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A phylogenetic analysis of the tribe Zopherini with a review of the species and generic classification (Coleoptera: Zopheridae)

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Abstract

A morphology-based phylogenetic analysis of all known species (excluding the well-revised *Zopherus* Gray) of the tribe Zopherini was performed. The genus *Sesaspis* Casey is elevated from synonymy, redescribed and two new species are described from Central America, *Sesaspis ashei* NEW SPECIES and *Sesaspis triplehorni* NEW SPECIES. The following NEW COMBINATIONS are proposed: *Noserinus furcatus* (Kirsch), *Phloeodes venustus* (Champion), *Sesaspis emarginata* (Horn), *Sesaspis lutosa* (Champion), *Sesaspis sylvatica* (García-París *et al.*), and *Sesaspis doyeni* (García-París *et al.*). The following NEW SYNONYMIES are proposed: *Phloeodes pustulosus* LeConte of *Phloeodes diabolicus* LeConte, *Nosoderma prominens* Casey, *Nosoderma senex* Casey, *Nosoderma brevicollis* Casey, and *Nosoderma subglabrus* Casey of *Eurychora inaequale* Say *as Verodes inaequalis* (Say), *Nosoderma insigne* Champion of *Nosoderma interruptum* Champion as *Verodes interruptus* (Champion), *Noserodes squalidus* Casey of *Nosoderma guatemalense* Champion as *Verodes guatemalensis* (Champion), *Scoriaderma congolense* Fairmaire of *Nosoderma scabrosum* Solier as *Verodes scabrosus* (Solier), and *Scoriaderma comoriense* Fairmaire of *S. cordicolle* Waterhouse. A revised key to the world genera is provided, as well as keys to all species of the tribe, save those of *Zopherus*, including the multispecies genera *Noserinus* Casey, *Nosoderma* Guérin-Méneville, *Phloeodes* LeConte, *Sesaspis* Casey, and *Verodes* Casey. A synoptic catalog of the described species is provided, with brief comments on the taxonomic histories of the tribe, genera, and species. All recognized species are illustrated and diagnosed, with information on their types, taxonomic history and geographic distributions.

Key words: Coleoptera, Zopheridae, new species, taxonomy

Introduction

The tribe Zopherini represents the majority of the beetles commonly referred to as “ironclad” beetles (excluding only the genus *Phellopsis* LeConte). This very diverse tribe is most species-rich in southern North America (*i.e*. Central America, Mexico and the southwestern USA), but species also occur in Africa, Australia, Cuba, peninsular Malaysia, and South America.

Several recent publications on the Zopherini have rendered the species-level taxonomy virtually indiscernible. For example, the reasonably common California species’ epithet *Nosoderma plicatum* LeConte has changed generic combination in every modern paper dealing with the tribe. This species was placed in *Noserus* LeConte by Doyen and Lawrence (1979), *Phloeodes* LeConte by Ślipiński and Lawrence (1999), and *Nosoderma* Solier (*not* Guérin-Méneville) by García-París *et al.* (2006). To confuse the issue even more, the correct authorship and type species of *Nosoderma* Guérin-Méneville was recently determined (Foley and Ivie 2007), which, if the classification of García-París *et al.* (2006) is followed, results in an additional change in the generic combination to *Verodes* Casey. Obviously, the taxonomic history of the tribe is very confusing, and hopefully, this paper will clear up, rather than add to, the confusion within the ironclad beetles.

As evidenced above, the historic nomenclature of the Zopherini is very unstable (Solier 1841, LeConte 1862, LeConte and Horn 1883, Casey 1907b, Gebien 1936) and more recent attempts to resolve the issues within the tribe have not fared much better (Doyen and Lawrence 1979, García-París *et al.* 2001, García-París *et al.* 2006). The problems with the prevailing taxonomic work on the group are the result of either under-sampling for synthetic works (Doyen and Lawrence 1979, Ślipiński and Lawrence 1999) or random species descriptions with questionable and unsupported generic placements (García-París *et al.* 2001, García-París *et al.* 2006). The generic concepts that follow here basically mirror the findings of the phylogenetic analysis of Ślipiński and Lawrence (1999) and the proposed changes result from the inclusion of additional taxa not examined by those authors.

The confusion in this group centers on the North American species and their generic limits, where the majority of the diversity occurs. The old world genera are now all monotypic: *Zopherosis* White (Australia), *Zopher* Ślipiński and Lawrence (Malaysia) and *Scoriaderma* Fairmaire (Africa, rendered monotypic after a species is removed and another synonymized below). These, as well as the large American genus *Zopherus* Gray have been recently defined in essentially the same form as treated here (Ślipiński and Lawrence 1999).

However, for the genera of zopherines with 10-segmented antennae, a notable lack of useful defining characters (LeConte 1862, Casey 1907b, Gebien 1936) was a significant obstacle to placing several Central American species in one of the two genera recognized by Ślipiński and Lawrence (1999)—*Phloeodes* LeConte and *Nosoderma* Solier (*not* Guérin-Méneville). Therefore, all named and unnamed species of the Zopherini (excluding the recently revised and well-defined genus *Zopherus* Gray, represented by exemplars) were reevaluated based on type specimens and all available museum material, using morphological characters. This resulted in a reclassification of the genera, including the elevation from synonymy of *Sesaspis* Casey, several changes in the species assigned to various genera, and correct usage of *Nosoderma* Guérin-Méneville (=*Meralius* Casey of Ślipiński and Lawrence 1999, see Foley and Ivie 2007). Of the 21 species of Zopherini with 10-segmented antennae (Nosodermini of Casey 1907b) recognized here that were known when Ślipiński and Lawrence (1999) revised the genera of Zopheridae, only 6 remain in the generic combinations they recognized.

Included in the Zopherini Solier (*sensu* Ślipiński and Lawrence 1999) are all of the genera of larger zopherids, of the typical "ironclad" appearance that have always formed the core of the zopherid complex, except *Phellopsis* LeConte (Phellopsini, see Foley and Ivie 2008). With the exclusion of the genus *Phellopsis*, the remaining members of the Zopherini form a stable, probably monophyletic group (Ślipiński and Lawrence 1999). Members of the tribe Zopherini exhibit an immense amount of intraspecific variation (Triplehorn 1972), which has made species-level definitions complex and difficult to establish. While the higher-level

relationships of the subfamily Zopherinae appear well resolved (Ślipiński and Lawrence 1999), many problems exist in the definition and placement of individual species.

Taxonomic history of the Zopherini

Gray (1832) published the first description of what would become know as "ironclad beetles" when he described *Zopherus chilensis* Gray and *Z. mexicanus* Gray. Guérin-Méneville (1838) described the first valid species of *Nosoderma*, *N. echinatum* from Cuba. The tribe Zopherini was originally proposed by Solier (1841, as Zophérites), for the New World genera *Zopherus*, *Nosoderma*, and *Dicerode*res (the last now in the Tenebrionidae, Gebien 1936) and expanded both zopherine genera adding several New World species.

White (1859) next described the monotypic genus *Zopherosis* from Australia. While it has remained unchanged for almost 150 years, the other genera have not been nearly as stable. LeConte (1862) moved several species described in *Nosoderma* and *Bolitophagus* Illiger into 3 new genera, recognizing 5 genera of Zopherini in his tenebrionid subfamily Tentyriinae: *Noserus* LeConte, *Nosoderma*, *Phellopsis*, *Phloeodes* LeConte, and *Zopherus*.

Further additions to the Zopherini included the African genus *Scoriaderma* Fairmaire 1894, for *Nosoderma cordicolle* Waterhouse 1880, and *Scoriaderma congolense* Fairmaire, 1894. *Scoriaderma* was described without explicit tribal placement but with noted affinities to *Nosoderma echinatum* Guérin-Méneville 1838.

The vast majority of names (many questionable) applied to species of zopherids (*sensu* Solier) were described in the late 19th and early 20th centuries (e.g. Champion 1884, Casey 1907a, 1907b). Champion (1884) described 10 new species of *Zopherus* (of which only 2 names are currently considered valid *vide* Triplehorn, 1972), and 13 new species of *Nosoderma* (of which 9 are valid based on the current analysis). Casey (1907b) divided what is now the Zopherini into three tribes: the Zopherini, Nosodermini and Zopherosini, the first containing *Zopherus* and Casey's now-synonymized genera *Megazopherus* Casey, *Zopherodes* Casey, *Zopherinus* Casey. The Nosodermini included the rest of the large ironclads with 10-segmented antennae: *Meralius* Casey, *Noserus*, *Noserinus* Casey, *Noserodes* Casey, *Nosoderma*, *Phloeodes*, *Sesaspis* Casey, *Verodes* Casey and *Phellopsi*s. The Zopherosini included the Australian *Zopherosis*. This tribal-level separation was not recognized by Gebien (1936), or subsequent authors (Triplehorn 1972, Doyen and Lawrence 1979, Ślipiński and Lawrence 1999, etc.) and is not recognized here.

Casey's papers (1907a, 1907b) created a plethora of generic and specific synonyms. *Megazopherus*, *Zopherinus*, and *Zopherodes* were synonymized with *Zopherus* by Triplehorn (1972) and *Noserodes*, *Sesaspis*, and *Verodes* were synonymized with *Nosoderma* by Doyen and Lawrence (1979). Casey created 21 specific synonyms and 1 subspecies in *Zopherus* (Triplehorn 1972), 10 in *Phloeodes* (discussed later), 6 in *Nosoderma* (discussed later), 1 in *Noserinus* (Doyen and Lawrence 1979), and 2 in *Phellopsis* (Foley and Ivie 2008). Casey described 42 species of zopherids and only two, *Zopherus uteanus* (Casey 1907a), and *V. championi* appear to be truly valid species (Triplehorn 1972, and below). These are perfect examples of Casey's well-known approach to taxonomy where he described individual variation rather than true species (Triplehorn 1972).

Gebien (1936) established several specific synonyms, moved *Nosoderma furcatus* Kirsch 1866 to *Meralius*, and added the South American genus *Exeniotis* Pascoe 1871 to the Zopherini (later returned to the Tenebrionidae, Doyen and Lawrence 1979). In the first phylogenetic analysis of the group, Ślipiński and Lawrence (1999) made additional changes to the Zopherini by synonymizing *Noserus* LeConte with *Phloeodes* LeConte (discussed later) and describing the genus *Zopher* from Southeast Asia. García-París *et al.* described two species of Zopherini (2001, 2006), and questioned the independent status of *Phloeodes* (=*Noserus*), synonymizing that genus with *Nosoderma*, without any phylogenetic data. Their conclusion is rejected based on the findings of Ślipiński and Lawrence (1999) and the current research which included all described taxa.

Previous to this study the Zopherini contained 8 genera (*sensu* Ślipiński and Lawrence 1999): *Meralius*, *Noserinus*, *Nosoderma*, *Phloeodes* LeConte, *Scoriaderma* Fairmaire, *Zopher* Ślipiński and Lawrence, *Zopherosis* White, and *Zopherus*.

The true authorship and type species of *Nosoderma* Guérin-Méneville has recently been established (Foley and Ivie 2007), and its use restricted to those species previously placed in *Meralius* Casey. The replacement name *Verodes* Casey was proposed for those species formerly placed in *Nosoderma sensu* Solier *not* Guérin-Méneville (Foley and Ivie 2007), and that dramatically changed nomenclature is followed here.

Materials—Morphology

The current study was based on the examination of several thousand specimens of Zopherini. With the exception of some species of *Zopherus*, which was adequately represented by specimens from species that are easily identifiable using Triplehorn's (1972) revision, all definable species belonging to the tribe were represented. Primary type material was examined for all but 6 named taxa of non-*Zopherus* Zopherini (*Nosoderma echinatum* Guérin-Méneville, *Nosoderma furcatus* Kirsch, *Nosoderma cordicolle* Waterhouse, *Nosoderma duponchelii* Solier, *Nosoderma sylvaticum* García-París *et al.*, and *Noserus doyeni* García-París *et al.*), but paratypes were examined for *N. doyeni*. Availability of adult specimens was sufficient to complete a thorough examination of morphology and delimit each species and genus. Types and other material for this investigation were obtained on loan from the 60 entomological collections listed below and cited in the text by the following codens (the curator responsible for the loan is listed in parentheses).

AAPC	Albert Allen Personal Collection, Boise, Idaho, USA (Albert Allen).
ANIC	Australian National Insect Collection, Canberra, ACT, Australia (S. Adam Ślipiński).
ASUT	Arizona State University, Tempe, Arizona, USA (David Pearson).
BMNH	The Natural History Museum, London, United Kingdom (Maxwell V. L. Barclay).
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, USA (Alistair S. Ramsdale).
BYUC	Brigham Young University, Provo, Utah, USA (Shawn M. Clark).
CASC	California Academy of Sciences, San Francisco, California (Norman Penny and David H. Kavanaugh).
CMNC	Canadian Museum of Nature, Ottawa, Ontario, Canada (François Génier).
CNCI	Canadian National Collections of Insects, Ottawa, Ontario, Canada (Patrice Bouchard).
CSCA	California State Collection of Arthropods, Sacramento, California, USA (Charles Bellamy).
CSUC	Colorado State University, Fort Collins, Colorado, USA (Boris C. Kondratieff).
DBTC	Donald B. Thomas Personal Collection, Weslaco, Texas, USA (Donald Thomas).
DEI	Deutsches Entomologisches Institut, Leibniz-Zentrums für Agrarlandschaftsforschung, Müncheberg, Germany (Lothar Zerche).
DKYC	Daniel K. Young Personal Collection, Madison, Wisconsin, USA (Daniel K. Young).
EMEC	University of California, Berkeley, California, USA (Cheryl Barr).
ENMU	Eastern New Mexico University, Portales, New Mexico, USA (Darren A. Pollock).
FMNH	Field Museum, Chicago, Illinois, USA (James H. Boone).
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, USA (Paul E. Skelley).
FZMC	Fernando de Zayas Muñoz collection, Havana, Cuba (Teressa de Zayas Revuelta).
HNHM	Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl).
HUMB	Humboldt State University, Arcata, California, USA (Michael Camann).
IESC	Instituto de Ecologia y Sistematica, Academia de Ciencia, Havana, Cuba (Ileana Fernandez, Rayner Nuñez Aguila, Nayla García Rodriquez).
IEXA	Instituto de Ecologia, Academia de Ciencias, Xalapa, Veracruz, Mexico (Miguel Angel Morón Ríos).

INBC	Instituto de Biologia, Santo Domingo, Costa Rica (Angel Solis).
INHS	Illinois Natural History Survey, Champaign, USA (Colin Favret).
IRCW	University of Wisconsin, Madison, Wisconsin, USA (Steven Krauth).
JEWC	James E. Wappes Personal Collection, Bulverde, Texas, USA (James E. Wappes).
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, USA (Weiping Xie).
LSAM	Louisiana State Arthropod Museum, Baton Rouge, Louisiana, USA (Victoria Bayless).
LUND	Lund University, Lund, Sweden (Roy Danielsson).
MCPM	Milwaukee Public Museum, Milwaukee, Wisconsin, USA (Susan Borkin).
MAIC	Michael A. Ivie Private Collection, Bozeman, Montana, USA.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (Philip D. Perkins).
MIZ	Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland (Wioletta Tomaszewska).
MNHC	Museo Nacional de Historia Natural, Havana (Esteban Gutierrez).
MNHN	Museum National d'Histoire, Pairs, France
MSUC	Michigan State University, East Lansing, Michigan, USA (Gary L. Parsons).
MTEC	Montana Entomology Collection, Montana State University Bozeman, Montana, USA (Michael A. Ivie).
NCSU	North Carolina State University Insect Collection, Raleigh, North Carolina, USA (Robert Blinn).
NHMB	Natural History Museum Basel, Switzerland (Michael Brancucci and Eva Sprecher).
NHMW	Naturhistorisches Museum Wien, Vienna, Austria (Heinrich Schönmann).
NMNH	National Museum of Natural History, Washington D.C., USA (Warren E. Steiner).
NMPC	National Museum of Natural History, Prague, Czech Republic (Svatopluk Bílý).
OHGC	Orlando H. Garrido, Personal Collection, Havana, Cuba (Orlando H. Garrido).
OSAC	Oregon State Arthropod Collection, Oregon State University, Corvallis, USA (Andrew Brower).
OSUC	The Ohio State University, Columbus, Ohio, USA (Charles A. Triplehorn).
RLAC	Rolf L. Aalbu Personal Collection, Sacramento, California, USA (Rolf L. Aalbu).
ROME	Royal Ontario Museum, Toronto, Ontario, Canada (Brad Hubely).
SBMN	Santa Barbara Museum of Natural History, California, USA (Michael S. Caterino).
SEMC	Snow Entomological Collections, University of Kansas, Lawrence, Kansas, USA (Zachary H. Falin).
SMDV	Spencer Entomological Museum, University of British Columbia, Vancouver (Karen M. Needham).
TAMU	Texas A&M University, College Station, Texas, USA (Edward G. Riley).
UTSC	Utah State University, Logan, Utah, USA (Colin Brammer).
UASM	Strickland Museum, University of Alberta, Edmonton, Canada (Danny Shpeley).
UCDC	Bohart Museum of Entomology, University of California, Davis, California, USA (Steve L. Heydon).
UCMC	University of Colorado Museum, Boulder, Colorado, USA (Virginia Scott).
UCRC	University of California, Riverside, California, USA (Douglas Yanega).
UGCA	Georgia Museum of Natural History, Athens, Georgia, USA (Cecil L. Smith).
UMMZ	University of Michigan, Ann Arbor, Michigan, USA (Mark F. O'Brien).
UNSM	University of Nebraska State Museum, Lincoln, Nebraska, USA (Federico C. Ocampo).
WFBM	William F. Barr Entomological Museum, University of Idaho, Moscow, Idaho, USA (Frank W. Merickel).
WSUC	Washington State University, Pullman, Washington, USA (Richard Zack).
ZIN	Institute of Zoology Russian Academy of Sciences, St. Petersburg, Russia (Mark G. Volkovitsh).

Methods—Morphology

This review was based on morphological characters of adult specimens following the phylogenetic species concept of Wheeler and Platnick (2000). This concept views species as the smallest group of populations or lineages diagnosable by a unique combination of character states. These unique characters can be inherited, and therefore used to delimit species and genera. This concept was applied to populations of the tribe to determine individual species limits.

Frequently specimens of the tribe are encrusted with a greasy exudate as well as accumulated environmenal debris. This makes morphological structures very difficult to examine. In order to examine external morphological structures, specimens were cleaned. To clean the specimens they were first relaxed in hot water (90–100° C) for 5–10 minutes. Once relaxed, specimens were placed in an ammonium hydroxide solution (Parsons'® household ammonia) in an ultrasonic cleaner for 10–15 minutes, followed by a distilled water rinse. Any remaining obstructions were then scraped away using the point of an insect pin. The cleaning process significantly enhances the visibility of the surface sculpture, without compromising the specimen. Dissection and disarticulation were used to study certain morphological characters (i.e. mouthparts, genitalia) of relaxed specimens.

Specimens were studied under a Leica® Wild M3C stereoscope equipped with a 150w fiber optic illuminator. Habitus images of larger specimens were made using an Olympus DP11 digital camera system, mounted to a NIKON® micro-NIKKOR 105mm lens. Images of smaller morphological characters and structures were made using a JVC (DC Ky-F75U) digital camera mounted on a Leica® MS5 stereoscope, attached to an IBM IntelliStation M Pro® with a 1GHz Pentium4® processor. Enhancements to digital images were made using the Syncroscopy AutoMontagePro® version 5.03.0020 Beta 2005 software and edited in Adobe PhotoShop® 5.5. Line drawings were made by tracing digital images with a drawing tablet in Adobe PhotoShop® 5.5.

Nomenclature of morphological structures follows Doyen (1966), Doyen and Lawrence (1979), Lawrence and Britton (1991) and Ślipiński and Lawrence (1999). A tubercle is defined as a rounded protuberance of the cuticle that has a single inserted seta. This differs from a nodule, which is used to refer to the large rounded or tear-drop shaped elevation of an entire cuticular area that may have multiple setae and/or tubercles on the surface. Specifically, the "male nodule" refers to an elevated circular-to-elliptical area near the base of the femora of the male in many species of Zopherini. The term "setiferous fossae" was recently used in *Noserus* (García-París *et al.* 2001) to refer to pits of the cuticular surface with single inserted setae; we use "setose punctures" to refer to these features following Harris (1979). Other sculpture definitions follow Harris (1979) and Nichols (1989).

The label transcription for type specimens follows Ivie (1985). Data on each line within a label is separated by ";" (semicolon); each individual label is separated by a "/" (backslash).

The distribution of each species is recorded as COUNTRY: PROVINCE or STATE: county (when available).

Materials and methods-phylogenetic analysis

A cladistic analysis was conducted based on 32 morphological characters in order to determine the generic placement of the species, and to hypothesize evolutionary relationships among the genera. This analysis included 29 species of Zopherini representing all genera, and all known species of *Verodes*, *Noserinus*, *Nosoderma*, *Phloeodes*, *Scoriaderma*, *Zopher*, and *Zopherosis*. Since the monophyly of *Zopherus* was not in question, and the species already revised, a representative exemplar was used for that genus. *Phellopsis porcata* was included as an outgroup. Table 1 lists the primary vouchers for character state coding.

Parsimony analysis was conducted using PAUP* 4.0b10 (Swofford 2003). All characters were unordered

and equally weighted. Branch-and-bound searches for maximum parsimony were computed heuristically with the "MaxTrees" setting=5000, branches collapsed if the maximum branch length was zero, with the "MultTrees" option in effect, and topological constraints not enforced.

Phellopsis porcata (LeConte) was used as the designated outgroup because it has been historically placed with the larger zopherines and in the results of the phylogenetic analysis of Ślipiński and Lawrence (1999) *Phellopsis* is part of the lineage that is sister to the Zopherini + Pycnomerini. The character states represented by *Phellopsis* are also shared by most members of the other basal lineages of the subfamily (Ślipiński and Lawrence 1999), and are assumed to be plesiomorphic.

The 32 characters used in the analysis include a mixture of those used by Ślipiński and Lawrence (1999) and newly employed ones. The primary purpose of the phylogenetic analysis was not to resolve the species relationships, but rather to place individual species within phylogentically supported monophyletic genera. To this end, many characters which represented autapomorphies, were uniform throughout the in-group, or were otherwise phylogentically uninformative were discarded from the data matrix. The characters and their states are listed below, and the resulting matrix of 32 characters X 30 taxa is presented in Table 2.

TABLE 1. Locality data and repository for representative specimens used in the phylogenetic analysis.

Species	Locality	Collection
Zopherus nodulosus	USA: Texas, Burleson Co.	UCRC
Phloeodes diabolicus	USA: California, Orange Co.	CASC
Phloeodes plicatus	USA: California, Los Angeles Co.	LACM
Zopherosis georgei	AUSTRALIA: Victoria	MAIC
Sesaspis emarginata	USA: Texas, Bexar Co.	TAMU
Sesaspis denticulata	MEXICO: Nuevo Leon	MAIC
Sesaspis sylvatica	MEXICO: Tamaulipas	TAMU
Phloeodes venustus	COSTA RICA: Guanacaste Prov.	INBC
Sesaspis doyeni	MEXICO: Nuevo Leon	MAIC
Sesaspis ashei	MEXICO: Hidalgo	SEMC
Verodes inaequalis	MEXICO: Puebla	UCMC
Verodes interruptus	MEXICO: Oaxaca	UCMC
Verodes scabrosus	MEXICO	MNHN
Verodes exsculptus	MEXICO: Oaxaca	HNHM
Sesaspis triplehorni	BELIZE: Toledo Dist.	NMNH
Sesaspis lutosa	MEXICO: Oaxaca	MAIC
Verodes zunilensis	HONDURAS: Olancho	CMNC
Verodes guatemalensis	MEXICO: Chiapas	CMNC
Verodes sparsus	GUATEMALA: Quezalten	CMNC
Verodes aequalis	MEXICO: Oaxaca	MAIC
Noserinus dormeanus	ARGENTINA: Iguazu	AAPC
Nosoderma echinatum	CUBA	MAIC
Nosoderma turquinense	CUBA	OHGC
Noserinus furcatus	VENEZUELA: Merida	MAIC
Scoriaderma cordicolle	KENYA: Kwale Dist.	MAIC
Zopher iviei	MALAYSIA: Cameron Highlands	MAIC
Phellopsis porcata	USA: California, Nevada Co.	UCDC

TABLE 2. Character matrix.

Taxon\Character	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Phellopsis porcata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zopherus nodulosus	2	1	0	0	0	1	0	1	1	1	1	2	0	1	1	0	0	1	1	2	0	2	2	0	0	1	2	1	2	2	1	1
Phloeodes diabolicus	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	2	0	1	0	2	2	1	0	1	1	1
Phloeodes plicatus	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	3	0	1	0	2	2	1	0	1	1	1
Phloeodes venustus	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	3	0	1	0	2	2	1	0	1	1	1
Zopherosis georgei	0	1	0	1	0	2	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	2	1	0	0	0	2	1	2	1	1	0
Sesaspis emarginata	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	2	4	1	0	1	2	1	1	1	1	1	1
Sesaspis denticulata	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	2	4	1	0	0	2	1	1	1	1	1	1
Sesaspis lutosa	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	2	4	1	0	0	2	1	1	1	1	1	1
Sesaspis sylvatica	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	2	4	1	0	0	2	1	1	1	1	1	1
Sesaspis doyeni	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	4	1	0	0	2	1	1	1	1	1	1
Sesaspis ashei	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	4	1	0	0	2	1	1	1	1	1	1
Sesaspis triplehorni	1	1	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	0	4	1	0	0	2	1	1	1	1	1	1
Verodes zunilensis	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	5	0	1	0	2	1	1	0	0	1	1
Verodes guatemalensis	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	5	0	1	0	2	1	1	0	0	1	1
Verodes sparsus	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	5	0	1	0	2	1	1	0	0	1	1
Verodes aequalis	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	1	0	5	0	1	0	2	1	1	0	0	1	1
Verodes inaequalis	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	5	0	1	0	2	0	1	0	0	1	1
Verodes interruptus	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	5	0	1	0	2	0	1	0	0	1	1
Verodes scabrosus	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	5	0	1	0	2	0	1	0	0	1	1
Verodes exsculptus	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	5	0	1	0	2	0	1	0	0	1	1
Verodes carinatus	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	5	0	1	0	2	0	1	0	0	1	1
Verodes asperatus	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	5	0	1	0	2	0	1	0	0	1	1
Verodes championi	1	0	1	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0	0	0	0	5	0	1	0	2	0	1	0	0	1	1
Noserinus dormeanus	1	0	1	0	1	2	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	5	2	1	0	2	0	1	1	0	1	1
Nosoderma echinatum	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	0	0	1	0	0	4	2	1	0	2	0	1	1	1	1	1
Nosoderma turquenense	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	0	0	1	0	0	4	2	1	0	2	0	1	1	1	1	1
Noserinus furcatus	1	0	1	0	0	2	1	1	0	0	0	1	1	0	1	1	0	0	1	0	0	5	2	1	0	2	0	1	1	0	1	1
Scoriaderma cordicolle	1	1	0	1	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	0	0	1	2	0	1	2	0	1	1	1	1	1
Zopher iviei	0	0	1	0	1	2	1	1	0	0	0	0	0	0	1	0	0	0	1	0	0	5	2	1	0	2	0	1	1	0	1	0

Characters, states and definitions are as follows:

0. Number of antennomeres: (0) 11 (Fig. 3); (1) 10 (Fig. 2); (2) 9 (Fig. 1). The difference in number involves only antennomeres 9–11, as the terminals become fused together.
1. Antennal cavity: (0) absent; (1) present. The size, shape, presence or absence of antennal cavities on the prothorax is highly variable. The antennal cavity is present if a small distinct cavity (Figs. 42, 54) or broad depression that clearly can receive the antenna (Figs. 39–41) is present. In the case of *Ph. venustus*, the cavity is weakly defined but is coded as present (1) because the anterior portion of the hypomeron is "rolled over" the pleurosternal suture, producing a distinct groove for the antenna, and the hypomeral face is concave laterad the pleurosternal suture in a weak but clear indication of the cavity. In all cases of the cavity being truly absent (0) the hypomeron is either flat or concave laterad the pleurosternal suture.
2. Nodule on male femora: (0) absent on all femora; (1) present on at least two pairs of femora. This second-

ary sexual character (Figs. 50–53) in the male is found only within the Zopherini, and is absent from all other tribes in the Zopherinae. The character was not used in the analysis by Ślipiński and Lawrence (1999), and is variable within the tribe. The nodule is present on all femora in *Phloeodes*, *Zopher*, *Noserinus*, most *Verodes*, and some *Sesaspis* but is absent on some or all femora in *Nosoderma*, some *Sesaspis*, and rarely *Verodes*. This character is totally absent in members of *Scoriaderma*, *Zopherus*, and *Zopherosis*.

