly protruding, eye facets more or less forming a smooth surface.

Eye facets coarse is defined as the individual eye facet distinctly protruding, eye facets more or less forming a rough, raspberry like surface.

THORAX

Prothorax – Pronotum

Mid-lateral secretory pore: *Pronotum with obvious mid-lateral secretory por*e is defined as the presence of a clear pore near the lateral margin of the pronotum at middle. This pore secretes an exudate which aids in the adherence of debris to the dorsal surface, therefore the specimen must be thoroughly cleaned for the pore to be visible. This character is only present in two genera (*Lobogestoria*, *Antilissus*)

Pronotum without mid-lateral secretory pore is defined as no such pore being present.

Pronotal width – anterior and posterior: *Pronotum distinctly wider anteriorly than* *basally* is defined by the anterior portion of the pronotum greatly expanded, or the pronotum tapering strongly towards the base. This should not be scored if the lateral margins are arcuate with the anterior portion only slightly wider than basal portions.

*Pronotum subquadrate or distinctly wider basally than anteriorl*y is defined as the pronotal width being nearly equal or distinctly wider basally than anteriorly. This should be scored if the lateral margins are arcuate with the anterior or basal portion slightly wider than opposite portions.

Sublateral carinae on pronotal disc – presence: *Pronotum with paired sublateral carinae* is defined by the presence of a distinct pair of carinae located sublaterally on the pronotal disc. Most often, these carinae are straight to subtly curved to slightly sinuate, but never complexly sinuate or forming an interlacing network (as in *Sesaspis*, *Lasconotus*).

Pronotum lacking paired sublateral carinae is defined by the absence of a distinct pair of carinae located sublaterally on the pronotal disc. In cases where the pronotal carinae (if present at all) are complexly sinuate or forming an interlacing network (as in *Sesaspis*, *Lasconotus*), this was scored as lacking.

Metathorax – Metacoxae

Metacoxal separation: *Metacoxae nearly contiguous or narrowly separated, intercoxal process usually acute* is defined at the distance between the metacoxae distinctly less than 0.75x the width of one coxa.

Metacoxae moderately to widely separated, intercoxal process usually broadly *rounded to truncate* is defined at the distance between the metacoxae around or more than 0.75x the width of one coxa.

ELYTRA

<u>Elytral ornamentation:</u> *Elytra without carinae or tubercles* is defined as the lack distinct, cuticular carinae and/or tubercles on the elytra. Raised areas of setae are not considered tubercles, and elytral intervals that are slightly elevated (but not distinctly raised or keeled, as in some *Lasconotus*) are not considered carinate.

Elytra with carinae or tubercles is defined as the presence of distinct, cuticular carinae and/or tubercles on the elytra. In some taxa (e.g. some Lasconotus), suberect setae that converge at the elytral margins may give the impression of underlying carinae, but in fact are not. There must be distinct tubercles or well-defined carinae for the state to be scored.

<u>Elytra color/pattern – presence:</u> *Elytra solid colored, patterned* is defined as the cuticle of the elytra unicolorous, not creating a distinct, clearly visible pattern, regardless of setae color.

Elytra bi-colored and with patterns/maculations is defined as the cuticle of the elytra varying in color to create a distinct, clearly visible pattern. Setae that are lighter or darker in color than the elytra and form a pattern should not be scored.

LEGS

<u>Protibia – spine:</u> *Apex of protibia without stout, apical spine(s)* is defined as lacking any sort of distinct, stout, curved spine or pair of straight, stout spines.

Apex of protibia armed with single, stout, curved apical spine is defined as having such spine (e.g. *Aulonium*, *Colydium*, *Lasconotus*, *Nematidium*). Generally the spine is as long as or slightly longer than the first tarsomere. For taxa in which the apex of the protibia bears a single short spine or row of spines, these should not be scored for this state.

Apex of protibia armed with two subequal, short, stout, straight spines: In some taxa (most Zopherini), the apex of the protibia (and usually all tibia) bears a single or pair of straight, short, stout spines. These are distinct from the previous state in that they are shorter, paired, and not distinctly curved.

Identifying Ironclad and Cylindrical Bark Beetles

The family Zopheridae is an extremely diverse assemblage of beetles that, at one time or another, have been a part of 3 separate families (Monommatidae, Zopheridae, Colydiidae). Due to this tremendous heterogeneity, it can often be difficult to correctly identify a zopherid based on any consistent set of diagnostic features. In general, zopherids possess the following features: antennae 9-11 segmented with a usually abrupt, 1-3 segmented club, antennal insertions concealed from above, closed mesocoxal cavities, 4-4-4 or 5-5-4 tarsal formula, heteromeroid trochanters, and a tenebrionoid aedeagus (male genitalia). Due to the great diversity within the group, it is useful to state the diagnostic features of the subfamilies and tribes found in North America to better help separate identifiable groups. Note: the characters listed can be regarded as superficial and cannot be applied to all members of the group on a worldwide scale. The characters given below should be used strictly for the fauna found in North America.

Colydiinae : 4-4-4 tarsi (also found in *Pycnomerus* in Zopherinae) (sometimes appearing 3-3-3), antennal insertions concealed from above, antennae 10- to 11-segmented with an abrupt 1-3 segmented club, open procoxal cavities (most) or with closed procoxal cavities (some; if closed, then apex protibia bearing a stout, curved spine); procoxae usually narrowly separated.

Zopherinae: 5-5-4 tarsi (except 4-4-4 in *Pycnomerus*), closed procoxal cavities (most); procoxae usually broadly separated; eyes narrower, extending well onto dorsal surface of head (except eyes round in *Pycnomerus*).

Colydiinae

Tribe: **Colydiini**: Includes the North America genera *Aulonium* and *Colydium*.
Diagnostic features: With paired, lateral carinae on pronotum; eye emarginated, with canthus (also in some Synchitini); apex of protibia bearing a stout, curved spine; antennae 11-segmented with 3 segmented antennal club; procoxal cavities closed.

Tribe: **Synchitini**: Includes the North American genera *Acolobicus*, *Antilissus*, *Bitoma*, *Colobicus*, *Coxelus*, *Denophloeus*, *Endeitoma*, *Eucicones*, *Eudesma*, *Lasconotus*, *Lobogestoria*, *Lyreus*, *Megataphrus*, *Microprius*, *Microsicus*, *Namunaria*, *Neotrichus*, *Paha*, *Phloeonemus*, *Pseudocorticus*, *Stephaniolus*, *Synchita*.
Diagnostic features: This is a very diverse group and difficult to diagnose. In most cases, apex of protibia lacking a stout, curved spine (except present in*Lasconotus*); antennae 10-

11 segmented with a 1- or 2-segmented club (3-segmented in *Lasconotus,* some *Bitoma*); antennae lacking scale-like setae; procoxal cavities open (closed in *Lasconotus*).

Tribe: **Adimerini**: Includes the North America genus *Monoedus*.
Diagnostic features: Tarsomere 1 greatly enlarged, often concealing tarsomere 2 or 2+3; antennae 10-segmented with a small, 1-segmented club.

Tribe: **Rhagoderini**: Includes the North America genus *Rhagodera*.
Diagnostic features: Wingless; narrow hind-coxae; antennae 11-segmented with weak, gradual, 3-segmented club; antennae with scales.

Tribe: **Nematidiini**: Includes the North America genus *Nematidium*.
Diagnostic features: Long, cylindrical body; mandibular bases exposed; antennae 11 segmented with 2-segmented club; procoxal cavities closed.

<u>Zopherinae</u>
Tribe: **Zopherini**: Includes the North America genera *Zopherus*, *Sesaspis*, and *Phloeodes*.
Diagnostic features: body large, constricted between prothorax and pterothorax; antennae 9-10 segmented; eyes extending well onto dorsal surface of head but not nearly meeting; hypomeron with at least some development of an antennal cavity; procoxal cavities closed; scutellum not visible; tarsal formula 5-5-4.

Tribe: **Pycnomerini**: Includes the North America genus *Pycnomerus*.

Diagnostic features: Body small, parallel-sided, glabrous, often shiny; eyes not extending well onto dorsal surface of head; hypomeron lacking antennal cavities; procoxal cavities closed; elytra with distinct puncture rows/striae; tarsal formula 4-4-4.

Tribe: **Phellopsini**: Includes the North America genus *Phellopsis*.

Diagnostic features: body large, constricted between prothorax and pterothorax; antennae 11-segmented; eyes extending well onto dorsal surface of head but not nearly meeting; hypomeron lacking antennal cavities; procoxal cavities open; scutellum visible; tarsal formula 5-5-4.

Tribe: **Usechini**: Includes the North America genera *Usechus* and *Usechimorpha*.

Diagnostic features: body smaller, constricted between prothorax and pterothrax; antennae 11-segmented with a 3-segmented club; pronotum with distinctive dorsal antennal grooves; eyes extending well onto dorsal surface of head but not nearly meeting; dorsal surface with setae; tarsal formula 5-5-4.

Tribe: **Monommatini**: Includes the North America genera *Hyporhagus*, *Spinhyporhagus*, and *Aspathines*.

Diagnostic features: body oval, dorsally convex, glabrous; procoxal cavities open; eyes extending well onto dorsal surface of head, nearly meeting; 4 abdominal ventrites connate; hypomeron with distinct antennal groove to receive antenna.

Fact Sheets

Below are the fact sheets for North American zopherid genera.

<u>Genus: *Acolobicus*</u>

Diagnostic Features

Description: Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves present, as long as eyes. Eyes large, well-developed, facets moderately coarse. Pronotal disc convex, with several pair of faint. weak carinae. Lateral pronotal margins widest posteriorly, distinctly explanate. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra unicolored, weakly carinate with two fine, well-separated puncture rows between carinae. Elytral margins slightly explanate. Tarsal formula 4-4-4.

Similar genera: The genus *Acolobicus* is similar in general appearance to the genus *Eucicones*. The absence of carinae on the pronotal disc, presence of thick, flattened, club-shaped setae and variegated dorsal surface serve to distinguish *Eucicones*.

Known Distribution

Southeast (SC, FL), South Central (TX) USA.

Biology

Acolobicus erichsoni has been collected at UV/MV lights or from under the bark of dead trees.

Abundance: Uncommon.

North American Species (1)

Acolobicus erichsoni (Reitter, 1877)

Potential Problems with Identification

Stephan (1989) and Ivie (2002a) remark that the genus has 10-segmented antennae with a distinct 1-segmented club. Upon close examination, it appears *Acolobicus erichsoni* has a 2-segmented club with the club segments compact, of equal size and completely flush, superficially resembling a 1-segmented club.

Selected References

Ivie 2002a, Reitter 1877b, Stephan 1989.

Genus: *Antilissus*

Diagnostic Features

Description: Body cylindrical. Antennae 10-segmented with a distinct, 1-segmented club. Antennal setation sparse. Subantennal grooves present, extending behind eyes. Eyes small coarsely faceted, with scale-like interfacetal setae. Head with small, distinct temples behind eyes. Pronotal disc convex, lateral margins and pronotal disc with distinct network of pits, grooves and channels, raised areas with short, flattened, pale setae. Procoxal cavities closed. Metacoxae narrowly separated, separation less than metacoxal length. Elytra with distinct striae composed of coarse punctures. Abdominal ventrites 1-3 connate, ventrite 5 with a deep preapical groove. Tarsal formula apparently 3-3-3 (actually 4-4-4, tarsomeres 1 and 2 partially fused). Dorsal surface with short, flattened, pale setae.

Similar genera: The genus *Antilissus* is similar to the genus *Lobogestoria* in having an apparently 3-3-3 tarsal formula and grooved pronotum, but *Lobogestoria* is easily distinguished by the large, horn-like projections of the pronotum extending well over the head. Superficially, *Antilissus* resembles the genus Neotrichus, but the 1-segmented antennal club and distinctive network of pits, grooves and channels of the pronotum serve to distinguish *Antilissus.*

Known Distribution

Known only from Hawai'i, USA.

Biology

Antilissus aper have been collected off of *Sideroxylon* (Sapotaceae).

Abundance: Rarely encountered.

North American Species (1)

Antilissus aper Sharp, 1879

Selected References

Ivie 2002a, Sharp 1879**,** Ślipiński and Lawrence 1997.

Genus: *Aspathines*

Diagnostic Features

Description: Body small, convex, round to oval, size under 3 mm. Antennae 11-segmented with a 2-segmented club. Antennal setation sparse. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Groove around dorsal edge of eye paralleling eye facets for entire length. Lateral margins of pronotum arcuate. Pronotal disc simple. Hypomeron with deep antennal cavities. Antennal groove and cavity recurved dorsally, meeting or nearly meeting lateral margin of hypomeron. Antennal cavity not concealed by prothoracic leg when retracted. Procoxal cavities open. Metacoxae widely separated, separation as wide or wider than metacoxal length. Scutellum small, triangular, visible. Abdominal ventrite 5 simple. Tarsal formula 5-5-4. Dorsal surface punctate, glabrous, shiny.

Similar genera: The genus *Aspathines* is similar to the monommatine genera *Hyporhagus* and *Spinhyporhagus*, can immediately be distinguished by the smaller size and more oval body, the 2-segmented antennal club, the antennal groove and cavity strongly recurved dorsally and ending near lateral margin of hypomeron, and the antennal cavity not concealed by the prothoracic leg when retracted.

Known Distribution

Southeast (FL) USA.

Biology

Members of the Monommatini are associated with rotting vegetable matter and are suspected to feed on fungus (Ivie 2002)

Abundance: rare.

North American Species (1)

Aspathines aenus ovatus Champion, 1888

Species Diagnoses

***Aspathines aenus ovatus*:** This is the only member of the genus thought to occur in North America. The description and differentiation from similar genera above serve to distinguish this species from all other North American monommatines. NOTE: Several subspecies are recognized, but due to the need of revisionary work on the genus, only the subspecies *A. aenus ovatus* will be referred to in this resource.

Known Distribution

Florida Keys, Florida, USA.

Discussion

This predominantly occurs from Paraguay to Mexico, and it is possible it may be found in the border states.

Potential Problems with Identification

If correctly identified to Zopheridae, the small size and antennal characters will easily separate this species from all others.

Selected References

Champion 1888, Freude 1993, Ivie 2002b

Genus: *Aulonium*

Diagnostic Features

Description: Body elongate, subcylindrical to subdepressed. Antennae 11-segmented with a 3-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes ovate, well-developed, coarsely faceted. Eyes emarginate anteriorly by projection of frons, forming a distinct canthus. Pronotum subquadrate to elongate, sides nearing parallel. Pronotal disc often with pair of sublateral carinae and pair of faint submedial lines, anterior portion of disc usually with pair of sulci or knob-like tubercles. Procoxal cavities narrowly closed. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Apex of protibia expanded, armed with a stout, apical spine. Dorsal surface glabrous, moderately shiny.

Similar genera: The genus *Aulonium* is superficially similar in general appearance to *Colydium*. The carinate elytral declivity and presence of a pair of long setae near the apical margin of the last abdominal ventrite serve to distinguish *Colydium*. The genus *Phloeonemus* also has emarginated eyes formed by a projection of the frons, but is readily distinguished from *Aulonium* and *Colydium* by the 2-segmented antennal club, lack of a stout apical spine on the protibia, explanate lateral pronotal margins, very different sculpturing of the pronotal disc.

Known Distribution

Northwest (ID, MT, OR, WA), Southwest (AZ, CA, CO, NM, NV, UT), North Central (SD, IL, IN, MI, OH), Northeast (DC, DE, NJ, NY, MA, MD, PA, WV, VA), Southeast (AL, FL, GA, KY, NC, SC, TN), South Central (AR, LA, MS, OK, TX) USA, and British Columbia, Canada.

Biology

Aulonium has been collected at MV/UV lights and from under the bark of various dead hardwoods and conifers. Adults and larvae of *Aulonium* have been found in the galleries of scolytine weevils (Curculionidae), and they are suspected to feed on the larvae of those beetles within the galleries (Ivie 2002; Craighead 1920; Marshall 1978; Podoler *et al.* 1990). This genus is a beneficial insect, attacking destructive wood boring beetles.

Abundance: Moderately common.

North American Species (5)

Aulonium aequicolle LeConte, 1859

Aulonium ferrugineum Zimmermann, 1869

Aulonium longum LeConte, 1866

Aulonium parallelopipedum (Say, 1826)

Aulonium tuberculatum LeConte, 1863

Species Diagnoses

***Aulonium aequicolle*:** Western species. Pronotum quadrate, as long as wide. Anterior pronotal margin nearly straight. Sublateral carinae slightly curved basally, not distinctly raised anteriorly, merge with raised anterior margin of pronotum. Submedial lines diverge apically and basally, narrowed in apical 1/3. Pronotal disc more or less convex, slightly depressed in between submedial lines. Tubercles of anterior margin of pronotum not sexually dimorphic – in both sexes tubercles extremely reduced or absent. Strial rows of elytra distinct, punctures larger. Color usually piceus. Rarely collected. Associated with oaks.

Distribution: Arizona, California, USA.

***Aulonium ferrugineum*:** Eastern species. Body more elongate, 3.6x longer than wide. Pronotum nearly quadrate, distinctly longer than wide. Anterior pronotal margin concave. Sublateral carinae straight basally, distinctly raised and strongly carinate anteriorly. Tubercles of anterior margin of pronotum not sexually dimorphic – in both sexes tubercles extremely reduced or absent. Submedial lines parallel in anterior half, diverging in basal half. Pronotal disc more or less convex, slightly depressed in between submedial lines. Strial rows of elytra indistinct, punctures minute. Color ferrugineous throughout. Associated with pines.

Distribution: Pennsylvania, Florida, Georgia, Oklahoma, Texas, Alabama, North Carolina, South Carolina, USA.

***Aulonium longum*:** Western species. Pronotum quadrate, slightly longer than wide. Anterior pronotal margin sinuate. Sublateral carinae straight basally, distinctly raised and strongly carinate anteriorly. Submedial lines parallel, weak, only present in basal half. Pronotal disc strongly excataved in central 1/3. Tubercles of anterior margin of pronotum sexually dimorphic in males, tubercles strongly raised, in females, tubercles reduced, only slightly raised. Strial rows of elytra indistinct, punctures minute. Color usually reddish brown. Commonly collected. Associated with pines.

Distribution: Arizona, California, New Mexico, Idaho, Nevada, Oregon, Utah, Washington, Colorado, Montana, South Dakota, USA; British Columbia, Canada.

***Aulonium parallelopipedum*:** Eastern species. Body slightly broader and shorter, 3x longer than wide. Pronotum quadrate. Sublateral carinae slightly curved basally, not distinctly raised anteriorly, merge with raised anterior margin of pronotum. Anterior pronotal margin slightly sinuate. Submedial lines diverge apically and basally, narrowed in apical 1/3. Pronotal disc more or less convex, slightly depressed in between submedial lines. Tubercles of anterior margin of pronotum not sexually dimorphic in both sexes, tubercles present but not distinctly produced, slightly larger in males. Strial rows of elytra distinct, punctures larger. Color piceus. Associated strictly with hardwoods.

Distribution: Washington D.C., Delaware, Illinois Indiana, Massachusetts, Maryland, Michigan, New Jersey, New York, Ohio, Pennsylvania, Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, Virginia, Oklahoma, Texas, USA.

***Aulonium tuberculatum*:** Eastern species. Body more elongate, 3.6x longer than wide. Pronotum nearly quadrate, distinctly longer than wide. Anterior pronotal margin sinuate. Sublateral carinae straight basally, distinctly raised and strongly carinate anteriorly in males, not strongly raised anteriorly in females. Tubercles of anterior margin of pronotum distinctly sexually dimorphic in males, tubercles strongly raised, with an additional pair of raised areas beneath, in females, tubercles absent. Submedial lines parallel, extremely weak. Pronotal disc weakly excataved in central 1/5 in males only. Strial rows of elytra indistinct, punctures minute. Color ferrugineous, with elytral apex darker. Associated with pines.

Distribution: Washington, D.C., Indiana, Maryland, New Jersey, New York, Pennsylvania, Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Virginia, West Virginia, Oklahoma, Texas, USA.

Potential Problems with Identification

The species of *Aulonium* seem to fall into two distinct groups, the *A. aequolle*, *A. parallelopipedum* group defined by the larger, darker body and lack of tubercles near the anterior margin of the pronotum, and the *A. longum*, *A. tuberculatum, A. ferrugineum* group, with the more elongate body and presence of tubercles (except in *A. ferrugineum*) near the anterior margin of the pronotum. These species can be distinguished by the characters given above, but separation of species within the genus becomes much more difficult on a worldwide scale.

Selected References

Ivie 2002a, LeConte 1859, 1863, 1866, Say 1826, Stephan 1989, Zimmermann 1869.

Genus: *Bitoma*

Diagnostic Features

Description: Antennae 11-segmented with a distinct, 2-segmented club (rarely antennomere 9 expanded apically, causing club to appear 3-segmented). Antennal setation sparse. Subantennal grooves greatly reduced to a small depressed area or absent. Eyes large, well-developed, finely to coarsely faceted, nearly always with obvious interfacetal setae. Antennal segment 3 slightly elongate (only slightly longer than 4) Pronotal disc carinate, with at least 2 pairs of longitudinal carinae, lateral margins (in most) slightly to strongly explanate, serrulate to denticulate. Pronotum usually wider than long. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Dorsal surface consisting of thin, fine, hair-like setae (rarely clothed in velvet-like setae).

Similar genera: The genus *Bitoma* is similar in general appearance to *Microprius*, *Paha* and *Lasconotus*. In *Microprius*, the antennal groove is long and reaches to the posterior margin of the eye. *Bitoma* differs from *Paha* and *Lasconotus* in having a 2-segmented antennal club (1-segmented in *Paha* and 3-segmented in *Lasconotus*). In *Lasconotus*, the procoxal cavities are closed.

Known Distribution

Northeast (VA, WV, MD, DE, NJ, NY, CT, MA, NH, VT), North Central (IA, MO, IN, OH), Southeast (NC, SC, TN, GA, AL, FL), South Central (TX, OK, MS), Northwest (OR, WA, ID), Southwest (NM, AZ, CO, NV, CA) USA; Ontario, Canada.

Biology

Bitoma has been collected at MV/UV lights and from injured or dead cacti (*B. gracilis*), in leaf axils of dying agave and yucca (*B. gracilis*), in the nest piles of packrats (*B. gracilis, B. sulcata*), in flood debris (*B. ornata*), and under the bark of dead hardwoods and pines, including: mesquite and palo verde, sotol (*B. neglecta, B. gracilis*), cottonwoods (*B. sulcata*, *B. ornata*), maples (*B. ornata*, *B. quadricollis*), pines (*B. pinicola*), oaks (*B. quadricollis*, *B. sulcata*, *B. carinata*), and beech (*B. quadricollis*).

Abundance: some species are common.

North American Species (14)

Bitoma brevipes (Sharp, 1894)

Bitoma carinata (LeConte, 1863)

Bitoma crenata (Fabricius, 1775)

Bitoma discolor Schaeffer, 1907

Bitoma exarata (Pascoe, 1863b)

Bitoma gracilis Sharp, 1894

Bitoma granulata (Blatchley, 1910)

Bitoma ornata (LeConte, 1858)

Bitoma neglecta Stephan, 1989

Bitoma pinicola Schaeffer, 1907

Bitoma quadricollis (Horn, 1885)

Bitoma quadriguttata (Say, 1826)

Bitoma sulcata (LeConte, 1858)

Bitoma vittata Schaeffer, 1907

Common Species:

Bitoma quadriguttata (eastern) and *B. ornata* (western) are, by far, the most abundant species.

Species Diagnoses

Bitoma brevipes**:** Eastern species. *B. brevipes* can be readily distinguished by the dark, cylindrical body, pronotm distinctly longer than wide, with 2 pairs of well-defined, full-length, slightly curved to sinuate carinae and an additional pair of short carinae anteromedially, and reduced interfacetal setae. This species can be separated from the similar *B. carinata* by the additional short pair of carinae on the anterior portion of the pronotal disc and less granulate pronotum.

Distribution: Known from Fort Meyers, Florida, although this is probably an introduction. *B. brevipes* is known from Mexico, Panama, and Costa Rica. This species may also occur in the Southwest USA and it is unclear whether or not this species has been established in the United States.

Bitoma carinata**:** Eastern species. *B. carinata* can be readily distinguished by the dark, cylindrical body, pronotm distinctly longer than wide, distinctly granulate with 2 pairs of well-defined, full-length, slightly curved to sinuate carinae, and reduced interfacetal setae. This species can be separated from the similar *B. brevipes* by the lack of an addition short pair of carinae on the anterior portion of the pronotal disc and more granulate pronotum.

Distribution: Alabama, Florida, Georgia, Mississippi, South Carolina, Virginia, USA.

Bitoma crenata**:** Eastern species. This species can be distinguished by the large red spots and apically enlarged 9th antennal segment, causing the antennal club to appear 3-segmented. *B. crenata* most closely resembles *B. sulcata*, but can be separated by the more smooth central area of the pronotal disc, eyes flattened and not nearly as protruding, reduced to absent interfacetal setae, generally bi-colorous body, and geographic distribution. This species is locally common.

Distribution: Indiana, New York, Ohio, Vermont, Washington, USA; Ontario, Canada. This species has been introduced from Europe (apparently twice).

Bitoma discolor**:** Eastern species. *B. discolor* can be distinguished from other *Bitoma* by the larger eyes with dense, stout, curved interfacetal setae, larger antennal club, and distinctly denticulate lateral pronotal margins. This species is most similar to the more common *B. quadricollis*, and can be separated by the dark elytra with lighter spots and geographical distribution. This species is rare.

Distribution: southern Florida and the Florida Keys, USA. This species is also found in Cuba.

Bitoma exarata**:** Western species. The larger size and distinctive dorsal ornamentation consisting of carinae and granules clothed in velvety scales (tomentose) should adequately distinguish this species.

Distribution: extreme southern Arizona, USA. This species also occurs from Brazil to Mexico.

Bitoma gracilis**:** Western species. Most similar to *B. neglecta*, but differs in having a sparsely setose/glabrous prosternum, eyes set closer apart ventrally, narrower pronotum, more elongate, generally lighter in color and smaller in size.

Distribution: Arizona, California, New Mexico, Texas, USA.

Bitoma granulata**:** Central/eastern species. *B. granulata* can be easily separated from the remaining North American *Bitoma* by the greatly reduced eyes and the extremely flattened body. This species is extremely rare.

Distribution: Missouri, Indiana, Iowa, USA.

Bitoma ornata**:** Western species. Most similar to the introduced *B. crenata*, but differs in the smaller 9th antennal segment. This is the only native western species with red spots.

Distribution: Arizona, California, Idaho, Nevada, Oregon, Colorado, USA.

Bitoma neglecta**:** Western species. Most similar to *B. gracilis*, but differs in having a setose prosternum, eyes set farther apart ventrally, wider pronotum, less elongate, generally darker in color and larger in size.

Distribution: Arizona, USA.

Bitoma pinicola**:** Eastern species. This species can be separated from all other eastern species by the larger size, greatly flattened body, and widely separated eyes (ventrally).

Distribution: Delaware, Massachusetts, New Jersey, North Carolina, USA.

Bitoma quadricollis**:** Eastern species. *B. quadricollis* can be distinguished from other *Bitoma* by the larger eyes with dense, stout, curved interfacetal setae, larger antennal club, and distinctly denticulate lateral pronotal margins. This species is most similar to the rarer *B. discolor*, and can be separated by the unicolorous elytra and geographical distribution. This species is uncommon.

Distribution: New Jersey, Maryland, Ohio, Florida, Mississippi, North Carolina, Tennessee, West Virginia, Virginia, Oklahoma, USA.

Bitoma quadriguttata**:** Eastern species. This species varies widely in coloration, and is most often confused with *B. quadricollis*, *B. granulata* (darker specimens), and *B. gracilis*, *B. discolor* (redder specimens). Dark *B. quadriguttata* can be distinguished by the size and position of the eyes. *B. quadriguttata* can be distinguished from *B. gracilis* by the less narrow body, eyes closer together ventrally, and inner pair of pronotal carinae curved outward. *B. quadriguttata* can be distinguished from *B. discolor* by the more well-separated eyes ventrally and more granulate prosternum.

Distribution: Connecticut, Delaware, Indiana, Maryland, New Jersey, New Hampshire, New York, Ohio, Alabama, Florida, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, West Virginia, Virginia, Oklahoma, Texas, USA; Ontario, Canada. This is by far the most commonly encountered North American species of *Bitoma*.

***Bitoma sulcata*:** Western species. This species can be distinguished by the apically enlarged 9^{th} antennal segment, causing the antennal club to appear 3-segmented. *B. sulcata* most closely resembles *B. crenata*, but can be separated by the more rugose and setose central area of the pronotal disc, eyes rounder and greatly protruding, interfacetal setae more prominent and dense, generally uni-colorous body, and geographic distribution. This species is locally common.

Distribution: Arizona, California, Texas, USA.

***Bitoma vittata*:** Western species. *B. vittata* can be immediately distinguished from the other North American *Bitoma* by the lateral margins of the pronotum greatly explanate and distinctly narrowed basally. This species is uncommon.

Distribution: extreme southern Texas, USA.

Discussion

On a regional level, the genus *Bitoma* appears stable, although the defining characters break down on a worldwide scale. The overall generic concept is still in question, with many aberrant forms currently included in this large, cosmopolitan genus. A worldwide revision of the genus and a closer investigation of the generic definitions of the genera within the tribe Synchitini is the only way to resolve this issue.

Potential Problems with Identification

The North American species within this genus all appear very similar and will be hard to differentiate without a synoptic collection. Most of the species are rarely encountered. If identification is uncertain, it is suggested the specimens are checked against the most common species for that particular geographic region. Teneral specimens are much paler in color and may not exhibit the standard patterns of coloration diagnostic for the species.

Selected References

Blatchley 1910, Fabricius 1775, Horn 1885, Ivie 2002a, LeConte 1858, 1863, Pascoe 1863, Say 1826, Schaeffer 1907, Sharp 1894, Stephan 1989.

Genus: *Colobicus*

Diagnostic Features

Description: Body distinctly flattened. Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Antennomere 3 distinctly elongate (at least twice as long as 4). Subantennal grooves long, reaching posterior margin of eye. Eyes round, well-developed, facets fine. Pronotum simple, with flattened, short, recumbent setae. Pronotal lateral margins smooth, widest basally, distinctly explanate. Procoxal cavities narrowly open. Metacoxae narrowly separated, separation less than metacoxal length. Elytral lateral margins weakly explanate. Elytra with distinct striae composed flattened, short, recumbent setae. Tarsal formula 4-4-4.

Similar genera: The genus *Colobicus* is superficially similar to the genera *Acolobicus* and *Eucicones*. The smaller size, presence of faint carinae on the pronotal disc, lack of thick, flattened, club-shaped setae and unicolored dorsal surface serve to distinguish *Acolobicus*. The smaller size, variegated elytra, rougher dorsal surface, and distinctly more setose vestiture serve to distinguish *Eucicones*.

Known Distribution

Hawai'i, and Southeastern (LA) USA.

Biology

Colobicus parilis has been found at UV/MV light and from under the bark of a number of trees. It has been noted that this species has been found on commercial shipments and in stores of sweet potatoes and other crops, where it is suspected to spread fungal disease (Hinton, 1945; Ivie, 2002a). Due to the destruction of crops from fungal disease spread by this beetle, it should be considered harmful.

Abundance: Rare.

North American Species (1)

Colobicus parilis Pascoe, 1860

Discussion

This genus is found throughout the Australo-Pacific region. It has likely been introduced into the United States, possibly on crop products.

Selected References

Ford 1968, Ivie 2002a, Pascoe 1860, Ślipiński and Lawrence 1997.

Genus: *Colydium*

Diagnostic Features

Description: Body elongate, subcylindrical. Antennae 11-segmented with a 3-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes ovate, well-developed, coarsely faceted. Eyes weakly to distinctly emarginate anteriorly by projection of frons, forming a distinct canthus. Pronotum subquadrate to elongate. Pronotal disc often with pair of sublateral sulci and single medial sulcus. Procoxal cavities narrowly closed. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Apex of protibia expanded, armed with a stout, apical spine. Dorsal surface glabrous, moderately shiny.

Similar genera: The genus *Colydium* is superficially similar in general appearance to *Aulonium*. The non-carinate elytral declivity and absence of a pair of long setae near the apical margin of the last abdominal ventrite serve to distinguish *Aulonium*. The genus *Phloeonemus* also has emarginated eyes formed by a projection of the frons, but is readily distinguished from *Colydium* and *Aulonium* by the 2-segmented antennal club, lack of a stout apical spine on the protibia, explanate lateral pronotal margins, very different sculpturing of the pronotal disc.

Known Distribution

Northwest (ID, MT, OR, WA), Southwest (AZ, CA, CO, NM, NV, UT), North Central (SD, IL, IN, MI, OH), Northeast (DC, DE, NJ, NY, MA, MD, PA, WV, VA), Southeast (AL, FL, GA, KY, NC, SC, TN), South Central (AR, LA, MS, OK, TX) USA, and British Columbia, Canada.

Biology

Aulonium has been collected at MV/UV lights and from under the bark of various dead hardwoods and conifers. Adults and larvae of *Colydium* have been found in the galleries of scolytine weevils (Curculionidae), and they are suspected to feed on the larvae of those beetles within the galleries (Ivie, 2002; Lawrence, 1991; Węgrzynowicz, 1999). It is unclear whether or not this genus can be considered beneficial, as the feeding on wood boring beetles may be circumstantial.

Abundance: Moderately common.

North American Species (5)

Colydium glabriculum Stephan, 1989

Colydium lineola Say, 1826

Colydium nigripenne LeConte, 1863

Colydium robustum Stephan, 1989

Colydium thomasi Stephan, 1989

Species Diagnoses

***Colydium glabriculum*:** Apex of clypeus glabrous, labrum distinctly setose. Anterior angles of pronotum rounded, not projecting forward. Lateral margins of pronotum narrowing basally. Sublateral sulci of pronotal disc distinct. Elytral carinae distinctly raised basally and for apical half, indistinctly raised medially. Body reddish, apex of elytra darker.

Distribution: Arizona and New Mexico, USA.

***Colydium lineola*:** Body 5x longer than wide. Apex of clypeus and labrum both distinctly setose. Anterior angles of pronotum rounded, not projecting forward.

Lateral margins of pronotum narrowing basally. Sublateral sulci of pronotal disc faint to absent. Elytral carinae distinctly raised for entire length. Body dark red to black.

Distribution: Washington D.C., Delaware, Illinois, Indiana, Maryland, New Jersey, New York, Pennsylvania, Alabama, Arkansas, Florida, Georgia, Louisiana, Mississippi, South Carolina, Tennessee, Arizona, California, Oklahoma, Texas, Oregon, Washington, Missouri, USA; British Columbia, Ontario, Canada.

***Colydium nigripenne*:** Apex of clypeus and labrum both distinctly setose. Anterior angles of pronotum rounded, not projecting forward. Lateral margins of pronotum narrowing basally. Sublateral sulci of pronotal disc distinct. Elytral carinae distinctly raised for entire length. Head and pronotum reddish, elytra black.

Distribution: Washington D.C., Maryland, Illinois, New Jersey, Alabama, Arkansas, Florida, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, Oklahoma, Texas, USA.

***Colydium robustum*:** Body 4x longer than wide. Apex of clypeus and labrum both distinctly setose. Anterior angles of pronotum angulate, distinctly projecting forward. Lateral margins of pronotum evenly curved. Sublateral sulci of pronotal disc distinct. Elytral carinae distinctly raised for entire length. Body dark red to black.

Distribution: Arizona, USA.

***Colydium thomasi*:** Apex of clypeus glabrous, labrum distinctly setose. Anterior angles of pronotum rounded, not projecting forward. Lateral margins of pronotum narrowing basally. Sublateral sulci of pronotal disc faint to absent. Elytral carinae distinctly raised for entire length. Body reddish, apex of elytra darker.

Distribution: Florida Keys, Florida, USA, USA.

Selected References

Ivie 2002a, LeConte 1863, Say 1826, Stephan 1989, Węgrzynowicz 1999.

Genus: *Coxelus*

Diagnostic Features

Description: Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes small, reduced, coarsely faceted. Pronotal disc convex, lateral margins emarginate. Procoxal cavities open. Metacoxae moderately separated, separation slightly less than metacoxal length. Elytra with distinct striae composed of coarse , nearly confluent punctures. Tarsal formula 4-4-4. Dorsal surface with curved, recumbent setae.

Similar genera: The genus *Coxelus* is similar to the genera *Stephaniolus* and *Megataphtus* in having reduced eyes and wings absent. The distinctive antennal cavities on the hypomeron serve to distinguish *Megataphrus*, and the presence of subantennal grooves serve to distinguish *Stephaniolus.*

Known Distribution

Southern coastal range of California, USA.

Biology

Coxelus serratus have been collected sifting duff from Redwood trees, as well as under the bark of Douglas fir.

Abundance: Rarely encountered.

North American Species (1)

Coxelus serratus Horn, 1885

Selected References

Horn 1885, Ivie 2002a, Stephan 1989.

Genus: ***Denophloeus***

Diagnostic Features

Description: Body larger (6-7mm), elongate, somewhat cylindrical. Surfaces opaque, very dark in color (dark brown to black). Antennae 11-segmented with a 2-segmented club (club may appear 3-segmented due to slightly enlarged antennomere 9). Antennal setation sparse. Subantennal grooves present, wide, longer than eyes. Eyes small, round, well-developed, finely faceted. Eyes deeply emarginate anteriorly by projection of frons, forming a distinct canthus. Pronotal disc convex, with a pattern of sinuate carinae. Pronotal lateral margins widest anteriorly, distinctly explanate. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra with irregularly shaped, blunt carinae and several small tubercles near apical declivity. Tarsal formula 4-4-4. Dorsal surface sparsely pubescent, composed of short, curved, thin setae. Body usually encrusted with dirt or debris.

Similar genera: The genus *Denophloeus* is superficially similar in general appearance to *Phloeonemus* and *Acolobicus* but is immediately distinguished by the larger body size, sculpturing of the pronotum and elytra, and distribution.

Known Distribution

Northwestern (Southern OR) and Southwestern (Northern CA) United States.

Biology

Denophloeus nosodermoides has been collected under loose bark and around the stumps of dead conifers.

Abundance: Moderately common locally.

North American Species (1)

Denophloeus nosodermoides (Horn, 1878)

Selected References

Horn 1878, Ivie 2002a, Stephan 1989.

Genus: *Endeitoma*

Diagnostic Features

Description: Antennae 11-segmented with a subtle, 2-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes large, well-developed, finely faceted. Antennal segment 3 distinctly elongate (at least twice as long as 4) Pronotal disc convex, simple. Lateral pronotal margins widest at middle, distinctly denticulate. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Dorsal surface consisting of thin, fine, hair-like setae. Members of this genus are frequently convered in a pale, whitish exudate.

Similar genera: The genus *Endeitoma* is similar in general appearance to the other genera with 10-segmented antennae and a 1-segmented club that lack a subantennal groove, including *Microsicus*, *Synchita*, and *Paha*. *Microsicus* differs in antennal segment 3 not distinctly elongate, dorsal surface with strongly curved, flattened, multi-colored elytral setae. The genus *Synchita* differs in antennal segment 3 not distinctly elongate and the dorsal surface with short, bristle-like setae. *Paha* differs in antennal segment 3 not distinctly elongate, pronotal disc with two parallel, longitudinal carinae, the lateral margins widest anteriorly and distinctly explanate, and the dorsal pubescence is minute or lacking. In *Endeitoma*, the third antennal segment is distinctly elongate (at least twice as long as segment 4), the lateral pronotal margins are distinctly denticulate, and a dorsal pubescence consists of thin, fine, hair-like setae.

Known Distribution

Northeast (DE, MD, PA, WV), North Central (IN, MO), Southeast (AL, FL, GA, MS, NC), South Central (OK, TX) USA.

Biology

Endeitoma has been collected from under the bark of dead hardwoods and pines.

Abundance: Moderately common.

North American Species (2)

Endeitoma granulata (Say, 1826)

Endeitoma dentata (Horn, 1885)

Species Diagnoses

***Endeitoma granulata*:** Pronotal lateral margin weakly explanate and moderately translucent, appearing bi-colored. Length of antennal club shorter than diameter of eye.

Distribution: Delaware, Indiana, Maryland, Pennsylvania, Alabama, Florida, Georgia, Mississippi, North Carolina, West Virginia, Oklahoma, Texas, Missouri, USA.

***Endeitoma dentata*:** Pronotal lateral margin not explanate, unicolored. Length of antennal club equal to or longer than diameter of eye.

Distribution: Mississippi, Florida, Georgia, Oklahoma, USA.

Potential Problems with Identification

Members of this genus are frequently convered in a pale, whitish exudate which may conceal many of the important features used for identification. Ivie (2002a) remarks that the genus has 10-segmented antennae with a distinct 1-segmented club. Ślipiński and Lawrence (1997) state that the genus has 11-segmented antennae with a distinct, 2-segmented club. In comparison with other *Endeitoma* from around the world, it is clear the North American species also have a 2-segmented club with the last segment being much smaller than the 10^{th}.

Selected References

Horn 1885, Ivie 2002a, Say 1826, Stephan 1989.

Genus: *Eucicones*

Diagnostic Features

Description: Antennae 10-segmented with a distinct, 1-segmented club. Antennal setation sparse. Subantennal grooves present, as long as eyes. Eyes large, well-developed, facets moderately coarse. Pronotal disc convex, simple. Lateral pronotal margins widest posteriorly, distinctly explanate. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra variegated, multi-colored. Elytral margins slightly explanate. Tarsal formula 4-4-4. Dorsum with short, thick, flattened, club-shaped setae.

Similar genera: The genus *Eucicones* is similar in general appearance to the genus *Acolobicus*. The presence of faint carinae on the pronotal disc, lack of thick, flattened, club-shaped setae and unicolored dorsal surface serve to distinguish *Acolobicus*.

Known Distribution

Northeast (DC, NJ, PA), North Central (IL, IN, KS, MO), Southeast (TN, AL, FL), South Central (OK, TX) USA, and Ontario, Canada.

Biology

Eucicones marginalis has been collected from under the bark of dead oaks and elms.

Abundance: Uncommon.

North American Species (1)

Eucicones marginalis (Melsheimer, 1846)

Selected References

Ivie 2002a, Melsheimer 1846, Stephan 1989.

Genus: *Eudesma*

Diagnostic Features

Description: Body cylindrical, elongate. Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves present, as long as eyes. Eyes large, well-developed, facets fine. Pronotum subquadrate, with several raised areas and depressions. Lateral pronotal margins finely serrate. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra weakly carinate, with two rows of large, nearly contiguous punctures between carinae. Tarsal formula 4-4-4. Dorsal surface bi-colored, vestiture consisting of patches of pale setae.

Similar genera: The genus *Eudesma* is extremely distinctive and is not readily confused with other zopherid genera.

Known Distribution

Northeast (PA, VA) and North Central (IL, IN, OH) USA.

Biology

Eudesma undulata has been collected from under the bark of dead trees, including buckeye (*Aesculus glabra*) and oak (*Quercus*).

Abundance: Rare.

North American Species (1)

Eudesma undulata (Melsheimer, 1846)

Selected References

Cockerell 1906, Ivie 2002a, Melsheimer 1846, Stephan 1989.

Genus: *Hyporhagus*

Diagnostic Features

Description: Body larger, convex, elongate-oval, size over 3.5 mm. Antennae 11-segmented with a 3-segmented club. Antennal setation sparse. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Groove around dorsal edge of eye paralleling eye facets for entire length. Lateral margins of pronotum arcuate. Pronotal disc simple. Hypomeron with deep antennal cavities. Antennal groove and cavity slightly curved (not recurved dorsally), ending before lateral margin of hypomeron. Antennal cavity concealed by prothoracic leg when retracted. Procoxal cavities open. Metacoxae widely separated, separation as wide or wider than metacoxal length. Scutellum small, triangular, visible. Abdominal ventrite 5 with deep, curved preapical groove. Tarsal formula 5-5-4. Dorsal surface punctate, glabrous, shiny.

Similar genera: The genus *Hyporhagus* is most similar to the other monommatine genera *Aspathines* and *Spinhyporhagus*. *Hyporhagus* can be separated from *Aspathines* by the larger size, 3-segmented anntennal club, antennal groove and cavity not strongly recurved dorsally and not ending near lateral margin of hypomeron, and antennal cavity concealed by the prothoracic leg when retracted. *Hyporhagus* can be separated from *Spinhyporhagus* by the lack of a thin cuticular process on the dorsal margin of the eye.

Known Distribution

Southwest (AZ, CA, NM, NV, UT), Southcentral (TX, OK, LA), Southeast (FL) USA.

Biology

Members of the Monommatini are associated with rotting vegetable matter and are suspected to feed on fungus (Ivie, 2002). *H. gilensis* was found in *Yucca* stems (Lawrence, 1991).

Abundance: rare.

North American Species (4)

Hyporhagus gilensis Horn, 1872

Hyporhagus opaculus LeConte, 1866

Hyporhagus pseudogilensis Freude, 1955

Hyporhagus punctulatus Thomson, 1860

Species Diagnoses

***Hyporhagus gilensis*:** Western species. Body sub-opaque. DORSAL: Lateral margins of pronotum nearly straight, with a distinct angle separating lateral from anterior margins. Anterior pronotal margin nearly straight, distinctly shorter than basal margin. Posterior pronotal angles obtuse, posterior pronotal margin more sharply angled, distinctly convex. VENTRAL: maxillary palpi not distinctly swollen, terminal palpomere subcylindrical, widest at apex, not distinctly wider than preceding palpomeres, apex distinctly truncate. Strip of cuticle between eye and mouthparts wide, expanding towards base of eye. Eye at base mostly concealed, not distinctly expanded. Intercoxal process of abdominal ventrite I shallower, abdominal ventrite I shorter or nearly as long as ventrites 2-4. Male protarsus with 2 tarsomeres dilated and pubescent.

Distribution: Arizona, California, Nevada, New Mexico, Utah, Texas, Oklahoma, USA.

***Hyporhagus opaculus*:** Western species. Body sub-opaque. DORSAL: Lateral margins of pronotum arcuate, curvature smoothly continuing to anterior margin. Anterior pronotal margin nearly straight, slightly shorter than basal margin. Posterior pronotal angles acute, posterior pronotal margin more subtly convex. VENTRAL: maxillary palpi swollen, terminal palpomere bulbous, widest at middle, distinctly wider than preceding palpomeres. Strip of cuticle between eye and mouthparts wide, expanding towards base of eye. Eye at base mostly concealed, not distinctly expanded. Intercoxal process of abdominal ventrite I shallower, abdominal ventrite I about at long as ventrites 2-4. Male protarsus with 3 tarsomeres dilated and pubescent.

Distribution: California, Arizona, New Mexico, Texas, USA.

Hyporhagus pseudogilensis**:** Western species. Body sub-opaque. DORSAL: Lateral margins of pronotum arcuate, with a slight angle separating lateral from anterior margins (curvature into anterior margin not seamless. Anterior pronotal margin slightly sinuate, distinctly shorter than basal margin. Posterior pronotal angles obtuse, posterior pronotal margin more sharply angled, distinctly convex. VENTRAL: maxillary palpi slightly swollen, terminal palpomere subcylindrical, widest at middle, narrowing slightly towards apex, only slightly wider than preceding palpomeres, apex distinctly truncate. Strip of cuticle between eye and mouthparts wide, expanding towards base of eye. Eye at base mostly concealed, not distinctly expanded. Intercoxal process of abdominal ventrite I shallower, abdominal ventrite I shorter or nearly as long as ventrites 2-4. Male protarsus with 2 tarsomeres dilated and pubescent.

Distribution: Texas, Arizona, USA.

Hyporhagus punctulatus**:** Eastern species. Body shining. DORSAL: Lateral margins of pronotum arcuate, curvature smoothly continuing to anterior margin. Anterior pronotal margin nearly straight, slightly shorter than basal margin. VENTRAL: maxillary palpi swollen, terminal palpomere bulbous, widest at middle, distinctly wider than preceding palpomeres. Strip of cuticle between eye and mouthparts narrower, nearly parallel sided towards base of eye. Eye at base exposed, distinctly expanded inward. Intercoxal process of abdominal ventrite I more acute, abdominal ventrite I longer than ventrites 2-4. Male protarsus with 3 tarsomeres dilated and pubescent.

Distribution: Florida, Louisiana, USA.

NOTE: Several subspecies are recognized for *H. gilensis, H. punctulatus,* and *H. opaculus*, but due to the need of revisionary work on the genus, only the nominal species for each will be referred to in this resource.

Potential Problems with Identification

Members of this genus are extremely difficult to identify without representatives of each species at hand. The group requires extensive revision.

Selected References

Freude 1955, 1993, Horn 1872, Ivie 2002b, Lawrence 1991b, LeConte 1866, Thomson 1860.

<u>Genus: *Lasconotus*</u>

Diagnostic Features

Description: Antennae 11-segmented with a distinct, 3-segmented club. Antennal setation sparse. Subantennal grooves weakly developed or absent. Eyes large, well-developed, finely faceted. Antennal segment 3 longer than 4, but not as long as 4+5. Pronotal disc with one or two pairs of longitudinal ridges or carinae, often with depressed areas. Lateral pronotal margins variable, subparallel to sinuate. Procoxal cavities closed (narrowly open in *L. fitzgibbonae* and *L. coronatus*). Metacoxae narrowly separated, separation less than metacoxal length. Elytra with distinct carinae. Abdominal ventrite 5 with a deep preapical groove. Tarsal formula 4-4-4. Apex of protibia expanded, armed with a stout, apical spine and several smaller spines. Dorsal surface consisting of thin, fine, hair-like setae, occasionally with tufts of long, thin, golden setae.

Similar genera: The genus *Lasconotus* is similar in general appearance to the genera *Bitoma* and *Microprius*. *Lasconotus* can be immediately distinguished with the distinctly 3-segmented antennal club, closed procoxal cavities, apically expanded protibia armed with a stout apical spine and several smaller spines, and carinate pronotum and elytra.

Known Distribution

Northeast (Washington D.C., MD, NH, NJ, NY, PA, VA), North Central (IN, MO, MI, NK, OH, SD), Southeast (AL, FL, GA, NC, SC), South Central (LA, MS, OK, TX), Southwest (AZ, CA, CO, NM, NV, UT), Northwest (ID, MT, OR, WA, WY), Alaska, USA; Ontario, British Columbia, Northwest Territories, Canada.

Biology

Lasconotus has been collected by beating vegetation, at MV/UV lights, and from under the bark of dead pines, including the root bark of *Pinus edulis* and *Pinus leiophylla* (*Lasconotus fitzgibbonae*). It has been noted that some *Lasconotus* are predators of scolytine weevils (Curculionidae), and are therefore possibly beneficial.

Abundance: Some species are moderately common.

North American Species (~22)

Lasconotus bitomoides Kraus, 1912

Lasconotus borealis Horn, 1878

Lasconotus complex LeConte, 1859

Lasconotus concavus Casey, 1890

Lasconotus coronatus (Hinton, 1935)

Lasconotus fiskei Kraus, 1912

Lasconotus fitzgibbonae Kingsolver, Stephan, and Moser, 2006

Lasconotus flexuosus Kraus, 1912

Lasconotus intricatus Kraus, 1912

Lasconotus knulli Stephan, 1989

Lasconotus laqueatus LeConte, 1866

Lasconotus linearis Crotch, 1874

Lasconotus mexicanus Kraus, 1912

Lasconotus nucleatus Casey, 1890

Lasconotus pertenuis Casey, 1890

Lasconotus planipennis Kraus, 1912

Lasconotus pusillus LeConte, 1863

Lasconotus referendarius Zimmermann, 1869

Lasconotus servus Horn, 1885

*Lasconotus simplex*LeConte, 1866

Lasconotus subcostulatus Kraus, 1912

Lasconotus tuberculatus Kraus, 1912

Lasconotus vegrandis Horn, 1885

Species Diagnoses

***Lasconotus bitomoides*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly concave in from elytral interstitial intervals 1 to 5 for nearly entire length on both elytra and the carina of elytral interstitial interval 5 markedly more raised than other carinae. *L. bitomoides* and *L. fiskei* each have a long, nearly complete pair of sublateral carinae on the pronotum (between central depression and lateral margin). *L. bitomoides* can be separated by the greater elytral concavity, more granulate central depression, and greater distribution from Texas to California.

Distribution: Arizona, California, New Mexico, Texas, USA.

Lasconotus borealis**:** Northern species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, pronotum with network of curving carinae crested with setae, and elytral intervals with 2-3 rows of short setae. *L. borealis* is most similar to *L. intricatus*, but can be separated by the piceus color and the pronotum wider than long.

Distribution: Alaska, Michigan, New Hampshire, New York, USA; Ontario, Northwest Territories, Canada.

Lasconotus complex**:** Western species. This species is distinguished by the reflexed lateral margin of the pronotum forming a distinct longitudinal depression between the lateral margin and the 1st pair of pronotal carina and carina of elytral interstitial interval 3 more distinctly raised near apex than other carinae. *L. complex* and *L. tuberculatus* are readily distinguished by the internal pair of carinae on the prontal disc interrupted into small tubercles. *L. complex* is distinguished from *L. tuberculatus* by the more parallel, sinuate lateral margins of the pronotum, the inner pair of pronotal carinae less distinctly interrupted into tubercles, and the posterior angles of the pronotum nearly right angles, not projecting posteriorly.

Distribution: California, Idaho, Oregon, Utah, Washington, USA; British Columbia, Canada.

***Lasconotus concavus*:** Western species. This species is in a group of *Lasconotus* with the pronotum lacking any distinct carinae, instead, two raised ridges laterally bordering a larger central depression, sinuate anterior margin of pronotum, and elytra distinctly concave in from elytral interstitial intervals 1 to 5 for nearly entire length on both elytra and the carina of elytral interstitial interval 5 markedly more raised than other carinae. *L. concavus* can be separated from the other similar *Lasconotus* by the more flattened, wider body, absence of a distinctly carinate anterior margin of pronotum, and the concave portion of the elytra without clear striae.

Distribution: Arizona, New Mexico, Colorado, Montana, USA.

***Lasconotus coronatus*:** Western species. *L. coronatus* is most similar to *L. fitzgibbonae* and forms a distinct group within *Lasconotus*. These two species can be separated by the remainder of the genus by the distinctive paired tufts of long golden setae at the anterior margin of the pronotum, narrowly open procoxal cavities, and antennal segment 3 longer than either 2 or 4. *L. coronatus* differs from *L. fitzgibbonae* in being slightly larger (~4.5 mm compared to ~3.25 mm in *L. fitzgibbonae*), the marginal pronotal carinae with a deep depression at midpoint, a more acute pronotal margin and broader anterior angles of the pronotum.

Distribution: Colorado, USA.

***Lasconotus fiskei*:** Southcentral species. This species is in a group of *Lasconotus* with the elytra distinctly concave in from elytral interstitial intervals 1 to 5 for nearly entire length on both elytra and the carina of elytral interstitial interval 5 markedly more raised than other carinae. *L. fiskei* and *L. bitomoides* each have a long, nearly complete pair of sublateral carinae on the pronotum (between central depression and lateral margin). *L. fiskei* can be separated by the slighter elytral concavity, less granulate central depression, and distribution restricted to Texas.

