A REVIEW OF THE IRONCLAD BEETLES OF THE WORLD (COLEOPTERA ZOPHERIDAE: PHELLOPSINI AND ZOPHERINI)

by

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May 2006

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TABLE OF CONTENTS

TABLE OF CONTENTS-CONTINUED

TABLE OF CONTENTS-CONTINUED

APPENDICES

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

Figure Page

ABSTRACT

Phellopsis LeConte is revised. *Phellopsis porcata* (LeConte) is returned to valid status and *P. yulongensis* NEW SPECIES is described. *Phellopsis montana* Casey NEW SYNONYMY (NS) and *P. robustula* Casey NS = *P. porcata* (LeConte). *Phellopsis imurai* Masumoto = *P. amurensis* (Heyden) NS. Species redescriptions, a key to species and notes on the history, biology and biogeography of the group are provided.

Phylogenetic analyses support several changes to sustain monophyletic genera of Zopherini because the genera *Meralius* Casey, *Nosoderma* Solier, and *Phloeodes* LeConte were found to be polyphyletic.

The genus *Sesaspis* Casey NEW STATUS is re-recognized, and redescribed to include the following species: *Sesaspis denticulata* (Solier), *S. emarginatus* (Horn) NEW COMBIATION (NC), *S. lutosus* (Champion) NC, *S. doyeni* (García-París et al.) NC, *S. adami* NEW SPECIES, *S. ashei* NEW SPECIES, and *S. triplehorni* NEW SPECIES.

Phloeodes LeConte is clarified with 10 new synonymies [*P. diabolicus* (LeConte) = *P. pustulosus* (LeConte) NS, *P. latipennis* Casey NS, *P. ovipennis* Casey NS, *P. elongatus* Casey NS, *P. scaber* Casey NS, *P. angustus* Casey NS, and *P. remotus* Casey NS). *Phloeodes plicatus* (LeConte) = *Noserus torvus* Casey NS, *Noserus collaris* Casey NS, *Noserus corrosus* Casey NS, *Noserus convexulus* Casey NS]. *Phloeodes venustus* (Champion) NC is supported as a member of this clade extending the known range of the genus into Central America.

Noserinus furcatus (Kirsch) NC is moved from *Meralius* Casey. *Meralius clavapilus* NEW SPECIES is described from Venezuela. Eleven new synonyms are proposed in *Nosoderma* Solier (*N. championi* Casey NS, *N. prominens* Casey NS, *N. senex* Casey NS, *N. brevicolle* Casey NS, and *N. subglabrum* Casey NS = *N. inaequalis* (Say); *N. interruptum* Champion NS = *N. insigne* Champion; *N. carinatum* Champion NS, *N. anceps* Champion NS, *N. impressum* Champion NS, and *N. longipennis* Casey NS = *N. exsculptum* Champion; and *N. squalidus* Casey NS = *N. guatemalensis* Champion). *Scoriaderma congolense* Fairmaire NS is a junior synonym of *Nosoderma scabrosum* Solier.

Keys to the genera of Zopherini and species of *Meralius* Casey, *Noserinus* Casey, *Nosoderma* Solier, *Phloeodes* LeConte and *Sesaspis* Casey are provided, with illustrations of all included species of the genera mentioned.

Disclaimer: This thesis is not intended to meet the provision of the ICZN (1999) regarding publication of new nomenclatural acts [Art. 8.2]. No name or nomenclatural act proposed herein should be considered available as defined by the ICZN

CHAPTER 1

THE FAMILY ZOPHERIDAE

Introduction

The family Zopheridae (*sensu* Ślipiński & Lawrence 1999) is a diverse-looking combination of species that were recently placed in three different families (Zopheridae, Monommatidae, and Colydiidae) (e.g. Lawrence & Newton 1995). The sense of the Zopheridae includes two subfamilies, Zopherinae, and Colydiinae. The Colydiinae were not well represented in the analysis of Ślipiński & Lawrence (1999) and the demonstration of the monophyly of that group has been questioned (Ivie 2002a, c). On the other hand, although highly variable in general morphological appearance, the definition of the subfamily Zopherinae (including the Monommatidae) is well supported by morphological phylogenetic analysis (Ślipiński & Lawrence 1999, Ivie 2002a, c).

The large, often rough-bodied members of this subfamily commonly referred to as ironclad beetles are now placed in two zopherid tribes -- the Zopherini and Phellopsini. My research focused on these two tribes and the taxonomic problems that exist therein. Prior to this study these tribes contained a total of 72 valid species names, many of which were poorly defined and of uncertain taxonomic status. The problem within this group is that taxa have been defined by the intensity of the dorsal sculpture and vestiture. These types of characters have been found to be highly variable and almost always only useful in a presence/absence sense, i.e. ridge in 3rd elytral interval present or not, intertuberculate setae present or not. This study has better defined individual species, and significantly improved the confused species-level taxonomy of the ironclad beetles.

Diagnostic Morphology

The Zopheridae belong to the superfamily Tenebrionoidea (Lawrence and Newton 1995), and share many morphological characters with typical members of the Tenebrionidae, including antennal insertions concealed under a lateral expansion of the frons (suprantennal ridge) and a maximum of 5-5-4 tarsal formula. The Zopheridae can be distinguished from the Tenebrionidae based on the four connate ventrites (three in Tenebrionidae) and procoxal cavities closed (or nearly so, rarely broadly open as in *Usechimorpha*) by a laterad expansion of the prosternal process rather than a mesad expansion of the hypomeron. In larvae, the presence of thoracic and/or abdominal asperities and the dorsal surface of the head with lyriform or v-shaped frontal arms are also useful as diagnostic characters, but known larvae are quite rare and remain undescribed for many genera.

Taxonomic History of the Zopheridae

Historical references to zopherid species have mostly been based on the large, hard-bodied and rough appearance of flightless species with heteromerus (5-5-4) tarsi commonly referred to as ironclad beetles. Originally placed within the Tenebrionidae, the group has recently received broad support as a family taxon (Doyen and Lawrence 1979, Ślipiński & Lawrence 1999, Ivie 2002a, b, c, d)

Most of the species of Zopherinae (*sensu* Ślipiński & Lawrence 1999) were described before the broad recognition of the group as a family taxon. Based on this history, the current higher-level components of the subfamily are discussed in a chronological manner.

The family-group name was first proposed as the tribe Zophérites by Solier (1834), for the New World genus *Zopherus* Gray. Solier (1841) expanded the definition to include his New World (Mesoamerica and Cuba) genus *Nosoderma* Solier. These two genera contain a majority of the species in, and are the historical core of the current Zopherini.

Horn (1870) proposed the tribe Usechini in the Tentyriinae for the atypical North American and Japanese genus *Usechus* Motschulsky 1845.

In Casey's (1907a, 1907b) revision of the zopherid complex, he proposed a classification of four tribes and 14 genera: Usechini (*Usechus*), Zopherini (*Megazopherus* Casey, *Zopherodes* Casey, *Zopherinus* Casey, *Zopherus*), Nosodermini (*Meralius* Casey, *Phloeodes*, *Noserus*, *Noserinus* Casey, *Noserodes* Casey, *Nosoderma*, *Phellopsis*, *Sesaspis* Casey, and *Verodes* Casey) and the Australian Zopherosini (*Zopherosis georgei* White).

Zopheridae were first elevated to family rank by Böving and Craighead (1931). Their action was based on the larval characters of divided cardines, the lack of a frontoclypeal suture (fused frontoclypeal region), lyriform frontal arms and distinct hypostomal rods.

Gebien (1936), in his catalog of tenebrionids, did not recognize the zopherids as a distinct family, and returned to Horn's (1870) tribal classification, recognizing only two zopherid tribes, the Zopherini and Usechini, but moved them to the tenebrionid subfamily

Asidinae. While Gebien (1936) ignored Casey's tribes Nosodermini and Zopherosini, he did recognize all of the genera Casey described (1907a, 1907b), and added the South American genus *Exeniotis* Pascoe 1871 to the Zopherini.

Crowson (1955) returned the Zopheridae to the family-level definition of Böving and Craighead (1931), i.e. with the tribes Zopherini and Nosodermini, and modified and expanded it with supporting adult characters. Crowson (1955) noticed marked structural similarities between specimens of *Phellopsis* and *Monomma* (Monommatidae) in the antennae, general head structure, the incompletely closed pro-coaxal cavities, metendosternite, largely connate abdominal ventrites, and oblique impressions of the fifth ventrite. He also noticed metendosternite similarities between *Phellopsis*, the Colydiidae, and the Mycetophagidae. Kamiya (1963) tentatively moved the Usechini to the Zopheridae, based on similar adult structural characters. Boddy (1965) used open procoxal cavities (*Phellopsis*, *Usechus*, and *Usechimorpha*), and clavate antennae with last 3 segments suddenly wider to define the group, primarily based on *Phellopsis*. Watt (1967, 1974) added further support for the recognition of the family. Other authors (Arnett 1963, 1971, 1973; Triplehorn 1972; Arnett and Jacques 1981; Downie and Arnett 1996) continued to argue that the group belonged as a tribe or tribes within the tenebrionid subfamily Asidinae, all without providing phylogenetic evidence.

Watt (1974) performed the first phylogenetic analysis of the zopherid group using adult and larval synapomorphies to construct overall similarity matrices for the Tenebrionidae and related taxa. He showed that Zopheridae and Tenebrionidae are closely related but have significant dividing characters, such as the zopherid-type of procoxal cavity closure. To his definition of the Zopheridae, Watt (1974) also added 5 Tenebrionidae genera (*Arthopus* Sharp, *Brouniphylax* Strand, *Exohadrus* Broun, *Parahelops* Waterhouse, *Syrphetodes* Pascoe), the Ulodini (*Dipsaconia* Pascoe, *Ganyme* Pascoe, *Trichulodes* Carter and *Ulodes* Latreille), as well as the Australian genera *Cotulades* Pascoe and *Docalis* Pascoe from the Stenosini and *Latometus* Erichson from the Bolitophagini. Watt (1974) stated that the Ulodinae all resemble Zopheridae in the transversely flat prosternal process expanded behind the coxae to partly close the procoxal cavity; the simple, lightly scelerotized tegmen; and the aedeagus with setose parameres that lack the inflected alae (winglike structure) characteristic of true tenebrionids.

The family Merycidae was established (Crowson 1955) for the genus *Meryx* Latrielle from Australia. This genus was suggested to belong to the Zopheridae (Watt 1974), and was formally so placed in the Ulodinae by Doyen and Lawrence (1979)

Doyen and Lawrence (1979) explored the relationship and higher classification of the Zopheridae and suggested a relationship with the Colydiidae and Monommatidae based on the procoxal structure, preapical groove of ventrite 5, and structure of the aedeagus. They removed *Exeniotis* from the Zopherini (Gebien 1936) and returned it to the Tenebrionidae (*sensu stricto*) and divided the Zopheridae into three subfamilies: Zopherinae, Usechinae, and Ulodinae, adding 3 Tenebrionidae genera to the Ulodinae (*Notocerastes* Carter, *Phaennis* Champion, and *Trachyderas* Philippi). They also returned *Trichulodes* to the Tenebrionidae and noted that *Cotulades*, *Docalis*, and *Latometus* were closely related to the Usechinae, but placed them *incertae sedis*. Doyen et al. (1989) added the Australian genus *Melytra* to the Zopheridae without specific infrafamilial placement.

Lawrence and Britton (1991) recognized the Zopherinae but divided the Ulodinae (*sensu* Doyen and Lawrence 1979) into three subfamilies: Ulodinae, Parahelopinae, and Merycinae. In Lawrence's (1994) phylogenetic analysis of the Perimylopidae, Zopheridae, and Chalcodryidae, he showed that the Zopherinae, Usechinae, and *Cotulades* form a monophyletic group with the Colydiidae and Monommatidae which are more closely related to each other than any of the components are to the Ulodinae (*sensu* Doyen and Lawrence 1979). He excluded the Ulodinae from the Zopheridae and recognized that group as the family Ulodidae. Based on his analysis Lawrence (1994) modified the components of the Ulodidae (from Ulodinae *sensu* Doyen and Lawrence 1979) by adding *Pteroderes* Germain and *Trachyderastes* Kaszab and moving *Parahelops* Waterhouse and *Melytra* Pascoe to the Perimylopidae. Lawrence and Newton's (1995) classification followed Lawrence (1994), limiting the family to two subfamilies: Usechinae and Zopherinae, with 3 (*Cotulades*, *Docalis*, and *Latometus*) *incertae sedis* genera. In a typographical error, the Zopheridae are stated to include the Merycidae (p. 891, line 8), even though the only genus, *Meryx* Latreille, is correctly placed within the Ulodidae.

Ślipiński and Lawrence (1999) examined the phylogenetic relationship of the families Colydiidae, Monommatidae, and Zopheridae. Their results suggest that the three families form a monophyletic group, and proposed a new definition of the family Zopheridae, dividing it into two subfamilies: Colydiinae and Zopherinae. This definition was followed by Lawrence et al. (1999 b) but not Lawrence et al. (1999 a). In the new sense, the Colydiinae contain the old colydiids (*sensu* Ivie and Ślipiński 1990) minus the Pycnomerinae which are placed in the Zopherinae with the core zopherids. The Zopherinae also include the old Monommatidae. They recognized six tribes within their Zopherinae: Latometini (3 genera), Usechini (2 genera), Monommatini (16 genera), Phellopsini (1 genus), Pycnomerini (4 genera), and Zopherini (8 genera).

Table. 1. Changes in the Zopheridae from Doyen and Lawrence (1979) to Ślipiński and Lawrence (1999).