3. Transverse groove on prosternum: (0) absent; (1) present (Fig. 24). A transverse groove anterior of the procoxal cavities is present in some species.
4. Flight wings: (0) reduced to membranous flap or absent; (1) present and fully developed. Most members of the Zopherinae have lost flight capabilities.
5. Area between tarsal claw: (0) simple exposed insertions (Fig. 49); (1) with expanded dermal lobes that completely enclose the insertion points (Fig. 9); (2) with setose and/or membranous empodium (Fig. 13). In *Zopherus* dermal lobes are present that overlap between the tarsal claws and enclose the base of the claw (1), often there is a tuft of setae on the dorsal surface. In those species with a large scutellum, the area between the insertions of the tarsal claws has a membranous (Fig. 13) and/or setose empodium that may have a few or a tuft of setae (2). The assumed plesiomorphic condition (0) of simple exposed insertions between the claws is present in most members of the Zopherini (Fig. 49)
6. Epipleuron: (0) tuberculate/smooth; (1) with distinct ridge (Fig. 14).
7. Labial palp insertions: (0) dorsal/lateral (Figs. 30–31, 47–49); (1) ventral (Fig. 56).
8. Labial palp insertions: (0) exposed; (1) concealed by mentum (Fig. 21).
9. Scutellum: (0) present; (1) absent.
10. Eye: (0) wide, greater than 10 facets at narrowest point; (1) narrow, fewer than 10 facets at narrowest point.
11. Antennal-club number of apparent segments enlarged: (0) 3 segments (Fig 3); (1) 2 segments (Fig. 2); (2) 1 segment (Fig. 1).
12. Penultimate antennomere with sensillae: (0) on both sides; (1) protruding on lateral sides (Fig. 2); (2) absent. All of the species of Zopherini with 10-segmented antennae have a protruding area that is variably covered in sensillae.
13. Apical antennomere with micro-setose field: (0) covering most of apex (Fig. 4); (1) depressed and emarginate (Fig. 5).
14. Mandibular membranous prostheca: (0) present (Fig. 34); (1) reduced or absent (Figs. 32–33)
15. Lateral margin of pronotum: (0) smooth; (1) with distinct teeth or lobes.
16. Maxillary palp with last segment: (0) pointed/rounded at apex; (1) flattened at apex (Fig. 31). The apex is considered flattened if the apical sensilla area is longer than wide, and the apex is wider than the base.
17. Maxillary palpomere 2: (0) not or slightly expanded at base; (1) strongly and abruptly expanded at base.
18. Subgenal ridge: (0) weak (Fig. 55); (1) strong (Fig. 54).
19. Secondary setose vestiture on pronotum: (0) present (Fig. 70); (1) absent; (2) entire pronotum glabrous. The secondary setose vestiture is that which is present or absent between the setae that are singly inserted on tubercles.
20. Apical margin of at least first antennomere: (0) similar setose density to other surfaces; (1) with very short golden setae; (2) with dense patch of setae.
21. Hypomeron with: (0) no antennal cavity, including cases with thumb-like projection where prosternal suture meets margin (Figs. 55); (1) broad depression (Fig. 15); (2) complete cavity (Figs. 39, 41); (3) incomplete (Fig. 40, 42); (4) arcuate depression (Fig. 54); (5) with thumb-like projection where prosternal suture meets margin.
22. Ventral surface with: (0) tubercles with single setae (Fig. 71); (1) setose punctures (Fig. 72); (2) only setae.

23. Ligula: (0) with margin evenly setose; (1) with tufts of setae inserted in fossae (Fig. 48).
24. Antennomere 3: (0) elongate, longer than 4; (1) transverse, subequal in length to 4.
25. Preapical groove of last ventrite: (0) divided; (1) sinuate; (2) single narrow groove along nearly entire margin.
26. Tarsal strip: (0) absent; (1) weak, usually tufts of golden setae; (2) well developed, (Fig. 43).
27. Procoxal-cavities: (0) externally open; (1) externally closed.
28. Dorsal sculpture: (0) combination of setae and tubercles; (1) only setae and punctures; (2) mostly glabrous.
29. Vestiture on legs: (0) uniformly setose; (1) bi-setose (Fig. 25); (2) glabrous with strip of bare cuticle. A bi-setose vestiture consists of setae of two distinctly different lengths and widths.
30. Submentum: (0) with setose pit; (1) without setose pit. The pit is present (0) in all other tribes of Zopherinae, but is absent in the Zopherini (Ślipiński and Lawrence 1999).
31. Apical and pre-apical antennomeres: (0) distinct and free (Fig. 3); (1) partly or entirely fused together (Figs. 1–2).

Results-phylogenetic analysis

With *Phellopsis porcata* as the outgroup, four most parsimonious trees were found, each with identical statistics (Length=81, CI= 0.5679, RI= 0.8087, HI= 0.4321) (Fig. 73). The strict consensus option retains only those monophyletic groups occurring in all input trees (Schuh 2000), and resolves the group at all of the higher branches.

We interpret the strict consensus cladogram to support the recognition of 9 monophyletic genera of Zopherini (Table 3, Fig. 73). The clade *Zopherus* + *Zopherosis* is supported as basal to the rest of the Zopherini by the synapomorphy of maxillary palpomere 2 strongly and abruptly expanded at the base, as was found in the analysis of Ślipiński and Lawrence (1999). In that analysis the *Zopher* + *Noserinus* lineage arose within the rest of the Zopherini, but as a distinct group. The present analysis supports *Zopher* as a succesively independent lineage from the rest of the Zopherini. *Zopher* and the independent *Noserinus* clade are shown as basal to the remaining Zopherini. The remaining genera share several hypothesized synapomorphies: the presence of a setose empodium between the tarsal claws, distinct epipleural ridge, large scutellum, and a widened eye. The relationship between *Zopher* and *Noserinus* warrants further investigation.

For those species possessing 10-segmented antennae and lacking a visible scutellum, Ślipiński and Lawrence (1999) recognized four genera. The current analysis supports recognition of five genera, with the re-recognition of *Sesaspis* Casey. Interestingly, given this result, no species currently supported as members of *Sesapis* were included in the analysis by Ślipiński and Lawrence. It is reasonable to assume that if a species of the group had been included in that analysis a similar conclusion would have been reached by those authors. The independent status of the genus *Sesapis* from the *Verodes* + *Phloeodes* lineage, where all of its previously described members were placed, is well supported by the arcuate depression on the hypomeron, patch of setae on the apical margin of the basal antennomeres, ventral body surfaces with setose punctures, and the weak tarsal strip. The hypothesized sister-relationship between *Sesaspis* and *Nosoderma* + *Scoriaderma* is not unreasonable based on the generally similar morphological appearance of *Nosoderma turquinense* (Garrido) from Cuba and some species of *Sesaspis*.

Our results support changing the generic placement of several species as discussed under the generic descriptions below. Both *Noserinus furcatus* and *Phloeodes venustus* expanded the concepts of the genera where they are being placed. The alternative is to recognize additional genera, but we did not believe that the present evidence requires the recognition of additional monotypic genera within the tribe when evidence for placement of them in monophyletic genera is available.

Taxonomy

Key to world genera of Zopherini

1 Antennae 9-segemented, club composed of 3 fused antennomeres (Fig. 1); femora and tibia with paired rows of golden setae on inner surface; dorsum glabrous. Southwestern U.S., Central America. Figs. 6–7 ..... *Zopherus* Gray

- Antennae 10 or 11-segemented; club variable, weakly 1-segmented to distinctly 3-segmented (Figs. 2–3); dorsal vestiture variable 2

2 Antennae 11-segmented with weak to strong 3-segmented club 3

- Antennae 10-segmented with 1 or 2-segmented club 4

3 Scutellum partially visible; flight wings absent; hypomeron with complete cavity to contain antennae (Fig. 40); weak 3-segmented antennal club (Fig. 3); dorsal surface glabrous, sculpture strongly nodulate. Australia. Fig. 8..... *Zopherosis* White

- Scutellum large and visible; functional flight wings present; hypomeron lacking antennal cavity; strong 3-segmented antennal club; dorsal surface with dense patchy pubescence. Penninslar, Malaysia. Fig. 10..... *Zopher* Ślipiński and Lawrence

4 Scutellum large and visible; epipleural ridge distinct in basal 2/3rd of elytra (Fig. 14); setose empodium present between tarsal claws (Fig. 13). South America. Figs. 11–12..... *Noserinus* Casey NEW SENSE

- Scutellum not visible or very small; epipleural ridge totally absent; lacking empodium between tarsal claws..... 5

5 Lateral margin of pronotum with distinct teeth or lobes (Figs. 16, 22–23); prosternum densely setose with transverse groove (Fig. 24) 6

- Lateral margin of pronotum without distinct lobes, at most irregularly denticulate; prosternum densely setose to tuberculate, rarely with broad transverse depression 7

6 Sensilla area at apex of last antennomere medially constricted, reduced and recessed, not visible laterally, (Fig. 5); hypomeron with shallow antennal cavities; labial palps inserted laterally concealed by mentum (Fig. 21); apical portion of pronotum with sinuate channel (Fig. 20); thin ridge connecting suprantennal and sub-genal ridge present, enclosing apical margin on antennal insertion (Fig. 15). Africa, Comoro Islands. Fig. 16..... *Scoriaderma* Fairmaire

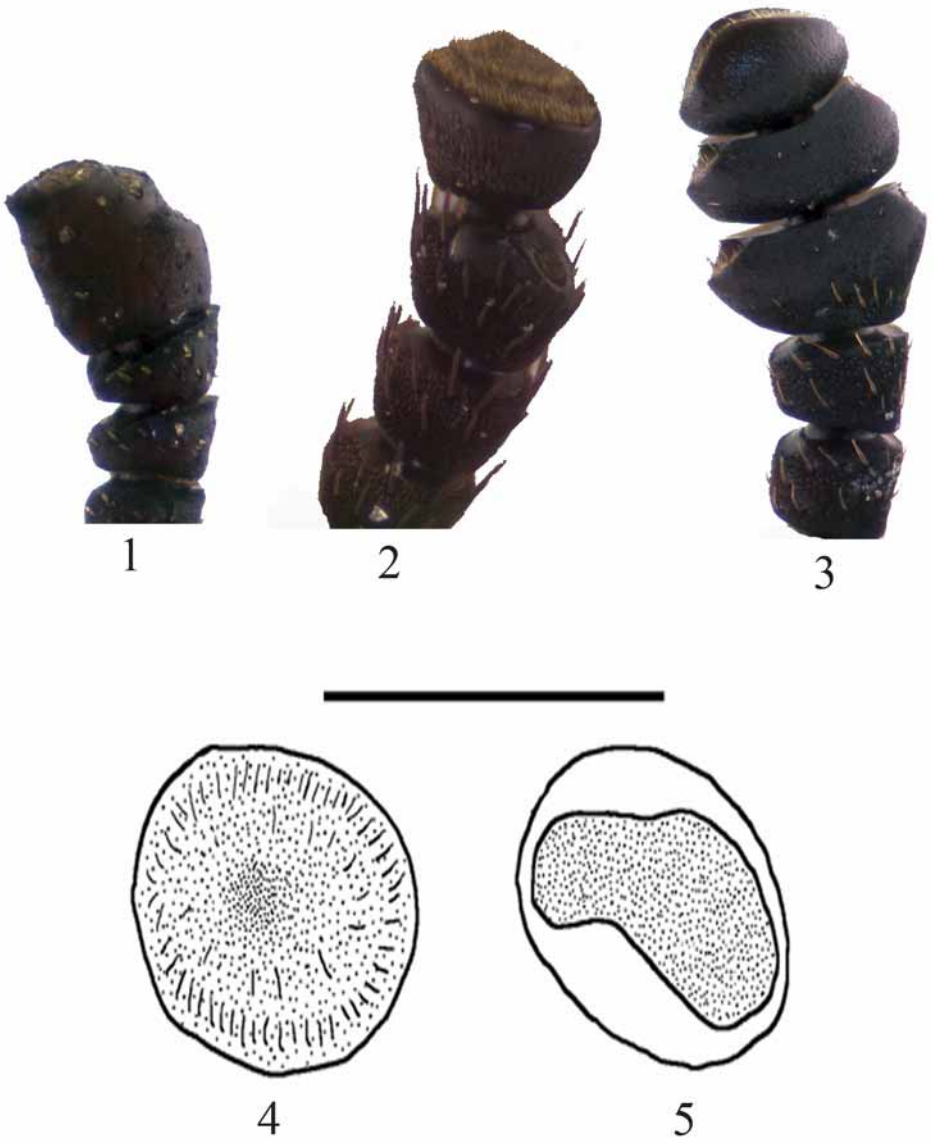
- Sensilla area at apex of last antennomere large (Fig. 4), covering approximately half of antennomere, visible laterally; labial palps inserted ventrally, visible; pronotal hypomeron without antennal cavity; apicolateral portion of pronotum with indistinct arcuate depression; thin ridge between suprantennal and sub-genal ridges absent. Cuba. Figs. 22–23..... *Nosoderma* Guérin-Méneville

7 Ventral surfaces with setose punctures (Fig. 72), setation often very dense obscuring punctures; apical margin of hypomeron with short arcuate depression (Fig. 54). Central America and Southwestern U.S. Figs. 17–19, 26–29..... *Sesaspis* Casey NEW SENSE

- Ventral surfaces with tubercles (Fig. 71); hypomeron variable from small break in margin to complete antennal cavity 8

8 Mandible with large membranous prostheca (Fig. 34); hypomeron without large antennal cavity, occasionally with weak straight depression (Fig. 55); ventral surface of head with dense flattened tubercles lateral of gula; gula with punctures; sub-genal ridge weak, slightly arcuate with median depression; last segment of maxillary palp with flattened apical margin, flat sensillary surface of apex wider than base (Fig. 31). Central America. Figs. 57–68 ..... *Verodes* Casey NEW SENSE

- Mandible without large membranous prostheca (Figs. 32–33); hypomeron with complete antennal cavity to weak depression (Figs. 39–42); ventral surface of head variable; gula densely setose; sub-genal ridge strong with distinct curve toward base of head; last segment of maxillary palp acutely narrowed at apex, sensillary surface of apex narrower than base. California Floristic Province and Central America. Figs. 35–38 ..... *Phloeodes* LeConte NEW SENSE



FIGURES 1–5. 1–3. Antennal clubs. 1. *Zopherus nodulosus*; 2. *Sesaspis sylvatica*; 3. *Zopherosis georgei***. 4–5.** Apex of last antennomere. 4. *Nosoderma echinatum*; 5. *Scoriaderma cordicolle*. Scale bar = 1 mm.

Genus *Zopherus* Gray
Figs. 1, 6–7, 9

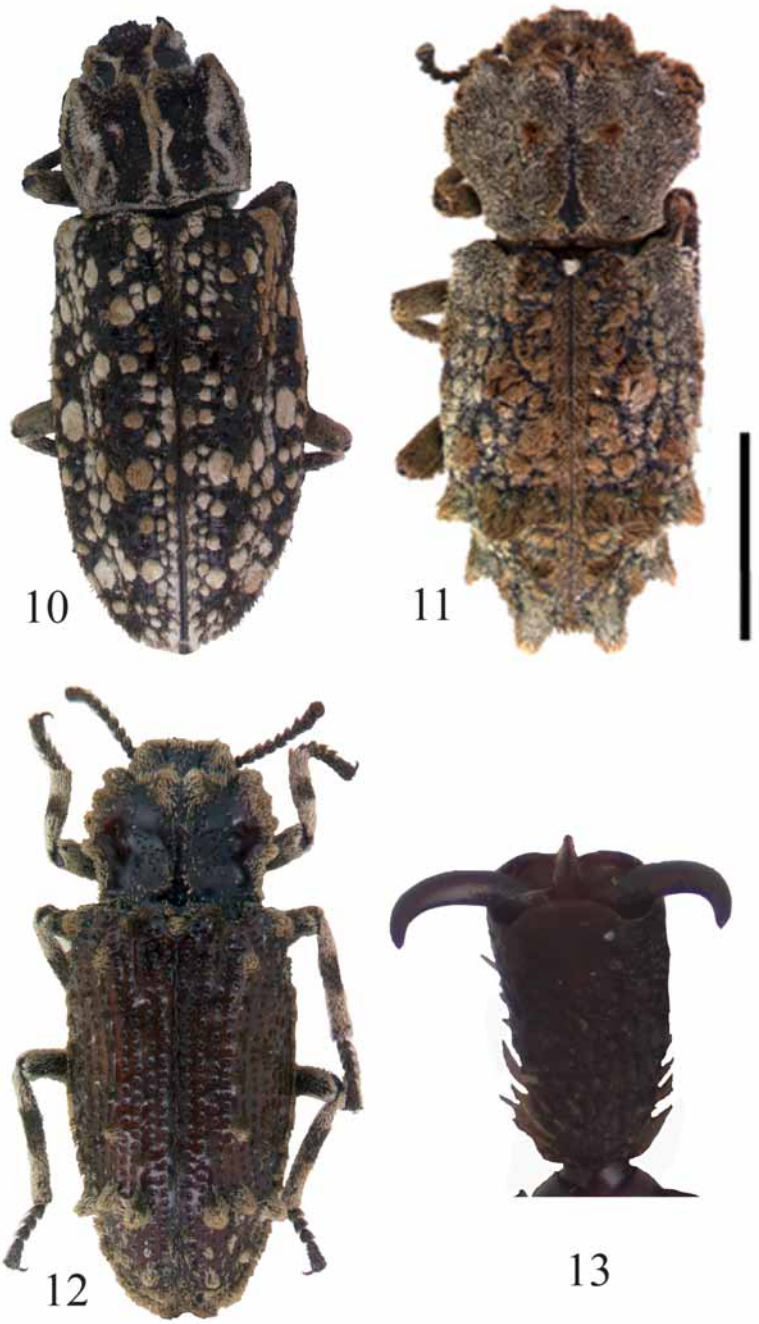
Zopherus Gray, 1832: 796. Blanchard, 1861: pl. 7A, fig. 6. Guérín-Méneville, 1844: 18. Lucas, 1852: XXIII. Solier, 1841: 42–46. Sturm, 1842: 349. Sallé, 1849: 301. LeConte, 1851: 130. Horn, 1867: 160–162. Horn, 1870: 271–272. Champion, 1884: 39–43. Horn, 1885: 160. Champion, 1892: 489. Casey, 1907a: 36–41. Casey, 1907b: 464–467. Casey, 1924: 304–305. Blaisdell, 1931: 111. Gebien, 1936: 665. Blackwelder, 1945: 514. Triplehorn, 1972: 1–24. Doyen and Lawrence, 1979: 344. Ślipiński and Lawrence, 1999: 17. Ivie, 2002: 49. García-París *et al.*, 2006: 216. (Type species *Zopherus mexicanus* Gray, 1832, subsequent designation by Casey, 1907a).
Megazopherus Casey, 1907a: 36. Gebien, 1936: 665. Blackwelder, 1945: 514. (Synonymy by Triplehorn, 1972: 3).
Zopherinus Casey, 1907a: 36. Gebien, 1936: 666. Blackwelder, 1945: 514. (Synonymy by Triplehorn, 1972: 3).
Zopherodes Casey, 1907a: 36. Gebien, 1936: 666. Blackwelder, 1945: 514. (Synonymy by Triplehorn, 1972: 3).

Diagnosis: The genus can be distinguished from all other Zopheridae by having 9-segmented antennae with the club composed of 3 fused segments, and complete antennal cavities on the hypomeron.

Description: See Triplehorn (1972), Ślipiński and Lawrence (1999).

Notes: The genus was described by Gray (1832) and the type species was subsequently designated by Casey (1907a) as *Zopherus mexicanus* Gray 1832. This is the largest genus in the tribe with 19 valid species, and is the only one that has been critically examined (Triplehorn 1972). It is well supported based on several synapomorphies including the 9-segmented antennae with the apical 3 segments fused, the overlapping cuticle between the tarsal claws, glabrous pronotum and ventrite 5 with a sinuate preapical groove. For a key to species and excellent revision, see Triplehorn (1972).

FIGURES 6–9. 6–8. Dorsal habiti. 6. *Zopherus championi*, Mexico, Nuevo Leon ; 7. *Z. jansoni*, Costa Rica; 8. *Zopherosis georgei*, Australia, Victoria. **9.** *Zopherus nodulosus* apex of tarsal claw. Scale bars = 5mm.



FIGURES 10–13. 10–12. Dorsal habiti. 10. *Zopher iviei*, Penninsular. Malaysia ; 11. *Noserinus furcatus*, Venezuela; 12. *Noserinus dormeanus*, Brazil. **13.** *Noserinus dormeanus* apex of tarsal claw. Figs. 10–12, Scale bar = 5mm.

Genus *Zopherosis* White
Figs. 3, 8

Zopherosis White, 1859: 121. Masters, 1872: 171. Gebien, 1936: 667. Ślipiński and Lawrence, 1999: 19. Ivie, 2002b: 461. Hawkeswood 2003: 93. (Type species *Zopherosis georgei* White, 1859 by monotypy).

Diagnosis: Distinguished from other flightless species by having 11-segmented antennae and a small scutellum. The presence of complete antennal cavities on the hypomeron will distinguish this species from all Zopherini except *Zopherus* (9-segmented antennae) and *Phloeodes diabolicus* (10-segmented antennae).

Description: See Ślipiński and Lawrence (1999).

Notes: This monotypic genus was described by White (1859), with the type species *Zopherosis georgei*

White 1859 by monotypy. Casey (1907b) described the separate tribe, Zopherosini, for this genus but this division never was subsequently recognized (Gebien 1936, Doyen and Lawrence 1979, Ślipiński and Lawrence 1999).

This genus is clearly distinct from *Zopherus*, and is defined by a combination of characters including the 11-segmented antennae, scutellum present, groove on prosternum present and lightly setose vestiture (glabrous in *Zopherus*).

Adults of *Zopherosis georgei* have been observed feeding on fruiting bodies of the fungi *Ganoderma applanatum* (Fries) Karsten on a standing dead coachwood tree (*Ceratopetalum apetalum* D. Don. Cunoniaceae) in coastal rainforests (Hawkeswood 2003).

Distribution: The coastal rainforests of eastern Australia.

Recorded distribution: A summary of the 3 specimens examined is AUSTRALIA: VICTORIA and NEW SOUTH WALES.

TYPES (*Zopherosis georgei* White)**:** The holotype was examined at the Natural History Museum (BMNH).

Genus *Zopher* Ślipiński and Lawrence

Fig. 10

Zopher Ślipiński and Lawrence, 1999: 11. Ivie, 2002b: 460. (Type species *Zopher iviei* Ślipiński and Lawrence, 1999 by original designation)

Diagnosis: The only Zopherini genus with 11-segmented antennae and functional flight wings. The distinct 3-segmented club and smooth lateral pronotal margins lacking lobes or teeth will distinguish this species from the closely related *Noserinus*.

Description: See Ślipiński and Lawrence (1999).

Notes: This monotypic genus was described by Ślipiński and Lawrence (1999) for *Zopher iviei* Ślipiński and Lawrence. The relationship with the genus *Noserinus* is unresolved but the two genera share many characters (see brief discussion under *Noserinus*) and are probably sister-genera.

This stunning genus is known only from Pahang State, Malaysia, and specimens are extremely rare with fewer than 10 known in museums. Since the description, additional old material has been found in the BMNH collection, and at least one specimen was recently collected by Czech entomologists (pers. comm. with M. Barclay at the BMNH).

Distribution: Peninsular Malaysia.

Recorded distribution: A summary of the type series is MALAYSIA: PAHANG: Cameron Highlands.

Types (*Zopher iviei* Ślipiński and Lawrence)**:** Holotype in BMNH. Paratypes, 2-BMNH, 2-BPBM, 1-MAIC, 1-MIIZ (see Ślipiński and Lawrence 1999). Paratype examined ♂ in MAIC: *Zopher iviei*: MALAYA: Cameron; Highlands, Mt.; Brichang, 2-7.I.59/ L. W. Quata; Collector/ blue rectangle PARATYPE; ZOPHER; IVIEI; SLIP. & LAWR.

Genus *Noserinus* Casey

Figs. 11–14

Noserinus Casey, 1907b: 470. Gebien, 1936: 669. Doyen and Lawrence, 1979: 345. Costa *et al.*, 1988: 212. Ślipiński and Lawrence, 1999: 13. (Type species: *Noserinus annulatipes* Casey, 1907b, by original designation).

Diagnosis: The presence of a large setose scutellum and 10-segmented antennae is unique among the Zopherini.

Description (male): With the inclusion of *Noserinus furcatus* (Kirsch) NEW COMBINATION, the generic description of *Noserinus* should be slightly modified as follows from Ślipiński and Lawrence (1999). Length 13–24 mm. Flight wings present or absent. Anterior clypeal margin deeply to weakly emarginate. Pronotal sides weakly to strongly lobed. Male femora with nodules on meso and metafemora only.

Notes: The genus *Noserinus* was described by Casey for his new Brazilian species *Noserinus annulatipes* Casey 1907b (Type species *Noserinus annulatipes* Casey 1907, by original designation). Casey mentioned that his species was related to *Nosoderma dormeanum* Fairmaire 1889, but this species was not officially moved to *Noserinus* until Gebien (1936) synonymized the Casey species with *Noserinus dormeanus*.

The species *Noserinus dormeanus*, *Zopher iviei*, and *Meralius furcatus* share the following characters: the presence of a large setose scutellum, distinct epipleural ridge and an empodium present between the tarsal claws. Therefore, *Meralius furcatus* is moved to *Noserinus*, rather than recognizing a third monotypic genus.

Key to Species of *Noserinus* Casey

1 Functional flight wings present; apical margin of elytra smooth. Central South America. Fig. 12 .... *N. dormeanus* (Fairmaire)

- Functional flight wings absent; apical margin of elytra with strongly projecting conical nodules. Northern South America. Fig. 11..... *N. furcatus* (Kirsch)

***Noserinus dormeanus* (Fairmaire)**
Figs. 12–13

Nosoderma dormeanus Fairmaire, 1889: xxxii. Casey, 1907b: 470.
Noserinus dormeanus; Gebien, 1936: 669. Blackwelder, 1945: 515. Costa *et al.*, 1988: 212. Ślipiński and Lawrence, 1999 :15.
Noserinus annulatipes Casey, 1907b: 471. (Synonymy by Gebien, 1936: 669)

Diagnosis: This is the only species of Zopherini with 10-segmented antennae, a large setose scutellum, and fully functional flight wings. It can be distinguished from *N. furcatus* (which also has 10-segmented antennae and a setose scutellum) by having the apical margin of the elytra smooth, lacking projections.

Distribution: South America.

Recorded distribution: A summary of the 64 specimens examined is ARGENTINA: MISSIONES. BRAZIL: ESPIRITO SANTO, PARANA, RIO GRANDE DO SOL, SANTA CATARINA. PARANA. PARAGUAY: ALTO PARANA.

Types: *Noserinus dormeanus*: COTYPE: ♀, in NHMB-Frey Collection. Hand written on paper what appears to be Brazil; Dep "unknown word"/ pink rectangle label hand written *Noserinus*; printed Cotype; hand written *dormeanus*.

Noserinus annulatipes: LECTOTYPE, here designated: ♀, in NMNH, missing all tarsal claws except left meso, and right meta. Hand written Blumenau (Brazil)/ Casey; bequest; 1925/ {orange rectangle} Type NMNH; 46391/ *Noserinus*; *annulatipes*; Csy./ Lectotype; *Noserinus*; *annulatipes*; Casey 1907; desg. Foley & Ivie '07.

Notes: The larva of *Noserinus dormeanus* was described by Costa *et al.* (1988).

***Noserinus furcatus* (Kirsch), NEW COMBINATION**
Figs. 11, 14

Nosoderma furcatus Kirsch, 1866: 189.
Nosoderma furcatum; Foley and Ivie, 2007: 68.
Meralius furcatus; Gebien, 1936: 669. Blackwelder, 1945: 515.
Meralius furcatum: Garrido, 2004: 56.

Diagnosis: The species *N. furcatus* differs from *Noserinus dormeanus* in lacking functional flight wings and possessing small pits along the basal margin of the pronotum. The strongly projecting nodules at the apex of the elytra will also distinguish this species from *N. dormeanus*.

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FIGURES 14–15. 14. *Noserinus furcatus* epipleuron. **15.** *Scoriaderma cordicolle*. Prothoracic hypomeron. Scale bars = 1mm.

Distribution: Northern South America.

Recorded distribution: A summary of the 143 specimens examined is COLOMBIA: NORTE DE SANTANDER; Felipe Ovalle. PERU: SAN MARTIN; BRAZILIAN FRONTIER; UPPER RIO HUALLAGA.VENEZUELA: FALCÓN, LARA, MÉRIDA.

Types: Not examined.

Notes: The species *Nosoderma furcatus* Kirsch 1866 was stated to resemble *Scoriaderma cordicolle* (Fairmaire 1894b), but was placed in *Meralius* by Gebien (1936) without comment. *Meralius furcatus* (Kirsch) does not fit the definition of the genus (*sensu* Ślipiński and Lawrence 1999; now considered a synonym of *Nosoderma*, Foley and Ivie 2007) and is incorrectly placed. It differs from true *Nosoderma* Guérin-Méneville species most obviously in having a large scutellum and lacking a groove on the prosternum which is only broadly depressed. Coincidentally, there is a specimen of *Nosoderma* from Venezuela that was represented in Gebien's collection (label data: "Sammlung H. Gebien") and probably assumed to be *Nosoderma furcatus*. Gebien (1936) could have based his placement of *Nosoderma furcatus* in *Meralius* (*sensu* Ślipiński and Lawrence 1999) based on this specimen. This specimen is actually a species described by Garrido (2004) from Cuba, it is unclear if this species actually occurs in Venezuela, or was mislabeled.

This species, as with many Zopherini, is morphologically variable across its distribution. This distinctive species has large laterally projecting tubercles and a highly patterned setose vestiture that is highlighted with arcuate markings ranging in color from white to gold to black. Specimens are highly variable in coloration, pattern, and sculptural intensity. No consistent morphological differences could be found in the large number of mostly historical specimens examined to warrant the recognition of more than a single species.