Distribution: Texas, USA.

***Lasconotus fitzgibbonae*:** Western species. *L. fitzgibbonae* is most similar to *L. coronatus* and forms a distinct group within *Lasconotus*. These two species can be separated by the remainder of the genus by the distinctive paired tufts of long golden setae at the anterior margin of the pronotum, narrowly open procoxal cavities, and antennal segment 3 longer than either 2 or 4. *L. fitzgibbonae* differs from *L. coronatus* in being slightly smaller (~3.25 mm compared to ~4. 5 mm in *L. coronatus*), the lateral pronotal carinae with a shallow depression at midpoint, a more straight pronotal margin and narrower anterior angles of the pronotum.

Distribution: Arizona, South Dakota, USA.

***Lasconotus flexuosus*:** Western species. This species is distinguished by the reflexed lateral margin of the pronotum forming a distinct longitudinal depression between the lateral margin and the 1st pair of pronotal carina, the carina of elytral interstitial interval 3 more distinctly raised near apex than other carinae, and the presence of a strong flexure or bend in the pronotum slightly ahead of midline (only when viewed laterally).

Distribution: Washington, USA.

***Lasconotus intricatus*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, pronotum with network of curving carinae crested with setae, and elytral intervals with 2-3 rows of short setae. *L. intricatus* is most similar to *L.*

borealis, but can be separated by the ferrugineus color and the pronotum longer than wide.

Distribution: Idaho, Oregon, Washington, USA; British Columbia, Northwest Territories, Canada.

***Lasconotus knulli*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length and with all elytral carinae similarly raised. *L. knulli* can be distinguished by the restricted distribution, extremely small size, elytra with no distinct carina, pronotum longer than wide with only a hint of paired cainae.

Distribution: Arizona, USA.

***Lasconotus laqueatus*:** Western species. This species is in a group of *Lasconotus* with the pronotum lacking any distinct carinae, instead, two raised ridges laterally bordering a larger central depression, sinuate anterior margin of pronotum, and elytra distinctly concave in from elytral interstitial intervals 1 to 5 for nearly entire length on both elytra and the carina of elytral interstitial interval 5 markedly more raised than other carinae. *L. laqueatus* can be separated from the other similar *Lasconotus* by the presence of a distinctly carinate, double "U" shaped anterior margin of pronotum, the width of the centralpronotal depression greater than 1/2 the total width of pronotum, and the concave portion of the elytra for majority of elytral length. *L. laqueatus*differs from *L. pusillus* by its western distribution.

Distribution: Arizona, California, New Mexico, Texas, Nevada, South Dakota, Montana, Wyoming USA.

***Lasconotus linearis*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, pronotum with network of curving carinae crested with setae, and elytral intervals with a single row of recumbent setae. *L. linearis* is most similar to *L. pertenuis*, but can be separated by the usually bicolored elytra and antennomere 9 as long as 10.

Distribution: California, USA.

***Lasconotus mexicanus*:** This species is distinguished by the reflexed lateral margin of the pronotum forming a distinct longitudinal depression between the lateral margin and the 1st pair of pronotal carina and elytral carinae all equally elevated. To date, *L. mexicanus* does not occur in North America north of Mexico, but is included because it is likely this species will be discovered in the Southwest USA.

Distribution: Mexico.

***Lasconotus nucleatus*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length and with all elytral carinae similarly raised. *L. nucleatus* is readily distinguished by the rounded anterior angles of the pronotum, dorsal vestiture consisting of short, recurved setae, and elytra with numerous small tufts of round, silver-white setae.

Distribution: California, Oregon, Washington, USA.

***Lasconotus pertenuis*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, pronotum with network of curving carinae crested with setae, and elytral intervals with a single row of recumbent setae. *L. pertenuis*is most similar to *L.linearis*, but can be separated by the unicolored elytra and antennomere 9 distinctly shorter and narrower than 10.

Distribution: California, USA.

Lasconotus planipennis**:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, and pronotum with indistinct carinae (never with network of curved carinae crested with setae). *L. planipennis* can be separated from similar species by the western distribution, smaller size (2.5 mm or less), absence of a distinct pair of sublateral pronotal carinae, and elytra distinctly convex.

Distribution: Arizona, California, New Mexico, Idaho, Washington, South Dakota, Montana, Wyoming, USA; British Columbia, Canada.

Lasconotus pusillus**:** Eastern species. This species is in a group of *Lasconotus* with the pronotum lacking any distinct carinae, instead, two raised ridges laterally bordering a larger central depression, sinuate anterior margin of pronotum, and elytra distinctly concave in from elytral interstitial intervals 1 to 5 for nearly entire length on both elytra and the carina of elytral interstitial interval 5 markedly more raised than other carinae. *L. pusillus* can be separated from the other similar *Lasconotus* by the presence of a distinctly carinate, double “U” shaped anterior margin of pronotum, the width of the central pronotal depression greater than 1/2 the total width of pronotum, and the concave portion of the elytra for majority of elytral length. *L. pusillus* differs from *L. laqueatus* by its eastern distribution.

Distribution: Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, Ohio, Oklahoma, Texas, USA.

***Lasconotus referendarius*:** Eastern species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, and pronotum with indistinct carinae (never with network of curved carinae crested with setae). *L. referendarius* can be separated from similar species by the eastern distribution, smaller length to width ratio, and lack of distinct pronotal carinae.

Distribution: Washington D.C., Indiana, Maryland, New Jersey, Pennsylvania, Alabama, Florida, Georgia, North Carolina, South Carolina, Virginia, Oklahoma, Texas, USA.

***Lasconotus servus*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, and pronotum with indistinct carinae (never with network of curved carinae crested with setae). *L. servus* can be separated from similar species by the western distribution, larger size (3mm +), and presence of a distinct pair of sublateral pronotal carinae.

Distribution: Arizona, California, New Mexico, USA.

***Lasconotus simplex*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, and pronotum with indistinct carinae (never with network of curved carinae crested with setae). *L. simplex* can be separated from similar species by the western distribution, smaller size (2.5 mm or less), absence of a distinct pair of sublateral pronotal carinae, and elytra distinctly flattened.

Distribution: Arizona, California, New Mexico, USA.

Lasconotus subcostulatus**:** Western species. This species is in a group of *Lasconotus* with the pronotum lacking any distinct carinae, instead, two raised ridges laterally bordering a larger central depression, sinuate anterior margin of pronotum, and elytra distinctly concave in from elytral interstitial intervals 1 to 5 for nearly entire length on both elytra and the carina of elytral interstitial interval 5 markedly more raised than other carinae. *L. subcostulatus* can be separated from the other similar *Lasconotus* by the presence of a distinctly carinate, double "U" shaped anterior margin of pronotum, the width of the central pronotal depression 1/3 to 1/2 total width of pronotum, and the concave portion of the elytra for posterior half only.

Distribution: California, Idaho, Nevada, Oregon, Washington, South Dakota, Montana, Nebraska, USA.

Lasconotus tuberculatus**:** Western species. This species is distinguished by the reflexed lateral margin of the pronotum forming a distinct longitudinal depression between the lateral margin and the 1st pair of pronotal carina and carina of elytral interstitial interval 3 more distinctly raised near apex than other carinae. *L. tuberculatus* and *L. complex* are readily distinguished by the internal pair of carinae on the prontal disc interrupted into small tubercles. *L. tuberculatus* differs from *L. complex* by the more arcuate, sinuate lateral margins of the pronotum, the inner pair of pronotal carinae more distinctly interrupted into tubercles, and the posterior angles of the pronotum distinctly angulate, projecting posteriorly.

Distribution: Arizona, California, New Mexico, Oregon, Washington, Utah, South Dakota, Wyoming, USA; British Columbia, Canada.

***Lasconotus vegrandis*:** Western species. This species is in a group of *Lasconotus* with the elytra distinctly convex to flattened (never concave) for entire length, with all elytral carinae similarly raised, and pronotum with indistinct carinae (never with network of curved carinae crested with setae). *L. vegrandis* can be separated from similar species by the pronotal width distinctly narrower than the elytral width.

Distribution: California, Idaho, Oregon, Washington, USA; British Columbia, Canada.

Discussion

Due to a unique combination of morphological characters, the placement of *Lasconotus* within the tribe Synchitini remains in question.

Selected References

Casey 1890, Crotch 1874, Hinton 1935, Horn 1878, 1885, Ivie 2002a, Kingsolver, Stephan, and Moser 2006, Kraus 1912, LeConte 1859, 1863, 1866, Stephan 1989, Zimmermann 1869.

Genus: *Lobogestoria*

Diagnostic Features

Description: Body cylindrical. Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes well-developed, round, finely faceted. Pronotal disc with pair of large, forward projecting horns. Pronotum longer than wide, lateral margins parallel-sided. Pronotum with a mid-lateral secretory pore situated in a lateral, longitudinal channel. Procoxal cavities narrowly open. Metacoxae narrowly separated, separation less than metacoxal length.

Elytral with 9 rows of evenly spaced, round punctures. Abdominal ventrites 1-3 fused, distinctly convex, ventrite 4 narrow, with transverse groove, ventrite 5 flat. Tarsal formula apparently 3-3-3 (actually 4-4-4, tarsomeres 1 and 2 partially fused). Dorsal surface glabrous.

Similar genera: The genus *Lobogestoria* is similar to the genus *Antilissus* in having an apparently 3-3-3 tarsal formula and grooved pronotum, but *Lobogestoria* is easily distinguished by the large, horn-like projections of the pronotum extending well over the head.

Known Distribution

Southeastern (AL, FL, GA, SC) and South Central (LA) United States.

Probable Distribution

South Central United States (MS).

Biology

Nothing is known about the biology of this group.

Abundance: Rare.

North American Species (1)

Lobogestoria gibbicollis Reitter, 1878

Discussion

This genus is also found in Cuba, parts of South America, and the Australo-Pacific region. It has likely been introduced into the United States.

Selected References

Ivie 2002a, Reitter 1878, Stephan 1989.

Genus: *Lyreus*

Diagnostic Features

Description: Body extremely small. Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse, except for club densely setose. Subantennal grooves present, distinct, extending to rear of head. Eyes absent. Pronotal disc with large, irregular tubercles, lateral margins weakly serrate. Procoxal cavities narrowly open. Metacoxae narrowly separated, separation less than metacoxal length. Elytral smooth, with finely impressed striae. Tarsal formula 4-4-4. Dorsal surface covered in large, flattened, nearly contiguous tubercles. Body usually encrusted with dirt or debris.

Similar genera: The genus *Lyreus* is extremely distinctive and is not readily confused with other zopherid genera.

Known Distribution

Southeastern (AL) United States.

Biology

Lyreus alleni is known only from a limestone sinkhole in Alabama.

Abundance: Uncommon.

North American Species (1)

Lyreus alleni Ivie and Ślipiński, 2001

Discussion

The only other known species of *Lyreus* is European, creating an odd distribution for the genus.

Selected References

Ivie 2002a, Ivie and Ślipiński 2001.

<u>Genus: *Megataphrus*</u>

Diagnostic Features

Description: Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves present, grooves extent into antennal cavities on hypomeron. Eyes small, reduced, coarsely faceted. Pronotal disc convex. Procoxal cavities open. Metacoxae moderately separated, separation slightly less than metacoxal length. Elytra fused, with weak punctate striae and carinae. Tarsal formula 4-4-4. Dorsal surface sparsely setose. Body usually encrusted with dirt or debris.

Similar genera: The genus *Megataphrus* is similar to the genera *Stephaniolus* and *Coxelus* in having reduced eyes and wings absent. The presence of antennal cavities on the hypomeron serve to distinguish *Megataphrus* from the other two.

Known Distribution

Northwestern United States (OR), Southwestern United States (CA, AZ).

Biology

Members of this genus are flightless and ground-dwelling. They are most commonly collected by Berlese extraction from the debris of redwood, fir, eucalyptus, laurel, chinquapin (*Castanopsis*), *Ceanothus* (Rhamnaceae) and under the bark of various stumps.

Abundance: Rarely encountered.

North American Species (3)

Megataphrus tenuicornis Casey, 1890

Megataphrus arizonicus Stephan, 1989

Megataphrus chandleri Stephan, 1989

Species Diagnoses

***Megataphrus tenuicornis*:** Antennal cavities on hypomeron margined both on the inside and outside. Elytron with 3 carinae between suture and margin.

Distribution: California and Oregon, USA.

***Megataphrus arizonicus*:** Antennal cavities on hypomeron margined on the outside only. Elytron with 4 carinae between suture and margin.

Distribution: Arizona, USA.

***Megataphrus chandleri*:** Antennal cavities on hypomeron margined on the outside only. Elytron with 3 carinae between suture and margin.

Distribution: Oregon, USA.

Potential Problems with Identification

Members of this genus are frequently encrusted with dirt and other debris which may conceal the pronotal and elytral characters.

Selected References

Casey 1890, Ivie 2002a, Stephan 1989.

Genus: *Microprius*

Diagnostic Features

Description: Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves long, reaching posterior margin of eye. Eyes elongate, well-developed, facets fine. Pronotal disc with network of connecting, bifurcating carinae. Pronotal lateral margins subparallel, minutely serrate, slightly explanate.. Procoxal cavities narrowly open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra carinate, with 9 rows of regularly spaced, deep punctures. Tarsal formula 4-4-4. Dorsal surface with minute setae.

Similar genera: The genus *Microprius* is extremely similar to *Bitoma*, and seems to differ only by the length of antennal groove on the ventral side of the head (short to absent in *Bitoma*).

Known Distribution

Southwestern (CA) and Northeastern (VA) USA.

Probable Distribution

This species is widespread throughout the Old World and will likely be found throughout the US.

Biology

Microprius rufulus has been found at UV/MV light and from under the bark of a number of trees.

Abundance: Rare.

North American Species (1)

Microprius rufulus (Motschulsky, 1863)

Selected References

Ivie 2002a, Ivie *et al.* 2001b, Motschulsky 1863.

<u>**Genus: *Microsicus***</u>

Diagnostic Features

Description: Antennae 10-segmented with a distinct, 1-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes large, well-developed, finely faceted. Pronotal disc convex, simple. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Dorsal surface with strongly curved, flattened, multi-colored setae.

Similar genera: The genus *Microsicus* is similar in general appearance to the other genera with 10-segmented antennae and a 1-segmented club that lack a subantennal groove, including *Synchita*, *Paha*, and *Endeitoma*. *Synchita* differs in having short, bristle-like, unicolored setae. The genus *Paha* differs in lacking obvious dorsal pubescence, lateral pronotal margins widest anteriorly and distinctly explanate, and having paired carinae on the pronotal disc. *Endeitoma* differs in having a long third antennal segment (at least twice as long as segment 4), lateral pronotal margins distinctly denticulate, and a dorsal pubescence consisting of thin, fine, hair-like setae. In *Microsicus*, the pronotal disc is simple, the lateral margins are not distinctly denticulate, antennal segment 3 is not distinctly elongate, and the dorsal pubescence consists of strongly curved, flattened, multi-colored setae.

Known Distribution

Northeast (DE, MD, PA, WV, VA), North Central (IN), Southeast (FL, GA, NC), South Central (AR, OK), Northwest (OR, ID), Southwest (CA, AZ) USA.

Biology

Microsicus has been collected at MV/UV lights, but can commonly be found under the bark of various dead trees, including cottonwood (*M. variegatus*), oak (*M. parvulus*, *M. obscurus*), and hickory (*M. parvulus*, *M. obscurus*).

Abundance: Moderately common.

North American Species (3)

Microsicus variegatus (LeConte, 1858)

Microsicus parvulus (Guérin-Méneville, 1829)

Microsicus obscurus (Horn, 1885)

Species Diagnoses

Microsicus variegatus**:** Elytra variegated, with weak carinae, west of 100th meridian.

Distribution: Idaho, Oregon, California, and Arizona, USA.

Microsicus parvulus**:** Elytra without carinae, eyes large, elongate, head without temples, east of 100th meridian.

Distribution: Delaware, Indiana, Maryland, Pennsylvania, Arkansas, Florida, Georgia, North Carolina, West Virginia, Virginia, and Oklahoma, USA.

Microsicus obscurus**:** Elytra without carinae, eyes smaller, round, protruding, head with temples, east of 100th meridian.

Distribution: Washington D.C., Pennsylvania, New Jersey, and Oklahoma, USA. The true distribution of this species is probably much larger than records indicate.

Discussion

This genus is most closely allied to *Synchita*, with little difference other than setation type and pattern to distinguish between the two.

Selected References

Guérin-Méneville 1829, Horn 1885, Ivie 2002a, LeConte 1858, Stephan 1989.

Genus: ***Monoedus***

Diagnostic Features

Description: Antennae 10-segmented with a distinct, 1-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes small, round to reniform, finely faceted. Pronotal disc simple, pronotum longer than wide, widest anteriorly, lateral margins weakly serrate. Procoxal cavities narrowly open. Metacoxae narrowly separated, separation less than metacoxal length. Elytral with 9 rows of evenly spaced, round punctures. Tarsal formula 4-4-4 with first tarsomere dilated and encompassing small 2nd and 3rd segments. Dorsal surface glabrous. Elytra pale with a number of small, dark spots. Dorsum with small, curved, pale setae. Body usually encrusted with a pale, waxy exudate.

Similar genera: The genus *Monoedus* is extremely distinctive and is not readily confused with other zopherid genera.

Known Distribution

Southeastern (Southern FL, Florida Keys) United States.

Biology

Monoedus guttatus can be found on milkweed (*Cynanchum scoparium*) (Ivie, 2002a).

Abundance: Locally not rare.

North American Species (1)

Monoedus guttatus Horn, 1882

Discussion

This genus is also found in Central and South America and the West Indies. It has likely been introduced into the United States.

Potential Problems with Identification

Members of this genus are frequently encrusted with a pale, waxy exudate which may conceal many of the important features used for identification.

Selected References

Horn 1882, Ivie 2002a, LeConte 1882, Stephan 1989.

Genus: *Namunaria*

Diagnostic Features

Description: Antennae 11-segmented with a 2-segmented club. Antennal setation sparse. Subantennal grooves present, short, not reaching past eyes. Eyes round, well-developed, finely faceted. Eyes deeply emarginate anteriorly by projection of frons, forming a distinct canthus. Pronotal disc convex, without distinguishing sculpture. Pronotal lateral margins widest at middle, distinctly explanate, finely serrate. Procoxal cavities closed. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Dorsal surface with patches of dark and pale, flattened, curved setae.

Similar genera: The genus *Namunaria* is superficially similar in general appearance to *Pseudocorticus*. *Pseudocorticus* can be readily distinguished by the open procoxal cavities, antennae covered in dense, short, scale-like setae, antennal club one-segmented, lack of antennal grooves on head, and dorsum covered in short, scale-like setae.

Known Distribution

Northwest (OR, WA), Southwest (CA), South Central (OK, TX, MS), North Central (IN, OH), Northeast (NJ, NY, MD, PA, WV, VA), Southeast (NC, TN) USA, Ontario and British Columbia, Canada.

Biology

Namunaria has been collected at MV/UV lights and from under the bark of various dead hardwoods and conifers.

Abundance: Moderately common.

North American Species (2)

Namunaria guttulata (LeConte), 1863

Namunaria pacifica (Horn), 1878

Species Diagnoses

Namunaria guttulata**:** Antennal segment 3 1.5 times length of segment 4.

Distribution: Indiana, New Jersey, New York, Ohio, Maryland, Pennsylvania, North Carolina, Mississippi, Tennessee, West Virginia, Virginia, Oklahoma, Texas, USA. Ontario, Canada.

Namunaria pacifica**:** Antennal segment 3 subequal or only slightly larger than segment 4.

Distribution: California, Oregon, Washington, USA; British Columbia, Canada.

Selected References

Horn 1878, Ivie 2002a, LeConte 1863, Stephan 1989.

Genus: *Nematidium*

Diagnostic Features

Description: Body extremely elongate, cylindrical. Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves present, distinct. Eyes well-developed, round, finely faceted, flush with head. Pronotal disc simple, pronotum longer than wide, lateral margins with large, shallowly depressed area. Procoxal cavities broadly closed. Metacoxae narrowly separated, separation less than metacoxal length. Elytral smooth, with finely impressed striae. Tarsal formula 4-4-4. Dorsal surface glabrous, densely and minutely punctured.

Similar genera: The genus *Nematidium* is extremely distinctive and is not readily confused with other zopherid genera.

Known Distribution

Southeastern (AL, FL, GA, SC, NC, TN) and South Central (LA) United States.

Probable Distribution

South Central United States (MS).

Biology

Nematidium filiforme had been collected at MV/UV lights. Adults and larvae of *Nematidium* have been found in the galleries of ambrosia beetles (Curculionidae: Platypodinae), and they are suspected to feed on the larvae of those beetles within the galleries (Ivie, 2002a; Beeson, 1941; Roberts, 1977). This genus is a beneficial insect, attacking destructive wood boring beetles.

Abundance: Uncommon.

North American Species (1)

Nematidium filiforme LeConte, 1863

Discussion

This genus occurs worldwide, from South America to Indo-Malaysia.

Selected References

Ivie 2002a, LeConte 1863, Stephan 1989.

Genus: *Neotrichus*

Diagnostic Features

Description: Body cylindrical. Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Antennomere 3 distinctly elongate (at least twice as long as 4). Subantennal grooves short to absent. Eyes round, well-developed, facets coarse. Pronotum subquadrate, disc with small, raised, dense tubercles. Pronotal lateral margins distinctly serrate, with a mid-lateral secretory pore, difficult to see. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra with striae composed of alternating weak punctures and tubercles. Abdominal ventrites 1-3 fused. Tarsal formula apparently 3-3-3. Dorsal surface with small, bristle-like, erect, golden setae. Body usually encrusted with dirt or debris.

Similar genera: The genus *Neotrichus* superficially resembles the genus *Endeitoma*. The 4-4-4 tarsi, narrower antennal club, abdominal ventrites 1-3 not fused, and distribution readily distinguish *Endeitoma*.

Known Distribution

Hawai'i, USA.

Biology

Neotrichus latiusculus has been collected from under the bark of dead *Pipturus* and *Terminalia.*

Abundance: Rare.

North American Species (1)

Neotrichus latiusculus (Fairmaire, 1881)

Discussion

This genus is found throughout the Australo-Pacific region. It has likely been introduced into the United States.

Selected References

Ford 1968, Ivie 2002a, Jamieson 1999, Nishida 1992, Ślipiński and Lawrence 1997.

Genus: *Paha*

Diagnostic Features

Description: Antennae 10-segmented with a distinct, 1-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes large, well-developed, finely faceted. Pronotal disc convex with central depression, with two parallel, longitudinal carinae. Pronotal lateral margins widest anteriorly, distinctly explanate. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Dorsum lacking obvious pubescence (if visible, then not distinct).

Similar genera: The genus *Paha* is similar in general appearance to the other genera with 10-segmented antennae and a 1-segmented club that lack a subantennal groove, including *Microsicus*, *Synchita*, and *Endeitoma*. *Microsicus* differs in lacking pronotal carinae, and the dorsal surface with strongly curved, flattened, multi-colored elytral setae. The genus *Synchita* differs in lacking pronotal carinae, lateral pronotal margins widest at middle and not as distinctly explanate, and the dorsal surface with short, bristle-like setae. *Endeitoma* differs in having a long third antennal segment (at least twice as long as segment 4), pronotal disc lacking carinae, lateral pronotal margins distinctly denticulate, and a dorsal pubescence consisting of thin, fine, hair-like setae. In *Paha*, the pronotal disc has two parallel, longitudinal carinae, the lateral margins are widest anteriorly, distinctly explanate, antennal segment 3 is not distinctly elongate, and the dorsal pubescence is minute or lacking.

Known Distribution

Northeast (DC, MD, NY, PA, VA), North Central (IN), Southeast (TN, AL, FL, MS, NC), South Central (OK) USA.

Biology

Paha laticollis has been collected from under the bark of dead oaks.

Abundance: Uncommon.

North American Species (1)

Paha laticollis (LeConte, 1863)

Selected References

Ivie 2002a, LeConte 1863, Stephan 1989.

<u>Genus: *Phellopsis*</u>

Diagnostic Features

Description: Antennae 11-segmented with a 3-segmented club. Antennal setation sparse. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Males with setose pit on submentum. Lateral margins of pronotum arcuate to sinuate, without distinct lobes. Pronotal disc with several depressions and numerous small, round tubercles. Hypomeron without depressions or antennal cavities. Prosternum without distinct transverse groove. Procoxal cavities narrowly open. Metacoxae widely separated, separation as wide or wider than metacoxal length. Scutellum small, visible. Abdominal ventrite 5 with a deep preapical groove divided medially into two setose depressions. Tarsal formula 5-5-4. Dorsal surface granulose, tomentose. Dorsal and ventral surfaces commonly encrusted with dirt and debris.

Similar genera: The genus *Phellopsis* is similar to the genera *Sesaspis*, *Phloeodes*, and *Zopherus*, but can immediately be distinguished by the 11-segmented antennae with a 3-segmented club, narrowly open procoxal cavities, hypomeron with lack of depression/antennal cavity, and a small but visible scutellum.

Known Distribution

Southwest (CA, NV), Northwest (AK, ID, MT, OR, WA), Northeast (CT, MA, ME, MD, NH, NJ, NY, PA, VA, VT, WV), North Central (MI, WI), Southeast (GA, NC, TN) USA; Alberta, British Columbia, New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, Canada.

Biology

Phellopsis feeds on fungus found in old growth boreal forests. *P. obcordata* have been reported to feed on *Piptoporus betulinus* (Polyporales) on birch (*Betula papyrifera*, *B. lenta*) and *Heterobasidion annosum* (Bondarzewiaceae) on balsam fir (*Abies balsamea*). *P. porcata* have been reported to feed on fungi on western hemlock (*Tsuga heterophylla*) and on *Lentinus* (Polyporaceae).

Abundance: moderately common.

North American Species (2)

Phellopsis obcordata (Kirby, 1837)

Phellopsis porcata (LeConte, 1853)

Species Diagnoses

***Phellopsis obcordata*:** Eastern species. Hypomeron lacking dense setation in between tubercles.

Distribution: Connecticut, Georgia, Massachusetts, Maryland, Maine, Michigan, North Carolina, New Hampshire, New Jersey, New York, Pennsylvania, Tennessee, Virginia, Vermont, Wisconsin, West Virginia, USA, New Brunswick, Newfoundland, Nova Scotia, Ontario, Quebec, Canada.

***Phellopsis porcata*:** Western species. Hypomeron with dense setation in between tubercles.

Distribution: California, Nevada, Alaska, Idaho, Montana, Oregon, Washington, USA; Alberta, British Columbia, Canada.

Discussion

The taxonomic history of this genus in North America is quite complex, but following the thorough revision by Foley and Ivie (2008), only two species are currently recognized.

Potential Problems with Identification

Members of this genus are frequently encrusted with dirt and other debris which may conceal the diagnostic characters.

Selected References

Foley and Ivie 2008a,b, Ivie 2002c , Kirby 1837, LeConte 1853, Ślipiński and Lawrence 1999, Steiner 1992.

Genus: *Phloeodes*

Diagnostic Features

Description: Antennae 10-segmented with a 2-segmented club. Antennal setation sparse, with stout, bristle-like setae. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Lateral margins of pronotum arcuate to sinuate, without distinct lobes. Pronotal disc with several depressions and numerous small, round tubercles. Apical margin of hypomeron variable, with weak depression to complete antennal cavity. Prosternum without distinct transverse groove. Procoxal cavities closed. Metacoxae widely separated, separation as wide or wider than metacoxal length. Scutellum greatly reduced or absent from view. Abdominal ventrite 5 with an irregular preapical groove. Tarsal formula 5-5-4. Dorsal surface granulose. Dorsal and ventral surfaces commonly encrusted with dirt and debris.

Similar genera: The genus *Phloeodes* is similar to the genera *Sesaspis*, *Phellopsis*, and *Zopherus*. *Phloeodes* is most similar to *Sesaspis*, but can be distinguished by antennomere 3 distinctly longer than 4 (in *Sesaspis*, antennomere 3 only slightly longer than 4) and the pronotal disc mostly flat, bearing small, round tubercles (in *Sesaspis*, with more well-defined raised ridges). *Phellopsis* can immediately be distinguished by the 11-segmented antennae with a 3-segmented club, narrowly open procoxal cavities, hypomeron with lack of depression/antennal cavity, and a small but visible scutellum. The genus *Zopherus* can immediately be distinguished by the 9-segmented antennae with a 1-segmented club composed of 3 fused segments, the deep antennal cavities on the prothoracic hypomera, and the paired rows of fine golden setae on all femora and tibiae.

Known Distribution

Southcentral (TX), Southwest (AZ, CA), Northwest (OR) USA.

Biology

It is speculated that some members may be morphologically adapted (as larvae) for boring into sound wood (Doyen and Lawrence, 1979; Ślipiński and Lawrence, 1999).

Abundance: moderately rare.

North American Species (2)

Phloeodes diabolicus (LeConte, 1851)

Phloeodes plicatus (LeConte, 1859)

Species Diagnoses

***Phloeodes diabolicus*:** Antennal cavities of prothoracic hypomeron complete, clearly limited (enclosed) posteriorly. Elytral apical declivity with several small, round tubercles and one larger raised area. Body generally dark black, elytra often with pale velvety patches of setae at humeral angles and apex.

Distribution: Arizona, Oregon, California, USA.

***Phloeodes plicatus*:** Antennal cavities of prothoracic hypomeron incomplete, not limited (enclosed) posteriorly. Elytral apical declivity with several large, irregular tubercles/raised areas, each elytron with three main nodules. Dorsal vestiture even throughout, generally clothed in lighter colored setae.

Distribution: Arizona, California, USA.

Discussion

Other specimens of *Phloeodes* have been seen bearing locality data from Alaska, Washington, Oklahoma, Pennsylvania, Texas and Wisconsin, but these records are questionable. It is doubtful natural populations occur there.

Potential Problems with Identification

Members of this genus are frequently encrusted with dirt and other debris which may conceal the diagnostic characters.

Selected References

Foley and Ivie 2008 a, b, LeConte 1851, 1859, Ivie 2002c, Ślipiński and Lawrence 1999.

<u>Genus: *Phloeonemus*</u>

Diagnostic Features

Description: Antennae 11-segmented with a 2-segmented club (club may appear 3-segmented due to slightly enlarged antennomere 9). Antennal setation sparse. Subantennal grooves present, as long as eyes. Eyes large, well-developed, finely faceted. Eyes deeply emarginate anteriorly by projection of frons, forming a distinct canthus. Pronotal disc convex, with a pattern of sinuate carinae. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra carinate, with two rows of punctures between carinae. Tarsal formula 4-4-4. Dorsal surface glabrous.

Similar genera: The genus *Phloeonemus* is superficially similar in general appearance to *Denophloeus* and *Acolobicus* but is immediately distinguished by the deeply emarginate eyes.

Known Distribution

South Central (TX), Southwest (AZ, CA) USA.

Probable Distribution

Southwestern United States (NM).

Biology

Phloeonemus has been collected at MV/UV lights and from under the bark of mesquite.

Abundance: Moderately common.

North American Species (2)

Phloeonemus catenulatus Horn, 1878

Phloeonemus interruptus Reitter, 1877

Species Diagnoses

***Phloeonemus catenulatus*:** Elytral carinae uniterrupted, solid.

Distribution: California, Arizona, Texas, USA.

***Phloeonemus interruptus*:** Elytral carinae numerously interrupted.

Distribution: Extreme South Texas, USA.

Selected References

Horn 1878, Ivie 2002a, Reitter 1877a, Stephan 1989.

Genus: ***Pseudocorticus***

Diagnostic Features

Description: Antennae 10-segmented with a distinct, 1-segmented club composed of 2 connate segments. Antennal setation dense, covered in short, flattened, scale-like setae at base and thin, hair-like setae for terminal segments. Subantennal grooves absent to very weakly developed. Eyes well-developed, round, coarsely faceted and densely setose. Pronotal disc with pair of median tubercles. Pronotal lateral margins widest anteriorly, distinctly explanate. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Tarsal formula 4-4-4. Dorsal surface sparsely covered with short, scale-like, light and dark colored setae.

Similar genera: The genus *Pseudocorticus* superficially resembles the genera *Rhagodera* and *Namunaria.* The distinctly carinate elytra and weak, 3-segmented antennal club serve to distinguish *Rhagodera*. The lack of scale-like setae on the antennae, presence of antennal grooves, a distinctly 2-segmented antennal club, and closed procoxal cavities and serve to distinguish *Namunaria*.

Known Distribution

South Central (TX) and Southwestern United States (NM).

Probable Distribution

Southwestern United States (AZ).

Biology

Members of this genus have been found under the bark of dead hackberry (Celtis reticulata) and oak (*Quercus muhlenbergii*).

Abundance: Rare.

North American Species (1)

Pseudocorticus blairi Hinton, 1935

Potential Problems with Identification

Antennal segments and antennal club segments are often difficult to count due to dense, scale-like setae. The antennae appears to be 10-segmented with a one-segmented club composed of apparently 2 fused (connate) segments, denoted by an annulation, or 11-segmented with a composite, 2-segmented club.

Selected References

Hinton, 1935, Ivie 2002a.

Genus: *Pycnomerus*

Diagnostic Features

Description: Body elongate, subdepressed. Antennae 10- or 11-segmented with distinct, 1- or 2-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes large, well-developed, finely faceted. Submentum in male with a setose pit. Pronotal disc convex, simple, sometimes with medial depressions. Procoxal cavities broadly closed. Metacoxae widely separated, separation as wide as or greater than metacoxal length. Tibia with outer angle expanded and produced into a tooth. Tarsal formula 4-4-4. Abdomen with ventrites 1-3 connate. Elytron with 10 distinct striae. Dorsal surface glabrous, shiny.

Similar genera: The genus *Pycnomerus* is distinct among the genera of North America zopherids in having 4-4-4 tarsi, widely separated metacoxae, sparse antennal setation, and a shiny, glabrous body.

Known Distribution

Northeast (DE, MD, NJ, NY, PA, VA), North Central (IL, IN, OH), Southeast (AL, FL, GA, NC, SC, TN), South Central (AR, LA, MS, OK, TX), Northwest (OR, ID), Southwest (AZ) USA. Ontario, Canada

Biology

Pycnomerus is commonly collected under the bark of dead, rotting wood (both hardwoods and pines), on rotting palm fronds, and at MV/UV lights at night.

Abundance: Very common.

North American Species (7)

Pycnomerus arizonicus Stephan, 1989

Pycnomerus haematodes (Fabricius, 1801)

Pycnomerus quercus Stephan, 1989

Pycnomerus reflexus (Say, 1826)

Pycnomerus sulcicollis LeConte, 1863

Pycnomerus thrinax Ivie and Ślipiński, 2000

Species Diagnoses

***Pycnomerus arizonicus*:** Western species. Antennal club 1-segmented. Pronotum convex, without median, longitudinal depressions. Punctures of pronotum more or less uniform in size. Lateral margins of pronotum straight to slightly sinuate. Pronotal disc evenly convex to lateral margins. Anterior angles of pronotum angulate, distinct, posterior angles rounded.

Distribution: Arizona, USA.

***Pycnomerus haematodes*:** Eastern species. Antennal club 2-segmented. Pronotum with 2 median, longitudinal depressions. Punctures of pronotum more or less uniform in size. Lateral margins of pronotum sinuate. Pronotal disc with central area flattened or subdepressed. Anterior and posterior angles of pronotum angulate, distinct.

Distribution: Indiana, Maryland, New Jersey, New York, Ohio, Pennsylvania, Alabama, Florida, Georgia, Mississippi, South Carolina, Virginia, Oklahoma, Texas, USA.

***Pycnomerus quercus*:** Western species. Antennal club 2-segmented. Pronotum convex, without median, longitudinal depressions. Punctures of pronotum more or less uniform in size. Lateral margins of pronotum arcuate. Pronotal disc evenly convex to lateral margins. Anterior angles of pronotum angulate, distinct, posterior angles rounded.

Distribution: Arizona, USA.

***Pycnomerus reflexus*:** Eastern species. Antennal club 2-segmented. Pronotum convex, without median, longitudinal depressions. Punctures of pronotum more or less uniform in size. Lateral margins of pronotum arcuate. Pronotal disc evenly convex to lateral margins. Anterior and posterior angles of pronotum angulate, distinct.

Distribution: Illinois, Indiana, Maryland, New Jersey, Ohio, Pennsylvania, Georgia, Mississippi, North Carolina, Louisiana, South Carolina, Tennessee, Virginia, USA; Ontario, Canada.

Pycnomerus sulcicollis**:** Eastern species. Antennal club 1-segmented. Pronotum with 2 median, longitudinal depressions. Punctures of pronotum variable in size, punctures in central portion of disc larger than surrounding punctures. Lateral margins of pronotum arcuate. Pronotal disc with central area flattened or subdepressed. Anterior and posterior angles of pronotum angulate, distinct.

Distribution: Delaware, Indiana, New Jersey, Alabama, Arkansas, Florida, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, Virginia, Oklahoma, USA.

Pycnomerus thrinax**:** Eastern species. Antennal club 2-segmented. Pronotum convex, without median, longitudinal depressions. Punctures of pronotum more or less uniform in size. Lateral margins of pronotum arcuate. Pronotal disc with central area flattened or subdepressed. Anterior and posterior angles of pronotum rounded.

Distribution: Known only from the Florida Keys, Florida, USA.

Potential Problems with Identification

It is possible that a West Indian species, Pycnomerus infimus Grouvelle, might also occur in the Florida Keys area. This species is extremely similar to Pycnomerus thrinax (above), and can be differentiated from P. infimus in having round pronotal punctures, pronotum lacking longitudinal wrinkles, and sides of elytra sinuate medially. In P. infimus, the pronotal punctures are elongate, londitudinal wrinkles on the pronotum are present, and the sides of the elytra are straight.

Selected References

Fabricius 1801, Ivie 2002c, Ivie and Ślipiński 2000, LeConte 1863, Say 1826, Stephan 1989, Ślipiński and Lawrence 1999.

Genus: *Rhagodera*

Diagnostic Features

Description: Antennae 11-segmented with an indistinct, 3-segmented club. Antennal setation dense, scaly. Subantennal grooves/depressions present or absent. Eyes small, coarsely faceted, with scale-like interfacetal setae. Pronotal disc with a pair of costae. Lateral margin of pronotum serrate, appearing curved or sinuate when teeth are filled with debris. Procoxal cavities narrowly open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra fused. Each elytron with 3 costae. Tarsal formula 4-4-4. Body usually encrusted with sand, dirt, or debris.

Similar genera: The genus *Rhagodera* is superficially similar to the genus *Pseudocorticus*. The lack of elytral carinae and 1-segmented antennal club serve to distinguish *Pseudocorticus*.

Known Distribution

Southwestern United States (CA, AZ, TX), Mexico.

Probable Distribution

Southwestern United States (NM).

Biology

Members of this genus are flightless and ground-dwelling. They inhabit arid, deserted regions. The larvae are unknown. Little is known about the biology of this group.

Abundance: Rarely encountered.

North American Species (4)

Rhagodera tuberculata Mannerheim, 1843

Rhagodera interrupta Stephan, 1989

Rhagodera costata Horn, 1867

Rhagodera texana Stephan, 1989

Species Diagnoses

***Rhagodera tuberculata*:** Subantennal groove/depression present. Antennal segment 3 not greatly elongate. No elytral costae join near apex. Second elytral costa not interrupted before apex. Epipleural fold does not reach apex of elytra.

Distribution: California and Arizona, USA.

***Rhagodera interrupta*:** Subantennal groove/depression absent. Antennal segment 3 greatly elongate. No elytral costae join near apex. Second elytral costa interrupted before apex. Epipleural fold does not reach apex of elytra.

Distribution: California, USA.

***Rhagodera costata*:** Subantennal groove/depression present. Antennal segment 3 not greatly elongate. Lateral margin of pronotum appearing sinuate when filled with debris. Elytral costae 1 and 2 joined near apex. Epipleural fold reaches apex of elytra.

Distribution: Southern Arizona, USA.

***Rhagodera texana*:** Subantennal groove/depression present. Antennal segment 3 not greatly elongate. Lateral margin of pronotum appearing evenly curved when filled with debris. Elytral costae 1 and 2 joined near apex. Epipleural fold reaches apex of elytra.

Distribution: Texas, USA.

Discussion

Members of this genus are quite distinct from all other members of the subfamily Colydiinae, with a number of characters separating it as a distinct group. The specific placement of this genus in the overall classification of the family is uncertain.

Potential Problems with Identification

Members of this genus are frequently encrusted with sand and other debris, which may conceal the pronotal and elytral characters. *Rhagodera costata* and *Rhagodera texana* are very similar. Although unsatisfactory, their distribution serves as the best diagnosis.

Selected References

Horn 1867, Ivie 2002a, Mannerheim 1843, Stephan 1989.

Genus: *Sesaspis*

Diagnostic Features

Description: Antennae 10-segmented with a 2-segmented club. Antennal setation sparse, with thick, bristle-like setae. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Lateral margins of pronotum arcuate to sinuate, without distinct lobes. Pronotal disc with several raised ridges. Apical margin of hypomeron with short, arcuate depression. Prosternum without distinct transverse groove. Procoxal cavities closed. Metacoxae widely separated, separation as wide or wider than metacoxal length. Scutellum greatly reduced or absent from view. Abdominal ventrite 5 with a narrow arcuate preapical groove. Tarsal formula

5-5-4. Dorsal surface tomentose. Ventral surface with punctures from which a single seta arises. Dorsal and ventral surfaces commonly encrusted with dirt and debris.

Similar genera: The genus *Sesaspis* is similar to the genera *Phloeodes*, *Phellopsis*, and *Zopherus*. *Sesaspis* is most similar to *Phloeodes*, but can be distinguished by antennomere 3 only slightly longer than 4 (in *Phloeodes*, antennomere 3 distinctly longer than 4) and the pronotal disc with more well-defined raised ridges (in *Phloeodes*, mostly flat, bearing small, round tubercles). *Phellopsis* can immediately be distinguished by the 11-segmented antennae with a 3-segmented club, narrowly open procoxal cavities, hypomeron with lack of depression/antennal cavity, and a small but visible scutellum. The genus *Zopherus* can immediately be distinguished by the 9-segmented antennae with a 1-segmented club composed of 3 fused segments, the deep antennal cavities on the prothoracic hypomera, and the paired rows of fine golden setae on all femora and tibiae.

Known Distribution

Southcentral (TX), Southwest (NM) USA.

Biology

Sesaspis has been collected from under loose bark of pine and oak.

Abundance: uncommon.

North American Species (1)

Sesaspis emarginata (Horn, 1878)

Potential Problems with Identification

Members of this genus are frequently encrusted with dirt and other debris which may conceal the diagnostic characters.

Selected References

Foley and Ivie 2008, Horn 1878, Ivie 2002c, Ślipiński and Lawrence 1999.

Genus: *Spinhyporhagus*

Diagnostic Features

Description: Body larger, convex, elongate-oval, size over 4 mm. Antennae 11-segmented with a 3-segmented club. Antennal setation sparse. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Groove around dorsal edge of eye paralleling a narrow cuticular process directed away from eye for partial length. Lateral margins of pronotum arcuate. Pronotal disc simple. Hypomeron with deep antennal cavities. Antennal groove and cavity slightly curved (not recurved dorsally), ending before lateral margin of hypomeron. Antennal cavity concealed by prothoracic leg when retracted. Procoxal cavities open. Metacoxae widely separated, separation as wide or wider than metacoxal length. Scutellum small, triangular, visible. Abdominal ventrite 5 simple. Tarsal formula 5-5-4. Dorsal surface punctate, glabrous, shiny.

Similar genera: The genus *Spinhyporhagus* is most similar to the other monommatine genera *Aspathines* and *Hyporhagus*. *Spinhyporhagus* can be separated from *Aspathines* by the larger size, 3-segmented anntennal club, antennal groove and cavity not strongly recurved dorsally and not ending near lateral margin of hypomeron, and antennal cavity concealed by the prothoracic leg when retracted. *Spinhyporhagus* can be separated from *Hyporhagus* and *Aspathines* by the presence of a thin cuticular process on the dorsal margin of the eye.

Known Distribution

Southcentral (TX) USA.

Biology

Members of the Monommatini are associated with rotting vegetable matter and are suspected to feed on fungus (Ivie, 2002)

Abundance: known from only a single specimen.

North American Species (1)

Spinhyporhagus cuneispinatus Freude, 2000

Species Diagnoses

***Spinhyporhagus cuneispinatus*:** Southcentral species. This is the only member of the genus thought to occur in North America. The description and differentiation from similar genera above serve to distinguish this species from all other North American monommatines.

Distribution: Texas, USA.

Discussion

According to Ivie (2002), Freude (2000) described *S. cuneispinatus* from a single specimen labeled "Texas." No specimens of this species have been seen, and it is unclear whether or not the genus is established in the United States or if this species is valid.

Potential Problems with Identification

The nature of the head usually contracted within the pronotum will make this species difficult to separate from the genus *Hyporhagus* unless the head is removed.

Selected References

Freude 1993, 2000, Ivie 2002b, Ślipiński and Lawrence 1999.

<u>Genus: *Stephaniolus*</u>

Diagnostic Features

Description: Antennae 11-segmented with a distinct, 2-segmented club. Antennal setation sparse. Subantennal grooves/depressions present, open internally. Eyes small, reduced, coarsely faceted. Pronotal disc simple. Procoxal cavities open. Metacoxae moderately separated, separation slightly less than metacoxal length. Elytra with distinct striae composed of coarse, nearly confluent punctures. Tarsal formula 4-4-4. Dorsal surface sparsely covered with hair-like setae.

Similar genera: The genus *Stephaniolus* is similar to the genera *Coxelus* and *Megataphtus* in having reduced eyes and wings absent. The distinctive antennal cavities on the hypomeron serve to distinguish *Megataphrus*, and the absence of subantennal grooves serve to distinguish *Coxelus.*

Known Distribution

Southwestern United States (SE AZ). High-elevation mountains.

Probable Distribution

Southwestern United States (NM). High-elevation mountains.

Biology

Members of this genus have been found on the bark of old pine stumps.

Abundance: Rarely encountered.

North American Species (1)

Stephaniolus longus (Stephan, 1989)

Selected References

Ivie 2002a, Ivie *et al.* 2001a, Stephan 1989.

<u>Genus: *Synchita*</u>

Diagnostic Features

Description: Antennae 10-segmented with a distinct, 1-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes large, well-developed, finely faceted. Pronotal disc convex, simple. Procoxal cavities open. Metacoxae narrowly separated, separation less than metacoxal length. Elytra with serially arranged, thick, upright setae. Tarsal formula 4-4-4.

Similar genera: The genus *Synchita* is similar in general appearance to the other genera with 10-segmented antennae and a 1-segmented club that lack a subantennal groove, including *Microsicus*, *Paha*, and *Endeitoma*. *Microsicus* differs in having strongly curved, flattened, multi-colored elytral setae. The genus *Paha* differs in lacking obvious dorsal pubescence, lateral pronotal margins widest anteriorly and distinctly explanate, and having paired carinae on the pronotal disc. *Endeitoma* differs in having a long third antennal segment (at least twice as long as segment 4), lateral pronotal margins distinctly denticulate, and a dorsal pubescence consisting of thin, fine, hair-like setae. In *Synchita*, the pronotal disc is simple, the lateral margins are not distinctly denticulate, antennal segment 3 is not distinctly elongate, and the dorsal pubescence consists of short, bristle-like, unicolored setae.

Known Distribution

Northeast (DC, NH, NH, NJ, ME, MD, PA, WV), North Central (IL, IN, MO, OH), Southeast (FL, NC, SC), South Central (AR, OK, TX) USA, and Ontario, Canada.

Biology

Synchita fuliginosa has been collected at MV/UV lights, but can commonly be found under the bark of various dead trees, including oak, hickory, elm, maple, and pecan.

Abundance: Moderately common.

North American Species (1)

Synchita fuliginosa Melsheimer, 1846

Selected References

Ivie 2002a, Melsheimer 1846, Stephan 1989.

Genus: *Usechimorpha*

Diagnostic Features

Description: Antennae 11-segmented with a 3-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Submentum in male with a setose pit. Pronotum with anterolateral antennal cavities/grooves located above lateral margin, clearly visible from above. Pronotum narrowed anteriorly, distinctly margined laterally. Pronotal disc distinctly setose. Procoxal cavities open. Metacoxae widely separated, separation as wide as metacoxal length. Abdominal ventrite 5 with a thin preapical groove. Tarsal formula 5-5-4. Dorsal surface with patches of short, thick, pale setae. Dorsal and ventral surfaces commonly encrusted with dirt and debris.

Similar genera: The genus *Usechimorpha* is similar to the genus *Usechus*. *Usechimorpha* can be readily distinguished by the more abrupt and compact antennal club, open procoxal cavities, truncate apex of the prosternal process, and the posterolateral depressions of pronotum connected by a transverse groove at the base. In *Usechus*, the antennal club is less compact, the procoxal cavities are closed, the apex of the prosternal process is distinctly widened, and the posterolateral depressions of pronotum are not connected by a transverse groove at base.

Known Distribution

Northwest (OR), Southwest (CA) USA, Vancouver Island, British Columbia (Canada).

Biology

Usechimorpha has been collected sifting leaf litter and detritus in conifer forests and from decaying fruiting bodies of *Laetiporus sulphureus* (Polyporaceae).

Abundance: Moderately rare.

North American Species (2)

Usechimorpha barberi Blaisdell, 1929

Usechimorpha montanus Doyen and Lawrence, 1979

Species Diagnoses

***Usechimorpha barberi*:** Clypeus densely setose. Elytra with a number of setose tubercles. Elytral setae distributed throughout, but more dense on elytral tubercles.

Distribution: California, Oregon, USA; British Columbia, Canada.

***Usechimorpha montanus*:** Clypeus sparsely setose or glabrous. Elytral intervals 1, 2, and 4 regular, not carinate. Elytral setae more or less evenly distributed.

Distribution: California, USA.

Potential Problems with Identification

Members of this genus are frequently encrusted with dirt and other debris which may conceal the diagnostic characters.

Selected References

Blaisdell 1929, Boddy 1965, Doyen and Lawrence 1979, Ivie 2002c, Ślipiński and Lawrence 1999.

Genus: *Usechus*

Diagnostic Features

Description: Antennae 11-segmented with a 3-segmented club. Antennal setation sparse. Subantennal grooves absent. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Submentum in male with a setose pit. Pronotum with anterolateral antennal cavities/grooves located above lateral margin, clearly visible from above. Pronotum narrowed anteriorly, distinctly margined laterally. Pronotal disc distinctly setose. Procoxal cavities closed. Metacoxae widely separated, separation as wide as metacoxal length. Abdominal ventrite 5 with a thin preapical groove. Tarsal formula 5-5-4. Dorsal surface with patches of short, thick, pale setae. Dorsal and ventral surfaces commonly encrusted with dirt and debris.

Similar genera: The genus *Usechus* is similar to the genus *Usechimorpha*. *Usechus* can be readily distinguished by the less compact antennal club, closed procoxal cavities, distinctly widened apex of the prosternal process, and posterolateral depressions of pronotum not connected by a transverse groove at base. In *Usechimorpha*, the antennal club is more abrupt and compact, procoxal cavities are open, the apex of the prosternal process is truncate, and the posterolateral depressions of pronotum are connected by a transverse groove at base.

Known Distribution

Northwest (OR, WA), Southwest (CA) USA.

Biology

Usechus has been collected sifting leaf litter and detritus of oaks, maples and conifers. *Usechus lacerta* larvae and pupae have been collected in *Quercus* and associated with fungus under bark of dead maple (*Acer macrophyllum*) (Doyen and Lawrence, 1979).

Abundance: Moderately rare.

North American Species (2)

Usechus lacerta Motschulsky, 1845

Usechus nucleatus Casey, 1889

Species Diagnoses

***Usechus lacerta*:** Elytral intervals 1, 3, and 5 merge at elytral base to form a transverse carina that does not project forward. Pronotum more uniformly setose except for glabrous posterolateral depressions.

Distribution: California, USA.

***Usechus nucleatus*:** Elytral intervals 1, 3, and 5 merge at elytral base to form an abruptly raised tubercle that projects forward. Pronotum less uniformly setose, with larger glabrous posterolateral depressions and a glabrous mediobasal depression.

Distribution: California, Oregon, Washington, USA.

Discussion

Blaisdell (1929) divided the genus Usechus into two species, *U. nucleatus* and *U. lacerta.* He further divided U. lacerta into 4 varieties (*U. lacerta lacerta*, *U. l. santaclarae*, *U. l. horni*, and *U. l. trinitatis*). For the purposes of this work, all *Usechus lacerta* varieties will be treated under one species.

Potential Problems with Identification

Members of this genus are frequently encrusted with dirt and other debris which may conceal the diagnostic characters.

Selected References

Blaisdell 1929, Boddy 1965, Casey 1889, Doyen and Lawrence 1979, Ivie 2002c, Motschulsky 1845, Ślipiński and Lawrence (1999)

Genus: *Zopherus*

Diagnostic Features

Description: Antennae 9-segmented with a 1-segmented club composed of 3 fused segments. Antennal setation sparse. Eyes well-developed, elongate-oval, somewhat reniform, coarsely faceted, extending well onto dorsal portion of head. Males without setose pit on submentum. Lateral margins of pronotum arcuate to sinuate, without distinct lobes, narrowed posteriorly. Hypomeron with deep antennal cavities. Prosternum with or without distinct transverse groove. Procoxal cavities closed. Metacoxae moderately separated, separation slightly narrower than metacoxal length. Scutellum small, visible to indistinct. Abdominal ventrite 5 with an undivided preapical groove. Femora and tibia with paired rows of golden setae on inner face. Tarsal formula 5-5-4. Dorsal surface glabrous, piceus to bicolored with white and black.

Similar genera: The genus *Zopherus* is similar to the genera *Sesaspis*, *Phloeodes*, and *Phellopsis*, but can
immediately be distinguished by the 9-segmented antennae with a 1-segmented club composed of 3 fused segments, the deep antennal cavities on the prothoracic hypomera, and the paired rows of fine golden setae on all femora and tibiae.

Known Distribution

Southwest (AZ, CA, CO, NM, NV, UT), Southcentral (TX) USA; Mexico.

Biology

Zopherus occurs in rotting wood and plant matter. It is speculated that some members may be morphologically adapted (as larvae) for boring into sound wood (Doyen and Lawrence, 1979; Ślipiński and Lawrence, 1999). Larvae of *Zopherus nodulosus* has been found in pecan timber (*Carya* sp.) and larvae of *Z. granicollis* have been collected from the root crown of *Pinus monophylla* (Doyen and Lawrence, 1979).

Abundance: Some species are locally common.