Historical Taxa	**1979 Placement**	**1999 Placement**
ulodids (12 genera)	sub-family Ulodinae	family Ulodidae
Usechus	Usechinae	Usechini
Usechimorpha	Usechinae	Usechini
Phellopsis	Zopherinae	Phellopsini
Meralius	Zopherinae	Zopherini
Noserinus	Zopherinae	Zopherini
Noserus	Zopherinae	syn. of *Phloeodes*
Nosoderma	Zopherinae	Zopherini
Phloeodes	Zopherinae	Zopherini
Scoriaderma	Zopherinae	Zopherini
Zopherosis	Zopherinae	Zopherini
Zopherus	Zopherinae	Zopherini
Zopher	gen. nov. in 1999	Zopherini
Cotulades	*incertae sedis*	Pycnomerini
Docalis	*incertae sedis*	Pycnomerini
Latometus	*incertae sedis*	Latometini
Orthocerodes	gen. nov. in 1999	Latometini
Notorthocerus	gen. nov. in 1999	Latometini
Pycnomerus	Colydiidae: Pycnomerini	Zopherinae: Pycnomerini
Pycnomerodes	Colydiidae: Pycnomerini	Zopherinae: Pycnomerini
Monommatidae	Family-taxon	Monommatini
Colydiidae	Family-taxon	Colydiinae of Zopheridae

While the higher level relationships have been critically reviewed, many problems still exist in the definition and placement of individual species. Ślipiński & Lawrence (1999) have provided an excellent framework (Table 1) to examine the genera of

Zopherinae at the species level, and most species of Zopherini (excluding *Zopherus*) are reviewed in the second chapter of this thesis. The need for species-level revisions in this group has been noted repeatedly (Campbell 1991, Ivie 2002c, Garcia-Paris 2001).

CHAPTER 2

A REVISION OF THE GENUS *PHELLOPSIS*

Introduction

The genus *Phellopsis* LeConte is the only component of the tribe Phellopsini (Ślipiński and Lawrence 1999), and can be separated from other large Zopherinae by having 11-segmented antennae and slightly-open procoxal cavities. It forms a distinct cluster based on a unique combination of characters (Ślipiński and Lawrence 1999) and hypothesized synapomorphies including the laterally lobed ventrites and tuberculate body surfaces. The members of *Phellopsis* are widely distributed in the Holarctic, but exhibit very little interspecific morphological diversity. This similarity between species has led to considerable taxonomic confusion. This revision is the first for the entire genus, and I provide a key, full species descriptions, illustrations, taxonomic history and distribution maps for all included species.

Taxonomic History

LeConte (1862) described *Phellopsis* for *Bolitophagus obcordatus* Kirby 1837, from Canada and New England, and *Nosoderma porcatum* LeConte 1853, from California and Oregon. In his 1853 description LeConte noted the strong resemblance between *P. porcata* and *P. obcordata*, an observation that started the confused history of the taxonomy of the North American species.

Several authors have dealt with the problem of distinguishing these allopatric species in North America. Horn (1870) stated that the species were difficult to diagnose, but treated them as distinct species based on color and sculpture. Henshaw (1881) first synonymized the two species in his catalog of species described by LeConte. LeConte's speculation about the species' validity continued even after his death in 1881. In a posthumous (for LeConte) publication, LeConte and Horn (1883) stated that the two named populations were likely parts of a single species, but then retained both names as valid. Casey (1907a), adding to the quandary, stated that they were in fact quite distinct and also supported both as full species. No further changes were made for over 80 years and the purported species were distinguished by geographic origin due to the lack of a good diagnostic character (C.A. Triplehorn pers. com. to M.A. Ivie). Then, without comment, Campbell (1991) returned to Henshaw's (1881) placement of *P. porcata* as a junior synonym of *P. obcordata*. This placement was recognized and commented on by Ivie (2002b).

In the meantime, Casey (1907a) described two additional western species, *P. robustula* Casey from Idaho and *P. montana* Casey from California. These names have been mostly ignored, and were mentioned only by Boddy (1965) and Ivie (2002b), and in some catalogs and checklists (e.g. Gebien 1936). A decisions on their official status has languished for almost 100 years.

The Asian species have a very different taxonomic history. In 1885, Heyden described *Pseudonosoderma* Heyden 1885 (Type species *Pseudonosoderma amurensis* Heyden 1885) from the Russian Far East. Unfortunately, the genus was mistakenly placed in the Byrrhidae section of the Zoological Record of 1885 (Sharp 1886, Champion 1894, Lewis 1895) and was not recognized as a zopherid when *Phellopsis suberea* Lewis

1887 was described from Japan and Russia. Fellow Russian, Semenow (1893), did note the correct relationship of Heyden's genus, and added *Pseudonosoderma chinense* from the Gansu Province of China.

The following year Champion (1894) synonymized *Pseudonosoderma* and *Phellopsis*. The fact that *P. suberea* was based on a series of specimens from both Japan and Russia (Lewis 1887) led Champion (1894) to place *P. suberea* as a synonym of the Russian *P. amurensis*. Lewis contradicted Champion's synonymy in a note (Lewis 1895) asserting that the two were in fact distinct species. He acknowledged that the single specimen he originally cited (Lewis 1887) from Russia as *P. suberea* was in fact *P. amurensis*, and restricted the former name to the Japanese populations. However, since no holotype was established, the syntype series was mixed, and no lectotype has been designated, the correct interpretation of Lewis's name remained uncertain. Establishment in this paper of a lectotype from the Japanese syntypes finally solidifies Lewis' and subsequent authors view as the correct one.

The most recent species addition to *Phellopsis* is *P. imurai* Masumoto 1990 from South Korea. Masumoto (1990) also provided the first key to the Asian *Phellopsis.* However, he based that key at least in part on misidentified specimens, further adding to the confusion in this difficult genus.

At the beginning of this study, we were left with one recognized Trans-North-American species, and two North American names of uncertain status, as well as four east-temperate Asian species of confused definition. My work has shown that there are two North American and four Asian species, these being significantly different in their species limits from the previous assessment.

Materials

The current study was based on the examination of over 3,400 adult specimens of the genus *Phellopsis*, as well as an equal number of related genera. The number of North American specimens available for the current work is considerably larger than that of the Asian species and is a better representation of the expected variability of the species. The numbers of adults examined in each species are: *P. porcata* (n = 2628), *P. obcordata* (n = 752), *P. amurensis* (n = 22), *P. suberea* (n = 61), *P. chinensis* (n = 12), *P. yulongensis* NEW SPECIES (n = 10). The availability of adult specimens was sufficient to complete a thorough examination of morphology and delimit each species. Larval representatives were examined for only the North American species, with a single late instar of each species examined. The larva of *P. amurensis* is described from Russia, but specimens were not available for examination, and the larval character used in the phylogenetic analysis for this species is based on the published description (Keleinikova and Mamaev 1971).

The material for this investigation was obtained on loan from most of the North American entomological collections, as well as many collections in Europe, and a few Asian collections. It proved extremely difficult to obtain loans from Chinese institutions, and I was ultimately unsuccessful. All of the material examined from China is housed in collections outside of that country. Specimens were obtained from or are deposited in the following institutions and collections (the curator responsible for the loan is listed in parenthesis):

AAPC - Albert Allen Personal Collection, Boise, Idaho (Albert Allen).

ASUT - Arizona State University, Tempe, Arizona (David Pearson).

BMNH - The Natural History Museum, London, United Kingdom (Maxwell V. L. Barclay).

BPBM - Bernice P. Bishop Museum, Honolulu, Hawaii (Alistair S. Ramsdale).

BYUC - Brigham Young University, Provo, Utah (Shawn M. Clark)

CASC- California Academy of Sciences, San Francisco, California (Norm Penny and David H. Kavanaugh).

CHICO - Chico State University, Chico, California (Donald Miller).

CMNC - Canadian Museum of Nature, Ottawa, Ontario (François Génier).

CNCI - Canadian National Collections of Insects, Ottawa, Ontario (Patrice Bouchard).

CSCA - California State Collection of Arthropods, Sacramento, California (Chuck Bellamy).

CSUC - Colorado State University, Fort Collins, Colorado (Boris C. Kondratieff).

DBTC - Donald B. Thomas Personal Collection, Weslaco, Texas (Donald Thomas).

DEI - Deutsches Entomologisches Institut, Leibniz-Zentrums für Agrarlandschaftsforschung, Müncheberg, Germany.

DKYC - Daniel K. Young Personal Collection, Madison, Wisconsin (Daniel K. Young).

EIHU - Hokkaido University, Sapporo, Japan (Mashiro Ohara).

EMEC - University of California, Berkeley, California (Cheryl Barr).

ENMU - Eastern New Mexico University, Portales, New Mexico (Darren A. Pollock).

FMNH - Field Museum, Chicago, Illinois (James H. Boone).

FSCA - Florida State Collection of Arthropods, Gainesville, Florida (Paul E. Skelley).

HNHM - Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl).

HUMB - Humboldt State University, Arcata, California (Michael Camann).

INHS - Illinois Natural History Survey, Champaign (Colin Favret).

IRCW - University of Wisconsin, Madison, Wisconsin (Steven Krauth).

JEWC - James E. Wappes Personal Collection, Bulverde, Texas (James E. Wappes).

LACM - Natural History Museum of Los Angeles County, Los Angeles, California (Weiping Xie).

LSAM - Louisiana State Arthropod Museum, Baton Rouge, Louisiana (Victoria Bayless).

LUND - Lund University, Lund, Sweden (Roy Danielsson).

MCPM - Milwaukee Public Museum, Milwaukee, Wisconsin (Susan Borkin).

MAIC - Michael A. Ivie Private Collection, Bozeman, Montana (Michael. A. Ivie).

MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (Philip D. Perkins).

MIZ - Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland (Wioleta Tomaszewska).

MSUC - Michigan State University, East Lansing, Michigan (Gary L. Parsons).

MTEC - Montana Entomology Collection, Montana State University Bozeman (Michael A. Ivie).

NCSU - North Carolina State University Insect Collection, Raleigh, North Carolina (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. (Warren E. Steiner).

NMPC - National Museum of Natural History, Prague, Czech Republic (Svatopluk Bílý).

OSAC - Oregon State Arthropod Collection, Oregon State University, Corvallis (Andrew Brower).

RLAC - Rolf L. Aalbu Personal Collection, Sacramento, California (Rolf L. Aalbu).

ROME - Royal Ontario Museum, Toronto, Ontario (Brad Hubely).

SBMN - Santa Barbara Museum of Natural History, California (Michael S. Caterino).

SEMC - Snow Entomological Collections, University of Kansas, Lawrence (Zachary H. Falin).

SMDV - Spencer Entomological Museum, University of British Columbia, Vancouver (Karen M. Needham).

TAMU - Texas A&M University, College Station (Edward G. Riley).

UTSC -Utah State University, Logan (Colin Brammer).

UASM - Strickland Museum,University of Alberta, Edmonton (Danny Shpeley).

UCDC - Bohart Museum of Entomology, University of California-Davis (Steve L. Heydon).

UCMC - University of Colorado Museum, Boulder (Virginia Scott).

UCRC - University of California-Riverside (Douglas Yanega).

UGCA - Georgia Museum of Natural History, Athens (Cecil L. Smith).

UMMZ - University of Michigan, Ann Arbor (Mark F. O'Brien).

WFBM - William F. Barr Entomological Museum, Univ. of Idaho, Moscow (Frank W. Merickel).

WSUC - Washington State University, Pullman (Richard Zack).

WVDA - West Virginia Dept. of AgricultureCharleston (Laura T. Miller).

ZIN - Russian Academy of Sciences, St. Petersburg (Mark G. Volkovitsh).

Methods -- Morphology

This revision was based on morphological characters primarily of adult specimens following the operational species concept of Whitehead (1972). This concept assumes that if one group of organisms shares a set morphological characters which are absent in another group, then the difference is due to genetic differences between the groups. If these supposedly genetically-based gaps between the groups are significant, then the groups are defined as different species.

Specimens were initially separated based on geographic location, and then compared to other populations looking for unique morphological characters that would support the recognition of different species. Because all members of the genus *Phellopsis* are relatively homogeneous morphologically, a set of informative species-level characters did not exist. I was able to identify a working set of morphological characters that varied within the genus, and allowed for discrimination of the species, as well as phylogenetic comparison between the species.

Frequently, specimens of the genus are encrusted with a greasy exudate as well as accumulated debris, such as sand and soil, making structures difficult to examine. In order to examine both external and internal morphological structures, specimens were relaxed and cleaned (Ivie 2002d) by first placing them 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 encrustations 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. Specimens thus prepared were then ready for dissection and disarticulation, which was used to study structures such as mouthparts and genitalia.

Nomenclature of morphological structures follows Doyen (1966), Doyen and Lawrence (1979), Lawrence and Britton (1991) and Ślipiński and Lawrence (1999). Definitions specific to this study are few. A tubercle is defined as 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 its surface. The term "setiferous fossae" was recently used in the Zopherinae (García-París et al. 2001) to refer to pits in the cuticular surface with a single inserted seta. Here they are referred to as setose punctures following Harris (1979). Other sculpture definitions follow Harris (1979) and Nichols

(1989).

Specimens were studied on 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 5005 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.

Type specimens were examined for all named species except *P. amurensis* (DEI) which was not available for loan. Specimens of this species were examined from the type locality and confidently represent the true identity of the species.

Transcription of label data from type specimens follows Ivie (1985): the end of each line on a label is indicated by a ";" (semicolon); the individual labels are separated by a "/" (backslash). The summarized distribution data follows the format COUNTRY: PROVINCE or STATE: County, Borough, Census Area, or Municipality.