Genus *Scoriaderma* Fairmaire

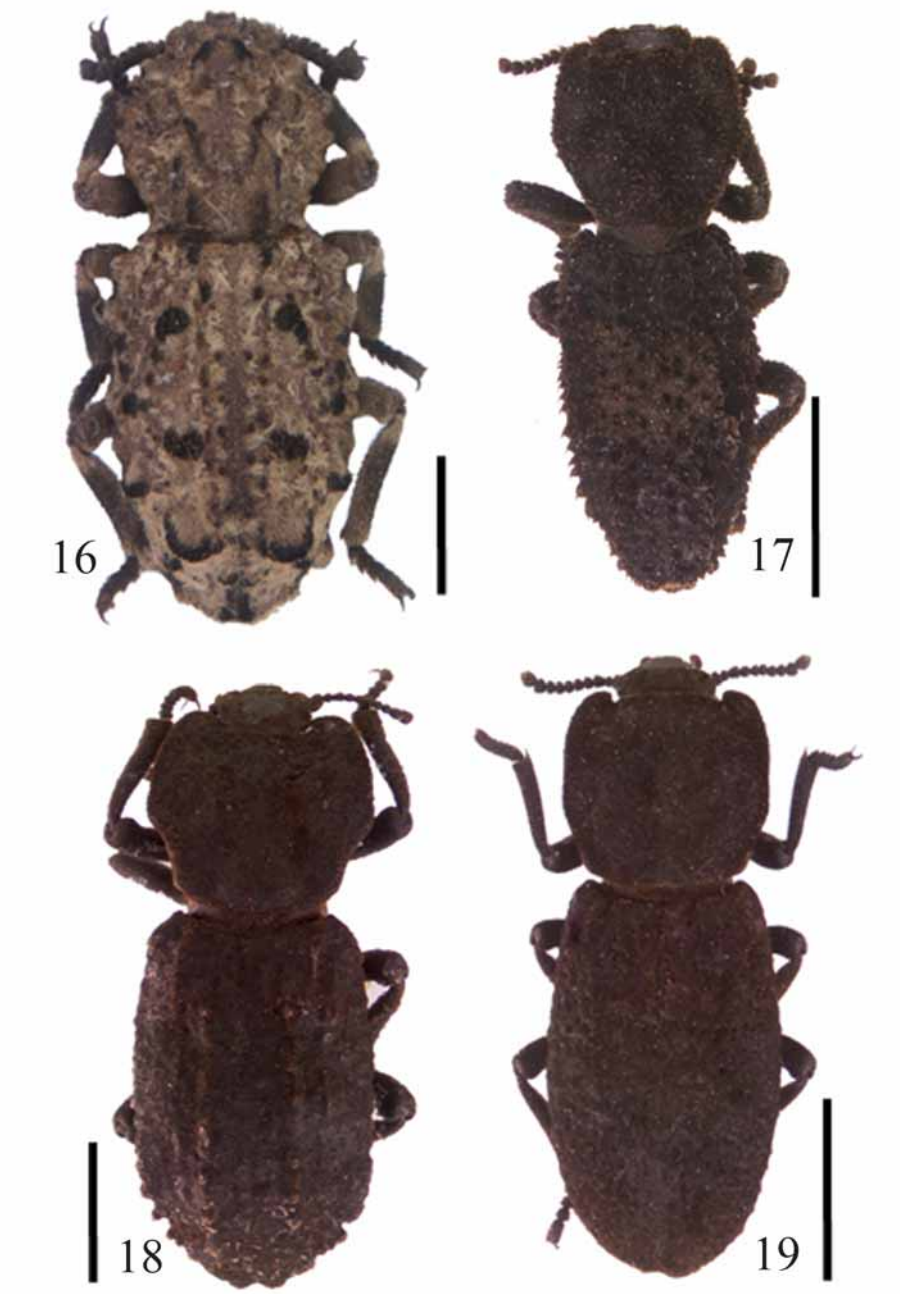
Figs. 15–16, 20–21

Scoriaderma Fairmaire, 1894a: C. Gebien, 1936: 670. Doyen and Lawrence, 1979: 345. Ślipiński and Lawrence, 1999:15. (Type species *Scoriaderma comoriense* Fairmaire 1894, by monotypy).

Diagnosis: Similar in general appearance to *Nosoderma echinatum* from Cuba, with a dense tomentose vestiture and lobed lateral pronotal margins, but *Scoriaderma* is distinguished from *Nosoderma* by having a sinuate channel near the apical margin of the pronotum (Fig. 20), a lateral bridge between the suprantennal ridge and subgenal ridge that encloses the antennal insertion apically (Fig. 15), the labial palpal insertions concealed by the mentum (Fig. 21), the micro-setose field of the last antennomere depressed and emarginate at the apex (Fig. 5), a well developed but incomplete antennal cavity on the hypomeron, and lack of femoral nodules in the male.

Notes: For such a small genus, with so little literature, *Scoriaderma* is plagued with a surprisingly high amount of taxonomic/nomenclatural error, confusion and uncertainty. The problems revolve around a pair of papers published by Leon Fairmaire (1894a, 1894b), one in the Bulletin de la Société Entomologique de France, and the other in the Annales de la Société Entomologique de Belgique. Because these papers appeared in the same year, and were printed in different journals, it was critical to establish which paper actually appeared first in order to determine the type species of *Scoriaderma*, and details of the original texts, and their interpretation by subsequent workers, further complicates the issue.

The cover of the Annales de la Société Entomologique de France 1894, deuxieme et troisieme trimesters, which includes the Bulletin des Séances that includes the pages of Fairmaire's 1894a paper, bears the mailing date of 25 November 1894. The Annales de la Société Entomologique de Belgique issue 12 for 1894, which includes pages of his 1894b paper includes the minutes from the Assemblee Mensuelle of 01 December 1894, so that the earliest possible (although improbable) date of mailing is 02 December 1894. However, as pointed out by Evenhuis (2002), there was a second version of the Bulletin de la Société Entomologique de France from 1873–1894, known informally as the "Bulletin Bimensuel." It had the same pagination as, but was issued twice-monthly, and in advance of, the version issued quarterly with the Annales. Thus, *Scoriaderma* Fairmaire 1894 was validated upon the mailing of issue 8 of the Bulletin Bimensuel, on 05 May 1894 (Evenhuis 2002).



FIGURES 16–19. Dorsal habiti. 16. *Scoriaderma cordicolle*, Tanzania; 17. *Sesaspis denticulata*, Mexico, Nuevo Leon; 18. *Sesaspis ashei*, Mexico, Hidalgo; 19. *Sesaspis doyeni*, Mexico, Nuevo Leon. Space bar = 5mm.

In that note, Fairmaire (1894a) explicitly described the genus for his new species *Scoriaderma comoriense* Fairmaire 1894 from the Comoro Islands. In the subsequent paper, he (1894b), described *Scoriaderma congolense*, but did not mention *S. comoriense* at all. In both papers, he mentioned the east African *Nosoderma cordicolle* Waterhouse, 1880 when diagnosing the new species. In the first (1894a), he suggested that *N. cordicolle* might belong in *Scoriaderma*. In the second (1894b), clearly after more study, he stated that it did indeed belong in *Scoriaderma*. With the establishment of the fact that the 1894a paper was published first, the type species of *Scoriaderma* must be taken from species included in that paper.

Yet, interpretation of the text has lead to disagreement about the correct type species. Fairmaire did not designate a type species. However, Gebien (1936), citing Fairmaire (1894a) as the validation of the generic name, designated *N. cordicolle* as the type species, which would constitute a subsequent designation, but

Ślipiński and Lawrence (1999) listed *Scoriaderma comoriense*, citing monotypy. The legitimacy of these designations rests on whether Fairmaire included one or two species in the original paper. The dispute here revolves around the interpretation of the following paragraph:

"Ce curieux insecte ressemble beaucoup à *Nosoderma echinatum*, de Cuba. J'en dois la communication à notre collègue M. R. Obenthür. Déjà M. Waterhouse a signalé un Insecte de ce groupe trouvé dans les montagnes de l'Afrique orientale et qu'il a rapporté au genre *Nosoderma*, *N. cordicolle* (...). It est intéressant de voir ce genre américain passer, en se modifiant, de la Californie dans l'Amour (…), puis dans le Japon (…), et franchir les presqu'iles indiennes pour retrouver en Afrique. L'insect de M. Waterhouse doit appartenir tres probablement au nouveau genre." (Fairmaire 1894a: CI)

[English translation by MAI, corrected and validated by Rolf Aalbu] "This curious insect much resembles *Nosoderma echinatum* of Cuba. I owe the communication of it to our colleague Mr. R. Obenthür. Earlier Mr. Waterhouse described an insect of this group, found in the mountains of Eastern Africa, and referred it to the genus *Nosoderma*, *N cordicolle* (...). It is interesting to see this American genus passing, while changing, from California to the Amur (...), then in Japan (...), and jumping over the Indian peninsula to be found again in Africa. The insect of Mr. Waterhouse most probably belongs to this new genus."

Does "probablement" constitute inclusion in the genus? ICZN (1999) Article 67.2.5 expressly excludes from eligibility any species "doubtfully or conditionally included" in the original genus. As such, Gebien's designation is invalid, and *Scoriaderma comoriense* Fairmaire 1894 is indeed the type species, by monotypy.

Not to be outdone, Waterhouse managed to double-publish the name *Nosoderma cordicolle* as well (Waterhouse 1880a, 1880b). The species was validated either by a description in the Annals and Magazine of Natural History, or by indication (ICZN 1999, Art. 12.1, 12.2.7), the name accompanying an illustration on plate iii of Westwood's "Aid to the Identification of Insects." The date of publication of the journal article is 01 March 1880 (Evenhuis 2003), that of the plate is unknown to us. Luckily in this case, the order does not affect the stability of the name, as both the description and the indication are based on the same specimen. Given that the known publication date is early in the year, we have arbitrarily chosen the journal article as the validation, and list the plates as a subsequent use. Should reversal of this become necessary by future scholarship, it will not affect the interpretation of the name.

Not even *Scoriaderma congolense* escaped problems, as the label data on the type were misinterpreted by Fairmaire (1894b), and that Mexican species was placed in the African genus based on geography, not characters. It is here placed as a synonym of *Verodes scabrosus* (Solier) (see below under *Verodes*). This restricts *Scoriaderma* to the drier upland forests of Eastern Africa and possibly the Comoro Islands (see below).

The now-monotypic genus *Scoriaderma* is grouped in the strict consensus tree (Fig. 73) with the 2 species in the Cuban endemic *Nosoderma*. It is tempting to synonymize the 2 genera based on the small number of species and the overall similarity of the groups. However, since the generic name is already available, we will continue to recognize it for the time being.

Scoriaderma shares several characters with one or both of the basal *Zopherus* and *Zopherosis* (Ślipiński and Lawrence 1999). These include: absence of femoral nodules on all femora in the male (also homoplastic with *Sesaspis emarginata* and *Verodes aequalis*), labial palp insertions concealed by the mentum, sensilla area at apex of last antennomere recessed and emarginate, and antennomere 3 transverse (also occurs in *Sesaspis emarginata*). The lateral bridge between the suprantennal ridge and subgenal ridge that encloses the antennal insertion apically (Fig. 15) is probably an synapomorphy for the genus.

***Scoriaderma cordicolle* (Waterhouse)**
Figs. 15–16, 20–21

Nosoderma cordicolle Waterhouse, 1880a: 214; Waterhouse, 1880b: plate iii.
Scoriaderma cordicolle; Gebien, 1936: 670.
Scoriaderma comoriense Fairmaire, 1894a: C. NEW SYNONYMY

Diagnosis: See above, under genus.

Distribution: Upland forests of southeastern Africa at elevations around 1500 meters, and the Comoro Islands.

Recorded distribution: A summary of the 39 specimens of the genus examined is COMORO ISLANDS. KENYA: Kwale District, Makadara Forest, Shimba Hills Res. TANZANIA: Usambara Hills. ZIMBABWE.

Types: *Nosoderma cordicolle* Waterhouse 1880a. Probably lost, see Notes below.

Scoriaderma comoriense Fairmaire: LECTOTYPE here designated, of undetermined sex, intact in MNHN. Handwritten Comores/ red rectangle TYPE/ *Scoriaderma; comorianum*; n-g.; J- Comores/ light blue rectangle Muséum Paris; 1906; Coll. L. Fairmaire/ red square LECTOTYPE; *Scoriaderma*; *comoriense*; Fairmaire 1894; designated; I. A. Foley 2006. PARALECTOTYPE here designated, of undetermined sex, missing right protarsus, in NHMB-Frey Collection. Handwritten (in same hand as Lectotype) J. Comores/ on pink card hand written; typed Cotype; handwritten *comoriense*/ red square PARALECTOTYPE; *Scoriaderma*; *comoriense*; Fairmaire 1894; designated; I. A. Foley 2006.

Notes: We have not been able to locate the holotype of *Nosoderma cordicolle*, which seems to have been lost. Waterhouse (1880a, 1880b) stated it was in the "possession of Colonel Shelley," and it is not among Waterhouse's types deposited in the BMNH (Maxwell V. L. Barclay, *in lit*.), nor is it in the Hope Museum at Oxford (James Hogan, *in lit*.). We do not know anything further of Shelley or his collection. There was an ornithologist by the name of G. E. Shelley who worked in Africa, and sold a collection of beetles in 1889 (Horn and Kahle 1937), but in 1896, when G. E. Shelley published "The Birds of Africa," he held the rank of Captain (Shelley 1896), so he would not have been the 1880 Colonel Shelley. At this point, we must assume that the type of *Nosoderma cordicolle* has been lost, but it may still exist in one of the smaller British or European museums. No Neotype is deemed necessary for *N. cordicolle*, as no taxonomic confusion is involved in the interpretation of the single species in east Africa.

We base our interpretation of the species on Waterhouse's (1880a) description, the beautifully rendered illustration (1880b), the opinions of previous workers, and material from the mountain ranges of the Kenya/ Tanzania border region that produced Waterhouse's type.

With the removal of *S. congolense* to *Verodes*, the remaining 39 specimens of *Scoriaderma* examined represent a single variable species. Although there is a large amount of individual variation in color pattern and intensity of elytral sculpture (like many members of the tribe), no consistent geographical differences could be found, not even between the types from the Comoro Islands, and populations on the mainland of Africa. Because there seem to be no recent collections of the genus from the Comoro Islands, it is possible that those types were mislabeled or are part of an introduced population from the mainland. In any case, the name *S. comoriense* is a junior synonym of *S. cordicolle* NEW SYNONYMY. This conclusion will need testing with additional specimens.

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FIGURES 20–21. *Scoriaderma cordicolle.* 20. Dorsal surface of head and pronotum; 21. Ventral surface of head and prosternum. Scale bars = 1mm.

Genus *Nosoderma* Guérin-Méneville

Figs. 4, 22–25

Nosoderma Dejean, 1834: 207 *nomen nudum*. Dejean 1836: 207 *nomen nudum*.

Nosoderma Guérin-Méneville, 1838: 280. Sherborn, 1928: 4412. Neave, 1939: 347. Foley and Ivie, 2007: 65. (Type species *Nosoderma echinatum* Guérin-Méneville 1838: 280, by monotypy).

Meralius Casey, 1907b: 470. Gebien, 1936: 669. Neave, 1939: 105. Blackwelder, 1945: 515. Marcuzzi, 1957: 128. Marcuzzi, 1962: 43. Doyen and Lawrence, 1979: 342. Marcuzzi, 1984: 75. Lawrence and Newton, 1995: 891. Ślipiński and Lawrence, 1999: 15. García-París *et al.*, 2001: 145. Ivie, 2002: 460. Garrido, 2004: 56. (Type species *Nosoderma duponchelii* Solier, 1841, by original designation) (Synonymy by Foley and Ivie, 2007).

Diagnosis: The combination of the transverse groove on the prosternum (Fig. 24), distinct pit on the metasternum, and lobed lateral margins of the pronotum will separate this genus from all Zopherini with 10-segmented antennae except *Scoriaderma*. It can be distinguished from *Scoriaderma* by the ventrally inserted labial palps not concealed by the mentum, sensilla at the apex of last antennomere covering the apical half of the segment, presence of nodules on the femora of the male, and a very narrow groove at least along the apical third of the lateral margin of the pronotum.

FIGURES 22–25. 22–23. Dorsal habiti. 22. *Nosoderma echinatum*, Cuba; 23. *N. turquinense***,** Cuba. **24.** *N. echinatum* ventral surface of prosternum. **25.** *N. turquinense* leg surface.

Description: The generic definition of Ślipiński and Lawrence (1999) for *Meralius* Casey, matches the concept of *Nosoderma* used here.

Notes: The genus *Nosoderma* was first validated by Guérin-Méneville based on the inclusion of his species *Nosoderma echinatum* Guérin-Méneville 1838 (type species based on monotypy). The genus *Meralius* was later described by Casey 1907 (Type species *Nosoderma duponchelii* Solier 1841, by original designation) without examining any actual specimens of the genus. It was distinguished based on the crenulate lateral margins of the prothorax, and being the only member of the tribe from the West Indies (Cuba). The Casey type species was later synonymized with *Nosoderma echinatum* Guérin-Méneville 1838 (Gebien 1936). *Meralius* Casey was recently synonymized with *Nosoderma* Guérin-Méneville (Foley and Ivie 2007).

No new species were added to this genus for nearly 140 years until 2004, when two new species were

described from Cuba. Garrido (2004) added two questionable species to the genus: *Meralius turquinensis* and *Meralius montanus*. These species were differentiated based on size, sculpture and variation in the femoral nodules of the male, all of which are variable within species of Zopherini. The male nodule is a particularly variable character across species, within species, and even within individual specimens. Rare specimens of the genera *Sesaspis* and *Verodes* have the nodules occurring asymmetrically, present on one leg but not the other in a single individual.

This genus is defined by having ventrally inserted labial palps (also occurs in *Verodes*), the presence of a very narrow groove, at least along the apical third of the lateral margin of the pronotum occurs nowhere else in the Zopherini and is probably a synapomorphy, similar pronotal grooves occur in different position in *Scoriaderma*, *Noserinus* and *Zopher.*

A specimen of this genus in the NHMB-Frey Collection, bears a label identifying the specimen as *Meralius furcatus*, as well as a label that places it in the collection of Gebien. This specimen is not a member of *Nosoderma furcatus* Kirsch, but a misidentified specimen of *Nosoderma turquinense* (Garrido). This clarifies that when Gebien (1936) moved *Nosoderma furcatus* Kirsch to *Meralius*, he was in fact examining a misidentified specimen, leading to decades of confusion about the distribution and characters of what was, until recently, known as *Meralius*. The actual entity belonging to the name *N. furcatus* is supported as more closely related to *Noserinus dormeanus*, and is now placed in *Noserinus*.

Key to species of *Nosoderma*

1. Elytral margin, from level of hind coxa posteriad, with 5–6 more-or-less equal sized and evenly spaced nodules (Fig. 22); discal nodule on declivity of subequal size to these 5; secondary setation on legs uniformly thickened and apressed; apex of elytra along suture smooth to weakly emarginate; body form more stout, approximately 0.58X as long as wide at widest point; femoral calus of male with raised marginal bead, disc depressed below this bead. Cuba. Figs. 22, 24..... *N. echinatum* (Guérin-Méneville)
-. Elytral margin, from level of hind coxa posteriad, with 3 larger, unequal nodules and 2–3 smaller ones (Fig. 23); disc of declivity with single large median nodule, and 2 or 3 weak elevations; secondary setation on legs very long, projecting, and club shaped (Fig. 25); apex of elytra along suture strongly emarginate; body form more elongate approximately 0.65X as long as wide at widest point; femoral calus of male with calus domed, lacking marginal bead. Cuba. Figs. 23, 25 .....*N. turquinense* (Garrido)

***Nosoderma echinatum* Guérin-Méneville**
Figs. 4, 22, 24

Nosoderma echinatum Guérin-Méneville, 1838: 280. Fairmaire, 1894: CI. Foley and Ivie, 2007: 65.
Meralius echinatus; Gebien, 1936: 669. Blackwelder, 1945: 515. Marcuzzi, 1984: 75. Garrido, 2004: 56.
Nosoderma duponchelii Solier, 1841: 34. (synonymy by Gebien 1936: 669).
Meralius duponchelii; Casey, 1907b: 470.

Diagnosis: Distinguished by the short stout form, with at least 5 small subapical elytral nodules, and secondary setae which are not club shaped.

Distribution: Widespread on Cuba and Isla de la Juventud from sea level to 1,700 meters (Garrido 2004).

Recorded distribution: A summary of the 78 specimens examined is CUBA: Pinar del Rio, La Habana, Matanzas, Sancti Spíritus, Camagüey, Holguín, Santiago de Cuba, Isla de la Juventud.

Types: Not seen.

***Nosoderma turquinense* (Garrido)**
Figs. 23, 25.

Meralius turquinense Garrido, 2004: 56.
Nosoderma turquinense; Foley and Ivie 2007: 68.
Meralius montanus Garrido, 2004: 59. **NEW SYNONYMY.**
Nosoderma montanum; Foley and Ivie 2007: 68.

Diagnosis: This species is distinguished from *N. echinatum* by the elongate form, large elytral nodules, and long club-shaped secondary setose vestiture (Fig. 25). In general form it resembles some species of *Sesaspis* but it is easily distinguished from that genus by lacking setose punctures on the ventral surface, and the presence of the distinct prosternal groove.

Redescription (of male): 17.5 mm. Fig. 107. Brachypterous. Dorsal vestiture multicolored tomentose, consisting of short, apressed scales; secondary setation of long club shaped golden setae. Anterior clypeal margin weakly concave; bridge connecting suprantennal ridge and subgenal ridge absent; subgenal ridge strongly developed; antennomere 3 approximately 1.75 X longer than 4; labial palps inserted ventrally; labial margin with tufts of setae inserted in fossae; mentum acute at apex. Scutellum not visible; lateral margin of pronotum with distinct teeth; apical angle with large posteriorly directed fin-shaped tooth; hypomeron with short arcuate groove near apical margin; well developed transverse groove medially on prosternum. Elytra elongate, approx. 1.75 X as long as wide, 1.78 X longer than pronotum; lateral margin of declivity with two strongly projecting, acute nodules; apex with similar large nodules one either side of suture, creating deeply emarginate tip; start of declivity with large nodule medially. Metasternum with distinct small pit. Profemora only, with small nodule; tibial spurs present but short, barely extending beyond setose fringe; tarsal strip absent. Ventrites 1–4 rounded; margin between ventrites 1–3 with median groove; ventrite 5 with narrow preapical groove flattened at apex.

Distribution: The higher areas of the Sierra Maestra, Cuba.

Recorded distribution: A summary of the 30 specimens examined -- CUBA: Santiago de Cuba.

Rejected record: VENEZUELA: N. Grenada, this specimen (NHMB) mentioned in the generic notes is undoubtedly a mislabeled Cuban specimen.

Types: *Meralius turquinense* Garrido. Holotype female (IESC): Cuba; Pico Turquino, S. M.; 1500 m. 31/ 7 1990; L. de Armas (IESC) PARATYPES: 1 male—La Siberia; Sierra Maestra, Ote; 7 VI 1963; Cols. Zayas, García/ Zopheridae; Ident OHG 2564; Meralius turquinensis; Garrido 200 (OHGC). 1 female—La Siberia; Sierra Maestra, Ote; 7 VI 1963; Cols. Zayas, García/ [should have a label that says "Zopheridae; Ident OHG 2566; Meralius turquinensis; Garrido 200" but it is missing] (OHGC). 1 female—Sierra Maestra, Cuba; Julio 10–20 de 1922; Col. C. H. Guillou y; S. C. Bruner; 1076–350m/ Zopheridae; Ident OHG 2568; Meralius turquinensis; Garrido 200 (OHGC). 1 female – El Joaquin; y La Platica; Turquino; P. Valdéz/ Zopheridae (OHGC). 7 females – 29-11-2000; Bajo; corteza/ Zopheridae; Ident OHG [2592, 2693, 2594, 2595, 2596, 2598]; Meralius turquinensis; Garrido 200 [seventh specimen is missing the second label, and is #2567] (OHGC).

Meralius montanus Garrido. Garrido (2004) reports the holotype to be in the IESC. There are four male specimens in the IESC that match the reported data of the holotype of *M. montanus*. None are the specimen illustrated in the original paper, but that illustration is probably one of the paratypes in the Garrido collection (OHGC). None of the IESC specimens bear a holotype label, but the one that has been dissected is considered the holotype: La Gran Piedra; Stgo de Cuba; 1100m 21/7; L. de Armas. On the underside of this label is "♂ Bajo; corteza." The three other male specimens with same label in IESC are not paratypes. PARATYPES: 3 males—La Gran Piedra; Stgo de Cuba; 1100m 21/7; L. de Armas/ Zopheridae; Ident OHG [2557, 2559, 2565]; Meralius montanus; Garrido 200 [some minor variation exists among the exact lettering of the first label] (OHGC). 1 male – La Gran Piedra; VI – 1971; Oriente Cuba; Col. R. Gonzales/ Zopheridae; Ident OHG

2556; Meralius montanus; Garrido 200 [this specimen is included in the type series via the OHG number, although the first label does not strictly agree with the Holotype as indicated in the enumeration of types in Garrido 2004] (OHGC).

Notes: [In the discussion below, *Meralius turquinensis* and *Meralius montanus* are used to discuss the original concepts of Garrido (2004), while *Nosoderma turquinensis* is used in reference to our concept of a single species.] As defined by Garrido (2004), *Meralius turquinensis* (from Pico Turquino) is geographically separated from *M. montanus* (from La Gran Piedra). Both localities are in the Sierra Maestra, but that area includes several different ranges with different origins. Garrido (2004) reported two unnamed specimens from a third Sierra Maestra range, between the two type localities—the Loma del Gato in the Sierra del Cobre.

Femoral caluses of *M. turquinensis* and *M. montanus* do indeed differ. However, there is only one reported male of *M. turquinensis*, and it is the largest male known. It has a correspondingly exaggeratedly large femoral calus ("cayo femoral"), but otherwise is similar to those of *M. montanus*. Two additional males from Pico Turquino in the IESC have smaller caluses. The variation in lateral serration of the elytron and pronotum, as well as the size of elytral and pronotal tubercles does not show any geographic consistency. The single Loma del Gato male (Male 254) is in fact a *N. turquinensis* that is in form intermediate between the 2 named populations. It has a smaller femoral calus than the reported *M. turquinensis*, but of the depressed form of that population. Variation in this character is extremely wide in many species, scattered across the Zopherini as a whole, and this specimen is the best argument for the synonymy of *M. turquinensis* and *M. montanus*. It is labeled: Loma del Gato, Sie-;rra del Cumbre, O-;riente Cuba, Oc-;tober 12, 1935/ Zopheridae; Ident. OHG 2–54; Meralius sp. n. (OHGC). We can find no other difference to support the separation of these into species.

The Loma del Gato Female 340 mentioned by Garrido (2004, pg 61) is in fact a typical *N. turquinensis* with the apex of the elytra glued into the posterior opening in the prothorax, and the mesothoracic opening directed caudally, explaining why it looks "totally different." It is labeled: Loma del Gato, Sie-;rra del Cumbre, O-;riente Cuba, Oc-;tober 1–2, 1935/ J. Acuña, S. C.; Bruner, elv.; 2600–3525 ft. (OHGC). A second, undamaged, female with the same label data is in the IESC.

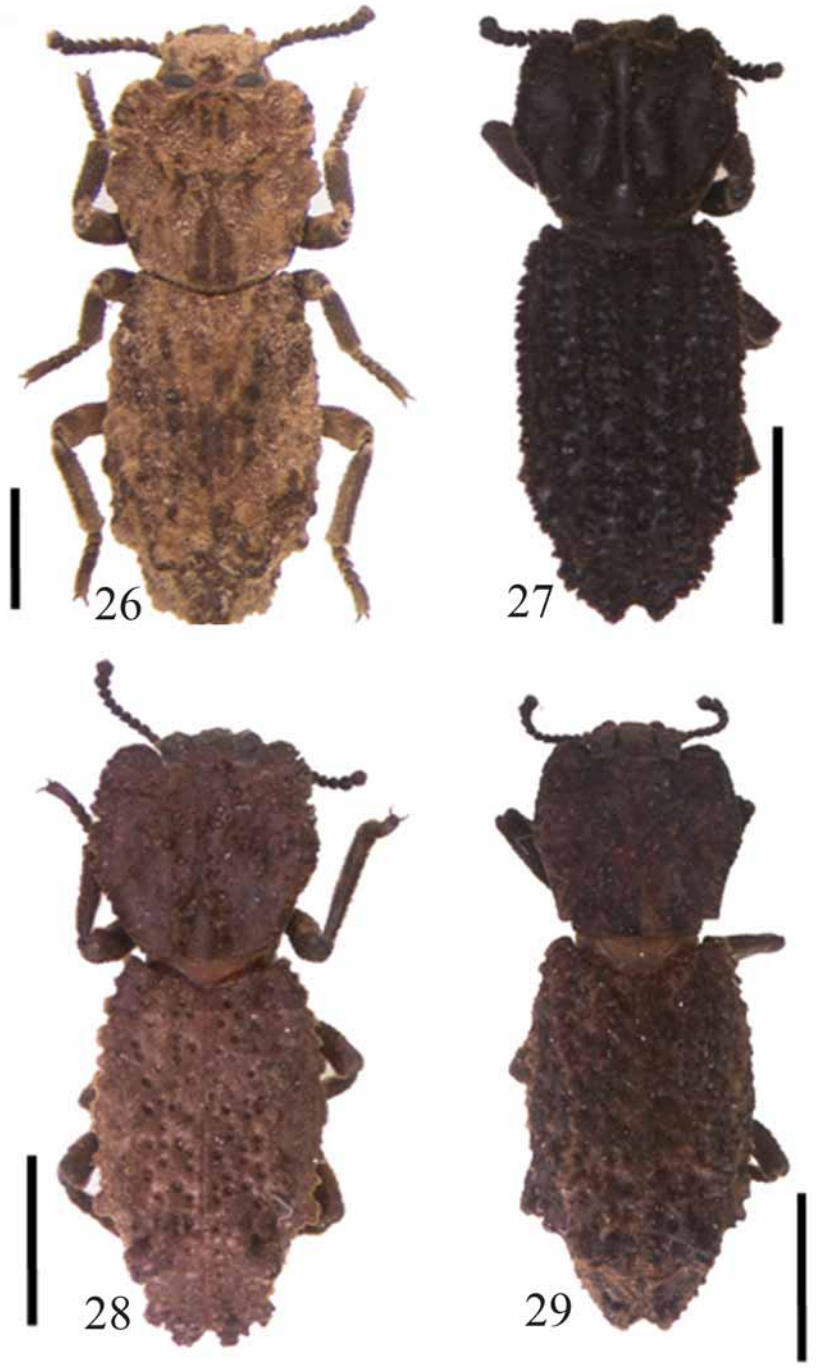
This species is sympatric with *N. echinatum*, which is much wider in distribution.

Genus *Sesaspis* Casey NEW SENSE
Figs. 2, 17–19, 26–29, 30, 33, 54, 72

Sesaspis Casey, 1907b: 469. Gebien, 1936: 669. Neave, 1939: 182. Blackwelder, 1945: 514. Doyen and Lawrence, 1979: 341. (Type species *Nosoderma denticulata* Solier, 1841: 33 by original designation).
Sesapis Doyen and Lawrence, 1979: 341. (*lapsus calami*).

Diagnosis: This genus is defined by having the ventral body surfaces covered by punctures with single inserted setae (tubercles in *Phloeodes* and *Verodes*) and the presence of a short arcuate cavity on the hypomeron (also present in *Nosoderma*, but that genus has a distinct transverse groove on the prosternum).