North American Species (11)

Zopherus championi Triplehorn, 1972

Zopherus concolor LeConte, 1851

Zopherus elegans Horn, 1870

Zopherus gracilis Horn, 1867

Zopherus granicollis Horn, 1885

Zopherus opacus Horn, 1867

Zopherus nodulosus Solier, 1841

Zopherus sanctaehelenae (Blaisdell, 1931)

Zopherus tristis LeConte, 1851

Zopherus uteanus (Casey, 1907)

Zopherus xestus Triplehorn, 1972

Species Diagnoses

***Zopherus championi*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side and the lateral margins of the elytra and pronotum bordered in white (some specimens lack white lateral margins). This species is most similar to *Z. elegans*, and can be distinguished by pronotal surface consisting of simple punctures (compared to small, scabrous bumps or tubercles in *Z. elegans*) and the prosternum anterad of procoxae with punctured but lacking distinct tubercles. This species may sometimes be covered in a greasy exudate, rendering the specimen almost entirely black in color. If this is the case, *Z. championi* will greatly resemble *Z. gracilis*, but can be separated by the distribution, more convex pronotal disc, punctures on pronotal disc deeper, and a hint of coloration on the elytra.

Distribution: Texas, USA; Mexico.

***Zopherus concolor*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side, solid black body, pronotum with small, deep, moderately sparse punctures, and distinctly scabrous, irregularly tuberculate elytral sculpture (as opposed to vermiculate in other species). *Z. concolor* is most similar to *Z. tristis*, but can be distinguished by the shallower and more sparse pronotal punctures and the elytral scabrous tublercles more distinctly raised and prominent.

Distribution: New Mexico, Texas, USA.

***Zopherus elegans*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side and the lateral margins of the elytra and pronotum bordered in white (some specimens lack white lateral margins). This species is most similar to *Z. championi*, and can be distinguished by pronotal surface consisting of small, scabrous bumps or tubercles (compared to simple punctures in *Z. championi*) and the prosternum anterad of procoxae with distinct tubercles, not punctures. This species may sometimes lack the whitish lateral pronotal and elytral margins, rendering the specimen almost entirely black in color. If this is the case, *Z. elegans* will greatly resemble *Z. granicollis* and *Z. uteanus*, but can be separated by the evenly curved anterior margin of the pronoum (when viewed anteriorly), as opposed to bisinuate in *Z. granicollis* and *Z. uteanus*.

Distribution: Arizona, New Mexico, Utah, USA.

***Zopherus gracilis*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side and the pronotum smooth, impunctate, the elytra impunctate, smooth to slightly wrinkled, and the solid black dorsum. *Z. gracilis* is most similar to *Z. gracilis* but can immediately be distinguished by the 2 slightly swollen oblique ridges at the elytral apex, whereas in *Z. xestus* the elytral apex bears 2 large, swollen, oval tubercles.

Distribution: Arizona, New Mexico, USA; Mexico.

***Zopherus granicollis*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side, solid black body, pronotum and elytra bearing small, regular scabrous tubercles subequal in size and more or less evenly distributed. *Z. granicollis* is most similar to *Z. uteanus*, but differs in the prosternal process between the coxae more densely punctate (as opposed to sparsely punctate in *Z. uteanus*), coarser clypeal punctures, and pronotum usually narrower than elytra.

NOTE: This species has two subspecies, *Z. granicollis granicollis* and *Z. granicollis ventriosus*. *Z. granicollis granicollis* can be separated from *Z. granicollis ventriosus* in the overall larger size of the elytral tubercles and lateral tubercles of the elytra similar in size and shape to those on rest of elytra, whereas in *Z. granicollis ventriosus*, the elytral tubercles are overall smaller in size and the lateral tubercles of the elytra are transversely elongate.

Distribution: Arizona, California, Nevada, USA; Mexico.

Zopherus opacus**:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side, solid black body, pronotum with small, moderately dense punctures, and distinctly vermiculate and minutely tuberculate or bumpy elytral sculpture (as opposed to with scabrous, flattened tubercles in other species) The similar size and density of the small bumps/tubercles of the pronotum and elytra serve to separate this species.

Distribution: California, Nevada, Utah, USA.

Zopherus nodulosus**:** This species can be readily distinguished by the elytral apex bearing 4 distinct tubercles, the inner pair being smaller than the outer, and the bicolorous, black and white dorsum.

NOTE: This species has two subspecies, *Z. nodulosus nodulosus* and *Z. nodulosus haldemani*. *Z. nodulosus nodulosus* can be separated from *Z. nodulosus haldemani* in the pronotum and elytra mostly white with black coloration mostly restricted to midline, whereas in *Z. nodulosus haldemani*, the black coloration is more widespread. There can also be darker color morphs (nearly all black) of both subspecies. *Z. nodulosus nodulosus* occurs in Mexico whereas *Z. nodulosus haldemani* occurs in Texas and Mexico. This species may sometimes be covered in a greasy exudate, rendering the specimen almost entirely black in color. If this is the case, *Z. nodulosus* can still be easily recognized by the 4 distinct tubercles at the elytral apex.

Distribution: Texas, USA; Mexico.

***Zopherus sanctaehelenae*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side, solid black body, pronotum with small, moderately sparse punctures, and distinctly vermiculate and minutely punctate elytral sculpture (as opposed to with scabrous, flattened tubercles in other species).

Distribution: California, USA.

***Zopherus tristis*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side, solid black body, pronotum with small, deep, moderately sparse punctures, and distinctly scabrous, irregularly tuberculate elytral sculpture (as opposed to vermiculate in other species). *Z. tristis* is most similar to *Z. concolor*, but can be distinguished by the deeper and more dense pronotal punctures and the elytral scabrous tublercles less distinctly raised.

Distribution: Arizona, California, Colorado, Texas, USA; Mexico.

***Zopherus uteanus*:** This species can be readily distinguished by the elytral apex bearing 2 swollen, oblique ridges on each side, solid black body, pronotum and elytra bearing small, regular scabrous tubercles subequal in size and more or less evenly distributed. *Z. uteanus* is most similar to *Z. granicollis*, but differs in the prosternal process between the coxae sparsely punctate (as opposed to more densely punctate in *Z.*

granicollis), clypeal punctures smaller and sparser, and pronotum usually as wide or wider than elytra.

Distribution: Arizona, California, Nevada, Utah, USA.

***Zopherus xestus*:** This species can be readily distinguished by the elytral apex bearing 2 distinct tubercles, the pronotum smooth, impunctate, the elytra impunctate, smooth to slightly wrinkled, and the solid black dorsum. *Z. xestus* is most similar to *Z. gracilis* but can immediately be distinguished by the 2 tubercles at the elytral apex large, swollen, and oval in shape, whereas in *Z. gracilis* the elytral apex bears a slightly swollen oblique ridge.

Distribution: Texas, USA.

Potential Problems with Identification

Many of the North American members of this genus are quite similar in general appearance and can be difficult to accurately identify. The species which exhibit patterns of black and white coloration also have black forms, which greatly hinder identification. This black coloration is caused by a greasy exudate, which conceals the white coloration and many of the surface sculpture. The exudate can be removed by soaking the specimen in a grease solvent.

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CHAPTER 2

Illustrated Catalogue and Type Designations of the New Zealand Zopheridae (Coleoptera: Tenebrionoidea).

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Appendix G contains the figures 1–421 for Chapter 2 and is available as a supplementary file via LoboVault. See PDF titled "Appendix_G_Figures_Chapter2".

Abstract

This paper provides a comprehensive catalogue of the New Zealand members of the family Zopheridae Solier (Coleoptera: Tenebrionoidea) in an effort to stabilize the nomenclature preceding extensive revisionary taxonomy within the group. A checklist of the 17 New Zealand zopherid genera and an account for each of the 189 species (by current combination) is provided. Type material for nearly all species was examined, and type specimens are designated herein (89 confirmed holotypes, 103 lectotypes, 283 paralectotypes). Images of all primary type specimens and labels examined are provided. *Pycnomerus sulcatissimus* Sharp, 1886 is a junior synonym and secondary homonym of *Pycnomerus sulcatissimus* (Reitter, 1880). One replacement name is proposed, *Chorasus beckae* **nom. nov.**, for *Chorasus subcaecus* (Broun), and 24 new combinations are given.

Introduction

Zopheridae (= Colydiidae) are cosmopolitan, litter-dwelling or saproxylic beetles that feed on dead plant material or fungi. Of a total of 190 genera and over 1,700 species, a disproportionate diversity (nearly half) is restricted to the Australo-Pacific region (Ślipiński and Lawrence 2010). Zopherids are well-represented in New Zealand in particular, constituting the fourth most speciose family (Leschen *et al.* 2003). Based on the current classification (Ślipiński and Lawrence 2010; Bouchard *et al.* 2011), the New Zealand fauna consists of species contained in both subfamilies: Zopherinae (*Pycnomerodes* Broun, *Pycnomerus* Erichson) and Colydiinae (all other genera). Despite their extraordinary diversity in New Zealand, the family has not been studied in great detail and no new species have been described since Broun (1923).

Several workers documented the New Zealand fauna fragmentally; six different workers described a total of 16 species prior to 1880; David Sharp described a large portion (33 species) from the mid-1870s through to the mid-1880s; the remaining species were described by the prolific Thomas Broun. In one of his earlier works on the fauna, Sharp (1876: 18) listed 24 species of Zopheridae and speculated that the number of known colydiids was sure to increase ("...highly probably even quadrupled"), and "...it is pretty certain that, like the Atlantic islands, New Zealand will prove to be very rich in species closely allied to *Tarphius* Erichson…I anticipate that some very interesting comparisons will be suggested when the New Zealand forms of the family are better known, as I hope may soon be the case." Thomas Broun, a New Zealand beetle specialist, military man, and teacher, had initially sent specimens to the British Museum of Natural History. He was soon encouraged by Sharp to describe the fauna, and Broun did so impetuously (though not without some early objections by Sharp 1882: 73–76), describing large numbers of New Zealand Zopheridae (=Colydiidae) from 1880 until 1923. Altogether, Broun described 146 species of zopherids. Surprisingly, all but three (as secondary homonyms) of Broun's names are currently valid, but revisions are needed for species validations and generic assignments. Description of New Zealand zopherids ended with Broun's last publication in 1923. Thereafter, work on the fauna was nil, though species were catalogued or listed by Hutton (1904), Hudson (1923), Hetschko (1930), and Maddison (2010) with numbers of species from Hudson (1923) recapitulated in Watt (1982a), and Klimaszewski and Watt (1997).

Ślipiński and Lawrence (1997) presented a comprehensive generic revision and a key to the Australo-Pacific colydiine genera, providing a suitable starting point for focused studies of the New Zealand species. Most species can readily be identified to genus, though some difficulties are encountered, especially with smaller specimens and those covered by waxy excretions and encrustations (*e.g.* Figs. 39, 121, 158, 169). Closer examination of the named species, notably the type material, yields further problems with identification. For example, in related population studies (Marske *et al.* 2011), a cursory examination types and dissections of *Epistranus* Sharp and the *Pristoderus bakewellii* group (= *Enarsus* Pascoe) did not indicate well-defined species breaks that correlated with well-supported haplotype lineages. Phenotypic variation, therefore, requires careful scrutiny, especially in lineages of New Zealand saproxylic beetles that have been subjected to a rather unique set of of geographic, climatic, and geologic processes confined to a relatively small landmass separated from the rest of Gondwana for some 65–80 my (Marske *et al.* 2012).

We are part of a small team of researchers studying the systematics of New Zealand zopherids employing a combined morphological and molecular approach to document species diversity, classification, and their evolution in New Zealand (a sister study is under way by our counterparts in Australia; *e.g.*, Turco *et al.* 2012). Because of the hyperdiversity that exists in New Zealand, it is imperative that sound taxonomic work begins with a study of the primary literature and museum specimens. For this paper, we examined nearly all types, photorecorded primary types and associated labels, designate lecto- and paralectotypes, and provide synonymies and replacement names where necessary. The purpose of this paper is to stabilize the nomenclature of the New Zealand species in a critical foundational step before proceeding with revisionary studies. This paper does not attempt to make any taxonomic changes outside of the new combinations, a synonymy, and a single replacement name given via an application of current genus-group names.

Materials and Methods

Literature and format

Most relevant taxonomic and primary literature for New Zealand Zopheridae was checked by the authors, including major catalogues and checklists (*e.g.* Hutton 1904; Hudson 1923; Hetschko 1930; Ivie and Ślipiński 1990). An attempt was made to include all spelling errors within publications and the Zoological Records. Pagination of combinations given in abstracts and indices at the beginning and end of works were omitted. In order to provide additional interpretability to the nomina listed in the synonymical tables, a comma is used between the author and year for attributions of original combinations (*e.g. Ablabus brevis* Broun, 1882: 292), whereas a comma is *not* used between the author and year for citations of original combinations (*e.g. Ablabus brevis* Maddison 2010: 426). Subsequent combinations of nomina are separated by a colon from the citations for that combination (*e.g. Notoulus brevis*: Hutton 1904: 168).

Format largely follows Leschen and Gimmel (2012). A complete synonymical listing, type locality, Broun number (see below), remarks, and type material examined sections are presented under each species entry. Where possible, detailed information about the type specimens (including mounting method, damage, etc.) is recorded in each account.

Label data for all type specimens are recorded under the following conventions: double quotes ("") enclose label data quoted verbatim; double forward slashes (//) separate labels; brackets [ ] enclose our comments or notes. Label text is typed, unless noted in brackets. All primary types (incl. card-mounts, if informative) and type labels were imaged (Figs. 1–421). Images of primary types were taken on a Visionary Digital Passport Imaging system utilizing a Canon 40D DSLR camera, stacked using Zerene Stacker v. 1.04, and edited in Adobe Photoshop CS5.

Remark on Broun Numbers

Thomas Broun allocated unique numbers to the 4,000 plus species of New Zealand Coleoptera treated throughout his works (though some were omitted, see May 1967) and also listed or described several varietal forms to which he often gave unique names (*e.g. Vitiacus costatus* var. *incertus* Broun, 1895: 195). We treated these varieties as species in the cases where a new name was provided (accompanied by a description and generally a Broun number), as these were usually listed as formal species in later works (*e.g.* Hetschko 1930).

Examination and designation of type material

An effort was made to examine all holotypes and syntypes and designate primary and (when applicable) secondary types for each of the New Zealand species in accordance with Art. 74.7 of the International Code of Zoological Nomenclature. The following collections were examined (museum coden and curator in parentheses): Auckland War Memorial Museum (AMNZ; John Early), Muséum National d'Histoire Naturelle, Paris, France (MNHN; Thierry Deuve, Azadeh Taghavian), Natural History Museum, London (BMNH; M. Barclay, Roger Booth) and the New Zealand Arthropod Collection, Auckland (NZAC). The Hungarian Natural History Museum, Budapest (HNHM; Otto Merkl) and the Museum für Naturkunde, Berlin (MNHUB; Bernd Jaeger, Manfred Uhlig) were also consulted for potential Reitter material. It is possible (and in some cases, probable) that additional syntype specimens not identified in this paper exist. Material was frequently traded between workers (*e.g.*, Broun, Sharp, and Brookes) and some syntypic series were split up, re-sorted, and in some instances and re-labeled in various collections (*e.g.* Broun material in MNHN, Brookes Collection in NZAC). Primary type specimens were located for all but the following species: *Bolitophagus anguliferus* Blanchard (MNHN?), *Ectomida lacerata* Pascoe (BMNH? Presumed lost), and *Penthelispa acutangulum* Reitter (Presumed lost). All type specimens examined and designated were affixed with appropriate labels by the authors with the following form (*e.g.*) "LECTOTYPE *Ulonotus plagiatus* Broun, 1911 designated by N.P. Lord and

R.A.B. Leschen, 2010". Red labels were affixed to holotypes and lectotypes; blue labels were affixed to paralectotypes. For the sake of brevity, our type labels are not included in the label data and figures.

Remarks on Syntype Material

Handwriting on card-mounts and labels was confirmed by the authors using Horn *et al.* (1990) and with assistance from R. Booth (BMNH) and Trevor Crosby (NZAC). The following conventions were used in determining members of syntypic series of previously described species:

Many BMNH specimens, especially those contained in the Broun and Sharp collections, bear a round label with a red/orange or blue border and the word "TYPE." These specimens should be regarded as potential syntypes, but not as definitive holotypes, lectotypes, or paratypes as may be indicated by the affixed labels. Over the course of the BMNH Coleoptera Collection's history, various parts of the collection were moved and later re-amalgamated. Curators went through the collection and placed these labels on specimens in a conservative fashion (R. Booth, personal communication). When there was some doubt of the constituents of the syntypic series, conservative lectotype and paralectotype designations were made by us where specific information in the original descriptions or on specimens/labels was ambiguous or incomplete.

Much of Sharp's material is labeled as "Type" or "Ind. typ.", usually written at the base of the card-mount in his distinctive hand. It is unclear what Sharp meant by "Ind. type," as these were probably syntypes or material compared to his concept of his "type" specimens. When possible, we regard this material as part of the syntypic series. This assertion is strengthened when the locality information, collector, and/or collection dates on the specimens match those of the original descriptions.

The labels on Broun material are often diagnostic for syntypes. If written in Broun's hand, labels with a full stop (.) after the determination and/or Broun number labels usually indicate syntypic material. This information helped to confirm syntypical material held in other collections outside of the principal Broun collection maintained at the BMNH (i.e., MNHN and NZAC). There are a number of presumed Broun syntype specimens in the NZAC with labels in Albert Brookes' (a late contemporary of Broun, see preface for Broun, 1923: 667) distinctive hand, confirmed from handwriting on other labels and texts (including a Hutton catalogue annotated by Brookes himself). Broun and Brookes exchanged material, and several of the NZAC specimens match the exact date and locality given in the original description. These specimens are most likely original Broun material and were either originally or subsequently labeled by Brookes. Thus, we consider many of these specimens to be syntypes.

Remark on Type Localities

In an attempt to conform to Article 76.2, the place of origin of a designated lectotype becomes the type locality of the nominal species-group taxon. In some instances, the locality recorded on the labels was lacking or less specific than that pubished in the original description (*e.g.* label data states "Otago," whereas original description states "Moeraki," which is in the Otago Region). In these cases the more specific of the two localities is given, or the locality was inferred from collector data (*e.g.* "New Zealand Helms Reitter" = Greymouth, as Reitter received Helms' material from

Greymouth; much of Sharp's (1876) material was received from Broun from Tauria, but not labeled as such). Occasionally, the localities on designated paralectotypes rather than the designated lectotype more accurately matched the locality given in the original description (*e.g. Ablabus nodosus* Broun). In these instances, the additional information listed in the section above (*e.g.* Sharp "Type" on card-mount, Broun hand-written determination labels, label formatting) was taken into account in order to select the most appropriate specimen for type designation. Additional information from the original descriptions or labels is provided in brackets ([]).

Nomenclatural Acts

We present 24 new combinations. All remaining New Zealand members of the genus *Coxelus* Dejean, 1821 are herein moved to *Notocoxelus* Ślipiński and Lawrence 1997. For the sake of clarity, all combinations of species-group names resulting from genus-group synonymies within Ivie and Ślipiński 1990 and Ślipiński and Lawrence 1997 that were not explicitly stated as new combinations in those works are listed as "implied combinations" herein. The majority of these combinations was later given in Maddison 2010 and are listed as such in the synonymical tables for each species.

One replacement name is proposed**:** *Chorasus beckae*, replacement name for *C. subcaecus* (Broun), 1921a: 528, preoccupied by *Chorasus subcaecus* Sharp, 1882: 80.

One new synonymy is reported: *Pycnomerus sulcatissimus* Sharp, 1886 is a junior synonym and secondary homonym of *Pycnomerus sulcatissimus* (Reitter, 1880).

CHECKLIST OF THE GENERA OF NEW ZEALAND ZOPHERIDAE

(species numbers = N.Z. species)

Subfamily: Colydiinae, Tribe: Synchitini (154 spp.)

1. *Ablabus* Broun, 1880 (= *Notoulus* Broun, *Symphysius* Broun) (19 spp.)

2. *Allobitoma* Broun, 1921 (1 sp.)

3. *Bitoma* Herbst, 1793 (= *Ditoma* Illiger, *Eulachus* Erichson, *Euditomum* Gistel, *Phormesa* Pascoe, *Coniophaea* Pascoe, *Xuthia* Pascoe, *Synchytodes* Crotch) (18 spp.)

4. *Chorasus* Sharp, 1882 (= *Vitiacus* Broun) (10 spp.)

5. *Ciconissus* Broun, 1893 (= *Caanthus* Champion) (1 sp.)

6. *Epistranus* Sharp, 1878 (= *Epistrophus* Sharp, *nec* Kirsch) (8 spp.)

7. *Glenentela* Broun, 1893 (2 spp.)

8. *Heterargus* Sharp, 1886 (= *Protarphius* Broun, *Gathocles* Broun) (17 spp.)

9. *Lasconotus* Erichson, 1845 (= *Illestus* Pascoe, *Ithris* Pascoe, *Lado* Wankowicz, *Othismopteryx* J. Sahlberg, *Chrysopogonius* Hinton) (1 sp.)

10. *Norix* Broun, 1893 (1 sp.)

11. *Notocoxelus* Ślipiński and Lawrence, 1997 (22 spp.)

12. *Pristoderus* Hope, 1840 (= *Ulonotus* Erichson, *Sparactus* Erichson, *Enarsus* Pascoe, *Tarphiomimetes* Wollaston, *Dryptops* Broun, *Recyntus* Broun) (41 spp.)

13. *Rytinotus* Broun, 1880 (= *Edalus* Broun) (1 sp.)

14. *Syncalus* Sharp, 1876 (= *Acosmetus* Broun) (9 spp.)

15. *Tarphiomimus* Wollaston, 1873 (= *Ectomida* Pascoe) (3 spp.)

Subfamily: Zopherinae, Tribe: Pycnomerini (35 spp.)

16. *Pycnomerodes* Broun, 1886 (1 sp.)

17. *Pycnomerus* Erichson, 1842 (= *Pycnomorphus* Motschulsky, *Dechomus* Jacquelin du Val, *Penthelispa* Pascoe, *Endectus* LeConte, *Pycnomeroplesius* Ganglbauer) (34 spp.)

CATALOGUE

Family ZOPHERIDAE Solier, 1834: 505.

Subfamily COLYDIINAE Billberg, 1820: 394.

Tribe SYNCHITINI Erichson, 1845: 254. Type genus: *Synchita* Hellwig, 1792.

ABLABUS Broun, 1880

Ablabus Broun, 1880: 183. Type species: *Ablabus ornatus* Broun, 1880, designated by Ivie and Ślipiński 1990: 9.

Notoulus Broun, 1886: 947. Type species: *Ablabus ornatus* Broun, 1880, designated by Ivie and Ślipiński 1990: 9. Objective synonymy with *Ablabus* Broun, listed in Ivie and Ślipiński 1990: 9.

Symphysius Broun, 1909a: 391. Type species: *Symphysius serratus* Broun, 1909, designated by Ivie and Ślipiński 1990: 8. Synonymized with *Ablabus* Broun by Ślipiński and Lawrence 1997: 351.

Remarks: *Notoulus* was listed as an objective synonym of *Ablabus* by Ivie and Ślipiński 1990: 9. Hetschko (1930: 37) listed *Ablabus obscurus* (Blackburn) from "Neu-Seeland" in error, as this species was described from South Australia.

Ablabus brevis Broun, 1882

(Figs. 1–3)

Ablabus brevis Broun, 1882: 292. Broun 1886: 763 (reprinted from Broun 1882). Broun 1886: 894. Hetschko 1930: 37. Maddison 2010: 426 (incorrectly attributed to "Broun 1886").

Notoulus brevis: Hutton 1904: 168. Broun 1912: 420. Broun 1914a: 97. Hudson 1923: 368.

Type locality: Tairua (Auckland).

Broun number: 1353.

Remarks: The description of this species was re-printed in Part III of Broun's Manual of New Zealand Coleoptera (1886: 763). Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ablabus brevis*.

Type material examined: *Lectotype* (BMNH): mounted on same acetate card as paralectotype, top specimen is the lectotype, "Type [round label with red border] // 1353. [green label] // Tairua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus brevis - [in Broun's hand]". *Paralectotype* (BMNH): mounted on same acetate card as lectotype, bottom specimen is a paralectotype, mounted venter-up, labels same as lectotype.

Ablabus crassulus (Broun, 1914)

(Figs. 4–5)

Notoulus crassulus Broun, 1914a: 96. Broun 1921a: 526. Hudson 1923: 368. Hetschko 1930: 37. Kuschel 1990: 33, 63.

Ablabus crassulus: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus crassulus: Maddison 2010: 426.

Type locality: Mount Te Aroha.

Broun number: 3405.

Remarks: Broun mentioned that he based this species on two specimens collected in November, 1910. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Notoulus crassulus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 3405. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Te Aroha. Nov^{r} 1910. [in Broun’s hand] // Notoulus crassulus. [in Broun’s hand]”. *Paralectotype* (BMNH): mounted venter-up, “3405. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Te Aroha. Nov^{r} 1910. [in Broun’s hand] // Notoulus crassulus [in Broun’s hand]”.

Ablabus demissus (Broun, 1912)

(Figs. 6–7)

Notoulus demissus Broun, 1912: 419. Broun 1914a: 97. Hudson 1923: 368. Hetschko 1930: 37.

Ablabus demissus: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9).

Ablabus demissus: Maddison 2010: 426.

Type locality: Mount Pirongia.

Broun number: 3224.

Remarks: Broun based this species on a single specimen collected in December, 1909.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3224 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pirongia. Decr. 1909. [in Broun's hand] // Notoulus demissus. [in Broun's hand]".

Ablabus discors (Broun, 1921)

(Figs. 8–9)

Notoulus discors Broun, 1921a: 526. Hudson 1923: 368. Hetschko 1930: 37.

Ablabus discors: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus discors: Combination byMaddison 2010: 426.

Type locality: Titirangi.

Broun number: 4048.

Remarks: Broun based this species on a single specimen collected on 21 November, 1914.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 4048. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Titirangi - 21.11.1914. [in Broun's hand] // Notoulus discors. [in Broun's hand]".

Ablabus facetus (Broun, 1893)

(Figs. 10–11)

Notoulus facetus Broun, 1893b: 1341. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 37.

Ablabus facetus: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus facetus: Maddison 2010: 426.

Type locality: Moeraki.

Broun number: 2353.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2353. [in Broun's hand] // Otago // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus facetus [in Broun's hand]".

Ablabus fervidulus Broun, 1880

(Figs. 12–13)

Ablabus fervidulus Broun, 1880: 186. Hetschko 1930: 37. Maddison 2010: 426.

Notoulus fervidulus: Hutton 1904: 168. Hudson 1923: 368.

Type locality: Tairua.

Broun number: 329.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 329 [green label] // Tairua [black underline, in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus fervidulus. [in Broun's hand]".

Ablabus libentus (Broun, 1886)

(Figs. 14–15)

Notoulus libentus Broun, 1886: 947. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 37. Hudson 1934: 58.

Ablabus libentus: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus libentus: Maddison 2010: 426.

Type locality: Waitakere Range, Auckland.

Broun number: 1705.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the material of *Notoulus libentus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1705. [in Broun's hand] // Waitakerei // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // libentis [sic] [in Broun's hand]".

Ablabus lobifer (Broun, 1909)

(Figs. 16–17)

Symphysius lobifer Broun, 1909a: 392. Hudson 1923: 369. Hetschko 1930: 37. May 1967: 178.

Ablabus lobifer: Implied combination based on synonymy of *Symphysius* with *Ablabus* in Ślipiński and Lawrence 1997: 351, figs. 9–11 on pg. 352 (Note: figs. 9–11 labeled as *Ablabus lobifer* (Sharp), but this is a misidentification, as illustration is of *Ablabus serratus* (Broun), and authority is incorrectly attributed to Sharp).

Ablabus lobiferus: Maddison 2010: 426. Incorrect subsequent spelling, not available.

Ablabus lobifer: Maddison 2010: 426.

Type locality: Invercargill.

Broun number: 2776 (as given in May 1967: 178).

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2776 [in Broun's hand] // Invercargill // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Symphysius lobifer. [in Broun's hand]".

***Ablabus longipes* (Broun, 1914)**

(Figs. 18–19)

Notoulus longipes Broun, 1914b: 176. Hudson 1923: 368. Hetschko 1930: 37.

Ablabus longipes: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus longipes: Maddison 2010: 426.

Type locality: Hump Ridge, near Invercargill.

Broun number: 3543.

Remarks: Broun mentioned that he based this species on two specimens collected in February, 1912. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Notoulus longipes*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3543. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hump Ridge. Feby. 1912. [in Broun's hand] // Notoulus longipes [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "3543. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hump Ridge Feby. 1912. [in Broun's hand] // Notoulus longipes. [in Broun's hand]".

Ablabus nodosus Broun, 1886

(Figs. 20–21)

Ablabus nodosus Broun, 1886: 894. Broun 1893b: 1342. Hetschko 1930: 37. Maddison 2010: 426.

Notoulus nodosus: Hutton 1904: 168. Hudson 1923: 368.

Type locality: Hooper's Inlet; near Dunedin [Otago Region].

Broun number: 1594.

Remarks: Broun mentioned that he based this species on a specimen from Hooper's Inlet and "2 or 3" others from near Dunedin. Two specimens from Dunedin and Otago, respectively, were located in the BMNH. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ablabus nodosus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1594 [in Broun's hand] // Otago // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus nodosus. [in Broun's hand]". *Paralectotype*

(BMNH): “1594. [in Broun’s hand] // Dunedin // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482.”

Ablabus ornatus **Broun, 1880**

(Figs. 22–23)

Ablabus ornatus Broun, 1880: 184. Broun 1882: 292. Broun 1886: 763 (reprinted from Broun 1882). Hetschko 1930: 37. Ivie and Ślipiński 1990: 9. Ślipiński and Lawrence 1997: 351. Maddison 2010: 426.

Notoulus ornatus: Broun 1886: 947. Hutton 1904: 168. Hudson 1923: 368.

Type locality: Mount Manaia [Whangarei Heads].

Broun number: 326.

Remarks: Broun mentioned that he based this species on five specimens. Two specimens with similar localities were located at the BMNH. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ablabus ornatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 326. [green label] // Manaia // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus ornatus [in Broun’s hand]”. *Paralectotype* (BMNH): “326. [green label] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482.”

Ablabus pallidipictus **Broun, 1880**

(Figs. 24–25)

Ablabus pallidipictus Broun, 1880: 185. Hetschko 1930: 37. Maddison 2010: 426.

Notoulus pallidipictus: Hutton 1904: 168. Hudson 1923: 368.

Type locality: Parua Bay [vicinity ofWhangarei Harbour].

Broun number: 327.

Remarks: Broun mentioned that he based this species on four specimens from Whangarei Harbour, but only two specimens were located in the BMNH. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ablabus pallidipictus*.

Type material examined: *Lectotype* (BMNH): mounted on acetate card with green strip at base, "Type [round label with red border] // 327. [green label] // Parua. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus pallidipictus [in Broun's hand]". *Paralectotype* (BMNH): "327. [green label] // Parua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482."

Ablabus punctipennis Broun, 1880

(Figs. 26–27)

Ablabus punctipennis Broun, 1880: 186. Hetschko 1930: 37. Maddison 2010: 426.

Notoulus punctipennis: Hutton 1904: 168. Hudson 1923: 368.

Type locality: Tairua.

Broun number: 330.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 330 [green label] // Tairua [black underline, in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus punctipennis [in Broun's hand]".

Ablabus scaber Broun, 1880

(Figs. 28–29)

Ablabus scabra Broun, 1880: 185.

Ablabus scabrous: Maddison 2010: 426. Incorrect subsequent spelling, not available.

Notoulus scabrus: Hutton 1904: 168. Hudson 1923: 368. Hudson 1934: 58.

Type locality: Tairua.

Broun number: 328.

Remarks: Note that the male gender ending of the Latin "*scabr-*" is formed as *scaber* (as listed above). Broun based this species on a single specimen. Broun's determination label on the holotype reads "Notoulus scabrus," but the name given in the original description is *Ablabus scabra*.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 328 [green label] // Tairua [black underline, in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus scabrus. [sic] [in Broun's hand]".

Ablabus sellatus (Sharp, 1886)

(Figs. 30–32)

Bitoma sellata Sharp, 1886: 385, pl. 12, fig. 20. Broun 1893b: 1081 (reprinted excerpt of Sharp 1886: 385). Hutton 1904: 169. Hetschko 1930: 19.

Notoulus sellata: transferred from *Bitoma* by Broun 1912: 420. Hudson 1923: 368. Hudson 1934: 58.

Ablabus sellata: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus sellatus: Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 1927.

Remarks: Note that the male gender ending of the Latin "*sellata*" is formed as *sellatus* (as listed above). Sharp did not mention the number of specimens examined. Sharp lists the specimen data as "Greymouth. Helms, No. 289." In the BMNH there are 21 specimens identified by Sharp from Greymouth, with Sharp's distinctive handwriting on the card-mount. There are two specimens with "Types" hand-written by Sharp on the same card, and we designate the specimen on the right as the lectotype, the left specimen as a paralectotype. All remaining specimens in the assumed syntypic series have the "Greymouth New Zealand [red underline] Helms." label, and the "Sharp Coll. 1905-313." label. In order to stabilize this name, a lectotype and 20 paralectotypes are **here designated** from the material of *Bitoma sellata*. There is one card-mounted specimen in the BMNH bearing the labels "Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." another card-mounted specimen [card has five black lines] bearing the labels: "Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313. // sellatus n.sp. [handwritten, appears to be in Sharp's hand]", and three specimens card-mounted together with a determination label of "Bitoma sellata Greymouth" in Sharp's hand, but the bottom label states "N.Zeal / [red line] / 86 20". We do not regard these as syntypes due to the lack of a determination and different card style.

Type material examined: *Lectotype* (BMNH): mounted on same card as a paralectotype, right specimen is the lectotype, "Bitoma sella- ta. Types. D.S. Greymouth. N. Zeal^{d}. Helms. [written at base of card in Sharp's hand] // Type [round label with red border] //

Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313. // BMNH(E) #651699". *Paralectotype* (BMNH): mounted on same card as lectotype, left specimen is a paralectotype, labels same as lectotype. *Paralectotype* (BMNH): 1, card-mounted individually, "Bitoma sellata D.S. Greymouth N.Zd [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): eight total, four pairs of paralectotypes card-mounted on separate cards and pins, with identical labels, "Bitoma sellata D.S. Greymouth N.Z. Helms. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 3, mounted together on single card, "Bitoma ~~Tarphiomimus~~ sellata Greymouth N.Zd Helms. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted together on single card, right specimen mounted venter-up, "Bitoma sellata D.S. Greymouth. NZ. Helms. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted together on single card, venter-up, "Bitoma sellata Greymouth Helms [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 3, mounted together on single card, right specimen mounted venter-up, "Bitoma sellata D.S. Greymouth N.Z. Helms. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313."

Ablabus serratus **(Broun, 1909)**

(Figs. 33–34)

Symphysius serratus Broun, 1909a: 391. Hudson 1923: 369. Hetschko 1930: 37. May 1967: 178. Ivie and Ślipiński 1990: 8.

Ablabus serratus: Ślipiński and Lawrence 1997: 351, based on synonymy of *Symphysius* with *Ablabus*. *Ablabus lobifer sensu* Ślipiński and Lawrence 1997: 352, figs. 9–11, not Broun 1909 [misidentification].

Type locality: Southland.

Broun number: 2775 (as given in May 1967: 178).

Remarks: Broun mentioned that he based this species on three specimens: two specimens from "Southland" and one with the number "5237" on it sent by J.H. Lewis that was caked with dried sap and dirt. The two specimens from "Southland" were located and are mounted on the same card type, but we did not locate the specimen with the "5237" number as Broun described. There are two specimens with "Greymouth Lewis" labels, one of which bears a "37" label, the other lacking this label and mounted ventrally on the card. We assume that Broun miscounted the number of specimens and/or also quoted or miswrote the Lewis batch label. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Symphysius serratus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2775. [in Broun's hand] // Southland // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Symphysius serratus. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "2775. [in Broun's hand] // Southland // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Symphysius serratus [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "2775. [in Broun's hand] // 37.

[handwritten] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Greymouth. Lewis - [in Broun's hand]".

Ablabus sparsus (Broun, 1886)

(Figs. 35–36)

Notoulus sparsus Broun, 1886: 947. Hutton 1904: 168. Hudson 1923: 368. Hetschko, 1930: 37.

Ablabus sparsus: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus sparsus: Maddison 2010: 426.

Type locality: Stratford, base of Mount Egmont [Taranaki Region].

Broun number: 1704.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype and three paralectotypes are **here designated** from the material of *Notoulus sparsus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1704. [in Broun's hand] // Taranaki // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus sparsus. [in Broun's hand]". *Paralectotype* (BMNH): "1704. [in Broun's hand] // Taranaki // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482." *Paralectotypes* (NZAC): 2, individually mounted on separate cards and pins, with identical labels, "Stratford Taranaki [in Brookes' hand] // 1704 [in Brookes' hand] // Notoulus sparsus Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection".

***Ablabus truncatus* (Broun, 1914)**

(Figs. 37–38)

Notoulus truncatus Broun, 1914b: 175. Hudson 1923: 368. Hetschko 1930: 37.

Ablabus truncatus: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus truncatus: Maddison 2010: 426.

Type locality: McClennan's Bush, near Methven.

Broun number: 3542.

Remarks: Broun mentioned that he based this species on two specimens collected on 15 March, 1912. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Notoulus truncatus.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3542 [in Broun's hand] // McClennans. 15.3.1912. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus truncatus [in Broun's hand]". *Paralectotype* (MNHN): card-mounted, "McClennans. 15.3.1912. [in Broun's hand] // Notoulus truncatus [in Broun's hand] // 3542. [in Broun's hand]".

***Ablabus varicornis* (Broun, 1910)**

(Figs. 39–40)

Notoulus varicornis Broun, 1910b: 38. Broun 1914b: 176. Hudson 1923: 368. Hetschko 1930: 37.

Ablabus varicornis: Implied combination based on *Notoulus* as an objective synonym of *Ablabus* in Ivie and Ślipiński 1990: 9.

Ablabus varicornis: Maddison 2010: 426.

Type locality: Dunedin.

Broun number: 3086.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3086. [in Broun's hand] // Dunedin 9.5.09 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus varicornis [in Broun's hand]".

ALLOBITOMA Broun, 1921

Allobitoma Broun, 1921a: 526. Type species: *Allobitoma halli* Broun, 1921, fixed by monotypy.

Allobitoma halli Broun, 1921

(Figs. 41–42)

Allobitoma halli Broun, 1921a: 527. Hudson 1923: 368. Hetschko 1930: 20. Ivie and Ślipiński 1990: 5. Ślipiński and Lawrence 1997: 355, figs. 29–37, 356. Maddison 2010: 426.

Type locality: Glenhope.

Broun number: 4049.

Remarks: Broun mentioned that he based this species on two specimens collected on 20 December, 1914. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Allobitoma halli*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type. [red underline, in Broun’s hand] // 4049. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Glen Hope. 20.12.1914. [in Broun’s hand] // Allobitoma. halli - [in Broun’s hand] // SYN- TYPE [round label with light blue border]”. *Paralectotype* (MNHN): card-mounted, “Glen Hope. 20.12.1914. [in Broun’s hand] // Allobitoma halli - [in Broun’s hand]”.

BITOMA Herbst, 1793

Bitoma Herbst, 1793: 25. Type species: *Tritoma crenata* Fabricius, 1775, by subsequent designation of Latreille, 1810: 431.

Ditoma Illiger, 1807: 320, unjustified emendation of *Bitoma* Herbst. Type species: *Tritoma crenata* Fabricius, 1775, by subsequent designation of Latreille, 1810: 431.

Eulachus Erichson, 1845: 275. Type species: *Eulachus costatus* Erichson, 1845, by monotypy. Synonymized with *Bitoma* Herbst by Ślipiński and Lawrence 1997: 361.

Euditomum Gistel, 1857: 26 (also cited as p. 524). Type species: *Ditoma unicolor* Gistel, 1857, fixed by monotypy.

Phormesa Pascoe, 1863a: 31. Type species: *Phormesa lunaris* Pascoe, 1863, designated by Ivie and Ślipiński 1990: 6. Synonymized with *Bitoma* Herbst by Ślipiński and Lawrence 1997: 361.

Coniophaea Pascoe, 1863b: 90. Type species: *Coniophaea exarata* Pascoe, 1863, by monotypy. Synonymized with *Bitoma* Herbst by Ślipiński and Lawrence 1997: 361.

Xuthia Pascoe, 1863c: 128. Type species: *Xuthia siccana* Pascoe, 1863, designated by Ślipiński 1985: 478. Synonymized with *Bitoma* Herbst by Arrow 1909: 193.

Synchytodes Crotch, 1873: 45. Type species: *Bitoma quadriguttata* Say, 1827, designated by Ivie and Ślipiński 1990: 5.

Synchitodes Reitter, 1882: 130. Incorrect subsequent spelling, not available.

***Bitoma auriculata* Sharp, 1886**

(Figs. 43–45)

Bitoma auriculata Sharp, 1886: 385. Broun 1893b: 1082 (reprinted excerpt of Sharp 1886: 385). Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 16. Maddison 2010: 426.

Type locality: New Zealand.

Broun number: 1928.

Remarks: Sharp based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Bitoma auric- ulata Type D.S. N. Zealand. Murray [written at base of card in Sharp's hand] // Type [round label with red border] // ? Gen. Ablabus Broun. [handwritten] // Sharp Coll. 1905-313. // BMNH(E) #651710".

***Bitoma brouni* (Hetschko, 1928)**

(Figs. 46–47)

Bitoma brouni (Hetschko, 1928: 141; as *Ditoma*). Replacement name for *Bitoma obsoleta* Broun 1914b: 176, preoccupied by *Bitoma obsoleta* Grouvelle, 1903: 182. Hetschko 1930: 16. Maddison 2010: 426.

Bitoma obsoleta Broun: Hudson 1923: 369.

Type locality: Rakaia Gorge, near Methven.

Broun number: 3544.

Remarks: Broun based his *Bitoma obsoleta* on a single specimen collected on 1 November, 1912. This was given the replacement name *Bitoma brouni* (Hetschko, 1928: 142; as *Ditoma*).

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3544. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Rakaia. 1.11.1912. [in Broun's hand] // Bitoma obsoleta - [in Broun's hand]".

***Bitoma costicollis* (Reitter, 1880)**

(Figs. 48–49)

Phormesa costicollis Reitter, 1880c: 174. Broun 1910b: 38. Hudson 1923: 368. Hetschko 1930: 23.

Bitoma costicollis: Implied combination based on synonymy of *Phormesa* with *Bitoma* in Ślipiński and Lawrence 1997: 361.

Bitoma costicollis: Maddison 2010: 426 (attributed to Reitter, although author and year were not in parentheses).

Type locality: Greymouth.

Broun number: 3085.

Remarks: Reitter did not mention the number of specimens examined. In order to stabilize this name, a lectotype and seven paralectotypes are **here designated** from the material of *Phormesa costicollis.*

Type material examined: *Lectotype* (MNHN): card-mounted, "Now. Zeeland Helms Reitter. [label bordered with thin black line] // Phorm. Costicollis m [in Reitter's hand] // Phormesa costicollis Rtt & SYNTYPES [red label, in S.A. Ślipiński's hand]". *Paralectotypes* (MNHN): 5, individually mounted on separate cards and pins, with identical labels, "EX. COLL. REITTER". *Paralectotypes* (MNHN): 2, individually mounted on separate cards and pins, with identical labels, "New Zealand Helms Reitter".

Bitoma discoidea Broun, 1880

(Figs. 50–51)

Bitoma discoidea Broun, 1880: 195. Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 17. Maddison 2010: 426.

Type locality: Mount Manaia [Whangarei Heads].

Broun number: 349.

Remarks: Broun mentioned that he based this species on two specimens. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Bitoma discoidea*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 349 [green label] // Mount Manaia. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Bitoma discoidea [in Broun's hand]".

Paralectotype (BMNH): "349. [green label] // Manaia. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482."

***Bitoma distans* Sharp, 1876**

(Figs. 52–54)

Bitoma distans Sharp, 1876: 26. Sharp 1877c: 399 (reprinted from Sharp 1876). Broun 1880: 193. Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 17. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 345.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and four paralectotypes are **here designated** from the material of *Bitoma distans*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Bitoma distans Type N Zeald D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 4, individually mounted on separate cards and pins, with identical labels, "Bitoma distans Ind. typ. N.Zeald D.S. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313."

***Bitoma distincta* Broun, 1880**

(Figs. 55–56)

Bitoma distincta Broun, 1880: 194. Hutton 1904: 169. Broun 1921b: 613. Hudson 1923: 368. Hetschko 1930: 17. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 348.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 348 [green label] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Tairua. [black underline, in Broun's hand] // Bitoma distincta [in Broun's hand]".

Bitoma guttata Broun, 1886

(Figs. 57–58)

Bitoma guttata Broun, 1886: 895. Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 18. Maddison 2010: 426.

Type locality: near Dunedin [Otago Region].

Broun number: 1597.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1597. [in Broun's hand] // Otago [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Bitoma guttata. [in Broun's hand]".

Bitoma insularis White, 1846

(Figs. 59–61)

Bitoma insularis White, 1846: 18. Sharp 1876: 18, 26. Sharp 1877c: 391, 399 (reprinted from Sharp 1876). Broun 1880: 192. Hutton 1904: 169. Broun 1912: 420. Hudson 1923: 368. Hetschko 1930: 18. Hudson 1934: 59. Kuschel 1990: 33, 63. Maddison 2010: 426.

Type locality: Port Nicholson.

Broun number: 343.

Remarks: White did not mention the number of specimens examined. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Bitoma insularis*.

Type material examined: *Lectotype* (BMNH): mounted on same card as paralectotype, left specimen is the lectotype, "Type [round label with red border] // Port. Nicholson N. Zealand [dark green label with black border, in White's hand] // 67. 78- [round blue label, handwritten] // Bitoma insularis White. Zool. Ereb & Terro [handwritten]". *Paralectotype* (BMNH): mounted on same card as lectotype, right specimen is a paralectotype, mounted on right side and missing head and prothorax, labels same as lectotype.

Bitoma lobata Broun, 1886

(Figs. 62–63)

Bitoma lobata Broun, 1886: 833, 895. Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 18. Maddison 2010: 426.

Type locality: Woodhill, near Waitakere Range.

Broun number: 1482.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted. "Type [round label with red border] // 1482. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Woodhill. Waitakerei. [in Broun's hand] // Bitoma lobata. [in Broun's hand]".

***Bitoma morosa* Broun, 1921**

(Figs. 64–65)

Bitoma morosa Broun, 1921b: 613. Hudson 1923: 369. Hetschko 1930: 18. Maddison 2010: 426.

Type locality: Lake Rotoiti, Nelson.

Broun number: 4181.

Remarks: Broun based this species on a single specimen collected on 17 March, 1916.

Type material examined: *Holotype* (BMNH): card-mounted, "4181. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Rotoiti. 17.3.1916 [in Broun's hand] // Bitoma morosa - [in Broun's hand]".

***Bitoma mundula* Sharp, 1886**

(Figs. 66–68)

Bitoma mundula Sharp, 1886: 386. Broun 1893b: 1083 (reprinted excerpt of Sharp 1886: 386). Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 18. Maddison 2010: 426.

Type locality: Picton.

Broun number: 1930.

Remarks: Sharp based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Bitoma mundu- la Type D.S. Picton N. Zeal$^{d.}$ Helms [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll 1905-313. // BMNH(E) #651700".

***Bitoma nana* Sharp, 1876**

(Figs. 69–71)

Bitoma nana Sharp, 1876: 27. Sharp 1877c: 400 (reprinted from Sharp 1876). Broun 1880: 194. Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 18. Kuschel 1990: 33, 63. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 347.

Remarks: Sharp based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Bitoma nana Type N. Zeal[d] D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll 1905-313."

Bitoma novella Hetschko, 1929

(Figs. 72–73)

Bitoma novella Hetschko, 1929: 94, replacement name for *Bitoma maura* Broun, 1912: 420, preoccupied by *Bitoma maura* (Pascoe, 1863c: 129; as *Xuthia*). Maddison 2010: 426.

Bitoma maura Broun, 1912: 420. Hudson 1923: 369.

Type locality: Waimarino.

Broun number: 3225.

Remarks: Broun based this species on a single specimen collected in January, 1910.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3225. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Waimarino Jany. 1910. [in Broun's hand] // Bitoma maura [in Broun's hand]".

Bitoma picicornis Broun, 1909

(Figs. 74–75)

Bitoma picicorne Broun, 1909a: 385. Hudson 1923: 369. May 1967: 178.

Bitoma picicornis: Broun 1914b: 177. Hetschko 1930: 19. Maddison 2010: 426.

Type locality: Broken River.

Broun number: 2762 (as given in Broun 1914b: 177; May 1967: 178).

Remarks: Note that the female gender ending of the Latin "*picicorn*-" is formed as *picicornis* (as listed above). Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2762. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Broken River. [in Broun's hand] // Bitoma picicorne - [in Broun's hand]".

Bitoma rugosa Sharp, 1876

(Figs. 76–78)

Bitoma rugosa Sharp, 1876: 26. Sharp 1877c: 399 (reprinted from Sharp 1876). Broun 1880: 193. Broun 1886: 833, 895. Hutton 1904: 169. Broun 1909a: 386. Hudson 1923: 368. Hetschko 1930: 19. Hudson 1934: 59. Kuschel 1990: 33, 63. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 346.

Remarks: Sharp did not mention the number of specimens examined. One specimen labeled as "var" [handwritten] was not considered a syntype because it did not have "Ind.

typ" written on the card mount in Sharp's hand. In order to stabilize this name, a lectotype and five paralectotypes are **here designated** from the material of *Bitoma rugosa*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Bitoma rugosa Type N. Zeal[d] D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, individually mounted on separate cards and pins, with identical labels, "Bitoma rugosa Ind. typ. N. Zeald [written at base of card mount in Sharp's hand] // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 3, individually mounted on separate cards and pins, with identical labels, "Bitoma rugosa Ind. typ. N. Zeald D.S. [written at base of card mount in Sharp's hand] // Sharp Coll. 1905-313."

Bitoma scita Broun, 1886

(Figs. 79–80)

Bitoma scita Broun, 1886: 895. Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 19. Maddison 2010: 426.

Type locality: Whangarata, near Tuakau.

Broun number: 1596.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1596. [in Broun's hand] // Whangarata // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Bitoma scita - [in Broun's hand]".

Bitoma serraticula Sharp, 1886

(Figs. 81–83)

Bitoma serraticula Sharp, 1886: 386. Broun 1893b: 1083 (reprinted excerpt of Sharp 1886: 386). Hutton 1904: 169. Hudson 1923: 368. Hetschko 1930: 19. Maddison 2010: 426.

Type locality: New Zealand.

Broun number: 1929.

Remarks: Sharp based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Bitoma serratic- ula Type D.S. New Zealand. Murray [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651701".

Bitoma vicina Sharp, 1876

(Figs. 84–86)

Bitoma vicina Sharp, 1876: 25. Sharp 1877c: 398 (reprinted from Sharp 1876). Broun 1880: 193. Hutton 1904: 169. Broun 1912: 420. Hudson 1923: 368. Hetschko 1930: 20. Hudson 1934: 59. Watt 1982b: 303. Kuschel 1990: 33, 63. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 344.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Bitoma vicina*. There are five additional specimens, one singleton and two pairs card-mounted on separate pins (one pair with right specimen mounted venter-up, with pin head removed) that bear only "Sharp Coll. 1905-313" labels. These appear to be on the same card and pin type as the lectotype and paralectotypes and may be part of a split-up series. These specimens are not regarded as syntypes, however, due to lack of information.

Type material examined: *Lectotype* (BMNH): card-mounted, "Bitoma vicina Type N. Zeal[d] D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted individually on separate cards pins, with identical labels, "Bitoma vicina Ind. typ. N. Zeald D.S. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313."

CHORASUS Sharp, 1882

Chorasus Sharp, 1882: 79. Type species: *Chorasus subcaecus* Sharp, 1882, fixed by monotypy.

Vitiacus Broun, 1893b: 1087. Type species: *Vitiacus costatus* Broun, 1893, fixed by monotypy. Synonymized with *Chorasus* Sharp by Ślipiński and Lawrence 1997: 368.

***Chorasus beckae*, NEW NAME**

(Figs. 87–88)

Chorasus beckae, replacement name for *Chorasus subcaecus* (Broun, 1921a: 528; as *Vitiacus*), preoccupied by *Chorasus subcaecus* Sharp, 1882: 80.

Vitiacus subcaecus Broun, 1921a: 528. Hudson 1923: 369.

Chorasus subcaecus (Broun): Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Type locality: Hollyford.

Broun number: 4051.

Remarks: Broun based this species on a single specimen collected on 20 February, 1914.

Etymology: The specific epithet of the replacement name honors Becky Freeman for her support during the preparation of this work.

Type material examined: *Holotype* (BMNH): card-mounted, "4051 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hollyford. 20.2.1914 [in Broun's hand] // Vitiacus subcaecus. [in Broun's hand]".

Chorasus costatus (Broun, 1893)

(Figs. 89–90)

Vitiacus costatus Broun, 1893b: 1087. Broun 1895: 195. Hutton 1904: 169. Broun 1921a: 530. Hudson 1923: 369. Hetschko 1930: 48. Ivie and Ślipiński 1990: 11.

Chorasus costatus: Ślipiński and Lawrence 1997: 368, based on synonymy of *Vitiacus* with *Chorasus* (p. 368). Maddison 2010: 426.

Type locality: Moeraki.

Broun number: 1937.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1937. [in Broun's hand] // Moeraki - Otago - [in Broun's hand] // New

Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Vitiacus costatus. [in Broun's hand]".

Chorasus costicollis (Broun, 1893)

(Figs. 91–92)

Vitiacus costicollis Broun, 1893b: 1442. Hutton 1904: 169. Broun 1921a: 529. Hudson 1923: 369. Hetschko 1930: 48.

Chorasus costicollis: Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Chorasus costicollis: Maddison 2010: 426.

Type locality: Capleston.

Broun number: 2501.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2501. [in Broun's hand] // Capleston Westland // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Vitiacus costicollis [in Broun's hand]".

Chorasus incertus (Broun, 1895)

(Figs. 93–94)

Vitiacus incertus Broun, 1895: 195. Broun 1921a: 530. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 48. May 1967: 178.

Chorasus incertus: Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Chorasus incertus: Maddison 2010: 426.

Type locality: Mount Te Aroha.

Broun number: 2774 (as given in Broun 1921a: 530; May 1967: 178).

Remarks: Broun mentioned that he based this species on two specimens collected in March, 1894. Broun (1895: 195) originally listed this taxon as a varietal form of *V. costatus* to be treated further when more material of both forms became available. Hetschko (1930: 48) also listed it as a variety of *Vitiacus costatus* Broun. However, *V. incertus* was listed as a distinct species in later works (*e.g.* May 1967), thus we regard this species as distinct and not a varietal form. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Vitiacus incertus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2774. [in Broun's hand] // Mount TeAroha. [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Vitiacus incertus. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "2774 [in Broun's hand] // Mount. Te Aroha [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Vitiacus incertus [in Broun's hand]".