Methods -- Phylogenetic Analysis

A cladistic analysis was conducted based on morphological characters and was used to produce a hypothesis of the relationship between the six known species of *Phellopsis*. Outgroups were chosen using Ślipiński and Lawrence's (1999) phylogeny, with a choice of one exemplar from the sister-group and one from the next-lower clade. Species with available larvae were chosen as exemplars. Following the conventions of WINCLADA, *Usechus lacerta* Motschulsky was coded as the designated outgroup, and the Monommatini *Hyporaghus* sp. was included within the ingroup, representing the reported sister-linage to *Phellopsis* (Ślipiński and Lawrence 1999).

Fourteen characters represented by 34 states were ultimately selected for the analysis and construction of cladograms. The initial matrix contained over 40 characters, but most were discarded because they were plesiomorphies shared by all taxa in the analysis, autapomorphies for individual species, or phylogenetically uninformative.

Characters, states and definitions are as follows (adult characters unless noted) [Character state numbering starts with “0”, because this is the data entry format used by WINCLADA.]:

0. Lateral margin of elytra appearing: (0) smooth, Figs. 10, 11, 57, 60; (1) serrate, Figs. 14-17, 53-56. In the dorsal view the lateral margin of the elytra appears serrate due to protruding tubercles and nodules in the 7th elytral interval.
1. Subgenal sculpture: (0) with setose punctures, Fig. 37; (1) with distinct raised tubercles, Fig. 36; (2) with indistinct, flat tubercles, Fig. 35. In the Chinese species of *Phellopsis*, the ventral surface of the head is relatively smooth, because the tubercles are flattened and merged together. In the other species, the tuberculation in this area is similar to other surfaces of the body. The sculpture of both outgroup taxa consists of setose punctures. Subgenal tubercles occur as a

homoplasy in some members of the Zopherini (*Phloeodes*), but are hypothesized as independently derived synapomorphy in *Phellopsis*.

2. Lateral margins of ventrites 3 and 4: (0) even; (1) posterolaterally expanded, Figs. 30-31. Ventrites 3 and 4 of all *Phellopsis* species are lobed along the lateral margin. This character is not seen in any of the other Zopherinae, and represents a hypothesized synapomorphy for *Phellopsis*. It is found in some other flightless species of beetles including members of the Ulodidae and Tenebrionidae, but this is considered as a homoplasy in distantly related derived taxa.
3. Elytral punctures: (0) rounded, Figs. 10-11, 14; (1) elongate, Figs. 14-17. The puncture on the dorsal surface of the elytra in several species are fused together or indistinct (1), or rounded and in regular rows.
4. Subgenal ridge: (0) longer, extending below eye, eye set below surface of gena; (1) shorter, produced forward, eye even with gena; (2) absent. The subgenal ridge is well defined in the genus, but varies in the relative position. Species with a longer ridge (1) also have a median depression on the margin.
5. Ventrites: (0) with setose punctures; (1) tuberculate, Figs. 30-31. All species of *Phellopsis* have tubercles, *Usechus* and *Hyporaghus* have setose punctures. Tubercles on the ventral surface of the body have independently evolved in other lineages of Zopherini (*Phloeodes* and *Nosoderma*).
6. Lateral margin of epistoma anterior to suprantennal ridge: (0) fused; (1) short, Figs. 22- 23; (2) long, Fig. 19-21; (3) short due to median depression on dorsal surface of head, Fig. 18. The distance from the apicolateral angle of the epistoma to the

insertion of the suprantennal ridge is either shorter or longer than the 3rd antennomere, or entirely fused with the epistoma. Character state 3 occurs as an autapomorphy in *P. suberea* where

7. Profemur grooved ventrally: (0) complete; (1) incomplete. The ventral surface of the profemur is grooved for the reception of the tibia. It either extends to the base of the femur (0) or ends short of the base (1).
8. Tubercles on head between frons: (0) absent, with punctures; (1) present and weak, Fig. 19-23; (2) present and strong, Fig. 18. Distinct large tubercles are present on the apex of the head in *P. suberea*. These tubercles decrease in intensity in the other species, and are weakly present in many Zopherinae. The presence of clearly visible large tubercles on the dorsal surface of the head is a hypothesized synapomorphy for *Phellopsis*.
9. Hypomeron: (0) without intertuberculate setae, Fig. 12; (1) with dense intertuberculate setae, Fig. 13.
10. Scutellum: (0) visible; (1) not visible.
11. Larva: ventral asperites of A8: (0) absent; (1) present, Figs. 32-33. This character shows up as a synapomorphy for *Phellopsis*, but because of missing data in 3 of 6 species (and many other members of the subfamily), this is poorly supported. Ventral asperities are also present in some Zopherini (*Zopherus*).
12. Male parameres in lateral view: (0) without basal stop, Fig. 27; (1) with clear basal stop, Figs. 24-26, 28.

13. Tarsomere with: (0) simple setae only; (1) with ventral setae thickened, modified as tiny spurs, distinctly heavier than dorsal surface, Fig. 38; (2) with dense setose pads.

Table 2. Character matrix used for phylogenetic analysis.

Taxon\Character	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Usechus lacerta	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hyporaghus sp.	0	0	0	0	2	0	0	0	0	0	0	0	1	2
P. porcata	0	1	1	0	0	1	1	1	1	1	0	1	1	0
P. obcordata	0	1	1	0	0	1	1	1	1	0	0	1	1	0
P. chinensis	1	2	1	1	1	1	2	0	1	1	0	?	0	1
P. yulongensis (n. sp)	1	2	1	1	1	1	2	0	1	0	0	?	1	1
P. suberea	1	1	1	1	1	1	3	1	2	0	0	?	1	1
P. amurensis	1	1	1	0	1	1	2	1	1	0	0	1	1	1

Parsimony analysis was conducted using the software programs WINCLADA version 1.00.08 (Nixon 2002) and NONA 2.0 (Goloboff 1999). All characters, except 1 and 6, were treated as unordered using non-additive Fitch parsimony (Wiley 1981, Wiley et al. 1991, Lipscomb 1998, Maddison and Maddison 2000). Characters 1 and 6 were treated as additive using Farris optimization, because intermediate states are hypothesized in these characters. All characters were equally weighted. Missing characters were coded as question marks ("?"). All searches relied on heuristic parsimony approaches of NONA 2.0 (Goloboff 1999) run with WINCLADA version 1.00.08 (Nixon 2002) as a shell program to find the most parsimonious trees. The commands 'hold 1000', '500 mult*N', '1 hold/' were used for the unconstrained multiple TBR + TBR 'mult*ma*' search strategy (TBR is the tree bisection-reconnection method of branch-swapping). Bootstrap support was estimated for nodes with the 'bootstrap' option in NONA based on 1000 replicates and 'max TBR'. Characters were traced on the most parsimonious tree using WINCLADA. The relationships between taxa are hypothesized on the assumption of synapomorphies and parsimony. The cladistic principles delineated by Wiley (1981), Wiley et al. (1991), Lipscomb (1998), and Maddison and Maddison (2000), were used to infer relationships based on the results of the analysis.

Taxonomy of the Genus *Phellopsis* LeConte

(Figs. 10-36, 38-59, 62)

Phellopsis LeConte 1862: 216. (Type species *Bolitophagus obcordatus* Kirby 1837, designated by Casey 1907b: 470). Horn 1870: 271, 273. Henshaw 1881: 203, 255. LeConte and Horn 1883: 365. Champion 1884: 44. Fairmaire 1894: C1. Lewis 1887: 218-220. Lewis 1894: 379, pl. xiii, fig. 1. Champion 1894: 114. Lewis 1895: 447. Casey 1907a: 44-46. Casey 1907b: 470, 480-481. Reitter 1916: 130-131. Leng 1920: 223. Bradley 1930: 183, 322. Böving and Craighead 1931: 41, pl. 52. Gebien 1936: 668. Crowson 1955: 127. Arnett 1962: 650, 668. Boddy 1965: 77-78, pl. x. Arnett 1968: 650, 668. Arnett 1971: 650, 668. Keleinikova and Mamaev 1971: 125-128. Arnett 1973: 650, 668. Doyen 1976: 267, 270-271. Doyen and Lawrence 1979: 341-345. Papp 1984: 162-163. Arnett 1985: 350. Masumoto 1990: 87-91. Campbell 1991: 252. Lawrence 1991: 518-519. Egorov 1992: 504-505. Steiner 1992: 25-30. Lawrence 1994: 341-344. Ślipiński and Lawrence 1999: 21, 23. Steiner 1999: 125, 138-139. García-París et. al. 2001: 145. Ivie 2002: 460.

Pseudonosoderma Heyden 1885: 305. (Type species *Pseudonosoderma amurensis*

Heyden 1885 by monotypy). Semenow 1893: 499. Synonymy by Champion 1894: 114.

Diagnosis: The members of this genus are easily distinguished from all other large (> 9mm) Zopherinae by the presence of 11-segmented antennae (Fig. 39) associated with slightly open procoxal cavities (Figs. 41 and 42).

Description (male): Length 11-22mm. Body elongate, parallel sided; elytra 1.9-2.4X longer than pronotum; reddish brown to black; dorsal surface granulose, covered in small dark tubercles, each with single setae; secondary vestiture setose; elytral and pronotal sculpture forming similar pattern in all species (Figs. 53-57), pronotum with lyriform ridge and lateral nodule, elytra with parallel ridges, two subapical nodules, and single nodule near apex.

Head with suprantennal ridges distinctly raised above widely separated antennal insertions (Figs. 18-23); not constricted behind eyes; dorsal surface of head with varying intensity of tubercles between suprantennal ridges and frons; margin of suprantennal ridge emarginate, flat, or convex. Antennae 11-segmented (Fig. 49), not reaching beyond middle of prothorax; capitate with moderate 3 segmented club antennomere 2 transverse, shorter than 1 or 3; antennomere 3 slightly elongate but less than twice as long as wide, shorter than 4 and 5 combined; antennomeres 9 and 10 with lateral patch of sensilla, 11 with apex covered in sensilla. Subgenal ridges present. Eye emarginate, coarsely faceted, frontal margin with golden setae; area directly behind with small elevated glabrous piece. Labrum visible, transverse, punctate, apical margin with dense fringe of setae. Mandible acutely bidentate, apex curved mesally (Figs. 43-44); median tooth, setose-fringed membranous prostheca, and mola present. Maxillary surfaces with setae inserted in small punctures, variably sculptured; maxillary palpifer and basistipes with long bristle-like setae; apical maxillary palpomere rounded; galea and lacinia densely setose, lacinia hooked laterally, with one or two small teeth (Figs. 45-46). Labial palps broadly separated, inserted laterally; ligula shallowly emarginate to smooth, setose. Submentum with setose pit (Fig. 36). Gula strongly narrowed or not; posterior tentorial pits present along suture, often indistinct.

Pronotum with lyriform ridge divided by midline; large apicolateral nodule; lateral margin slightly explanate or thickened; pronotum widest anterior to midline, anterior angles produced and broadly rounded; posterior angles obtuse; base narrower than elytral base; lateral margin of pronotum variably arcuate, with dense intertuberculate setae at margin, presence of setae varying in species on hypomeron. Hypomeron lacking any hint of antennal cavities. Prosternum in front of procoaxe longer than midlength between procoxal cavities; prosternum anterior to procoaxe at midline longer than prosternal process; prosternal process gradually expanded then narrowed, apical margin concave or biconcave; strongly elevated and curved dorsally behind coxae; procoxal cavities circular, widely separated, and narrowly open.

Scutellum abruptly elevated, notched anteriorly to rounded; elytron with scutellary striole; with 7 rows distinct to obscure, rounded, irregular or elongate punctures; epipleuron complete; distinct paired tubercles on elytron at top of apical declivity, a single tubercle near apex, apex rounded and slightly emarginate; elytra not fused.

Mesepisternum widely separated, with round fovea or vermiculate, occasionally with small tubercles (Figs. 41-42); mesocoxal cavities closed laterally, moderately separated; mesoventral process extending to middle of mesocoxal cavity.

Exposed portion of metepisternum long and narrow; metaventral median line long; metacoxal extending laterally to reach elytron; cavities moderately separated. Brachypterous, flight wings reduced to small elongate or rounded membranous pads.

Tarsal formula 5-5-4; tarsi and claws simple; tarsal setae on ventral surface of tarsomeres variably shorter and thicker than dorsal surface (Fig. 38); all tibia with paired apical spurs; apical margin ringed with small spines; femora and tibia with length of pro<meso<meta; length of meta- tibia 0.06-0.12X longer than the femur; ventral surfaces of all femora with elongate glabrous area.

Intercoxal process of Ventrite 1 (V1) broadly truncate; abdomen with 5 ventries; first 4 connate, V1 weakly to strongly depressed behind the coxae, V5 with preapical groove divided into two sinuous pits (Figs. 21 and 22); V3 and V4 with laterally expanded lobes, V2 occasionally with hint of expansion; laterotergite 3 variably expanded and coupled with internal surface of elytron. Adeagus as in Figs. 30-31.

Female: The female lacks the setose pit on the submentum, but is similar in all other external morphological characters. The female genitalia (Fig. 50) distally terminates in a single-segmented, elongate gonostylus that is setose on the apex. Tergite eight and the proctiger are densely clothed in appressed setae. The pleated membrane lacks setation, and the coxite is setose laterally and at the apex.

Larva: (see description of the larva of *P. obcordata* below).