DESCRIPTION (of male): Length 11–19 mm. Brachypterous. Dorsal vestiture tomentose to densely setose; vestiture consisting of dense bristle-like setae, or combination of very short matted woolly setae and golden setae inserted in punctures, never with obvious tubercles; ventral surface similar with setae inserted in punctures. Head not constricted behind eyes; suprantennal ridges distinctly raised above antennal insertions. Anterior clypeal margin relatively straight to concave. Subgenal ridges present and strong. Eye elongate oval, posterior margin slightly emarginate. Antenna 10-segmented; antennomere 2 shorter than 1 or 3; antennomere 3 short and transverse equal in size to 4, or slightly to considerably longer than 4; at least antennomere 1 and up to basal 6 antennomeres with dense patch of golden setae on apical margin; antennal club 2-segmented, weak. Mandible (Fig. 33) bidentate, without membranous prostheca; last segment of maxillary palp acutely acuminate; labial palps inserted laterally, insertions exposed; apical margin of labium with setose fringe or setae inserted in fossae.



FIGURES 26–29. Dorsal habiti. 26. *Sesaspis triplehorni*, Belize; 27. *S. emarginata*, Texas, Comal Co.; 28. *S. lutosa*, Mexico, Oaxaca; 29. *S. sylvatica*, Mexico, Tamaulipas. Scale bar = 5mm.

Lateral margin of pronotum weakly arcuate to weakly bisinuate; disc with strong lyriform to weakly arcuate ridge laterally, simple along midline to paired parallel ridges running entire length, more strongly elevated at apex and base; anterior angles rounded, produced forward. Hypomeron with distinct short arcuate cavity near apical margin, shallow depression behind cavity; prosternal process 2.0–2.5X as wide as coxal cavity, apex concave; procoxal cavities externally closed.

Scutellum not visible. Elytra with or without distinct ridges and nodules; with 8 rows of fairly regular

punctures; never with obvious tubercles.

Mesocoxae separated by distance subequal in width to coxal cavity; laterally closed. Tarsal formula 5-5-4, tarsi with all segments with dense patches of golden setae creating weak median strip; apex between claws simple without setose empodium. Nodules on femora absent, present on all legs, or present only on pro and mesofemora. Abdomen with ventrites 1–4 medially flattened or rounded; with setose punctures, never with tubercles; ventrite 5 with narrow arcuate preapical groove.

FEMALE: Similar to male except lacking nodules on femora. When the nodules are totally absent in the male (*S. emarginata*), there is no discernable external difference.

Distribution: The genus occurs in Central America north up the Sierra Madre Oriental into Texas. This is a relatively small geographic area to support 7 species, but the mountainous pine forest of this area are highly fragmented sky islands that have led to the formation of several allopatric species.

Notes: This genus was described by Casey without examining actual specimens and was based on the published description of *Nosoderma denticulata* Solier, the type species, by original designation. *Sesaspis* was later synonymized with *Nosoderma* Solier by Doyen and Lawrence (1979). The current morphological analysis supports the recognition of *Sesaspis* as a distinct genus that occurs from Mesoamerica to Texas. The five described species placed in this genus were most recently placed in the genera *Nosoderma* (*not* Guérin-Méneville) (*S. denticulata*, *S. lutosa*, and *S. sylvatica*) and *Phloeodes* (=*Noserus*) (*S. emarginata* and *S. doyeni*). The independent phyletic lineages of *Noserus* (*sensu* Doyen and Lawrence 1979) were recognized by García-París *et al.* (2001), who suggested the genus was possibly paraphyletic, with a Mexican Gulf and Pacific lineage, but took no action to correct the generic definition or component species. García-París *et al.* (2001) also returned *Noserus* to valid status after it had been synonymized with *Phloeodes* (Ślipiński and Lawrence 1999). From this sense of *Noserus*, *Noserus plicatus* is confirmed as a member of *Phloeodes* (Ś lipiński and Lawrence 1999, Ivie 2002) and the other two described species are here placed in *Sesaspis*.

The name *Nosoderma denticulata* has historically been applied to a species that is relatively common in Central America. Based on the examination of the Solier type of this species these identifications are incorrect. Solier (1841) described the species *Nosoderma denticulata* from Mexico, but only a single specimen of the presumed species has been examined from Mexico, and it was in southern Chiapas (IEXA). The true identity of *Nosoderma denticulata* lies with a species that has only been recorded from a handful of localities in eastern and central Mexico and is closely related (possibly the sister-species) to *Noserus emarginatus* Horn from Texas. Both of the species that the name *Nosoderma denticulata* has been applied to are supported as true members of the genus *Sesaspis* Casey. Therefore the type species of the new sense of the genus remains *Nosoderma denticulata* Solier 1841.

While there has been some confusion about species identity, amazingly there are no synonyms described in *Sesaspis*. This could be due to the fact that the genus is rarer and more isolated in habitat than the genera *Phloeodes* and *Verodes*. For example, *Noserus emarginatus* was described in 1878 from Texas. This species has been reported from a relatively wide geographic area of southern Texas, including highly populated areas, but relatively few specimens (very few when compared to *Phloeodes*) have been collected. The rarity of specimens (Casey never saw any 1907a, b) during a time of questionable taxonomy, saved the genus from the accumulation of synonyms that have plagued the related genera. The two new species described here, and the two most recent species additions to the tribe (García-París *et al.* 2001 and 2006), both belong in this genus and are the result of relatively recent collecting efforts in northern Mexico and Central America.

General relatedness patterns can be identified among the species based on morphology. The species *Sesaspis doyeni* and *Sesaspis ashei*, *Sesaspis emarginata* and *Sesaspis denticulata*, and *Sesaspis lutosa* and *Sesaspis sylvatica* are all probably sister-species pairs. This leaves the species *Sesaspis triplehorni* relatively isolated in Central America and sharing general sculptural patterns with four of the other species (*S. emarginata*, *S. denticulata*, *S. lutosa* and *S. sylvatica*) which almost certainly represent a separate clade within *Sesapis* defined by the loss of the male nodule on at least one femora, the dense setose vestiture, and distinct sculpture

of elevated ridges and nodules. On the other hand, *Sesaspis doyeni* and *Sesaspis ashei* are similar in the reduced elytral sculpture, and presence of nodules on all femora of the male. The little biological information that is available for these species suggests that *S. doyeni*, *S. ashei*, *S. sylvatica*, and possibly *S. lutosa* all occur in high elevation cloud forests, while *S. triplehorni* and *S. emarginata* occur in lowland hardwood forests.

García-París *et al.* (2006) at least partially based their synonymy of *Noserus* and *Phloeodes* with *Nosoderma* (Solier *not* Guérin-Méneville) on the conclusion that *N. sylvaticum* was intermediate between the genera. In actuality, the species currently placed in *Sesaspis*-, share more characters with the species correctly placed in *Nosoderma* Guérin-Méneville from Cuba, including many similarities in the vestiture and surface sculpture.

At least two species have been collected from oak (*Quercus* sp., label data), *Sesapis doyeni* was described from under loose bark of dead pine stumps (García-París *et al.* 2001), and *S. sylvatica* from rotten fungus covered logs in cloud forests (García-París *et al.* 2006).

Key to species of *Sesaspis* Casey

1 Elytral sculpture reduced, at most a faint straight elevation of the 3rd or 5th elytral interval, and weak elevation at start of declivity; apex of elytra almost smooth, if weakly emarginate not swollen along suture 2

- Elytral sculpture well developed with any combination of distinct parallel or arcuate ridges and large nodules; apex of elytra weakly to strongly emarginate, if weakly emarginate then swollen along suture 3

2 Elytra with faint elevation in 5th interval; lateral margin of apical declivity smooth. Mexico, Nuevo Leon. Fig. 19 ... . *S. doyeni* (García-París *et al.*)

- Elytra with faint elevation in 3rd interval; lateral margin of apical declivity weakly serrate. Mexico, Hidalgo. Fig. 18 ..... *S. ashei* NEW SPECIES

3 Elytra with two distinct almost straight parallel ridges from base to declivity, ridge in 3rd terminating in small nodule before apical margin; apex of elytra strongly emarginate; antennomere 3 short and transverse subequal in size to 4; male nodules absent on all femora. Texas, New Mexico. Tamalipas. Fig. 27 ..... *S. emarginata* (Horn)

- Ridge in 3rd elytral interval weak, indistinct, or series of disconnected nodules for most of length, ridge in 5th if present strongly arcuate; apex of elytra weakly emarginate; antennomere 3 slightly to obviously elongate, longer than 4; male nodules present on at least pro and mesofemora 4

4 Elytral ridge in 3rd interval reduced medially, distinct apically, extending almost to apical margin; apex of elytra only slightly emarginate; nodule at start of apical declivity weak, connected to ridge; vestiture of dense bristle-like setae. Mexico. Fig. 17 ..... *S. denticulata* (Solier)

- Elytral ridge in 3rd interval reduced to almost absent, or consisting of series of rounded nodules; 3rd interval terminating in large round or arcuate nodule at start of apical declivity; vestiture tomentose 5

5 Ridge in 3rd elytral interval formed by disconnected round nodules; elytral suture at apex not swollen; nodules at start of declivity strongly rounded or conical; subgenal ridge strongly thickened with enclosed median depression or pit. Mexico, Chiapas and Central America. Fig. 26..... *S. triplehorni* NEW SPECIES

- Ridge in 3rd elytral interval indistinct, elytra flattened dorsally; elytral suture strongly to weakly swollen; nodules at start of declivity arcuate; subgenal ridge well developed but with distinct posterior bend 6

6 Apical margin of elytra bifid with two distinct nodules, suture weakly swollen; posterior angles of pronotum obtuse and rounded; dorsal surface of head with apical margin of frons flat, margin of suprantennal ridge slightly emarginate, channels at base of suprantennal ridge straight. Mexico, Oaxaca. Fig. 28 .... *S. lutosa* (Champion)

- Apex of elytra with single nodule, suture strongly swollen with short ridge; posterior angles of pronotum expanded, sharpened to approximately 90° angle; dorsal surface of head with apical margin of frons concave, margin of suprantennal ridge rounded, channels at base of suprantennal ridge arcuate. Mexico. Fig. 29 .. *S. sylvatica* (García-París *et al.*)

***Sesaspis denticulata* (Solier) RESTORED COMBINATION**
Fig. 17

Nosoderma denticulatum Solier, 1841: 33. García-París *et al.*, 2006: 229.
Sesaspis denticulata; Casey, 1907b: 469. Gebien, 1936: 669. Blackwelder, 1945: 514.
Verodes denticulatus; Foley and Ivie, 2007: 71.
Nosoderma sylvaticum; (in part); García-París *et al.*, 2006: 222.

Diagnosis: Vestiture similar to *S. emarginata*, consisting of dense bristle-like setae, but with the elytral ridges arcuate rather than straight and strongly parallel, and with femoral nodules present in the male. Additionally, the elytral apex is only slightly emarginate, the nodule at the start of apical declivity is weak and connected to a ridge. These characters will distinguish this species from other members of *Sesaspis* with obvious elytral sculpture.

Distribution: Northeastern Mexico in high elevation cloud forests of the Sierra Madre Oriental between 750–2050m.

Recorded distribution: A summary of the 21 specimens examined is MEXICO: HIDALGO: NUEVO LEON: Chipinque Mesa. TAMAULIPAS: Gómez Farías.

Types: *Nosoderma denticulata*: HOLOTYPE ♂ intact in MNHN. Small green square Denti-;culatum/ green circle nosoderm.; denticulata.; May Sol.; Det. 61/red rectangle TYPE/ Solier-9641-34; Mus. Paris/ denticulatum Sol 33, 1 Mex/ hand written nosoderma; denticulatum; Sol.; mexique; on backside of same label microglossa; denticulata Sol; mexique (m. gory.).

***Sesaspis emarginata* (Horn) NEW COMBINATION**
Fig. 27

Noserus emarginatus Horn, 1878: 55. Gebien, 1936: 668. García-París *et al.*, 2001: 144–155.
Nosoderma emarginatum; García-París *et al.*, 2006: 229.
Phloeodes emarginatus; Ivie, 2002: 461.

Diagnosis: Distinguished by very dense bristle-like setose vestiture, antennomere 3 transverse and subequal in length to 4, distinct parallel ridges running almost entire length of elytra, elytra strongly emarginate at apex and male lacking nodules on all femora (also occurs in *Verodes aequalis*).

Distribution: Widespread but uncommon throughout central Texas, a single specimen has been examined each from Mexico (UCMC) and New Mexico (OSUC).

Recorded distribution: A summary of the 71 specimens examined is MEXICO: TAMAULIPAS: Corona. UNITED STATES: NEW MEXICO: Eddy. TEXAS: Bexar, Brooks, Burnet, Comal, Dimmit, Duval, Hidalgo, Jim Hogg, Jones, Kennedy, Kerr, Kimble, Kleberg, Llano, Medina, San Patricio, Sutton, Travis, Uvalde, Webb.

Types: HOLOTYPE of undetermined sex, mounted on card, with left meso-tarsus glued to card in MCZ. Small square label Tex(as)/red rectangle Holotype label with #3924 crossed out/red square label MCZ; Holotype 33955/ Noserus emarginatus Horn/Jan-Jul. 2005; MCZ Image Database.

***Sesaspis lutosa* (Champion) NEW COMBINATION**
Fig. 28

Nosoderma lutosa Champion, 1884: 46.
Noserodes lutosus; Gebien, 1936: 670.
Noserodes lutosa; Blackwelder, 1945: 515.

Nosoderma lutosum; García-París *et al.*, 2006: 230.
Verodes lutosus; Foley and Ivie, 2007: 71.

Diagnosis: Similar to *S. sylvatica*, but distinguished by the non-prominent posterior angles of the pronotum, and bifid tubercle at the elytral apex. See discussion of *S. sylvatica* below.

Distribution: Southcentral Mexico.

Recorded distribution: A summary of the 4 specimens examined is MEXICO: OAXACA: VERACRUZ.

Types: *Nosoderma lutosum*: LECTOTYPE ♂, intact in BMNH. Orange ringed circle Type/Orizaba-Mexico.; Salle Coll./Nosoderma lutosum,; Champ. MS/1674 light blue square/Phellopsis sp. Salle/Sp. Figured/ B.C.A.Col.IV.1.; Nosoderma lutosum/red square Lectotypus; *Nosoderma*; *lutosum*; Champion; García-París des 2000. PARALECTOTYPE ♀, intact in BMNH. Same data as LECTOTYPE except no type or 1674 label.

***Sesaspis sylvatica* (García-París, Coca-Abia, & Parra-Olea) NEW COMBINATION**
Fig. 29

Nosoderma sylvaticum García-París, Coca-Abia, & Parra-Olea, 2006: 215–230.

Diagnosis: The species is closely related to *S. lutosa*, but can be distinguished from that species by the acutely pointed hind angles of the pronotum, concave anterior clypeal margin, weakly serrate lateral pronotal margin and single dominant nodule expanded along the apex of the elytral suture, compared to the bifid large nodule at the apex in *S. lutosa* and strongly serrate lateral margin of the pronotum.

Description: See García-París *et al.* (2006).

Distribution: Known from the Mexican states of Tamaulipas, Queretaro, and Hidalgo, where the species occurs at elevations between 700–1,400 meters in the Sierra Madre Oriental.

Recorded distribution: A summary of the 47 specimens examined is MEXICO: HIDALGO, NUEVO LEON, TAMAULIPAS, QUERETARO.

Types: Not examined, holotype in Colección Nacional de Insectos del Instituto de Biología, Universidad Nacional Autónoma de México, México (García-París *et al.* 2006).

Notes: *Sesaspis lutosa* apparently replaces *S. sylvatica* in more southern Mexican locales such as Oaxaca. Three specimens were associated with oak (*Quercus* sp.) and several others were collected in "mesófilos", mountain forests or cloud forests (label data).

***Sesaspis doyeni* (García-París, Coca-Abia, & Parra-Olea) NEW COMBINATION**
Fig. 19

Noserus doyeni García-París, Coca-Abia, and Parra-Olea, 2001: 144–155.
Nosoderma doyeni; García-París *et al.*, 2006: 229.

Diagnosis: Distinguished from all members of *Sesaspis* except *S. ashei* by smooth, non-prominent dorsal and lateral tuberculation, completely covered by dense but very short tomentose setae. Distinct from *S. ashei* based on the thinner body, and very weakly elevated ridge present in the 5th rather than 3rd elytral interval.

Description: See García-París *et al.* (2001).

Distribution: Known only from the type locality, MEXICO: NUEVO LEON, Cerro Potosi between 2,800–3,350 meters and a single additional locality near Cerro Potosi in the Sierra Madre Oriental, San Antonio de Peña Heveda.

Recorded distribution: A summary of the 47 specimens examined is MEXICO: NUEVO LEON: Cerro Potosi, San Antonio de Peña Heveda.

Types: *Noserus doyeni*: Holotype not examined, holotype in Colección Nacional de Insectos del Instituto de Biología, Universidad Nacional Autónoma de México, México (García-París *et al.* 2001). PARATYPES #5–33 in EMEC. MEX: Nuevo Leon, Cerro Potosi; 10,300' IX-25-75/J. Powell, J. Chemsak & T. Friedlander/ red rectangle *Noserus doyeni* García-París, Coca-Abia, & Parra-Olea 2000, Paratipo. #5 with Nosoderma n. sp., Det. J. Doyen, 1989. #32 with Noserus sp., Det. J. Doyen, 1987.

PARATYPES #34–36 in CASC. Cerro Potosi, 11000', Galena, Nuevo Leon, Mex., AUG. 5,1938, Harry Hoogstraal/ under pine bark/ Gift to the California Academy of Sciences from Nevada Dept. of Agriculture via Robert C. Bechtel received 26 October 1990/ *Noserus doyeni* García-París, Coca-Abia, & Parra-Olea 2000, Paratipo.

***Sesaspis ashei* Foley and Ivie NEW SPECIES**
Fig. 18

Diagnosis: This species is closely related to *S. doyeni*, but can be distinguished from that species by the weakly serrate lateral elytral margin of the declivity, the weak elytral ridge in the 3rd rather than 5th interval, shallow dorsal elytral depressions medio-laterally, and a noticeably thicker body – visually the epipleuron is wider than the metepisternum for nearly the entire length.

DESCRIPTION (male): Length 17.5–22.5 mm. Black to dark brown; in natural state covered in greasy exudate and environmental debris; cleaned specimens have the cuticle uniformly dark red to black. Dorsal vestiture of very short bristle-like setae slightly expanded, secondary vestiture of short golden setae. Anterior clypeal margin weakly concave. Antennomere 3 approximately 1.25 X longer than 4; antennomeres 1–6 with short dense golden setae on apical margin. Labium with thin fringe of setae. Pronotum with weak arcuate lateral ridges; lateral margin smooth; hind angles obtusely rounded. Elytral sculpture with weak elevation running nearly entire length in interval 3, slightly more elevated at start of declivity; lateral margin of declivity weakly serrate. Femoral nodules large and distinct on all femora. Ventrites 1–3 flattened medially. Parameres emarginate at apex, sides not strongly projecting forward.

Distribution: Known only from the Mexican states of Hidalgo and Puebla.

Types: HOLOTYPE: ♂, MEXICO: Hidalgo; 4.4 km N Tlanchinol; Hwy. 105, 8 July 1992; 1420 m, J. S. Ashe #31; ex: misc. collecting/ red rectangle HOLOTYPE; Sesaspis; ashei; ♂; Foley & Ivie 2007 (SEMC).

PARATYPES: 1 ♂, 1 ♀, MEXICO, Hgo.,; La Mojonera,; 28.X.1992,; leg. J. Pál (HNHM). 1 ♂ - Vera Cruz,; 2-IX-51 MEXICO; Ben A. Foote (FMNH). 1 ♂ - MEX., PUE., 6800'; 1 mi. S. Honey,; VII-6-71; A. Newton.266 (FMNH). All paratypes with blue rectangle label PARATYPE; Sesaspis; ashei; ♂; Foley & Ivie 2007.

ETYMOLOGY: This species is named in honor of our friend and colleague, the late Dr. James Stephen "Steve" Ashe, who was the collector of the holotype and a significant number of other Central American Zopherini.

Notes: This species is probably the sister species to *S. doyeni* which is restricted to higher elevations of Nuevo León. The two species are restricted to sky islands in the Sierra Madre Oriental, and are divided by a considerable distance of unsuitable habitat.

No biological information is present on the label data. *Sesaspis doyeni*, the most closely related species, has been reported under the loose bark of dead pine trees (*Pinus* sp.*)* (García-París *et al.* 2001), and this species probably inhabits a similar high elevation pine-oak forest ecosystem.

***Sesaspis triplehorni* Foley and Ivie NEW SPECIES**
Fig. 26

Diagnosis: Resembles *S. emarginata* (Texas) and *S. denticulata* (Mexico), in the dense setose vestiture, but is quite distinct in sculpture. The pronotum has sub-parallel ridges along the midline that have weakly divided elevations at the apex and base (not quite as strong as *S. emarginata*), the elytral sculpture consists of arcuate rows of small round nodules, with one distinctly larger and teardrop shaped nodule at the start of the apical declivity. The dense mottled tomentose vestiture and banded apex of the parameres are also quite distinct.

DESCRIPTION (male): Length 11–22 mm. Vestiture consisting of dense setae, short and bristle like to tomentose, color mottled darks and light. Anterior clypeal margin concave. Antennomere 2 short and transverse; 3 only slightly longer than 4; antennomeres 1–6 with short dense golden setae on apical margin. Labium with two lateral tufts and few median setae inserted in broad depression; subgenal ridge thickened with median depression or pit. Pronotum with arcuate lateral ridges; lateral margin sinuate with weak notch; hind angles obtusely rounded. Elytral sculpture with arcuate rows of nodules in 3rd and 5th elytral intervals; large teardrop shaped nodule in 3rd interval at start of declivity. Femoral nodules present only on pro and meso femora. Ventrites 1–3 flattened medially.

Parameres strongly narrowed at the tip almost fused, weakly emarginate; near apex with distinct color band, light yellow at the tip.

Distribution: Far southern Mexico through Central America as far south as Nicaragua.

Types: HOLOTYPE: ♂ - BELIZE: Toledo Dist.; Blue Creek Village; 16 June 1981; W. E. Steiner/ EARTHWATCH Belize; Expedition 1981; D. H. Messersmith,; W. E. Steiner, *et al.*/ red rectangle HOLOTYPE; Sesaspis; triplehorni; ♂; Foley & Ivie 2007 (NMNH). PARATYPES: 7 ♂♂, 5 ♀♀ - same data as Holotype (NMNH). 3 ♂♂, 3 ♀♀ - same data as Holotype, except 1 July 1981 (NMNH). 1 ♂ - BELIZE: Orange Walk District; Rio Bravo Conservation Area; Mahogany Trail; 17°50'N, 89°01'W 4May1996; C.E. Carlton Lot#093/ LSAM0024746 (LSAM). 2 ♂♂ - BELIZE, 28.v.1997; Chiquibul For. Res.; Las Cuevas Field Station; 88°59'W, 16°44'N/ Pitfall with (1 specimen) dung/ (1 specimen) meat; coll. D. Inward; BMNH{E}; 2005-78 (BMNH). 1 ♀ - BELIZE, V–VI 1997; Chiquibul For. Res.; Las Cuevas field station; 88°59'W, 16°44'N; 500–700m, D. Inward; BMNH{E}; 2005-78 (BMNH). 2 ♂♂ - BELIZE (Cayo); Chiquibul Forest Reserve; Las Cuevas Research Station; 16°44'N 88°59'W; June 2006; BMNH {E} 2006-141; C. Gillett & J. Kitson (BMNH). 4 ♀♀ - BELIZE: Orange Walk Dist.; Rio Bravo Conserv. Area; Mahogany Trail, 2-3.IX.1995, P. W. Kovarik, coll.; taken on logs at night (1 MAIC, 1 OSUC). 1 ♀ - BELIZE: Cayo District; San Ignacio, San Ignacio; Hotel, 290m., VI-25-VII-1-1992; MV & FLUOR. lgts., broadleaved-: hardwood for., J. Rifkind & P. Gum (WFBM). 1 ♂ - BELIZE: Cayo District, mtn. Pine; Ridge, Pine Ridge Chito Line at; Little Vaqueros Ck. 525m.VI-26&28;-1992. broadleaf hardwood forest; slash area, J. Rifkind & P. Gum (WFBM). 1 ♀ - BELIZE: Orange Walk.; Dist. Rio Bravo Cons.; Area 8/16 -IV- 1996; mushroom pitfall trap (OSUC). 4 ♂♂, 1 ♀ - (BELIZE): 2 mi. S Orange Walk; Cayo, Br. Honduras; VIII-14-56 400'; B. & B. Valentine (OSUC). 1 ♀ BELIZE: Orange Walk; Dist. Rio Bravo Cons. Area, Well Trail near; "Texas Camp" 11-18.VII.;1996 P. W. Kovarik, coll.; yellow pan traps (OSUC). 1 ♂ BELIZE: Orange Walk Dist.; Rio Bravo Conservation Area; vic. La Milpa ruins, 17.IV.1995 P. W. Kovarik, coll./ collected as pupa; from within rotting; log/ Rio Bravo Coleoptera; Survey ZOP0001 (OSUC). 3 ♀♀ - HONDURAS, Liberia; 2-IX-1984 (rain; forest), C.W. O'Brien (HNHM). 2 ♂♂ - HONDURAS, Liberia; 6-IX-1984 (rain; forest), C.W. O'Brien (HNHM). 1 ♂ - HONDURAS: Atlantida; Lancetilla Bot. Grd., Tela; 10 m, 22 June 1994; 15°46'N, 87°27'W; J. Ashe, R. Brooks #181; ex: fogging fungusy log/ Zopheridae; det. K. J. Ahn 1994 (SEMC). 1 ♀ - HONDURAS: Atlantida Dpt.; Parque Nacional Pico Bonito,; Rio Secate, 15-III-2002; 15°41.700'N, 86°55.892'W; Caesar, Cognato, Harlin & Torres (TAMU). 1 ♂ - GUATEMALA: Tikal; 20-22.VII.1970; J. & M. Sedlacek (BPBM). 1 ♂ - MEXICO: CHIAPAS; Boca de Chajul; 27-VIII-1984 Alt. 110 m; Fragoso-Villalobos, cols./ TM-20; Colecta general.; En troncos podridos (IEXA). 1 ♀ - NICARAGUA: Rio San Juan Dept.; 60 km SE San Carlos Refugio; Bartola

100m 10°58.40'N 84°20.30'W; 26-V-2002, R. Brooks, Z. Falin,; S. Chatzimanolis ex. pyrethrum; fogging fungusy logs, NIC1BFC02 074/ Bar Code label with; SM0531635; KUNHM-ENT (SEMC). All paratypes with blue rectangle label PARATYPE; Sesaspis; triplehorni; ♂; Foley & Ivie 2007.

ETYMOLOGY: This species is named in honor of Dr. Charles A. Triplehorn, our academic parent (to MAI) and grandparent (to IAF), whose excellent species level revision of *Zopherus* was motivation to understand the other genera of the tribe, and in recognition of the considerable unpublished observations on the group which were kindly shared with us.

Notes: Specimen data report individuals collected from the trunk of a rotten tree, another on logs at night, and a handful on "fungusy" logs. Specimens were collected from 10–290 m and apparently inhabit lowland tropical wet forests. A long series of specimens was collected over several days in a rain-forested creek valley with steep sides among large rotten tree trunks covered with a garden of different bracket fungi and mushrooms both on and under the logs (W. Steiner pers. comm.).

Genus *Phloeodes* LeConte

Figs. 32, 35–53

Phloeodes LeConte, 1862: 216. LeConte, 1853: 235. Horn, 1870: 272–273. LeConte and Horn, 1883: 364. Champion, 1884: 44. Casey, 1907a: 42–43. Casey, 1907b: 471–473. Leng, 1920: 223. Essig, 1926: 429. Bradley, 1930: 183,322. Böving and Craighead, 1931: 41. Gebien, 1936: 667–668. Arnett, 1973: 651. Doyen, 1976: 267–272; fig. 1–11. Doyen and Lawrence, 1979: 341–345. Powell and Hogue, 1979: 295,297. Doyen and Miller, 1980: 3. White, 1983: 250, fig.107. Arnett, 1985: 350. Costa *et al.*, 1988: 213. Hogue, 1993: 296,298. Ślipiński and Lawrence, 1999: 19, fig. 69–82. Ivie, 2002: 458–461. Caterino, 2004: 7. García-París *et al.*, 2006: 215–230. (Type species *Nosoderma diabolicum* LeConte, 1851, designated by Casey 1907b).

Noserus LeConte, 1862: 216. Horn, 1870: 273. LeConte and Horn, 1883: 365. Champion, 1884: 44. Casey, 1907a: 43–44. Casey, 1907b: 473–474. Leng, 1920: 223. Bradley, 1930: 183,322. Böving and Craighead, 1931: 41. Gebien, 1936: 668. Arnett, 1960: 651,668. Arnett, 1968: 651,668. Arnett, 1973: 668. Arnett, 1983: 16. Doyen and Lawrence, 1979: 345. Doyen, 1980: 3. Arnett and Jacques, 1981: 145. Arnett, 1985: 350. Ślipiński and Lawrence, 1999: 19. García-París *et al.*, 2000: 473. García-París *et al.*, 2001: 151–153. Ivie, 2002c: 461. Foley *et al.* 2003: 103. García-París *et al.*, 2006: 215–230. (Type species: *Nosoderma plicatum* LeConte, 1859, by monotypy). (Synonymy by Ślipiński and Lawrence 1999).

Ageonoma Pascoe, 1866: 478. Horn, 1870: 272. (Type species: *Nosoderma diabolicum* LeConte, 1851, by monotypy). (Synonymy by Horn 1870).

Phoeodes Arnett, 1962: 668 (*lapsus calami*).

Noserosus Doyen and Lawrence, 1979: 345 (*lapsus calami*).

Noserodes [in part] Gebien, 1936: 670.