Chorasus lateralis **(Broun, 1921)**

(Figs. 95–96)

Vitiacus lateralis Broun, 1921a: 531. Hudson 1923: 369. Hetschko 1930: 49.

Chorasus lateralis: Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Chorasus lateralis: Maddison 2010: 426.

Type locality: Erua.

Broun number: 4056.

Remarks: Broun based this species on a single specimen collected in January, 1909. A duplicate specimen was located in the MNHN Broun Collection, but we do not recognize this as a syntype since it lacked Broun's handwritten "4056." and Broun (1921a: 531) indicated only having examined a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "4056. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Erua. Jany. 1909. [in Broun's hand] // Vitiacus. lateralis. [in Broun's hand]".

Chorasus posticalis (Broun, 1921)

(Figs. 97–98)

Vitiacus posticalis Broun, 1921a: 529. Hudson 1923: 369. Hetschko 1930: 49.

Chorasus posticalis: Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Chorasus posticalis: Maddison 2010: 426.

Type locality: Hollyford.

Broun number: 4052.

Remarks: Broun based this species on a single specimen collected on 20 February, 1914.

Type material examined: *Holotype* (BMNH): card-mounted, "4052. [in Broun's hand] // Hollyford 20.2.1914 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Vitiacus posticalis [in Broun's hand]".

Chorasus purus (Broun, 1921)

(Figs. 99–100)

Vitiacus purus Broun, 1921a: 529. Hudson 1923: 369. Hetschko 1930: 49.

Chorasus purus: Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Chorasus purus: Maddison 2010: 426.

Type locality: Hollyford.

Broun number: 4053.

Remarks: Broun based this species on a single specimen collected on 16 February, 1914.

Type material examined: *Holotype* (BMNH): card-mounted, "4053. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hollyford 16.2.1914 [in Broun's hand] // Vitiacus purus. [in Broun's hand]".

Chorasus setarius (Broun, 1921)

(Figs. 101–102)

Vitiacus setarius Broun, 1921a: 531. Hetschko 1930: 49.

Chorasus setarius: Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Chorasus setarius: Maddison 2010: 426.

Type locality: Erua, near Waimarino.

Broun number: 4055.

Remarks: Broun mentioned that he based this species on two specimens collected in January, 1909 and 1910. Only one of the two specimens matching the date and locality was located BMNH Broun collection. In order to stabilize this name, a lectotype is **here designated** from the material of *Vitiacus setarius.*

Type material examined: *Lectotype* (BMNH): card-mounted, “4055. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Erua. Jany. 1910. [in Broun’s hand] // Vitiacus setarius. [in Broun’s hand]”.

Chorasus subcaecus Sharp, 1882

(Figs. 103–105)

Chorasus subcaecus Sharp, 1882: 80. Broun 1893b: 1093 (reprinted excerpt of Sharp 1882: 80). Hutton 1904: 170. Broun 1921a: 529. Hudson 1923: 369. Hetschko 1930: 49. Ivie and Ślipiński 1990: 13. Ślipiński and Lawrence 1997: 368. Maddison 2010: 426.

Chorasus subcoecus: Hetschko 1930: 59. Incorrect subsequent spelling, not available.

Type locality: Greymouth.

Broun number: 1943.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and eight paralectotypes are **here designated** from the material of *Chorasus subcaecus*. There are an additional six specimens in the BMNH that appear to be on the same card and pin type as the syntypic series. While it is possible these specimens are also part of the syntypic series, we do not regard them as such due to the discrepancy in label data (*e.g.*, one specimen was dated 1885).

Type material examined: *Lectotype* (BMNH): card-mounted, “Chorasus subcaecus Type D.S. Greymouth. [written at base of card in Sharp’s hand] // Type [round label with red border] // Greymouth, [red underline] New Zealand. Helms. // Sharp Coll. 1905-313.” *Paralectotype* (BMNH): 1, card-mounted, “Chorasus subcaecus Ind. typ. D.S. Greymouth [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): 1, card-mounted venter-up, "Chorasus subcaecus D.S. Greymouth Helms. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted on same card, "Chorasus subcaecus Greymouth. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 4, mounted on same card, one disarticulated, "Chorasus sub- caecus Greymouth N. Zd. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313."

Chorasus suturalis **(Broun, 1921)**

(Figs. 106–107)

Vitiacus suturalis Broun, 1921a: 530. Hudson 1923: 369. Hetschko 1930: 49.

Chorasus suturalis: Implied combination based on synonymy of *Vitiacus* with *Chorasus* in Ślipiński and Lawrence 1997: 368.

Chorasus suturalis: Maddison 2010: 426.

Type locality: Mount Owen.

Broun number: 4054.

Remarks: Broun based this species on a single specimen collected on 27 December, 1914.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [red underline, in Broun's hand] // 4054 [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit.

Mus. 1922-482. // M^{t} Owen. 27.12.1914. [in Broun's hand] // Vitiacus suturalis [in Broun's hand]".

CICONISSUS Broun, 1893

Ciconissus Broun, 1893a: 185. Type species: *Ciconissus granifer* Broun, 1893, by monotypy.

Caanthus Champion, 1894: 378. Type species: *Caanthus gibbicollis* Champion, 1894, by monotypy. Synonymized with *Ciconissus* Broun by Ślipiński and Lawrence 1997: 372.

***Ciconissus granifer* Broun, 1893**

(Figs. 108–109)

Ciconissus granifer Broun, 1893a: 186. Hutton 1904: 171. Hudson 1923: 369. Hetschko 1930: 48. May 1967: 178. Ivie and Ślipiński 1990: 11. Ślipiński and Lawrence 1997: 373. Maddison 2010: 426.

Type locality: Mount Pirongia.

Broun number: 2773.

Remarks: Broun mentioned that he based this species on seven specimens collected in December, 1892. Three specimens in the BMNH and one in the NZAC matching this data were located. In order to stabilize this name, a lectotype and three paralectotypes are **here designated** from the material of *Ciconissus granifer*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 2773 [in Broun’s hand] // Pirongia // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ciconissus granifer. [in Broun’s hand]”. *Paralectotype* (BMNH): card-mounted venter-up, “2773 [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1933-482. // Pirongia. Decr. 1892. [in Broun’s hand] // Ciconissus granifer. [in Broun’s hand].” *Paralectotype* (MNHN): card-mounted, “Pirongia. Dec^{r} 1892. [in Broun’s hand] // 2773. [in Broun’s hand]”. *Paralectotype* (NZAC): card-mounted “Mt. Pirongia [in Brookes’ hand] // 2773. [in Brookes’ hand] // T. Broun Collection // A.E. Brookes Collection”.

EPISTRANUS Sharp, 1877

Epistrophus Sharp, 1876: 22 [*nec* Kirsch, 1868]. Type species: *Epistrophus lawsoni* Sharp, 1876, fixed by monotypy.

Epistranus Sharp, 1877c: 395. Replacement name for *Epistrophus* Sharp, 1876.

Remarks: The genus was originally described by Sharp as *Epistrophus* (1876: 22). In 1877, Sharp re-printed his 1876 paper and replaced the name *Epistrophus* with *Epistranus* (1877c: 395) followed by a later paper (Sharp 1878: 36) re-stating this replacement name on account of being preoccupied by *Epistrophus* Kirsch, 1868. Ivie and Ślipiński (1990: 11) incorrectly attributed this replacement to Sharp 1878: 36 (not Sharp, 1877c: 395).

Epistranus fulvus **Reitter, 1880**

(Figs. 110–111)

Epistranus fulvus Reitter, 1880c: 174. Broun 1910b: 37. Hudson 1923: 369. Hetschko 1930: 52. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 3083.

Remarks: Reitter did not mention the number of specimens examined. In order to stabilize this name, a lectotype and five paralectotypes are **here designated** from the material of *Epistranus fulvus.*

Type material examined: *Lectotype* (MNHN): card-mounted [card with two black lines near base], "Now. Zeeland Helms Reitter. [label bordered with thin black line] // Epistranus fulvus m. [in Reitter's hand] // Epistranus fulvus Reitter, LECTOTYPE, design. By R. Leschen 2009 [red label] // Epistranus fulvus Reit. [red label, in S.A. Ślipiński's hand]". *Paralectotypes* (MNHN): 2, individually mounted on separate cards and pins [card with three black lines near base, middle line thicker], with identical labels, "Now. Zeeland Helms Reitter. [label bordered with thin black line] // Epistranus fulvus Reitter PARALECTOTYPE design. By R. LESCHEN 2009 [blue label]". *Paralectotypes* (MNHN): 2, individually mounted on separate cards and pins [card with two black lines near base], with identical labels, "Now. Zeeland Helms Reitter. [label bordered with thin black line] // Epistranus fulvus Reitter PARALECTOTYPE design. By R. LESCHEN 2009 [blue label]". *Paralectotype* (MNHN): card-mounted [card without black lines], "Now. Zeeland Helms Reitter. [label bordered with thin black line] // Epistranus fulvus Reitter PARALECTOTYPE design. By R. LESCHEN 2009 [blue label]".

Epistranus hirtalis Broun, 1893

(Figs. 112–113)

Epistranus hirtalis Broun, 1893a: 187. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 52. May 1967: 178. Kuschel 1990: 33, 63. Maddison 2010: 426.

Type locality: Mount Pirongia.

Broun number: 2772.

Remarks: Broun (1893) did not designate a unique species number for this species that he based on two specimens from Pirongia collected in December, 1892. We located two specimens in the BMNH, though the second specimen lacks the locality label, both specimens are considered syntypes. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Epistranus hirtalis*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2772 [in Broun's hand] // Pirongia // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Epistranus hirtalis [in Broun's hand]". *Paralectotype* (BMNH): card-mounted venter-up, "2772 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Epistranus hirtalis [in Broun's hand] // ? [handwritten on left side] SYN- TYPE [round label with light blue border]".

Epistranus humeralis Broun, 1880

(Figs. 114–115)

Epistranus humeralis Broun, 1880: 203. Broun 1881: 670. Broun 1886: 950. Broun 1893b: 1344. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 52. Watt 1982b: 303. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 363.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 363 [green label] // Tairua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Epistranus humeralis [in Broun's hand]".

Epistranus lawsoni **(Sharp, 1876)**

(Figs. 116–118)

Epistrophus lawsoni Sharp, 1876: 22.

Epistranus lawsoni Sharp 1877c: 395 (reprinted, with corrections, from Sharp 1876).

Combination from genus-group replacement name *Epistranus* Sharp, 1876 for *Epistrophus* Sharp, 1877c. Sharp 1878: 36. Broun 1880: 203. Broun 1893a: 187. Broun 1893b: 1344. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 52. Ivie and Ślipiński 1990: 11. Kuschel 1990: 33, 63. Ślipiński and Lawrence 1997: 383. Maddison 2010: 426. Marske *et al.* 2011: 90. Marske *et al.* 2012: 1863.

Type locality: Auckland.

Broun number: 362.

Remarks: Sharp based this species on a single specimen "sent from Auckland by Mr. T. Lawson…" which is labeled as a type by Sharp, but also bears a (presumably) erroneous Greymouth label.

Type material examined: *Holotype* (BMNH): card-mounted, "Epistrophus lawsoni Type D.S. N. Zeal[d] [written at base of card in Sharp's hand] // Type [round label with red border] // Greymouth, [red underline] New Zealand. Helms. // Sharp Coll. 1905-313. // Altered to Epistranus Lawsoni, D.S. [in Sharp's hand]".

Epistranus optabilis Broun, 1893

(Figs. 119–120)

Epistranus optabilis Broun, 1893b: 1343. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 52. Maddison 2010: 426.

Type locality: Moeraki.

Broun number: 2357.

Remarks: Broun mentioned that he based this species on two specimens. These were located in the BMNH Broun collection, mounted on the same card. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Epistranus optabilis*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2357. [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Epistranus optabilis [in Broun's hand] // SYN-TYPE [round label with light blue border]". *Paralectotype* (BMNH): card-mounted venter-up, "2357. [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Epistranus optabilis [in Broun's hand] // SYN-TYPE [round label with light blue border]".

Epistranus parvus Broun, 1886

(Figs. 121–122)

Epistranus parvus Broun, 1886: 950. Broun 1893b: 1344. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 52. Maddison 2010: 426.

Type locality: near Howick.

Broun number: 1712.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, the single specimen of *Epistranus parvus* in the BMNH Broun collection is **here designated** as the lectotype.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 1712. [in Broun’s hand] // Howick // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Epistranus parvus [in Broun’s hand]”.

Epistranus sharpi Reitter, 1880

(Figs. 123–124)

Epistranus sharpi Reitter, 1880c: 173. Broun 1910b: 37. Hudson 1923: 369. Hetschko 1930: 52. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 3082.

Remarks: Reitter did not mention the number of specimens examined. In order to stabilize this name, a lectotype and eight paralectotypes are **here designated** from the material of *Epistranus sharpi*.

Type material examined: *Lectotype* (MNHN): card-mounted, “Now. Zeeland Helms Reitter. [label bordered with thin black line] // Epistranus Sharpi m. [in Reitter’s hand] // Epistranus sharpi Reitter, LECTOTYPE, design. By R. Leschen 2009 [red label] // Epistranus Sharpi Rtt [red label, in S.A. Ślipiński’s hand]”. *Paralectotypes* (MNHN): 3, individually mounted on separate cards and pins [card with two black lines near base], with identical labels, “Now. Zeeland Helms Reitter. [label bordered with thin black line] // Epistranus sharpi Reitter PARALECTOTYPE design. By R. LESCHEN 2009 [blue label]”. *Paralectotypes* (MNHN): 4, individually mounted on separate cards and pins [card with three black lines near base, middle line thicker], with identical labels, "Now. Zeeland Helms Reitter. [label bordered with thin black line] // Epistranus sharpi Reitter PARALECTOTYPE design. By R. LESCHEN 2009 [blue label]". *Paralectotype* (MNHN): 1, card-mounted [card with three black lines near base, middle line thicker], "Epistranus sharpi Reitter PARALECTOTYPE design. By R. LESCHEN 2009 [blue label]".

Epistranus valens Broun, 1881

(Figs. 125–126)

Epistranus valens Broun, 1881: 670. Broun 1886: 950. Broun 1893a: 187. Broun 1893b: 1344. Hudson 1923: 369. Hetschko 1930: 52. Maddison 2010: 426.

Type locality: Mount Manaia [Whangarei Heads].

Broun number: 1168.

Remarks: Broun based this species on a single specimen missing one antenna.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1168. [green label] // Manaia // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Epistranus valens. [in Broun's hand]".

GLENENTELA Broun, 1893

Glenentela Broun, 1893b: 1089. Type species: *Glenentela serrata* Broun, 1893, fixed by monotypy.

Glenentela costata Broun, 1921

(Figs. 127–128)

Glenentela costata Broun, 1921a: 527. Hudson 1923: 369. Hetschko 1930: 52. Maddison 2010: 426.

Type locality: Glenhope.

Broun number: 4050.

Remarks: Broun mentioned that he based this species on four specimens collected on 18 July, 1915. Three specimens in the BMNH and two in the NZAC matching this date were located. We assume Broun mis-reported the number of specimens before him. In order to stabilize this name, a lectotype and four paralectotypes are **here designated** from the material of *Glenentela costata*.

Type material examined: *Lectotype* (BMNH): card-mounted, "4050 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Glen Hope. 18.7.1915. [in Broun's hand] // Glenentela costata. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up and missing the head, "4050 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Glen Hope 18-7-1915. [in Broun's hand] // Glenentela costata. [in Broun's hand]". *Paralectotype* (BMNH): "4050. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Glen Hope. 18-7-1915. [in Broun's hand] // Glenentela costata. [in Broun's hand]". *Paralectotypes* (NZAC): 2, individually mounted on separate cards and pins (one venter-up), with identical labels, "Glenhope Nelson [in Brookes' hand] // T. Hall. 18-7-1915 [in Brookes' hand] // 4050 [in Brookes' hand] // Glenentela costata Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection".

Glenentela serrata Broun, 1893

(Figs. 129–130)

Glenentela serrata Broun, 1893b: 1090. Hutton 1904: 170. Broun 1921a: 528. Hudson 1923: 369. Hetschko 1930: 52. Ivie and Ślipiński 1990: 11. Kuschel 1990: 33, 63. Ślipiński and Lawrence 1997: 385. Maddison 2010: 426.

Type locality: Howick.

Broun number: 1940.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the single specimen of *Glenentela serrata* in the BMNH Broun collection.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1940. [in Broun's hand] // Howick // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Glenentela serrata. [in Broun's hand]".

HETERARGUS Sharp, 1886

Heterargus Sharp, 1886: 384. Type species: *Heterargus rudis* Sharp, 1886, fixed by monotypy.

Protarphius Broun, 1893a: 193. Type species: *Protarphius ruficornis* Broun, 1893, designated by Ivie and Ślipiński 1990: 11. Synonymy with *Heterargus* Sharp by Ślipiński and Lawrence 1997: 385.

Gathocles Broun, 1893b: 1086. Type species: *Gathocles nodosus* Broun, 1893, fixed by monotypy. Synonymy with *Heterargus* Sharp by Ślipiński and Lawrence 1997: 385.

***Heterargus angulifer* (Broun, 1914)**

(Figs. 131–132)

Gathocles angulifer Broun, 1914b: 178. Hudson 1923: 369. Hetschko 1930: 48.

Heterargus angulifer: Implied combination based on synonymy of *Gathocles* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus angulifer: Maddison 2010: 426.

Type locality: McClennan's Bush, near Methven [Mount Hutt also given in original description].

Broun number: 3547.

Remarks: Broun mentioned that he based this species on 12 specimens collected at Mount Hutt in April, 1912, which is the same locality as McLennan's Bush. Ten specimens in the BMNH, MNHN, and NZAC with the same date ranges were located. There is one specimen in the NZAC labeled as "3547 var." from McClennans Bush, which we do not consider a syntype. In order to stabilize this name, a lectotype and nine paralectotypes are **here designated** from the material of *Gathocles angulifer*. Broun's determination label on the lectotype reads "Heterargus angulifer," but the name given in the original description is *Gathocles angulifer*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3547. [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit.

Mus. 1922-482. // M^{c}Clennans. 23.4.1912. [in Broun's hand] // Heterargus angulifer. [in Broun's hand]". *Paralectotype* (BMNH): "3547. [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Mt. Hutt 12.4.1912. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "3547. [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Mt. Hutt 12.4.1912. [in Broun's hand] // Heterargus angulifer. [in Broun's hand]". *Paralectotype* (MNHN): card-mounted, "M^{t} Hutt. 12.4.1912. [in Broun's hand] // 3547. [in Broun's hand] // Heterargus angulifer. [in Broun's hand]". *Paralectotype* (MNHN): card-mounted, "M^{c}Clennans 23.4.1912. [in Broun's hand] // 3547 [in Broun's hand]". *Paralectotype* (NZAC): card-mounted, "Mt. Hutt. Methven Canterbury [in Brookes' hand] // Coll. T. Hall. 4-1912 [in Brookes' hand] // 3547 [in Brookes' hand] // Gathocles anguilifer Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted, "Mt. Hutt. Methven [in Brookes' hand] // T. Hall. 4-1912 [in Brookes' hand] // 3547 [in Brookes' hand] // Gathocles anguilifer Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted venter-up, "Mt. Hutt. Methven [in Brookes' hand] // T. Hall. 4-1912 [in Brookes' hand] // 3547 [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted, "Mt. Hutt. Methven [in Brookes' hand] // T. Hall. 12-4-1912 [in Brookes' hand] // 3547 [in Brookes' hand] // Gathocles anguilifer Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted, "McClennans Bush, Methven Canterbury [in Brookes' hand] // T. Hall. 4-1912 [in Brookes' hand] // 3547 [in Brookes' hand] // Gathocles anguilifer Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection".

Heterargus crassus (Broun, 1881) NEW COMBINATION

(Figs. 133–134)

Ablabus crassus Broun, 1881: 669. Hetschko 1930: 37. Maddison 2010: 426.

Protarphius crassus: transferred from *Ablabus* by Broun 1893a: 184. Hutton 1904: 170. Broun 1914a: 98. Hudson 1923: 369.

Heterargus crassus: Implied combination based on synonymy of *Protarphius* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Type locality: Parua.

Broun number: 1167.

Remarks: Broun mentioned that he based this species on two specimens. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ablabus crassus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 1167. [green label] // Parua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius crassus. [in Broun’s hand]”. *Paralectotype* (BMNH): “1167. [green label] // Parua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482.”

Heterargus decorus (Broun, 1914)

(Figs. 135–136)

Protarphius decorus Broun, 1914a: 97. Hudson 1923: 369. Hetschko 1930: 52. Kuschel 1990: 33, 63.

Heterargus decorus: Implied combination based on synonymy of *Protarphius* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus decorus: Maddison 2010: 426.

Type locality: Great Barrier Island.

Broun number: 3407.

Remarks: Broun mentioned that he based this species on two specimens collected in March, 1911. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Protarphius decorus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3407 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // G$^{\underline{t}}$ Barrier. March 1911. [in Broun's hand] // Protarphius decorus. [in Broun's hand]". *Paralectotype* (BMNH): "3407. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // G$^{\underline{t}}$ Barrier. March 1911. [in Broun's hand] // Protarphius decorus [in Broun's hand]".

***Heterargus fuscus* (Broun, 1923)**

(Figs. 137–138)

Gathocles fuscus Broun, 1923: 684. Hudson 1923: 369. Hetschko 1930: 48.

Heterargus fuscus: Implied combination based on synonymy of *Gathocles* with *Heterargus* in Ślipiński and Lawrence, 1997: 385.

Heterargus fuscus: Maddison 2010: 426.

Type locality: Mount Dick, near Kingston.

Broun number: 4281.

Remarks: Broun did not mention the number of specimens examined, but stated they were collected on 17 March, 1914. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Gathocles fuscus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // M[t] Dick. 17.3.1914. [in Broun's hand] // Gathocles fuscus. [in Broun's hand]". *Paralectotype* (BMNH): "New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // M[t] Dick. 17.3.14. [in Broun's hand] // Gathocles fuscus. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // M[t] Dick. 17.3.1914. [in Broun's hand] // Gathocles fuscus [in Broun's hand]".

Heterargus grossanus (Broun, 1886) NEW COMBINATION

(Figs. 139–140)

Coxelus grossanus Broun, 1886: 927. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Gathocles grossanus: transferred from *Coxelus* by Broun 1893b: 1087.

Heterargus grossanus: Implied combination based on synonymy of *Gathocles* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Type locality: Dunedin.

Broun number: 1662.

Remarks: Broun did not mention the number of specimens examined. We located one specimen in the BMNH matching his description, though there was an additional specimen in the BMNH with a printed "Otago" label, a printed "Purakanui" label, and a handwritten "*Gathocles grossanus*" determination label. This specimen is not regarded as being part of the syntypic series due to the difference in locality with the original description. In order to stabilize this name, a lectotype is **here designated** from the material of *Coxelus grossanus.*

Type material examined: *Lectotype* (BMNH): card-mounted venter-up, "Type [round label with red border] // 1662 [in Broun's hand] // Dunedin // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Gathocles grossanus [in Broun's hand]".

Heterargus indentatus (Broun, 1893)

(Figs. 141–142)

Protarphius indentatus Broun, 1893a: 185. Broun 1909a: 391. Broun 1910b: 38. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 52. May 1967: 178.

Heterargus indentatus: Implied combination based on synonymy of *Protarphius* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus indentatus: Maddison 2010: 426.

Type locality: Taranaki, near Stratford.

Broun number: 2769.

Remarks: Broun mentioned that he based this species on two specimens. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Protarphius indentatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2769. [in Broun's hand] // Taranaki // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius indentatus [in Broun's hand]". *Paralectotype*

(BMNH): mounted venter-up, “2769. [in Broun’s hand] // Taranaki // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius indentatus [in Broun’s hand]”.

***Heterargus interruptus* (Broun, 1923)**

(Figs. 143–144)

Gathocles interruptus Broun, 1923: 685. Hudson 1923: 369. Hetschko 1930: 48.

Heterargus interruptus: Implied combination based on synonymy of *Gathocles* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus interruptus: Maddison 2010: 426.

Type locality: Wellington.

Broun number: 4282.

Remarks: Even though this species was described by Broun under the name “*Gathocles interruptus*” in the original description, both specimens carry a “*Glenentela interrupta*” determination label and were located under *Glenentela* and above the “*interruptus*” tag in the BMNH Broun collection. Broun did not mention the number of specimens examined, but stated they were collected on 24 April, 1916. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Gathocles interruptus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Wellington. 24.4.1916. [in Broun’s hand] // Glenentela interrupta. [in Broun’s hand]”. *Paralectotype* (BMNH): “New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Wellington. 24.4.1916. [in Broun’s hand] // Glenentela interrupta. [in Broun’s hand]”. *Paralectotype* (NZAC): card-mounted venter-up, “Wellington [in Brookes’ hand] // A.C. O’Connor 24-4-1916. [in Brookes’ hand] // 4282 [in Brookes' hand] // Gathocles interruptus Broun [in Brookes' hand] // A.E. Brookes Collection".

Heterargus nodosus (Broun, 1893)

(Figs. 145–146)

Gathocles nodosus Broun, 1893b: 1086. Hutton 1904: 169. Broun 1914b: 179. Broun 1923: 685. Hudson 1923: 369. Hetschko 1930: 48. Ivie and Ślipiński 1990: 11.

Heterargus nodosus: Ślipiński and Lawrence 1997: 387, based on synonymy of *Gathocles* with *Heterargus* (p. 385). Maddison 2010: 426.

Type locality: Moeraki.

Broun number: 1936.

Remarks: Broun based this species on a single specimen. There is an additional specimen in the BMNH that matches the information given in the original description bearing the following label data: "1936. [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Gathocles nodosus [in Broun's hand]". Upon comparison, both specimens appeared to be of the same species. It is impossible to determine which the one specimen Broun had before him was. Therefore, we chose to recognize as the holotype the cleaner of the two specimens. Additionally, the handwritten determination label of the holotype has a period following the name, which was common on Broun's type specimens.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1936 [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Gathocles nodosus. [in Broun's hand]".

Heterargus obliquicostatus (Broun, 1909)

(Figs. 147–148)

Gathocles obliquicostatus Broun, 1909a: 388. Hudson 1923: 369.

Gathocles obliquecostatus: Hetschko 1930: 48. Incorrect subsequent spelling, not available.

Gathocles obliquisignatus: May 1967: 178. Incorrect subsequent spelling, not available.

Heterargus obliquicostatus: Implied combination based on synonymy of *Gathocles* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus obliquecostatus: Maddison 2010: 426. Incorrect subsequent spelling, not available.

Heterargus obliquicostatus: Maddison 2010: 426.

Type locality: Otara, Southland.

Broun number: 2767 (as given in May 1967: 178).

Remarks: Broun did not mention the number of specimens examined. Two specimens in the NZAC matching the locality were located. Three specimens in the BMNH matching the locality were located, but one is labeled as a variety and not considered a syntype. This varietal specimen was mentioned in the description as having fewer antennal segments (one side has a few funicle segments fused, but the 2-segmented club exists for both sides). In order to stabilize this name, a lectotype and four paralectotypes are **here designated** from the material of *Gathocles obliquicostatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2767. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Otara. Southland. [in Broun's hand] // Gathocles obliquicosta. [sic –

name abbreviated or perhaps label was cut] [in Broun's hand]". *Paralectotype* (BMNH): "2767. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Var. antenna [in Broun's hand] // Otara. Southland. [in Broun's hand]". *Paralectotype* (BMNH): "2767. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Otara. Southland. [in Broun's hand] // Gathocles obliquicost. [in Broun's hand]". *Paralectotypes* (NZAC): 2, individually mounted on separate cards and pins, with identical labels, "Otara Southland [in Brookes' hand] // Coll. A. Philpott [in Brookes' hand] // 2767 [in Brookes' hand] // Gathocles obliquicostatus Broun [in Brookes' hand] // A.E. Brookes Collection".

Heterargus pallens **(Broun, 1914)**

(Figs. 149–150)

Protarphius pallens Broun, 1914b: 179. Hetschko 1930: 52.

Protarphius palleus: Hudson 1923: 369. Incorrect subsequent spelling, not available.

Heterargus pallens: Implied combination based on synonymy of *Protarphius* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus pallens: Maddison 2010: 426.

Type locality: McClennan's Bush, near Methven.

Broun number: 3548.

Remarks: Broun did not mention the number of specimens examined, but stated they were collected in April, 1912. In order to stabilize this name, a lectotype and eight paralectotypes are **here designated** from the material of *Protarphius pallens*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3548. [in Broun's hand] // McClennans. 23.4.1912. [in Broun's hand] //

New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius pallens - [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "3548 [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // M^{c}Clennans. 23.4.1912. [in Broun's hand] // Protarphius pallens. [in Broun's hand]". *Paralectotype* (BMNH): "3548 [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // M^{c}Clennans. 23.4.1912. [in Broun's hand] // Protarphius pallens [in Broun's hand]". *Paralectotype* (BMNH): "3548. [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // M^{c}Clennans. 23.4.1912. [in Broun's hand]". *Paralectotype* [card-mounted] (MNHN): "M^{c}Clennans. 23.4.1912. [in Broun's hand] // 3548. [in Broun's hand]". *Paralectotypes* (NZAC): 2, individually mounted on separate cards and pins, with identical labels, "McClennan's Bush, Methven [in Brookes' hand] // T. Hall. April, 1912 [in Brookes' hand] // 3548 [in Brookes' hand] // Protarphius pallens Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection". *Paralectotypes* (NZAC): 2, individually mounted on separate cards and pins, with identical labels, "McClennans Bush, Methven [in Brookes' hand] // T. Hall. 23-4-1912 [in Brookes' hand] // 3548 [in Brookes' hand] // Protarphius pallens Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection".

Heterargus parallelus **Broun, 1914**

(Figs. 151–152)

Heterargus parallelus Broun, 1914b: 178. Hudson 1923: 369. Hetschko 1930: 48. Maddison 2010: 426.

Type locality: Hump Ridge, near Invercargill.

Broun number: 3546.

Remarks: Broun did not mention the number of specimens examined, but stated they were collected in February, 1912. In order to stabilize this name, a lectotype and three paralectotypes are **here designated** from the material of *Heterargus parallelus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “3546 [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hump Range. Dec^{r} 1911. [in Broun’s hand] // Heterargus parallelus. [in Broun’s hand]”. *Paralectotype* (BMNH): “TYPE [round label with red border] // 3546. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hump Ridge. Feby. 1912. [in Broun’s hand] // Heterargus parallelus [in Broun’s hand]”. *Paralectotype* (BMNH): “3546. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hump Ridge. Feby. 1912. [in Broun’s hand]”. *Paralectotype* [card-mounted] (MNHN): “Hump Ridge. Feby. 1912. [in Broun’s hand] // 3546 [in Broun’s hand]”.

***Heterargus posticalis* (Broun, 1909)**

(Figs. 153–154)

Protarphius posticalis Broun, 1909a: 390. Hudson 1923: 369. Hetschko 1930: 52. May 1967: 178.

Heterargus posticalis: Implied combination based on synonymy of *Protarphius* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus posticalis: Maddison 2010: 426.

Type locality: Otara, Southland.

Broun number: 2771 (as given in May 1967: 178).

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the material of *Heterargus posticalis.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2771. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Otara. Southland [in Broun's hand] // Protarphius posticalis. [in Broun's hand]".

Heterargus rudis Sharp, 1886

(Figs. 155–157)

Heterargus rudis Sharp, 1886: 384, pl. 12, fig. 17. Broun 1893b: 1086 (reprinted excerpt of Sharp 1886: 384). Hutton 1904: 169. Broun 1909a: 389. Broun 1914a: 97. Hudson 1923: 369. Hetschko 1930: 48. Ivie and Ślipiński 1990: 11. Ślipiński and Lawrence 1997: 387. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 1935.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and eight paralectotypes are **here designated** from the material of *Heterargus rudis*.

Type material examined: *Lectotype* (BMNH): mounted on same card as one paralectotype, left specimen is the lectotype, "Heterargus rudis Types D.S. N. Zealand. Greymouth. Helms. [written at base of card in Sharp's hand] // Type [round label with red border] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): mounted on same card as lectotype, right specimen is a paralectotype, labels same as lectotype. *Paralectotypes* (BMNH): 2, mounted on same card and pin, right specimen mounted venter-up, "Heterargus rudis D.S. Greymouth NZd Helms. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Heterargus rudis D.S. Greymouth NZd Helms 1883 [written at base of card in Sharp's hand] // I 17 [handwritten] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted on same card and pin, Heterargus rudis D.S. Greymouth N.Zd [written at base of card in Sharp's hand]". *Paralectotypes* (BMNH): 2, mounted venter-up on same card and pin, Heterargus rudis D.S. Greymouth [written at base of card in Sharp's hand]".

***Heterargus ruficornis* (Broun, 1893)**

(Figs. 158–159)

Protarphius ruficornis Broun, 1893a: 184. Hutton 1904: 170. Broun 1909a: 390. Broun 1914b: 180. Hudson 1923: 369. Hetschko 1930: 52. May 1967: 178. Ivie and Ślipiński 1990: 11.

Heterargus ruficornis: Ślipiński and Lawrence 1997: 387, based on synonymy of *Protarphius* with *Heterargus* (p. 385). Maddison 2010: 426.

Type locality: Mount Pirongia.

Broun number: 2768.

Remarks: Broun mentioned that he based this species on two specimens collected in December, 1892. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Protarphius ruficornis*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 2768_ [in Broun’s hand] // Pirongia // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius ruficornis [in Broun’s hand]”. *Paralectotype* (BMNH): mounted venter-up, “2768. [in Broun’s hand] // Mount Pirongia. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius ruficornis [in Broun’s hand]”.

Heterargus serricollis Broun, 1893

(Figs. 160–161)

Heterargus serricollis Broun, 1893b: 1441. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 48. Maddison 2010: 426.

Type locality: Capleston.

Broun number: 2500.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 2500. [in Broun’s hand] // Capleston Westland [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Heterargus serricollis [in Broun’s hand]”.

Heterargus subaequus Broun, 1914

(Figs. 162–163)

Heterargus subaequus Broun, 1914a: 97. Broun 1914b: 178. Hudson 1923: 369. Hetschko 1930: 48. Maddison 2010: 426.

Type locality: Hakapoua, Southland.

Broun number: 3406.

Remarks: Broun based this species on a single specimen collected on 1 March, 1911. There was an additional specimen in the BMNH that bears a "Hakapoua, Southland" label (in Broun's hand), but this was not considered a syntype because the specimen lacked a Broun identification label.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3406. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hakapoua. March 1911 - // Heterargus subaequus. [in Broun's hand]".

***Heterargus tricavus* (Broun, 1909)**

(Figs. 164–165)

Protarphius tricavus Broun, 1909a: 389. Broun 1914b: 180. Hudson 1923: 369. Hetschko 1930: 52. May 1967: 178.

Heterargus tricavus: Implied combination based on synonymy of *Protarphius* with *Heterargus* in Ślipiński and Lawrence 1997: 385.

Heterargus tricavus: Maddison 2010: 426.

Type locality: Broken River, Canterbury.

Broun number: 2770 (as given in May 1967: 178).

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Protarphius tricavus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2770 [in Broun's hand] // Broken River. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius tricavus. [in Broun's hand]”. *Paralectotype* (BMNH): “2770. [in Broun’s hand] // Broken River. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius tricavus. [in Broun’s hand]”. *Paralectotype* (BMNH): mounted venter-up, “2770. [in Broun’s hand] // Broken River. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Protarphius tricavus [in Broun’s hand]”.

LASCONOTUS Erichson, 1845

Lasconotus Erichson, 1845: 258. Type species: *Lasconotus complex* LeConte, 1859, by subsequent monotypy.

Illestus Pascoe, 1863a: 33. Type species: *Illestus terrenus* Pascoe, 1863, fixed by monotypy. Synonymized with *Lasconotus* Erichson by Hinton 1935: 204.

Ithris Pascoe, 1863c: 134. Type species: *Ithris decisa* Pascoe, 1863, fixed by monotypy. Synonymized with *Lasconotus* Erichson by Pope 1955: 245.

Lado Wankowicz, 1867: 249. Type species: *Bitoma jelskii* Wankowicz, 1867. Synonymized with *Lasconotus* Erichson by Hinton 1935: 204.

Othismopteryx J. Sahlberg, 1871: 441. Type species: *Othismopteryx carinatus* J. Sahlberg, 1871, fixed by monotypy. Synonymized with *Lado* by Reitter 1882: 131.

Chrysopogonius Hinton, 1935: 207. Type species: *Chrysopogonius coronatus* Hinton, 1935, by original designation. Synonymized with *Lasconotus* Erichson by Ivie and Ślipiński 1990: 6.

***Lasconotus gracilis* (Sharp, 1876)**

(Figs. 166–168)

Ithris gracilis Sharp, 1876: 23. Sharp 1877c: 396 (reprinted from Sharp 1876). Broun 1880: 205. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 33. Watt 1982b: 303. Kuschel 1990: 33, 63.

Lasconotus gracilis: Implied combination based on synonymy of *Ithris* with *Lasconotus* in Pope 1955: 245.

Lasconotus gracilis: Maddison 2010: 426.

Type locality: Auckland.

Broun number: 365.

Remarks: Sharp based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Ithris gracilis Type N. Zeal[d] D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll 1905-313."

NORIX Broun, 1893

Norix Broun, 1893b: 1090. Type species: *Norix crassus* Broun, 1893, fixed by monotypy.

***Norix crassus* Broun, 1893**

(Figs. 169–170)

Norix crassus Broun, 1893b: 1091. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 37. Ivie and Ślipiński 1990: 8. Ślipiński and Lawrence 1997: 404. Maddison 2010: 426.

Type locality: Mokohinou Island.

Broun number: 1941.

Remarks: Broun based this species on a single specimen missing a leg.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1941. [in Broun's hand] // Mokohinau // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Norix crassus [in Broun's hand]".

NOTOCOXELUS Ślipiński and Lawrence, 1997

Notocoxelus Ślipiński and Lawrence, 1997: 404. Type species: *Coxelus helmsi* Reitter, 1880, fixed by monotypy.

Remarks: Sharp remarked on the affinities of the New Zealand *Coxelus* (= *Notocoxelus*) with that of the European *Coxelus*, suggesting it was near enough to not require a separate genus. However, Ślipiński and Lawrence (1997: 404) erected the genus *Notocoxelus* for the New Zealand members of the genus *Coxelus*, but neglected to formally designate all New Zealand species as new combinations under *Notocoxelus* (Adam Ślipiński, pers. comm.). Below we formally combine these names for the New Zealand *Coxelus*.

Notocoxelus bicavus (Broun, 1909) NEW COMBINATION

(Figs. 171–172)

Coxelus bicavus Broun, 1909a: 388. Hudson 1923: 369. Hetschko 1930: 46. May 1967: 178. Maddison 2010: 426.

Notocoxelus bicavus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Invercargill.

Broun number: 2766 (as given in May 1967: 178).

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2766. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Invercargill. - A. Philpott - [in Broun's hand] // Coxelus bicavus, Brn. - [handwritten]".

Notocoxelus chalmeri (Broun, 1886) NEW COMBINATION

(Figs. 173–174)

Coxelus chalmeri Broun, 1886: 949. Broun 1893b: 1084. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus chalmeri: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Purakanui, on the coast north of Dunedin [Otago Region].

Broun number: 1711.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the material of *Coxelus chalmeri*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1711. [in Broun's hand] // Otago // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus chalmeri [in Broun's hand]".

Notocoxelus clarus (Broun, 1882) NEW COMBINATION

(Figs. 175–176)

Coxelus clarus Broun, 1882: 294. Broun 1886: 766 (reprinted from Broun 1882). Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus clarus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Parua.

Broun number: 1357.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1357 [in Broun's hand] // Parua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus clarus [in Broun's hand]".

Notocoxelus dubius (Sharp, 1876) NEW COMBINATION

(Figs. 177–179)

Coxelus dubius Sharp, 1876: 19. Sharp 1877c: 393 (reprinted from Sharp 1876). Broun 1880: 196. Reitter 1880c: 175. Broun 1882: 295. Broun 1886: 766 (reprinted from

Broun 1882). Broun 1893b: 1084. Broun 1895: 194. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Kuschel 1990: 33, 63. Maddison 2010: 426.

Notocoxelus dubius: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Auckland and Tairua.

Broun number: 350.

Remarks: Sharp did not mention the number of specimens examined sent to him "…from Auckland and Tairua by Mr. Lawson and Captain Broun." In the BMNH, there is one specimen from Auckland with "Ind. typ." another specimen with "N Zeal[d]" and "type" written at the base of the cards, both of which bear "Greymouth, New Zealand, Helms" labels, probably attached in error. There are a number of other specimens in the BMNH from Greymouth with Sharp's handwriting at the base of the card-mount, but we do not regard these as part of the syntypic series due to the discrepancy in type locality. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Coxelus dubius*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Coxelus dubius Type N. Zeal[d] D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313. // NZl-Greymouth [handwritten in red pen] // BMNH(E) #651718". *Paralectotype* (BMNH): card-mounted, "Coxelus dubius Ind. typ. Auckland D.S. [written at base of card in Sharp's hand] // Greymouth. New Zealand [red underline] Helms. // Sharp Coll. 1905-313."

Notocoxelus elongatus (Broun, 1909) NEW COMBINATION

(Figs. 180–181)

Coxelus elongatus Broun, 1909a: 386. Broun 1914b: 178. Hudson 1923: 369. Hetschko 1930: 47. May 1967: 178. Maddison 2010: 426.

Notocoxelus elongatus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Broken River.

Broun number: 2764 (as given in Broun 1914b: 178; May 1967: 178).

Remarks: Broun mentioned that he based this species on three specimens. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Coxelus elongatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2764. [in Broun's hand] // Broken River. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus elongatus - [in Broun's hand]". *Paralectotype* (BMNH): card-mounted venter-up, "2764. [in Broun's hand] // Broken River- [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus elongatus. [in Broun's hand]". *Paralectotype* (MNHN): card-mounted, "Broken River. [in Broun's hand] // 2764. [in Broun's hand] // Coxelus elongatus [in Broun's hand]".

Notocoxelus graniceps (Broun, 1893) NEW COMBINATION

(Figs. 182–183)

Coxelus graniceps Broun, 1893b: 1343, 1441. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus graniceps: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Moeraki.

Broun number: 2356.

Remarks: Broun mentioned that he based this species on three specimens from Moeraki, but only two specimens in the BMNH specimens are labeled Otago or Moeraki. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Coxelus graniceps*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2356. [in Broun's hand] // Otago [topside, in Broun's hand] Moeraki [underside, in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus graniceps [in Broun's hand]". *Paralectotype* (BMNH): card-mounted, venter up, "2356. [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit Mus. 1922-482. // Coxelus graniceps [in Broun's hand]".

***Notocoxelus helmsi* (Reitter, 1880)**

(Figs. 184–185)

Coxelus helmsi Reitter, 1880c: 175. Broun 1886: 949. Broun 1910b: 37. Broun 1914b: 178. Hudson 1923: 369. Hetschko 1930: 47.

Notocoxelus helmsi: transferred to *Notocoxelus* by Ślipiński and Lawrence, 1997: 404, 406, 436, fig. 478. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 3084.

Remarks: Reitter did not mention the number of specimens examined. In order to stabilize this name, a lectotype and 13 paralectotypes are **here designated** from the material of *Coxelus helmsi*.

Type material examined: *Lectotype* (MNHN): card-mounted, "Now. Zeeland Helms Reitter. [label bordered with thin black line] // Lectotypus [red label] // Coxelus n sp. Helmsi m. Now. Zeeland [in Reitter's hand] // Coxelus helmsi Reitter LECTOTYPE S.A. Ślipiński, 1997 // TYPE [red label] // Museum Paris ex. Coll. R. Oberthur [pink label]". *Paralectotypes* (MNHN): 8, 3 on same pin but card-mounted seperately, 5 card-mounted on separate cards and pins, cards with two thin black lines and one thick black line at base, "Now. Zeeland Helms Reitter. [label bordered with thin black line] // TYPE [red label] // Museum Paris ex. Coll. R. Oberthur [pink label] // Paralectotypus [light orange label] // Coxelus helmsi Reitter PARALECTOTYPE S.A. Ślipiński, 1997". *Paralectotypes* (MNHN): 2, individually mounted on separate cards and pins, cards with two thick black lines at base, "Now. Zeeland Helms Reitter. [label bordered with thin black line] // TYPE [red label] // Museum Paris ex. Coll. R. Oberthur [pink label] // Paralectotypus [light orange label] // Coxelus helmsi Reitter PARALECTOTYPE S.A. Ślipiński, 1997". *Paralectotypes* (MNHN): 2, individually mounted on separate cards and pins, cards with two thin black lines and one thick black line at base, "EX. COLL. REITTER // TYPE [red label] // Museum Paris ex. Coll. R. Oberthur [pink label] // Paralectotypus [light orange label] // Coxelus helmsi Reitter PARALECTOTYPE S.A. Ślipiński, 1997". *Paralectotypes* (MNHN): 1, individually mounted on separate cards and pins, cards with one thin black line at base, "EX. COLL. REITTER // TYPE [red label] //

Museum Paris ex. Coll. R. Oberthur [pink label] // Paralectotypus [light orange label] // Coxelus helmsi Reitter PARALECTOTYPE S.A. Ślipiński, 1997”.

Notocoxelus instabilis **(Broun, 1914) NEW COMBINATION**

(Figs. 186–187)

Coxelus instabilis Broun, 1914b: 177. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus instabilis: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: McClennan’s Bush, near Methven [Pudding Hill also given in original description].

Broun number: 3545.

Remarks: Broun mentioned that he based this species on “about twenty specimens” from McClennan’s Bush and Pudding Hill during April and May, 1912, but only five specimens in the BMNH and six specimens in the NZAC matching this data were located. In order to stabilize this name, a lectotype and ten paralectotypes are **here designated** from the material of *Coxelus instabilis*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 3545 [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // $M^{\underline{c}}$Clennans. 23.4.1912. [in Broun’s hand]”. *Paralectotype* (BMNH): card-mounted, “3545 [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pudding Hill. 4.5.1912. [in Broun’s hand]”. *Paralectotype* (BMNH): card-mounted, “3545. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pudding Hill. 4.5.1912. [in Broun’s hand] // Coxelus instabilis [in

Broun's hand]". *Paralectotype* (BMNH): card-mounted venter-up, "3545 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pudding Hill. 4.5.1912. [in Broun's hand] // Coxelus instabilis [in Broun's hand]". *Paralectotype* (BMNH): card-mounted, "3545 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // McClennans. 23.4.1912. [in Broun's hand] // Coxelus instabilis [in Broun's hand]". *Paralectotypes* (NZAC): 2, individually mounted on separate cards and pins, with identical labels, "Methven. Canterbury. [in Brookes' hand] // T. Hall. 1912. [in Brookes' hand] // 3545 [in Brookes' hand] // Coxelus instabilis Broun [in Brookes' hand] // Cotype. [in Brookes' hand] // Paratype [blue label] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted venter-up, "Methven. Canterbury. [in Brookes' hand] // T. Hall. 1912. [in Brookes' hand] // 3545. [in Brookes' hand] // Coxelus instabilis Broun [in Brookes' hand] // Cotype [in Brookes' hand] // Paratype [blue label] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted, "Methven. Canterbury. [in Brookes' hand] // T. Hall. 1912. [in Brookes' hand] // 3545. [in Brookes' hand] // Coxelus instabilis Broun [in Brookes' hand] // Paratype [blue label] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted, "Methven. Canterbury. [in Brookes' hand] // T. Hall. 1912. [in Brookes' hand] // 3545 [in Brookes' hand] // Coxelus instabilis Broun [in Brookes' hand] // Paratype [handwritten on blue label] // T. Broun Collection // A.E. Brookes Collection". *Paralectotype* (NZAC): card-mounted, "Methven. Canterbury. [in Brookes' hand] // T. Hall. 4-5-1912. [in Brookes' hand] // 3545. [in Brookes' hand] // Coxelus instabilis Broun [in Brookes' hand] // Cotype. [in Brookes' hand] // Paratype [blue label] // T. Broun Collection // A.E. Brookes Collection".

Notocoxelus longulus (Broun, 1893) NEW COMBINATION

(Figs. 188–189)

Coxelus longulus Broun, 1893b: 1085. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus longulus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Moeraki.

Broun number: 1934.

Remarks: Broun mentioned that he based this species on three specimens. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Coxelus longulus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1934. [in Broun's hand] // Otago [topside, in Broun's hand] Moerak [underside, in Broun's hand; label was cut and the "i" in "Moeraki" was inadvertently cut off] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus longulus [in Broun's hand]". *Paralectotype* (BMNH): card-mounted venter-up, "1934. [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482." *Paralectotype* (NZAC): card-mounted, "Moeraki, ~~Canterbury~~ Otago [in Brookes' hand] // Coll. Sandanger. [in Brookes' hand] // 1934 [in Brookes' hand] // Coxelus longulus Broun [in Brookes' hand] // T. Broun Collection // A.E. Brookes Collection".

Notocoxelus mucronatus (Broun, 1911) NEW COMBINATION

(Figs. 190–191)

Coxelus mucronatus Broun, 1911: 98. Hudson 1923: 369. Hetschko 1930: 47. Emberson 1998: 44. Maddison 2010: 426.

Notocoxelus mucronatus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Pitt Island.

Broun number: This species was listed as number 61 in the paper, but this is not a "Broun number" in the standard sense.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype and seven paralectotypes are **here designated** from the material of *Coxelus mucronatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "61. ♂. [in Broun's hand] // ♂ [handwritten] // Chatham Is. [red underline] Broun Coll. B.M. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand] // Coxelus mucronatus. [in Broun's hand]". *Paralectotype* (BMNH): card-mounted, "61. ♀. [in Broun's hand] // ♀ [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand]". *Paralectotypes* (BMNH): 2, individually mounted on separate cards and pins, with identical labels, "61. ♂ [in Broun's hand] // ♂ [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand]". *Paralectotype* (BMNH): card-mounted, "61. ♂ [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand] // Coxelus ♂ mucronatus. [in Broun's hand]". *Paralectotype* (NZAC): card-mounted, "61. ♀. [in Broun's hand] // New Zealand, [typed] Chatham Is. Broun Coll. [in J.C Watt's hand] // A.E. Brookes Collection". *Paralectotypes* (NZAC): 2, individually mounted on separate cards and pins, "c.m.♂. [in Broun's hand] // 61. [in Broun's hand] // New Zealand, [typed] Chatham Is. Broun Coll. [in J.C Watt's hand] // A.E. Brookes Collection // [green label] SYNTYPE [typed] Coxelus mucronatus Broun, 1911 [in J.C Watt's hand]".

Notocoxelus oculator (Broun, 1893) NEW COMBINATION

(Figs. 192–193)

Coxelus oculator Broun, 1893b: 1342. Broun 1895: 195. Hutton 1904: 169. Broun 1909a: 388. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus oculator: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Moeraki.

Broun number: 2354.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2354. [in Broun's hand] // Otago [topside, in Broun's hand] Moerak [underside, in Broun's hand; label was cut and the "i" in "Moeraki" was inadvertently cut off] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus oculator. [in Broun's hand]".

Notocoxelus ovicollis (Broun, 1893) NEW COMBINATION

(Figs. 194–195)

Coxelus ovicollis Broun, 1893b: 1084. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus ovicollis: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Moeraki [Otago Region].

Broun number: 1933.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1933. [in Broun's hand] // Otago // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus ovicollis [in Broun's hand]".

Notocoxelus picicornis (Broun, 1893) NEW COMBINATION

(Figs. 196–197)

Coxelus picicornis Broun, 1893b: 1342. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus picicornis: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Moeraki.

Broun number: 2355.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2355. [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus picicornis [in Broun's hand]".

Notocoxelus posticalis (Broun, 1893) NEW COMBINATION

(Figs. 198–199)

Coxelus posticalis Broun, 1893b: 1084. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus posticalis: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Moeraki.

Broun number: 1932.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1932. [in Broun's hand] // Otago [topside, in Broun's hand] oerak [underside, in Broun's hand; label was cut and the "M" in "Moeraki" was inadvertently cut off] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus posticalis [in Broun's hand]".

***Notocoxelus punctatus* (Broun, 1910) NEW COMBINATION**

(Figs. 200–201)

Coxelus punctatus Broun, 1910a: 294. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus punctatus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Sunday Island.

Broun number: This specimen was not given a number by Broun.

Remarks: Broun based this species on a single specimen. In the Broun Collection Kermadecs Island drawer at the BMNH, there is a label stating "Transferred to Auckland Institute and Museum, New Zealand, 30/10/1969. *ref.* Trustee's Meeting Oct.23.69". This refers to the holotype in the AMNZ.

Type material examined: *Holotype* (AMNZ): card-mounted, "11. [square label, in Broun's hand] // Kermadec Is. [red underline] Broun Coll. B.M. 1922-482. // Coxelus punctatus. [in Broun's hand] // Kermadecs. Sunday Isd. [in Broun's hand] // Type [round label with red border] // Ex B.M. (N.H.) ~~Duplicate~~ ["Duplicate" crossed through in black pen] // =xanthonyx Br. [in R.D. Pope's hand] R.D. Pope det. 1969 [typed] // AMNZ 21826 AUCKLAND MUSEUM NEW ZEALAND".

Notocoxelus regularis **(Broun, 1893) NEW COMBINATION**

(Figs. 202–203)

Coxelus regularis Broun, 1893b: 1440. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus regularis: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Ashburton.

Broun number: 2499.

Remarks: Broun mentioned that he based this species on two specimens from Ashburton. Two specimens labeled "Canterbury" with "Ashburton" hand-written underneath were located in the BMNH. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Coxelus regularis*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2499. [in Broun's hand] // Canterbury [topside, in Broun's hand] Ashburton [underside, in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus regularis [in Broun's hand]". *Paralectotype* (BMNH): card-mounted venter-up, "2499. [in Broun's hand] // Canterbury [topside, in Broun's hand]

Ashburton [underside, in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus regularis [in Broun's hand]".

Notocoxelus robustus (Broun, 1880) NEW COMBINATION

(Figs. 204–205)

Coxelus robustus Broun, 1880: 197. Broun 1882: 295. Broun 1886: 766 (reprinted from Broun 1882). Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus robustus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Mount Manaia [Whangarei Heads].

Broun number: 352.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 352 [green label] // Manaia // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus robustus [in Broun's hand]".

Notocoxelus rufus (Broun, 1893) NEW COMBINATION

(Figs. 206–207)

Coxelus rufus Broun, 1893b: 1084. Broun 1895: 195. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Maddison 2010: 426.

Notocoxelus rufus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Taieri, Otago.

Broun number: 1931.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 1931. [in Broun’s hand] // Taieri // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus rufus [in Broun’s hand]”.

Notocoxelus similis (Sharp, 1876) NEW COMBINATION

(Figs. 208–210)

Coxelus similis Sharp, 1876: 20. Sharp 1877c: 393 (reprinted from Sharp 1876). Broun 1880: 196. Broun 1882: 295. Broun 1886: 766 (reprinted from Broun 1882). Broun 1886: 949. Broun 1895: 194. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 47. Kuschel 1990: 33, 63. Maddison 2010: 426.