Notes: The generic identity of this group has been relatively stable since LeConte's description. The only issue was Heyden's description of *Pseudonosoderma*, which contained *P. amurensis* and *P. chinensis* for a short time. *Pseudonosoderma* is clearly synonymous with *Phellopsis* (Champion 1894).

Biology

Adults and larvae both feed on fungi associated with decaying trees in old growth boreal forests (Steiner 1992, Ivie 2002). Adults are surface feeders, while larvae burrow into the substrate.

Adults of the genus have been collected on a variety of xylophilous fungi growing on both coniferous and deciduous trees in various states of decay (label data, pers. obs., Steiner 1992, Ivie 2002). Several reports in the literature have associated adults with specific habitats. *Phellopsis obcordata* adults have been reported feeding on *Piptoporus betulinus* (Bull.:Fr.) P. Karst. on a paper birch log (*Betula papyrifera* Marsh), and *Fomes annosus* (Fr.) Cooke on dead balsam fir (*Abies balsamea* Mill.) in Maine, and from *P. betulinus* on sweet birch (*Betula lenta* L.) in Maryland (Steiner 1992). *Phellopsis porcata* adults have been associated with fungi on western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) on Vancouver Island (Guppy 1951) and on *Lentinus* fungus in Montana (Russell 1968). In Japan, *P. suberea* was described from *Boletus* fungus on large oak trees (*Quercus* sp.) (Lewis 1894). *Phellopsis amurensis* was reported on Poriaceae fungi from a mixed forest of spruce, fir, birch, and other deciduous trees in the Sikhote-Alin Mountains of southern Primorski Krai, Russia (Lafer 2002).

Adults use thanatosis (death feigning) as a predator avoidance mechanism, a behavior that has been 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). When disturbed, adults drop to the ground with appendages retracted, and remain motionless for a significant time period (pers. obs., Steiner 1992). Their rough bodies blend perfectly with bark chips and detritus at the base of trees or litter on the ground, making a good search image critical to collecting species of this group.

The larvae of *Phellopsis obcordata* have been found living in shelf fungi in dense woodland (Peterson 1951) and conks of the fungi *Piptoporus betulinus* (Polyporales: Fomitopsidaceae) (Steiner 1999). In Western North America, the larvae of *P. porcata* bore through soft wood, where they feed on white sheet fungi between the laminae of large rotting spruce (*Picea sp.*) stumps (Ivie 2002). Wood boring has also been reported for the larva of *P. amurensis* (Keleinikova and Mamaev 1971), but this is probably another case of fungal association.

Key to the Species of *Phellopsis*

1\. Lateral margin of elytra appearing smooth in dorsal view (Figs. 10-11); North America……………………………………………..…………………….……..2

1’. Lateral margin of elytra appearing serrate in dorsal view (Figs. 14-17); Asia ……………..…………………………………………………………………3

2. Hypomeron lacking intertuberculate setae (Fig. 12); lateral margin of pronotum strongly bisinuate in lateral view (Fig. 58); elytral punctures large, discal tubercles less than ¼ diameter of puncture; posterior margin of prointercoxal process straight to weakly concave (Fig. 51). Eastern North America.
…………………………………………………….…………….*P. obcordata* (Kirby)

2’. Hypomeron with dense setae between tubercles (Fig. 13); lateral margin of pronotum arcuate to weakly bisinuate in lateral view (Fig. 59); elytral punctures small, discal tubercles about ½ diameter of punctures; posterior margin of prointercoxal process bi-sinuate. Western North America..........................*P. porcata* (LeConte)

3. Outer margin of suprantennal ridge emarginate; head between frons with very large tubercles (Fig. 18); gula at narrowest point approximately 0.2X the width the apex of the submentum (Fig. 35). Japan………………………………*P. suberea* Lewis

3’. Outer margin of suprantennal ridge straight to convex (Fig. 19-23); head between frons with at most small indistinct tubercles (Fig. 19-23); gula approximately 0.65X width of the apex of the submentum (Fig. 34, 36). Mainland Asia.
……………..…..4

4. Elytral humerus with nearly 90° notch (Fig. 14); striae with linear series of rounded punctures; subgena with raised tubercles. Russian Far East and Korean Pennisula.
…………………………………………………..……………*P. amurensis* (Heyden)

4’. Elytral humerus rounded or flattened but not distinctly notched (Fig. 15-17); striae with irregular punctures; subgena with indistinct, flat tubercles (Fig. 34, 36).
……………………………………………………………………………...………..5

5. Setae of pronotal disc broad, scale-like, golden (fig. 39); elytral disc irregularly squarrose; ventrites with very large flat tubercles (Fig. 30); pronotal disc between and anterior to lyriform ridges lacking distinct tubercles; disc of hypomeron with intertuberculate setae. Central China……………………..…*P. chinensis* (Semenow)

5’. Setae of pronotal disc narrow, hair-like, red (Fig. 40); elytral disc plain and striate; ventrites with smaller tubercles (Fig. 31); pronotal disc between and anterior to lyriform ridges with distinct tubercles; disc of hypomeron lacking intertuberculate setae. Western China…..………………..………..*P. yulongensis* NEW SPECIES

Species Descriptions

Phellopsis obcordata (Kirby)

(Fig. 1, 10, 12, 22, 24, 32, 48, 51, 57, 58)

Bolitophagus obcordatus Kirby 1837: 236.

Boletophagus obcordatus LeConte 1853: 235. LeConte 1862: 216. LeConte and Horn 1883: 365. Casey 1907b: 470. Ślipiński and Lawrence 1999: 23. (*lapsus calami*)

Nosoderma obcordatum: Heyden 1885: 307. LeConte 1853: 235.

Phellopsis obcordata: Horn 1870: 273. Hubbard and Schwarz 1878: 640. Henshaw 1881: 255 [in part]. Lewis 1887: 219. Champion 1894: 114. Hamilton 1895: 341. Leng 1920: 223. Leonard 1928: 401. Böving and Craighead 1931: pl. 52. Chagnon 1935: 278. Geiben 1936: 668. Brimley 1938: 190. Triplehorn 1952: 1-3. Peterson 1960: 180, fig. C48. Dillon and Dillon 1961: 464, pl. xlvi. Boddy 1965: 78. Pielou 1966: 1235. Pielou and Verma 1968: 1184. Keleinikova and Mamaev 1971: 125.

Arnett 1983: 17. Papp 1984: 162. Lawrence 1991: 518-519. Campbell 1991: 252[in part]. Steiner 1992: 25-30. Lawrence 1994: 341. Downie and Arnett 1996: 1080. Ślipiński and Lawrence 1999: 21. Steiner 2000: 138-139. Ivie 2002: 458-460[in part]. Triplehorn and Johnson 2005: 435.

Type Material Examined: LECTOTYPE, here designated: Specimen of undetermined sex in the BMNH. Circle label with "N. Scotia" on backside; "5969, B" on front/ Round red-ringed "Type" label/ Bolitoph obcordatus; N. Scotia 5969; Rev. W. Kirby/ white card Lectotype underlined in red, Bolitophagus obcordatus; Kirby 1873; designated by M.A. Ivie 2005.

Diagnosis: Distinguished from the other North American species, *P. porcata*, by the lack of intertuberculate setae on the hypomeron (Fig. 12). Other useful characters include, the presence of large distinct round punctures on the elytra, 10-13 between the apical edge of the scutellary striole and subapical nodule, the ridge in the 3rd elytral interval very weak or absent medially and more strongly arcuate around the scutellum, strongly bisinuate lateral margin of the pronotum, the basal connecting ridge between the 1st and 3rd elytral interval smooth and lacking a depression, and the lateral subapical nodule of the declivity strongly directed away from the plane of the body. This species can also be confused with *P. amurensis*, but has the tuberculation on the apical half of the pronotum stronger, and the lateral elytral margin smooth rather than serrate.

Description (male): Length 11-16mm. Reddish brown to dark brown; dorsal setose vestiture sporadic; most elytral punctures large and clearly visible; vestiture consisting of short, slightly thickened setae, lacking significant intertubercle setation on prothoracic and elytral surfaces. Head on dorsal surface with weak indistinct tubercles between frons; outer margin of suprantennal ridges concave; lateral margin of epistoma anterior to suprantennal ridge short (0.12-0.17mm, Fig. 22); ventral surface of head with distinct and regular tubercles; gula wide; subgenal ridge rounded, with slight depression medially; subgenal ridge longer, extending below eye; eye set below genal surface. Post-occipital suture deep and narrowly divided. Last antennomere with micro-setose patch of sensilla oval; preapical patches oblong. Ligula shallowly emarginate.

Pronotum evenly tuberculate; paired elevations on apical margin of pronotum broadly and weakly divided at midline; lateral margin of pronotum strongly bisinuate (Fig. 58); hypomeron without intertuberculate setae, cuticular surface between tubercles with smooth microsculpture.

Dorsal elytral surfaces with small, often obscure tubercles; humerus slightly flattened; scutellum oval, shallowly set below elytral ridges; scutellary striole distinct; 10-13 large, rounded elytral punctures along midline between scutellary striole and large nodule at start of apical declivity; median subapical elytral nodule usually noticeably larger than lateral nodule; lateral nodule of apical declivity usually strongly projected away from body plane at approximately 45° angle; paired nodules considerably larger than single nodule near apex; ridges in 3rd and 5th elytral intervals, overlapping at most only at base and apex but not medially; nodule in 3rd interval never connected to ridge; area around elytral suture weakly elevated and flattened, never with large tubercles. Metasternum with small, relatively uniform tubercles (Fig. 48); ventrite tuberculation reduced medially, uniformly spaced laterally. Tarsal setation denser on ventral surface, setae relatively uniform in thickness.

Aedeagus (Fig. 24), relatively short and broad; apex of parameres almost straight; apical margin of basal stop with moderate concave depression medially, and lightly setose.

Female: Same as male except lacking setose pit on submentum.

Variation: The dorsal elytral sculpture is less variable than in *P. porcata*. Southern Appalachian specimens (North Carolina, Tennessee, West Virginia, Georgia) frequently have the humeri more flattened and pointed apically.

Larva: (modified from Peterson 1951 and Lawrence 1991). Body elongate, 15-25mm when extended, subcylindrical, white or creamy in color; head, pronotum, asperites, and legs lightly sclerotized; tarsal claws, urogomphi, and mouthparts heavily sclerotized.

Head subquadrate, lateral margins rounded, dorsoventrally flattened, prognathus, with sparse patches of short setae, 5 stemmata on each side, frontal arms lyriform. Antennae 3-segmented, anterolaterally inserted. Mandibles large, prognathus, apical tip bidentate. Maxilla thick and fleshy, with apical setae; cardo bifid.

Prothorax enlarged, partly enclosing head when retracted. Meso-and metathorax with arcuate rows of asperites, followed by sparse patches of asperites; spiracles annular-biforous.

Abdominal segments subequal in size, segments 1-6 with dorsal rows and patches of asperites, 9 with sclerotized granulate basal spots and well-developed recurved urogomphi; ventral surface of 2-8 with progressively strong patches of asperites, 8 with dense patch (Fig. 32). Legs short, 5-segmented; coxae large and transverse, short setae concentrated on apical surfaces, claw elongate hook.

Distribution (Fig. 1): Restricted to boreal forests of eastern portions of North America, widespread but uncommon from Newfoundland south to Northern Georgia and west to northern Wisconsin and the Upper Peninsula of Michigan. In more southern locales the species appears to be confined to higher elevations of the Appalachian Mountains.

Recorded Distribution: The full data for individual specimens are recorded in Appendix A. A summary of the distribution is presented here as COUNTRY: PROVINCE or STATE: county (when available).

CANADA: NEW BRUNSWICK, NEWFOUNDLAND, NOVA SCOTIA, ONTARIO, QUEBEC. UNITED STATES: CONNECTICUT: Litchfield. GEORGIA: Rabun. MASSACHUSETTS: Worcester. MARYLAND: Garrett. MAINE: Cumberland, Hancock, Kennebec, Knox, Lincoln, Penobscot, Piscataquis, Washington. MICHIGAN: Cheboygan, Emmet, Marquette, Schoolcraft. NORTH CAROLINA: Avery, Buncombe, Burke, Haywood, Macon, Watauga. NEW HAMPSHIRE: Coos, Grafton, Rock, Carr. NEW JERSEY: Hudson (Steiner 1992) NEW YORK: Erie, Essex, Franklin, Herkimer, St. Lawrence, Tompkins, Ulster, Wayne. PENNSYLVANIA: Dauphin, Forest, Huntington, Monroe, Westmoreland. TENNESSE: Blount, Carter, Sevier, Tusculum. VIRGINIA: Albemarle, Giles, Highland, Lee, Madison, Page, Washington. VERMONT: Addison, Bennington, Lamoille. WISCONSIN: Florence, Forest. WEST VIRGINIA: Greenbrier, Pendleton, Pocahontas, Preston.

Notes: The name *P. obcordata* has recently been applied to an assumed Trans-

North American species (Campbell 1991, Ivie 2002, label data), but is here restricted to the species occurring in Eastern North America. The historical discussion of the North American species names has been tumultuous and has included very little diagnostic support. A summary of this history is provided in the Introduction. The difficulty in separating the two species was frequently acknowledged by ambiguous characterizations of the relationship (LeConte 1853, Horn 1870, LeConte and Horn 1883), or stated as very clearly defined (Casey 1907a). I have found that 100% of specimens can be assigned to one of the 2 North American species recognized here using the characters in the key and diagnosis. These characters are 100% correlated with a geographic division across the North American Great Plains. This division is well supported based on the glaciation and subsequent drying out of the North American Great Plains (Kavanaugh 1988, Marek and Kavanaugh 2005). Hopefully the taxonomic confusion has now been resolved.