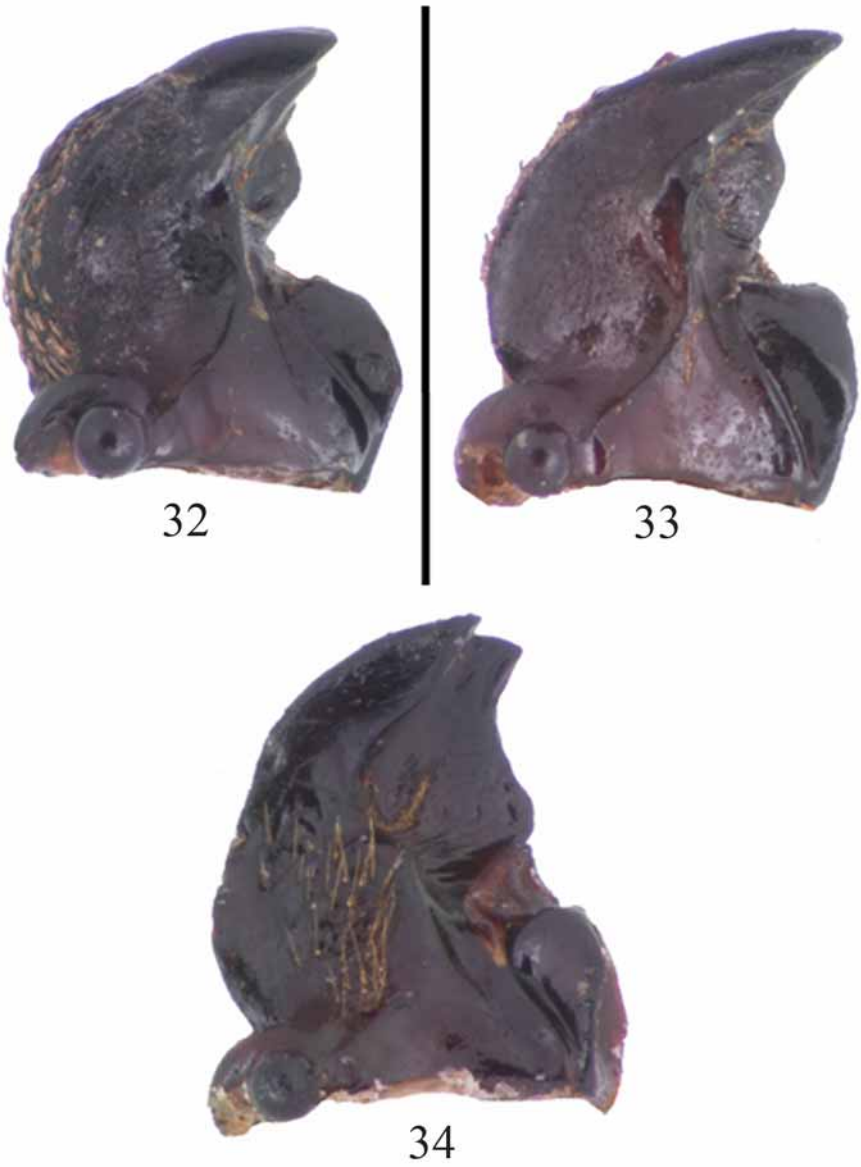
Diagnosis: This genus is supported based on the well-developed glabrous tarsal strip (Fig. 43) and at least partial, broad, well developed antennal cavities on the prothoracic hypomeron. The glabrous tarsal strip also occurs as a homoplasy in the distantly related *Zopherus*, and weakly in some *Verodes*, but *Zopherus* has 9-segmented antennae (10 in *Phloeodes*) and *Verodes* has no hint of an antennal cavity (well developed in *Phloeodes*, Figs. 39–42). This genus is very closely related to the genus *Verodes*, and can be further distinguished from that genus (Ślipiński and Lawrence 1999) by the lack of a mandibular prostheca, the broad mentum, and the laterally inserted labial palps. The presence of a tomentose whitish vestiture on the humeri and apical declivity in many specimens of *Phloeodes diabolicus*, and covering a large portion of the body in *Phloeodes venustus* will separate those two species from all other Zopherini with 10-segmented antennae that lack a scutellum (golden vestiture present in some *Sesaspis* species). The third member of the genus, *Phloeodes plicatus* is usually uniformly colored, but rarely has whitish patches of scale-like setae on the body.

30

31

FIGURES 30–31. Ventral surface of the head. 30. *Sesaspis sylvatica*; 31. *Verodes aequalis*. Scale bars = 1mm.

Notes: The genera *Phloeodes* LeConte and *Noserus* LeConte were originally described for species described in *Nosoderma sensu* Solier 1841. The taxonomic histories of those species have followed separate paths since 1862. These paths recently converged when *Noserus* was synonymized with *Phloeodes* (Ślipiński and Lawrence 1999). This synonymy was not recognized by García-París *et al.* (2000, 2001) who described a Mexican species, *Noserus doyeni* García-París *et al.* 2001, in the old sense of *Noserus* which returned the genus to independent status. Ivie (2002) restored it to synonymy following Ślipiński and Lawrence (1999), but little actual analysis of this question has been conducted.



FIGURES 32–34. Dorsal view of left mandibles. 32. *Phloeodes diabolicus*; 33. *Sesaspis sylvatica*; 34. *Verodes aequalis*. Scale bar = 1mm.

The genus *Phloeodes* originally included two California species, *Nosoderma diabolicum* LeConte 1851, and *Nosoderma pustulosum* LeConte 1859 (LeConte 1862). This genus was differentiated from *Zopherus* Gray and *Phellopsis* LeConte by having 10-segmented antennae and from *Noserus* LeConte by the degree of closure of the prothoracic antennal cavity. *Verodes* (*Nosoderma* Solier *not* Guérin-Méneville), occurring in Central America, was not included in LeConte's generic key (1862), but he did mention that it differed from *Phellopsis* in the number of antennal segments (10 vs. 11). He did not comment on any differences between the three genera with 10-segmented antennae.

Casey described 6 new species of California *Phloeodes*: *P. latipennis* Casey 1907a, *P. ovipennis* Casey 1907a, *P. elongatus* Casey 1907a, *P. scaber* Casey 1907a, *P. angustus* Casey 1907a, and *P. remotus* Casey 1907b. Casey's (1907a) contention was that the two LeConte *Phloeodes* species were divided into a northern species (*Phloeodes diabolicus*) and a southern species (*Phloeodes pustulosus*) separated by the presence of a dense pale whitish vestiture on the apical declivity of the elytra. To this interpretation, Casey (1907a, 1907b) then described his 6 new *Phloeodes* species from few or single specimens. These specimens were distinguished in typical Casey key format based on variations in sculpture, body proportions, velvety spots on the

elytra, and vestiture of the apical declivity. All of these characters have been observed to be highly variable within the genus, frequently because the external appearance of individuals is concealed by the accumulation of exudate and collected environmental debris. Casey had some inkling of this condition when he commented that some of his species may prove to be subspecies (1907a) and that some of his previously described *Phloeodes* species seemed doubtful (1907b). Despite these reservations, he concluded after examining additional specimens, that all of the species were valid and proceeded to described *Phloeodes remotus* from a single specimen (Casey 1907b). LeConte did not recognize a type species when he erected the genus, therefore Casey (1907b) designated *Phloeodes diabolicus* as the type species. The first Casey name to be synonymized was *Phloeodes latipennis*, which was listed as a junior synonym of *Phloeodes pustulosus* by Gebien (1936). The tradition of synonymy recently continued when García-París *et al.* (2006) synonymized the remainder of the Casey names with either, *P. diabolicus* or *P. pustulosus*.

LeConte (1862) described the genus *Noserus*, in the same paper that he described *Phloeodes*, with *Nosoderma plicatum* LeConte 1859 from California as the sole member of the genus. *Noserus emarginatus* Horn 1878 was added from Texas, considerably expanding the geographic range of the genus.

In a situation similar to his treatment of *Phloeodes*, Casey (1907a, 1907b) also revised *Noserus*. In addition, he recognized the close relationship between *Phloeodes* and *Noserus* and noted that in both groups the species forms were difficult to define (Casey 1907b). However, Casey described several new California *Noserus* species based on single or a few specimens as he had done in *Phloeodes*: *Noserus torvus* Casey 1907a, *Noserus collaris* Casey 1907a, *Noserus corrosus* Casey 1907b, and *Noserus convexulus* Casey 1907b. In describing these taxa, Casey primarily used differences in the strength of elytral ridges and tubercles as well as degree of body convexity; these characters are highly variable in most members of the tribe and are not useful in defining species limits. All of these Casey species were recently synonymized with *P. plicatus* (García-París *et al.* 2006).

When *Noserus* LeConte was synonymized with *Phloeodes* LeConte by Ślipiński and Lawrence (1999) in their review of the genera of Zopherinae, the synonymy was based on the fact that there are no distinguishing characters between the taxa besides the extent of the antennal cavity. All available evidence supports that *Phloeodes diabolicus* and *Phloeodes plicatus*, the respective type-species of the genera *Phloeodes* and *Noserus*, belong to the same genus, and that synonymy is recognized here.

The problems with the classification of *Phloeodes* in this sense comes from the described species that occur outside of California, *Noserus emarginatus* from Texas, New Mexico and Northern Mexico (García-París *et al.* 2000)], and *Noserus doyeni* García-París *et al.*, from Nuevo Leon, Mexico. Casey, who divided the Zopherini (*sensu* Ślipiński and Lawrence 1999) into several genera that were later synonymized (Triplehorn 1972, Doyen and Lawrence 1979) was the first to acknowledge that true *Phloeodes* would probably be confined to California (1907b). Even though Casey did not examine specimens of *Noserus emarginatus*, he stated that it would prove to be generically different and possibly belong to the genus *Nosoderma* Solier (*not* Guérin-Méneville) of Central America (now *Verodes*). The independent status of the genus *Phloeodes* was recently questioned by García-París *et al.* (2001, 2006). Based on previous difficulties assigning a species to the appropriate genus (*Noserus doyeni*), and perhaps realizing the problematic generic concepts in the Zopherini, García-París *et al.* (2006), lumped the genera *Phloeode*s and *Noserus* into *Nosoderma* (=*Verodes*). Little support was found for this conclusion, and three independent monophyletic lineages of this group are here recognized at the generic level.

The two species of old "*Noserus*" differ from the current diagnosis of *Phloeodes* in having setiferous punctures on the ventral body surfaces, a different type of antennal cavity, a poorly defined tarsal strip, variation in the male nodules, and the generally dense setose vestiture. They also differ from species of *Verodes* in lacking a membranous mandibular prostheca, in the presence of ventral setose punctures and laterally inserted labial palps. Therefore, these two species are removed from the genus *Phloeodes*, and added to the genus *Sesaspis*

Phloeodes (*sensu stricto*) is here restricted to the two California species (*Phloeodes diabolicus* and *Phloeodes plicatus*) and the Central American *Phloeodes venustus* (Champion) NEW COMBINATION, which was discovered to be a member of *Phloeodes* during the course of this study. The species here considered members of *Phloeodes* LeConte represent quite distinct forms. While the habitat and geographic range of the California species seem to overlap entirely, the two species are easily distinguishable. *Phloeodes venustus*, moved into *Phloeodes* from *Nosoderma* Solier (*not* Guérin-Méneville), was called the "finest and most distinct" of all the Central American species (Champion 1884), so it is also readily identifiable.

The inclusion of *Phloeodes venustus* in this genus is based on the absence of a membranous mandibular prostheca (which excludes it from *Verodes*), presence of tubercles on all body surfaces (which excludes it from *Sesaspis*), a well defined tarsal strip, broad apical margin of the mentum, and laterally inserted labial palps. The whitish vestiture that is seen in many specimens of *Phloeodes diabolicus*, and was the historical distinction between that species and *Phloeodes pustulosus*, is exactly the same vestiture that covers nearly the entire surface of the body in *Phloeodes venustus*. This whitish vestiture is seen in no other species of Zopherini with tuberculate sculpture, 10-segmented antennae, and hidden scutellum.

A general evolutionary trend towards wood boring larvae has been suggested in the Zopherini (Triplehorn 1972, Doyen 1976, Doyen and Lawrence 1979, Ślipiński and Lawrence 1999, Ivie 2002). The larval morphology of *Phloeodes diabolicus* is obviously modified for a wood-boring habitat possessing an enlarged thoracic region and reduced legs (Doyen 1976). The larva of *Phloeodes diabolicus* was described from cottonwood logs (*Populus* sp.), oak logs (*Quercus* sp.), and mulberry roots (*Morus* sp.) and was suggested as a non-specific decomposer that utilizes a variety of tree species (Doyen 1976). While for many larval Zopherinae the associated substrate is rotting wood, the nutritive source may be associated fungi (Doyen 1976, Ivie 2002), possibly white rot fungi (Lawrence 1991).

Adults of *Phloeodes diabolicus* and *Phloeodes plicatus* are most commonly collected under bark of decaying oak (*Quercus* sp.) and cottonwood (*Populus* sp.) trees, but have also been found associated with woody material of willow (*Salix* sp.), alder (*Alnus* sp.), sycamore (*Platanus* sp.), walnut (*Juglans* sp.), eucalyptus, cedar (*Cedrus* sp.), pine (*Pinus* sp.), madrone (*Arbutus* sp.), and laurel (*Umbellularia* sp.), as well as under several shrubs (including *Salicornia* sp. and *Baccharis* sp.), on fungi, in leaf litter, and under rocks. Multiple individuals of both species were found in the same microhabitat, with both species being relatively abundant under the same standing dead oak trees in Monterey Co., California in 2005 (pers. obs.).

Typically species of Zopherini are covered in a waxy cuticular secretion that accumulates environmental debris. Such secretions have been hypothesized to be mechanisms to protect against water loss, for sexual attraction, and defense (Lawrence and Hlavac 1979). All three functions seem reasonable within the Zopherini. The secretions in *Phloeodes* probably serve at least some sexual attractant function, this is attributed to the apparent secretory pores on the secondary sexual character of the male (Figs. 50–53). These waxy secretions would also provide a useful barrier against water loss in the dry summer months that occur in the southwestern United States and Central America, where many members of the tribe are found.

Many Zopherinae have the ability to feign death (thanatosis), a behavior documented in several groups of beetles (Chemsak and Linsley 1970, Allen 1990, Oliver 1996, Miyatake 2001, and Miyatake *et al.* 2004) and specifically in the Zopherini (Evans and Hogue 2004). Both species of the genus *Phloeodes* in California when disturbed will drop from an attached substrate and become immobile for an extended period of time, probably as a defense mechanism (pers. obs.).

Individuals have also been reported (label data) to have the ability to survive long periods of time without food or water. This potential has also been documented in members of *Zopherus* (Sallé 1849, Triplehorn 1972).

Distribution: As defined here, the genus occurs in two disjunct geographic areas with two species (*P. diabolicus*, *P. plicatus*) occurring in the California Floristic Province and one (*P. venustus*) in Central America.

Key to the species of *Phloeodes*

1 Prothoracic hypomera with deep antennal cavities that are clearly limited posteriorly, and completely contains the antennae while in repose (Figs. 39, 41); elytra usually with at least partially visible velvety arcuate patches; elytra with elevated sculpture reduced, at most to single weak median nodule at start of apical declivity. California Floristic Province. Figs. 35–36 ..... *P. diabolicus* (LeConte)

- Prothoracic hypomera with deep antennal cavities that are incomplete and not limited posteriorly (Fig. 40), or broad shallow depression (Fig. 42); elytral vestiture variable; elytra with three distinct nodules at start of declivity, two offset medially, and one laterally 2

2 Prothoracic hypomera with deep antennal cavity that is not limited posteriorly (Fig. 40); elytral vestiture uniform in coloration from dark red to black; with only three nodules in area of declivity; length rarely over 20mm. California Floristic Province. Fig. 37 ..... *P. plicatus* (LeConte)

- Prothoracic hypomera with shallow depression, lacking distinct cavity (Fig. 42); elytral vestiture mottled whitish to black, with velvety spots along suture and on ridges; with three nodules in declivity area and fourth nodule near apex of elytra; length usually over 20mm. Central America. Fig. 38 ..... *P. venustus* (Champion)

***Phloeodes diabolicus* (LeConte)**
Figs. 32, 35–36, 39, 41, 44, 47, 50–51

Nosoderma diabolicum LeConte, 1851: 130. LeConte, 1853: 235. LeConte, 1857: 49, pl. 2. LeConte, 1859: 77. Pascoe, 1866: 487. Heyden, 1885: 307. García-París *et al.*, 2006: 229.

Phloeodes diabolicus: Horn, 1870: 273. Casey, 1907a: 42. Leng, 1920: 223. Essig, 1926: 429. Gebien, 1936: 667. Doyen, 1976: 267–272; fig. 1–11. Powell and Hogue, 1979: 295, 297. Arnett, 1983: 16. White, 1983: 250, fig. 107. Costa *et al.*, 1988: 213. Ślipiński and Lawrence, 1999: 19, figs. 69–81. Ivie, 2002: 458, 461.

Nosoderma diabolica: Casey, 1907b.

Ageonoma diabolica Pascoe, 1866: 487.

Nosoderma pustulosum LeConte, 1859: 77. García-París *et al.*, 2006: 230.

Phloeodes pustulosus: Horn, 1870: 273. Casey, 1907a: 43. Leng, 1920: 223. Essig, 1926: 428. Gebien, 1936: 668. Doyen, 1980: 3. Arnett, 1983: 16. White, 1983: 250. Hogue, 1993: 296, 298. Ivie, 2002: 461. NEW SYNONYMY.

Phloeodes latipennis Casey, 1907a: 43. Casey, 1907b: 472. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 16. (Synonymy by Gebien 1936)

Phloeodes ovipennis Casey, 1907a: 42. Casey, 1907b: 472. Leng, 1920: 223. Gebien, 1936: 667. Arnett, 1983: 16. (Synonymy by García-París *et al.* 2006)

Phloeodes elongatus Casey, 1907a: 42. Casey, 1907b: 472. Leng, 1920: 223. Gebien, 1936: 668. (Synonymy by García-París *et al.* 2006).

Phloeodes scaber Casey, 1907a: 43. Casey, 1907b: 472. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 16. (Synonymy by García-París *et al.* 2006).

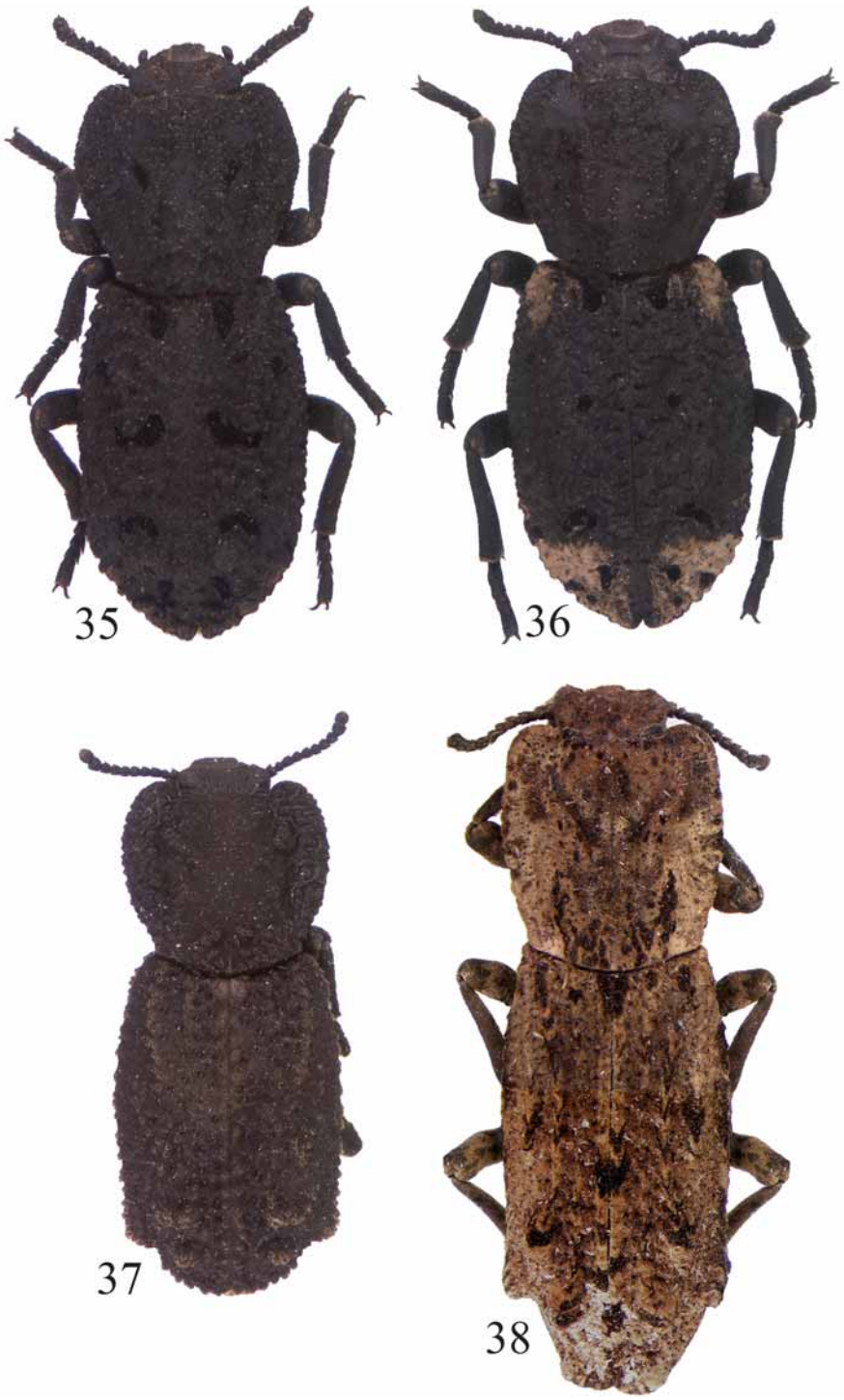
Phloeodes angustus Casey, 1907a: 43. Casey, 1907b: 472. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 16. (Synonymy by García-París *et al.* 2006).

Phloeodes remotus Casey, 1907b: 472. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 16. (Synonymy by García-París *et al.* 2006).

Diagnosis: The presence of large antennal cavities that are clearly limited posteriorly and completely contain the antennae while in repose (Figs. 39, 41), a few arcuate velvety spots on the elytra, and the reduced pattern of elevated ridges to at most one small nodule at the start of the declivity will distinguish individuals of the species from all other Zopherini with 10-segmented antennae.

Description: See García-París *et al.* (2006).

Distribution: California Floristic Province as far north as Shasta county, possibly all the way to Umatilla county in Oregon (3 specimens: 2-OR label only [NHMB, FMNH], 1-OR: Umatilla [UGCA], and east possibly to the edge of Arizona (6 specimens: 4-AZ label only [INHS, CASC, MSUC], 1-Yuma [INHS], 1-"Grand Canon"/VII-1924; Van Dyke [CAS]), and south into California. Specimens have also been recorded from Alaska, Oklahoma, Oregon, Pennsylvania, Texas and Wisconsin though none are from specific localities and can almost certainly be discounted as labeling errors, or hitchhiking individuals.



FIGURES 35–38. Dorsal habiti. 35. *Phloeodes diabolicus*, California, San Diego Co.; 36. *Phloeodes diabolicus*, California, Napa Co.; 37. *P. plicatus*, California, Los Angeles Co.; 38. *P. venustus*, Costa Rica.

Recorded distribution: A summary of the 3,878 specimens examined is (for complete label data, see Foley 2006) MEXICO: BAJA CALIFORNIA: Ensenada. UNITED STATES: ARIZONA: Yuma. CALIFORNIA: Alameda, Amador, Calaveras, Contra Costa, El Dorado, Fresno, Glenn, Humboldt, Imperial, Kern, Kings, Lake, Los Angeles, Madera, Mariposa, Merced, Mono, Monterey, Napa, Orange, Placer, Riverside, Sacramento, San Benito, San Bernadino, San Diego, San Joaquin, San Jose, San Luis Obispo, Santa Barbara, Santa Clara, Santa Cruz, Shasta, Solano, Stanislaus, Tulare, Tuolumne, Ventura, Yolo. OREGON: Umatilla.

Types: *Nosoderma diabolicum*: LECTOTYPE here designated: ♂ intact. Hand written *Phloeodes diaboli-*

cus (LeC.)/ Red square Type-4505/ gold circle/ Jan.-Jul MCZ image database/ red rectangle Lectotype; Nosoderma ♂; diabolicum LeConte 1851; designated by I. A. Foley 2006.

Nosoderma pustulosum: HOLOTYPE ♀, missing left meso, and right meta tarsomeres in MCZ. . Red square Type 4506/ hand written *P. pustulosus*: (LeC.): Tejon/ Jan.-Jul. 2005 MCZ Image Database.

Phloeodes latipennis: LECTOTYPE, here designated: ♂, intact in NMNH. Cal.(ifornia)/ Casey; bequest; 1925;/ orange rectangle Type NMNH; 46376/ hand written latipennis; Csy./ Casey determ.; pustulosus-10/ red square Lectotype; *Phloeodes*; ♂ *latipennis*; Casey 1907; designated I. A. Foley 2006.

Phloeodes ovipennis: LECTOTYPE, here designated: ♀, right pro leg missing last two tarsomeres in NMNH. Cal.(ifornia)/ Casey; bequest; 1925;/ orange rectangle Type NMNH; 46375/ hand written ovipennis Csy./ Casey determ.; elongatus- 4/ red square Lectotype; *Phloeodes*; ♀ *ovipennis*; Casey 1907; designated I. A. Foley 2006. PARALECTOTYPE, here designated: ♂, intact in NMNH. Cal.(ifornia)/ Casey; bequest; 1925/ orange rectangle ovipennis-2; Paratype NMNH; 46375/ Casey determ.;elongatus-5/ red square Paralectotype; *Phloeodes*; ♀ *ovipennis*; Casey 1907; designated I. A. Foley 2006.

Phloeodes elongatus: LECTOTYPE, here designated: ♂, missing left meso tarsus in NMNH. Kern; Co. Cal.,(ifornia)/ Casey; bequest; 1925/ orange rectangle Type NMNH 46374/ hand written elongatus; Csy./ red square Lectotype; *Phloeodes*; ♂ *elongatus*; Casey 1907; designated I. A. Foley 2006.

Phloeodes scaber: LECTOTYPE, here designated: ♂, intact in NMNH. Handwritten S. Diego/ Casey; bequest; 1925/ Casey determ.; scaber – 4/ orange rectangle Probably; original; TYPE; of scaber/ red square Lectotype; *Phloeodes*; ♀ *scaber*; Casey 1907; designated I. A. Foley 2006. Of the 7 specimens identified as *Phloeodes scaber* by Casey, only 2 are from San Diego, and the one designated the Lectotype is closer to the length of the specimen in the original description.

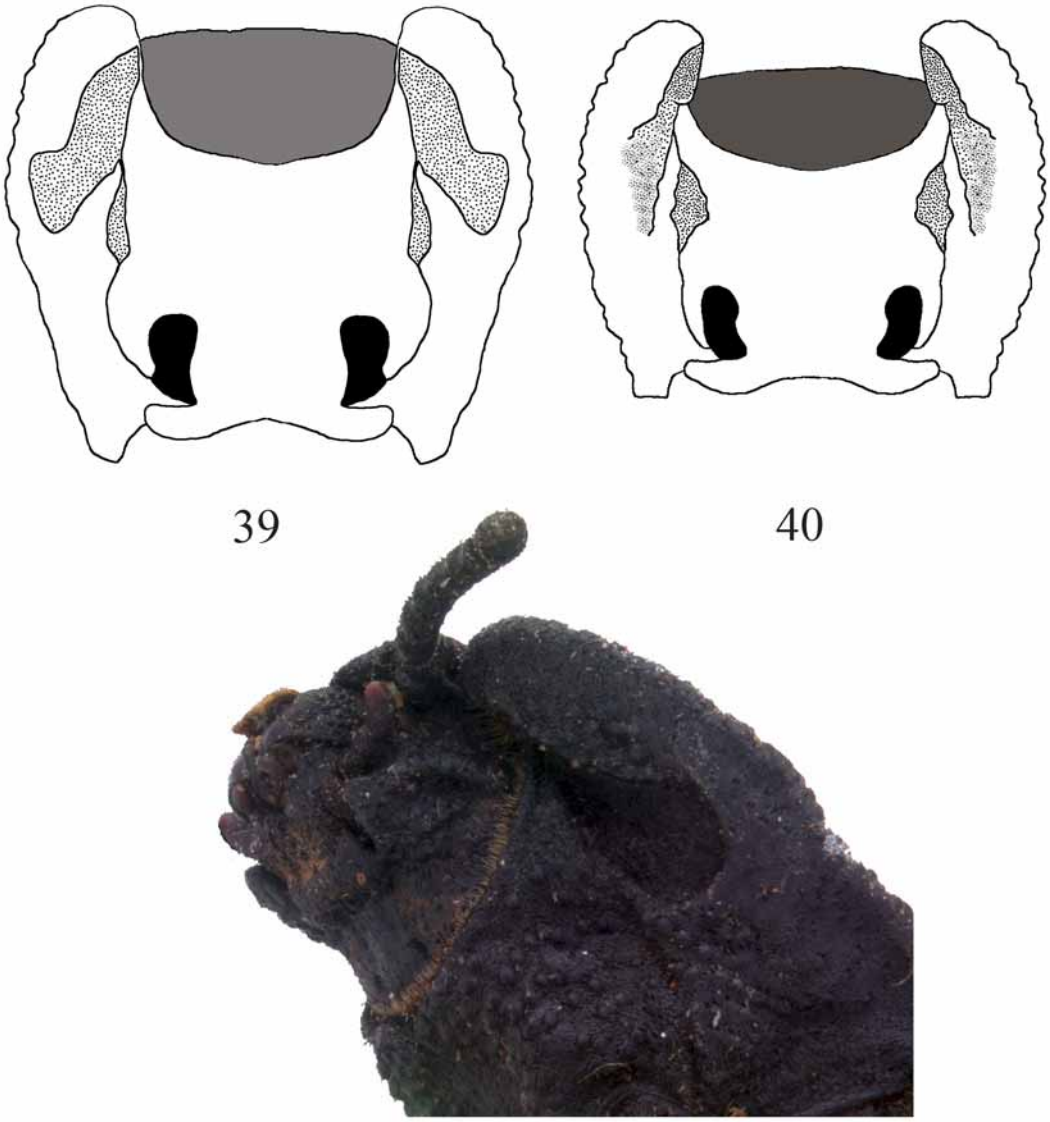
Phloeodes angustus: LECTOTYPE, here designated: ♀, left antenna missing last two antennomeres in NMNH. S. Cal.(ifornia)/ Morrison/ Casey; bequest; 1925/ red rectangle Neo-; Type NMNH; 46378, hand written angustus; Csy./ red square Lectotype; *Phloeodes*; ♀ *angustus*; Casey 1907; designated I. A. Foley 2006.

Phloeodes remotus: LECTOTYPE, here designated: ♂, right meta-tarsus missing in NMNH. No locality label/ Casey; bequest; 1925/ Casey determ.; remotus – 4/ red square Lectotype; *Phloeodes*; ♂ *remotus*; Casey 1907; designated I. A. Foley 2006. This species was differentiated by Casey based on the femoral swelling in the male, this specimen is the only male of the 4 *Phloeodes remotus* identified by Casey. It is also from an unrecorded locality as the original description states.