Notocoxelus similis: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Auckland.

Broun number: 351.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Coxelus similis*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Coxelus similis Type N. Zeal[d] D.S. [written at base of card in Sharp’s hand] // Type [round label with red border] // Sharp Coll 1905-313. // NZl- Greymouth [handwritten in red pen] // BMNH(E) #651717”. *Paralectotype* (BMNH): “Coxelus similis Ind. typ. N. Zeald D.S. [written at base of card in Sharp’s hand] // Sharp Coll. 1905-313.”

Notocoxelus thoracicus (Broun, 1895) NEW COMBINATION

(Figs. 211–212)

Coxelus thoracicus Broun, 1895: 194. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 48. May 1967: 178. Maddison 2010: 426.

Notocoxelus thoracicus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Wellington.

Broun number: 2763 (as given in May 1967: 178).

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Coxelus thoracicus*. There is an additional specimen (card-mounted venter-up) in the BMNH Broun collection that matches the type locality, but we do not consider this to be a syntype because Broun's determination label identifies it as a variety of *C. thoracicus*. Additionally, the locality label is handwritten rather than typed, as is the case with the lectotype (BMNH) and paralectotype (MNHN).

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2763. [in Broun's hand] // Wellington // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus thoracicus [in Broun's hand]". *Paralectotype* (MNHN): card-mounted, "Wellington // 2763. [in Broun's hand] // Coxelus thoracicus [in Broun's hand]".

Notocoxelus variegatus (Broun, 1909) NEW COMBINATION

(Figs. 213–214)

Coxelus variegatus Broun, 1909a: 387. Hudson 1923: 369. Hetschko 1930: 48. May 1967: 178. Maddison 2010: 426.

Notocoxelus variegatus: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Invercargill.

Broun number: 2765 (as given in May 1967: 178).

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2765 [in Broun's hand] // Invercargill // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Coxelus variegatus [in Broun's hand]".

Notocoxelus xanthonyx (Broun, 1910) NEW COMBINATION

(Figs. 215–216)

Coxelus xanthonyx Broun, 1910a: 294. Hetschko 1930: 48. Maddison 2010: 426.

Notocoxelus xanthonyx: Implied combination based on the erection of the genus *Notocoxelus* (Ślipiński and Lawrence, 1997: 404).

Type locality: Raoul Island [Sunday Island].

Broun number: This specimen was not given a number by Broun.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "10. [in Broun's hand] // Kermadec Is. [red underline] Broun Coll. B.M. 1922-482. // Kermadecs Sunday Isd. [in Broun's hand] // Coxelus xanthonyx [in Broun's hand] // = punctatus Br. [in R.D. Pope's hand] R.D. Pope det. 1969".

PRISTODERUS Hope, 1840

Pristoderus Hope, 1840: 145. Type species: *Dermestes scaber* Fabricius, 1775, by original designation.

Ulonotus Erichson, 1845: 255. No type species included in original description. Type species: *Bolitophagus antarcticus* White, 1846, subsequent monotypy by Lacordaire 1854: 360. Synonymized with *Pristoderus* Hope by Ivie and Ślipiński 1990: 9.

Sparactus Erichson, 1845: 256. Type species: *Ditoma interrupta* Erichson, 1842, by monotypy. Synonymized with *Pristoderus* Hope by Ślipiński and Lawrence 1997: 406.

Pristiderus Agassiz, 1846: 135. Incorrect subsequent spelling, not available.

Enarsus Pascoe, 1866: 444. Type species: *Enarsus bakewellii* Pascoe, 1866, fixed by monotypy. Synonymized with *Pristoderus* Hope by Ślipiński and Lawrence 1997: 406.

Tarphiomimetes Wollaston, 1873: 9. Type species: *Tarphiomimetes lawsoni* Wollaston, 1873, designated by Ivie and Ślipiński 1990: 9. Synonymized with *Ulonotus* Erichson by Sharp 1876: 17.

Dryptops Broun, 1882: 292. Type species: *Dryptops dorsalis* Broun, 1882, designated by Ivie and Ślipiński 1990: 8. Synonymized with *Pristoderus* Hope by Ślipiński and Lawrence 1997: 406.

Recyntus Broun, 1882: 293. Type species: *Ulonotus tuberculatus* Broun, 1880, by original designation. Synonymized with *Pristoderus* Hope by Ślipiński and Lawrence 1997: 406.

Remarks: The genus *Pristoderus* was removed from synonymy and recognized as valid by Ivie and Ślipiński (1990: 9), stating: "This senior synonym of *Ulonotus* cannot be suppressed, and is the proper name of the genus currently known as *Ulonotus*." Pascoe (1876: 51) stated that Fabricius' *Dermestes scaber* is congeneric with White's *Pristoderus antarcticus* and Erichson's *Ulonotus* was probably based on one of these two species, although Erichson did not formally describe any species when he erected the genus. Sharp (1876: 17) stated that the name *Pristoderus* Hope "may be with advantage dropped into oblivion" due to lack of characters provided by Hope for the genus.

Pristoderus aberrans **(Broun, 1880)**

(Figs. 217–218)

Ulonotus aberrans Broun, 1880: 189. Broun 1886: 949. Waterhouse 1884: pl. 149. Hutton 1904: 168. Hudson 1923: 368.

Recyntus aberrans: Hetschko 1930: 56.

Pristoderus aberrans: Combination by Hudson 1934: 58. Maddison 2010: 426.

Pristoderus abberans: Hudson 1934: 58. Incorrect subsequent spelling, not available.

Type locality: Tairua, Whangarei Heads.

Broun number: 338.

Remarks: Broun mentioned that he based this species on three specimens, two from Tairua and one from Whangarei Heads, but only one matching these localities was located. Broun remarked that he sent material of this species to Sharp, who informed him it was not *U. lawsoni*. It is possible the other two syntypes are amongst Sharp's material at the BMNH. In order to stabilize this name, a lectotype is **here designated** from the material of *Ulonotus aberrans.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 338 [green label] // Tairua [in Broun's hand] // Ulonotus aberrans. [in Broun's hand]".

***Pristoderus acuminatus* (Broun, 1880)**

(Figs. 219–220)

Tarphiomimus acuminatus Broun, 1880: 183.

Dryptops acuminatus: transferred from *Tarphiomimus* by Broun 1882: 293. Broun 1886: 764 (reprinted from Broun 1882). Hutton 1904: 168. Broun 1921a: 527. Hudson 1923: 368. Hetschko 1930: 35.

Pristoderus acuminatus: Implied combination based on synonymy of *Dryptops* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus acuminatus: Emberson 1998: 44. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 325.

Remarks: Broun based this species on a single specimen. Broun (1880: 183) stated that this species might be more closely allied to *Ulonotus* due to the structure of the tarsi (lacking a lobed first tarsomere, as is found in *Tarphiomimus*). Broun (1882: 293) later moved the species to his newly-described genus *Dryptops*. *Dryptops* was subsequently synonymized with *Pristoderus* by Ślipiński and Lawrence (1997). Interestingly, Broun mentions this species in his description of *Allobitoma*, referring to it as *Tarphiomimus acuminatus* (probably disregarding his previous transfer to *Dryptops*), stating that the species "will no doubt be placed in another genus apart from *Tarphiomimus*" (Broun 1921a: 527).

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 325. [green label] // Tairua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Tarphiomimus acuminatus [in Broun's hand]".

***Pristoderus aemulus* (Broun, 1923)**

(Figs. 221–222)

Ulonotus aemulus Broun, 1923: 684. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus aemulus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus aemulus: Maddison 2010: 426.

Type locality: Belgrove.

Broun number: 4280.

Remarks: Broun based this species on a single specimen collected on 10 December, 1914.

Type material examined: *Holotype* (BMNH): card-mounted, "New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Belgrove. 10-12-14. [in Broun's hand] // Ulonotus aemulus. [in Broun's hand]".

Pristoderus affinis (Broun, 1923)

(Figs. 223–224)

Ulonotus affinis Broun, 1923: 683. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus affinis: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus affinis: Maddison 2010: 426.

Type locality: Martinborough.

Broun number: 4279.

Remarks: Broun based this species on a single specimen collected from Martinboro on 25 August, 1918. We could not locate a specimen matching this date. A single specimen in the BMNH Broun collection was located that matches the locality in Broun's description of the species. We assume this specimen is the holotype.

Type material examined: *Holotype* (BMNH): card-mounted, "New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Martinboro 2–3.1915. [in Broun's hand] // Ulonotus affinis. [in Broun's hand]".

Pristoderus antarcticus (White, 1846)

(Figs. 225–226)

Bolitophagus antarcticus White, 1846: 12, pl. 1, fig. 12. Sharp 1877b: 268. Sharp 1877c: 391 (reprinted from Sharp 1876), Ivie and Ślipiński 1990: 9.

Boleotophagus antarcticus: White 1846 pl. 1, fig. 12. *Lapsus calami*.

Ulonotus antarcticus: Combination by Lacordaire 1854: 360. Sharp 1876: 17. Sharp 1877c: 391 (reprinted from Sharp 1876). Broun 1880: 187. Broun 1886: 948.

Hutton 1904: 168. Heyne and Taschenberg 1908: 44 (reprint). Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus antarcticus: Pascoe, 1876: 51. Reitter 1880c: 173. Hudson 1934: 57. Watt 1983: 41, fig. 3g. Kuschel 1990: 63, fig. 65. Klimaszewski and Watt 1997: 59, 156, fig. 215. Maddison 2010: 426.

Type locality: Port Nicholson, New Zealand.

Broun number: 331.

Remarks: White did not mention the number of specimens examined of *Bolitophagus antarcticus.* In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Bolitophagus antarcticus*.

Type material examined: *Lectotype* (MNHN): pinned, "Port Nicholson N. Zealand [dark green label, handwritten] // Boletophagus [sic] antarcticus White Zool. Erebus & Terror [in White's hand] // Typicum Specimen [red text with red rectangular border]". *Paralectotype* (MNHN): pinned, "Port Nicholson N. Zealand [dark green label, handwritten] // Typicum Specimen [red text with red rectangular border]". *Paralectotype* (MNHN): pinned, "Port Nicholson N. Zeald [dark green label, handwritten]".

Pristoderus asper **(Sharp, 1876)**

(Figs. 227–229)

Ulonotus asper Sharp, 1876: 19. Sharp 1877c: 392 (reprinted from Sharp 1876). Broun 1880: 189. Broun 1886: 895. Hutton 1904: 168. Broun 1923: 684. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus asper: Combination by Hudson 1934: 58. Watt 1982b: 303. Kuschel 1990: 33, 63. Emberson 1998: 44. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 335.

Remarks: Sharp based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Ulonotus asper. Type N. Zeal[d]. D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651703".

Pristoderus atratus (Broun, 1880)

(Figs. 230–231)

Ulonotus atratus Broun, 1880: 190. Hutton 1904: 168. Hudson 1923: 368.

Recyntus atratus: Hetschko 1930: 56.

Pristoderus atratus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus atratus: Maddison 2010: 426.

Type locality: Tairua.

Broun number: 339.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 339 [green label] // Tairua [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus atratus. [in Broun's hand]".

Pristoderus bakewellii (Pascoe, 1866)

(Figs. 232–233)

Enarsus bakewellii Pascoe, 1866: 445, pl. 19, fig. 1. Sharp 1876: 17, 21. Sharp 1877c: 391, 394 (reprinted from Sharp 1876). Broun 1880: 199. Hutton 1904: 169. Hudson 1923: 369. Ivie and Ślipiński 1990: 8.

Enarsus bakewelli: Sharp 1877a: 190. Sharp 1886: 388. Broun 1893b: 1089. Heyne and Taschenberg 1908: 44 [reprint]. Sharp and Muir 1912: 516, pl. 57, fig. 92. Hetschko 1930: 36. Hudson 1934: 59. Kuschel 1990: 33, 63. Klimaszewski and Watt 1997: 120, fig. 43. Incorrect subsequent spelling, not available.

Pristoderus bakewellii: Ślipiński and Lawrence 1997: 407, based on synonymy of *Enarsus* with *Pristoderus* (p. 406).

Pristoderus bakewelli: Emberson 1998: 44. Maddison 2010: 426. Marske *et al.* 2011: 90. Incorrect subsequent spelling, not available.

Type locality: New Zealand.

Broun number: 355.

Remarks: Pascoe did not mention the number of specimens examined. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Enarsus bakewellii*.

Type material examined: *Lectotype* (BMNH): minuten-pinned into card, "Type [round label with red border] // New Zealand [green elliptical label, in Pasoe's hand] // Enarsus Bakewellii <u>type</u> Pasc. [in Pascoe's hand] // Pascoe Coll. 93-60 // BMNH(E) #651713". *Paralectotype* (BMNH): "Enarsus Bakewelli Pasco. Ind. typ. [written at base of card in Sharp's hand] // New Zealand [green elliptical label, in Pascoe's hand] // Enarsus Bakewelli Pasc. New Zealand. [in Pascoe's hand] // Sharp Coll. 1905-313."

Pristoderus brouni (Sharp, 1876)

(Figs. 234–236)

Ulonotus brouni Sharp, 1876: 18. Sharp 1877c: 392 (reprinted from Sharp 1876). Broun 1880: 188. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus brouni: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus brouni: Maddison 2010: 426.

Type locality: Tairua.

Broun number: 333.

Remarks: Sharp mentioned that he based this species on two specimens. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ulonotus brouni*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Ulonotus brouni Type N. Zeal[d]. D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651702". *Paralectotype* (BMNH): pin head removed, "Ulonotus brouni. Ind. typ. D.S. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313."

***Pristoderus carus* (Broun, 1886)**

(Figs. 237–238)

Ulonotus carus Broun, 1886: 947. Hutton 1904: 168. Broun 1914a: 96. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus carus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus carus: Maddison 2010: 426.

Type locality: Purakanui, near Dunedin.

Broun number: 1706.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1706. [in Broun's hand] // Otago // Purakanui // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus carus. [in Broun's hand]".

Pristoderus cinereus (Broun, 1886)

(Figs. 239–240)

Ulonotus cinereus Broun, 1886: 948. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus cinereus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus cinereus: Maddison 2010: 426.

Type locality: Mount Egmont.

Broun number: 1709.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, the single specimen of *Ulonotus cinereus* in the BMNH Broun collection is **here designated** as the lectotype.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1709. [in Broun's hand] // Egmont // Ulonotus cinereus [in Broun's hand]".

Pristoderus contractifrons (Broun, 1880)

(Figs. 241–242)

Enarsus contractifrons Broun, 1880: 200. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 36.

Pristoderus contractifrons: Implied combination based on synonymy of *Enarsus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus contractifrons: Maddison 2010: 426.

Type locality: Tairua.

Broun number: 358.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 358 [green label] // Tairua // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Enarsus contractifrons. [in Broun's hand]".

***Pristoderus cucullatus* (Sharp, 1886)**

(Figs. 243–245)

Enarsus cucullatus Sharp, 1886: 387, pl. 12, fig. 19. Broun 1893b: 1089 (reprinted excerpt of Sharp 1886: 387). Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 36. Hudson 1934: 59.

Pristoderus cucullatus: Implied combination based on synonymy of *Enarsus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus cucullatus: Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 1939.

Remarks: Sharp did not mention the number of specimens examined (listed as "Helms, No. 280" in the original description). Sharp stated that Mr. Helms sent him two specimens initially, then additional specimens at a later date, which we also regard as syntypes. In order to stabilize this name, a lectotype and seven paralectotypes are **here designated** from the material of *Enarsus cucullatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Enarsus cucullatus Type D.S. Greymouth N. Z[d]. Helms. [written at base of card in Sharp’s hand] // Type [round label with red border] // Greymouth, [red underline] New Zealand. Helms. // Sharp Coll. 1905-313. // BMNH(E) #651712”. *Paralectotype* (BMNH): “Enarsus cuculla- tus D.S. Greymouth. Helms [written at base of card in Sharp’s hand] // N. Zeal. [red underline] 86 20 // Sharp Coll. 1905-313.” *Paralectotypes* (BMNH): 2, mounted separately on individual cards and pins, with identical labels, “Enarsus cuculla- tus D.S. Greymouth. Helms. [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.” *Paralectotype* (BMNH): “Enarsus cuculla-tus D.S. Greymouth. N. Zd. [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.” *Paralectotype* (BMNH): “Enarsus cucullat us D.S. Greymouth. Helms. [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.” *Paralectotype* (BMNH): “Enarsus cucullatus D.S. Greymouth. N. Zd. [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.” *Paralectotype* (BMNH): “Enarsus cucullatus D.S. Greymouth. Helms. [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.”

***Pristoderus discalis* (Broun, 1921)**

(Figs. 246–247)

Ulonotus discalis Broun, 1921a: 525. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus discalis: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus discalis: Maddison 2010: 426.

Type locality: Routeburn, northwest of Lake Wakatipu.

Broun number: 4047.

Remarks: Broun based this species on a single specimen with a broken tibia collected on 11 February, 1914. This specimen was located in the BMNH beside a similar, fully intact specimen collected on 16 February, 1914.

Type material examined: *Holotype* (BMNH): card-mounted, "4047 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Routeburn. 11.2.1914_ [in Broun's hand] // Ulonotus discalis. [in Broun's hand]".

***Pristoderus discedens* (Sharp, 1877)**

(Figs. 248–250)

Ulonotus discedens Sharp, 1877b: 268. Broun 1880: 187. Broun 1886: 949. Hutton 1904: 168. Broun 1923: 684. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus discedens: Combination by Reitter 1880c: 173. Hudson 1934: 57. Maddison 2010: 426.

Type locality: West Coast.

Broun number: 332.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ulonotus discedens*. Since the paralectotype bears no labels other than the one listed below, it can be assumed this specimen is in the same series as the lectotype. Moreover, the pin and card are of the same stock and style.

Type material examined: *Lectotype* (BMNH): card-mounted, "Ulonotus discedens Type D.S. New Z^{d}. [written at base of card in Sharp's hand] // W.C. [abbreviation of "West Coast," handwritten] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651705". *Paralectotype* (BMNH): "Ulonotus discedens, Ind. typ. D.S. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313."

Pristoderus dissimilis **(Sharp, 1886)**

(Figs. 251–253)

Ulonotus dissimilis Sharp, 1886: 387, pl. 12, fig. 18. Broun 1893b: 1081 (reprinted excerpt of Sharp 1886: 387). Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus dissimilis: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus dissimilis: Maddison 2010: 426.

Type locality: Bealey [Greymouth and Picton also given in original description].

Broun number: 1926.

Remarks: Sharp did not mention the number of specimens examined but stated he was sent "an example from Captain Broun (with the No. 109 attached)," which "was found in numbers at Bealey and Picton by Helms," and is conspecific with a specimen that Reitter sent "some time ago from Greymouth…" In order to stabilize this name, a lectotype and 15 paralectotypes are **here designated** from the material of *Ulonotus dissimilis*.

Type material examined: *Lectotype* (BMNH): mounted on same card as 3 paralectotypes, left-most specimen is the lectotype, "Ulonotus dissimilis. Types D.S. Bealey. N. Zeal[d]. Helms. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651706". *Paralectotypes* (BMNH): 3, mounted on same card as lectotype, left-most specimen is the lectotype, right-most specimen is mounted venter-up, labels same as lectotype. *Paralectotypes* (BMNH): 4, mounted together on same card and pin, "Ulonotus dissimilis D.S. Bealey N.Z. Helms 1886 [written at base of card in Sharp's hand] // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 4, mounted together on same card and pin, "Ulonotus dissimilis Picton Helms 1884 [written at base of card in Sharp's hand] // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted together on same card and pin, "Picton, New Zealand. Helms. // Ulonotus dissimilis [in Sharp's hand] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Nov Zeeland Helms. Reitter [with black border] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "109 // Ulonotus dissimilis. Tairua Broun [in Sharp's hand] // Sharp Coll. 1905-313."

***Pristoderus dorsalis* (Broun, 1882)**

(Figs. 254–255)

Dryptops dorsalis Broun, 1882: 292. Broun 1886: 763 (reprinted from Broun 1882). Hutton 1904. Hudson 1923: 368. Hetschko 1930: 35. Ivie and Ślipiński 1990: 8.

Pristoderus dorsalis: Ślipiński and Lawrence 1997: 407, based on synonymy of *Dryptops* with *Pristoderus* (p. 406). Maddison 2010: 426.

Type locality: on the Waitakere Range.

Broun number: 1354.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1354. [green label] // Waitakerei // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Dryptops dorsalis [in Broun's hand]".

Pristoderus exiguus (Broun, 1882)

(Figs. 256–257)

Recyntus exiguus Broun, 1882: 294. Broun 1886: 765 (reprinted from Broun 1882). Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 56. Watt 1956: 59.

Pristoderus exiguus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus exiguus: Maddison 2010: 426.

Type locality: Parua Bay [near Whangarei Harbour].

Broun number: 1356.

Remarks: Broun based this species on a single specimen. This species description was re-printed in Part III of Broun's New Zealand Coleoptera (1886: 765).

Type material examined: *Holotype* (BMNH): mounted on an acetate card, "Type [round label with red border] // 1356. [in Broun's hand] // Parua. [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Recyntus exiguus [in Broun's hand]".

Pristoderus fulvus (Broun, 1893)

(Figs. 258–259)

Ulonotus fulvus Broun, 1893b: 1080. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus fulvus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus fulvus: Maddison 2010: 426.

Type locality: Moeraki.

Broun number: 1925.

Remarks: Broun based this species on a single specimen. We located one specimen in the BMNH Broun collection with a "1925" Broun number and identification label (but lacking a locality label), which we assume to be the holotype. Broun's determination label on the lectotype reads "Ulonotus fulvous," but the name given in the original description is *Ulonotus fulvus.*

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1925. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus fulvous [in Broun's hand]".

***Pristoderus fuscatus* (Broun, 1886)**

(Figs. 260–261)

Ulonotus fuscatus Broun, 1886: 948. Hutton 1904: 168. Broun 1914a: 96. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus fuscatus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus fuscatus: Maddison 2010: 426.

Type locality: Mount Egmont.

Broun number: 1707.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, the single specimen of *Ulonotus fuscatus* in the BMNH Broun collection is **here designated** as the lectotype.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1707. [in Broun's hand] // Egmont // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus fuscatus. [in Broun's hand]".

Pristoderus insignis (Broun, 1880)

(Figs. 262–263)

Ulonotus insignis Broun, 1880: 191.

Recyntus insignis: Broun 1882: 294. Broun 1886: 765 (reprinted from Broun 1882). Hutton 1904: 170. Broun 1923: 687. Hudson 1923: 369. Hetschko 1930: 56.

Pristoderus insignis: Implied combination based on synonymy of *Recyntus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus insignis: Maddison 2010: 426.

Type locality: Mount Manaia [Whangarei Heads].

Broun number: 341.

Remarks: Broun (1880: 191) mentioned that he based this species on two specimens while several others with different body proportions were listed as varieties. We located one specimen labeled "Mount Manaia" which we designate as the lectotype, and another with a similar "341" label which we designate as the paralectotype. Two additional specimens (card-mounted venter-up) were located and may be the varietal specimens Broun mentioned. In order to stabilize this name, a lectotype and paralectotype are **here**

designated from the material of *Ulonotus insignis*. Broun's determination label on the lectotype reads "Recyntus insignis," but the name given in the original description is *Ulonotus insignis.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 341 [green label] // Mount Manaia [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Recyntus insignis [in Broun's hand]". *Paralectotype* (BMNH): "341. [green label] // New Zealand. [red underline] / Broun Coll. Brit. Mus. 1922-482."

***Pristoderus integratus* (Broun, 1886)**

(Figs. 264–265)

Ulonotus integratus Broun, 1886: 949. Hutton 1904: 168. Broun 1914a: 96. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus integratus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus integratus: Maddison 2010: 426.

Type locality: Purakanui, Otago.

Broun number: 1710.

Remarks: Broun did not explicitly mention the number of specimens examined; however, the wording was ambiguous and he referred to "a small example" from Purakanui and provided a single length measurement. Only one specimen matching this data was located in the BMNH Broun collection, therefore we assume Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 1710. [in Broun’s hand] // Purakanui // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus integratus [in Broun’s hand]”.

Pristoderus isostictus (Broun, 1886)

(Figs. 266–267)

Ulonotus isostictus Broun, 1886: 926. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus isostictus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus isostictus: Maddison 2010: 426.

Type locality: Paparoa, near Howick.

Broun number: 1661.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, the single specimen of *Ulonotus isostictus* in the BMNU Broun collection is **here designated** as the lectotype. Broun’s determination label on the lectotype reads “Notoulus isostictus,” but the name given in the original description is *Ulonotus isostictus.*

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 1661. [in Broun’s hand] // Paparoa // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Notoulus isostictus [in Broun’s hand]”.

Pristoderus lawsoni (Wollaston, 1873)

(Figs. 268–269)

Tarphiomimetes lawsoni Wollaston, 1873: 11. Sharp 1877b: 268. Sharp 1877c: 391 (reprinted from Sharp 1876). Broun 1880: 189. Ivie and Ślipiński 1990: 9.

Ulonotus lawsoni: Sharp 1876: 18. Broun 1886: 949. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus lawsoni: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus lawsoni: Maddison 2010: 426.

Type locality: Auckland.

Broun number: 337.

Remarks: Wollaston did not mention the number of specimens examined. Sharp (1876: 18) moved this species to the genus *Ulonotus.* Ivie and Ślipiński (1990: 9) also designated this species as the type species for the genus *Tarphiomimetes* Wollaston. In order to stabilize this name, a lectotype is **here designated** from a single specimen we believe is the type of *Tarphiomimetes lawsoni.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Sharp Coll. 1905-313. // Tarphiomimetes Lawsoni, Woll. (<u>Nov. Zealandia</u>) [in Wollaston's hand]".

Pristoderus philpotti (Broun, 1914)

(Figs. 270–271)

Ulonotus philpotti Broun, 1914a: 95. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus philpotti: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus philpotti: Maddison 2010: 426.

Type locality: Tisbury, Southland.

Broun number: 3404.

Remarks: We assume Broun based this species on two specimens because he mentioned a "second (damaged) specimen…" in the description. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ulonotus philpotti*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3404. [in Broun's hand] // Tisbury [typed] 29.9.10 [handwritten] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus philpotti [in Broun's hand]". *Paralectotype* (BMNH): "3404. [in Broun's hand] // Tisbury [typed] 29/9/10 [handwritten] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus philpotti [in Broun's hand]".

***Pristoderus plagiatus* (Broun, 1911)**

(Figs. 272–273)

Ulonotus plagiatus Broun, 1911: 97. Hudson 1923: 368. Hetschko 1930: 38.

Utonotus plagiatus: Broun 1911: 97. *Lapsus calami*, no taxonomic status.

Pristoderus plagiatus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus plagiatus: Emberson 1998: 44. Maddison 2010: 426.

Type locality: Pitt Island.

Broun number: This species was listed as number 60 in the paper, but this is not a "Broun number" in the standard sense.

Remarks: Broun did not mention the number of specimens examined. Four specimens in the BMNH and one in the NZAC matching the locality were located. One of these specimens (BMNH) is labeled as a variant, which we do not consider a syntype. In order to stabilize this name, a lectotype and three paralectotypes are **here designated** from the material of *Ulonotus plagiatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "60. [in Broun's hand] // Chatham Is. [red underline] Broun Coll. B.M. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand] // Ulonotus plagiatus. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "60. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand] // Ulonotus plagiatus. [in Broun's hand]". *Paralectotype* (BMNH): "60. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand]". *Paralectotype* (NZAC): card-mounted, "60. [in Broun's hand] // New Zealand, [typed] Chatham Is. Broun Coll. [in J.C Watt's hand] // A.E. Brookes Collection // [green label] SYNTYPE [typed] Ulonotus plagiatus Broun, 1911 [in J.C Watt's hand]".

Pristoderus planiceps **(Broun, 1915)**

(Figs. 274–275)

Ulonotus planiceps Broun, 1915: 315. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus planiceps: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus planiceps: Maddison 2010: 426.

Type locality: Longwood Range, Southland.

Broun number: 3740.

Remarks: Broun based this species on a single specimen collected in January, 1913.

Type material examined: *Holotype* (BMNH): card-mounted, "New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Longwood. Jany. 1913 [in Broun's hand] // Ulonotus planiceps [in Broun's hand]".

Pristoderus probus (Broun, 1893)

(Figs. 276–277)

Enarsus probus Broun, 1893b: 1088. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 36.

Pristoderus probus: Implied combination based on synonymy of *Enarsus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus probus: Maddison 2010: 426.

Type locality: Taieri.

Broun number: 1938.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Enarsus probus*.

Type material examined: *Lectotype* (BMNH): pinned "Type [round label with red border] // 1938. [in Broun's hand] // Taieri // Enarsus probus. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482." *Paralectotype* (MNHN): pinned, "Taieri // 1938. [in Broun's hand]".

Pristoderus proprius (Broun, 1914)

(Figs. 278–279)

Ulonotus proprius Broun, 1914b: 174. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus proprius: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus proprius: Maddison 2010: 426.

Type locality: Rakaia Gorge, near Methven.

Broun number: 3541.

Remarks: Broun based this species on a single specimen collected on 5 June, 1912.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3541. [in Broun's hand] // Rakaia. 5.6.1912 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus proprius [in Broun's hand]".

***Pristoderus punctatus* (Broun, 1886)**

(Figs. 280–281)

Ulonotus punctatus Broun, 1886: 894. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 39.

Pristoderus punctatus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus punctatus: Maddison 2010: 426.

Type locality: Woodhill.

Broun number: 1595.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1595. [in Broun's hand] // Woodhill // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482."

Pristoderus reitteri (Sharp, 1882)

(Figs. 282–284)

Acosmetus reitteri Sharp, 1882: 80.

Recyntus reitteri: transferred from *Acosmetus* by Broun 1923: 686 (description reprinted from Sharp 1882: 80). Hudson 1923: 369. Hetschko 1930: 56.

Syncalus reitteri: Reitter 1880c: 173. *Nomen nudum*, see note below.

Pristoderus reitteri: Implied combination based on synonymy of *Recyntus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus reitteri: Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 4284.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and 11 paralectotypes are **here designated** from the material of *Acosmetus reitteri*. Reitter (1880c: 173) lists "Syncalus Reitteri Sharp. n. sp." without description and most likely refers to the species *Acosmetus reitteri*, soon-after described by Sharp (1882), who noted that "This very remarkable insect I first received from Mr. Reitter, of Vienna, and, supposing it might go into the genus *Syncalus*, proposed to call it *Syncalus Reitteri*. I find, however, it departs much from *Syncalus*…and I have therefore called it *Acosmetus Reitteri*…" Several specimens in the BMNH lacking handwritten labels by Sharp were not considered syntypes.

Type material examined: *Lectotype* (BMNH): card-mounted, "Acosmetus Reitteri Type D.S. Greymouth [written at base of card in Sharp's hand] // Type [round label with red border] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313."

Paralectotypes (BMNH): 2, individually mounted on separate cards and pins, with identical labels, "Acosmetus Reitteri Ind. typ. D.S. Greymouth [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): mounted venter-up and disarticulated, "Acosmetus Reitteri Ind. typ. D.S. Greymouth Helms [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 3, mounted together on single card, "Acosmetus reitteri D.S. Greymouth. N. Zealand. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 4 total, 2 mounted together on single card, two individually mounted on separate cards and pins, with identical labels, "Acosmetus reitteri D.S. Greymouth. N. Zd. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): card-mounted on single card, "Acosmetus reitteri D.S. Greymouth. N. Zd. 1882 Helms. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313."

***Pristoderus rudis* (Sharp, 1877)**

(Figs. 285–287)

Enarsus rudis Sharp, 1877a: 191. Broun 1880: 200. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 36.

Pristoderus rudis: Implied combination based on synonymy of *Enarsus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus rudis: Maddison 2010: 426.

Type locality: Christchurch.

Broun number: 357.

Remarks: Sharp did not mention the number of specimens examined; however, we located three specimens with the same card and pin stock, though the minutens pins varied in placement through the specimen. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Enarsus rudis*.

Type material examined: *Lectotype* (BMNH): minuten-pinned into card, "Enarsus rudis Type D.S. New Zealand. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651715". *Paralectotype* (BMNH): "Enarsus rudis D.S. New Zealand [written at base of card in Sharp's hand] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): minuten-pinned venter-up into card with abdomen and legs glued to card, "Enarsus rudis D.S. Nov. Zeal. Murray. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313."

***Pristoderus rufescens* (Broun, 1886)**

(Figs. 288–289)

Ulonotus rufescens Broun, 1886: 948. Hutton 1904: 168. Broun 1912: 419. Broun 1914a: 96. Hudson 1923: 368. Hetschko 1930: 39.

Pristoderus rufescens: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus rufescens: Maddison 2010: 426.

Type locality: Purakanui, Otago.

Broun number: 1708.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the single specimen of *Ulonotus rufescens* in the BMNH Broun collection.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1708 [in Broun's hand] // Purakanui // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Ulonotus rufescens. [in Broun's hand]".

Pristoderus salebrosus (Broun, 1880)

(Figs. 290–291)

Ulonotus salebrosus Broun, 1880: 192.

Recyntus salebrosus: Broun 1882: 294. Broun 1886: 765 (reprinted from Broun 1882). Hutton 1904: 170. Broun 1923: 687. Hudson 1923: 369. Hetschko 1930: 56.

Pristoderus salebrosus: Implied combination based on synonymy of *Recyntus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus salebrosus: Maddison 2010: 426.

Type locality: Tairua.

Broun number: 342.

Remarks: Broun mentioned that he based this species on two specimens, both of which were located in the BMNH and the MNHN. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Ulonotus salebrosus*. Broun's determination label on the lectotype reads "Recyntus salebrosus," but the name given in the original description is *Ulonotus salebrosus.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 342. [green label] // Tairua [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Recyntus salebrosus. [in Broun's hand]".

Paralectotype (MNHN): card-mounted, "Tairua [in Broun's hand] // 342. [green label]".

Pristoderus scaber **(Fabricius, 1775)**

(Figs. 292–296)

Dermestes scaber Fabricius, 1775: 57. Olivier 1790: 15, pl.2 fig. 14. Fabricius 1801: 318. Zimsen 1964: 77. Ivie and Ślipiński 1990: 9

Pristoderus scaber: Hope, 1840: 145. White 1846: 12. Lacordaire 1854: 359. Pascoe 1876: 51. Kuschel 1990: 33, 63. Ślipiński and Lawrence 1997: 407. Maddison 2010: 426.

Ulonotus scaber: Hetschko 1930: 39. Radford 1981: 188.

Bolitophagus anguliferus Blanchard, 1853: 167, pl. 11, fig. 3. Gerstaecker 1855: 177. Jouan 1868: 317. Synonymized with *Pristoderus scaber* (Fabricius) by Waterhouse 1875: 55.

Bolitophagus angulifer: Bates 1873: 473. Bates 1876: 283 (reprinted from Bates 1873). Waterhouse 1875: 55. Rye 1877: 341. Hutton 1904: 186. Gebien 1906: 219. Incorrect subsequent spelling, not available.

Ulonotus integer Sharp, 1877b: 268. Broun 1880: 189. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38. Synonymized with *Ulonotus scaber* Fabricius by Radford 1981: 188.

Pristoderus integer: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9. **New combination.**

Type locality: *Dermestes scaber* Fabricius: New Zealand. *Bolitophagus anguliferus* Blanchard: New Zealand. *Ulonotus integer* Sharp: Christchurch.

Broun number: *Dermestes scaber* Fabricius: none given. *Bolitophagus anguliferus* Blanchard: none given. *Ulonotus integer* Sharp: 336.

Remarks: Fabricius did not mention the number of specimens examined of *Dermestes scaber*, but a specimen in the Banks Collection at the BMNH was listed as the holotype by Radford (1981: 188). Blanchard did not mention the number of specimens examined of *Bolitophagus anguliferus*. Sharp based *Ulonotus integer* on a single specimen.

Type material examined: *Dermestes scaber* Fabricius: *Holotype* (BMNH): pinned through left elytron, "Derm. Scaber. [in Fabricius' hand] Fab. Entom. p. 57.16. [handwritten]". *Bolitophagus anguliferus* Blanchard: type material not examined. *Ulonotus integer* Sharp: *Holotype* (BMNH): card-mounted, "Ulonotus integer Type D.S. Christchurch. N.Z^{d}. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651704".

***Pristoderus tuberculatus* (Broun, 1880)**

(Figs. 297–298)

Ulonotus tuberculatus Broun, 1880: 191.

Recyntus tuberculatus: Broun 1882: 294. Broun 1886: 765 (reprinted from Broun 1882). Hutton 1904: 170. Broun 1923: 687. Hudson 1923: 369. Hetschko 1930: 56. Hudson 1934: 60. Ivie and Ślipiński 1990: 12. Kuschel 1990: 33, 64.

Pristoderus tuberculatus: Ślipiński and Lawrence 1997: 407, based on synonymy of *Recyntus* with *Pristoderus* (p. 406). Maddison 2010: 426.

Type locality: Tairua.

Broun number: 340.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 340 [green label] // 340. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Tairua Nov[r] 1875. [in Broun's hand] // Recyntus tuberculatus [in Broun's hand]".

Pristoderus undosus (Broun, 1882)

(Figs. 299–300)

Dryptops undosus Broun, 1882: 293. Broun 1886: 764 (reprinted from Broun 1882). Hudson 1923: 368. Hetschko 1930: 35. Hudson 1934: 59.

Dryptops undosis: Harris 2007: 29. Misspeling, no taxonomic status.

Pristoderus undosus: Implied combination based on synonymy of *Dryptops* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus undosus: Maddison 2010: 426.

Type locality: Outram [Taieri, Otago Region].

Broun number: 1355.

Remarks: Broun mentioned that he based this species on two specimens, one having been returned to Sydney W. Fulton. No specimens were located in the BMNH bearing an "Outram" locality label, but two were located with a "Taieri" label (more or less the same locality as Outram), one of which bears a handwritten determination label. A third specimen is presumably in the Otago Museum (OM), Dunedin, which is noted as a holotype by Harris (2007). This specimen was not confirmed by us due to restricted loaning policy by the OM, and is not considered a syntype until it can be examined. In order to stabilize this name, a lectotype is **here designated** from the material of *Dryptops undosus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1355. [in Broun's hand] // Taieri // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Dryptops undosus. [in Broun's hand]".

Pristoderus uropterus (Broun, 1912)

(Figs. 301–302)

Ulonotus uropterus Broun, 1912: 418. Broun 1914b: 175. Hudson 1923: 368. Hetschko 1930: 39.

Pristoderus uropterus: Implied combination based on *Ulonotus* as a junior synonym of *Pristoderus* in Ivie and Ślipiński 1990: 9.

Pristoderus uropterus: Maddison 2010: 426.

Type locality: Wairiri, Kaikoura.

Broun number: 3222.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3222 [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Wairiri. Kaikouras. [in Broun's hand] // Ulonotus uropterus. [in Broun's hand]".

Pristoderus viridipictus (Wollaston, 1873)

(Figs. 303–305)

Tarphiomimetes viridipicta Wollaston, 1873: 11. Sharp 1876: 17. Sharp 1877c: 391 (reprinted from Sharp 1876).

Tarphiomimetes viridipcta: Sharp 1877b: 268. Incorrect subsequent spelling, not available.

Tarphiomimetes viridipictus: Sharp 1876: 19. Sharp 1877c: 392 (reprinted from Sharp 1876).

Ulonotus viridipictus: Sharp 1876: 17. Broun 1880: 188. Broun 1886: 948. Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus viridipictus: Combination by Hudson 1934: 58. Maddison 2010: 426.

Type locality: Auckland.

Broun number: 334.

Remarks: Wollaston mentioned that he based this species on two specimens (listed as "exponents"). In order to stabilize this name, a lectotype is **here designated** from the material of *Tarphiomimetes viridipicta.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Tarphiomimetes viridipicta Woll. Ind. typ. N. Zeal[d]. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313. // Tarphiomimetes viridipicta, Woll. (Nov. Zealand) [in Wollaston's hand, confirmed by R.G. Booth]".

***Pristoderus wakefieldi* (Sharp, 1877)**

(Figs. 306–308)

Enarsus wakefieldi Sharp, 1877a: 190. Broun 1880: 199. Sharp 1886: 388. Broun 1893b: 1089. Hutton 1904: 169. Hudson 1923: 369. Hetschko 1930: 36. Hudson 1934: 59.

Pristoderus wakefieldi: Implied combination based on synonymy of *Enarsus* with *Pristoderus* in Ślipiński and Lawrence 1997: 406.

Pristoderus wakefieldi: Maddison 2010: 426.

Type locality: Peel Forest.

Broun number: 356.

Remarks: Sharp did not mention the number of specimens examined, but stated they were collected in March, 1874. In order to stabilize this name, a lectotype is **here designated** from the material of *Enarsus wakefieldi.* Three additional specimens associated with the lectotype were located in the BMNH, but due to incorrect locality information ("Oxford") and lack of Sharp handwriting on the card, we do not regard these as syntypes.

Type material examined: *Lectotype* (BMNH): card-mounted, "Enarsus Wakefieldi Type D.S. New Zealand. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313. // BMNH(E) #651714".

***Pristoderus wallacei* (Broun, 1912)**

(Figs. 309–310)

Ulonotus wallacei Broun, 1912: 419. Hudson 1923: 368. Hetschko 1930: 38.

Pristoderus wallacei: Combination by Hudson 1934: 58. Maddison 2010: 426.

Type locality: Wairiri, Seaward Kaikoura Range.

Broun number: 3223.

Remarks: Broun did not mention the number of specimens examined. Only four specimens were present in the BMNH, three that match the locality, one of which bears an additional "Moeraki" label. There are five specimens in the NZAC (three individually mounted on separate cards and pins, two pointed on separate cards on the same pins, one venter-up) with determination labels in Broun's hand and "Syntype" labels in J.C. Watt's hand. We do not regard these as syntypes because they lack locality labels. In order to stabilize this name, a lectotype and three paralectotypes are **here designated** from the material of *Ulonotus wallacei*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3223 [in Broun's hand] // Moeraki [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Wairiri. Kaikoura. [in Broun's hand] // Ulonotus Wallacei. [in Broun's hand]". *Paralectotype* (BMNH): "3223 [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Wairiri. Kaikoura [in Broun's hand]". *Paralectotype* (BMNH): "3223. [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Wairiri. Kaikoura [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "3223 [in Broun's hand] // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Wairiri. Kaikoura [in Broun's hand] // Ulonotus wallacei. [in Broun's hand]".

RYTINOTUS Broun, 1880

Rytinotus Broun, 1880: 204. Type species: *Rytinotus squamulosus* Broun, 1880, fixed by monotypy.

Rhytinotus: Waterhouse 1881: plate 42. Broun 1886: 834. Hutton 1898: 156. Incorrect subsequent spelling, not available.

Rhytidonotus: Kirby 1882: 44. Incorrect subsequent spelling, not available.

Edalus Broun, 1886: 834. Unjustified replacement name based on incorrect concept of homonymy.

Rytidinotus: Hutton 1904: 170. Incorrect subsequent spelling, not available.

Rhitidinotus: Broun 1909b: 146. Hutton 1904: 170 (cited in error as Broun 1904 by Emberson 2000: 23). Hudson 1923: 369. Hudson 1934: 60. Hudson 1950: 163. Pritchard 1953: 21. Emberson 1998: 45. Incorrect subsequent spelling, not available.

Remarks: Broun described the genus with an original spelling of *Rytinotus* (1880: 204). Later, Broun (1886:834) gave *Edalus* as a replacement name based on the similarity of his original *Rytinotus* to the genus *Rytinota*. This was an unjustified action based on an incorrect concept of homonymy. For a full discussion of the *Rytinotus* genus-group names, spellings and their usage, see Emberson 2000.

***Rytinotus squamulosus* Broun, 1880**

(Figs. 311–312)

Rytinotus squamulosus Broun, 1880: 204. Hetschko 1930: 37. Ivie and Ślipiński 1990: 8. Ślipiński and Lawrence 1997: 410, 411, 429, figs. 358–365, 447. Emberson 1998: 45. Maddison 2010: 426.

Rhytinotus squamulosus: Waterhouse 1881: plate 42. Incorrect subsequent spelling, not available.

Rhytidonotus squamulosus: Kirby 1882: 44. Hutton 1904: 170. Incorrect subsequent spelling, not available.

Rytidinotus squamulosus: Hutton 1904: 170. Incorrect subsequent spelling, not available.

Rhitidinotus squamulosus: Hudson 1923: 369. Hudson 1934: 60. Incorrect subsequent spelling, not available.

Type locality: Hunua Range, Auckland [Wairoa District].

Broun number: 364.

Remarks: Broun based this species on a single specimen. No specimens in the BMNH are labeled from the Wairoa district, but one from "Hunua Range" was located and is assumed to be the holotype. Broun's determination label on the holotype reads "Rhytidinotus squamulosus," but the name given in the original description is *Rytinotus squamulosus.*

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 364. [in Broun's hand] // Hunua Range. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Rhytidinotus squamulosus. [in Broun's hand]".

SYNCALUS Sharp, 1876

Syncalus Sharp, 1876: 20. Type species: *Syncalus hystrix* Sharp, 1876, designated by Ivie and Ślipiński 1990: 12.

Acosmetus Broun, 1880: 197. Type species: *Acosmetus oblongus* Broun, 1880, designated by Ivie and Ślipiński 1990: 12. Synonymized with *Syncalus* Sharp by Ślipiński and Lawrence 1997: 412.

Remarks: Sharp (1976:20–21) erected this genus and stated its affinities with and differences from *Tarphius*, suggesting that morphology would indicate members of the two genera probably share similar habits. Broun (1880: 197) erected *Acosmetus* to include members that appeared to be intermediate between *Coxelus* (=*Notocoxelus*) and *Syncalus*, while Sharp (1882: 81) considered *Acosmetus* to be a distinct genus.

Syncalus explanatus Broun, 1912

(Figs. 313–314)

Syncalus explanatus Broun, 1912: 417. Hudson 1923: 369. Hetschko 1930: 57. Maddison 2010: 426.

Type locality: Akatarawa, near Wellington.

Broun number: 3220.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 3220. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Akatarawa. Wellington. [in Broun’s hand] // Syncalus explanatus [in Broun’s hand]”.

Syncalus granulatus (Broun, 1880)

(Figs. 315–316)

Acosmetus granulatus Broun, 1880: 198. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 57. Watt 1982b: 303.

Syncalus granulatus: Implied combination based on synonymy of *Acosmetus* with *Syncalus* in Ślipiński and Lawrence 1997: 412.

Syncalus granulatus: Maddison 2010: 426.

Type locality: Parua, near Whangarei Harbour.

Broun number: 354.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 354. [green label] // Parua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Acosmetus granulatus [in Broun's hand]".

***Syncalus hystrix* Sharp, 1876**

(Figs. 317–319)

Syncalus hystrix Sharp, 1876: 22. Sharp 1877c: 395 (reprinted from Sharp 1876). Broun 1880: 202. Hutton 1904: 170. Broun 1923: 686. Hudson 1923: 369. Hetschko 1930: 57. Ivie and Ślipiński 1990: 12. Kuschel 1990: 33, 64. Ślipiński and Lawrence 1997: 414. Maddison 2010: 426.

Type locality: Tairua?

Broun number: 361.

Remarks: Sharp based this species on a single specimen sent by Broun. Although no locality was explicitly given in the description, it is likely the specimen was from Tairua, as Sharp received specimens of other species from Tairua from Broun (listed in descriptions in same paper).

Type material examined: *Holotype* (BMNH): card-mounted, "Syncalus hystrix Type D.S. [written at base of card in Sharp's hand] // Type [round border with red label] // Sharp Coll. 1905-313."

Syncalus munroi Broun, 1893

(Figs. 320–321)

Syncalus munroi Broun, 1893b: 1442. Hetschko 1930: 57. Maddison 2010: 426.

Syncalus monroi: Hutton 1904: 170. Hudson 1923: 369. Incorrect subsequent spelling, not available.

Type locality: Hunua Range, Clevedon.

Broun number: 2502.

Remarks: Broun mentioned that he based this species on three specimens, although only two were located in the BMNH Broun collection. There are two additional specimens (not regarded as syntypes) in the Broun collection with a "2502" label, but are from differing localities and are on different card types. There are also four specimens in the NZAC with labels in Brookes' hand that match the localities (two card-mounted venter-up). Because Broun mentioned only three specimens, we are electing to not regard the NZAC and additional BMNH specimens as syntypes, as two were located in the BMNH with appropriate Broun labels. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Syncalus munroi*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2502. [in Broun's hand] // Hunua Clevedon [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Syncalus munroi [in Broun's hand]”. *Paralectotype* (BMNH): “2502. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Hunua. Clevedon [in Broun’s hand]”.

Syncalus oblongus **(Broun, 1880)**

(Figs. 322–323)

Acosmetus oblongus Broun, 1880: 198. Hutton 1904: 170. Hudson 1923: 369. Hetschko 1930: 57. Ivie and Ślipiński 1990: 12.

Syncalus oblongus: Combination by Broun 1923: 686. Ślipiński and Lawrence 1997: 414 (note that this was listed as a new combination, but the earlier combination by Broun was apparently missed). Maddison 2010: 426.

Type locality: Whangarei Heads.

Broun number: 353.

Remarks: Broun did not mention the number of specimens examined. One specimen of *Syncalus oblongus* in the BMNH Broun collection bears a correct Broun number label and determination label, which we regard as the lectotype (**here designated**).

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 353. [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Syncalus oblongus. [in Broun’s hand]”.

Syncalus optatus **Sharp, 1876**

(Figs. 324–326)

Syncalus optatus Sharp, 1876: 21. Sharp 1877c: 394 (reprinted from Sharp 1876). Broun 1880: 201. Hutton 1904: 170. Broun 1923: 686. Hudson 1923: 369. Hetschko 1930: 57. Kuschel 1990: 33, 64. Maddison 2010: 426.

Type locality: Auckland.

Broun number: 359.

Remarks: Sharp based this species on a single "mutilated" specimen.

Type material examined: *Holotype* (BMNH): card-mounted [missing tarsomeres on the prolegs and right meso- and metalegs], "Syncalus optatus Type N. Zeal[d]. D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313."

Syncalus piciceps Broun, 1893

(Figs. 327–328)

Syncalus piciceps Broun, 1893b: 1092. Hutton 1904: 170. Hudson 1923: 369. Maddison 2010: 426.

Syncalus picipes: Hetschko 1930: 57. Incorrect subsequent spelling, not available.

Type locality: Wellington.

Broun number: 1942.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1942. [in Broun's hand] // Wellington // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Syncalus piciceps [in Broun's hand] // near_ 359. [in Broun's hand]".

Syncalus politus Broun, 1880

(Figs. 329–330)

Syncalus politus Broun, 1880: 201. Hutton 1904: 170. Broun 1923: 686. Hudson 1923: 369. Hetschko 1930: 57. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 360.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 360 [green label] // Tairua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Syncalus politus. [in Broun's hand]".

Syncalus solidus Broun, 1923

(Figs. 331–332)

Syncalus solidus Broun, 1923: 685. Hudson 1923: 369. Hetschko 1930: 57. Maddison 2010: 426.

Type locality: Tairua [Hunua Range, Waitakere, and Pakarau also given in original description].

Broun number: 4283.

Remarks: Broun did not mention the number of specimens examined. We located a specimen with a printed "Tairua" label which we regard as the lectotype and five specimens (three with a handwritten "Waitakere" label and two with a handwritten"Pakarau" label) which we regard as paralectotypes. No specimens were located, however, that are explicitly labeled from the Hunua Ranges. In order to stabilize this name, a lectotype and five paralectotypes are **here designated** from the material of *Syncalus solidus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Tairua // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Syncalus solidus. [in Broun’s hand]”. *Paralectotypes* (BMNH): 3, individually mounted on separate cards and pins, with identical labels, one mounted venter-up, “New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Waitakerei. 26.10.1914 [in Broun’s hand] // Syncalus solidus. [in Broun’s hand]”. *Paralectotype* (BMNH): “New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Pakarau. 24.3.15 [in Broun’s hand] // Syncalus solidus. [in Broun’s hand]”. *Paralectotype* (NZAC): card-mounted, “Parakau 24-3-18. [in Broun’s hand] // Syncalus solidus. [in Broun’s hand] // T. Broun Collection // A.E. Brookes Collection”.

TARPHIOMIMUS Wollaston, 1873

Tarphiomimus Wollaston, 1873: 12. Type species: *Tarphiomimus indentatus* Wollaston, 1873, fixed by monotypy.

Ectomida Pascoe, 1876: 51. Type species: *Ectomida lacerata* Pascoe, 1876, fixed by monotypy. Synonymized with *Tarphiomimus* Wollaston by Sharp 1876: 18.

Taphiomimus: Sharp and Muir 1912: fig. 93. Incorrect subsequent spelling, not available.

Tarphiomimus indentatus **Wollaston, 1873**

(Figs. 333–334)

Tarphiomimus indentatus Wollaston, 1873: 13. Sharp 1876: 18. Sharp 1877c: 391 (reprinted from Sharp 1876). Broun 1880: 182. Sharp 1882: 79. Broun 1893b:

1080. Hutton 1904. Broun 1912: 418. Sharp and Muir 1912: 516. Hudson 1923: 368. Hetschko 1930: 35. Hudson 1934: 59. Watt 1982b: 303. Ivie and Ślipiński 1990: 8. Kuschel 1990: 33, 64. Ślipiński and Lawrence 1997: 417, 418, 433, figs. 400–408, 466. Maddison 2010: 426. Buckley and Leschen 2012: 4.

Taphiomimus indentatus: Sharp and Muir 1912: pl. 57, fig. 93. Incorrect subsequent spelling, not available.

Ectomida lacerata Pascoe, 1876: 51. Synonymized with *Tarphiomimus indentatus* Wollaston by Sharp 1876: 391. Sharp 1877c: 391 (reprinted from Sharp 1876). Broun 1880: 183.

Ectomida laceratus: Hetschko 1930: 35 (listed as a jr. synonym of *Tarphiomimus indentatus)*. Incorrect subsequent spelling, not available.

Type locality: *Tarphiomimus indentatus* Wollaston: Auckland. *Ectomida lacerata* Pascoe: Auckland (Tairoa).

Broun number: *Tarphiomimus indentatus* Wollaston: 324. *Ectomida lacerata* Pascoe: none given.

Remarks: Sharp (1876:18) stated that Pascoe's *Ectomida lacerata* is identical with Wollaston's *Tarphiomimus indentatus* based on the descriptions and correspondence with Pascoe. Broun (1880: 183) also stated that this species agrees with Pascoe's *Ectomida lacerata*, placed within the Heteromera, but Wollaston's *Tarphiomimus indentatus* has priority due to date of publication. Pascoe did not mention the number of specimens examined of *Ectomida lacerata* and the type is apparently lost, as we could not locate specimens in the BMNH, MNHN, or NZAC. Wollaston did not mention the number of specimens examined of *Tarphiomimus indentatus*, though we examined seven with labels from Lawson. One of these bears a determination label in Wollaston's handwriting, and this specimen is designated as the lectotype. In order to stabilize this name, a lectotype and six paralectotypes are **here designated** from the material of *Tarphiomimus indentatus*. There is a specimen in the BMNH with a "Co-Type" label [round label with yellow border] that we do not consider a syntype due the the lack of Wollaston labels.