Roughly 40% of specimens examined were collected pre-1940. This may be an indication of a negative correlation between human disturbance in Eastern North America and habitat availability. The post-World War II distribution of this species appears to be restricted to highly fragmented old growth remnants of a historically widespread forested habitat.

Phellopsis porcata (LeConte)

(Fig. 1, 11, 13, 23, 25, 33, 50, 59)

Nosoderma porcatum LeConte 1853: 235. LeConte 1862: 216. LeConte and Horn 1883: 365.

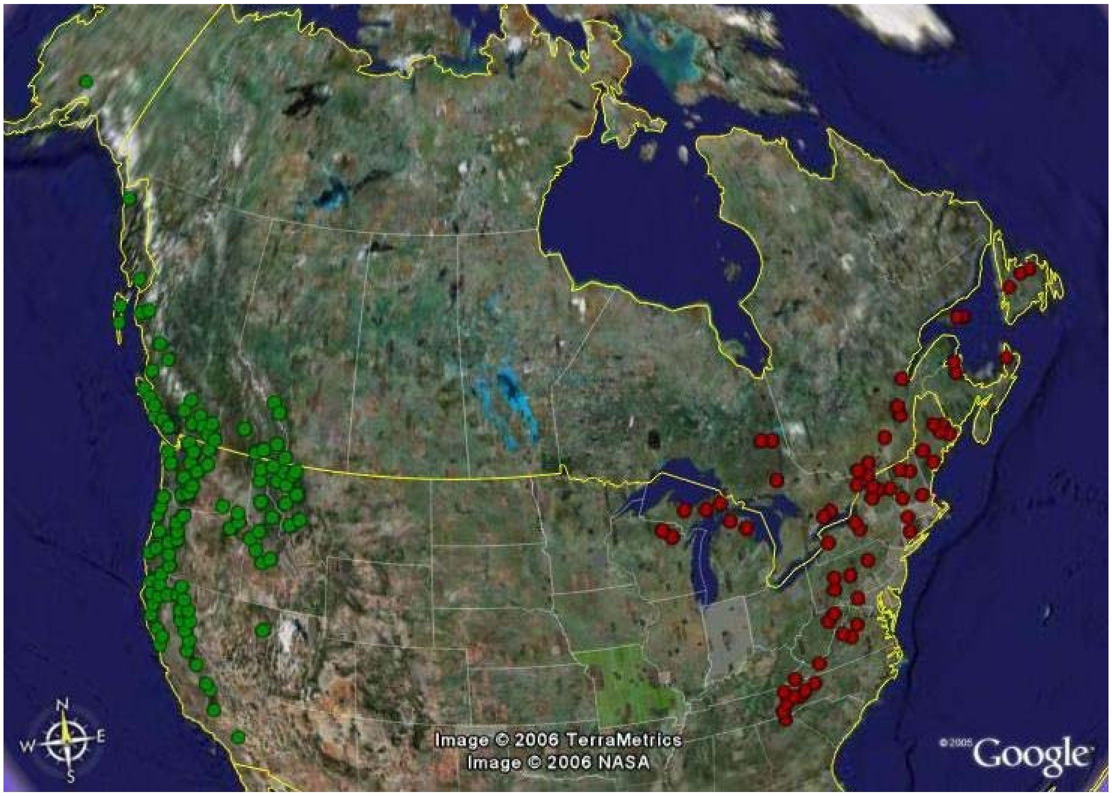

Fig. 1. The distribution of North American species of *Phellopsis*. *P. obcordata* red circles and *P. porcata* green circles.

Phellopsis porcata: Horn 1870: 273. Henshaw 1881: 255. LeConte and Horn 1883: 365. Champion 1894: 114. Casey 1907a: 44-45. Leng 1920: 223. Geiben 1936: 668. Guppy 1951: 28. Peterson 1960: 180, fig. C48. Boddy 1965: 78, pl. x. Papp 1984: 163. Campbell 1991: 252. Downie & Arnett 1996: 1080. Arnett 1983: 17. Boddy 1965: 78. Ivie 2002: 458-460.

Noserus plicatus (not LeConte) Milne and Milne 2000: 585, pl. 224.

Phellopsis robustula Casey 1907a: 45. Leng 1920: 223. Geiben 1936: 668. Boddy1965: 78. Arnett 1983: 17. NEW SYNONYMY

Phellopsis montana Casey 1907a: 46. Leng 1920: 223. Geiben 1936: 668. Arnett 1983:

17. NEW SYNONYMY

Phellopsis obcordata, (Not Kirby). Henshaw 1881: 255[in part]. Campbell 1991: 252[in part]. Ivie 2002: 460 [in part].

Type Material Examined: *Nosoderma porcatum* LeConte. HOLOTYPE in MCZ ♂ missing right meta-tarsus. Gold circle/ Red square type 4508 label/ Phellopsis porcata Lec./ Jan.-Jul. 2005 MCZ Image Database.

Phellopsis robustula Casey. HOLOTYPE in NMNH ♀ missing left pro-leg and antenna. "Id.[aho]./ Casey bequest 1925/ Orange rectangle Type USNM 46373/ hand written robustula Csy.".

Phellopsis montana Casey. HOLOTYPE in NMNH ♀ intact. "Cal.[ifornia]/ Casey bequest 1925/ orange rectangle Type USNM 46372/ hand written Montana Csy.". PARATYPE in NMNH ♀ missing right mesotarsus. USNM orange label stating "This ex.; clearly placed with porcata in Csy box; is doubtless the Placer Co. paratype of montana."/ Placer Co. Cal.

Diagnosis: Distinguished from the other North American species, *P. obcordata*, by having dense intertubercle setation on the hypomeron (Fig. 13). Other useful characters include, the 14-18 smaller elytral punctures between the apical edge of the scutellary striole and subapical nodule, arcuate lateral margin of the pronotum, more complete ridge in the 3rd elytral interval, generally denser setose vestiture, the basal connecting ridge between the 1st and 3rd elytral interval distinctly depressed, and the nodules of the apical declivity directed almost parallel with the body plane.

Description (male): Length 12-18mm. Reddish brown to black; dorsal vestiture very dense slightly obscuring elytral punctures; vestiture consisting of dense long, relatively thin setae; considerable amount of intertuberculate setation on pronotal and elytral surfaces.

Head on dorsal surface with weak indistinct tubercles between frons (Fig. 23); outer margin of suprantennal frontal ridges concave; lateral margin of epistoma anterior to suprantennal ridge short (0.04-0.10mm), almost in same plane; ventral surface of head with irregular tubercles; gula wide; sub-genal ridge rounded, with slight depression medially; sub-genal ridge longer, extending below eye; eye set below genal surface. Post occipital suture deep and narrowly divided. Last antennomere with micro-setose sensilla patch oblong. Ligula shallowly emarginate; maxillary palpifer with thickened setae; basistipes with paired thickened setae inserted laterally and strongly recurved; lacinia narrowed with median tuft of setae.

Pronotum evenly tuberculate across median portion; paired elevations on apical margin of pronotum broad and weakly divide by midline, nearly fused; lateral margin of pronotum arcuate to weakly bisinuate; hypomeron with dense intertuberculate setae.

Dorsal surface of elytra usually with obvious tubercles; humerus rounded; scutellum rounded set below elytral ridges, scutellary striole distinct; 14-18 elytral punctures along midline between scutellary striole and large median nodule at start of apical declivity; median and lateral nodule of declivity usually subequal in size; lateral nodule almost parallel with plane of body; paired nodules slightly smaller to subequal in size to single nodule near apex; ridges in 3rd and 5th elytral intervals usually overlapping weakly for most of length; nodule in 3rd elytral interval almost always connected to ridge.; area around elytral suture strongly elevated usually with row of distinct tubercles. Metasternum with uniform moderately sized tubercles; ventrite tuberculation reduced medially, uniformly spaced laterally. Tarsus with ventral setae slightly thickened and spur like, heavier than dorsal setae.

Aedeagus (Fig. 25) elongate, apical margin of basal stop with weak concave depression medially; parameres laterally with short setae along margin of basal stop; apex of parameres curved dorsally.

Female: Similar to male except lacking setose pit on the submentum. Genitalia (Fig. 50).

Larva: Differs from *P. obcordata* having more pronounced asperites on all surfaces with the patch on the ventral surface of A8 much denser (Fig. 33); urogomphus more strongly recurved; lyriform frontal arms more bulbous.

Variation: Probably the most variable of all *Phellopsis* species, this could be attributed to the fact that this species represents the greatest number of available specimens, and/or because it has the largest range. This variation includes the strength of the ridge in the 3rd elytral interval, size and shape of elytral punctures, and density of dorsal vestiture. Specimens from the inland forests east of the Columbia Plateau in Idaho, Montana, eastern Oregon and Washington, and eastern British Columbia and Alberta (including the Casey type of *P. robustula*) have the elytral humerus slightly flattened and sharpened apically, the depression between the 1st and 3rd connecting ridge weaker, the ridge in the 3rd sharpened apically, the pronotal margin more arcuate but not notched, and a generally denser setose vestiture. Specimens from Alaska and western British Columbia occasionally have the pronotal margins weakly bisinuate, a stronger connecting ridge between the 1st and 3rd elytral interval, more distinct elytral punctures, and reduced dorsal tuberculation. The 2 eastern Nevada specimens are typical of specimens found in California populations.

Notes: The confusion regarding the identity of this species is covered under *P. obcordata*. The type specimens and others identified by Casey as *P. robustula* or *P. montana* show typical variation of the species throughout the known range.

Distribution: Restricted to western North America, can be locally common in suitable habitat. This species tracks the forests of the western cordilleras from Alaska as far south as the Transverse Ranges of California and in the east from the western edge of Alberta south through western Montana and Idaho north of the Snake River. An outlying population in Nevada's Ruby Mountains needs more study.

Recorded Distribution: The full data for individual specimens is recorded in Appendix B. A summary of the distribution is presented here as COUNTRY: STATE or PROVINCE: County, Borough, or Census Area (when available).

CANADA: BRITISH COLUMBIA: ALBERTA. UNITED STATES: ALASKA: Haines, Ketchikan, Matanuska, Skagway-Hoonah-Angoon, Wrangell-Petersburg. CALIFORNIA: Alpine, Amador, Butte, Calaveras, Del Norte, Douglas, El Dorado, Glenn, Humboldt, Inyo, Lassen, Mendocino, Modoc, Nevada, Placer, Plumas, San Diego, San Bernadino, Santa Cruz, Shasta, Sierra, Siskiyou, Sonoma, Tehama, Trinity, Tuolumne, Yuba Co. IDAHO: Ada, Boise, Bonner, Boundary, Clearwater, Idaho.

Kootenai, Latah, Shoshone, Valley. MONTANA: Flathead, Glacier, Lake, Lincoln, Missoula, Ravalli. NEVADA: Elko, Washoe. OREGON: Benton, Clackamas, Coos, Deschutes, Douglas, Hood River, Jackson, Jefferson, Josephine, Kane, Klamath, Lane, Lincoln, Linn, Union, Wallowa, Wasco, Yamhill. WASHINGTON: Asotin, Chelan, Clallam, Clark, Cowlitz, Jefferson, King, Kitsap, Mason, Pacific, Pierce, San Juan, Skagit, Snohomish, Thurston, Walla Walla, Whatcom, Yakima.

Phellopsis suberea Lewis

(Fig. 2, 15, 18, 28, 35, 44, 46, 55)

Phellopsis suberea Lewis 1887: 219. Champion 1894: 114. Lewis 1894: 379, pl. xiii, fig. 1. Lewis 1895: 447. Reitter 1916: 131. Geiben 1936: 668. Nakane 1963: 235, pl. 118. Chujo 1985: 344, pl. 58. Masumoto 1990: 87-91. Kim et. al. 1994: 176.

Phellopsis suberosus Fairmaire 1894: C1. (*lapsus calami*)

Phellopsis subaenea Weon et. al. 2000: 119. (*lapsus calami*)

Type Material Examined: *Phellopsis suberea* Lewis. LECTOTYPE here designated, specimen of undetermined sex in BMNH mounted on card. Yuyama written in pencil on backside of card /round red-ringed type label / Phellopsis suberea Lewis Type/ Japan underlined in yellow; G. Lewis 1910-320; Yuyama 10.V.-14.V.81/ white card Lectotype underlined in red; *Phellopsis suberea*; Lewis 1887; designated by M.A. Ivie 2005. PARALECTOTYPES here designated: 8 specimens: 6 in BMNH with same data as lectotype, 1 in BMNH labeled in pencil Sapporo/Japan underlined in yellow; G. Lewis. 1910-320/Sapporo 5.VIII.-16.VIII.1880, 1 in the HNHM, Yuyama; 10.V.-

14.V.81/ Japan underlined in yellow; G. Lewis; 1910-320/ British Museum/ Suberea/ Sammiuna Adr. Schuster/ Rectangle red banded Paratypus label 1887; Phellopsis suberea; Lewis / white card Paralectotype underlined in red; *Phellopsis suberea*; Lewis 1887; designated by M.A. Ivie 2005.

The specimen that probably correlated to that mentioned by Lewis in the original description form "Chiuzenji" was excluded from the type series because the label date did not match the data that was published. Other specimens in the BMNH bearing the Lewis "Yuyama" label were excluded from the type series because they are clearly smaller than the described length, and were pinned unlike the card mounted types or were collected by Lewis from localities not mentioned in the description of the species.