Discussion of Casey types: The variation in the Casey types is typical of the species throughout its geographic range. The specimens uniquely identified by Casey in key format show the following variation: *Phloeodes remotus* is densely clothed throughout with a gray-brown vestiture, the velvety spots of the elytra are not black, but a more reddish-brown; in *Phloeodes angustus* the body is more elongate and narrower in form, the velvety spots indistinct, the dorsal surface is very unevenly and more sparsely tuberculate with large areas along the middle and lateral third devoid of tubercles; in *Phloeodes scaber* the prothorax is narrower than the elytra, the pronotum is strongly elevated along the median third, and the slopes of the median elevation on the prothorax are slightly concave and devoid of tubercles; in *Phloeodes elongatus* the prothorax is elongate, the finer tubercles are aggregated, the arcuate ridges are slightly stronger, the elytral velvety spots are large and distinct; *Phloeodes ovipennis* shows a paler grayish vestiture, the central velvety spot is slightly arcuate and oblique, the basal short, and the dorsal surface of the head has smaller tubercles.

Notes: Gebien (1936) listed a single Casey species, *Phloeodes latipennis*, as a synonym of *Phloeodes pustulosus* (LeConte). This synonymy was not recognized by García-París *et al.* (2006) who synonymized *P. scaber*, *P. angustus*, and *P. remotus* with *P. pustulosus*, as well as reporting the Gebien synonymy as new. The remaining Casey species, *P. ovipennis* and *P. elongatus*, were also synonymized, but with *P. diabolicus*. The species described by Casey (1907a, b) are all represented by individuals that are well within the normal character range of *Phloeodes diabolicus* LeConte. For example the type series of *Phloeodes scaber* Casey contains

seven specimens all of which are a fairly uniform chalky gray color, with the velvety spots on the dorsum of the elytra difficult to see. This is a common situation in specimens where environmental debris from the activity of the insect accumulates on the surface and obstructs some of the external structures. While this series appears slightly different from the other specimens in the Casey collection, it is clearly not a unique and distinct species across the spectrum of conditions that can be found in unprepared specimens of *Phloeodes diabolicus*. García-París *et al.* (2006) did not examine any type specimens of *Phloeodes*; therefore the opportunity to designate lectotypes is taken here.



FIGURES 39–41. 39–40. Ventral surface of pronotum. 39. *Phloeodes diabolicus*; 40. *P. plicatus*. **41.** Lateral view of *P. diabolicus* hypomeron.

García-París *et al.* (2006) retained *P. diabolicus* and *P. pustulosus* as independent taxa, and while they redescribed *P. diabolicus*, they provided no characters to distinguish between the two species. When LeConte (1859) described *P. pustulosus* he stated that it was of the "size and form" of *Phloeodes diabolicus*, but based his discrimination of the two types based on smaller and less regular tubercles, the lack of velvety spots on the elytra, and sculpture near the scutellum. These characters are all clearly variable, and do not justify the division of the continuous population into more than one true species. Clinal variation is seen in the presence (Fig. 36) or absence (Fig. 35) of the whitish vestiture on the elytral humeri, apical declivity, and on the apical ven-

trites. Most northern California populations show the whitish vestiture while central and southern populations are uniformly black or dark grey. A similar pattern is seen in the distribution of *Zopherus nodulosus nodulosus* Solier and *Zopherus nodulosus haldemani* Horn. Populations north of the Rio Grande River in Texas are predominately white, and those farther south in Mexico have a greater proportion of the dorsal surface black (Triplehorn 1972).

***Phloeodes plicatus* (LeConte)**
Figs. 37, 40, 45, 49, 52–53, 71

Nosoderma plicatum LeConte, 1859: 77. LeConte, 1862: 216. LeConte and Horn, 1883: 365. García-París *et al.*, 2006: 230.
Noserus plicatus: Horn, 1870: 273. Casey, 1907a: 44. Leng, 1920: 223. Gebien, 1936: 668. Doyen, 1980: 3. Arnett and Jacques, 1981: 145. Arnett, 1983: 16. Arnett, 1985: 350. Ślipiński and Lawrence, 1999: 19. García-París *et al.*, 2000: 473. Milne *et al.*, 2000: 585 (pl. 224 midentified as *Phellopsis porcata* LeConte). García-París *et al.*, 2001: 151–153.
Phloeodes plicatus: Ivie, 2002: 461.
Noserus torvus Casey, 1907a: 44. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 16. (Synonymy by García-París *et al.* 2006).
Noserus collaris Casey, 1907a: 44. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 17. (Synonymy by García-París *et al.* 2006).
Noserus corrosus Casey, 1907b: 474. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 17. (Synonymy by García-París *et al.* 2006).
Noserus convexulus Casey, 1907b: 474. Leng, 1920: 223. Gebien, 1936: 668. Arnett, 1983: 17. (Synonymy by García-París *et al.* 2006).
Phloeodes sp.: Ślipiński and Lawrence, 1999: 20, fig. 82.

Diagnosis: The presence of distinct antennal cavities that are not clearly limited posteriorly and a dorsal elytral sculpture consisting of a series of distinct arcuate ridges and tubercles will easily separate this species from *Phloeodes diabolicus*. The uniform coloration distinguishes it from *Phloeodes venustus*.

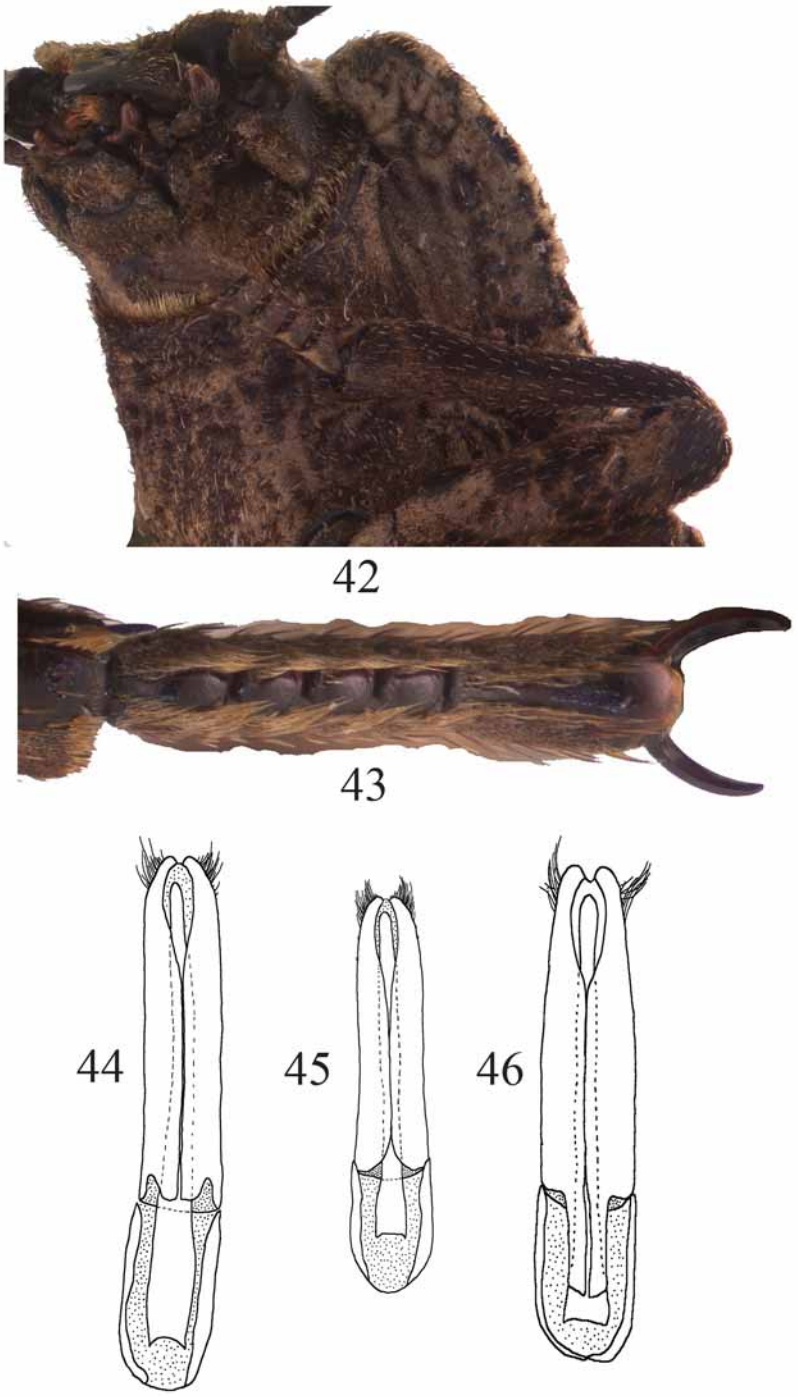
Description: See García-París *et al.* (2006).

Distribution: California Floristic Province as far north as Mendocino Co., east possibly to Arizona (1 specimen: AZ; Yuma; 3-VII-1936; D.L. Tiemann [EMEC]), south into Baja California, and west onto the California Channel Islands. Specimens have also been reported from Washington State and Oaxaca, Mexico, but are probably errors.

Recorded distribution: A summary of the 1,031 specimens examined is (for complete label data, see Foley 2006) MEXICO: BAJA CALIFORNIA: Ensenada. UNITED STATES: ARIZONA: Yuma. CALIFORNIA: Alameda, Contra Costa, Fresno, Kern, Lake, Los Angeles, Marin, Mendocino, Monterey, Napa, Orange, Placer, Riverside, San Benito, San Bernadino, San Diego, San Luis Obispo, San Mateo, Santa Barbara, Santa Clara, Santa Cruz, Santa Cruz Island, Sonoma, Trinity, Tulare, Ventura, Yolo.

Types: *Nosoderma plicatum*: LECTOTYPE, here designated: ♀, intact in MCZ. Cal.(ifornia)/ red square Type 4507/Noserus; plicatus (LeC.); Tejon/ Jan.-Jul. 2005 MCZ Image Database/ red rectangle Lectotype; *Nosoderma*; ♀ *plicatum*; LeConte 1859; designated by I. A. Foley 2006.

Noserus torvus: LECTOTYPE, here designated: ♀, intact in NMNH. Cal. (ifornia)/ Casey; bequest 1925/ Casey determ.; corrosus – 8/ orange rectangle probably; one of the; original; set of; *torvus*/ red square Lectotype *Noserus*; ♀ *torvus*; Casey 1907; designated; I.A. Foley 2006. All of the specimens in the Casey collection labeled *torvus* are ♂♂ rather then ♀ as stated in the description, therefore based on the note attached to the specimen this female is designated the Lectotype.



FIGURES 42–46. 42. Lateral view of *P. venustus* hypomeron. 43. Ventral view of tarsus of *P. venustus*. **44–46.** Male genitalia. 44. *P. diabolicus*; 45. *P. plicatus*; 46. *P. venustus*.

Noserus collaris: LECTOTYPE, here designated: ♂, missing right antenna in NMNH. Cal.(ifornia)/ Casey; bequest; 1925/ orange rectangle Type NMNH; 46380, hand written collaris; Csy./ Casey determ.; plicatus-5/ red square Lectotype *Noserus*; ♂ *collaris*; Casey 1907; designated; I.A. Foley 2006.

Noserus corrosus: LECTOTYPE, here designated: ♀, missing right metatibia and left metatarsus in NMNH. Hand written Los Angeles; Co.; Calif.(ornia)/ Casey; bequest; 1925/ orange rectangle Type NMNH; 46381/ hand written corrosus; Csy./ red square Lectotype *Noserus*; ♀ *corrosus*; Casey 1907; designated; I.A. Foley 2006. PARALECTOTYPE, here designated: ♀, several tarsi missing in NMNH. Same data as Lectotype/ orange rectangle corrosus-2, Paratype NMNH, 46381/ red square Paralectotype *Noserus*; ♀ *corrosus*;

Casey 1907; designated; I.A. Foley 2006.

Noserus convexulus: HOLOTYPE ♀, missing several tarsi in NMNH. Cal(ifornia)/ Casey; bequest; 1925/ orange rectangle Type NMNH; 46383/ hand written convexulus Csy./ red square Holotype *Noserus*; ♀ *convexulus*; Casey 1907; designated; I.A. Foley 2006.

Discussion of Casey types: The Casey types show typical variation of the species, and slightly vary in the following characterizations of their description: *Noserus torvus* is smaller and narrower than typical *Phloeodes plicatus*, with more obvious ridges, and larger lateral nodules; *Noserus collaris* has weaker basal ridges than *Phloeodes plicatus* and *Noserus torvus*, and a strongly elevated apical nodule; in *Noserus corrosus*, the elytral ridges and nodules are weak, and the exudate is thick, obscuring many of the tubercles; *Noserus convexulus* has a slightly rounded lateral elytral profile, stronger lateral tuberculation, slightly broader and shorter elytra, and smaller scattered ventral tubercles. Clearly all of these sculptural differences are well within the normal variation of the single recognized species *Phloeodes plicatus.*

Notes: García-París *et al.* (2006) did not designate lectotypes for any of the Casey species synonymized with *P. plicatus* or specifically mention any of the type specimens. Therefore, the opportunity to clarify the type specimens is taken here.

Phloeodes venustus (Champion) NEW COMBINATION

Figs. 38, 42, 46

Nosoderma venustus Champion, 1884: 45.
Nosoderma venustum; García-París *et al.*, 2006: 230.
Noserodes venusta; Casey, 1907b: 481. Gebien, 1936: 670. Blackwelder, 1945: 515. Arnett, 1983: 16.
Verodes venustus; Foley and Ivie, 2007: 71.

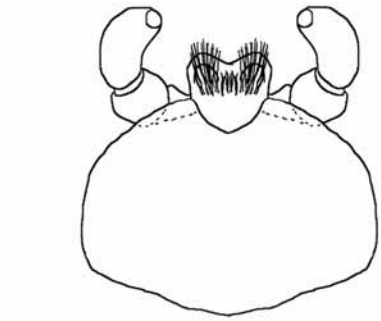
Diagnosis: This large elongate species is distinguished from all Zopherini with 10-segmented antennae by the lack of a visible scutellum, having tubercles present on the ventral body surface and the tomentose vestiture which is mottled in color, primarily whitish, golden, and dark brown to black. The species can appear largely black if the vestiture has worn off, or is obstructed by greasy exudate. The antennal cavity of *Ph. venustus* is weakly defined but the anterior portion of the hypomeron is produced ventrally relative to the pleurosternal suture, producing a distinct groove for the antenna. The central portion of the hypomeral face is concave laterad the pleurosternal suture in a weak but clear indication of the cavity.

Distribution: Central America from the countries of Costa Rica, Guatemala, Nicaragua, and Panama, at elevations between 600 – 1500 m.

Recorded distribution: A summary of the 22 specimens examined is (for complete label data, see Foley 2006) COSTA RICA: Guanacaste, Puntarenas. GUATEMALA: Escuintla. NICARAGUA: Matagalpa. PANAMA: Panamá.

Types: *Nosoderma venustum*: LECTOTYPE ♂, intact in BMNH. Orange ringed circle Type/V. de Atitlan, 25–3500 ft.; Champion./Nosoderma venustum; Champ MS./Sp. Figured/B.C.A.Col.IV.1.; Nosoderma venustum/red square Lectotypus; *Nosoderma*; *venustum* Champion; García-París des 2000. PARALECTOTYPE ♀, intact in BMNH. Zapote; Guatemala; G.C. Champion./Nosoderma venustum; Champ MS./Sp. Figured/ B.C.A.Col.IV.1.; Nosoderma venustum/red square ; Paralectotypus; *Nosoderma*; *venustum* Champion García-París des 2000.

Notes: This species was described in the genus *Nosoderma* but was placed in the genus *Noserodes* Casey by Gebien (1936) based on Casey's suggestion (1907b) that it was probably a member of that genus. The genus *Noserodes* was then synonymized with *Nosoderma* (Doyen and Lawrence 1979) moving the species back into the later genus. In comparison with the Californian species of this genus, very little information has been published on this large and very distinctive species.



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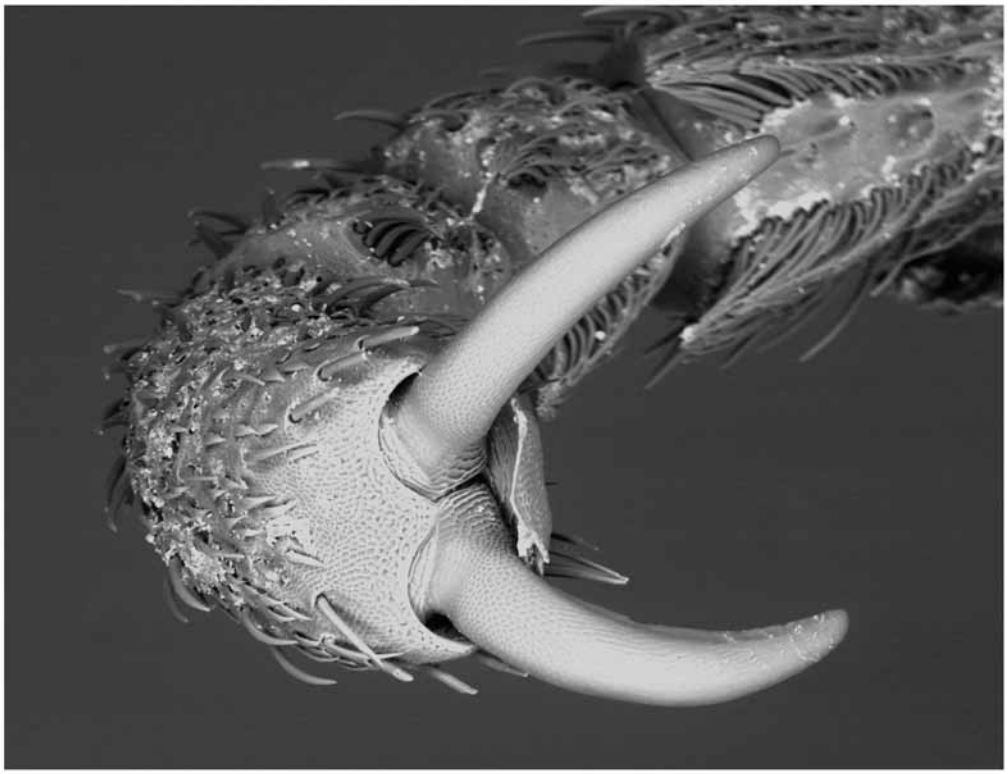

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FIGURES 47–49. 47–48. Labial palp insertions. 47. *Phloeodes diabolicus*; 48. *P. plicatus*. **49.** SEM of tarsal claw of *P. plicatus*.

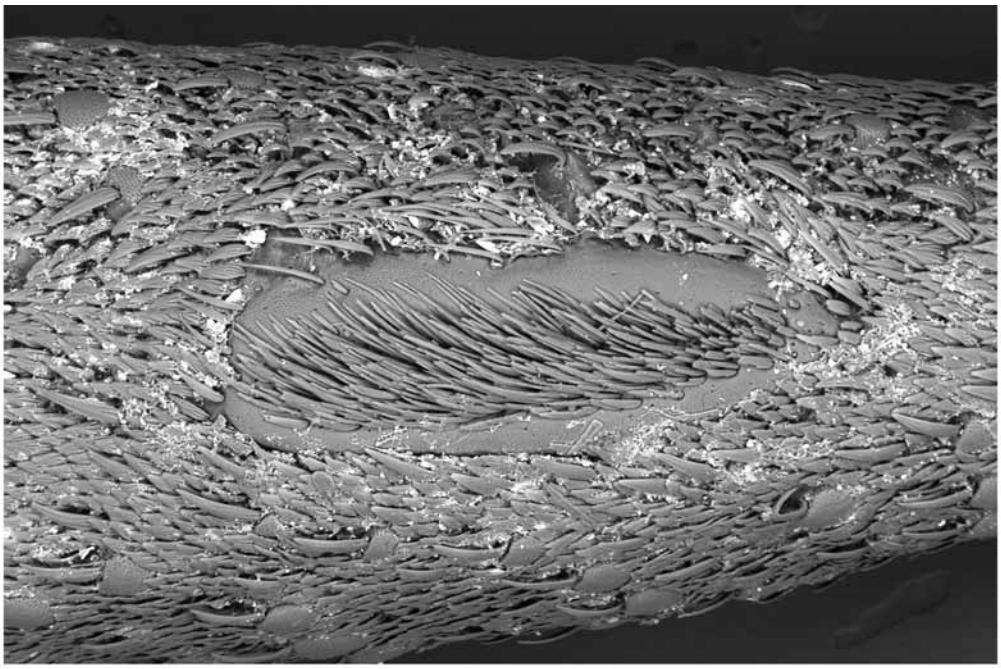
Genus *Verodes* Casey NEW SENSE
Figs. 31, 34, 55–68

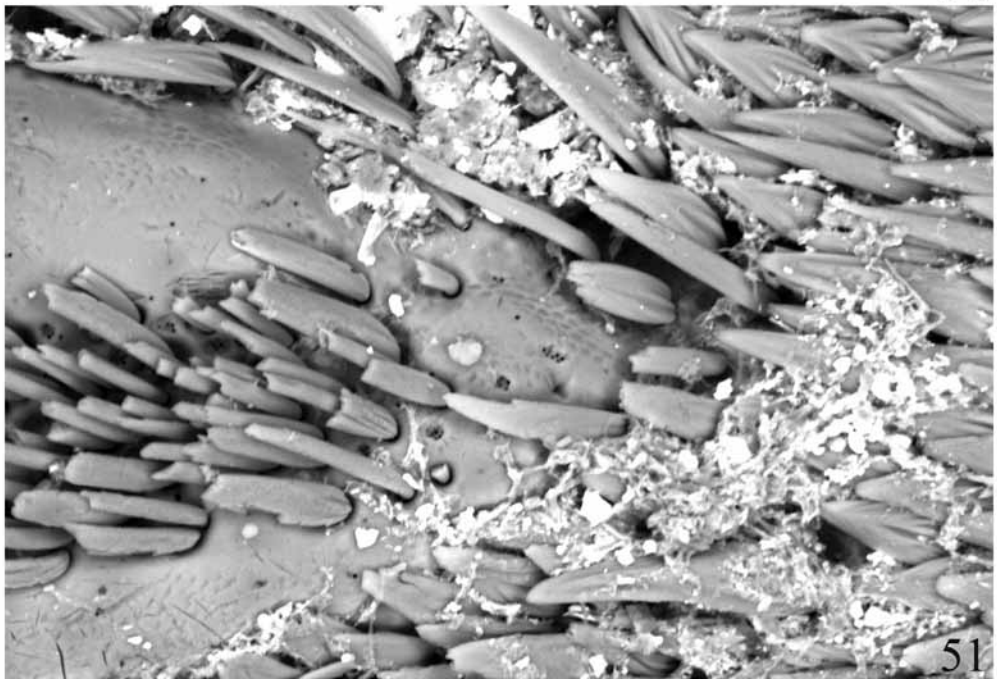
Homaloderes Solier, 1834: 31 (*nomen nudum*).

Nosoderma Solier, 1841: 31, *not* Guérin-Méneville, 1838: 280 [homonomy discussed by Foley and Ivie 2007] LeConte, 1851: 130. LeConte, 1853: 235. LeConte, 1859a: 77. LeConte, 1859b: 655. LeConte, 1862: 216. Kirsch, 1866: 189. Pascoe, 1866: 487. Champion, 1884: 44. Fairmaire, 1894b: 656. Casey, 1907a: 44. Casey, 1907b: 470. Gebien, 1936: 669. Blackwelder, 1945: 514. Triplehorn, 1972: 1. Doyen and Lawrence, 1979: 341. Lawrence, 1991: 518. Lawrence and Newton, 1995: 891. Ślipiński and Lawrence, 1999: 13. García-París *et al.*, 2000: 473. García-París *et al.*, 2001: 144. Ivie, 2002: 460. Garrido, 2004: 56. García-París *et al.*, 2006: 215-230. (Type species *Nosoderma morbillosum* Solier by subsequent designation of Gebien, 1936).

Verodes Casey, 1907b: 470. Gebien, 1936: 670. Neave, 1939: 635. Blackwelder, 1945: 515. Foley and Ivie, 2007: 69. (Type species *Nosoderma aequalis* Champion by original designation, Synonymy by Doyen and Lawrence, 1979: 342.).

Noserodes Casey, 1907b: 470 Gebien, 1936: 670. Neave, 1939: 346. Blackwelder, 1945: 515. (Type species *Noserodes squalidus* Casey, 1907b: 480 by original designation). (Synonymy by Doyen and Lawrence, 1979).

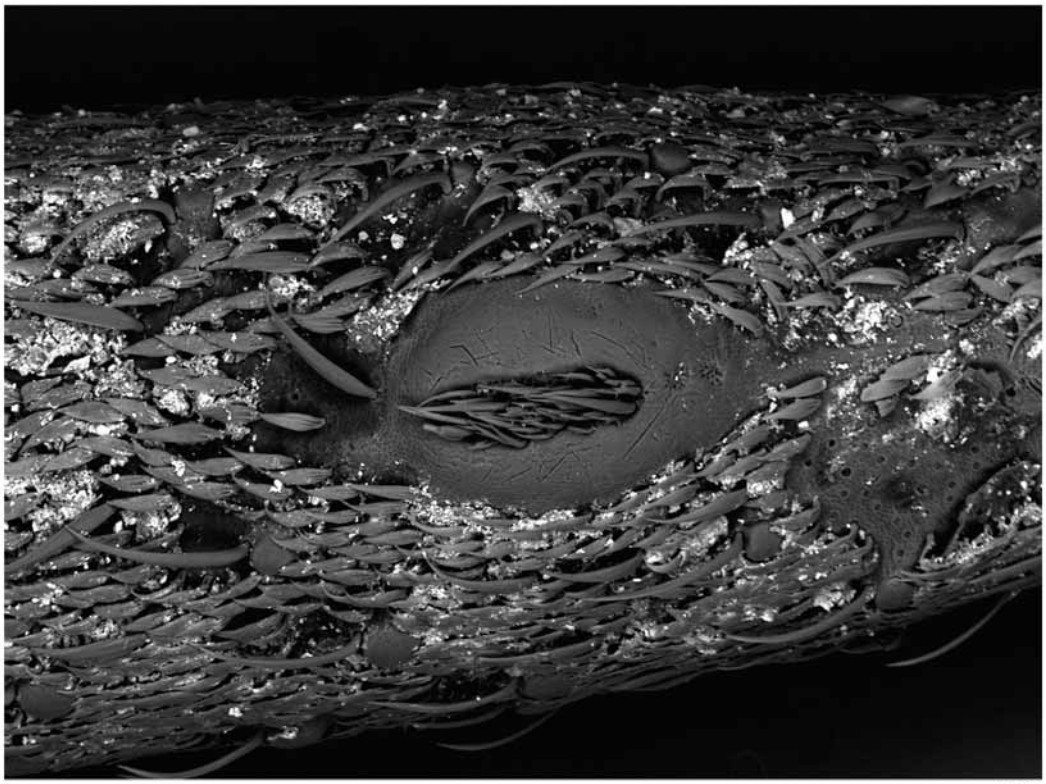


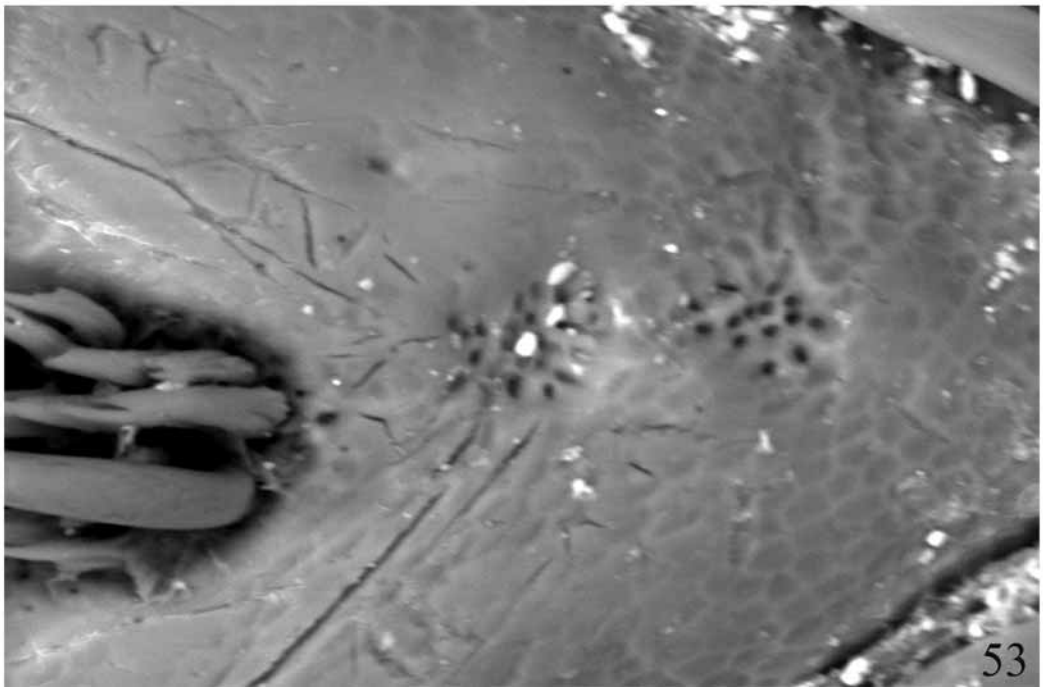


FIGURES 50–51. Femora of male *Phloeodes diabolicus*. 50. Male nodule. 51. Cuticular pores.

Diagnosis: The *Verodes* clade as recognized here is supported by the presence of a distinct membranous prostheca on the mandible (Fig. 34), ventrally inserted labial palps (Fig. 56), lack of an antennal cavity on the hypomeron (often a depression, or a small notch), and the presence of tubercles on the ventral surface (also in *Phloeodes*).

Description: See Ślipiński and Lawrence (1999). The previously published description of the genus *Nosoderma* is accurate as here classified based on the removal of two species to *Sesaspis* and one to *Phloeodes*.





FIGURES 52–53. Femora of male *Phloeodes plicatus*. 52. Male nodule. 53. Cuticular pores.