Type material examined: *Tarphiomimus indentatus* Wollaston: *Lectotype* (BMNH): card-mounted, "Auckland New Zeal. [red underline] Lawson [handwritten] // Sharp Coll. 1905-313. // Tarphiomimus indentatus, Woll (Nov. Zealand) [in Wollaston's hand]". *Paralectotypes* (BMNH): 3, mounted on the same card and pin, "Auckland New Zeal. [red underline] Lawson [in Wollaston's hand] // Sharp Coll. 1905-313. // Tarphiomimus indentatus Woll. Auckland Lawson [handwritten]". *Paralectotypes* (BMNH): 2, individually mounted on separate cards and pins, with identical labels, "Auckland New Zeal. [red underline] Lawson [in Wollaston's hand] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Auck- land [elliptical red label, in Wollaston's hand] // Sharp Coll. 1905-313. // Auckland New Zeal. [red underline] Lawson [in Wollaston's hand]". *Ectomida lacerata* Pascoe: type material not examined.

***Tarphiomimus tuberculatus* Broun, 1912**

(Figs. 335–336)

Tarphiomimus tuberculatus Broun, 1912: 417. Hudson 1923: 368. Hetschko 1930: 35. Maddison 2010: 426.

Type locality: Mount Greenland, near Ross.

Broun number: 3221.

Remarks: Broun did not mention the number of specimens examined. Only two specimens were located in the BMNH Broun collection. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Tarphiomimus tuberculatus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3221. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Mount Greenland. [in Broun's hand] // Tarphiomimus tuberculatus. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "3221 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Mount Greenland. [in Broun's hand] // Tarphiomimus tuberculatus. [in Broun's hand]".

Tarphiomimus wollastoni Sharp, 1882

(Figs. 337–339)

Tarphiomimus wollastoni Sharp, 1882: 79. Broun 1893b: 1080 (reprinted excerpt of Sharp 1882: 79). Hutton 1904: 168. Hudson 1923: 368. Hetschko 1930: 35. Maddison 2010: 426. Buckley and Leschen 2012: 4.

Type locality: Greymouth.

Broun number: 1924.

Remarks: Sharp did not mention the number of specimens examined. In order to stabilize this name, a lectotype and 13 paralectotypes are **here designated** from the material of *Tarphiomimus wollastoni*.

Type material examined: *Lectotype* (BMNH): mounted on same card as 3 paralectotypes, left-most specimen is the lectotype, "Tarphiomimus Wollastoni Types D.S. Greymouth. Helms. 1881. [written at base of card in Sharp's hand] // Type [round label with red border] // Greymouth, [red underline] New Zealand Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 3, mounted on same card as lectotype, left-most specimen is the lectotype, right-most specimen is mounted venter-up, labels same as lectotype. *Paralectotypes* (BMNH): 3, mounted on same card and pin, "Tarphiomimus wollastoni. Ind. typ. D.S. Greymouth [written at base of card in Sharp's hand] // Greymouth, [red underline] New Zealand Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): Tarphomimus Wollastoni. Greymouth N.Zd. [written at base of card in Sharp's hand] // Greymouth, [red underline] New Zealand Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted on same card and pin, "Tarphiomimus Wollastoni. Greymouth N. Zd. Helms [written at base of card in Sharp's hand] // Greymouth, [red underline] New Zealand Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted on same card and pin, "Tarphiomimus Wollastoni. D.S. Greymouth [written at base of card in Sharp's hand] // Greymouth, [red underline] New Zealand Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted on same card and pin, "Tarphiomimus Wollastoni. Greymouth N. Zd. Helms [written at base of card in Sharp's hand] // Greymouth, [red underline] New Zealand Helms. // N Zeal. [red underline] 86 20 [handwritten]".

Subfamily ZOPHERINAE Solier, 1834: 505.

Tribe PYCNOMERINI Erichson, 1845: 290. Type genus: *Pycnomerus* Erichson, 1842.

PYCNOMERODES Broun, 1886

Pycnomerodes Broun, 1886: 951. Type species, *Pycnomerodes peregrinus* Broun, 1886, by monotypy.

Pycnomerodes peregrinus Broun, 1886

(Figs. 340–341)

Pycnomerodes peregrinus Broun, 1886: 952. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 64. Ivie and Ślipiński 1990: 15. Maddison 2010: 426.

Type locality: near Howick.

Broun number: 1715.

Remarks: Broun did not mention how many specimens he "cut out from a log near Howick." Two specimens were located in the BMNH, one from Waitakere (affixed with a BMNH type label) and one from Paparoa. We regard the Paparoa specimen as the lectotype, because "Paparoa" is an old-use name for Howick. In order to stabilize this name, a lectotype is **here designated** from the material of *Pycnomerodes peregrinus.*

Type material examined: *Lectotype* (BMNH): card-mounted, "1715. [in Broun's hand] // Paparoa // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482."

PYCNOMERUS Erichson, 1842

Pycnomerus Erichson, 1842: 214. Type species: *Ips terebrans* Olivier, 1790, subsequent designaton by Dajoz 1977: 175.

Pycnomorphus Motschulsky, 1858: 139. Type species: *Colydium haematodes* Fabricius, 1801, fixed by monotypy. Synonymized with *Pycnomerus* Erichson by Ślipiński and Lawrence 1999: 30.

Dechomus Jacquelin du Val, 1859: 180. Type species: *Cerylon sulcicolle* Germar, 1824, fixed by monotypy. Synonymized with *Pycnomerus* Erichson by Ślipiński and Lawrence 1999: 30.

Penthelispa Pascoe, 1860: 111. Type species: *Penthelispa porosa* Pascoe, 1860, by monotypy. Synonymized with *Pycnomerus* Erichson by Sharp 1894: 474 (missed by Hetschko 1930).

Endectus LeConte, 1861: 91. Type species: *Lyctus reflexus* Say, 1827, designated by Ivie and Ślipiński 1990: 15. Synonymized with *Penthelispa* Pascoe by LeConte 1873: 328.

Pycnomeroplesius Ganglbauer, 1899: 885. Type species: *Pycnomerus inexpectus* Jacquelin du Val, 1859, fixed by monotypy. Synonymized with *Pycnomerus* Erichson by Kuhnt 1913: 558.

Remarks: Broun (1893b: 1094) listed the species *Pycnomerus pubescens* in the comparative section for *P. sinuatus,* but this name is probably a manuscript name as no specimens bearing this name were found in collections or in the literature.

Hetschko (1930: 65) listed *Penthelispa aequicolle* Reitter, 1878 from "Neu-Seeland" which is an error, as this species was described from "Portorico." It should be noted that *Pycnomerus aequicollis* (attributed to Reitter, although author and year were not in parentheses) was listed in Maddison (2010: 426) as occurring in New Zealand, a recapitulation from Hetschko (1930).

***Pycnomerus angulatus* Broun, 1893**

(Figs. 342–343)

Pycnomerus angulatus Broun, 1893b: 1443. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 61. Maddison 2010: 426.

Type locality: Maketu, Hunua Range.

Broun number: 2503.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2503. [in Broun's hand] // Hunua Maketu [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus angulatus [in Broun's hand]".

***Pycnomerus arboreus* Broun, 1886**

(Figs. 344–345)

Pycnomerus arboreus Broun, 1886: 927. Broun 1893b: 1443. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 61. Maddison 2010: 426.

Type locality: near Howick.

Broun number: 1663.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the material of *Pycnomerus arboreus.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1663. [in Broun's hand] // Howick // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // arboreus [in Broun's hand]".

***Pycnomerus arcuatus* Broun, 1914**

(Figs. 346–347)

Pycnomerus arcuatus Broun, 1914a: 98. Broun 1914b: 180. Hudson 1923: 370. Hetschko 1930: 61. Maddison 2010: 426.

Type locality: Broken River, Canterbury.

Broun number: 3408.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3408 [in Broun's hand] // Broken River – [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus – arcuatus. [in Broun's hand]".

***Pycnomerus basalis* Broun, 1882**

(Figs. 348–349)

Pycnomerus basalis Broun, 1882: 295. Broun 1886: 766 (reprinted from Broun 1882). Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 61. Maddison 2010: 426.

Type locality: Parua Bay [near Whangarei Harbour].

Broun number: 1359.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the material of *Pycnomerus basalis.*

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 1359. [in Broun’s hand] // Parua // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus basalis - [in Broun’s hand]”.

Pycnomerus caecus Broun, 1886

(Figs. 350–351)

Pycnomerus caecus Broun, 1886: 896. Broun 1886: 951. Hutton 1904: 171. Hudson 1923: 370. Maddison 2010: 426.

Pycnomerus coecus: Hetschko 1930: 61. Incorrect subsequent spelling, not available.

Type locality: Dunedin [Otago Region].

Broun number: 1599.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 1599. [in Broun’s hand] // Otago // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus caecus. [in Broun’s hand]”.

Pycnomerus candidus Broun, 1912

(Figs. 352–353)

Pycnomerus candidus Broun, 1912: 421. Hudson 1923: 370. Hetschko 1930: 61. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 3227.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 3227 [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Greymouth. -Lewis- [in Broun’s hand] // Pycnomerus candidus. [in Broun’s hand]”.

Pycnomerus carinellus Broun, 1886

(Figs. 354–355)

Pycnomerus carinellus Broun, 1886: 896. Hutton 1904: 171. Broun 1914a: 99. Hudson 1923: 370. Hetschko 1930: 61. Maddison 2010: 426.

Type locality: Woodhill (Kaipara Railway).

Broun number: 1598.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 1598. [in Broun’s hand] // Woodhill // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus carinellus. [in Broun’s hand]”.

Pycnomerus cognatus Broun, 1886

(Figs. 356–357)

Pycnomerus cognatus Broun, 1886: 951. Broun 1893b: 1094. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 61. Maddison 2010: 426.

Type locality: near Howick.

Broun number: 1714.

Remarks: Broun did not mention the number of specimens examined. We regard the Paparoa specimen as the lectotype, because "Paparoa" is an old-use name for Howick. In order to stabilize this name, a lectotype is **here designated** from the material of *Pycnomerus cognatus.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1714. [in Broun's hand] // Paparoa // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // cognatus [in Broun's hand]".

***Pycnomerus depressiusculus* (White, 1846)**

(Figs. 358–363)

Lyctus depressiusculus White, 1846: 18.

Pycnomerus depressiusculus: Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 62. Kuschel 1990: 33, 63. Maddison 2010: 426.

Pycnomerus sophorae Sharp, 1876: 24. Sharp 1877c: 397 (reprinted from Sharp 1876). Broun 1880: 208. Sharp 1886: 388. Broun 1893b: 1095, 1445. Broun 1903: 618. Hutton 1904: 171. Hudson 1923: 369. Hetschko 1930: 62. Klimaszewski and Watt 1997: 124, fig. 59. Maddison 2010: 426. Synonymized with *Lyctus depressiusculus* White by Arrow 1909: 194.

Penthelispa sophorae: Reitter 1880: 175.

Penthelispa acutangulum Reitter, 1878: 124. Sharp 1886: 388. Synonymy with *Pycnomerus sophorae* Sharp in Reitter 1880a: 508.

Pycnomerus acutangulus: Hetschko 1930: 61. Maddison 2010: 426.

Type locality: *Lyctus depressiusculus* White: Port Nicholson (Wellington). *Pycnomerus sophorae* Sharp: Tairua. *Penthelispa acutangulum* Reitter: New Zealand.

Broun number: *Lyctus depressiusculus* White: none given. *Pycnomerus sophorae* Sharp: 368. *Penthelispa acutangulum* Reitter: none given.

Remarks: White did not mention the number of specimens examined of *Lyctus depressiusculus*, though we located two specimens in the BMNH card-mounted together (the left specimen is the lectotype). Sharp did not mention the number of specimens examined of *Pycnomerus sophorae* from Tairua sent from Broun, and there are six specimens in the BMNH labeled by Sharp as types mixed in with specimens of *P. depressiusculus*.

We were unable to locate types of Reitter's (1878: 124) *Penthelispa acutangulum* and these are presumed lost. Based on the title of Reitter's (1878: 113) paper, type(s) should be deposited in Berlin, though types were not located in the Hungarian Natural History Museum (Otto Merkl, pers. comm) or the Museum für Naturkunde, Berlin (Bernd Jaeger and Manfred Uhlig, pers. comm.).

In order to stabilize these names, a lectotype and paralectotype are **here designated** from the material of *Lyctus depressiusculus* and a lectotype and five paralectotypes are **here designated** from the material of *Pycnomerus sophorae*.

Type material examined: *Lyctus depressiusculus* White: *Lectotype* (BMNH): mounted on same card as paralectotype, left specimen is the lectotype, "Type [round label with red border] // Port Nicholson N Zealand [green label, handwritten] // 67. 18- [round label, handwritten] // Lyctus depressiusculus White Zool. Ereb & Terror [in White's hand]". *Paralectotype* (BMNH): mounted on same card as lectotype, right specimen is a paralectotype, labels same as lectotype. *Pycnomerus sophorae* Sharp: *Lectotype* (BMNH): card-mounted, "Pycnomerus sophorae Type N. Zeal^{d}. D.S. [written at base of

card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313."
Paralectotypes (BMNH): 2, mounted together on same card and pin, "Pycnomerus sophorae Ind. typ. N. Zeal[d] DS. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313. // depressus = sophorae [handwritten in pencil] R.D. Pope det. 195_".
Paralectotypes (BMNH): 3, individually mounted on separate cards and pins, with the following labels on each: "Pycnomerus sophorae Ind. typ. N. Zeal[d] DS. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313." *Penthelispa acutangulum* Reitter: Type material not examined.

Pycnomerus ellipticus Broun, 1880

(Figs. 364–365)

Pycnomerus ellipticus Broun, 1880: 210. Broun 1882: 295. Broun 1886: 767 (reprinted from Broun 1882). Broun 1886: 896, 927. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Tairua.

Broun number: 372.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 372 [green label] // Tairua [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus ellipticus [in Broun's hand]".

Pycnomerus elongellus Broun, 1893

(Figs. 366–367)

Pycnomerus elongellus Broun, 1893b: 1444. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Mount Arthur.

Remarks: Broun based this species on a single specimen.

Broun number: 2505.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 2505. [in Broun’s hand] // Mount Arthur [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus elongellus. [in Broun’s hand]”.

Pycnomerus frontalis Broun, 1893

(Figs. 368–369)

Pycnomerus frontalis Broun, 1893b: 1443. Hutton 1904: 171. Broun 1921b: 614. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Howick.

Broun number: 2504.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 2504. [in Broun’s hand] // Howick // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus frontalis [in Broun’s hand]”.

Pycnomerus helmsi Sharp, 1886

(Figs. 370–372)

Pycnomerus helmsi Sharp, 1886: 389. Broun 1893b: 1095 (reprinted excerpt of Sharp 1886: 389). Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 1948.

Remarks: Sharp mentioned three specimens (listed as "No. 291, Helms" in the original description), and only one of these could be reliably identified as a syntype. There are four additional specimens (one specimen on one card and three specimens on another) which were labeled by Sharp but do not bear the handwritten word "type" at the base of the card. In order to stabilize this name, a lectotype is **here designated** from the material of *Pycnomerus helmsi.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Pycnomerus helmsi. Type D.S. Greymouth. NZ^{d}. [written at base of card in Sharp's hand] // Type [round label with red border] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313."

Pycnomerus hirtus Broun, 1886

(Figs. 373–374)

Pycnomerus hirtus Broun, 1886: 897. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Whangarata.

Broun number: 1600.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1600. [in Broun's hand] // Whangarata // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus hirtus - [in Broun's hand]".

Pycnomerus impressus Broun, 1893

(Figs. 375–376)

Pycnomerus impressus Broun, 1893b: 1094, 1444. Hutton 1904: 171. Broun 1909a: 394. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Hermitage, Mount Cook.

Broun number: 1946.

Remarks: Broun did not mention the number of specimens examined. In order to stabilize this name, a lectotype is **here designated** from the material of *Pycnomerus impressus.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1946. [in Broun's hand] // Hermitage Mt. Cook. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus impressus [in Broun's hand]".

Pycnomerus lateralis Broun, 1886

(Figs. 377–378)

Pycnomerus lateralis Broun, 1886: 897. Broun 1893b: 1094. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Tuakau.

Broun number: 1601.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 1601 [in Broun’s hand] // Tuakau // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus lateralis - [in Broun’s hand]”.

Pycnomerus latitans **Sharp, 1886**

(Figs. 379–381)

Pycnomerus latitans Sharp, 1886: 390. Broun 1893b: 1096 (reprinted excerpt of Sharp 1886: 390). Hutton 1904: 171. Broun 1912: 421. Hudson 1923: 370. Hetschko 1930: 62. Kuschel 1990: 33, 64. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 1950.

Remarks: Sharp did not mention the number of specimens examined. We located five specimens which we consider syntypes, including two pairs on separate cards with “1883” and “1885” handwritten on the cards, respectively. Four specimens (two pairs on separate cards) are labeled as variants and are not considered syntypes. In order to stabilize this name, a lectotype and four paralectotypes are **here designated** from the material of *Pycnomerus latitans*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Pycnomerus latitans Type D.S. Greymouth. Helms [written at base of card in Sharp’s hand] // Type [round label with red border] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.” *Paralectotypes* (BMNH): 2, mounted together on same card and pin, “Pycnomerus latitans D.S. Greymouth N. Zd Helms. [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.”

Paralectotype (BMNH): "Pycnomerus latitans D.S. Greymouth N. Zd Helms. 1883 [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted together on same card and pin, "Pycnomerus latitans D.S. Greymouth. 1885 [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313."

Pycnomerus longipes Broun, 1893

(Figs. 382–383)

Pycnomerus longipes Broun, 1893b: 1444. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Otago.

Broun number: 2506.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 2506. [in Broun's hand] // Tuakau // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus longipes [in Broun's hand]".

Pycnomerus longulus Sharp, 1886

(Figs. 384–386)

Pycnomerus longulus Sharp, 1886: 389, pl. 12, fig. 21. Broun 1893b: 1095 (reprinted excerpt of Sharp 1886: 389). Broun 1903: 618. Hutton 1904: 171. Broun 1911: 99. Broun 1912: 422. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Picton [Greymouth and Kumara also given in original description].

Broun number: 1947.

Remarks: Sharp did not mention the number of specimens examined. There were several specimens in the BMNH, and we considered six to be syntypes, not including specimens hand-labeled by Sharp as variants. In order to stabilize this name, a lectotype and five paralectotypes are **here designated** from the material of *Pycnomerus longulus*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Pycnomerus longulus Type D.S. Picton N. Zeal[d]. Helms [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313." *Paralectotypes* (BMNH): 2, mounted together on same card and pin, "Pycnomerus longulus D.S. Kumara N. Zd. Helms. 1884. [written at base of card in Sharp's hand] // I 21 [handwritten] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Pycnomerus longulus D.S. Picton N. Zd. Helms. 1884. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Pycnomerus longulus Greymouth [written at base of card in Sharp's hand] // N. Zeal. [red underline] 86 20 [handwritten] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Pycnomerus longulus D.S. Greymouth [written at base of card in Broun's hand] // Greymouth, [red line] New Zealand Helms. [handwritten] // Sharp Coll. 1905-313."

Pycnomerus marginalis Broun, 1893

(Figs. 387–388)

Pycnomerus marginalis Broun, 1893b: 1093. Hutton 1904: 171. Broun 1912: 421. Hudson 1923: 370. Hetschko 1930: 62. Maddison 2010: 426.

Type locality: Boatman's [Bay].

Broun number: 1944.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 1944 [in Broun's hand] // Boatmans Reefton [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus marginalis [in Broun's hand]".

Pycnomerus mediocris Broun, 1911

(Figs. 389–390)

Pycnomerus mediocris Broun, 1911: 99. Hudson 1923: 370. Hetschko 1930: 63. Emberson 1998: 44. Maddison 2010: 426.

Type locality: Pitt Island.

Broun number: This species was listed as number 62 in the paper, but this is not a "Broun number" in the standard sense.

Remarks: Broun did not mention the number of specimens examined. There are five specimens in the BMNH Chatham Islands Broun Collection and one in the NZAC. There is an additional specimen in the NZAC that lacks the "62." label, which we do not consider a syntype. In order to stabilize this name, a lectotype and five paralectotypes are **here designated** from the material of *Pycnomerus mediocris*.

Type material examined: *Lectotype* (BMNH): card-mounted, "62. [in Broun's hand] // Chatham Is. [red underline] Broun Coll. B.M. 1922-482. // Pitt Island. -T. Hall- [in Broun's hand] // Pycnomerus mediocris _ [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "62. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pitt Isd. -T. Hall- [in Broun's hand] // Pycnomerus mediocris. [in

Broun's hand]". *Paralectotypes* (BMNH): 3, individually mounted on separate cards and pins, with identical labels, "62. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pitt Isd. -Hall- [in Broun's hand]". *Paralectotype* (NZAC): card-mounted, "62. [in Broun's hand] // New Zealand, [typed] Chatham Is. Broun Coll. [in J.C Watt's hand] // A.E. Brookes Collection // [green label] SYNTYPE [typed] Pycnomerus mediocrus Broun, 1911 [in J.C Watt's hand]".

***Pycnomerus minor* Sharp, 1876**

(Figs. 391–393)

Pycnomerus minor Sharp, 1876: 25. Sharp 1877c: 398 (reprinted from Sharp 1876). Broun 1880: 209. Broun 1882: 295. Sharp 1886: 388. Broun 1886: 766 (reprinted from Broun 1882). Broun 1893b: 1094. Hutton 1904: 171. Broun 1909a: 395. Broun 1910a: 293. Hudson 1923: 370. Hetschko 1930: 63. Kuschel 1990: 33, 64. Maddison 2010: 426.

Penthelispa minor: Reitter 1880c: 175.

Type locality: Tairua?

Broun number: 371.

Remarks: Sharp did not mention the number of specimens examined. Although no locality was explicitly given in the description, it is likely the specimen was from Tairua, as Sharp received specimens of other species from Tairua from Broun (listed in descriptions in same paper).

Three specimens labeled as types were located in the BMNH. Two card-mounted specimens labeled as "Northland" were also in the BMNH, but these are not considered as syntypes because the card-stock differs from the presumed syntypes. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Pycnomerus minor*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Pycnomerus minor. Type N. Zeal[d]. D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Pycnomerus minor. Ind. typ. D.S. [written at base of card in Sharp's hand] // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Pycnomerus minor. Ind. typ. N. Zeal[d] D.S. [written at base of card in Broun's hand] // Sharp Coll. 1905-313."

Pycnomerus nitiventris Broun, 1903

(Figs. 394–395)

Pycnomerus nitiventris Broun, 1903: 617. Hutton 1904: 342. Hudson 1923: 370.

Pycnomerus nitidocularis: Hetschko 1930: 63. Incorrect subsequent spelling, not available.

Pycnomerus nitidiventris: Maddison 2010: 426. Incorrect subsequent spelling, not available.

Type locality: Westport.

Broun number: 2780 (as given in May 1967: 178).

Remarks: Broun mentioned two specimens from Walker's collection, which we assume are the two specimens in the BMNH Broun collection labeled from Westport. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Pycnomerus nitiventris*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2780. [in Broun's hand] // Westport. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus nitiventris [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "2780. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Westport [in Broun's hand]".

***Pycnomerus ocularius* Broun, 1914**

(Figs. 396–397)

Pycnomerus ocularius Broun, 1914a: 99. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: Mount Te Aroha.

Broun number: 3409.

Remarks: Broun mentioned that he based this species on three specimens collected in November, 1910. Three pins bearing only two specimens with labels matching this data were located in the BMNH Broun collection, though one specimen has come off the card and was not found in the drawer (this pin has all of the same labels as the lectotype, but no type label). In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Pycnomerus ocularius*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 3409 [in Broun's hand] // Te Aroha. Nov[r] 1910. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus ocularius. [in Broun's hand]". *Paralectotype* (BMNH): "3409 [in Broun's hand] // Te Aroha. Nov[r] 1910. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482."

Pycnomerus parvulus Broun, 1921

(Figs. 398–399)

Pycnomerus parvulus Broun, 1921b: 614. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: Karekare, west coast, near Auckland.

Broun number: 4182.

Remarks: Broun based this species on a single specimen collected on 23 February, 1916. One specimen, lacking a BMNH type label, bears a "Kerikeri" label (an alternate spelling of Karekare, which is located on the west coast of Auckland in the Waitakere ranges). We regard this specimen as the holotype.

Type material examined: *Holotype* (BMNH): card-mounted, "4182. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // KeriKeri. 23.2.1916 [in Broun's hand] // Pycnomerus parvulus. [in Broun's hand]".

Pycnomerus reversus Broun, 1912

(Figs. 400–401)

Pycnomerus reversus Broun, 1912: 421. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: Greymouth.

Broun number: 3226.

Remarks: Broun mentioned that he based this species on three specimens sent from Lewis. One specimen was found loose in the drawer and was subsequently re-glued by us to the appropriate elongate card. In order to stabilize this name, a lectotype and two paralectotypes are **here designated** from the material of *Pycnomerus reversus*.

Type material examined: *Lectotype* (BMNH): card-mounted, “Type [round label with red border] // 3226 [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Greymouth. -Lewis- [in Broun’s hand] // Pycnomerus reversus. [in Broun’s hand]”. *Paralectotype* (BMNH): mounted venter-up, “3226 [in Broun’s hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Greymouth. -Lewis- [in Broun’s hand] // Pycnomerus reversus. [in Broun’s hand]”. *Paralectotype* (BMNH): “Greymouth. -Lewis- [in Broun’s hand] // 3226. [in Broun’s hand]”.

Pycnomerus rufescens **Broun, 1882**

(Figs. 402–403)

Pycnomerus rufescens Broun, 1882: 295. Broun 1886: 766 (reprinted from Broun 1882). Broun 1893b: 1444. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: Parua Bay [near Whangarei Harbour].

Broun number: 1358.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 1358. [in Broun’s hand] // Parua // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus rufescens. [in Broun’s hand]”.

Pycnomerus ruficollis **Broun, 1909**

(Figs. 404–405)

Pycnomerus ruficollis Broun, 1909a: 394. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: Broken River, Canterbury.

Broun number: 2782 (as given in May 1967: 178).

Remarks: Broun did not mention the number of specimens examined, although he mentions a "good series" with some specimens that are a "little larger and darker" in color than "the type." Four specimens were located in the BMNH Broun collection. In order to stabilize this name, a lectotype and 3 paralectotypes are **here designated** from the material of *Pycnomerus ruficollis*.

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 2782. [in Broun's hand] // Broken River. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus ruficollis [in Broun's hand]". *Paralectotype* (BMNH): "2782 [in Broun's hand] // Broken River. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482." *Paralectotype* (BMNH): "2782. [in Broun's hand] // Broken River. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus ruficollis. [in Broun's hand]". *Paralectotype* (BMNH): mounted venter-up, "2782. [in Broun's hand] // Broken River. [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus ruficollis. [in Broun's hand]".

***Pycnomerus simplex* Broun, 1880**

(Figs. 406–407)

Pycnomerus simplex Broun, 1880: 209. Broun 1882: 295. Broun 1886: 767 (reprinted from Broun 1882). Hutton 1904: 171. Hudson 1923: 369. Hetschko 1930: 63. Watt 1982b: 303. Kuschel 1990: 33, 64. Maddison 2010: 426.

Type locality: Mount Manaia [Whangarei Heads].

Broun number: 370.

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 370 [green label] // Manaia // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus simplex _ [in Broun's hand]".

Pycnomerus simulans **Sharp, 1876**

(Figs. 408–410)

Pycnomerus simulans Sharp, 1876: 25. Sharp 1877c: 397 (reprinted from Sharp 1876). Broun 1880: 209. Sharp 1886: 388. Broun 1893b: 1443. Hutton 1904: 171. Hudson 1923: 369. Hetschko 1930: 63. Maddison 2010: 426.

Penthelispa simulans: Reitter 1880c: 175.

Type locality: Tairua

Broun number: 369.

Remarks: Sharp did not mention the number of specimens examined. None of the other specimens labeled by Sharp as *Pycnomerus simulans* matched the type locality (as most were labeled from localities in the South Island), therefore, we decided to recognize two specimens without specific geographic data as syntypes. In order to stabilize this name, a lectotype and paralectotype are **here designated** from the material of *Pycnomerus simulans*.

Type material examined: *Lectotype* (BMNH): mounted on same card as paralectotype, left specimen is the lectotype, "Pycnomerus simulans Type N. Zeal^{d}. D.S. [written at base of card in Sharp's hand] // Type [round label with red border] // Sharp Coll. 1905-313."

Paralectotype (BMNH): mounted on same card as lectotype, right specimen is a paralectotype, labels same as lectotype.

Pycnomerus sinuatus Broun, 1893

(Figs. 411–412)

Pycnomerus sinuatus Broun, 1893b: 1094. Hutton 1904: 171. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: Midhirst, near Mount Egmont.

Broun number: 1945.

Remarks: Broun did not mention the number of specimens examined. Two specimens were located in the BMNH Broun collection that matched this locality, and one was labeled as a variety. In order to stabilize this name, a lectotype is **here designated** from the material of *Pycnomerus sinuatus.*

Type material examined: *Lectotype* (BMNH): card-mounted, "Type [round label with red border] // 1945. [in Broun's hand] // Midhirst // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus sinuatus [in Broun's hand]".

Pycnomerus sulcatissimus (Reitter, 1880)

(Figs. 413–417)

Penthelispa sulcatissima Reitter, 1880b: 5. Reitter 1880c: 175. Hetschko 1930: 66.

Pycnomerus sulcatissimus: Maddison 2010: 426 (attributed to Reitter, although author and year were not in parentheses).

Pycnomerus sulcatissimus Sharp, 1886: 389, pl. 12, fig. 22. Broun 1893b: 1095 (reprinted excerpt of Sharp 1886: 389). Hutton 1904: 171. Broun 1912: 421. Hudson 1923: 370. Hetschko 1930: 63. **New Synonymy.**

Type locality: *Penthelispa sulcatissima* Reitter: assumed to be Greymouth, as Reitter received specimens from Helms, who collected extensively in Greymouth. *Pycnomerus sulcatissimus* Sharp: Greymouth.

Broun number: *Penthelispa sulcatissima* Reitter: none given. *Pycnomerus sulcatissimus* Sharp: 1949.

Remarks: The nomenclatural history of this species is complex. Reitter first described this species (1880b: 5) under the genus *Penthelispa.* Sharp (1886: 389) later describes the species *Pycnomerus sulcatissimus*, at the end of the description stating: “I have retained for this species the trivial name under whith it has been distributed by Herr Reitter.” It is apparent Sharp was unaware of Reitter’s earlier description, and, using material sent to him from Reitter, described the species under *Pycnomerus*. Sharp elected to not recognize the genus *Penthelispa*, as he stated (1876: 25): “Pascoe and Leconte have proposed to distinguish the *Pycnomeri* with distinctly 11-jointed antennae by the name of *Penthelispa*. Erichson, who pointed out this character [in his 1845 description of *Pycnomerini*], considered it unnecessary to make distinct generic names for the two forms; and the present species indicates the correctness of his judgement; for the antennae are just intermediate in structure between the two forms.” The genera *Pycnomerus* and *Penthelispa* were later synonymized by Sharp 1894: 474 (missed by Hetschko 1930); thus, *Pycnomerus sulcatissimus* Sharp is rendered a subjective synonym, as well as a secondary homonym, of *Pycnomerus sulcatissimus* (Reitter). Hetschko

(1930) listed both species under their respective genera. Reitter did not mention the number of specimens examined of *Penthelispa sulcatissima*. Sharp did not mention the number of specimens examined of *Pycnomerus sulcatissimus.* We considered all specimens not given as variants as syntypes. In order to stabilize these names, a lectotype and eight paralectotypes are **here designated** from the material of *Penthelispa sulcatissima* Reitter and a lectotype and four paralectotypes are **here designated** from the material of *Pycnomerus sulcatissimus* Sharp.

Type material examined: *Penthelispa sulcatissima* Reitter: *Lectotype* (MNHN): card-mounted, "TYP. REITTER // New Zeeland Helms sulcatissima m. [in Reitter's hand] // Penthelispa sulcatissima Rt TYPE Slip. 85 [green label, in S.A. Ślipiński's hand]". *Paralectotypes* (MNHN): 5, individually mounted on separate cards and pins [card with three black lines near base, middle line thicker], with identical labels, "Now. Zeeland Helms Reitter. [label bordered with thin black line]". *Paralectotype* (MNHN): card-mounted [card with three black lines near base, middle line thicker], lacking labels, but on with same card and pin type as lectotypes and other paralectotypes. *Paralectotype* (MNHN): card-mounted [card with three black lines near base, middle line thicker], "EX. COLL. REITTER". *Paralectotype* (MNHN): card-mounted [card with black border and one black line near base], "EX. COLL. REITTER". *Pycnomerus sulcatissimus* Sharp: *Lectotype* (BMNH): card-mounted, "Pycnomerus sulcatissimus Type D.S. Greymouth. Helms. [written at base of card in Sharp's hand] // Type [round label with red border] // Greymouth, [red underline] New Zealand. Helms. // Sharp Coll. 1905-313." *Paralectotype* (BMNH): "Pycnomerus sulcatissimus D.S. Greymouth. [written at base of card in Sharp's hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll.

1905-313.” *Paralectotype* (BMNH): “Pycnomerus sulcatissimus Greymouth. [written at base of card in Sharp’s hand] // I 22 [handwritten] Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.” *Paralectotype* (BMNH): “♂ Pycnomerus sulcatissimus D.S. Greymouth Helms [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.” *Paralectotype* (BMNH): “Pycnomerus sulcatissimus Greymouth, 1885 [written at base of card in Sharp’s hand] // Greymouth, New Zealand. [red underline] Helms. // Sharp Coll. 1905-313.”

***Pycnomerus suteri* Broun, 1909**

(Figs. 418–419)

Pycnomerus suteri Broun, 1909a: 393. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: The Hermitage, Mount Cook.

Broun number: 2781 (as given in May 1967: 178).

Remarks: Broun based this species on a single specimen.

Type material examined: *Holotype* (BMNH): card-mounted, “Type [round label with red border] // 2781. [in Broun’s hand] // Hermitage M[t] Cook. // New Zealand [red underline] Broun Coll. Brit. Mus. 1922-482. // Pycnomerus suteri. [in Broun’s hand]”.

***Pycnomerus tenuiculus* Broun, 1914**

(Figs. 420–421)

Pycnomerus tenuiculus Broun, 1914b: 180. Hudson 1923: 370. Hetschko 1930: 63. Maddison 2010: 426.

Type locality: McClennan's Bush, near Methven.

Broun number: 3549.

Remarks: Broun based this species on a single specimen collected on 23 April, 1912.

Type material examined: *Holotype* (BMNH): card-mounted, "Type [round label with red border] // 3549 [in Broun's hand] // New Zealand. [red underline] Broun Coll. Brit. Mus. 1922-482. // M^c^Clennan's 23.4.1912. [in Broun's hand] // Pycnomerus tenuiculus. [in Broun's hand]".

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CHAPTER 3

Phylogenetic Analysis of the Ironclad and Cylindrical Bark Beetles of the World (Coleoptera: Tenebrionoidea: Zopheridae).

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Appendix H contains the figures 1a–2d for Chapter 3 and is available as a supplementary file via LoboVault. See PDF titled "Appendix_H_Figures_Chapter3".

Abstract. We infer the first phylogenetic hypothesis for Zopheridae Solier, 1834 (Coleoptera: Tenebrionoidea). Portions of three genes (28S rDNA, cytochrome c oxidase I and histone III) were analyzed. One hundred eighty three zopherid species were included, representing 2/2 subfamilies, 15/15 tribes, and more than half of the currently recognized genera. Twelve outgroup taxa from eight other families of Tenebrionoidea were included. Parsimony and partitioned Bayesian analyses were performed on the combined data set. In both phylogenetic analyses, Zopheridae was not recovered as monophyletic. The subfamily Zopherinae was not recovered as monophyletic in both analyses, and the subfamily Corticariinae was recovered as monophyletic only in the Bayesian analysis.

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Introduction:

Zopheridae are cosmopolitan, small, litter-dwelling or subcortical beetles that exhibit tremendous morphological diversity. Members of the Zopheridae are thought to include both economically beneficial *and* harmful insects, as several genera (*Colydium*, *Aulonium*, *Nematidium*) are predaceous as both larvae and adults of destructive wood-boring insects, while others have been documented to transmit crop-destroying fungi (Ivie 2002a, b, c; Ślipiński and Lawrence 1997). Thus, studies of the taxonomy and natural history of the group is of economic relevance and has exhibited strong funding potential (*e.g.* USDA, see Lord *et al.* 2011). As proposed by Ślipiński and Lawrence (1999), Zopheridae (*sensu novo*) contains three previously separate families: the ironclad beetles (Zopheridae=Zopherinae *s.n.*), the monommatid beetles (Monommatidae=Zopherinae *s.n.*), and the cylindrical bark beetles (Colydiidae=Colydiinae *s.n.*) (for classification history of the groups, see Ślipiński and Ivie, 1990: 2–4). As currently constituted, Zopheridae contains nearly 180 genera, 15 tribes, and over 1,700 species, of which a disproportionate species diversity (nearly half) is restricted to the Australo-Pacific Region (Ślipiński and Lawrence 2010). Other large radiations and high levels of endemism (notably on islands or other isolated southern hemisphere landmasses) occur in Madagascar (13/35 endemic genera containing 90/100 endemic species), the Macronesian Islands (63 endemic species), and the Austral Region

(~28 genera, hundreds of endemic species) (Dajoz 1980; Ślipiński and Lawrence 1997; Amorim *et al.* 2012). The majority of the Zopheridae inhabiting these localities have profound morphological innovations such as loss of some major mouthparts, eye reduction and wing loss, traits that presumably decrease vagility resulting in low likelihood of long-distance dispersal. Due to high levels of diversity and endemism and niche specialization across a broad range of habitats, Zopheridae are ideal for investigating biogeographic patterns of paleoendemism, neoendemism, speciation, and ecological diversification throughout the Austral Region, as well as globally. However, before any interdisciplinary studies can be conducted, a phylogeny of the group is critically needed.

Despite their relative diversity and decent amounts of taxonomic attention by previous workers, the monophyly of the family is still strongly questioned. Seemingly few characters unite the groups included in Zopheridae, often making identification of its members quite difficult. In reference to the identification of North American Coleoptera, Ivie (2002a: 445) states: "However if it has 4-4-4 tarsi and doesn't fit somewhere else, try this family." Only two comprehensive catalogues to these groups exist: Hetschko (1930) and Ivie and Ślipiński (1990). Hetschko's catalogue validated the assertion of the group as a "wastebasket taxon" (Lawrence 1980: 305), as his concept of the family was later shown to contain members from ~85 genera across 14 other families of Coleoptera *not* currently recognized as Zopheridae (Ivie and Ślipiński 1990: 16-18). Ivie and Ślipiński's catalogue rectified many issues on the generic level, but higher-level groups remained problematic.

The first major work to progress the taxonomy of this family was Ślipiński and Lawrence (1997) which addressed the subfamily Colydiinae of the Australo-Pacific region and provided the first-ever key, diagnoses, and definitions to the genera of this surprisingly diverse subset. They defined each of the nine tribes, revealing a reliance on geographic distribution and characters that demonstrate high degrees of variability as the defining features of these groups (*e.g.* antennal segmentation, procoxal closure, tarsomere shape). Ślipiński and Lawrence stated (1997: 344) "The internal classification of the Colydiinae presents serious problems and suffers from inadequate analysis…most of these taxa are based on a few relatively superficial characters, and a cladistics analysis of the entire subfamily will probably lead to further reduction." In reference to the mega-diverse tribe Synchitini, they stated "It is probably that of the above tribes at least Acropini and Colydiini will also be included here." As is the case with many of the major works on the group, the generic concepts were well-addressed, but their higher-level relationships remained murky.

A later work by Ślipiński and Lawrence (1999) provided the most comprehensive analysis of the family and its constituents via a cladistic analysis based on 59 adult and larval morphological characters across 37 tenebrionoid taxa. Their analysis consisted of 5/9 colydiine tribes, 6/6 zopherine tribes, and representatives of 5 tenebrionoid families as outgroups. Results of their analyses led to the combination of the three previously-recognized families under a larger Zopheridae (Zopheridae, Monommatidae, Colydiidae). Their analyses provided a few morphological characters as potential synapomorphies for Zopheridae *sensu novo*, notably character #12, #30, and #39. Unfortunately, these characters were either mis-scored (#39, most likely due to poor taxon sampling) or are homoplasious when additional tenebrionoid groups are included (#12, #30). Their analyses recovered the family Ulodidae as sister to Zopheridae *sensu novo*, but the sampling lacked several other notable tenebrionoid families and only contained eight exemplars from the diverse colydiine subfamily. As a consequence, the monophyly of this heterogeneous family is still in question and higher-level relationships within the group remain tentative, likely due to the limited choice of in-group and out-group taxa as well as possible incorrect morphological character scoring (Lawrence 1980; Ivie 2002a, b, c; Ślipiński and Lawrence 1997, Ślipiński and Lawrence 2010). The monophyly of Zopheridae *sensu novo* has not been recovered in some molecular analyses (i.e. Hunt *et al*. 2007, Kanda *in prep*.) but has been recovered in one subsequent morphological analysis (with addition of Trichtenotomidae; Lawrence *et al.* 2011), although both these studies were severely limited by weak taxonomic sampling within the group. Ivie (2002) reviewed the zopherids for North America, but elected to retain separation under the previously-recognized family-group names.

Lower-level phylogenies within Zopheridae are practically non-existent, with the only exception being a cladistic analysis of Zopherini based on 32 adult morphological characters scored for nearly all species of Zopherini (Foley and Ivie 2008). Although the taxonomic sampling within the tribe was strong, Zopherini was assumed monophyletic, thus rendering many of the internal relationships insignificant if the tribe is actually para/polyphyletic. It is apparent that, although considerable attention had been paid to this somewhat small beetle group, the status of the higher-level classification of the family and member tribes are still in flux. In order to provide nomenclatural and taxonomic stability, the classification of Zopheridae (and higher Tenebrionoidea) need to be re-addressed. After this task is satisfactorily achieved, larger questions about the biogeography, natural history, and evolution of the group can be rigorously examined.

Objective

The objective of this study is to construct the first comprehensive molecular phylogeny of worldwide Zopheridae based on a representation of 15/15 tribes and over half of world genera, with particular emphasis on testing the monophyly of Zopheridae within the superfamily. A greater knowledge of the taxonomy and phylogeny of a difficult and diverse taxon will provide a suitable foundation for future studies investigating biogeographic hypotheses as well as the evolution and impact of several key morphological innovations throughout the family. In addition, the construction of this phylogeny has potential to elucidate higher-level coleopteran relationships of the superfamily Tenebrionoidea.

Materials and Methods

Taxon Sampling

Ingroup: In an effort to achieve comprehensive taxonomic coverage of Zopheridae on a worldwide scale, we accumulated large numbers of specimens from numerous localities around the world, including dense samples from critically important localities in the Palaearctic (USA, Denmark, Canaries, Japan), Neotropics (Panama, Costa Rica, French Guyana, Peru, Venezuela, Bolivia, Chile), Madagascar, continental Africa (Cameroon, South Africa, Zambia), Southeast Asia (PNG, Sarawak) and the Southwest Pacific (Fiji, New Caledonia, New Zealand). These analyses included 184 ingroup taxa representing both subfamilies, 15/15 tribes and ~90 genera, representing ~57% generic coverage (Table 1). Within the subfamily Zopherinae, the following generic sampling was achieved: 2/3 Latometini, 1/16 Monommatini, 1/1 Phellopsini, 3/4 Pycnomerini, 1/2 Usechini, and 4/9 Zopherini, representing ~34% generic coverage within the subfamily. Within the subfamily Colydiini, the following generic sampling was achieved: 2/4 Acropini, 2/2 Adimerini, 4/4 Colydiini, 4/6 Gempylodini, 1/1 Nematidiini, 1/3 Orthocerini, 1/1 Rhagoderini, 1/1 Rhopalocerini, and 62/~120 Synchitini (+ ~6 n.gen. or gen. undet.), representing nearly 55% generic coverage within the subfamily.

Outgroup: Also included in the analyses were 12 outgroup taxa representing eight of the other 28 tenebrionoid families: Archaeocrypticidae, Oedemeridae, Melandryidae, Mycetophagidae, Mycteridae, Tenebrionidae, Tetratomidae, and Ulodidae (Table 1). This selection was based on examining several previous works to determine the more closely related tenebrionoid families (e.g. Hunt et al. 2007; Lawrence et al. 2011). K. Kanda (Ph.D. candidate, Oregon State University) is currently conducting analyses of 4-6 loci across a comprehensive sampling of all beetle families within the superfamily Tenebrionoidea (in prep., 114 taxa across 28/28 Tenebrionoid families + outgroups from Cucujoidea). K. Kanda corroborated our outgroup selection based on the relatedness of those taxa to Zopheridae in his preliminary analyses and generously supplied DNA aliquots and partial sequence data for 11/12 outgroups. The topologies were rooted to KK180 Mycterus sp. (Mycteridae). We feel this is a strong taxonomic sampling and should serve to adequately address the monophyly of the family, subfamilies and tribes of Zopheridae worldwide.

Several taxa were not identified below the generic level due to the poor state of taxonomy in those groups and a great number of expected undescribed species. Primary voucher specimens and DNA extraction vouchers were deposited in the Museum of Southwestern Biology Division of Arthropods (MSBA) at the University of New Mexico (majority) and the Oregon State University Tissue collection (OSUIC) (some outgroups). Sequences were submitted to GenBank (accession numbers ####-####).

Data Sampling

DNA was extracted using Qiagen (Valencia, California, USA) DNEasy kit for animal tissues. The abdomen was removed prior to extraction, and the remainder of the specimen was placed in buffer. After incubation, each specimen was removed from the buffer, rinsed, and retained as a primary voucher specimen. Three genes were amplified and sequenced: 28S ribosomal DNA (28S), cytochrome c oxidase I (COI), and histone III (H3).

DNA fragments were amplified using PCR with TaKaRa Ex Taq (Takara Bio Inc., Otsu, Shiga, Japan) on an Eppendorf Mastercycler ep gradient S Thermal Cycler (Eppendorf, Hamburg, Germany) and visualized by gel electrophoresis. PCR purification was done using ExoSAP-IT (USB-Affymetrix, Cleveland, OH, USA) and cyclesequenced using ABI Prism Big Dye v3.1 (Fairfax, VA, USA) with the same primers used for amplification. Sequencing reaction products were purified using Sephadex G-50 Fine (GE Healthcare, Uppsala, Sweden) and sequenced with an ABI 3130xl Genetic Analyzer (Molecular Biology Facility, University of New Mexico). All gene regions were sequenced in both directions. PCR product yield, specificity and contamination were monitored using gel electrophoresis. Data editing and contig assembly was performed in Geneious® version 6.1.6 (created by Biomatters Ltd., available from http://www.geneious.com). All sequences were BLASTed against published GenBank sequences to detect possible contamination.

Gene Selection

We identified three mitochondrial and nuclear genes we think are appropriate for providing resolving signal at multiple levels within Zopheridae.

28S rRNA (28S): (~2200bp). This marker has become nearly universal in higher phylogenetics in insects. Despite challenges with alignment, it has considerable utility because it exhibits variation suitable for providing signal at multiple levels within phylogenetic reconstruction. We sequenced a partial ~1,000bp region that has previously proven successful in New Zealand Zopheridae (Buckley and Leschen, 2013).

Cytochrome c oxidase I (COI): (~1500bp). This gene has been used for phylogenetic analysis of numerous coleopteran groups. Primers for this gene have already been optimized to work across the Zopheridae (Marske *et al*. 2011; Buckley & Leschen, 2013) (for utility, see: Sandoval *et al*., 1998; Koulianos, 1999; Reyes *et al*., 1999; Ribera *et al*., 2001a; Ribera *et al*., 2001b; Klass *et al*., 2003; Miller *et al*., 2007; Miller and Edgerly, 2008). We sequenced a partial ~770bp region that has previously proven successful in New Zealand Zopheridae (Buckley and Leschen, 2013).

Histone III (H3): (328bp). This nuclear protein coding gene often exhibits considerable third position variation in Coleoptera (Bergsten and Miller, 2007; Miller *et* *al.*, 2007). This level of variation is often not suitable for higher level phylogenetics, but it makes it highly suitable for species- and population-level analysis.

Analytical Methods

Alignment: Alignment of COI and H3 was performed in Geneious® based on conservation of the codon reading frame. Alignment of 28S was done using Muscle (Edgar, 2004) under the default settings (max 16 iterations) as implemented in Geneious®. Gaps were treated as missing data. The individual loci datasets were exported from Geneious® as NEXUS files. An Incongruence Length Difference test (ILD, Farris *et al.* 1994) was performed in WinClada (Nixon, 2002) and revealed no significant incongruence between the datasets (p=0.1667). Therefore, the datasets were concatenated in Geneious® and exported as a NEXUS file. The combined dataset produced an alignment with 2,068 bases. Completeness of data for each taxon is provided in Table 1. Overall, sequence data from three loci for all taxa was as follows: 28S: 86% of taxa; COI 79% of taxa, H3 68% of taxa.

Parsimony: A combined parsimony analysis was performed in TNT v.1.1 (Goloboff *et al.* 2007) as implemented by WinClada with commands set to the following: Ratchet: 10,000 iterations per rep, perturbation 10% up- and down-weight; Drift: 50 iterations per rep; Tree Fusion: 5 round of fusion; 1000 total trees held, and TBR-Max. Bootstrap values were calculated in NONA as implemented by WinClada using 1,000 replications, 10 search reps (mults), one starting tree per rep, “don’t do max*(TBR)” and saving the consensus of each replication.

Bayesian: Optimal partitioning strategies and models of evolution for the dataset were calculated in PartitionFinder v.1.1.1 (Lanfear *et al.* 2012) under the following commands: branchlengths = linked; models of evolution = beast; modelselection = BIC; scheme = greedy; datablocks = charset 28S=1-969; charset COI_pos1=970-1740\3; charset COI_pos2=971-1740\3; charset COI_pos3=972-1740\3; charset H3_pos1=1742-2068\3; charset H3_pos2=1743-2068\3; charset H3_pos3=1741-2068\3. The optimal partitioning strategy and models of evolution recovered were as follows: by gene, by separate codon position (7 partitions); partition 1 = 28S under SYM+I+G; partition 2 = COI pos. 1 under GTR+I+G; partition 3 = COI pos. 2 under GTR+I+G; partition 4 = COI pos. 3 under GTR+I+G; partition 5 = H3 pos. 3 under SYM+I+G; partition 6 = H3 pos. 1 under GTR+I+G; partition 7 = H3 pos. 2 under K80+I. Bayesian analyses were conducted using BEAST v.1.7.5 (Drummond *et al.* 2012). A BEAST xml file NEXUS file of the combined data was generated in BEAUti v.1.7.5 (Drummond *et al.* 2012) under a lognormal relaxed clock with the tree prior set to Yule Process. Four separate Bayesian runs were run through use of the CIPRES Science Gateway ver. 3.1 (Miller *et al.*, 2010), each run for 10 x 10^7 generations, sampling every 1000 generations. The log files were then analyzed in Tracer v1.4.1 (Rambaut and Drummond, 2007) to determine an acceptable burn-in. To conserve estimation, the log files and tree files for each run, respectively, were combined with a removed burn-in per run of 8% generations and thinned under a lower sampling frequency (every 20,000 generations) in LogCombiner v.1.7.5 (Drummond *et al.* 2012). The combined log file was then analyzed in Tracer for acceptable stationarity and ESS values. The sampled trees in the combined tree file were summarized in TreeAnnotator v.1.7.5 (Drummond *et al.* 2012) onto a single “target” tree.

This tree was analyzed, rooted, and set to display posterior probabilities in FigTree v.1.3.1 (Rambaut 2006-2009).

Imaging and Tree Figures

Color habitus images were captured using a Visionary Digital^{TM} Passport and BK Plus imaging systems (www.visionarydigital.com), equipped with a Canon 40D or 7D DSLR camera. Image stacks were montaged in Zerene Stacker v.1.04 (Zerene Systems LLC, Richland, WA, USA). Images were edited in Adobe Photoshop CS5 v.12.0.4. Trees were digitally rendered in Adobe Illustrator CS5, v.15.0.2 (Adobe Systems, Inc., San Jose, CA, USA).

Results

The parsimony ratchet analyses resulted in 130 most parsimonious trees (L=21,580, Ci=9, Ri=37). The consensus tree (L=21,980, Ci=9, Ri=36) is displayed in Fig. 1. Low consistency and retention index values indicate considerable homoplasy in the data.

The results of the parsimony and Bayesian analyses differed greatly in higher-level topology, although the results at the tribal and genus-group levels were congruent in many important aspects (Figs. 1, 2b-d). Zopheridae *sensu lato* was recovered as polyphyletic with respect to several outgroup taxa in both the parsimony and Bayesian topologies. Within Zopheridae, the subfamily Colydiinae was recovered as monophyletic in the Bayesian topology, but paraphyletic with respect to several zopherine taxa and tenebrionoid outgroups in the parsimony topology. The subfamily Zopherinae was recovered as polyphyletic with respect to several colydiine taxa and tenebrionoid outgroups in the parsimony topology and paraphyletic with respect only to Tetratomidae in the Bayesian topology. Both topologies were very weakly supported at internal nodes and more better supported at the terminal nodes.

Bayesian Topology

Family-group: Within the outgroup taxa, the family Tenebrionidae was recovered as polyphyletic. Two tenebrionids within the tribe Cnemeplatiini were included in this analysis due to previous doubts about family-group placement (K. Kanda, pers. comm.). These two taxa were recovered within a larger clade containing exemplars from Mycetophagidae and Archaeocrypticidae with strong support (pp = 0.87), suggesting a re-evaluation of the larger Tenebrionoidea (and specifically Tenebrionidae) is needed. Zopheridae was not recovered as monophyletic, rendered polyphyletic by several tenebrionoid outgroup families (Oedemeridae, Tenebrionidae, Tetratomidae). The support for this grouping, however, was very weak (posterior probability, pp = 0.2, denoted by a red circle in Fig. 2a).

Subfamily-groups (Fig. 2a): The subfamily Zopherinae was not recovered as monophyletic, rendered paraphyletic with respect to Tetratomidae. The inclusion of Tetratomidae within Zopherinae was weakly supported (0.3 pp for entire "Zopherinae" clade), but its inclusion was marginally better supported within two internal zopherine clades (pp = 0.62 and 0.47, respectively, yellow highlighted region in Fig. 2a, b). The subfamily Colydiinae was recovered as monophyletic, although with weak support (pp = 0.25).