The incorrectly identified syntype mentioned by Lewis (1887) in the original description from Siberia that was later corrected to *P. amurensis* (Lewis 1895), was not present with the rest of the Lewis material in the BMNH. If found, it would qualify for paralectotype status.

Diagnosis: The species is probably the most distinct member of the genus and is easily separated from all other *Phellopsis* species by the large distinct tubercles on the apex of the head limited by a strong transverse depression (Fig. 18), the presence of a narrowed gula (Fig. 35), and emarginate outer margin of the suprantennal ridges (Fig. 18).

Description (male): Length 14.5-22 mm. Elongate species, light to dark brown; dorsal vestiture consisting of golden scale like setae. Dorsal surface of head (Fig. 18) with strong tuberculation between frons; suprantennal frontal ridges with outer margin distinctly emarginate; lateral margin of epistoma anterior to suprantennal ridge short (0.12-0.15mm); ventral surface of head with very large tubercles, lateral profile arced; gula strongly narrowed, narrowest point apical of gular pits; sub-genal ridge produced apically, rounded margin; sub-genal ridge shorter, not extending below eye, eye at same level as gena.

Ligula transverse with smooth apical edge; mandible (Fig. 44) with inner tooth rounded, small tooth apical of prostheca blunt, prostheca setose only on apex not wrapping around mola, molar surface smooth; maxilla (Fig. 46) with galea, palpifer, and basistipes ruggedly sculptured; galea with secondary row of setae; palpifer with setae of several widths, twice as wide as setae on galea and lacinia; two thick setae on basistipes set in deep fossae; cardo with depressed apical margin; lateral profile of galea arced; densely setose.

Pronotum evenly tuberculate, widest apical to midline and strongly angled to narrowed base; paired elevations on apical margin of pronotum narrowly pointed and well divide along midline; lateral margin of pronotum bisinuate; hypomeron with large tubercles, intertuberculate area glabrous. Mesepisternum with irregularly shaped elongate punctures and elevations.

Elytra narrow and elongate, only slightly wider than widest portion of pronotum; scutellum rounded, scutellary striole distinct; elytral humerus sharply produced posteriorly, not rounded or flattened laterally; lateral margins of elytra appearing strongly serrate; elytral punctures variable, typically elongate, but also rounded; 3rd and 4th rows of punctures indistinct from each other at midpoint, staggered and overlapping, not forming distinct rows; ridge in 1st elytral interval slightly elevated around scutellum; ridge in 3rd interval strongly elevated and almost straight in basal 1/3 becoming weak in middle terminating in large tear drop shaped tubercle; ridge in 5th interval indistinct in apical portion originating where ridge in 3rd weakens becoming strong and arcuate outwards, terminating in weak tubercle followed by a gap and then a large tubercle joining 5th and 7th lateral serrate ridge; paired nodules of apical declivity considerably larger than single nodule near apex. Metasternum bituberculate with small and large sized tubercles. Base of pro-tibia strongly narrowed and curved. Ventrites 1-3 obtusely ridged along midline. Tarsus with ventral setae modified as small spurs, distinctly heavier than dorsal setae.

Aedeagus (Fig. 28); apical margin of basal stop with v-shaped depression medially; lateral portion of parameres with elongate depression near base; tip of median lobe laterally flattened.

Female: Similar to male except lacking setose pit on the submentum.

Distribution: JAPAN: SHIKOKU: Ehime. HONSHU: Gumma, Mie, Shizuoka, Tochigi. KYŪSHŪ: Fukuoka, Ōita. HOKKAIDŌ: Sapporo.

Notes: This species has been mistakenly recorded from South Korea (Weon et al. 2000), but these records almost certainly refer to *P. amurensis*. The rather convoluted history of this species is covered in the introduction.

Variation: This species has been recorded from all of the large islands of Japan, and individual populations are presumed to be isolated on these islands, but no observable morphological variation between populations has been noted.

Fig. 2. The distribution of *P. suberea*, green circles, and *P. amurensis*, red circles.

Phellopsis amurensis (Heyden)

(Figs. 2, 14, 20, 41, 56)

Pseudonosoderma amurense Heyden 1885: 306. Semenow 1893: 499. Champion 1894: 114. Fairmaire 1894: C1. Lewis 1895: 447.

Phellopsis amurensis: Reitter 1916: 130. Leng 1920: 223. Geiben 1936: 668. Keleinikova and Mamaev 1971: 124-128. Gaedike 1986: 360. Masumoto 1990: 91. Egorov 1992: 505. Slipinski and Lawrence 1999: 23.

Phellopsis imurai Masumoto 1990: 87. NEW SYNONYMY.

Type Material Examined: *Pseudonosoderma amurense* Heyden. Holotype in DEI not examined.

Phellopsis imurai Masumoto. PARATYPE ♂ in HNHM with median lobe on card, missing both mesotarsi and left meta-leg. Chonwangbong, 950-;1500m, Mt. Chiri-san; Kyongsangnam-do; 7.VI.1989 [KOREA]; Imura & Mizunuma lg/ pink rectangle label Paratype; handwritten *Phellopsis*; *imurai* Masumoto. The holotype is deposited in the National Science Museum, Tokyo and was not examined.

Diagnosis: This species is similar in general elytral structure to *P. obcordata* but has the lateral elytral margins serrate and suprantennal frontal ridges strongly elevated like the other Asian species. It is distinguished from these species by the more stout form, rounded elytral punctures and presence of strongly notched humeri (Fig. 14).

Description (male): Length 14.5-19mm. Dark brown to black; dorsal vestiture consisting of golden hair-like setae. Head with dorsal surface (Fig. 20) with tuberculation between the frons weak; outer margin of suprantennal frontal ridges smooth; post occipital suture narrow and deep; lateral margin of epistoma anterior to suprantennal ridge longer (0.24-0.29mm); ventral surface of head distinct raised tubercles; gula wide, narrowest point at gular pits; sub-genal ridge produced apically, rounded margin; sub-genal ridge shorter, not extending below eye; eye at same level as gena. Ligula subquadrate with slightly emarginate apical edge; mandibular prostheca with brush of setae at apex.

Pronotum evenly tuberculate, apical margins acutely rounded; paired elevations on apical margin of pronotum distinctly separated along midline; lateral margin weakly bisinuate; hypomeron lacking intertuberculate setae.

Lateral profile of elytra flattened medially in dorsal plane; elytral humerus flattened with a distinct notch; lateral margins of elytra serrate; scutellum oval set well below elytral rides; scutellary striole distinct and deep; 10-12 rounded elytral punctures between striole and start of nodule at apical declivity; 3rd and 4th rows of punctures forming distinct rows at midpoint; ridge in 5th elytral interval starting at mid-point of meta-sternum and extending to the apical margin of ventrite 3, distinct gap between ridge and nodule of declivity; nodule in 3rd elytral interval connected to ridge; median subapical nodule larger than lateral one; nodule at apex of elytron smaller than median subapical nodule; paired subapical nodules of declivity overlapping for a significant width in the same lateral plane, almost entire width. Mesepisternum with regular small punctures (Fig. 41); metasternum bituberculate. Ventrites 1-3 flat, with numerous uniformly distributed small tubercles. Tarsus with ventral setae modified as spurs, distinctly heavier than dorsal setae.

Aedeagus with basal stop of parameres only moderately enlarged, shorter in length; apical margin of stop smooth.

Distribution: RUSSIA: Coastal mountains from Amur River valley to Khrebet Sikhote Alin Mountains north of Vladivostok, SOUTH KOREA: Chonwangbong.

Variation: Little morphological variation is seen in specimens throughout the species range.

Notes: While correctly identifying the generic synonymy of *Pseudonosoderma*, Champion (1894) incorrectly synonymized *P. suberea* with *P. amurensis.* Lewis (1895) corrected a previous misidentification of *P. amurensis* as a syntype of *P. suberea* and recognized both species as distinct returning all of the available Asian names to valid status within *Phellopsis.*

Masumoto (1990) commented that *P. imurai* was a relative of *P. amurensis*, but compared it to *P. suberea,* from which it clearly differs. A paratype of *P. imurai* is the only Korean specimen examined, and is lighter in color than many typical specimens of *P. amurensis*, but morphologically does not differ from Russian specimens.

While only reported from the Sikhote-Alin Mountain Range of the Primorski Krai, Amur River valley and mountainous regions of South Korea, I expect that *P. amurensis* occurs in suitable habitat areas all along the western slope of the Sea of Japan. This includes North Korea, and possibly far-eastern areas of the Jilin and/or Heilongjiang provinces of China in the Changbai Shan Mountains where deforestation may be less than total. Specimens from Korea (identified as *P. suberea* almost certainly incorrectly) have been reported from Cheongrangli, Hongcheon, Kangwon, Kwangheung, Kyeongki, and Seoul (Weon et al. 2000).

Phellopsis chinensis Semenow

(Fig. 3, 16, 21, 27, 30, 36, 38, 39, 47, 53)

Pseudonosoderma chinense Semenow 1893: 499.

Phellopsis chinensis: Champion 1894: 114. Reitter 1916: 131. Geiben 1936: 668. Masumoto 1990: 87-91.

Type Material Examined: *Pseudonosoderma chinense* Semenow HOLOTYPE ♂

in ZIN missing left protarsus. Hand written on card [in Russian] pass near village Morpin to south; 4.VII85/ folded piece of paper 2-4.811.85.; [in Russian] top of a pass from village of Morpin to the south/ handwritten on graph paper *Pseudonosoderma chinense*; m; typum, unknown character–II-92/ gold hexagon dot/ red rectangle label “Holotypus”/ yellow rectangle Zoological Institute; Russian Academy; of Sciences,; St. Petersburg, RUSSIA.

Material Examined: CHINA: GANSU: Min Shan Mts.,h-2700; 70km W. from Wudu; 15.06.2005.; Leg. A. Gorodinski (4 MAIC). Min Shan Range; 70km N.W. Wudu; 1 vi 1997; 2100m; Leg: A. Gorodinski (2 AAPC). Hin Shan Range; 2100m 70km N.W.; Hodo I-VI-97; Leg.A.Gorodinski (1 AAPC). Min Shan Mts.; 76km N.W. Wudu; 25 vii 2000; Leg: A. Gorodinski (1 AAPC). SICHUAN: Near Pingwu; 1.07.2005.; Leg. A. Gorodinski (3 MAIC). SHAANXI: 100km.S.W. of Xian; Taibai Shan Mt.; Near Houzhezi village; 30.07.2005.; Leg. A. Gorodinski (1 MAIC).

Diagnosis: This species can be distinguished from all other species of *Phellopsis* by the absence of the basal stop on the parameres of the male (Fig. 27). It can be differentiated externally from *P. amurensis* by the rounded to flat elytral humeri (Fig. 16), elongate and irregular elytral punctures, rugged nature of the elytral ridges (Fig. 53), and smooth ventral surface of the head (Fig. 36), and from *P. yulongensis* by the very large tubercles on the ventral surface (Fig. 30) and overall golden scale like vestiture (Fig. 39).

Description (male): Length 12.5-21mm. Robust species; dorsal setose vestiture golden consisting of dense flattened broad scale like setae (Fig. 39); dorsal elytral sculpture very rugged and squarrose.

Head with dorsal surface (Fig. 21) with tuberculation almost completely reduced; lateral margin of epistoma anterior to suprantennal ridge long (0.32-0.35mm); tubercles on ventral surface of head large and flattened creating a relatively smooth surface; gular sutures weakly defined; gula wide, narrowest point near gular pits; sub-genal ridge produced apically, rounded margin; sub-genal ridge shorter, not extending below eye; eye at same level as gena. Ligula subquadrate with slightly emarginate apical edge.

Pronotal disc between and anterior to lyriform ridges lacking distinct tubercles; paired elevations on apical margin of pronotum distinctly separated along midline; lateral margin of pronotum bisinuate, thickened; hypomeron with very large tubercles, dense intertuberculate setae present; prosternal process slightly bi-impressed. Metasternum bi-tuberculate with very large and very small tubercles (Fig. 47)

Lateral profile of elytra rounded in dorsal plane; elytral humerus broadly rounded; scutellum rounded; scutellary striole distinct and deep; lateral margin strongly serrate; ridge in 5th elytral interval starting at or just before meta-coxae and extending to mid point of ventrite 3; nodule at apex of elytron slightly smaller to subequal in size to lateral subapical nodule; medial subapical nodule larger than lateral and apical; paired subapical nodules overlapping for a modest width in the same lateral plane, slightly offset. Tubercles on ventrites large and flattened (Fig. 30). Tarsus with ventral setae modified as small spurs, distinctly heavier than dorsal setae (Fig. 38).

Aedeagus (Fig. 27); ventral surface of parameres broadly arcuate in lateral view, lacking basal stop.

Female: Similar to male but lacking setose pit on submentum

Distribution: CHINA: GANSU, SICHUAN, and SHAANXI.

Notes: The specimen identified as *P. chinensis* (HNHM), and assumedly examined by Masumoto (1990), does not accurately represent the holotype of *P. chinensis* Semenow (ZIN). That specimen is here designated a paratype of *P. yulongensis* NEW SPECIES. The misidentification *P. chinensis*, addition of *P. yulongensis,* and inclusion of *P. imurai* (here synonymized with *P. amurensis*) renders the key to Asian species (Masumoto 1990) outdated.