Notes: The genus *Verodes* is the second largest in the tribe behind *Zopherus*, and prior to this study contained 23 valid named species (*sensu* Foley and Ivie 2007). Morphological analysis of this group suggests that it is not monophyletic. The species group centered on *Verodes denticulata* forms a distinct group and is here recognized as the reconstituted Casey genus *Sesaspis* NEW SENSE. When *Sesaspis* is recognized as a genus, *Verodes*, *Phloeodes*, and *Sesaspis* all form monophyletic genera with the only remaining problem being the placement of *Verodes venustus*. This species does not fit the definition of either *Verodes* or *Sesaspis*. It is

excluded from *Verodes* because it lacks a membranous mandibular prostheca, and from *Sesaspis* because the ventral surface is densely tuberculate and it lacks an arcuate groove on the hypomeron. Based on this evidence, *Verodes venustus* is moved to *Phloeodes* NEW COMBINATION, and becomes the only member of that genus to occur outside the California Floristic Province.

The genus *Verodes* as here defined contains 11 species in two separate morphological clades. A group of seven species occurs generally from Oaxaca, Mexico, north possibly into the United States (there are unconfirmed localities of *Verodes exsculptus* in Texas with simply state data [NMNH]), and another group containing four species that generally occur from Oaxaca, Mexico, south into Central America.

FIGURES 54–56. 54–55. Hypomera. 54. *Sesaspis sylvatica*; 55. *Verodes exsculptus*. 56. Ventral surface of head and pronotum of *Verodes inaequalis*. Scale bars = 1mm.

The species-group occurring northwards from Oaxaca is generally restricted to high-elevation cloud forests and contains the two most widespread and morphologically diverse species of *Verodes*, *V. inaequalis* and *V. exsculptus*, and five that are quite rare. *Verodes championi*, the only species in the genus described by Casey that appears valid, is similar in appearance to *V. inaequalis*, but has a unique elytral sculpture that approaches the pattern of *V. exsculptus*. *Verodes carinatus* is most similar to *V. exsculptus* but can be distinguished by the stout body form and differing elytral sculpture. *Verodes insignis* is known only from the state of Oaxaca, and the elytral sculpture of this species, consisting of ridges that are hooked at the apex, is unique in *Verodes*. *Verodes scabrosus* and *V. asperatus* appear to be sister-species that are isolated to high elevation cloud forests.

The lineage occurring in more southern locales of Mexico and into Central America contains the species that Casey placed into the genera *Noserodes* (*V. zunilensis*, *V. guatemalensis*, and *V. sparsus*) and *Verodes* (*sensu* Casey 1907b) (*V. aequalis*). The three species previously placed in *Noserodes* are closely allied, and *V. zunilensis* and *V. guatemalensis* are probably sister-species. The species formerly placed in its own genus by Casey, *V. aequalis*, is distinct among species of *Verodes* in having the elytral sculpture completely reduced, even more so than *Sesaspis doyeni* and *S. ashei*, and lacking nodules on all femora of the male, but these characters do not warrant generic distinction based on the current analysis.

Most species of *Verodes* are highly variable in morphology, especially in the intensity of the nodules and ridges that form the elytral and pronotal sculpture. The key below uses this sculpture extensively which makes the identification of a single specimen more difficult than several representatives of a species.

Distribution: Many specimens of this genus were collected in the days of the Biologia Centralia-Americana during the 19th century and therefore often lack accurate locality information. The majority of specimens have simply "Mexico" or a few localities common to the above mentioned publication such as "Jalapa", "Las Vigas", "Guerrero", and others, but a general distribution pattern for the genus does appear to form. The majority of the diversity in the genus occurs around Oaxaca, Mexico, with radiations north though the Sierra Madre Occidental and south along the western coastal ranges of Central America. Interestingly, the genus *Sesaspis* (although the genera do co-occur at the same localities in Mexico) appears to occur in the other half of Mexico radiating through the Sierra Madre Oriental, and occurring in the lowland tropical forests of the eastern edge of Central America. Some of these distributional patterns were recognized by García-París *et al.* (2001, 2006) but they did not recognize *Sesaspis* as an independent lineage.

Key to the species of *Verodes* Casey

1 Dorsal surface of pronotum with all setae singly inserted at the base of tubercles; tubercles on pronotum uniformly distributed 2
- Dorsal surface of pronotum with dense setae between tubercles inserted directly on cuticular surface; tubercles on pronotum more dense on ridges, and absent in intervening areas 5
2 Pronotal and elytral surface smooth with dense flattened tubercles lacking any distinct ridges or nodules; male femoral nodules absent. Mexico, Oaxaca. Fig. 68 ..... *V. aequalis* (Champion)
- Pronotal and elytral surfaces with distinct ridges and nodules; male femoral nodules present on at least meso and metafemora 3
3 Metepisternum irregularly foveolate; elytra elongate, 1.95–2.05 X longer than widest point; elytra smooth at apex. Guatemala. Fig. 62 ..... *V. sparsus* (Champion)
- Metepisternum tuberculate; elytra more stout, 1.60–1.75 X longer than widest point; elytra very shallowly to deeply emarginate at apex. Mexico and Central America 4
4 Elytra shallowly emarginate at apex, rounded; subapical area of elytra with single elevated nodule. Mexico and Central America. Fig. 64 ..... *V. guatemalensis* (Champion)
- Elytra deeply emarginate at apex, sharply pointed; subapical area of elytra with nodule with two distinct elevations. Mexico and Central America. Fig. 63 ..... *V. zunilensis* (Champion)
5 Ridge or nodule in 5th elytral interval very short, or long, but never reaching the base of the elytra 6

- Ridge in 5th elytral interval very short, or moderately long, but always reaching the base of the elytra 8
6 Third elytral interval with short ridge at base; 5th elytral interval with arcuate ridge from level of just behind mesocoxal cavities to the suture between ventrites 2 and 3; apical third of elytron with three moderate sized nodules subequal in size, one near apex slightly smaller than subapical two. Mexico. Fig. 57 ..... *V. inaequalis* (Say)
- Third elytral interval with nodule at base, may be fused to short ridge in 5th; 5th elytral interval with disconnected nodules arranged in a row approximately from the level of the midpoint of metasternum to suture between ventrites 1 and 2; apical third of elytron with three large projecting conical nodules, lateral subapical one very large, much larger than one near apex. Mexico 7
7 Apical margin appearing very strongly serrate; subapical nodules extremely large and conical. Mexico, Hidalgo. Fig. 59..... *V. asperatus* (Champion)
- Apical margin of elytra weakly serrate; subapical nodules rounded. Mexico. Fig. 60..... *V. scabrosus* (Solier)
8 Apical half of elytra with 6 distinct nodules not connected to ridges. Mexico. Fig. 67 ..... *V. championi* (Casey)
- Apical half with 4 or fewer nodules not connected to ridges..... 9
9 Fifth elytral interval with ridge distinctly hooked at apex; apex of elytra with swollen ridge around suture; ridge starting at base of elytra curved towards midline. Mexico. Fig. 61..... *V. interruptus* (Champion)
- Fifth elytral interval with straight to arcuate ridge, but never hooked at apex; apex of elytra along suture flattened; ridge starting at base of elytra straight..... 10
10 Subapical nodule in 3rd elytral interval extending farther towards apex than nodule in the 5th interval; nodules and ridges relatively weakly elevated. Mexico. Figs. 55, 58 ..... *V. exsculptus* (Champion)
- Subapical nodule in 5th elytral interval extending farther towards apex than nodule in the 3rd interval; nodules and ridges more distinctly elevated 11
11 Ridge in 5th elytral interval extending continuously from the base to beyond the level of the start of ventrite 2. Mexico. Fig. 66 ..... *V. carinatus* (Champion)
- Ridge in 5th elytral interval distinctly interrupted into basal and apical half, with median lateral depression across elytra near the level of the metacoxae. Mexico. Fig. 65 ..... *V. impressus* (Champion)

***Verodes aequalis* (Champion)**
Figs. 31, 34, 68

Nosoderma aequale Champion, 1884: 44, pl. 2, fig. 14. García-París *et al*., 2006: 229.
Nosoderma aequalis; Casey, 1907b: 470 [as type species of *Verodes*]. Ślipiński and Lawrence, 1999: 13.
Verodes aequalis; Gebien, 1936: 670. Blackwelder, 1945: 515. Foley and Ivie, 2007: 69.

Diagnosis: This species can be distinguished from all species of *Verodes* by the smooth and shiny dorsal surface of the pronotum and elytra which lack any distinct ridges or nodules, and uniformly distributed flattened tubercles with single inserted setae.

Distribution: Mexico: Oaxaca at elevations between 2,400–3,400 meters.

Recorded distribution: A summary of the 22 specimens examined is MEXICO: OAXACA.

Types: *Nosoderma aequale*: HOLOTYPE: ♀, left antennae broken, left pro and meso tarsus broken, right meso and metatarsus broken in BMNH. Orange ringed circle Type/Parada/1654 light blue square/Mexico.; Salle Coll./Nosoderma aequale; Champ. MS./Sp. Figured/B.C.A.Col.IV.1.;Nosoderma aequale/red square Holotypus *Nosoderma aequale* García-París des 2000.

***Verodes inaequalis* (Say)**
Figs. 56–57

Eurychora inaequale Say, 1835: 182.
Nosoderma inaequale; Gebien, 1936: 669. García-París *et al.*, 2006: 230.
Nosoderma inaequalis; Casey, 1907b: 470. Blackwelder, 1945: 514.

Nosoderma morbillosum Solier, 1841: 37. (Synonymy by Gebien, 1936: 669.)
Nosoderma morbillosa; Casey, 1907b: 475. Ślipiński and Lawrence, 1999: 13.
Nosoderma vicinum Solier, 1841: 38. (Synonymy by Gebien, 1936: 669.)
Nosoderma vicina; Casey, 1907b: 476.
Nosoderma prominens Casey, 1907b: 478. Gebien, 1936: 669. Blackwelder, 1945: 514. García-París *et al.*, 2006: 230. NEW SYNONYMY.
Verodes prominens; Foley and Ivie, 2007: 70.
Nosoderma senex Casey, 1907b: 479. Gebien, 1936: 669. Blackwelder, 1945: 514. García París *et al.*, 2006: 230. NEW SYNONYMY.
Verodes senex; Foley and Ivie, 2007: 70.
Nosoderma brevicollis Casey 1907b: 478. Blackwelder 1945: 514. García-París *et al.*, 2006: 229. NEW SYNONYMY.
Nosoderma brevicolle; Gebien, 1936: 669.
Verodes brevicollis; Foley and Ivie, 2007: 71.
Nosoderma subglabra Casey, 1907b: 478. Blackwelder, 1945: 514. NEW SYNONYMY.
Nosoderma subglabrum; Gebien, 1936: 669. García-París *et al.*, 2006: 230.
Verodes subglabrus; Foley and Ivie 2007: 70.

Diagnosis: This species can be distinguished by the ridge in the 5th elytral interval not reaching the base of the elytra, and strongly expanded hind angles of the pronotum lacking the very large conical nodules seen in *V. scabrosus*.

Distribution: Central Mexico north through the Sierra Madre Occidental at elevations between 2,000–4,000 meters.

Recorded distribution: A summary of the 284 specimens examined is MEXICO: DISTRITO FEDERAL, DURANGO, GUANAJUATO, GUERRERO, HIDALGO, JALISCO, MÉXICO, MORELOS, PUEBLA, SINALOA, SONORA, VERACRUZ.

Types: *Eurychora inaequale*: The confusion surrounding the species epithet *inaequale* of Dejean and *inaequalis* of Say and the fact that Say's types have been lost requires the designation of a Neotype for *Eurychora inaequalis* Say 1835. Casey (1907b) recognized this need and identified a specimen which is here designated the NEOTYPE of *Eurychora inaequalis*. NEOTYPE: ♀, intact in NMNH. Mex./ Casey; bequest; 1925/ Eurychora; inaequalis; Say/ NEOTYPE; *Eurychora*; *inaequalis*; ♀ Say, 1835; desg. Foley & Ivie '07.

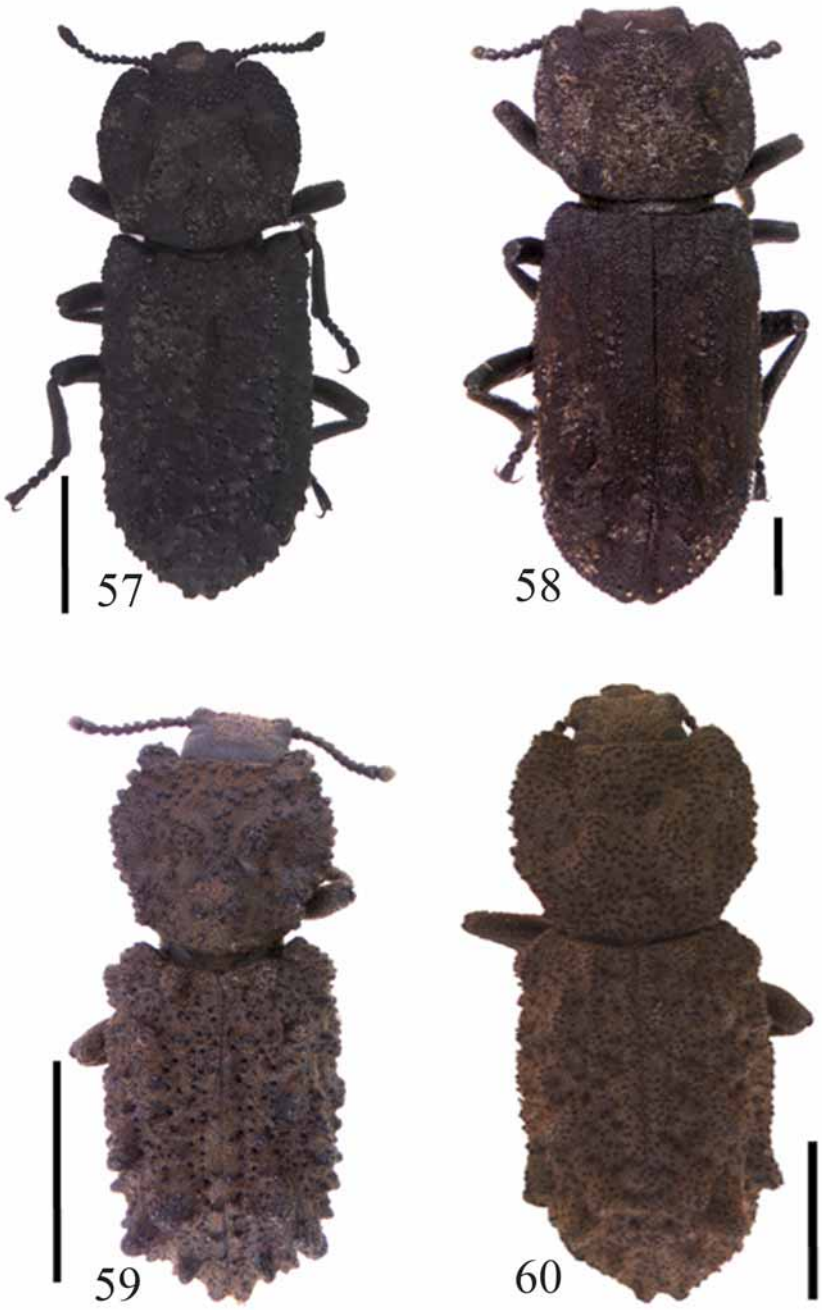
Nosoderma prominens: LECTOTYPE, here designated: ♀, missing right mesotarsus, in NMNH. Omilteme,; Guerrero,; 8000 ft.; H. H. Smi/ Casey; bequest; 1925/ N. inaequale Say; morbillosum/ Type NMNH; 46386/ prominens; Csy./ red rectangle label Lectotype; *Nosoderma*; *prominens*; ♀ Casey, 1907; desg. Foley & Ivie '07.

Nosoderma senex: LECTOTYPE, here designated: ♂, missing left meta leg, in NMNH. Las Vigas; Mexico; Hoege/ Casey; bequest; 1925/ Type NMNH; 46384/ senex; Csy./ red rectangle label Lectotype; *Nosoderma*; *senex*; Casey, 1907; desg. Foley & Ivie '07.

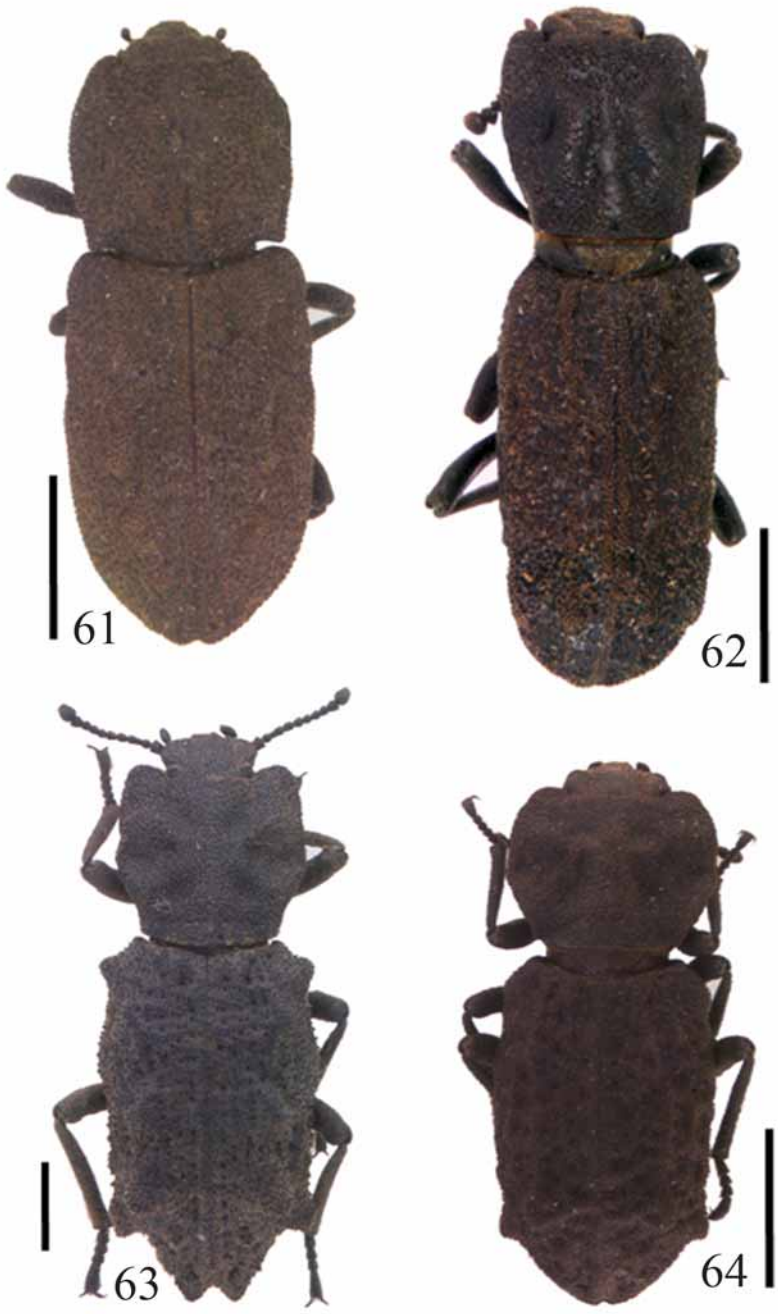
Nosoderma brevicollis: LECTOTYPE, here designated: ♂, intact, in NMNH. Mex./ Casey; bequest; 1925/ Type NMNH; 46387/ brevicollis; Csy./ red rectangle label Lectotype; *Nosoderma*; *brevicollis*; ♂ Casey, 1907; desg. Foley & Ivie '07.

Nosoderma brevicollis: LECTOTYPE, here designated: ♂, missing right antenna and protarsus, in NMNH. Guer./ Casey; bequest; 1925/ Type NMNH; 46385/ Nosoderma; subglabra; Csy./ red rectangle label Lectotype; *Nosoderma*; *subglabra*; ♂ Casey, 1907; desg. Foley & Ivie '07. PARALECTOTYPE, here designated: ♂, intact in NMNH. Same data as Lectotype.

Notes: One of the most commonly collected, widespread, and morphologically diverse members of the genus. Some of this variation is represented in the Casey types; this includes variation in the expansion of the hind angles of the pronotum, strength of the elytral punctures, and general shape of the elytral apex. All of the variation seen within the Casey types is well within the range for the species throughout its distribution.



FIGURES 57–60. Dorsal habiti. 57. *Verodes inaequalis*, Mexico, Puebla.; 58. *V. exsculptus*, Mexico, Oaxaca; 59. *V. asperatus*, Mexico, Hidalgo; 60. *V. scabrosus*, Mexico. Scale bars = 5mm.



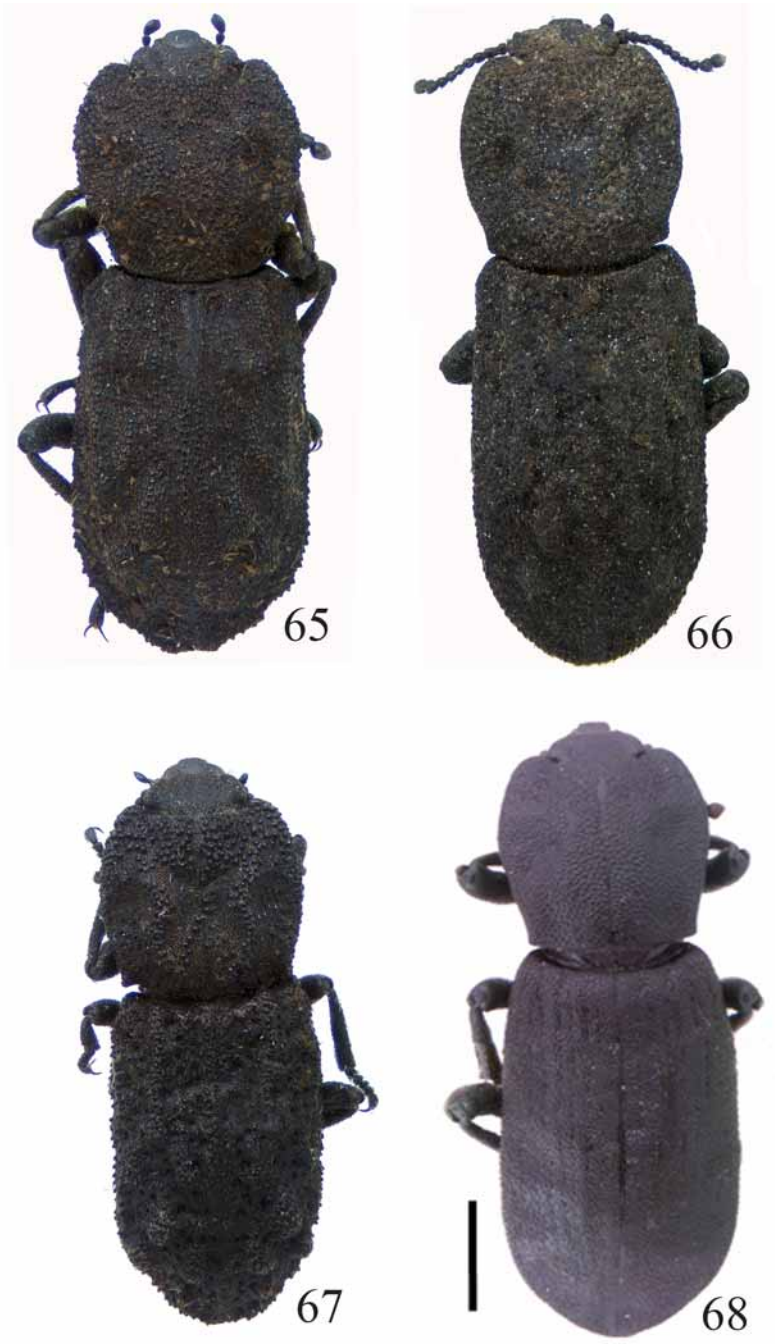
FIGURES 61–64. Dorsal habiti. 61. *Verodes interruptus*, Mexico, Oaxaca; 62. *V. sparsus*, Guatemala; 63. *V. zunilensis*, Mexico, Chiapas; 64. *V. guatemalensis*, Mexico, Chiapas. Scale bars = 5mm.

***Verodes championi* (Casey)**
Fig. 67

Nosoderma championi Casey, 1907b: 476. Gebien, 1936: 669. Blackwelder, 1945: 514. García-París *et al.*, 2006: 229. *Verodes championi*; Foley and Ivie, 2007: 70.

Diagnosis: This species is similar in general appearance to *V. inaequalis*, but can be distinguished from that species by having 6 distinct nodules in the apical half of the elytra not connected to ridges versus 3 or 4 in *V. inaequalis*.

Distribution: Mexico: Guerrero, Oaxaca and Veracruz.

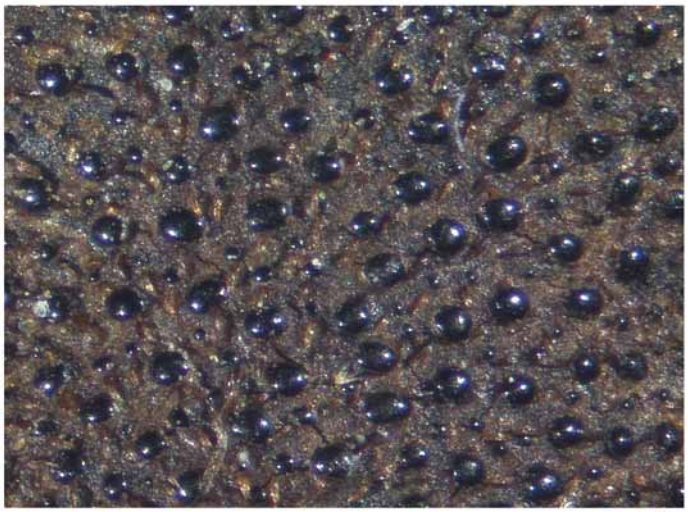


FIGURES 65–68. Dorsal habiti. 65. *Verodes impressus*, Mexico, Veracruz; 66. *V. carinatus*, Mexico, Veracruz; 67. *V. championi*, Mexico, Oaxaca ;68. *V. aequalis*, Mexico, Oaxaca. Scale bar = 5 mm.

Recorded distribution: A summary of the 9 specimens examined is MEXICO: GUERRERO, OAXACA, VERACRUZ.

Types: *Nosoderma championi:* LECTOTYPE, here designated: ♂, intact in NMNH. Mex./ Casey; bequest; 1925/ Type NMNH; 46388/ championi; Csy./ red rectangle label Lectotype; *Nosoderma*; *championi*; ♂ Casey, 1907; desg. Foley & Ivie '07. PARALECTOTYPES, here designated: 1 ♂, 1 ♀, in NMNH. Guer./ Casey; bequest; 1925/ championi 2 & 3; Paratype NMNH; 46388/ blue rectangle label Paralectotype; *Nosoderma*; *championi*; Casey, 1907; desg. Foley & Ivie '07.

Notes: One of only two apparently valid species described by Casey in the Zopherini. Besides the types, 6 additional specimens (BMNH) were examined that show the same distinct morphological pattern.



69

70

FIGURES 69–70. Dorsal surface sculpture of pronotum. 69. *Verodes guatemalensis*; 70. *V. inaequalis*.

***Verodes interruptus* (Champion)**
Fig. 61

Nosoderma interruptum Champion, 1884: 47. Gebien, 1936: 669. García-París *et al.*, 2006: 230.
Nosoderma interupta Blackwelder, 1945: 514 [*lapsus calami*].
Nosoderma insigne Champion, 1884: 48, pl. 2, fig, 13. Gebien, 1936: 669. García-París *et al.*, 2006: 230. NEW SYNONYMY.
Nosoderma insignis; Blackwelder, 1945: 514.
Verodes interruptus; Foley and Ivie, 2007: 70.

Diagnosis: This species can be distinguished from all other members of the genus by its unique elytral sculpture which consists of arcuate ridges that are hooked or recurved at the apex.

Distribution: Mexico: Oaxaca at elevations between 2,000–3,200 meters.

Recorded distribution: A summary of the 18 specimens examined is MEXICO: OAXACA.

Types: *Nosoderma interruptum*: LECTOTYPE: ♀, missing left antenna, tarsus on card in BMNH. Orange

ringed circle Type/ Las Vigas, Mexico; Hoege./ Nosoderma interruptum Champ./ B.C.A.Col.IV.1.; Nosoderma interruptum/ red square Lectotypus; *Nosoderma*; *interruptum* Champion; García-París des 2000. PARALECTOTYPE: ♂, intact in BMNH. Same data as LECTOTYPE without circle type label.

Nosoderma insigne: LECTOTYPE ♀, intact in BMNH. Orange ringed circle Type/Capulalpam/1657 on light blue square/Mexico; Salle Coll./Nosoderma insigne Champ. MS/B.C.A.Col.IV.1.;Nosoderma insigne/ red square Lectotypus; *Nosoderma*; *insigne* Champion; García-Paris des 2000. PARALECTOTYPE: ♀, last 4 antennomeres glued on, palps broken, in BMNH. Same data as LECTOTYPE, without type label/1656/pink F on white square/ M. García-París el al det. 2002.

Notes: The two Champion species described in the same publication (Champion 1884), and synonymized here, only vary slightly in the strength or orientation of the ridges, and do not warrant individual specific status.

***Verodes scabrosus* (Solier)**
Fig. 60

Nosoderma scabrosum Solier, 1841: 36. Gebien, 1936: 669.
Nosoderma scabrosa; Casey, 1907b: 476. Blackwelder, 1945: 514.
Verodes scabrosus; Foley and Ivie, 2007: 70.
Scoriaderma congolense Fairmaire 1894b: 656. Gebien, 1936: 670. **NEW SYNONYMY**

Diagnosis: This species and *V. asperatus* can be distinguished from all members of the genus by having rounded nodules (or very short ridges) at the base of the elytra in intervals 3 and 5 rather than elongated ridges. *Verodes scabrosus* can be distinguished from *V. asperatus* by the more typical rounded tubercles rather than the strongly conical ones seen in the later species.

Distribution: Mexico: Oaxaca and Durango.

Recorded distribution: A summary of the 9 specimens examined is MEXICO: OAXACA, DURANGO.