Tribal and Genus-groups: Within the subfamily Zopherinae, the tribes Monommatini, Latometini, Phellopsini, Usechini, and Pycnomerini were recovered as monophyletic with pp = 1 (Fig. 2b). The tribe Zopherini was rendered polyphyletic with respect to the remaining zopherine tribes. All included zopherine genera were recovered as monophyletic, and several interesting relationships were found. Zopherinae is composed of two major clades (although with weak support: pp = 0.4). In clade 1, the tribe Monommatini was shown to be sister to the *Verodes*+*Phloeodes* portion of Zopherini with marginally high support (pp = 0.76). This clade is sister to the Tetratomidae+??Zopheridae n.gen clade, although only with moderate support (pp = 0.62). Phellopsini was recovered sister to Usechini with high support (pp = 0.98), and together formed the sister clade to Latometini (pp = 0.88). In clade 2 (pp = 0.34), Pycnomerini was recovered as sister to the rest of Zopherini. The Gondwanan genus *Pycnomerodes* was recovered as sister to the Australian *Docalis*, and together they were sister to the cosmopolitan *Pycnomerus*.

Within the subfamily Colydiinae, the following tribes were recovered as monophyletic: Adimerini (pp = 0.89), Rhagoderini (pp = 1), Acropini (pp = 0.93), Nematidiini (pp = 0.98), Orthocerini and Rhopalocerini. The following tribes were recovered as polyphyletic: Gempylodini, Colydiinae, and Synchitini. The only included member of the tribe Orthocerini (*Orthocerus clavicornis*) was recovered as sister to the synchitine genus *Paryphus* with strong support (pp = 1). The gempylodine *Pseudendestes australis* was recovered outside the remaining genera within the tribe, rendering Gempylodini polyphyletic. Nematidiini was recovered as sister to a clade containing the single representative of the monogeneric tribe Rhopalocerini (*Rhopalocerus rondanii*) and several genera within the tribe Synchitini. Interestingly, these synchitine genera form a separate group on the basis of morphological characters as well, all members having a reduced first tarsomere (apparently 3-3-3 tarsal formula), and a mid-lateral secretory pore present on the pronotum ("3-3-3" clade, Fig. 2d). A number of the colydiine genera with morphological apomorphies clustered together. Adimerini (whose members bear a distinctly lobed first tarsomere) was recovered as sister to the stalk-eyed Acropini (*Plagiope*+*Acropis*) + the Chilean member of new, presumably Gondwanan genus ("*Ślipińskius"*), and this clade was recovered as sister to the enigmatic North American Rhagoderini. The nominal tribe of the subfamily, Colydiini, was recovered as polyphyletic. Two of the four genera within Colydiini (*Anarmostes* and *Colydium*) grouped together with decent support (pp = 0.72), but the remaining two genera, although grouping together with weak support (*Pseudaulonium* and *Aulonium*, pp = 0.11) were nested within a clade of Synchitini.

Taxa of interest: There were a few notable relationships among taxa of interest. Among the first group of Synchitini, a clade of presumably Gondwanan groups was nested within a greater sampling of synchitine genera (upper green highlighted portion – Fig. 2d). The genera *Notocoxelus*, *Isotarphius*, and *"Coxelus"* from Chile all share morphological similarities. In studies of the New Zealand members, it has been suggested that the Australian *Namunaria*, New Zealand *Notocoxelus* and Chilean *Coxelus* all constitute a single Gondwanan genus (NPL, T. Buckley, and R.A.B. Leschen, *in prep*). Interestingly, the monotypic genus *Isotarphius* was recovered nested within this clade, and the larger clade does not appear to be closely related to many of the remaining New Zealand and Australian zopherids (lower green highlighted portion, Fig. 2d). This large clade of strictly Australian and New Zealand zopherids is moderately well-supported (pp = 0.67), but it is apparent from the relationships recovered that the generic relationships need to be re-evaluated (*e.g. Pristoderus, Ablabus, Bitoma* “NEW”). A denser sampling of taxa from the Australo-Pacific was intentional 1) due to the zopherid diversity in the region (see Introduction) and 2) due to on-going work by NPL, T. Buckley and R.A.B. Leschen. The results from this phylogeny support a strong radiation of zopherids throughout the region.

Parsimony Topology

Due to the extremely poor resolution of the parsimony tree, only a brief summary of the findings will be given. Clades or relationships congruent with the Bayesian topology will be mentioned below. See discussion for remarks on parsimony performance.

<u>Family- / Subfamily-groups (Fig. 1):</u> Within the outgroup taxa, the family Tenebrionidae was recovered as polyphyletic. As in the Bayesian topology, members of the tribe Cnemeplatiini grouped together, but separately from the remaining tenebrionids. Unlike the Bayesian topology in which nearly all outgroups were at or very near the base of the rooted tree, the parsimony analyses resulted in a tenebrionoid (col172: *Tanylypa morio*) and an oedemerid (KK175: *Copidita quadrimaculata*) nested within clades of zopherines, as well as two members of Tenebrionidae forming a clade sister to the greater Colydiinae. Unlike the Bayesian topology, a clade of “basal” colydiines was recovered sister to a clade of tenebrionoid outgroups. This arrangement was weakly supported and may be an

artifact of missing data, as morphology would indicate the subfamily Zopherinae should hold this position (as in Bayesian topology).

Tribal and Genus-groups: Within the subfamily Zopherinae, the tribes Monommatini, Latometini, Phellopsini, Usechini, and Pycnomerini were recovered as monophyletic (boostraps: Latometini = 88; Usechini = 100) (Fig. 1). The tribe Zopherini was rendered paraphyletic with respect to Oedemeridae and the presumably new genus (Ngen160 – groups with Tetratomidae in Bayesian topology). As in the Bayesian results, Phellopsini was recovered as the sister to Usechini with relatively high support (bootstrap = 63), although this group was not recovered as sister to Latometini. Similar again to the Bayesian results, a *Phloeodes+Verodes* Zopherini clade was separate from the *Zopherosis+Zopherus* Zopherini clade. Pycnomerini was recovered as sister to the rest of Zopherini. Interestingly, the zopherine tribe Pycnomerini was recovered as monophyletic, but nested well within the Colydiinae. Within the subfamily Colydiinae, the following tribes were recovered as monophyletic: Adimerini, Rhagoderini (bootstrap = 55), Acropini (bootstrap = 81), Nematidiini, Orthocerini and Rhopalocerini. The following tribes were recovered as polyphyletic: Gempylodini, Colydiinae, and Synchitini. As in the Bayesian topology, the tribe Orthocerini (*Orthocerus clavicornis*) was recovered sister to the synchitine genus *Paryphus*, although with weak support. The gempylodine *Endestes* sp. Bolivia grouped with Rhopalocerini, and *Pseudendestes australis* was once again recovered outside the remaining genera within the tribe, rendering Gempylodini polyphyletic. Nematidiini was recovered within a basal clade of Colydiinae, sister to several members of the tribe Synchitini. As in the Bayesian analyses, a number of the colydiine genera with morphological apomorphies clustered together. Adimerini was again recovered as sister to the stalk-eyed Acropini (*Plagiope*+*Acropis*), although the placement of this clade differed than in the Bayesian topology. The nominal tribe of the subfamily, Colydiini, was recovered as polyphyletic. Two of the four genera within Colydiini (*Anarmostes* and *Colydium*) grouped together, but the remaining two genera were recovered elsewhere throughout the subfamily.

Taxa of interest: As with the Bayesian topology, several relationships among taxa of interest were elucidated. Among the larger group of Synchitini, the clade of presumably Gondwanan groups was again nested within a greater sampling of synchitine genera (although with weak support), but also includes of a species of *Lascotonus* from Malaysia. Again, this clade does not appear to be closely related to many of the remaining New Zealand and Australian zopherids. A large clade of strictly Australian and New Zealand zopherids is present, and it is again apparent from the relationships recovered that the generic relationships need to be re-evaluated. Interestingly, this clade was recovered sister to the Rhopalocerinin, although with weak support. A clade of the "3-3-3-like tarsi" was recovered, although not sister to Rhopalocerini as in the Bayesian topology. The consensus parsimony cladogram resulted in an unresolved polytomy of the "*Bitoma*" groups, the enigmatic gempylodine *Pseudendestes australis*, and several other synchitine and colydiine taxa. This polytomy was recovered as sister to the *Anarmostes*+*Colydium* clade.

Discussion

Taxonomic Implications – Family-group Relationships

Both topologies suggest a non-monophyletic Zopheridae. In order for the classification of Tenebrionoidea to be consistent with these findings, Zopheridae *sensu lato* will need to be divided into family groupings more similar to previously-held concepts (*e.g.* as reviewed in Ślipiński and Lawrence, 1999). This would include a resurrection of the family-groups Colydiidae and Zopheridae, although the previously-recognized family-group Monommatidae would continue to be retained as a tribe within Zopheridae. In order to address the polyphyly of the subfamily Zopherinae, A) the tenebrionoid family Tetratomidae would need to be subsumed within a larger Zopheridae *sensu novo* (in reference to the Bayesian topology), or B) further family-group level divisions would need to be made, elevating various clades within the subfamily to family-group status (*e.g.* Tetratomidae + Monommatidae + [*Verodes*+*Phloeodes*]). If the Bayesian topology is accepted, the monophyletic subfamily Colydiinae would be returned to family-group status as the former Colydiidae. If the Parsimony topology is accepted, the definitions of families and subfamilies across the Tenebrionoidea will need to be re-evaluated to reflect monophyletic clades.

Taxonomic Implications – Tribal-group Relationships

<u>Zopherinae:</u> The zopherine-tribal relationships recovered in this analysis are incongruent with those put forth by Ślipiński and Lawrence (1999) based on morphology alone; however, many of the larger findings of that study are supported (1999: 8). Similar results included recovering the expanded Pycnomerini within Zopherini, more or less two major clades of Zopheridae including a clade of the true zopherines, a monophyletic Usechini,

and a monophyletic Latometini within Zopheridae. In our analyses, however, the tribe Phellopsini was not recovered as the sister group to Monommatini. Within the tribe Zopherini, our results are also incongruent with those recovered in a morphological analysis presented by Foley and Ivie (2008), but this is likely due to the lack of other zopherine tribes and assumed monophyly of Zopherini in that analysis. In both Foley and Ivie (2008) and this work, however, *Verodes* was recovered sister to *Phloeodes* and *Zopherosis* as sister to *Zopherus*. In order to remedy these discrepancies, the tribal classification will need to be re-addressed through the inclusion of additional molecular markers, taxa, and morphological characters.

Colydiinae: Little work has been done to address the tribal relationships of the Colydiinae in any rigorous fashion, and the analyses conducted by Ślipiński and Ivie (1999) simply did not include a large enough taxon sampling of this diverse subfamily to draw any appreciable comparisons. In both our Bayesian and Parsimony analyses, the tribes Adimerini, Rhagoderini, Acropini, Nematidiini, Orthocerini and Rhopalocerini were recovered as monophyletic. The tribes Colydiini and Synchitini were recovered as polyphyletic, although this is not unexpected. Morphological investigations of members of these tribes have yet to result in any concrete characters for delimiting the majority of the currently-recognized groups and appear to be based on variable and/or apomorphic characters (*e.g.* Orthocerini, Rhopalocerini). If results from current analyses stand, the entire tribal classification system will need to be eliminated in favor of a "supertribe" as suggested by previous zopherid workers (M. Ivie, S.A. Ślipiński, R.A.B. Leschen, *pers. comm.*). It is possible the tribe Nematidiini and an expanded Adimerini

(Acropini+Adimerini) could be recognized, although this is dependent on placement within the greater Colydiinae.

Taxonomic Implications – Genus-group Relationships

It is apparent from several clades recovered throughout both analyses that the genus-group definitions are also in critical need of revision. Several genera (*e.g. Synchita*, *Ablabus, Pristoderus, Bitoma, Namunaria*) were recovered as para- or polyphyletic, although this comes as little surprise due to the fragmentary nature of alpha-level work within the group worldwide. A continued effort will be made to address the fauna of the Australo-Pacific region, as this zopherid subset shows promise for addressing previously-held hypotheses of southern hemisphere biogeography. Both analyses recovered a large clade of strictly Australian and New Zealand members, and the relationships between and within these genera will continue to be investigated via additional taxonomic sampling.

Topology Incongruence

As previously mentioned, there was significant incongruence in the Bayesian and Parsimony topologies. Missing data is a possible explanation for the shortcomings of the parsimony analyses, and gaps in data and sampling need to be filled prior to the acceptance of a preferred topology. It is also possible long-branch attraction is plaguing the parsimony analyses. Another explanation is that considerable homoplasy exists within the group, thus leading to poorly-resolved and poorly-supported topologies under a parsimony framework.

Future Directions - Increased Taxonomic and Molecular Sampling

In addition to the loci used in this study, we will continue to explore possible new markers being used in Coleoptera including other mitochondrial and nuclear genes, relying on the foundational work of Wild and Maddison (2008) and ongoing work on beetles and other groups of insects by Miller (*e.g.* Lord *et al.*, 2010; Miller *et al.* 2007, 2008) for primers and amplification and sequencing protocols. We hope some of these markers will aid in resolving the deeper divergences and provide more stability along the backbone of the tree. In addition, an effort will be made to obtain more exemplars of the smaller tribes throughout the family, allowing for a more accurate test of monophyly and sister-group relationships. Partitioned Bremer analyses on the data will be conducted to provide more insight on how the data is performing under parsimony, and problematic taxa will continue to be diagnosed. In addition, fossil calibrations will be implemented in Bayesian analyses in order to estimate lineage divergence times.

Conclusions

Although these analyses are a positive step in the direction towards a revised classification of Zopheridae, few concrete, actionable results were obtained. This phylogeny succeeded in confirming the fears of previous zopherid workers, demonstrating a messy and quite unresolved clustering of tenebrionoids. Encouragingly, the loci and taxa sampled for these analyses provided decent resolution at the more terminal nodes. While this begins to aid in the resolution of genus-group relationships and point out more glaring problems in our current tribal classifications, the poor resolution of the internal nodes needs to be remedied. Once accomplished, taxonomic alterations may be made to provide a more concrete definition of the included groups. As it stands, Zopheridae and the groups therein are still heavily under question, and this is complicated further by the highly convergent morphology within the Tenebrionoidea. It is our hope that additional molecular markers and taxon sampling can continue to aid in the resolution of this enigmatic group of LBBs (little brown beetles).

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Table 1. Taxon Sampling and Gene Coverage for the Molecular Phylogeny of Zopheridae.

Code	Family	Subfamily	Tribe	Genus	Species	28S	COI	H3
KK211	Archaeocrypticidae			*Enneboeus*	sp.	y	y	-
KK212	Melandryidae	Melandryinae	Serropalpini	*Dircaea*	*liturata*	y	y	y
KK182	Mycetophagidae			*Litargus*	*balteatus*	y	y	y
KK180	Mycteridae			*Mycterus*	sp.	y	y	y
KK175	Oedemeridae	Oedemerinae	Asclerini	*Copidita*	*quadrimaculata*	y	y	-
KK167	Tenebrionidae	Pimeliinae	Cnemeplatiini	*Actizeta*	sp.	y	-	y
KK208	Tenebrionidae	Pimeliinae	Cnemeplatiini	*Lepidocnemeplatia*	sp.	y	y	-
KK18	Tenebrionidae	Pimeliinae	Vacrotini	*Eupsophulus*	sp.	y	y	y
KK16	Tenebrionidae			*Peschalius*	sp.	y	y	-
col172	Tenebrionidae			*Tanylypa*	*morio*	y	y	y
KK173	Tetratomidae	Piseninae		*Triphyllia*	*elongata*	y	-	y
Mery31	Ulodidae			*Meryx*	*rugosa*	y	y	-
Acro171	Zopheridae	Colydiinae	Acropini	*Acropis*	n.sp. #14	y	y	y
Acro170	Zopheridae	Colydiinae	Acropini	*Acropis*	n.sp. #3	y	y	y
Plag35	Zopheridae	Colydiinae	Acropini	*Plagiope*	sp.	y	-	-
Moed174	Zopheridae	Colydiinae	Adimerini	*Monoedus*	sp. 2	y	-	y
Sten167	Zopheridae	Colydiinae	Adimerini	*Stenomonoedus*	sp.	y	y	y
Anar26	Zopheridae	Colydiinae	Colydiini	*Anarmostes*	sp.	-	y	y
Anar143	Zopheridae	Colydiinae	Colydiini	*Anarmostes*	sp.	y	y	y
Aulo37	Zopheridae	Colydiinae	Colydiini	*Aulonium*	*bidentatum*	y	y	y
Aulo144	Zopheridae	Colydiinae	Colydiini	*Aulonium*	sp.	y	y	y
Coly142	Zopheridae	Colydiinae	Colydiini	*Colydium*	prob. *elongatum*	y	y	y
Coly1	Zopheridae	Colydiinae	Colydiini	*Colydium*	*robustum*	y	y	-
Pseu24	Zopheridae	Colydiinae	Colydiini	*Pseudaulonium*	sp.	y	y	y
Ende4	Zopheridae	Colydiinae	Gempylodini	*Endestes*	sp.	y	y	y
Ende123	Zopheridae	Colydiinae	Gempylodini	*Endestes*	sp.	y	y	y
Gemp122	Zopheridae	Colydiinae	Gempylodini	*Gempylodes*	sp.	y	y	-
Mece25	Zopheridae	Colydiinae	Gempylodini	*Mecedanum*	*antennatum*	y	y	-
col1985	Zopheridae	Colydiinae	Gempylodini	*Pseudenestes*	*australis*	-	-	y
Nema140	Zopheridae	Colydiinae	Nematidiini	*Nematidium*	*elongatum*	y	y	y
col1987	Zopheridae	Colydiinae	Nematidiini	*Nematidium*	*poggii*	y	-	-
col1986	Zopheridae	Colydiinae	Nematidiini	*Nematidium*	*posticum*	y	y	-
Nema2	Zopheridae	Colydiinae	Nematidiini	*Nematidium*	sp.	y	-	-
Nema141	Zopheridae	Colydiinae	Nematidiini	*Nematidium*	sp.	y	-	-
Orth33	Zopheridae	Colydiinae	Orthocerini	*Orthocerus*	*clavicornis*	y	y	y
Rhag125	Zopheridae	Colydiinae	Rhagoderini	*Rhagodera*	nr. *texana*	y	y	y
Rhag3	Zopheridae	Colydiinae	Rhagoderini	*Rhagodera*	*tuberculata*	-	y	y
Rhop121	Zopheridae	Colydiinae	Rhopalocerini	*Rhopalocerus*	*rondanii*	y	y	y
Slip163	Zopheridae	Colydiinae	Synchitini	*Slipinskius n. gen.*	sp.	-	y	-
col1745	Zopheridae	Colydiinae	Synchitini	*Ablabus*	*bicolor*	y	y	y
col1746	Zopheridae	Colydiinae	Synchitini	*Ablabus*	*difficulis*	y	-	y
col1710	Zopheridae	Colydiinae	Synchitini	*Ablabus*	*mimus*	y	y	y
col1748	Zopheridae	Colydiinae	Synchitini	*Ablabus*	*pulcher*	y	y	y
col1747	Zopheridae	Colydiinae	Synchitini	*Ablabus*	*queenslandicus*	y	y	y
Abno78	Zopheridae	Colydiinae	Synchitini	*Ablabus (Notoulus)*	*discors*	y	-	-
Abtr79	Zopheridae	Colydiinae	Synchitini	*Ablabus "true"*	*sellata*	y	y	-
Acol56	Zopheridae	Colydiinae	Synchitini	*Acolobicus*	*erichsoni*	y	-	y
Acol135	Zopheridae	Colydiinae	Synchitini	*Acolobicus*	sp.	y	-	-
Allo73	Zopheridae	Colydiinae	Synchitini	*Allobitoma*	*halli*	y	y	y
col1738	Zopheridae	Colydiinae	Synchitini	*Antilissus*	*setosus*	y	y	y
Aspr23	Zopheridae	Colydiinae	Synchitini	*Asprotera*	*cylindrica*	y	y	-
col1972	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*cylindrica*	-	y	y
col1996	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*grouvellei*	-	y	y
col1997	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*grouvellei*	-	y	y
col1974	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*imperialis*	y	y	-
Bito21	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*jejuna*	y	y	y
col1711	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*notata*	y	y	-
col1973	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*notata*	y	y	y
col1742	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*serricollis*	-	y	y
Bito22	Zopheridae	Colydiinae	Synchitini	*Bitoma*	*siccana*	y	y	y
Bito116	Zopheridae	Colydiinae	Synchitini	*Bitoma*	sp.	y	-	-

Bito38	Zopheridae	Colydiinae	Synchitini	*Bitoma*	sp.	y	y	y
Lasc53	Zopheridae	Colydiinae	Synchitini	*Bitoma*	sp.	y	y	y
Btnw80	Zopheridae	Colydiinae	Synchitini	*Bitoma "NEW"*	*picicorne*	y	y	y
Bito20	Zopheridae	Colydiinae	Synchitini	*Bitoma (Coniophaea)*	*exarata*	y	y	y
Bolc169	Zopheridae	Colydiinae	Synchitini	*Bolcocius*	sp.	y	-	y
Caco45	Zopheridae	Colydiinae	Synchitini	*Cacotarphius*	*compressus*	y	y	-
col1992	Zopheridae	Colydiinae	Synchitini	*Caprodes*	*cinereus*	y	y	-
col1737	Zopheridae	Colydiinae	Synchitini	*Cebia*	*australis*	y	-	y
Cerc19	Zopheridae	Colydiinae	Synchitini	*Cerchanotus*	*asperulus*	y	y	y
Chor95	Zopheridae	Colydiinae	Synchitini	*Chorasus*	sp.	y	y	-
col1736	Zopheridae	Colydiinae	Synchitini	*Cicablabus*	*micros*	-	y	y
col1975	Zopheridae	Colydiinae	Synchitini	*Colobicones*	*alfa*	y	y	-
col1980	Zopheridae	Colydiinae	Synchitini	*Colobicones*	*australis*	y	y	-
col1982	Zopheridae	Colydiinae	Synchitini	*Colobicones*	*oculatus*	y	y	y
col1979	Zopheridae	Colydiinae	Synchitini	*Colobicones*	*papuanus*	y	y	-
Colo107	Zopheridae	Colydiinae	Synchitini	*Colobicus*	sp.	y	y	y
Colo126	Zopheridae	Colydiinae	Synchitini	*Colobicus*	sp.	y	y	y
Cold120	Zopheridae	Colydiinae	Synchitini	*Colydodes*	*gibbiceps*	y	-	-
Cold17	Zopheridae	Colydiinae	Synchitini	*Colydodes*	*mamilliaris*	y	-	-
Cold132	Zopheridae	Colydiinae	Synchitini	*Colydodes*	sp.	y	-	-
Coxc48	Zopheridae	Colydiinae	Synchitini	*Coxelus - Chile*	sp.	y	y	y
Dipl16	Zopheridae	Colydiinae	Synchitini	*Diplotoma*	*erichsoni*	y	y	y
Dito15	Zopheridae	Colydiinae	Synchitini	*Ditomoidea*	sp.	y	-	-
Dryp74	Zopheridae	Colydiinae	Synchitini	*Dryptops*	*dorsalis*	y	y	y
Enar76	Zopheridae	Colydiinae	Synchitini	*Enarsus*	*bakewellii* gp.	y	y	y
col1990	Zopheridae	Colydiinae	Synchitini	*Endeitoma*	*nigra*	y	y	-
col1988	Zopheridae	Colydiinae	Synchitini	*Endeitoma*	*perforata*	-	y	y
Endi14	Zopheridae	Colydiinae	Synchitini	*Endeitoma*	sp.	-	y	y
Endo124	Zopheridae	Colydiinae	Synchitini	*Endophloeus*	*serratus*	y	y	y
Euci136	Zopheridae	Colydiinae	Synchitini	*Eucicones*	sp.	y	y	y
Edsm66	Zopheridae	Colydiinae	Synchitini	*Eudesma*	*undulata*	y	y	-
Gath92	Zopheridae	Colydiinae	Synchitini	*Gathocles*	*nodosus/angulifer*	y	-	-
Bhut110	Zopheridae	Colydiinae	Synchitini	*Bhutania*	sp.	y	y	y
Glyp111	Zopheridae	Colydiinae	Synchitini	*Glyphocryptus*	sp.	y	-	-
Hybr113	Zopheridae	Colydiinae	Synchitini	*Hyberis gen. nr.*	sp.	y	-	-
Unkn165	Zopheridae	Colydiinae	Synchitini	*Gen. undet.*	sp.	y	y	-
Unkn166	Zopheridae	Colydiinae	Synchitini	*Gen. undet.*	sp.	y	-	y
Glen98	Zopheridae	Colydiinae	Synchitini	*Glenenetela*	sp.	y	y	y
Hetr91	Zopheridae	Colydiinae	Synchitini	*Heterargus "true"*	sp.	y	y	y
Holo51	Zopheridae	Colydiinae	Synchitini	*Holopleuridia*	sp.	y	y	y
Hybr112	Zopheridae	Colydiinae	Synchitini	*Hyberis*	sp.	y	y	-
Isot102	Zopheridae	Colydiinae	Synchitini	*Isotarphius*	*reitteri*	y	y	y
Labr43	Zopheridae	Colydiinae	Synchitini	*Labrotrichus*	sp.	y	-	-
Lasc129	Zopheridae	Colydiinae	Synchitini	*Lasconotus*	sp.	y	-	-
Last12	Zopheridae	Colydiinae	Synchitini	*Lascotonus*	sp.	y	y	-
Lobo119	Zopheridae	Colydiinae	Synchitini	*Lobogestoria*	sp.	y	-	-
Lobo55	Zopheridae	Colydiinae	Synchitini	*Lobogestoria*	sp.	y	y	-
Lobo139	Zopheridae	Colydiinae	Synchitini	*Lobogestoria*	sp.	y	y	-
Made11	Zopheridae	Colydiinae	Synchitini	*Madenophloeus*	*fairmairei*	y	y	y
Mama10	Zopheridae	Colydiinae	Synchitini	*Mamakius*	*conradti*	y	y	y
Micr67	Zopheridae	Colydiinae	Synchitini	*Microprius*	*decoratus*	y	y	y
Micr109	Zopheridae	Colydiinae	Synchitini	*Microprius*	*terrenus*	y	y	y
Micr131	Zopheridae	Colydiinae	Synchitini	*Microprius*	*terrenus*	y	y	y
Micr9	Zopheridae	Colydiinae	Synchitini	*Microprius*	*terrenus*	-	y	y
Mcsi59	Zopheridae	Colydiinae	Synchitini	*Microsicus*	sp.	y	y	-
Mcsi60	Zopheridae	Colydiinae	Synchitini	*Microsicus*	sp.	y	y	-
Ngen160	Zopheridae	Colydiinae	Synchitini	*N. gen.*	n.sp.	y	y	y
col1741	Zopheridae	Colydiinae	Synchitini	*Namunaria*	*communis*	y	y	y
col1740	Zopheridae	Colydiinae	Synchitini	*Namunaria*	*cylindrica*	y	y	-
Namu61	Zopheridae	Colydiinae	Synchitini	*Namunaria*	*pacifica*	-	y	-
Neot69	Zopheridae	Colydiinae	Synchitini	*Neotrichus*	sp.	y	y	y
Norx81	Zopheridae	Colydiinae	Synchitini	*Norix*	*crasssus*	y	-	y
Noto99	Zopheridae	Colydiinae	Synchitini	*Notocoxelus*	sp.	y	-	-
Pabu127	Zopheridae	Colydiinae	Synchitini	*Pabula*	*africana*	y	y	y
Paha41	Zopheridae	Colydiinae	Synchitini	*Paha*	*laticollis*	y	y	y
Paha42	Zopheridae	Colydiinae	Synchitini	*Paha*	n.sp.?	y	y	y

Pary168	Zopheridae	Colydiinae	Synchitini	*Paryphus*	sp.	y	y	y
Pary44	Zopheridae	Colydiinae	Synchitini	*Paryphus*	sp.	-	y	y
Phld40	Zopheridae	Colydiinae	Synchitini	*Phloeodalis*	nr. *raucus*	y	-	y
Phlo8	Zopheridae	Colydiinae	Synchitini	*Phloeonemus*	nr. *interruptus*	y	y	y
Phor70	Zopheridae	Colydiinae	Synchitini	*Phormesa*	sp.	-	y	-
Phor71	Zopheridae	Colydiinae	Synchitini	*Phormesa*	sp.	y	-	-
col1984	Zopheridae	Colydiinae	Synchitini	*Phorminx*	*lyrata*	y	y	y
Phre117	Zopheridae	Colydiinae	Synchitini	*Phreatus*	*immsi*	y	y	y
Pris86	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*aemulus*	y	y	y
Pris85	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*antarcticus*	-	y	y
col1733	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*bellus*	y	y	y
col1712	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*chloreus*	y	y	y
col1720	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*elongatus*	y	y	y
col1732	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*elongatus*	y	y	y
col1721	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*interruptus*	y	y	y
col1722	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*interruptus*	y	y	y
col1723	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*monteithi*	y	-	y
col1724	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*monteithi*	y	-	-
col1751	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*pustulosus*	-	y	y
col1752	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*queenslandicus*	-	y	y
col1719	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*saccaratus*	y	y	y
col1725	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*zigzag*	y	-	y
col1726	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*zigzag*	y	y	y
Sync88	Zopheridae	Colydiinae	Synchitini	*Pristoderus*	*salebrosus*	y	y	y
Rech7	Zopheridae	Colydiinae	Synchitini	*Rechodes*	sp.	y	y	y
Ryto94	Zopheridae	Colydiinae	Synchitini	*Rytinotus*	*squamulosus*	-	y	-
Sass104	Zopheridae	Colydiinae	Synchitini	*Sassaka*	n.sp.?	y	y	y
Spre68	Zopheridae	Colydiinae	Synchitini	*Sprecodes*	*madagascariense*	y	y	y
Symf77	Zopheridae	Colydiinae	Synchitini	*Symphysius*	*serratus*	y	y	y
Sync89	Zopheridae	Colydiinae	Synchitini	*Syncalus "True"*	*Sp.*	y	y	-
Sync6	Zopheridae	Colydiinae	Synchitini	*Synchita*	*fuliginosa*	y	y	-
Sync103	Zopheridae	Colydiinae	Synchitini	*Synchita*	*madagascariense*	y	y	y
col353	Zopheridae	Colydiinae	Synchitini	*Synchita*	sp.	y	y	y
Sync58	Zopheridae	Colydiinae	Synchitini	*Synchita*	sp.	y	-	-
Sync57	Zopheridae	Colydiinae	Synchitini	*Synchita - Chile*	sp.	y	y	-
Tabl84	Zopheridae	Colydiinae	Synchitini	*Tarphiababus*	n.sp. 2	y	y	y
Tubr75	Zopheridae	Colydiinae	Synchitini	*Tarphiomimus*	*tuberculatus* gp.	y	y	y
Tmim83	Zopheridae	Colydiinae	Synchitini	*Tarphiomimus*	*wollastoni*	y	y	y
Tsom105	Zopheridae	Colydiinae	Synchitini	*Tarphiosoma*	*indicus*	-	-	y
Tsom130	Zopheridae	Colydiinae	Synchitini	*Tarphiosoma*	*indicus*	y	-	y
Tarf72	Zopheridae	Colydiinae	Synchitini	*Tarphius*	*monstrosus*	-	y	y
col1739	Zopheridae	Colydiinae	Synchitini	*Todima*	*fulvicincta*	y	y	y
Trac5	Zopheridae	Colydiinae	Synchitini	*Trachypholis*	*similis*	-	y	y
Trac128	Zopheridae	Colydiinae	Synchitini	*Trachypholis*	sp.	y	y	y
col425	Zopheridae	Zopherinae	Latometini	*Latometus*	sp.	y	y	y
col503	Zopheridae	Zopherinae	Latometini	*Latometus*	sp.	y	y	y
col1709	Zopheridae	Zopherinae	Latometini	*Orthocerodes*	*australis*	y	y	y
Mono147	Zopheridae	Zopherinae	Monommatini	*Monomma*	sp.	y	y	y
Mono148	Zopheridae	Zopherinae	Monommatini	*Monomma*	sp.	y	-	-
Mono30	Zopheridae	Zopherinae	Monommatini	*Monomma*	sp.	-	y	-
Msc169	Zopheridae	Zopherinae	Phellopsini	*Phellopsis*	*porcata*	y	y	-
col424	Zopheridae	Zopherinae	Pycnomerini	*Docalis*	sp.	-	y	y
Pycd100	Zopheridae	Zopherinae	Pycnomerini	*Pycnomerodes*	*peregrinus*	y	-	-
Pycn27	Zopheridae	Zopherinae	Pycnomerini	*Pycnomerus*	*arizonicus*	y	y	y
Pycn65	Zopheridae	Zopherinae	Pycnomerini	*Pycnomerus*	sp.	y	y	y
Usec63	Zopheridae	Zopherinae	Usechini	*Usechus*	*lacerata*	y	y	y
Usec29	Zopheridae	Zopherinae	Usechini	*Usechus*	*lacerata*	y	y	y
Phde153	Zopheridae	Zopherinae	Zopherini	*Phloeodes*	*diabolicus*	-	-	y
Msc2105	Zopheridae	Zopherinae	Zopherini	*Phloeodes*	*plicatus*	y	y	y
Phde152	Zopheridae	Zopherinae	Zopherini	*Phloeodes*	*plicatus*	-	y	-
Phlo118	Zopheridae	Zopherinae	Zopherini	*Phloeodes*	*venustus*	y	-	-
Vero150	Zopheridae	Zopherinae	Zopherini	*Verodes*	*inaequalis*	y	y	y
col1731	Zopheridae	Zopherinae	Zopherini	*Zopherosis*	*georgei*	y	y	y
Zoph158	Zopheridae	Zopherinae	Zopherini	*Zopherus*	*concolor*	y	y	y
Zoph156	Zopheridae	Zopherinae	Zopherini	*Zopherus*	*gracilis*	y	y	y
Msc177	Zopheridae	Zopherinae	Zopherini	*Zopherus*	*granicollis*	-	y	y

Zoph155	Zopheridae	Zopherinae	Zopherini	*Zopherus*	*nodulosus*	y	y	y
Zoph154	Zopheridae	Zopherinae	Zopherini	*Zopherus*	*tristis*	-	y	y

CHAPTER 4

Novel Microscopy Techniques Reveal Multiple Evolutionary Origins of Metal Incorporation into Mandibles of the Megadiverse Beetles (Coleoptera).

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Appendix I contains the figures 1–17 for Chapter 4 and is available as a supplementary file via LoboVault. See PDF titled "Appendix_I_Figures_Chapter4". Appendix J contains the supplementary ESEM-EDS mandibular scans and is available as a supplementary file via LoboVault. See PDF titled "Appendix_J_EDS_Chapter4".

Abstract

It is well-documented that invertebrates incorporate various elements into their cuticle for reinforcement and wear resistance. High concentrations of heavy metals and halogens have previously been detected in a variety of invertebrate morphological structures. While numerous studies have investigated the types and locations of cuticular metals in assorted taxa, few have robustly investigated patterns of incorporation across a single order of diverse organisms within a phylogenetic framework. In doing so, potential evolutionary patterns of heavy metal incorporation can be revealed and may provide predictive ability to infer natural histories and phylogenetic relationships. Using a novel combination of microscopy instrumentation and analytical techniques, here we demonstrate the ability to rapidly and inexpensively visualize and analyze elemental incorporation and composition. Utilizing these techniques, we investigated metal incorporation within the mandibles of 117 taxa across the megadiverse order Coleoptera. Several lineages were found to incorporate zinc or manganese into various locations on the mandibular surface. To test for phylogenetic signal and evolutionary correlation between presence/absence of metals and adult mandibular use, we constructed a phylogeny under a Bayesian framework from a subsampling of a pre-existing dataset (Hunt *et al.* 2007), performed discrete statistical analyses on character evolution via *BayesTraits Discrete* (Pagel *et al.* 2004), and performed ancestral state reconstructions under both Parsimony and Bayesian frameworks via *Mesquite* (Maddison and Maddison 2011) and *BayesTraits Multistate* (Pagel *et al.* 2004). Resultant patterns of metal incorporation were strongly correlated with adult mandibular use and appear to have originated several times throughout Coleoptera. Additionally, the location and types of cuticular metals are demonstrated to be potentially valuable characters for taxonomic diagnoses. The utility of this instrumentation and analysis has broad-reaching impacts to the fields of material sciences, insect physiology, and systematics.

Introduction

The mandibles, ovipositors, tarsal claws, and mouth hooks of various invertebrates are structures that frequently contain significant amounts of heavy metals and halogens such as zinc, manganese, iron, copper, bromine, and chlorine (Figs. 1-10, Birkendal *et al.* 2006, Bone *et al.* 1993, Edwards *et al.* 1993, Hillerton and Vincent 1982, Hillerton *et al.* 1984, Lichtenegger *et al.* 2003, Schofield and Lefevre 1987, Quicke *et al.* 1998, Vincent and Wegst 2004). It has been demonstrated that the incorporation of these metals provides significant improvements in overall hardness and wear and fracture resistance (Fontaine *et al.* 1991, Morgan *et al*. 2003, Schöberl and Jäger 2006, for review of mandibular wear, see Chapman, 1995). While numerous studies have been conducted to identify the presence, types and locations of cuticular metals in particular groups of arthropods (Edwards *et al.* 1993, Fawke *et al.* 1997, Cribb *et al.* 2008a,b), few have focused on and sampled densely within any one major group. One possible reason for the lack of expansive research in this important area of invertebrate physiology lies in the methods and instrumentation currently employed. Some techniques presently being used to investigate cuticular metals such as Scanning Transmission Ion Microscopy (STIM), Proton Induce X-ray Emission (PIXE, *e.g.* Yoshiura *et al.* 2002), and Mass Spectrometry are quantitatively very accurate but are costly to run, require high levels of expertise and necessitate an irreparable alteration of specimens. Other techniques (environmental SEM, X-ray EDS), although more qualitative than quantitative, are becoming more readily available and are more easily accessible to a larger portion of the scientific community. Except for a few recent works (Schofield *et al.* 2001, 2002, 2003; Cribb *et al.* 2005, 2008a,b), the use and knowledge of this type of instrumentation has seemingly been restricted to physicists, insect physiologists and material scientists. Herein we describe a particular instrumentation set-up for the rapid and efficient qualitative analysis of cuticular elemental incorporation. We used this analytical combination to conduct a broad-scale survey of the incorporation of heavy metals in to the mandibles of adults across the order Coleoptera in order to investigate the prevalence and patterns of cuticular metals and examine possible correlations between metal incorporation and adult mandibular use.

Objectives

The objectives of this study are as follows:

1) Utilize cost-effective and time-efficient Scanning Electron Microscopy methods to reveal the presence/absence and types of metal incorporation in arthropod cuticle.

2) Conduct a broad survey across the megadiverse order Coleoptera to investigate the prevalence and patterns of metal incorporation in beetle mandibles.

3) Examine possible correlations between metal incorporation and adult mandibular use.

4) Determine the potential for new taxonomic characters.

Methods

<u>Mandibular Metal Analysis</u>

Taxon Sampling-Metal Analysis: The beetles (Coleoptera) comprise arguably the most diverse group of organisms on the planet, with an estimated 350,000 described species that occupy a broad array of habitats and ecological niches. In an attempt to decipher patterns of elemental incorporation, mandibles from 117 beetle taxa representing 4/4 suborders, 16/16 superfamilies, and over 25% of all known beetle families were analyzed for the presence/absence, types, and location of mandibular metals, with an emphasis on groups of economic importance (e.g. Curculionidae, Anobiidae) and/or exhibiting diverse adult food preferences and mandibular use (e.g. members of superfamily Cucujoidea).

Specimen Preparation: Adult beetle specimens were obtained from the University of Georgia Collection of Arthropods (Athens, GA) (majority), Museum of Southwestern Biology Division of Arthropods (MSBA) at the University of New Mexico), and several individuals (see acknowledgements). Each specimen was assigned a unique voucher number (e.g. NPL2009A12). Specimens were relaxed in warmed distilled water, cleaned via ultrasonication in dilute soapy water, and the mandibles were disarticulated from the head with fine tools. Mandibles were then submerged in 95% ethanol and left to dry. To allow for X-ray EDS analysis of the samples, the mandibles were not sputter coated. After drying, the mandibles were positioned on 260μm carbon conductive tabs (PELCO image tabs, TM, Ted Pella Inc., selected for increased thickness, high purity, and repositionable) placed on standard SEM stubs (12 mm aluminum). Two pairs of mandibles per species were mounted per tab, with right and left mandibles mounted dorsal and ventral surfaces up, respectively. Mandibular preparations and the remainder of the specimens are deposited as voucher specimens in the Museum of Southwestern Biology Division of Arthropods (MSBA) at the University of New Mexico.

Scanning Electron Microscopy: A traditional sample preparation for non-environmental SEM would include sputter-coating the sample with gold. This type of preparation is permanent, may damage the specimen, and is unsuitable for rare or delicate specimens. Sputter-coated samples also do not allow for elemental analysis of the specimen. Therefore, analysis and imaging was performed using a Zeiss JEOL 1450EP Variable Pressure Environmental Scanning Electron Microscope (ESEM) at the University of Georgia Center for Ultrastructural Research. A backscatter detector was used to generate the SEM images. Elemental analysis of the samples was conducted through the use of an equipped X-ray EDS system (see Goldstein *et al.* 2003, Newbury 1991, Perry *et al.* 1988, Roomans 1988, Schofield *et al.* 1988, Smith *et al.* 1992.

Energy-Dispersive X-ray Spectroscopy: The X-rays generated during SEM imaging were used to determine the elemental composition of the mandibles at the base and the apex. The beam excites electrons within inner shells of the sample (mandibles) causing electrons to be ejected from their orbitals. The empty electron holes are filled by higher-energy electrons from outer orbitals. The change in energy is released in the form of an X-ray. The emitted X-rays are collected and analyzed by an energy dispersive spectrometer (EDS). Elemental composition is determined based on the energy levels of the resulting X-rays from the region being exposed to the electron beam. Energy spectrum readouts (units in KeV) show peaks, the locations of which correspond to specific elements. By analyzing the peaks present and relative strength, it is possible to assess the elements present in the analyzed sample. Unlike more quantitative methods (STIM, PIXE), this type of analysis reveals incorporation only at the cuticular surface and is not appropriate for quantitative determination of amounts or percent composition throughout the mandible.

Phylogenetic Context

To date, the most robust phylogeny of the order Coleoptera is provided in Hunt *et al*. (2007) based on molecular data of three genes (16S ribosomal DNA, 18S ribosomal DNA, cytochrome c oxidase I) for an extensive taxonomic sampling of the group. In order to develop a phylogenetic framework to test character evolution across taxa, a representative phylogeny is needed. Therefore, molecular data for a taxonomic subset from Hunt *et al*.'s data (2007) was obtained to construct a representative phylogeny.

Taxon Sampling. In order to produce a data matrix with high levels of phylogenetic congruence to the taxa analyzed for mandibular metals, members of Hunt *et al.*'s (2007)1,880-taxon matrix were selected in order to achieve the highest taxonomic similarity. In many cases, the exemplars analyzed for metals were represented by the identical species in Hunt's dataset. When a one-to-one correlation was not possible, taxa were selected that were most closely related (according to current classifications) rather than completeness of gene coverage from Hunt *et al*.'s (2007) dataset. We feel this approach allows for the most accurate prediction of mandibular metal correlation on a resultant phylogeny of known taxa. It is possible the taxonomy of the groups selected may change or continue to be resolved, thus rendering some of our correlated selections inaccurate. While this cannot be predicted, every effort was made to follow current taxonomic classifications across the groups analyzed.

Data Sampling. Sequences of available loci of 86 taxa from Hunt *et al.*'s 2007 paper were downloaded from GenBank (GenBank accession numbers and data NEXUS files also available from the article supplementary material) via Geneious® version 6.1.6 (created by Biomatters Ltd., available from http://www.geneious.com). Sequence contig assembly was performed in Geneious®.

Analytical Methods

Alignment: Alignment of COI was performed in Geneious® based on conservation of the codon reading frame. Alignments of 16S and 28S were done using

Muscle (Edgar, 2004) under the default settings (max 16 iterations) as implemented in Geneious®. Gaps were treated as missing data. The individual loci datasets were exported from Geneious® as NEXUS files. An Incongruence Length Difference test (ILD, Farris *et al.* 1994) was performed in WinClada (Nixon, 2002) and revealed no significant incongruence between the datasets (p=0.1667). Therefore, the datasets were concatenated in Geneious® and exported as a NEXUS file. The combined dataset produced an alignment with 5,322 bases. Completeness of data for each taxon is provided in Table 2.

Bayesian: Optimal partitioning strategies and models of evolution for the dataset were calculated in PartitionFinder v.1.1.1 (Lanfear *et al.* 2012) under the following commands: branchlengths = linked; models of evolution = beast; modelselection = BIC; scheme = greedy; datablocks = charset 18S = 1-2788; charset 16S=2789-3704; charset COI_pos1=3705-5322\3; charset COI_pos2=3706-5322\3; charset COI_pos3=3707-5322\3. The optimal partitioning strategy and models of evolution recovered were as follows: by gene, by separate codon position (5 partitions); partition 1 = 18S under GTR+I+G; partition 2 = 16S under GTR+I+G; partition 3 = COI pos. 1 under GTR+I+G; partition 4 = COI pos. 2 under GTR+I+G; partition 5 = COI pos. 3 under TrN+I+G. Bayesian analyses were conducted using BEAST v.1.7.5 (Drummond *et al.* 2012). A BEAST xml file NEXUS file of the combined data was generated in BEAUti v.1.7.5 (Drummond *et al.* 2012) under a lognormal relaxed clock with the tree prior set to Yule Process. Four separate Bayesian runs were run through use of the CIPRES Science Gateway ver. 3.1 (Miller *et al.*, 2010), each run for 5×10^7 generations, sampling every 1000 generations. The log files were then analyzed in Tracer v1.4.1 (Rambaut and

Drummond, 2007) to determine an acceptable burn-in. To conserve estimation, the log files and tree files for each run, respectively, were combined with a removed burn-in per run of 4% generations and thinned under a lower sampling frequency (every 10,000 generations) in LogCombiner v.1.7.5 (Drummond *et al.* 2012). The combined log file was then analyzed in Tracer for acceptable stationarity and ESS values. The sampled trees in the combined tree file were summarized in TreeAnnotator v.1.7.5 (Drummond *et al.* 2012) onto a single "target" tree. This tree was analyzed, rooted, and set to display posterior probabilities in FigTree v.1.3.1 (Rambaut 2006-2009).

<u>Imaging and Tree Figures</u>

Trees were digitally rendered in Adobe Illustrator CS5, v.15.0.2 (Adobe Systems, Inc., San Jose, CA, USA).

<u>Correlations of Metals Presence with Adult Mandibular Use</u>

In order to test for phylogenetic correlation of the presence/absence of mandibular metals and/or mandibular use, the 86 taxon representative sampling was scored for two binary characters (char. #1 = mandibular metal presence; char. #2 = adult mandibular use) or for one composite multistate character (mandibular metal presence + mandibular use; see schemes and scoring below). Primary references on Coleoptera were surveyed to develop a character scoring for adult mandibular use (Arnett and Thomas 2001, Arnett *et al.* 2002, Beutel *et al.* 2005, Crowson 1981, Hunt *et al.* 2007, Lawrence and Britton 1991, Lawrence and Newton 1992, Lawrence *et al.* 1999, Lawrence *et al.* 2011, Leschen *et al.* 2010). An effort was made to make conservative scorings, as the mandibular use of many adult beetle groups is still either unknown or assumed. Character #1 was scored as: 0 = no mandibular metals present, 1 = mandibular metals present. We scored adult mandibular use (Char. 2) as “soft” use, “moderate” use, “hard” use, or some combination thereof. We broadly define these use categories as follows: SOFT (score = 0): fungivory, herbivory (primarily leaves and soft tissues), algivory, saprophagy, detritovory; MODERATE (score = 1): scavengery/predation (primarily invertebrate cuticle), xylophagy (soft wood), fungivory (bracket fungi); HARD (score = 2): xylophagy (hard wood, incl. boring, girdling), herbivory (incl. seminivory, nucivory, granivory); - = polymorphic / unknown. If habits were in question, the higher use value was selected (e.g. favoring harder).

In order to test for correlation among the two discrete binary characters (metal presence and mandibular use), we implemented a Likelihood Ratio Test on our resultant phylogeny using *BayesTraits Discrete* (Pagel *et al.* 2004) under a Maximum Likelihood analysis. To convert from a multistate mandibular use character (soft = 1, moderate = 2, hard = 3) to a binary character, we combined states as follows: Scheme 1 = multistate scorings of 0 and 1 converted to a binary scoring of 0, and a multistate scoring of 2 converted to a binary scoring of 1); Scheme 2 = multistate scorings of 0 converted to a binary scoring of 0, and multistate scorings of 1 and 2 converted to a binary scoring of 1). *BayesTraits Discrete* was run under both independent and dependent character settings under scheme 1 and scheme 2 utilizing a Maximum Likelihood framework. No restrictions were placed on the model of character evolution for either the dependent or independent character analyses. Results of discrete analyses of char. #1 and #2 demonstrated significant correlation between mandibular metal presence and mandibular use under both scoring schemes (see results). Therefore, additional analyses could be run utilizing *BayesTraits Multistate* (Pagel *et al.* 2004) to reconstruct ancestral states under a Maximum Likelihood framework. To run multistate analyses, scorings from characters #1 and #2 were merged into a single, multistate character. This effectively linked presence/absence of metals and mandibular use. Thus, the composite character scoring under the two schemes for our data is as follows:

<u>BayesTraits Multistate Analyses</u>

Scheme 1 – composite character produced from of individual chars. #1 and #2 (chars #1 and #2 converted to binary as above)

0 = char. #1: 0, char. #2: 0, no metals, “soft” use

1 = char. #1: 0, char. #2: 1, no metals, “medium” to “hard” use

2 = char. #1: 1, char. #2: 0, metals present, “soft” use

3 = char. #1: 1, char. #2: 1, metals present, “medium” to “hard” use

Scheme 2 – composite character produced from of individual chars. #1 and #2 (chars #1 and #2 converted to binary as above)

0 = char. #1: 0, char. #2: 0, no metals, “soft” to “medium” use

1 = char. #1: 0, char. #2: 1, no metals, “hard” use

2 = char. #1: 1, char. #2: 1, metals present, “heavy” use

3 = char. #1: 1, char. #2: 0, metals present, “soft” to “medium” use

NOTE: Under scheme 2, no taxa were scored for state 3.

BayesTraits Multistate was run utilizing a Maximum Likelihood framework. No restrictions were placed on transitions/transversions between character states (model of character evolution, e.g. shifts from one state to any other equally as likely). Scheme 1 resulted in a 12-rate model (0-1,0-2,0-3,1-0,1-2,1-3,2-1,2-3,3-0,3-1,3-2), and scheme 2 resulted in a 6–rate model (0-1, 0-2, 1-0, 1-2, 2-0, 2-1).

Ancestral State Reconstructions

Reconstructions of ancestral states were carried out under both Parsimony and Maximum Likelihood frameworks in *Mesquite* v. 2.75 (Maddison and Maddison 2011) and *BayesTraits Multistate* (Pagel *et al.* 2004). Ancestral state reconstructions on the Bayesian topology were calculated under a Parsimony framework in Mesquite for the following: presence/absence of mandibular metals (Fig. 12 – single character, no mandibular use included), Multistate Scheme 1 (Fig. 14 – single multistate character of composite presence/absence of metals + mandibular use), and Multistate Scheme 2 (Fig. 15 – single multistate character of composite presence/absence of metals + mandibular use). Ancestral state reconstructions on the Bayesian topology were calculated under a Likelihood framework in Mesquite for the following: presence/absence of mandibular metals (Fig. 13 – single character, no mandibular use included), Multistate Scheme 1 (Fig. 16 – single multistate character of composite presence/absence of metals + mandibular use), and Multistate Scheme 2 (Fig. 17 – single multistate character of composite presence/absence of metals + mandibular use). Note: With the exception of the initial Bayesian topology (Fig. 11), the taxa presented on the resultant topologies (Figs. 12-17) are *not* the taxa pulled from Hunt *et al.*'s dataset, but rather are the "taxonomic correlates” analyzed for mandibular metals (for full list, see Table 2). In Figures 13 and 16–17, likelihoods were reported as proportional, but the graphic of reconstruction does not showing reconstruction proportional to the likelihoods (e.g. higher likelihoods for states depicted by thicker branches).

Results

<u>ESEM / X-Ray EDS Mandible Analysis</u>

ESEM images were captured through the use of the backscatter detector on uncoated samples, yielding high-quality images. In instances where metals were incorporated into the cuticle, these higher density locations appeared much brighter than non-incorporated areas, resulting in a visually striking image (Figs. 1-10). Quantifiable incorporation of heavy metals was found in 13/46 families, 22/68 subfamilies, 42 genera, and 48/117 specimens. While the number of metal-incorporating taxa analyzed is largely dependent on taxon sampling (and may be higher due to increased sampling in certain groups, e.g. Curculionidae), the diversity of families shown to incorporate metals is quite high. Furthermore, there appear to be clear phylogenetic patterns associated with metal incorporation across various beetle lineages. Most notably, the following trends emerged:

1) Three out of four coleopteran suborders lack incorporation of quantifiable concentrations of heavy metals (Archostemata, Myxophaga, Adephaga).
2) Within the suborder Polyphaga, metal incorporation is widespread in Bostrichiformia, Cleroidea, Chrysomeloidea, and Curculionoidea.
3) Within Polyhaga, metal incorporation is conspicuously sparse or absent from Tenebrionoidea, Cucujoidea, and Elateriformia.

4) Metal incorporation is absent in aquatic Coleoptera; incorporation was recovered only in terrestrial groups.
5) Metal incorporation appears to have a phylogenetic correlation; major clades with or without widespread incorporation were recovered.
6) Presence of mandibular metals correlated with adult mandibular use – only taxa utilizing mandibles under “medium” to “hard” scorings displayed instances of incorporation.

Bayesian Phylogenetic Analyses

A consensus Bayesian topology was produced from trees sampled from the posterior distribution (at stationarity) of 86 representative taxa from Hunt *et al.* (2007) (Fig. 11 - values above nodes indicate posterior probabilities, values below nodes indicate node number). While the higher-level relationships among coleopteran groups recovered from these analyses differed in several aspects from the larger analyses presented in Hunt *et al.* 2007, our intent was not to replicate their results, but rather to produce a phylogeny with a taxonomic sampling correlating to the taxa analyzed for mandibular metals. This approach allows for the ability to carry out statistical tests of character correlation on a representative phylogeny for scored characters/states.

Correlations of Metals Presence with Adult Mandibular Use

BayesTraits Discrete Analyses

Scheme 1

Log-likelihood Dependent = -72.5184

Log-likelihood Independent = -81.7029

LR = 2[-72.5184 +81.7029] = 18.369

Chi-squared distribution, w/ 4 degrees of freedom: p-value > 0.001

Result = significant correlation between mandibular metal presence and mandibular use.