Variation: Two specimens from Gansu (1 ♂, 1 ♀) have the dorsal elytral sculpture reduced in intensity, and the lateral aspect of the elytra slightly flattened

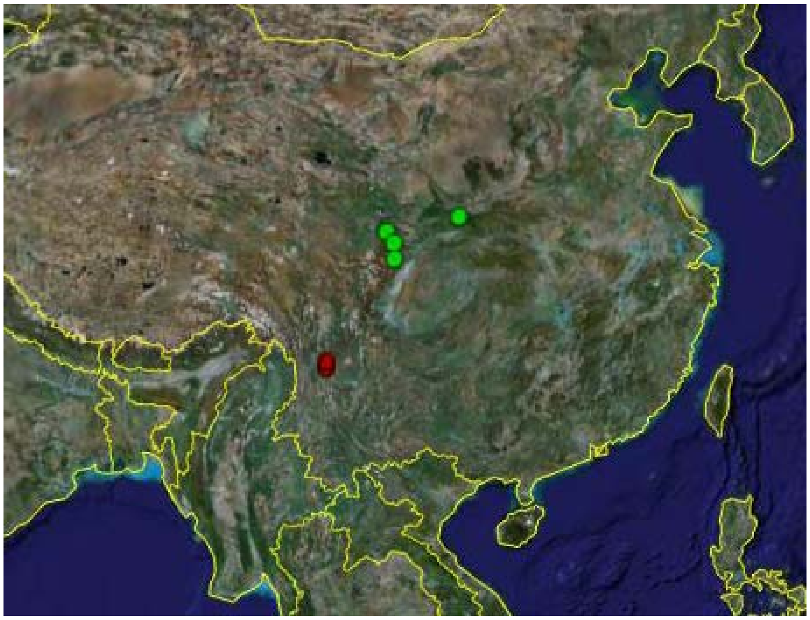

Fig. 3. The distribution of the species of Phellopsis found in China, *P. chinensis* green circles and *P. yulongensis* red circles.

Phellopsis yulongensis Foley and Ivie NEW SPECIES

(Fig. 3, 17, 19, 26, 29, 31, 34, 40, 42, 43, 45, 49, 52, 54)

Type Material: HOLOTYPE: CHINA: YUNNAN, 50km N. Lijiang, Yulongshan Nat. Res., 24-29-VI-1993, E. Jendek & O. Sausa leg. (MAIC). PARATYPES; CHINA: YUNNAN, 50km N. Lijiang, Yulongshan Nat. Res., 24-29-VI-1993, E. Jendek & O. Sausa leg. (4 MAIC). CHINA: YUNNAN, Heishui, 35km N Lijiang, 27°13’N 100°19’E, 1-19-VII-1992, E. Jendek leg. (2 MAIC --1 disarticulated). CHINA: YUNNAN, Heishui, 35km N Lijiang, 27°13’N 100°19’E, 1-19-VII-1992, S. Becvar lgt. (1 HNHM).

Etymology: This species is named for the type locality, the Yulongshan Nature Reserve, in acknowledgement of the role that the conservation of old growth habitat areas will play in the preservation of so many rare animals in all regions of the world, especially developing nations.

Diagnosis: This species can be distinguished from *P. amurensis* by having reduced tuberculation on the ventral surface of the head (Fig. 34), the humeri flattened not notched, and the elytral punctures elongate rather than rounded. It is distinguished from *P. chinensis* by having a more uniformly tuberculate pronotal disc, reduced sculptural intensity (Fig. 17), smaller and more frequent tubercles on the ventrites (Fig. 31), the vestiture reddish and composed of thin setae (Fig. 40), and the presence of a distinct stop at the base of the male parameres (Fig. 26, 29).

Description (male): 14-19mm long. Reddish to black; dorsal vestiture consisting of thin reddish thread like setae, red especially on vertex of head and pronotum (Fig. 40);

elytral sculpture consisting of sinuate ridges and distinct nodules.

Head with dorsal surface with tuberculation almost completely reduced (Fig. 19); lateral margin of epistoma anterior to suprantennal ridge long (0.34-0.37mm); antennomeres 9 and 10 with elongate sensilla patch extending partially around base of previous segment; antennomere 11 conical at apex (Fig. 49); tubercles on ventral surface of head large and flattened creating a relatively smooth surface; gular sutures weakly defined; gula wide, narrowest point at gular pits; sub-genal ridge produced apically, rounded margin; sub-genal ridge shorter, not extending below eye; eye at same level as gena.

Mandible (Fig. 43) with molar surface smooth without distinct ridges, membranous prostheca with short dense fringe of setae; maxilla (Fig. 45); lacinia with two small hooks laterally in the same plane, surrounded by a whorl of setae restricted to the margin creating hollow space in lateral width; palpifer with four thick setae, twice as wide as setae on galea and lacinia; basistipes with two thinner setae set in small fossae. Post occipital suture shallow and broad.

Pronotum with tuberculation uniformly distributed and similar in size; pronotal disc between and anterior to lyriform ridges with distinct tubercles; paired elevations on apical margin of pronotum broad and weakly divide by midline, nearly fused; lateral margin of pronotum arcuate to weakly bisinuate, weakly explanate; hypomeron with moderate sized tubercles, lacking intertuberculate setae; prosternal process bisinuate. Lateral profile of elytra flattened medially in dorsal plane; lateral margin weakly serrate; humerus flattened; scutellum oval, scutellary striole shallow; ridge in 5th elytral interval starting approximately at mid point of meta-sternum and extending to the mid-point of ventrite 3; paired nodules of declivity not overlapping for a considerable width in the same lateral plane, strongly offset; medial subapical nodule larger than lateral or apical; nodule at apex sub-equal in size to lateral subapical nodule. Metasternum bi-tuberculate, with moderate and small sized tubercles.

Tubercles on ventrites average sized and rounded (Fig. 31); laterotergite 3 not greatly expanded, in dorsal view with elytron removed; intercoxal process of V1 broad, flattened at the apex, strongly elevated. Tarsus with ventral setae slightly thickened, not distinctly spur like, heavier than dorsal setae.

Aedeagus (Figs. 26, 29); basal stop of parameres with well developed fringe of setae; apical margin concave medially.

Female: Similar to male but lacking setose pit on submentum.

Distribution: CHINA: YUNNAN.

Variation: The type series is morphologically very consistent.

Notes: The two species found to occur in China are narrowly divided by the boundary between the Southwest China and Central China zoogeographic regions (Jach and Ji 1995). The area of Southwest China where *P. yulongensis* is found has been considered one of the most diverse temperate regions in the world (UNESCO 2005).

Synoptic Catolog of the *Phellopsis* Species

Phellopsis LeConte 1862

Pseudonosoderma Heyden 1885

P. obcordata (Kirby) 1837

P. porcata (LeConte) 1853, RETURN TO VALID STATUS

- *P. robustula* Casey 1907, NEW SYNONYMY
- *P. montana* Casey 1907, NEW SYNONYMY

P. amurensis (Heyden) 1885

- *P. imurai* Masumoto 1990, NEW SYNONYMY

P. suberea Lewis 1887

P. chinensis (Semenow) 1893

P. yulongensis Foley and Ivie, NEW SPECIES

Results -- Phylogenetic Analysis

The present analysis was conducted primarily for insight into the species-area and biogeographic relationships shown by the disjunct distribution of this genus. A single most parsimonious tree (MPT, Fig. 62) was found using heuristic methods in NONA 2.0. The most parsimonious tree required 23 steps, had a Consistency Index (CI) of .86 and Retention Index (RI) of .87. Bootstrap support values are shown for all well (>50) supported nodes.

This cladogram provides strong support for a monophyletic Phellopsini based on the synapomorphies of the tuberculate subgenal sculpture 1; (1, 2), ventrites 3 and 4 laterally expanded 2; (1), and tuberculate ventrites 5; (1).

The only poorly supported internal node is that between the two North American species. A sister-species relationship is weakly supported in the analysis because there are no known apomorphies that hold these species together. The uniting characters (0 (0) smooth lateral margin of the elytra, 4 (0) long sub-genal ridge, 13 (0) tarsomere with simple setation, and 6 (1) short lateral margin of epistoma) are plesiomorphies shared with one or more of the outgroups. However, both species posses all of the defining synapomorphies of the genus and a unique combination of these characters with the above mentioned plesiomorphies weakly support the sister-species relationship of the North American species.

Strong support is given for an Asian group derived from the North American lineage. The Asian species are a well supported monophyletic group based on the synapomorphies of the serrate elytra margin 0; (1), short subgenal ridge 4; (1), extended lateral epistomal margin 6; (2), (secondarily modified as an autapomorphy in *P. suberea* 6; (3)) and thickened or spur like tarsal setation 13; (1). The mainland Asian group (*P. amurensis* + the Chinese species) is not supported as a monophyletic group. Likewise, the data also does not support a sister group relationship between the two species across the Sea of Japan, even though these two species are geographically close. These data support *P. amurensis* as basal to the remaining lineage *P. suberea* + Chinese species, with this group defined by the irregular and elongate elytral punctures 3; (1). The species from Japan is the most divergent of all the *Phellopsis* species and is defined by several autapomorphies including the large tubercles on the dorsal surface of the head 8; (2).

The Chinese species are shown to be sister-species based on the subgenal sculpture of large flattened tubercles 1; (2). Reversals occur in the Chinese species for character 7 (complete groove on the ventral surface of the prefemora) and in *P. chinensis* for character 12 (male parameres lacking basal stop).

A homoplasy occurs in character 9 (hypomeron with dense intertuberculate setae, state 1), with the setae occurring only in *P. porcata* and *P. chinensis*.

Biogeography

The genus *Phellopsis* shows a disjunct distribution pattern across the northern Pacific Ocean. This Nearctic-Eastern Palearctic distribution pattern has been found in a variety of organisms (Sanmartin et. al. 2001, Xiang et. al. 1998, Enghoff 1995, Enghoff 1993, Campbell 1993, etc.) and was identified as a possible result of the vicariance of a pan-Holartcic ancestor (Enghoff 1993) with subsequent extinctions in adjacent areas (Sanmartin et. al. 2001) such as Eurasia and the North American Great Plains (Marek and Kavanaugh 2005). During the last glacial maximum members of the genus *Phellopsis* were probably restricted to refugial areas of suitable mesic forest habitat, and individuals have subsequently weakly dispersed into the current limited species ranges. Or, they dispersed north and uphill with the glaciers' retreat, remaining in refugial mountains in the south, but becoming more continuous in northern boreal forests as those forests expanded. There is evidence for glacial refugia in or adjacent to all known species ranges, such as the Southern Appalachians in North America (Campbell 1980), and areas of the Pacific Coast of North America (Howden 1970, Lavoie 2001, Kavanaugh 1988, Marek and Kavanaugh 2005), the southern Russian Primorye region (Serizawa 2002), Western

Yunnan (Ren E.M. et al 1957) and coastal areas of Japan (Tsukada 1985, Ono 1991, Shoda et al. 2003).

Fauna and flora diversity is variable between the different Holarctic infraregions, with the Eastern Palearctic usually the richest, and the Western Palearctic the most depauperate (Sanmartin et. al. 2001). *Phellopsis* fits this pattern well with four species present in the Eastern Palearctic and none documented from the Western Palearctic. This difference in diversity has been explained by two hypotheses. The refugium argument suggests the climactic effects of the Pleistocene glaciations were less in Asia, and the extent of land recently covered by ice was considerably smaller, leaving areas of suitable mesic forest habitat (Sanmartin et al. 2001). The other argument is the diversification hypothesis that contends the Eastern Palearctic was already more diverse in the Tertiary, and more of this diversity survived the Quaternary climactic hardships (Sanmartin et al. 2001). The absence of the genus in the Western Palearctic can possibly be explained by extinction during the Pleistocene glaciations due to climatic changes (Sanmartin et. al. 2001). It has also been suggested that increased diversification in Asia is more important than extinction in Europe, and that this explains the difference in diversity between the regions (Latham & Ricklefs 1993). Eastern Asia has been suggested as the center of origin of boreotropical floral and faunal elements because of its high present-day diversity (Sanmartin et. al. 2001). This diversification is hypothesized to be driven by topological diversity which provided a rich variety of habitats and climates (Sanmartin et. al. 2001) and presumably accelerated speciation rates compared to the other Holarctic infraregions. This is a possible explanation of the species diversity of the genus

Phellopsis and other groups of insects in Asia (Qian & Ricklefs 2000, Nordlander et. al. 1996, Enghoff 1993).

Phellopsis is its present on islands off both the Atlantic and Pacific coasts of North America and the Pacific coast of Asia. The presence of large flightless beetles on islands has previously been explained by the theory of dispersal over large emergent coastal areas during times of lowered sea level (Howden 1970). However, these emergent areas which could have been part of the mainland during the Pleistocene could have served as glacial refugia (Kavanaugh 1988). In places such as Alaska and Northern British Colombia where the genus reaches its northern limits but is only reported from islands and coastal areas, these populations may represent vicariant remnants from the Pliestocene. Another possibility that has been proposed in other flightless tenebrionoid beetles (Peck 1994, Finston and Peck 1995, Finston, Peck and Perry 1997) is dispersal by oceanic drift on pleuston or floating debris, which could explain the presence of *Phellopsis* on coastal islands. The large size of these beetles make it an unlikely candidate to travel any significant distance through aerial pleustonic methods, but individuals could float on woody debris. Ulke (1902) supports the possibility of the genus traveling considerable distances floating on woody debris with this note: "The Potomac River every spring carries down quantities of flood debris from the mountain districts, containing insects which properly belong to higher elevations, for example, *Phellopsis obcordata*".