Types: *Nosoderma scabrosus*: HOLOTYPE: ♀ missing right meta tarsus in MNHN. Red rectangle TYPE/ Solier-9641-34; Mus. Paris; hand written on green square Nosoderma; scabrosum. Solier; denticla? (Chev. Dej.); Mexico/ scabrosus Sol 36, 3 Mex Bves/ Museum Paris; Coll. De. Marseul; 2842-90.

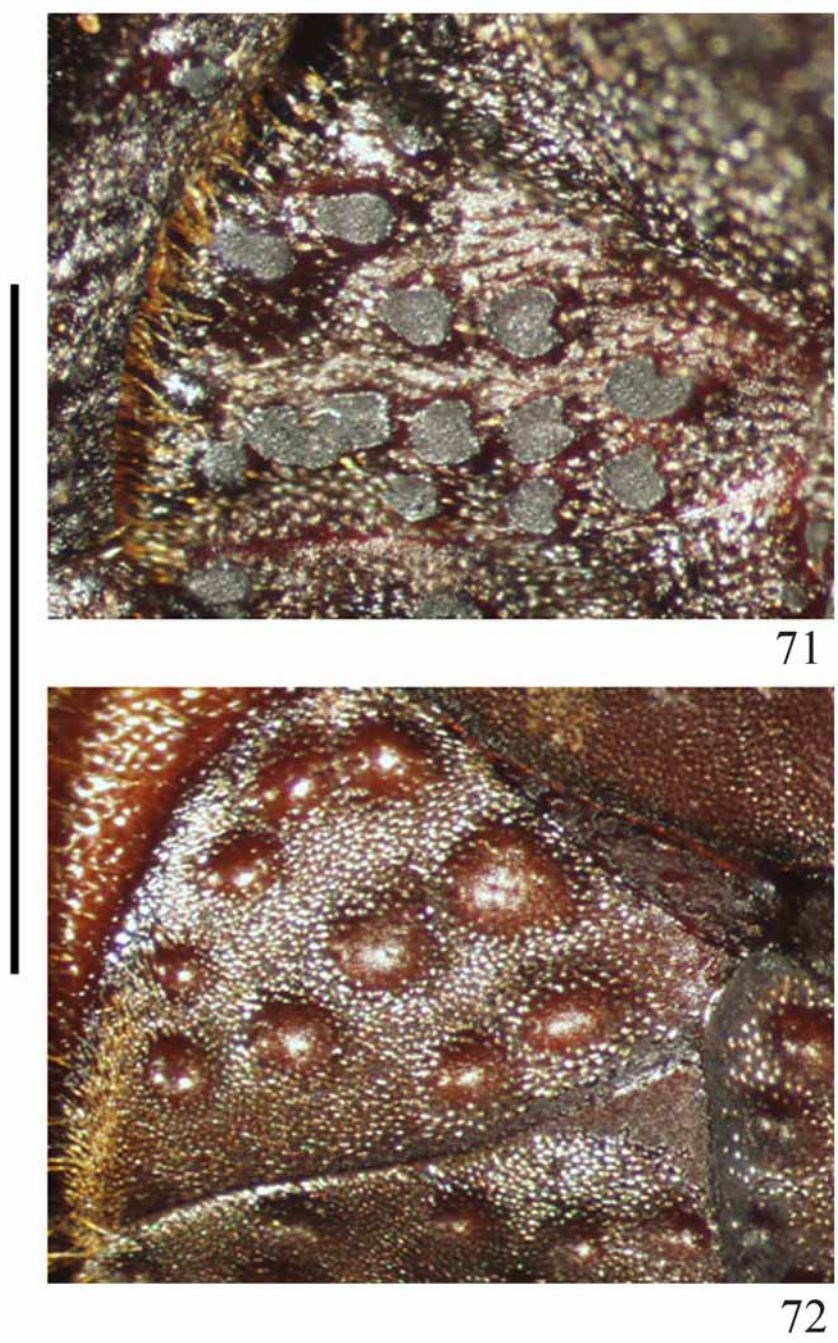
Scoriaderma congolense: HOLOTYPE: ♂, missing right proleg and left protarsus in MNHN. Handwritten on rectangle Congo/ red rectangle TYPE/ Scoriaderma; congolense; Fairmaire 1894; Congo./ light blue rectangle Muséum Paris; 1906; Coll. L. Fairmaire.

Notes: The label of the type of *Scoriaderma congolense* was misinterpreted. The handwritten "Congo" was interpreted (not unreasonably) to mean the African region of that name, but the specimen is actually a specimen of *Verodes scabrosus* (Solier) and clearly not congeneric with *S. comoriense*. The label apparently refers to the Mexican town of El Congo (25° 58' N, 105° 12' W), located in the Mexican state of Durango, which is within the range of this species.

***Verodes asperatus* (Champion)**
Fig. 59

Nosoderma asperatum Champion, 1884: 45, pl. 2, fig. 9. Gebien, 1936: 669. García-París *et al.*, 2006: 229.
Nosoderma asperata; Casey, 1907b: 476. Blackwelder, 1945:514.
Verodes asperatus; Foley and Ivie, 2007: 70.

Diagnosis: This species can be distinguished by the strongly projecting conical nodules in the apical half of the elytra and lateral elytral margins which appear strongly serrate.



FIGURES 71–72. Surface of mesepimeron. 71. *Phloeodes plicatus*; 72. *Sesaspis sylvatica*. Scale bar = 1mm.

Distribution: Central Mexico at elevations around 1,500 meters in the Sierra Madre Oriental.

Recorded distribution: A summary of the 9 specimens examined is MEXICO: HIDALGO, PUEBLA, SAN LUIS POTOSI, VERACRUZ.

Types: *Nosoderma asperatum*: LECTOTYPE: ♂, both antennae broken off in BMNH. Orange ringed circle Type/ Mexico; Salle Coll./ Nosoderma; asperatum Champ MS/ Sp. Figured.;B.C.A.Col.IV.1./ red square Lectotypus; *Nosoderma*; *asperatum* Champion; García-París des 2000. PARALECTOTYPE: ♂, right antennae broken off in BMNH. 1671 on light blue square/ Mexico; Salle Coll./ chewed up label no visible lettering/ Nosoderma; asperatum Champ MS/B.C.A.Col.IV.1.;Nosoderma asperatum/Foto on white square/ red square Paralectotipo; *Nosoderma*; *asperatum* Champion; M. García-París et al det. 2002.

***Verodes exsculptus* (Champion)**
Figs. 55, 58

Nosoderma exsculptum Champion, 1884: 49. Gebien, 1936: 669. García-París *et al.*, 2006: 229.
Nosoderma exsculpta; Casey, 1907b: 476. Blackwelder, 1945: 514.
Verodes exsculptus; Foley and Ivie, 2007: 70.
Nosoderma anceps Champion, 1884: 50. Gebien, 1936: 669. Blackwelder, 1945: 514. (Synonymy by García-París *et al.*, 2006: 229).
Verodes anceps; Foley and Ivie, 2007: 71.
Nosoderma longipennis Casey, 1907b: 477. Blackwelder, 1945: 514. García-París *et al.*, 2006: 230. **NEW SYNONYMY.**
Nosoderma longipenne; Gebien, 1936: 669.
Verodes longipennis; Foley and Ivie, 2007: 71.

Diagnosis: This species can be distinguished from all other members of the genus by having the subapical nodule in the 3rd elytral interval closer to the elytral apex than the one in the 5th.

Distribution: Southern Mexico associated with pine (*Pinus* sp.) forests between 2,500–3,400 meters.

Recorded distribution: A summary of the 111 specimens examined is MEXICO: OAXACA, PUEBLA, VERACRUZ.

Types: LECTOTYPE: ♀, right pro-leg missing in BMNH. Orange ringed circle Type/Jalapa, Mexico; Hoege./ ♀ on square/ Nosoderma; exsculptum Champ- B.C.A.Col.IV.1.; Nosoderma exsculptum/ red square *Nosoderma*; *exsculptum* Champion; Lectotype García-París 2000. PARALECTOTYPES: 1 ♂, intact and 1 ♂, missing left meta leg and left mesotarsus in BMNH. Jalapa, Mexico; Hoege./ 153 on square/ G.C. Champion Coll.; B.M. 1927/ 409/ red square Paralectotipo; Nosoderma; exsculptum Champion; M. García-París et al 2002.

Nosoderma anceps: LECTOTYPE: ♀, intact in BMNH. Orange ringed circle Type/ Jalapa, Mexico; Hoege./Nosoderma anceps; Champ. ;? var. exsculptum/B.C.A.Col.IV.1.; Nosoderma anceps/ red square Lectotypus; *Nosoderma anceps*; Champion; García-París 2000. PARALECTOTYPES: 2 ♂, intact in BMNH. Same data as LECTOTYPE.

Nosoderma longipennis: LECTOTYPE, here designated: ♀, missing left meta tarsus in NMNH. Jalapa; Mexico; Hoege/ Casey; bequest; 1925/ orange rectangle Type NMNH 46389/ *longipennis*; Csy/ red rectangle label Lectotype; *Nosoderma*; *longipennis*; ♀ Casey, 1907; desg. Foley & Ivie '07.

Notes: This species varies greatly in size with examined specimens ranging in size from 9–22 mm in length.

***Verodes carinatus* (Champion)**
Fig. 66

Nosoderma carinatum Champion, 1884: 49. Gebien, 1936: 669. García-París *et al.*, 2006: 229.
Nosoderma carinata; Casey, 1907b: 476. Blackwelder, 1945: 514.
Verodes carinatus; Foley and Ivie, 2007: 71.

Diagnosis: This species can be difficult to distinguish from *V. exsculptus* and *V. impressus*, but can be recognized by the long continuous ridge in the 5th elytra interval (interrupted in *V. impressus*) and having the subapical nodule in the 5th interval beyond that in the third (opposite in *V. exsculptus*).

Distribution: MEXICO: Veracruz.

Recorded distribution: A summary of the 12 specimens examined is MEXICO: VERACRUZ.

Types: *Nosoderma carinatum*: LECTOTYPE: ♂, intact in BMNH. Orange ringed circle Type/1659 on light blue square/Jacale, Mexico.; Salle Coll./Nosoderma carinatum, Champ./B.C.A.Col.IV.1.;Nosoderma

carinatum/red square Lectotypus; *Nosoderma*; *carinatum*; Champion; García-París des 2000. PARALECTOTYPES: ♀, broken right meso and meta tarsus in BMNH. Las Vigas, Mexico.; Hoege./G.C. Champion Coll.; B.M. 1927-409/red square Paralectotypus; *Nosoderma*; *carinatum*; Champion; García-París des 2000. ♀, intact in BMNH same data as above/ Paralectotipo M. García-Paris *et al.* det. 2002.

***Verodes impressus* (Champion)**
Fig. 65

Nosoderma impressum Champion, 1884: 50. Gebien 1936: 669. García-París *et al.*, 2006: 230.
Nosoderma impressa; Blackwelder, 1945: 514.
Verodes impressus; Foley and Ivie, 2007: 71.

Diagnosis: This species can be distinguished from all members of the genus by having the ridge in the 5th elytral interval distinctly interrupted by a broad lateral depression.

Types: *Nosoderma impressum*: LECTOTYPE: ♀, intact in BMNH. Orange ringed circle Type/1668 on light blue square/Jacale, Mexico; Salle Coll./ Nosoderma impressum, Champ. MS./ B.C.A.Col.IV.1.; Nosoderma impressum/ red square Lectotypus; Nosoderma; impressum; Champion; García-París des 2000. PARALECTOTYPE; ♂, missing right meta leg. Same data as LECTOTYPE without circle type label.

Distribution: Mexico: Veracruz around 2,400 meters.

Recorded distribution: A summary of the 11 specimens examined is MEXICO: VERACRUZ.

Notes: This uncommon species and *V. carinatus* appear to be closely related to *V. exsculptus* and occurs only in the Mexican state of Veracruz.

***Verodes zunilensis* (Champion)**
Fig. 63

Nosoderma zunilense Champion, 1884: 46, pl. 2, fig. 10. García-París *et al.*, 2006: 230.
Nosoderma zunilensis; Casey, 1907b: 481.
Noserodes zunilensis; Gebien, 1936: 670. Blackwelder, 1945: 515.
Verodes zunilensis; Foley and Ivie, 2007: 71.

Diagnosis: This species and *V. guatemalensis* can be distinguished from all other members of the genus by having a large lateral subapical nodule that is continuous with the lateral margin of the elytron. *Verodes zunilensis* can be distinguished from *V. guatemalensis* by having two distinct median subapical nodules versus a single nodule in *V. guatemalensis*. The apex of the elytra is also more deeply emarginate in *V. zunilensis*.

Distribution: Montane wet forests of Honduras.

Recorded distribution: A summary of the 9 specimens examined is HONDURAS: COMAYAGUA, OCOTEPEQUE, OLANCHO.

Types: *Nosoderma zunilense*: LECTOTYPE: ♀, missing left meta leg in BMNH. Orange ringed circle Type/ Cerro Zunil, 4000ft.; Champion./Nosoderma zunilense Champ; MS-Sp. Figured./ B.C.A.Col.IV.1.;Nosoderma zunilense/ red square Lectotypus *Nosoderma*; *zunilense*; Champion; García-París des 2000. PARALECTOTYPE: ♀, intact in BMNH. El Zumbador, 2500ft.; Champion./ Nosoderma; zunilense Champ MS; B.C.A.Col.IV.1. Nosoderma zunilense/ pink F on white square/ red square Paralectotipo *Nosoderma*; *zunilense*; Champion; García-París et al det. 2002.

Notes: See notes under *V. guatemalensis*.

***Verodes guatemalensis* (Champion)**
Fig. 64

Nosoderma guatemalense Champion, 1884: 47, pl. 2, fig. 11. García-París *et al.*, 2006: 230.
Nosoderma guatemalensis; Casey, 1907b: 481.
Noserodes guatemalensis; Gebien, 1936: 670. Blackwelder, 1945: 515.
Verodes guatemalensis; Foley and Ivie, 2007: 71.
Noserodes squalidus Casey, 1907b: 480. Gebien, 1936: 670. Ślipiński and Lawrence, 1999: 13. **NEW SYNONYMY.**
Noserodes squalida; Blackwelder, 1945: 515.
Nosoderma squalidum; García-París *et al.*, 2006: 230.
Verodes squalidus; Foley and Ivie, 2007: 72.

Diagnosis: See diagnosis of *V. zunilensis* above.

Distribution: Montane wet forests of Guatemala and southern Mexico between 1,500 and 2,600 meters.

Recorded distribution: A summary of the 73 specimens examined is GUATEMALA: EL PROGRESSO, ZACAPA. MEXICO: CHIAPAS.

Types: *Nosoderma guatemalense*: LECTOTYPE: ♂, intact in BMNH. Orange ringed circle Type/ Calderas, Guatemala; Champion./ Nosoderma guatemalense, Champ.; MS-Sp. Figured./ B.C.A.Col.IV.1.;Nosoderma guatemalense./ red square Lectotypus *Nosoderma*; *guatemalense*; Champion; García-París des 2000. PARALECTOTYPE: ♀, intact in BMNH. Same data as Lectotype.

Noserodes squalidus: LECTOTYPE, here designated: ♀, missing last 4 antennomeres of left antenna, all left tarsi, right pro-tarsus, and right meso leg in NMNH. Chiriqui; Costa Rica/ Casey; bequest; 1925/ orange rectangle Type NMNH; 46390/ *Noserodes*; *squalidus*; Csy./ red rectangle label Lectotype; *Noserodes*; *squalidus*; ♀ Casey, 1907; desg. Foley & Ivie '07.

Notes: This species and *V. zunilensis* are probably sister-species, with *V. zunilensis* documented only from Honduras, and *V. guatemalensis* occurring from Guatemala north into southern Mexico. The Casey type reported from Costa Rica is probably an error, as additional recent collecting efforts have not yielded new specimens, and the species that would be expected to occur in Costa Rica, if any, is *V. zunilensis*.

***Verodes sparsus* (Champion)**
Fig. 62

Nosoderma sparsum Champion, 1884: 50, pl. 2, fig. 12. García-París *et al.*, 2006: 230.
Nosoderma sparsa; Casey, 1907b: 481
Noserodes sparsus; Gebien, 1936: 670.
Noserodes sparsa; Blackwelder, 1945: 515.
Verodes sparsus; Foley and Ivie, 2007: 72.

Diagnosis: The species can be recognized based on its reduced elytral sculpture, with just a few weak ridges and nodules, and by the elongate body form with the elytra 1.95–2.05X longer than the widest point (some specimens of *V. exsculptus* also have an elongate body form, but that species has intertuberculate setae, and well defined ridges and nodules).

Distribution: Guatemala at elevations between 2,500 and 3,900 meters.

Recorded distribution: A summary of the 14 specimens examined is GUATEMALA: SAN MARCOS, SOLOLA, TOTONICAPÁN.

Types: *Nosoderma sparsum*: LECTOTYPE: ♀, missing left meso tarsus in BMNH. Orange ringed circle Type/Totonicapama,; 85–10,500 ft. Champion./ Nosoderma sparsum Champ./ Sp. Figured/ B.C.A.Col.IV.1.; Nosoderma sparsum/ red square Lectotypus *Nosoderma*; *sparsum*; Champion; García-París des 2000. PARALECTOTYPE: ♂, intact in BMNH. Same data as LECTOTYPE.

TABLE 3. Summary of the classification of the Zopherini Solier, 1834 (sensu Ślipiński & Lawrence 1999). Currently recognized names in **Bold**, with current combination. Synonyms in normal font, with original combination. For full synonymies, see text. For distribution data, SW USA = multiple states of USA, Mexico = multiple states of Mexico; S. America = multiple countries of South America, C. America = multiple countries of Central America, E. Australia = multiple states of Australia; and E. Africa = multiple countries of Eastern Africa and the Western Indian Ocean.

***Zopherus* Gray, 1832**	
Megazopherus Casey, 1907. (Syn. Triplehorn 1972)	
Zopherinus Casey, 1907 (Syn. Triplehorn 1972)	
Zopherodes Casey, 1907 (Syn. Triplehorn 1972)	
***Zopherus chilensis* Gray, 1832**	C. & S. America
Zopherus insignis Blanchard, 1861 (Syn. Gebien 1936)	
Zopherus bremei Guérin-Méneville (Syn. Gebien 1936)	
Zopherus moreletii Lucas, 1852 (Syn. Gebien 1936)	
***Zopherus nervosus* Solier, 1841: 42.**	Mexico
Zopherus pectoralis LeConte, 1851 (Syn. Gebien 1936)	
Zopherus reticulatus Champion, 1884 (Syn. Gebien 1936)	
Zopherus compactus Champion, 1884 (Syn. Triplehorn 1972)	
Zopherus marmoratus Casey, 1907 (Syn. Triplehorn 1972)	
***Zopherus nodulosus* Solier, 1841: 43.**	TX, Mexico
Zopherus variolosus Sturm, 1843 (Syn. Gebien 1936)	
Zopherus sallaei Champion, 1884 (Syn. Gebien 1936)	
Z. haldemani Horn, 1870 (Syn. Triplehorn 1972)	
Zopherus verrucosus Champion, 1884 (Syn. Gebien 1936)	
***Zopherus jourdani* Sallé, 1849**	C. America
Zopherus mexicanus (*auctorum*, not Gray)	
Zopherus costaricensis Champion, 1884 (Syn. Triplehorn 1972)	
***Zopherus jansoni* Champion, 1884**	C. America
***Zopherus mexicanus* Gray, 1832**	Mexico
Zopherus maculatus Champion, 1884 (Syn. Gebien 1936)	
***Zopherus angulicollis* Champion, 1884**	Chihuahua
***Zopherus laevicollis* Solier, 1841**	Mexico
Zopherus venosus Champion, 1884 (Syn. Triplehorn 1972)	
Zopherus tuberculatus Champion, 1884 (Syn. Triplehorn 1972)	
Zopherinus limbatus Casey, 1907a (Syn. Triplehorn 1972)	
***Zopherus xestus* Triplehorn, 1972**	TX
***Zopherus solieri* Triplehorn, 1972**	Durango
***Zopherus championi* Triplehorn, 1972**	Mexico
***Zopherus tristis* LeConte, 1851**	SW USA, Baja
Zopheroides aequalis Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides variabilis Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides incrustans Casey, 1907b (Syn. Triplehorn 1972)	
***Zopherus concolor* LeConte, 1851**	SW USA
Zopherus guttulatus Horn, 1867 (Syn. Triplehorn 1972)	
Zopheroides morosus Casey, 1907 (Syn. Triplehorn 1972)	
***Zopherus gracilis* Horn, 1867**	SW USA, Sonora

Zopheroides pudens Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides caudalis Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides lugubris Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides pruddeni Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides luctuosus Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides elongatus Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides germinatus Casey, 1907 (Syn. Triplehorn 1972)	
***Zopherus uteanus* (Casey), 1907**	SW USA
Zopheroides mormon Casey, 1907 (Syn. Triplehorn 1972)	
***Zopherus granicollis* Horn, 1885**	SW USA, Baja
Zopheroides induratus Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides californicus Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides prominens Casey, 1924. (Syn. Triplehorn 1972)	
Zopheroides ventriosus Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides parvicollis Casey, 1907 (Syn. Triplehorn 1972)	
Zopherus opacus Horn, 1867: 161.	SW USA
Zopherus elegans Horn, 1870: 272.	SW USA
Zopheroides otiosus Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides verrucipennis Casey, 1907 (Syn. Triplehorn 1972)	
Zopheroides circumductus Casey, 1924 (Syn. Triplehorn 1972)	
Zopheroides woodgatei Casey, 1924 (Syn. Triplehorn 1972)	
***Zopherus sanctaehelenae* (Blaisdell), 1931**	CA
***Zopherosis* White, 1859**	
Zopherosis georgei White 1859	E. Australia
***Phloeodes* LeConte, 1862**	
Noserus LeConte, 1862 (Syn. Ślipiński & Lawrence 1999)	
Ageonoma Pascoe, 1866 (Syn. Horn 1870)	
***Ph. diabolicus* (LeConte) 1851**	CA, Baja
Nosoderma pustulosus (LeConte) 1859 **[NEW SYNONYMY]**	
Ph. latipennis Casey 1907 (Syn. Gebien 1936)	
Ph. ovipennis Casey 1907 (Syn. García-París *et al.* 2006)	
Ph. elongatus Casey 1907 (Syn. García-París *et al.* 2006)	
Ph. scaber Casey 1907 (Syn. García-París *et al.* 2006)	
Ph. angustus Casey 1907 (Syn. García-París *et al.* 2006)	
Ph. remotus Casey 1907 (Syn. García-París *et al.* 2006)	
***Ph. plicatus* (LeConte) 1859**	CA, Baja
Noserus torvus Casey 1907 (Syn. García-París *et al.* 2006)	
Noserus collaris Casey 1907 (Syn. García-París *et al.* 2006)	
Noserus corrosus Casey 1907 (Syn. García-París *et al.* 2006)	
Noserus convexulus Casey 1907 (Syn. García-París *et al.* 2006)	
***Ph. venustus* (Champion) 1884: 45. [NEW COMBINATION]**	C. America
***Sesaspis* Casey, 1907b: 469. [NEW STATUS, NEW SENSE]**	
***Sesaspis denticulata* (Solier), 1841**	Mexico
***Sesaspis emarginata* (Horn), 1878 [NEW COMBINATION]**	SW USA, Tamaulipas
***Sesaspis triplehorni* [NEW SPECIES]**	C. America

***Sesaspis lutosa*(Champion), 1884 [NEW COMBINATION]**	Mexico
***Sesaspis sylvatica* (García-París *et al.*), 2006 [NEW COMBINATION]**	Mexico
***Sesaspis doyeni* (García-París *et al.*), 2001 [NEW COMBINATION]**	Nuevo Leon
***Sesaspis ashei* [NEW SPECIES]**	Mexico
***Verodes* Casey, 1907 (sensu Foley & Ivie 2007)**	
Nosoderma Solier, 1841 *not* Guérin-Méneville 1838	
Noserodes Casey, 1907 (Syn. Doyen & Lawrence 1979)	
***V. aequalis* (Champion), 1884**	Oaxaca
***V. inaequalis* (Say), 1835**	Mexico
Nosoderma morbillosum Solier, 1841: 37. (Syn. Gebien 1936)	
Nosoderma vicinum Solier, 1841: 38 (Syn. Gebien 1936)	
Nosoderma prominens Casey, 1907 [**NEW SYNONYMY]**	
Nosoderma senex Casey, 1907 **[NEW SYNONYMY]**	
Nosoderma brevicollis Casey, 1907 **[NEW SYNONYMY]**	
Nosoderma subglabrus Casey, 1907 **[NEW SYNONYMY]**	
***V. championi* Casey, 1907**	Mexico
***V. interruptus* (Champion), 1884**	Oaxaca
Nosoderma insigne Champion, 1884 **[NEW SYNONYMY]**	
***V. scabrosus* (Solier), 1841**	Oaxaca
Scoriaderma congolense Fairmaire 1894 **[NEW SYNONYMY]**	
***V. asperatus* (Champion), 1884**	Mexico
***V. exsculptus* (Champion), 1884**	Mexico
Nosoderma anceps Champion, 1884 (Syn. García-París *et al.* 2006)	
Nosoderma longipennis Casey, 1907b **[NEW SYNONYMY]**	
***V. carinatus* (Champion), 1884**	Veracruz
***V. impressus* (Champion), 1884**	Veracruz
***V. zunilensis* (Champion), 1884**	Honduras
***V. guatemalensis* (Champion), 1884**	C. America
Noserodes squalidus Casey, 1907 **[NEW SYNONYMY]**	
***V. sparsus* (Champion), 1884**	Guatemala
***Nosoderma* Guérin-Méneville, 1838**	
Meralius Casey, 1907 (Syn. Foley & Ivie 2007)	
***Nosoderma echinatum* Guérin-Méneville, 1838**	
Nosoderma duponchelii Solier, 1841 (Syn. Gebien 1936)	
***Nosoderma turquinense* (Garrido), 2004**	Cuba
M. montanus Garrido, 2004 **[NEW SYNONYMY]**	
***Noserinus* Casey, 1907**	
***Noserinus dormeanus* (Fairmaire) 1889**	S. America
Noserinus annulatipes Casey (Syn. Gebien 1936)	
***Noserinus furcatus* (Kirsch) [NEW COMBINATION]**	S. America
***Scoriaderma* Fairmaire, 1894**	
***Scoriaderma cordicolle* Waterhouse, 1880**	E. Africa
Scoriaderma comoriense Fairmaire, 1894 **[NEW SYNONYMY]**	
***Zopher* Ślipiński & Lawrence, 1999**	
***Zopher iviei* Ślipiński & Lawrence, 1999**	Malaysia

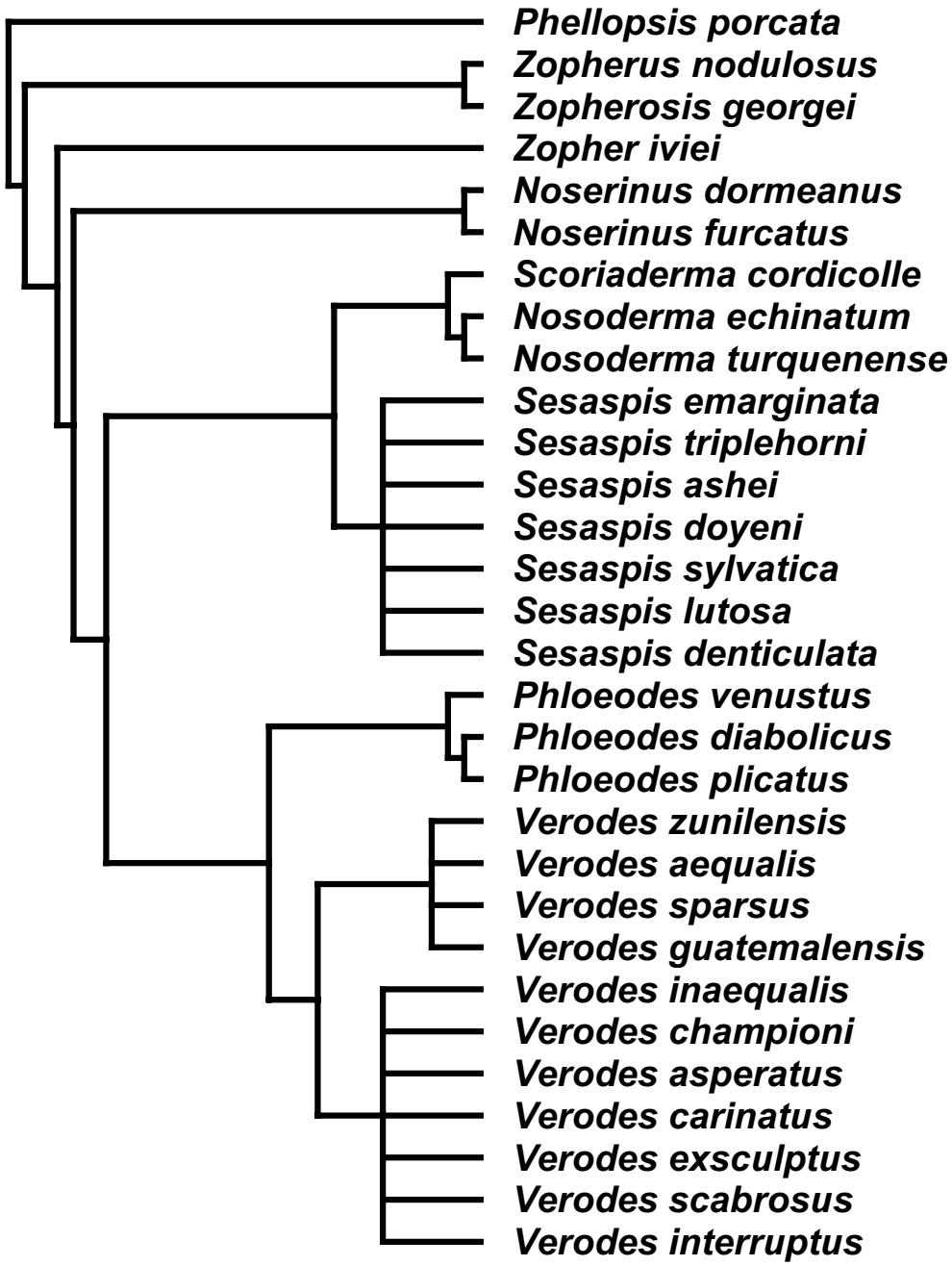


FIGURE 73. Strict consensus tree of 4 shortest trees found using PAUP.

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