Scheme 2

Log-likelihood Dependent = -67.6941

Log-likelihood Independent = -81.6452

LR = 2[-67.6941 + 81.6452] = 27.9022

Chi-squared distribution, w/ 4 degrees of freedom: p-value > 0.001

Result = significant correlation between mandibular metal presence and mandibular use.

Ancestral Character State Reconstructions

Ancestral state reconstructions on the Bayesian topology under the Parsimony framework for just the presence/absence of metals (Fig. 12) resulted in 11 to 12 instances of the evolution of metal incorporation. The only ambiguous ancestral state reconstruction occurred at the MRCA of Sphindidae–Curculionidae, as the most parsimonious result was either a single evolution and then a loss for *Sphindus americanus*, or two instance of evolution, one at the Anthribidae clade and another at the Curculionidae clade. Ancestral state reconstructions under a Likelihood framework for just presence/absence of metals recovered (Fig. 13) identical results as under the parsimony framework.

Ancestral state reconstructions under the parsimony framework under a composite multistate character via scheme 1 (Fig. 14) resulted in 10 to 12 instances of the evolution of metal incorporation. The only ambiguous ancestral state reconstructions occurred at the MRCA of Cerambycidae-Nitidulidae and Sphindidae–Curculionidae, respectively. Under this multistate character scoring scheme, additional information about the coevolution of mandibular metals and adult mandibular use can be seen. Green clades represent the presence of mandibular metals and a “soft” mandibular use, whereas black clades represent the presence of mandibular metals and a “moderate” to “hard” mandibular use. Multi-colored clades indicate equally most-parsimonious scorings. There were 3-4 origins of the “presence and soft use” character scoring, with the only ambiguous ancestral state reconstruction at the MRCA node for Anthribidae. All other instances of metal incorporation occurred with a “moderate” to “hard” mandibular use, and a shift to incorporation with “soft” use only occurred 1-2 times (Cleridae: *Enoclerus ichneumoneus* and possibly Anthribidae: *Euparius marmoreus*). Ancestral state reconstructions under the Likelihood framework under a composite multistate character via scheme 1 (Fig. 16) recovered identical results as under the Parsimony framework.

Ancestral state reconstructions under the Parsimony framework under a composite multistate character via scheme 2 (Fig. 15) resulted in as few as 3 but as many as 9 instances of the evolution of metal incorporation, but with multiple losses. Black clades represent the presence of mandibular metals and “hard” mandibular use. Green clades represent the absence of mandibular metals and “hard” mandibular use, and white clades represent the absence of mandibular metals and “soft” to “medium” mandibular use. Multi-colored clades indicate equally most-parsimonious scorings. Ancestral state reconstructions under the Likelihood framework under a composite multistate character via scheme 2 (Fig. 17) recovered similar results as under the Parsimony framework. If the highest likelihood value is accepted, the analysis resulted in 3 instances of the evolution of metal incorporation under scoring scheme 2 (Derodontidae: *Derodontus esotericus*, Eucnemidae: *Isorhipis obliqua*, and MRCA of Dermestidae+Silphidae through Curculionidae).

Discussion

The use of this type of ESEM microscopy and X-Ray EDS analysis allows for efficient analysis of the presence/absence of metals and is no more costly than traditional SEM imaging.

Types of mandibular metals: Of the taxa with detectable quantities of metals present in the mandibles, the most predominant metals were zinc in association with a chlorine halogen (occuring in 18/21 analyzed subfamilies with metal incorporation). Fewer of the positive taxa contained manganese (2/21 analyzed subfamilies: Dermestidae: Anthreninae; Cerambycidae: Lamiine), usually in much lower concentrations. Aluminum was recovered from Derodontidae, which represents the first documentation of this metal in quantifiable amounts. Another notable result was the recovery of high levels of potassium in Rhysodinae (Adephaga: Carabidae).

Location of mandibular metal incorporation: In previous studies, the specific location of metal incorporation in invertebrate mandibles has been mentioned only secondarily and has yet to be thoroughly investigated. The visually striking images produced by the VP-ESEM + backscatter detector allow for a rapid analysis of specific location of cuticular metals. Out of the 48 specimens analyzed that exhibited appreciable quantities of metals, the majority of incorporation was localized in the mandibular apices (e.g., *Anthrenus, Deretaphrus*, Figs. 1–2, 3, 6, appendix). In several groups (Trogossitidae, Cleridae, Figs. 7–8, appendix), areas of incorporation extended along the incisal edge of the mandible. In the scolytine weevil (*Ips grandicollis*, Fig. 4), metal incorporation appears restricted to a small tubercle near the base of the mandible, with the tubercle more than likely serving as a primary grinding surface. Location of incorporation is linked with the mechanical function of the mandible, as the areas of highest abrasion are subjected to the significant mechanical force and are thus more likely to be reinforced. Additional quantitative analyses would undoubtedly reveal metal incorporation in other high-wear areas of the mandibles (e.g. grinding plates, etc.), although in perhaps lower concentrations.

Sex-specific incorporation: Many members of the family Cerambycidae (Chrysomeloidea) are wood borers and are a group of major economic importance worldwide. Within this mega-diverse family, members of the tribe Onciderini exhibit a sexually dimorphic girdling behavior in which the females lay eggs in a branch and then girdle the branch, causing structural weakening and eventual detachment of the branch. Males do not girdle. Due to this dimorphism, members of this group were ideal in investigating the presence or absence of sex-specific incorporation of metals into mandibles. A male and female of *Oncideres cingulata* were analyzed, revealing incorporation of manganese in both sexes. This finding suggests that metals are incorporated universally in the mandibles of both sexes, lacking differentiation due to sex-specific natural histories.

Phylogenetic significance: Only one study has analyzed the presence or absence and types of metals within a phylogenetic framework (Cribb *et al.* 2008b), demonstrating that high quantities of zinc in the mandibles of one termite family could be used as a phylogenetically and taxonomically informative character. The presence or absence and types of cuticular metals incorporated in beetle mandibles does show strong phylogenetic signal with various clades exhibiting wide-scale incorporation of predominantly one metal (e.g. Polyphaga: Bostrichiformia/Bostrichoidea, Cleroidea, Curculionoidea) or lack of metals entirely (e.g. all Archostemata, Myxophaga, Adephaga except Rhysodines, and Polyphaga: Tenebrionoidea).

Mandibular Metal Presence Across Coleoptera under a Phylogenetic Context: It has been previously asserted that relatedness of taxa is the strongest predictor of metal incorporation, not natural histories or habitat (Cribb *et al.* 2008b). While the evolution of metal incorporation or types of heavy metals and halogens present in various invertebrate structures does seem to be expressed in a phylogenetic framework, our results indicate that mandibular use also plays a critical role in whether or not mandibles are reinforced in adult Coleoptera (see specifically Cucujoidea and Cleroidea). Mandibular use information as follows is given for all taxa that were shown to incorporate appreciable quantities of heavy metals in the mandibular cuticle, as gathered from primary references on Coleoptera (Arnett and Thomas 2001, Arnett *et al.* 2002, Beutel *et al.* 2005, Crowson 1981, Hunt *et al.* 2007, Lawrence and Britton 1991, Lawrence and Newton 1992, Lawrence *et al.* 1999, Lawrence *et al.* 2011, Leschen *et al.* 2010).

Derodontiformia (Derodontidae): The genus *Derodontus* feeds solely on homobasidiomycete fungi. These types of fungi range from soft to hard.

Bostrichiformia: with the exception of one subfamily of Dermestidae (Dermestinae), all members within the Bostrichiformia analyzed contained metals. This group of beetles is known for their wood-feeding and generally destructive habits, many of which are known as stored product and structural pests. The Bostrichiformia clade exhibits strong phylogenetic signal with metal incorporation.

<u>Dermestidae:</u> stored product pests, scavengers. Interestingly, members analyzed within the subfamily Dermestinae (*Dermestes*, *Thylodrias*) contained no metals, whereas the representative of the subfamily Anthreninae (*Anthrenus*) contained manganese, the only taxon to contain this metal other than a distantly related longhorn beetle (Cerambycidae: Lamiinae: *Oncideres cingulata*). *Anthrenus verbasci* is commonly known as the "varied carpet beetle" and are pests of carpets and other similar materials.

<u>Bostrichidae:</u> all members analyzed within the family Bostrichidae contained zinc and chlorine. Bostrichidae usually bore into dead or dying wood, and the taxa analyzed are both members of the subfamily Dinoderinae. The genus *Dinoderus* is commonly associated with bamboo, and the genus *Prostephanus* is known to feed on grains.

<u>Ptinidae (=Anobiidae):</u> Members of 5 different subfamilies were found to contain zinc and chlorine. With the exception of a puffball feeder, *Caenocara* sp. all ptinids contained metals. Most ptinids are stored product pests, and several bore into wood. Members of Dorcatominae are associated with fungi. Some members of Ptininae are wood boring, while others feed on animal matter.

Elateriformia: Eucnemidae: only the subfamily Melasinae within the Eucnemidae exhibited detectable metal incorporation. Eucnemids are associated with dead wood, and it is uncertain whether or not adults feed. The only other elateriform family tested, Phengodidae, did not exhibit metal incorporation.

Lymexyloidea: Lymexylidae are associated with wood and the larvae are wood boring. Their common name, the Ship-timber beetles, alludes to their nature as a structural pest of ship and other timbers. The representative analyzed (*Atractocerus* sp.) contained detectable quantities of aluminum, the only taxon to exhibit incorporation of this metal in detectable quantities in our analysis. It is possible, however, this result was an analytical artifact and should be re-evaluated.

Cucujoidea: within the large superfamily Cucujoidea, the only family shown to exhibit metal incorporation was Bothrideridae. Within that family, two genera from different subfamilies were analyzed. The genus *Deretaphrus* (subfamily Bothriderinae) contained significant quantities of zinc and chlorine (Figs. 1-2, appendix), whereas the mycophagous genus *Teredomorphus* (Bothrideridae: Teredinae) lacked quantifiable amounts of mandibular metals. Members of the subfamily Teredinae (metals absent) are fungivorous as larvae and adults, whereas members of the Bothriderinae (metals present) are thought be predaceous on wood-boring beetles and their larvae as adults.

Cleroidea: One of the more interesting findings of this study was the detection of high levels of zinc and chlorine in the mandibles of the largely predaceous cleroid families Trogossitidae and Cleridae. Within Trogossitidae, two genera were analyzed - the mycophagous *Calytis* contained no metals, whereas the stored grain pest *Tenebroides mauritanicus* contained zinc and chlorine. *Tenebroides mauritanicus* is also known to bore into wooden barrels. This case suggests a pattern of incorporation not due to incorporation in closely related lineages, but incorporation due to the natural history of the particular group (e.g. predisposition of boring into hard woods and grains as opposed to softer structures). Within the Cleridae, all three genera examined contained zinc and chlorine. The vast majority of clerids are predaceous on wood-boring beetles (including the tested *Thanasimus* and *Enoclerus*). The genus *Necrobia* is a stored product pest.

Chrysomeloidea: within this large superfamily, only the bruchine chrysomelids and cerambycids exhibited metal incorporation. The vast majority of chrysomeloids are phytophagous, but members of Bruchine are known as the “bean weevils” and frequently bore into hard seeds and nuts. Members of Cerambycidae bore out of sound wood after eclosion, and some groups girdle tree branches to aid in oviposition.

Curculionoidea: This superfamily contains many of the most economically important and destructive wood-boring beetle pests. Within the weevils and related taxa, both the families Anthribidae and Curculionidae were shown to incorporate metals. Most members of the Curculionidae subfamilies Platypodinae and Scolytinae bore into sound wood and then feed on resultant fungal growth. Other curculionids feed on nuts and seeds, but some (e.g. *Curculio*, analyzed, metals not present) feed on softer plant materials such as fruits and leaves). The curcuionoid family Anthribidae (the fungus weevils) commonly feed on polypore and/or pyrenomycete fungi, but some members are presumably phytophagous.

The findings presented here (in addition to Cribb, 2008b) make a strong case for the taxonomic and natural history implications of cuticular metal incorporation. Thus, the incorporation of metals into the mandibles likely has both taxonomic implications, potentially serving as a character for the separation of natural groups, as well as implications about the natural history of those groups. Based on the correlation of metal incorporation with adult mandibular use, it is expected that other groups of beetles also incorporate metals into their cuticle, e.g. members of subcortical, wood-inhabiting or wood-feeding groups (e.g. Histeridae, Passalidae, rhysodine Carabidae, Buprestidae, Zopheridae, Tenebrionidae, Ciidae, Silvanidae).

Conclusions

There is little doubt a far greater number of beetles incorporate metals into their mandibles in at least trace amounts than is currently documented, however, many of the more quantitative techniques have drawbacks of availability, cost, and time of operation.

Increased hardness and wear resistance of cuticular structures due to metal incorporation most likely plays a critical role in the evolution and natural histories of many invertebrate groups, but relatively little is known about this phenomenon. As of now, few studies have been conducted to investigate the presence and nature of this important physiological state across the vast majority.

From an instrumentation perspective, advances in SEM configurations now allow for an efficient, cost-effective solution for the investigation of the presence of cuticular metals.

Burgeoning areas of research would be to look at the incorporation of metals through both larval and adult life stages, as the natural history of each stage can differ greatly from one another. The bioavailability of metals in the environment and potential correlations with concentrations and types of metals found in invertebrate cuticles is in need of further investigation.

It can be assumed that metal incorporation across Coleoptera is more pervasive than currently documented and using more sensitive, quantitative techniques will reveal further patters of cuticular incorporation. However, the qualitative techniques used in this study are excellent indicators of easily-detectable, higher concentrations of metal incorporation on the cuticular surface. Although trace quantities of heavy metals are likely to occur in a great number of additional invertebrate groups, a rapid, cost effective analytical method is an appropriate investigative tool to begin to explore broad-scale patterns of metal incorporation across some of life's most diverse groups.

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Table 2. Taxon Sampling for Metals Analysis and Representative Taxa from Hunt *et al.* 2007.

	Superfamily	Family	Subfamily	Tribe	Genus	Species	Metals	Representative from Hunt *et al.*	Phylo. congruence	18S Acc. #	16S Acc. #	COI Acc. #
	-	Sialidae	-	-	-	-	-	*Sialis lutaria*	-	X89497	AY620141	-
	-	Chrysopidae	-	-	-	-	-	*Chrysoperla carnea*	-	X89482	AY620150	AB081321
	-	Rhaphidiidae	-	-	-	-	-	*Phaeostigma notata*	-	X89494	-	-
	ADEPHAGA	Carabidae	Cincindelinae	Cicidelini	*Cicindela*	sp. 1	-	*Cicindela* sp. BMH703842	genus	DQ337115	-	-
	ADEPHAGA	Carabidae	Cincindelinae	Cicidelini	*Cicindela*	sp. 2	-	*Cicindela* sp. BMH703842	genus	DQ337115	-	-
	ADEPHAGA	Carabidae	Cincindelinae	Cicidelini	*Cicindela*	sp. 3	-	*Cicindela* sp. BMH703842	genus	DQ337115	-	-
	ADEPHAGA	Carabidae	Cincindelinae	Megacephalini	*Megacephala*	*carolina*	-	*Megacephala klugi*	genus	AF423053	MIMKRGDB1	-
	ADEPHAGA	Carabidae	Harpalinae	Subtribe Harpalina	*Eurydersus*	*grossus*	-	*Discoderus cordicollis*	subtribe	AF002776	-	AJ583332
	ADEPHAGA	Carabidae	Rhysodinae		*Clinidium*	sp.	K	*Clinidium calcaratum*	genus	AF012521	-	-
	ADEPHAGA	Dytiscidae	Dytiscinae	Dytiscini	*Dytiscus*	sp.	-	*Rhantus grapii*	sister tribe	AJ318695	AF428195	AF428234
	ADEPHAGA	Dytiscidae	Hydroporinae	Hydroporini	*Hydroporus*	sp.	-	*Hydroporus erythrocephalus*	genus	AF201409	AF518261	AF518291
	ADEPHAGA	Gyrinidae	Gyrininae	Enhydrini	*Macrogyrus*	sp.	-	*Macrogyrus* sp. IR86	genus	AJ318664	-	-
	ADEPHAGA	Gyrinidae	Gyrininae	Gyrinini	*Gyrinus*	sp.	-	*Gyrinus* sp. VLS-1999	genus	AF201412	EF517575	-
	ADEPHAGA	Gyrinidae	Gyrininae	Orectochilini	*Patrus*	sp.	-	*Orectochilus villosus*	tribe	AJ318665	AY071789	AY071815
	ADEPHAGA	Haliplidae			*Haliplus*	sp.	-	*Haliplus lineatocollis*	genus	AJ318666	AY071777	AY071803
	ADEPHAGA	Haliplidae			*Peltodytes*	sp.	-	*Haliplus lineatocollis*	family	AJ318666	AY071777	AY071803
	ARCHOSTEMATA	Cupedidae			*Priacma*	*serrata*	-	*Distocupes* sp. VLS-1999	family	AF201421	-	-
	Bostrichoidea	Anobiidae	Anobiinae	Anobiini	*Hemicoelus*	*carinatus*	Zn, Cl	*Oligomerus ptilinoides*	tribe	EF213876	EF213837	-
	Bostrichoidea	Anobiidae	Anobiinae	Stegobiini	*Stegobium*	*paniceum*	Zn, Cl	*Stegobium paniceum*	species	EF363012	DQ202557	DQ221964
	Bostrichoidea	Anobiidae	Dorcatominae	Calymmaderini	*Calymmaderus*	*nitidus*	Zn, Cl	*Dorcatoma* sp. TJH-2004	tribe	AY748104	-	-
	Bostrichoidea	Anobiidae	Mesocoelopodinae	Tricorynini	*Tricorynus*	*confusus*	Zn, Cl	*Mesocoelopus* cf. sp. MSL2007	tribe	EF213903	EF213873	EF213955
	Bostrichoidea	Anobiidae	Ptininae		*Ptinus*	*clavipes*	Zn, Cl	*Ptinus fur*	genus	EF362997	-	-
	Bostrichoidea	Anobiidae	Xyletininae	Xyletinini	*Caenocara*	sp.	-	*Lasioderma serricorne* (chimera)	tribe	AY748105	-	DQ222030
	Bostrichoidea	Anobiidae	Xyletininae	Xyletinini	*Euvrilletta*	*peltata*	Zn, Cl	*Lasioderma serricorne* (chimera)	tribe	AY748105	-	DQ222030
	Bostrichoidea	Anobiidae	Xyletininae	Xyletinini	*Lasioderma*	*serricorne*	Zn, Cl	*Lasioderma serricorne* (chimera)	tribe	AY748105	-	DQ222030
	Bostrichoidea	Bostrichidae	Dinoderinae		*Dinoderus*	*japonicus*	Zn, Cl	*Rhyzopertha dominica*	subfamily	AY748108	-	-
	Bostrichoidea	Bostrichidae	Dinoderinae		*Prostephanus*	*punctatus*	Zn, Cl	*Rhyzopertha dominica*	subfamily	AY748108	-	-
	Bostrichoidea	Dermestidae	Anthreninae	Anthrenini	*Anthrenus*	*verbasci*	Mn	*Anthrenus verbasci*	species	AY748112	-	-
	Bostrichoidea	Dermestidae	Dermestinae	Dermestini	*Dermestes*	*lardarius*	-	*Dermestes murinus*	genus	EF213875	EF213831	EF213932
	Bostrichoidea	Dermestidae	Dermestinae	Dermestini	*Dermestes*	*maculatus*	-	*Dermestes murinus*	genus	EF213875	EF213831	EF213932
	Bostrichoidea	Dermestidae	Dermestinae	Thorictini	*Thylodrias*	*contractus*	-	Tribe not in Hunt et al. sampling	-	-	-	-
	Buprestoidea	Buprestidae	Agrilinae		*Agrilus*	*bilineatus*	-	*Agrilus sinuatus*	genus	AF451934	AJ862731	AJ862795
	Byrrhoidea	Dryopidae			*Helichus*	sp.	-	*Pomatinus substriatus*	family	AF451924	AJ862735	DQ266502
	Byrrhoidea	Heteroceridae	Heterocerinae	Heterocerini	*Neoheterocerus*	sp.	-	*Heterocerus* sp. IR-2002	tribe	AF451928	AJ862739	AJ862803
	Byrrhoidea	Psephenidae	Eubriinae		*Ectopria*	sp.	-	*Eubrianax* sp. UPOL 000M33	subfamily	DQ100485	DQ198632	DQ198555
	Chrysomeloidea	Cerambycidae	Cerambycinae	Callidiini	*Hylotrupes*	*bajulus*	Zn, Cl	*Phymatodes testaceus*	tribe	AY748116	DQ202535	-
	Chrysomeloidea	Cerambycidae	Cerambycinae	Elaphidiini	*Enaphalodes*	*rufulus*	-	*Elaphidion mucronatum*	tribe	AJ841525	AJ841404	AM283242
	Chrysomeloidea	Cerambycidae	Lamiinae	Lamiini	*Plectrodera*	*scalator* (female)	Mn	Tribe not in Hunt et al.	-	-	-	-

								sampling				
	Chrysomeloidea	Cerambycidae	Lamiinae	Onciderini	*Oncideres*	*cingulata* (female)	Mn	*Trachysomus* sp. BDF-2000	tribe	AF267410	-	-
	Chrysomeloidea	Cerambycidae	Lamiinae	Onciderini	*Oncideres*	*cingulata* (male)	Mn	*Trachysomus* sp. BDF-2000	tribe	AF267410	-	-
	Chrysomeloidea	Cerambycidae	Lamiinae		*Dorcadion*	*sulcipenne*	-	*Dorcadion* sp. BDF-2000	genus	AF267412	-	-
	Chrysomeloidea	Chrysomelidae	Bruchinae		*Caryobruchus*	*gleditsiae*	Zn, Cl	*Caryoborus gleditsiae*	subfamily	AF267421	-	-
	Chrysomeloidea	Chrysomelidae	Chrysomelinae		*Leptinotarsa*	*decimlineata*	-	*Leptinotarsa juncta*	genus	AJ841430	AJ841314	AM283131
	Cleroidea	Cleridae	Clerinae		*Enoclerus*	*ichneumoneus*	Zn, Cl	*Enoclerus* sp. TJH-2004	subfamily	AY748128	EF517585	-
	Cleroidea	Cleridae	Clerinae		*Thanasimus*	*dubius*	Zn, Cl	*Enoclerus* sp. TJH-2004	subfamily	AY748128	EF517585	-
	Cleroidea	Cleridae	Korynetinae		*Necrobia*	*rufipes*	Zn, Cl	*Necrobia rufipes*	species	EF209698	EF508044	EF508057
	Cleroidea	Trogossiidae	Calitinae		*Calitys*	sp.	-	Subfamily not in Hunt et al. sampling	-	-	-	-
	Cleroidea	Trogossiidae	Trogossitinae		*Tenebroides*	*mauritanicus*	Zn, Cl	*Tenebroides mauritanicus*	species	EF209680	-	-
	Cucujoidea	Bothrideridae	Bothriderinae		*Deretaphrus*	*puncticollis*	Zn, Cl	*Teredus cylindricus*	family	AY748141	DQ202533	EF517589
	Cucujoidea	Coccinellidae	Coccidulinae	Noviini	*Rodolia*	*cardinalis*	-	*Rhyzobius chrysomeloides*	subfamily	EF512320	EF512342	DQ155761
	Cucujoidea	Coccinellidae	Coccinellinae		*Coleomegilla*	*maculata*	-	*Coccinella septempunctata*	subfamily	AY748147	DQ202558	DQ155757
	Cucujoidea	Coccinellidae	Coccinellinae		*Psyllobora*	*vigintimaculata*	-	*Psyllobora vigintimaculata*	species	EF209854	-	-
	Cucujoidea	Coccinellidae	Epilachninae		*Epilachna*	*varivestris*	-	*Subcoccinella vigintiquatuorpunctata*	subfamily	AY748149	DQ202528	DQ155798
	Cucujoidea	Cucujidae			*Cucujus*	*clavipes*	-	*Cucujus clavipes*	species	AF423767	DQ202569	DQ222036
	Cucujoidea	Erotylidae	Languriinae		*Pharaxanotha*	*zamia*	-	*Pharaxonotha* sp. UPOL2173	genus	EF209808	-	-
	Cucujoidea	Nitidulidae	Carpophilinae		*Aphenolia*	*monogama*	-	*Carpophilus sexpustulatus*	subfamily	AY748172	DQ202545	-
	Cucujoidea	Nitidulidae	Cryptarchinae		*Pityophagus*	*rufipennis*	-	*Pityophagus ferrugineus*	genus	EF512332	-	-
	Cucujoidea	Nitidulidae	Nitidulinae		*Hebascus*	*aurantiacus*	-	*Cychramus luteus*	subfamily	AY748176	DQ202556	DQ155899
	Cucujoidea	Nitidulidae	Nitidulinae		*Lasiodactylus*	*kelleri*	-	*Cychramus luteus*	subfamily	AY748176	DQ202556	DQ155899
	Cucujoidea	Nitidulidae	Nitidulinae		*Lobiopa*	*falli*	-	*Cychramus luteus*	subfamily	AY748176	DQ202556	DQ155899
	Cucujoidea	Nitidulidae	Nitidulinae		*Platychora*	*decorata*	-	*Cychramus luteus*	subfamily	AY748176	DQ202556	DQ155899
	Cucujoidea	Nitidulidae	Nitidulinae		*Prometopia*	*sexmaculata*	-	*Prometopia quadrimaculata*	genus	EF209743	-	-
	Cucujoidea	Nitidulidae	Nitidulinae		*Psilotus*	*atratus*	-	*Prometopia quadrimaculata*	subfamily	EF209743	-	-
	Cucujoidea	Silvanidae	Silvaninae		*Ahasverus*	*advena*	-	*Silvanus unidentatus*	subfamily	AY748181	DQ202526	DQ155740
	Cucujoidea	Silvanidae	Silvaninae		*Cathartus*	*quadricollis*	-	*Silvanus unidentatus*	subfamily	AY748181	DQ202526	DQ155740
	Cucujoidea	Silvanidae	Silvaninae		*Oryzaephilus*	*mercator*	-	*Silvanus unidentatus*	subfamily	AY748181	DQ202526	DQ155740
	Cucujoidea	Silvanidae	Silvaninae		*Oryzaephilus*	*surinamensis*	-	*Silvanus unidentatus*	subfamily	AY748181	DQ202526	DQ155740
	Cucujoidea	Sphindidae	Sphindinae		*Sphindus*	*americanus*	-	*Sphindus dubius*	genus	AY748183	DQ202550	DQ222024
	Curculionoidea	Anthribidae	Anthribinae		*Euparius*	*marmoreus*	Zn, Cl	*Anthribus nebulosus*	subfamily	AJ849975	-	-
	Curculionoidea	Anthribidae	Choraginae		*Araecerus*	*fasciculatus*	Zn, Cl	*Choragus sheppardi*	subfamily	AJ849977	-	-
	Curculionoidea	Curculionidae	Cryptorhynchinae	Cryptorhynchini	*Cryptorhynchus*	*lapathi*	Zn, Cl	*Acalles ptinoides*	tribe	AJ850002	-	DQ155807
	Curculionoidea	Curculionidae	Curculioninae		*Curculio*	*caryae*	-	*Curculio glandium*	genus	AJ850003	-	AY327711
	Curculionoidea	Curculionidae	Platypodinae		*Euplatypus*	*compositus*	Zn, Cl	*Euplatypus hintzi*	genus	AJ850035	-	-
	Curculionoidea	Curculionidae	Platypodinae		*Myoplatypus*	*flavicornis*	Zn, Cl	*Euplatypus hintzi*	subfamily	AJ850035	-	-
	Curculionoidea	Curculionidae	Scolytinae	Hylesinini: Hylastina	*Hylastes*	*porculus*	Zn, Cl	*Hylastes porculus*	species	AF308339	-	AF375321
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Corthylina	*Corthylus*	*columbianus*	Zn, Cl	*Gnathotrupes* sp. SCL06	subtribe	AF375252	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Corthylina	*Gnathotrichus*	*materiarius*	Zn, Cl	*Gnathotrupes* sp. SCL06	subtribe	AF375252	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Ambrosiodmus*	*leconti*	Zn, Cl	*Xyleborinus saxeseni*	subtribe	AJ850038	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Anisandrus*	*sayi*	Zn, Cl	*Xyleborinus saxeseni*	subtribe	AJ850038	-	-

	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Euwallacea*	*validus*	Zn, Cl	*Xyleborinus saxeseni*	subtribe	AJ850038	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Premnobius*	*cavipennis*	Zn, Cl	*Xyleborinus saxeseni*	subtribe	AJ850038	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Xyleborinus*	*saxeseni*	Zn, Cl	*Xyleborinus saxeseni*	species	AJ850038	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Xyleborus*	*californicus*	Zn, Cl	*Xyleborus dispar*	genus	AJ850045	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Xyleborus*	*volvulus*	Zn, Cl	*Xyleborus dispar*	genus	AJ850045	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Xylosandrus*	*crassiusculus*	Zn, Cl	*Xylosandrus* sp. SCY05	genus	AF375263	-	-
	Curculionoidea	Curculionidae	Scolytinae	Scolytini: Xyleborina	*Xylosandrus*	*germanus*	Zn, Cl	*Xylosandrus* sp. SCY05	genus	AF375263	-	-
	Curculionoidea	Curculionidae	Scolytinae		*Dendroctonus*	*frontalis*	Zn, Cl	*Dendroctonus terebrans*	genus	AF308338	-	AF375315
	Curculionoidea	Curculionidae	Scolytinae		*Dendroctonus*	*tenebrans*	Zn, Cl	*Dendroctonus terebrans*	species	AF308338	-	AF375315
	Curculionoidea	Curculionidae	Scolytinae		*Ips*	*calligraphus*	Zn, Cl	*Ips grandicollis*	genus	AF250074	-	AF113349
	Curculionoidea	Curculionidae	Scolytinae		*Ips*	*grandicollis*	Zn, Cl	*Ips grandicollis*	species	AF250074	-	AF113349
	Curculionoidea	Curculionidae	Scolytinae		*Orthotomicus*	*caelatus*	Zn, Cl	*Orthotomicus caelatus*	subfamily	AF308343	-	AF113391
	Curculionoidea	Curculionidae	Scolytinae		*Scolytus*	*muticus*	Zn, Cl	*Scolytus multistriatus*	genus	AJ850043	-	AF375329
	Curculionoidea	Curculionidae	Scolytinae		*Scolytus*	*schevyrewi*	Zn, Cl	*Scolytus multistriatus*	genus	AJ850043	-	AF375329
	Dascilloidea	Dascillidae	Karumiinae		*Anorus*	*piceus*	-	*Dascillus cervinus*	family	AY745558	AJ862742	DQ221982
	Derodontoidea	Derodontidae	Derodontinae		*Derodontus*	*esotericus*	Zn, Al, P	*Laricobius erichsoni*	subfamily	AF427606	DQ202530	DQ155816
	Elateroidea	Eucnemidae	Melasinae		*Isorhipis*	*obliqua*	Zn, Cl	*Entomophthalmus americanus*	subfamily	DQ100491	DQ198638	-
	Elateroidea	Phengodidae	Phengodinae		*Phengodes*	*plumosa*	-	*Phengodes* sp. M29	genus	DQ100504	DQ198661	DQ198583
	Hydrophiloidea	Histeridae	Histerinae		*Platysoma*	sp.	-	*Platysoma punctigerum*	genus	AY028358	-	-
	Hydrophiloidea	Hydrophilidae	Hydrophilinae	Hydrophilini	*Hydrophilus*	sp.	-	*Enochrus testaceus*	tribe	AJ810719	DQ202576	DQ221978
	Lymelyloidea	Lymexylidae	Lymexilinae		*Atractocerus*	sp.	Zn, Cl	*Lymexylon navale*	subfamily	AY748185	DQ202588	DQ221992
	MYXOPHAGA	Hydroscaphidae			*Hydroscapha*	*natans*	-	*Hydroscapha natans*	species	AF012525	-	-
	Scarabaeoidea	Passalidae	Passalinae		*Odontotaenius*	*disjunctus*	-	*Odontotaenius disjunctus*	species	AY745573	-	DQ028966
	Scarabaeoidea	Passalidae	Passalinae		*Odontotaenius*	*disjunctus*	-	*Odontotaenius disjunctus*	species	AY745573	-	DQ028966
	Scirtoidea	Eucinetidae			*Eucinetus*	*morio*	-	*Eucinetus* sp. APV-2001	genus	AF427609	AJ862756	AJ862822
	Staphylinoidea	Silphidae	Nicrophorinae		*Nicrophorus*	sp. nr. *americanus*	-	*Nicrophorus humator*	genus	EF213789	-	-
	Staphylinoidea	Staphylinidae	Osoriinae		*Leptochirus*	sp.	-	*Osorius* sp. TJH-2004	subfamily	AY745623	-	-
	Tenebrionoidea	Ciidae	Ciinae		*Ceracis*	*thoracicornis*	-	*Cis nitidus*	subfamily	AY748191	DQ202540	DQ156020
	Tenebrionoidea	Meloidae	Meloinae		*Meloe*	*dianella*	-	*Meloe* sp. TJH2004	genus	AY748196	DQ202612	-
	Tenebrionoidea	Mordellidae	Mordellinae	Mordellini	*Mordella*	sp.	-	*Mordella brachyura*	genus	EF209922	EF490144	EF490172
	Tenebrionoidea	Mycetophagidae	Mycetophaginae		*Typhaea*	*stercorea*	-	*Mycetophagus quadripustulatus*	subfamily	AY748199	EF490159	DQ155907
	Tenebrionoidea	Mycteridae	Mycterinae		*Mycterus*	sp.	-	Family not in Hunt et al. sampling	-	-	-	-
	Tenebrionoidea	Oedemeridae	Nacerdinae		*Nacideres*	*melanura*	-	*Nacerdes hilleri*	genus	EF209974	EF490146	EF490174
	Tenebrionoidea	Rhipiphoridae	Rhipiphorinae	Macrosaigonini	*Macrosaigon*	sp.	-	*Macrosiagon* sp. UPOLZ086	genus	EF209933	-	-
	Tenebrionoidea	Tenebrionidae	Bolitophaginae	Bolitophagini	*Bolitotherus*	*cornutus*	-	*Bolitophagus reticulates*	tribe	EF362998	-	-
	Tenebrionoidea	Tenebrionidae	Diaperinae	Diaperini: Diaperina	*Neomida*	sp. nr. *bicornis*	-	*Diaperis lewisi*	subtribe	EF209946	EF490153	EF490183
	Tenebrionoidea	Tenebrionidae	Diaperinae	Diaperini: Diaperina	*Platydema*	sp.	-	*Diaperis lewisi*	subtribe	EF209946	EF490153	EF490183
	Tenebrionoidea	Tenebrionidae	Opatrinae		*Eleodes*	*carbonarius*	-	*Eleodes sulcipennis*	genus	AF423769	-	-
	Tenebrionoidea	Zopheridae	Monommatini		*Monomma*	sp.	-	Monommidae sp. UPOLZ110	tribe	EF209937	EF490142	EF490170
	Tenebrionoidea	Zopheridae	Zopherini		*Zopherus*	*concolor*	-	*Usechus lacerta*	subfamily	AY748216	DQ202562	EF517593

CONCLUSION

Although a decent amount of previous research has been conducted on the beetle family Zopheridae, a number of critical gaps in our collective knowledge of this economically important group exist. Aspects of identification, classitication, and phylogeny need to be addressed with greater rigor, and this was the aim of my individual dissertation chapters.

Accurate identification of zopherid species or even genera is often difficult due to the lack of available resources. IroncladID (Chapter 1) was constructed as an attempt to remedy this issue. IroncladID includes an interactive Key to Genera & Species, Genus Fact Sheets, species diagnoses, and hundreds of images to aid in the identification of Ironclad and Cylindrical Bark Beetles found in North America north of Mexico. Upon completion, the tool was peer reviewed by a number of taxonomic experts and then released for distribution. This tool is currently included in the larger USDA Wood Boring Beetle Resource, a comprehensive resource of identification and screening tools for wood boring beetles of the world (available from: http://wbbresource.org/).

Because of the zopherid hyperdiversity that exists in New Zealand, it is imperative that sound taxonomic work begins with a study of the primary literature and museum specimens. Thus, an illustrated catalogue to the new Zealand Zopheridae was constructed (Chapter 2). For this chapter, we examined nearly all types, photorecorded primary types and associated labels, designate lecto- and paralectotypes, and provide synonymies and replacement names where necessary. The purpose of this paper is to stabilize the nomenclature of the New Zealand species in a critical foundational step before proceeding with revisionary studies.

In order to assess the constitution, monophyly, and relationships within Zopheridae and among other tenebrionoid families, I conducted the first molecular phylogenetic analyses of the family (Chapter 3). Analyses suggest a non-monophyletic Zopheridae. In order for the classification of Tenebrionoidea to be consistent with these findings, Zopheridae *sensu lato* will need to be divided into family groupings more similar to previously-held concepts, including a resurrection of the family-groups Colydiidae and Zopheridae, although the previously-recognized family-group Monommatidae would continue to be retained as a tribe within Zopheridae. Our analyses recovered many of the previously-accepted tribes within the subfamilies Zopherinae and Colydiinae, however, a few of the tribes (*e.g.* Zopherini, Colydiini and Synchitini) were recovered as polyphyletic, although this is not unexpected. Morphological investigations of members of these tribes have yet to result in any concrete characters for delimiting the majority of the currently-recognized groups and appear to be based on variable and/or apomorphic characters (*e.g.* Orthocerini, Rhopalocerini). If results from current analyses stand, the entire tribal classification system will need to be eliminated in favor of a "supertribe" as suggested by previous zopherid workers (M. Ivie, S.A. Ślipiński, R.A.B. Leschen, *pers. comm.*). Although these analyses are a positive step in the direction towards a revised classification of Zopheridae, few concrete, actionable results were obtained. This phylogeny succeeded in confirming the fears of previous zopherid workers, demonstrating a messy and quite unresolved clustering of tenebrionoids. Encouragingly, the loci and taxa sampled for these analyses provided decent resolution at the more terminal nodes. While this begins to aid in the resolution of genus-group relationships and point out more glaring problems in our current tribal classifications, the poor resolution of the internal nodes needs to be remedied. Once accomplished, taxonomic alterations may be made to provide a more concrete definition of the included groups. As it stands, Zopheridae and the groups therein are still heavily under question, and this is complicated further by the highly convergent morphology within the Tenebrionoidea. It is our hope that additional molecular markers and taxon sampling can continue to aid in the resolution of this enigmatic group of LBBs (little brown beetles).

In Chapter 4, I conducted a broad-scale analysis of metal incorporation across the order Coleoptera using a unique microscopy set-up. From an instrumentation perspective, advances in SEM configurations now allow for an efficient, cost-effective solution for the investigation of the presence of cuticular metals. We demonstrated numerous instances of metal incorporation throughout the order. Resultant patterns of metal incorporation were strongly correlated with adult mandibular use and appear to have originated several times throughout Coleoptera. Additionally, the location and types of cuticular metals are demonstrated to be potentially valuable characters for taxonomic diagnoses. The findings presented here make a strong case for the taxonomic and natural history implications of cuticular metal incorporation. Thus, the incorporation of metals into the mandibles likely has both taxonomic implications, potentially serving as a character for the separation of natural groups, as well as implications about the natural history of those groups.

The over-arching goal of this dissertation was to add to our general knowledge of Coleoptera via a diversity of research questions and methodologies. Foundational studies on the enigmatic beetle family Zopheridae were conducted, and phylogenetic information pertaining to the incorporation of metals as a potential driver for coleopteran diversity was revealed. This research paves the way for additional investigations on these topics, and it is my sincere hope my work benefits entomology and science as a whole.

APPENDIX A

Lucid3 Key for Chapter 1 – IroncladID.

Available from: http://coleopterasystematics.com/ironcladid/IroncladID-key-portal.html

APPENDIX B

Gallery for Chapter 1 – IroncladID.

Available from: http://coleopterasystematics.com/ironcladid/IroncladID-gallery.html

APPENDIX C

Morphological Atlas for Chapter 1 – IroncladID.

Available from: http://coleopterasystematics.com/ironcladid/IroncladID-morphology.html

APPENDIX D

Glossary for Chapter 1 – IroncladID.

The following structures and descriptive terms are found throughout the Ironclad ID resource. The terms below have been defined using the Torre-Bueno Glossary of Entomology (Nichols 1989) and Lawrence *et al*. (1999, 2010).

Abdominal process (intercoxal process of abdominal ventrite I): projection on ventrite 1 which extends anteriorly between metacoxae.

Abdominal ventrite: visible ventral abdominal sclerite. Ventrite number does not correspond to true sternite number except in rare cases where sternite 1 is visible. Also called ventrite.

Acute: pointed; terminating in or forming less than a right angle.

Antennae: paired, segmental appendages, borne one on each side of head, functioning as sense organs and bearing a large number of sensilla.

Antennal club: an enlarged portion of the antennal apex, consisting of a variable number of antennomeres (often 3). In an incrassate, antenna the antennomeres gradually enlarge towards to apex, but if there is an abrupt change in length or width at some point, then the antennomeres beyond this are considered to be part of the club.

Antennal cavity: a prothoracic cavity for housing the whole antenna or a portion of the antenna (usually the club).

Antennal insertion: point of attachment for the antennae, consisting of an opening in the head capsule, sometimes with a reinforced sclerotized ring.

Antennomere: antennal segment; including scape, pedicel and flagellomeres.

NOTE: the flagellum is composed of all antennal segments proceeding the scape and pedicel. Any individual antennal segment is commonly called an antennomere

Anterior: in front; before.

Apex (pl. apices): end of any structure distad to the base.

Apical (apicad): an adjective (or adverb) denoting position near or movement toward the apex of a body part. The apex of the head or pronotum is at the anterior end while that of the abdomen or an elytron is at the posterior end; on the legs or antennae, apical and distal are synonymous.

Arcuate: arched or bowlike.

Basal (basad): an adjective (or adverb) denoting position near or movement toward the base of a body part. The base of the head or pronotum is at the posterior end while that of the abdomen or an elytron is at the anterior end; on the legs or antennae, basal and proximal are synonymous.

Bisinuate: with 2 sinuations or incisions.

Callosity: a rather flattened elevation not necessarily harder than the surrounding tissue.

Canthus (pl. canthi): a sclerotized bar encroaching on the eye.

Carina (pl. carinae): an elevated ridge or keel, not necessarily high or acute.

Clypeus: the area of the beetle head between the frontoclypeal suture and the labrum, or in the absence of a frontoclypeal suture, the area just behind the labrum and in front of the eyes. Also called the epistoma.

Concave: hollowed out; the interior of a sphere as opposed to the outer or convex surface.

Confluent: running together.

Connate: united at base, or along the entire length; fused.

Connate ventrites: ventrites which are immovably united, so that they can not slide over one another as they can when joined by membrane. This may be used as a synonym with fused ventrites, but they are always deparated by a groove or line, while fusion sometimes involves the disappearance of any joining line.

Convex: the outer curved surface of a segment of a sphere, as opposed to concave.

Cordate (cordiform): heart-shaped; triangular, with the corners of the base rounded; not necessarily emarginate at the middle of the base.

Coxa: the basal segment of the leg, by means of which it is articulated to the body.

Denticulate: set with little teeth or notches.

Depressed: flattened down as if pressed.

Distal (distad): an adjective (or adverb) denoting position near or at or movement toward the free end of an appendage or that furthest from the body.

Dorsal (dorsad): an adjective (or adverb) denoting position near or movement toward the upper side of the body or a body part.

Elytral declivity: the downward slope of the elytra, near the apex.

Elytral suture: the line formed when two elytra in folded or closed position meet along the midline.

Elytron (pl. elytra): the fore wing in Coleoptera, which is more or less uniformly sclerotized and in resting position is longitudinally oriented, usually meeting the opposite elytron along the midline.

Emarginate: notched at the margin.

Epipleuron (pl. epipleura): a lateral, infolded portion of the elytra, which is separated from the elytral disc by a distinct fold or carina and which usually fits against the lateral portions of the abdomen.

Epipleural fold: a fold in the elytron which separates the elytral disc from the epipleuron.

Explanate: spread out and flattened; applied to a margin.

Eye facet: individual parts of the external surface of the compound eye; often convex but sometimes more or less flattened.

Femur (pl. femora): the third and usually the stoutest segment of the beetle leg, articulated proximally with trochanter (or if the latter is absent, then the coxa) and distally with the tibia.

Ferrogino-testaceous: rusty yellow-brown

Ferrugineous: rusty red-brown

Frons: the area between the eyes and just behind the frontoclypeal suture. In Coleoptera it is not or only rarely separated from the vertex posteriorly.

Glabrous: without hairs (setae).

Heteromeroid (trochanter type): a type of strongly oblique trochantofemoral attachment with the base of the femur abutting the coxa.

Hypomeron (pl. hypomera): that portion of the pronotum which is visible from the ventral side; when there is a lateral pronotal carina, this is the portion below that carina (the pronotal disc being above it).

Impression: an indentation or depression on a surface.

In repose: at rest.

Interfacetal setae (of eye): setae arising between adjacent eye facets.

Interspaces (interval): the space between two structures or sculptures.

Interstria (interstice) (of elytra): the space between two lines, whether striate or punctate.

Labial palp: the one- to four-segmented appendage of the insect labium, borne on the palpiger.

Lateral (laterad): an adjective (or adverb) denoting position near or movement toward the sides of the body.

Lateral pronotal carina (pl. carinae): a sharp lateral edge on the prothorax separating the pronotal disc above and the hypomeron below.

Macula (pl. maculae): a spot or mark.

Maculate: spotted; with many superficial marks or spots.

Mandible: one of the paired lateral biting jaws in beetles, lying just below the labrum and just above the maxillae. The mandible is usually relatively stout and heavily sclerotized, with one or more apical teeth, a basal mola or grinding area, a membranous prostheca distal to the mola and sometimes one or more accessory teeth.

Matte: lacking or deprived of luster or gloss.

Maxillary palp: one- to seven-segmented appendage of the insect maxilla, carried by the stipes on its outer end, being sensory in function.

Medial fleck (of flight wings): binding patch located in the medial field. In Polyphaga this is located in front of MP3+4.

Median: on the midline.

Mesal (mesad): an adjective (or adverb) denoting position near or movement toward the midline of the body.

Meso-: prefix referring to a structure forming part of the mesothorax, including mid legs (e.g. mesocoxa, mesepisternum, mesotarsus, mesepisternum).

Mesocoxae: the coxae of the mesothorax.

Mesothorax: the second (middle) segment of the beetle thorax.

Mesotibia: the tibia of the mesoleg.

Meta-: prefix referring to a structure forming part of the metathorax, including hind legs (e.g. metacoxa, metepimeron, metatibia, metaventrite).

Metacoxae: the coxae of the metathorax.

Metathorax: the third (posterior) segment of the beetle thorax.

Metaventrite: ventral plate lying behind and between the mesocoxal cavities and delimited laterally by the metanepisterna.

Nodule: a small knot or swelling.

Oblique: slanting; any direction between perpendicular and horizontal.

Opaque: without any surface luster.

Palpomere: palp segment.

Pedicel: the second segment of the insect antenna, supporting the flagellum.

Piceus: black

Postcoxal process: mesal extension of the posterior part of the propleuron or hypomeron behind the procoxa, which may meet the prosternal process or the opposing postcoxsal process, thus closing the procoxal cavitiy externally.

Posteriad: toward the posterior end.

Posterior: hinder or hindmost, opposed to anterior; hind or rear.

Preapical groove (of abdominal ventrite V): a groove located just before the apex of abdominal ventrite V.

Pro-: prefix referring to a structure forming part of the prothorax, including fore legs (e.g. procoxa, prosternum, protrochantin, protarsus).

Procoxae: the coxae of the prothorax.

Procoxal cavities: countersunk prothoracic housing into which the procoxa fits. Formed in part by the prosternum and in part by the propleuron or pronotal hypomeron.

Procoxal cavities: external closure: externally closed when the postcoxal processes of the hypomera meet the prosternal process or meet one another.

Pronotal disc: the area of the pronotum which is visible dorsally and usually delimited laterally by the two lateral carinae. Contrasted with the paired pronotal hypomera, which extend onto the ventral surface.

Pronotum: dorsal portion of the pronotum, lying above the lateral pronotal carinae when these are present.

Prosternal process: projection of the mesal portion of the prosternum which extends between the procoxae and may overlap the mesoventrite or fit into the mesoventral cavity.

Prosternum: used for the entire ventral plate lying in front of and between the procoxae and between the notosternal or pleurosternal sutures.

Prothorax: the first segment of the beetle thorax.

Protrochantin: a precoxal sclerite articulating with the procoxa, prosternum and pleuron or sometimes fused to the pleuron or apparently absent.

Proximal: that part of an appendage nearest the body, as opposed to distal.

Pubescence: short, fine, soft, erect hair or down.

Pubescent: downy; clothed with soft, short, fine, loosely set hair.

Puncture: a small impression on the cuticle, like that made by a needle.

Quadrate: four-sided.

Recumbent: lying down; reclining.

Reniform: kidney-shaped.

Rugose: wrinkled.

Scabrous: irregularly and roughly rugose; possessing short, sharp projections or wrinkles.

Scape: the first or basal segment of the insect antenna.

Scutellar Shield: exposed portion of the mesoscutellum which lies between the bases of the elytra.

Scutellary striole: a shortened stria or puncture row lying just laterad of the scutellum but not extending very far posteriorly.

Scutellum: posterior portion of mesotergum. Often referring only to that portion of the scutellum which is visible between the bases of the elytra (see Scutellar Shield).

Secretory pore: a pore that exudes a glandular secretion.

Serrate: sawlike, i.e., with notched edges like the teeth of a saw.

Serrulate: finely serrated; with minute teeth or notches.

Seta (pl. setae): a sclerotized, hairlike (or scalelike) projection of cuticula arising from a single trichogen cell and surrounded at the base by a small cuticular ring.

Sinuate: wavy, applying specifically to edges and margins.

Spine: a multicellular, more or less thornlike process or outgrowth of the cuticle not separated from it by a joint.

Subantennal groove: groove or concavity lying below the antennal insertion and housing the base of the antenna. Placed between the eye (if present) and the mandibular articulation, and sometimes extends below or behind the eye.

Subequal: similar, but not equal in size, form or length.

Subgenal ridges: a pair of sharp longitudinal ridges extending from the maxillary articulations to the posterior region of the head and usually forming the lateral edges of a concavity. The subgenal ridges usually occur in conjunction with a strongly declined head and fit against the procoxae when the head is at rest.

Sublateral: just inside the lateral margin.

Sublateral pronotal carina: applied to various longitudinal carinae lying mesad of the lateral carinae. These may extend the length of the pronotal disc or be restricted to the posterior angles.

Tarsal claw: usually one of two articulated, sclerotized, claw-like processes attached to the apex of the tarsus. These claws and the empodium comprise the pretarsus. Occasionally, there is a single claw or none at all.

Tarsal formula: the number of tarsomeres on the fore, mid, and hind tarsi, respectively.

Tarsomere: one of the divisions of the tarsus.

Tarsus (pl. tarsi): the fifth segment of the beetle leg, which is articulated proximally with the tibia and distally with the pretarsus; almost always subdivided into two to five tarsomeres.

Temple: the lateral portion of the head between the posterior edge of the eye and an abrupt narrowing of the head to form a posterior neck.

Testaceous: brownish-yellow

Tibia (pl. tibiae): the fourth and often the longest segment of the beetle leg, articulated proximally with the femur and distally with the first tarsomere.

Tibial spur: an articulated, multicellular, spur-like process located at the apex of the tibia; usually paired but occasionally single, and sometimes absent.

Tomentose: covered with a form of pubescence composed of short, matted, woolly hair.

Trochanter: the second segment of the beetle leg, articulated proximally with the coxa and distally with the femur; usually a relatively small sclerite and occasionally highly reduced or absent.

Trochantin: a precoxal sclerite articulating with the coxa, sternum and pleuron or sometimes fused to the pleuron or apparently absent.

Truncate: cut off squarely at the tip.

Tubercle: a small knoblike or rounded protuberance.

Variegated: of several colors in indefinite pattern.

Ventral (ventrad): an adjective (or adverb) denoting position near or movement toward the lower side of the body or a body part.

Vestiture: the general surface covering comprised of cuticular projections, e.g., setae, scales, or spicules.

APPENDIX E

USDA Legal Jargon for Chapter 1 – IroncladID.

Ironclad ID was developed and published by the Center for Plant Health Science and Technology (CPHST) as part of a cooperative agreement with the University of New Mexico (UNM). The tool and fact sheets are available from the following web address (last updated 05 June, 2011): http://coleopterasystematics.com/ironcladid/

The interactive identification key runs as a Lucid3 Java Applet. Please read the Lucid3 system requirements for information regarding operating systems, web browsers, and other software needed to run the key.

This key has been constructed for identifying all genera and species of Ironclad and Cylindrical Bark Beetles known to occur in North America north of Mexico. This key does not include taxa known to occur in Mexico. It is very possible (and likely) additional zopherid taxa have been and will be introduced into or discovered within North America. If you believe you have a specimen that does not properly key to a listed entity, please contact the key author.

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Taxonomy: It should be noted that no taxonomic or nomenclatural changes are proposed in Ironclad ID. We feel that an identification tool is not the appropriate outlet for such changes, and any inconsistencies herein are purely out of error, rather than an explicit taxonomic statement.

Suggested Citation: Lord, N.P, Nearns, E.H., and K.B. Miller. 2011-2013. Ironclad ID: Tool for Diagnosing Ironclad and Cylindrical Bark Beetles (Coleoptera: Zopheridae) of North America north of Mexico. The University of New Mexico and Center for Plant Health Science and Technology, USDA, APHIS, PPQ.

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APPENDIX F

USDA Official Announcement of Tool Release for Chapter 1 – IroncladID.

Appendix F is available as a supplementary file via LoboVault. See PDF titled "Appendix_F_USDA_Announcement".

APPENDIX G

Figure Captions and Figures for Chapter 2 – Illustrated Catalogue and Type Designations of the New Zealand Zopheridae (Coleoptera: Tenebrionoidea).

Appendix G is available as a supplementary file via LoboVault. See PDF titled "Appendix_G_Figures_Chapter2".

APPENDIX H

Figures for Chapter 3 – Phylogenetic Analysis of the Ironclad and Cylindrical Bark Beetles of the World (Coleoptera: Tenebrionoidea: Zopheridae).

Appendix H is available as a supplementary file via LoboVault. See PDF titled "Appendix_H_Figures_Chapter3".

APPENDIX I

Figures for Chapter 4 – Novel Microscopy Techniques Reveal Multiple Evolutionary Origins of Metal Incorporation into Mandibles of the Megadiverse Beetles (Coleoptera).

Appendix I is available as a supplementary file via LoboVault. See PDF titled "Appendix_I_Figures_Chapter4".

APPENDIX J

ESEM EDS scans for Chapter 4 – Novel Microscopy Techniques Reveal Multiple Evolutionary Origins of Metal Incorporation into Mandibles of the Megadiverse Beetles (Coleoptera).

Appendix J is available as a supplementary file via LoboVault. See PDF titled "Appendix_J_Figures_Chapter4".