All speciation events in the genus appear to be the result of broad allopatric isolation, either on large islands (Japan), or by broad areas that were once or still are unsuitable habitat. In North America it seems that the boreal forest areas of Northern Canada would be suitable habitat for the genus, but specimens have not been reported east of Alberta, or west of Ontario. The absence of the genus in the north-central boreal forests could be the result of the previous isolation of the group to glacial refugia (Marek and Kavanaugh 2005). This isolation would have been followed by the inability of the species to recolonize suitable habitat based on its limited dispersal abilities. There may be a temperature limit on *Phellopsis* or its hosts that has restricted rebound into this area from the more temperate coastal areas, or there may simply not yet have been enough time for propigules to extend the range that far.

Habitat Conservation

The fact that this genus appears to require suitable old growth habitat could be a reason why the North American species were collected more commonly in the past (Post-1940). Recent collections frequently occur in protected "natural areas" of preserved old growth habitat in places such as Glacier and Great Smoky Mountain National Parks, and other protected U.S. Forest Service lands. The fragmentation of old growth boreal forests and limited dispersal abilities of the genus suggest that current populations are highly isolated and gene flow between them is perhaps non-existent. I would not expect flightless beetles to be capable of moving between fragmented areas like other more mobile animals.

Species of *Phellopsis* have drawn some interest as biological indicators of old growth forest habitat (Steiner 1992, USGS 2003). In Western North America, *P. porcata* was considered for indicator status of old growth habitat in Oregon but was ultimately rejected as a useful species because it could not be adequately collected (USGS 2003).

On the Asian continent species of *Phellopsis* have been collected in or near the protected habitat of large mammalian flagship conservation species including the Giant Panda (*Ailuropoda melanoleuca*) and the Amur or Siberian Tiger (*Panthera tigrus altaica*). The shared habitat of beetles requiring old growth habitat and large vertebrates that receive considerable international conservation support probably means that the habitats of this genus of beetles will be preserved as long as broader conservation efforts continue. The Amur Tiger range is mostly in the Russian Primorski Krai, and there are probably at most a handful of Amur Tigers inhabiting adjacent regions of northeast China (Lu Binxin 1993). These areas of possible tiger habitat directly coincide with a large area of the expected distribution of *P. amurensis*.

In South-Central China the two species of *Phellopsis* that occur along the edge of the Tibetan Plateau occur in areas protected in various nature reserves designated to protect Giant Panda habitat (Mittermeier et. al. 1999). Logging and encroachment of small-scale agriculture in a country where almost all available land is influenced by a dense human population are the major threats to suitable habitat for this sensitive species (Schaller 2005). The Yunnan province of China where *Phellopsis yulongensis* occurs had an estimated 23% forest covered area in 1996 (MacKinnon et. al. 1996) compared to 5.1-12% in the surrounding provinces. Several nature preserves have been established in Yunnan in recent years (MacKinnon et. al. 1996). This includes the United Nations Educational, Scientific and Cultural Organization (UNESCO) natural heritage site the

Three Parallel Rivers of Yunnan site (2003) which covers approximately 1.7 million hectares (UNESCO World Heritage Centre 2006).

The wide range persistence of the genus *Phellopsis* will require broad conservation efforts directed at the limited remaining suitable old growth habitat. There will be no reintroductions or captive breeding programs to increase population levels of an animal that few people ever see or notice alive. The persistence of relatively natural boreal and temperate forest ecosystems will be vital to the continued survival of this genus.

Future Research

Phellopsis is a group that is widely distributed geographically and theoretically old, but exhibits very little interspecific morphological diversity. This genus as a whole is an excellent candidate for future molecular studies if sufficient material from Asia can be obtained for data collection. If molecular data were available for all known species, it would significantly increase the available number of informative characters for the phylogenetic analysis and increase support for a hypothesis about the biogeographic and evolutionary history of the genus. At present only North American material is available in sufficient quantity and condition to be useful for molecular analysis.

In the western North American molecular data could be used to examine the population structure of *P. porcata* and recognize potential cryptic species in isolated populations. The Ruby and inland Rocky Mountain populations warrant future genetic study, to determine whether they are distinct at the species level. Comparison to other populations could also provide evidence about the biogeographic history, i.e. whether they are remnants of a widespread ancestor or recent introductions. The potential exists for other outlying populations of *P. porcata* to occur in the Black Hills of South Dakota as well as other Great Basin ranges. Population comparisons could also determine whether the genetic structure throughout the range follows a south to north diversity decline (as has been seen in other animals and plants, Kuchta and Tan 2005, Soltis et al. 1997) and hypothesize the age of Alaskan populations. The results of this analysis could also offer insight into the origins of *P. porcata*. If a south to north diversity decline is seen that would suggest a northward recolonization by a widespread ancestor. On the other hand, if Alaskan populations were found to be older that would suggest a colonization event from Asia across a Beringian land bridge and persistence in Pleistocene refugia along the coast.

The discovery of unknown populations in Asia in places such as the Kuril Islands and Kamchatka would require extensive specifically directed collecting effort because the genus is rarely collected in traps, with the vast majority of specimens being collected by hand. The possibility for the discovery of new species exists in the diverse temperate regions of Asia, but this also would require extensive collecting, and often an effort directed specifically at the under bark/shelf fungus micro-habitat occupied by these beetles.

CHAPTER 3

REVIEW OF THE ZOPHERINI

Introduction

In the process of revising the genus *Phloeodes* LeConte, and examining most members of the allied genera in the Zopherini, it became obvious that several member species were incorrectly placed. The generic definitions provided by Ślipiński and Lawrence (1999) are accurate based on the type species of each genus, and those definitions are not significantly modified here. The problems within the tribe arise in the placement of individual species. The historical lack of useful characters (LeConte 1862, Casey 1907b, Gebien 1936) to identify the genera of zopherines with 10-segmented antennae was a significant obstacle to placing individual Central American species in one of the two genera recognized by Ślipiński and Lawrence (1999), *Phloeodes* and *Nosoderma* Solier. This difficulty required a review of all known species of Zopherini in order to revise the genus *Phloeodes*. Therefore, all recognizable species of the Zopherini (excluding the revised and well-defined genus *Zopherus* Gray) were examined and a phylogenetic analysis was performed based on morphological characters of these species. This resulted in a reclassification of the genera, including the re-recognition of *Sesaspis* Casey. A key to the genera of Zopherini, keys to the species of *Nosoderma* Solier, *Sesaspis* Casey, *Meralius* Casey, *Noserinus* Casey and *Phloeodes* LeConte (in the following chapter) are provided, along with illustrations of most species, and the description of four new species.

Zopherini Solier

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. 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 exists in the definition and placement of individual species.

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

Taxonomic History of the Zopherini

The tribe Zopherini was originally proposed by Solier (1834) as Zophérites, for the New World genus *Zopherus*. Solier (1841) expanded this definition to include his New World (Mesoamerica and Cuba) genus *Nosoderma* and several new species. These two genera contain the majority of the species and represent the core of the current Zopherini.

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*, 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 echinatus* Guérin-Méneville 1838, later the type-species of *Meralius* Casey. The close relationship between *Scoriaderma* and *Meralius* has been confirmed (Ślipiński and Lawrence 1999, and here).

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 7 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 next the rest of the large ironclads with 10-segmented antennae (*Meralius*, *Noserus*, *Noserinus*, *Noserodes* Casey, *Nosoderma*, *Phloeodes*, *Sesaspis* Casey, and *Verodes* Casey) plus *Phellopsi*s, and the last for 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). Only two of the genera described by Casey, *Meralius* and *Noserinus*, are currently considered valid (Ślipiński & Lawrence 1999), although the current research supports the recognition of the genus *Sesaspis* Casey. Casey created 21 specific synonyms and 1 subspecies in *Zopherus* (Triplehorn 1972), 10 in *Phloeodes* (discussed in the following chapter), 7 in *Nosoderma* (listed below), 1 in *Noserinus* (Doyen and Lawrence 1979), and 2 in *Phellopsis* (discussed in the previous chapter). All in all, Casey described 42 species of zopherids and only one, *Zopherus uteanus* (Casey 1907a), appears to be a truly valid species (Triplehorn 1972). 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 which was later returned to the Tenebrionidae (Doyen and Lawrence 1979). Ślipiński and Lawrence (1999) made additional changes to the Zopherini by synonymizing *Noserus* LeConte with *Phloeodes* LeConte (discussed in following chapter) and describing the genus *Zopher* from Southeast Asia.

Materials

The current study was based on the examination of almost all definable species belonging to the tribe Zopherini (excluding a few species of *Zopherus*). The material for this investigation was obtained on loan from most of the North American entomological collections, as well as many collections in Europe, and a few Central American collections. The availability of adult specimens was sufficient to complete a thorough examination of morphology and delimit each species and genus, as well as generate a character matrix for phylogenetic analysis. At least representative type material was examined in all genera except *Zopherus* and *Zopherosis*, and these genera were adequately represented by specimens from the type localities or by species that are easily identifiable. Specimens were obtained from the institutions and collections listed in the following chapter (pgs. 135-138).

Methods -- Morphology

This review was based on morphological characters of adult specimens following the operational species concept of Whitehead (1972). This concept hypothesizes that unique morphological characters have a genetic basis. These unique characters can be inherited, and therefore used to delimit species and genera.

Frequently specimens of the tribe are encrusted with a greasy exudate as well as accumulated environment 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 on 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 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 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 a single inserted setae, I 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).

Methods -- Phylogenetic Analysis

A cladistic analysis was conducted based on morphological characters and was used to determine individual species placement and hypothesize evolutionary relationships between the genera. This analysis was based on 27 species of Zopherini representing all known genera, and all definable species possessing 10-segmented antennae. This extensive within genus sampling included all known species of *Meralius*, *Noserinus*, *Nosoderma*, *Phloeodes*, *Scoriaderma*, *Zopher*, and *Zopherosis*.

Parsimony analysis was conducted using the software programs WINCLADA version 1.00.08 (Nixon 2002) and NONA 2.0 (Goloboff 1999). All characters were treated as unordered throughout using non-additive Fitch parsimony (Wiley 1981, Wiley et al. 1991, Lipscomb 1998, Maddison and Maddison 2000) and were equally weighted. Missing characters were coded as question marks (?). All searches relied on heuristic parsimony approaches of NONA 2.0 (Goloboff 1999) run with WINCLADA version

1.00.08 (Nixon 2002) as a shell program to find the most parsimonious trees.

Table. 3. Locality data for species used in phylogenetic analysis.

Species	**Locality**	**Collection**
Zopherus n. haldemani	USA: Texas, Burleson Co.	UCRC
Phloeodes diabolicus	USA: California, Orange Co.	CAS
Phloeodes plicatus	USA: California, Los Angeles Co.	LACM
Zopherosis georgei	AUSTRALIA: Victoria	MAIC
Noserus emarginatus	USA: Texas, Bexar Co.	TXAM
Nosoderma denticulata	MEXICO: Nuevo Leon	MAIC
Sesaspis n. sp. 1	MEXICO: Tampaulipas	TXAM
Nosooderma venusta	COSTA RICA: Guanac. Prov.	INBC
Noserus doyeni	MEXICO: Nuevo Leon	MAIC
Noserus n. sp. nr. doyeni	MEXICO: Hidalgo	SEMC
Nosoderma inaquale	MEXICO: Puebla	UCMC
Nosoderma insigne	MEXICO: Oaxaca	UCMC
Nosoderma scabrosum	MEXICO	MNHN
Nosoderma exsculptum	MEXICO: Oaxaca	HNHM
Sesapis n. sp. 2	BELIZE: Toledo dist.	USNM
Nosoderma lutosus	MEXICO: Oaxaca	MAIC
Nosoderma zunilensis	HONDURAS: Olancho	CMN
Nosoderma guatemalensis	MEXICO: Chiapas	CMN
Nosoderma sparsus	GUATEMALA: Quezalten	CMN
Nosoderma aequalis	MEXICO: Oaxaca	MAIC
Noserinus dormeanus	ARGENTINA: Iguazu	AAPC
Meralius echinatus	CUBA	MAIC
Meralius n. sp. 1	VENEZUELA: N. Grenada	NHMB
Meralius furcatus	VENEZUELA: Merida	MAIC
Scoriaderma sp. 1	KENYA: Kwale Dist.	MAIC
Scoriaderma sp. 2	COMOROS	NHMB
Zopher ivie	MALAYSIA: Cameron Highlands	MAIC
Phellopsis porcata	USA: California, Nevada Co.	UCDC

The commands ‘hold 1000’, ‘500 mult*N’, ‘10 hold/’ were used for the unconstrained multiple TBR + TBR ‘mult*ma*’ search strategy (TBR is the tree bisection-reconnection method of branch-swapping). Bootstrap support was estimated for nodes with the ‘bootstrap’ option in NONA based on 1000 replicates. Characters were traced on the most parsimonious tree using WINCLADA. The relationships between taxa are hypothesized on the assumption of synapomorphies and parsimony.

The cladistic principles delineated by Wiley (1981), Wiley et al. (1991), Lipscomb (1998), and Maddison and Maddison (2000), were used to infer relationships based on the results of the analysis.

Two separate analyses were conducted, differing in the designated outgroup. The species *Phellopsis porcata* (LeConte) was used as the designated outgroup in the first analysis because it has been historically placed with the larger zopherines. In the results of the phylogenetic analysis of Ślipiński and Lawrence (1999), *Phellopsis* is part of the linage that is sister to the Zopherini + Pycnomerini. In the second analysis, *Zopherus nodulosus haldemani* Horn was used as the designated outgroup. This genus, along with *Zopherosis*, is the reported sister-clade to the rest of the Zopherini (Ślipiński and Lawrence 1999).

The 32 characters used in the analysis include a mixture of those used by Ślipiński and Lawrence (1999) and newly employed ones.

Characters, states and definitions are as follows: (Character numbering started with "0", because this is the data entry format used by WINCLADA).

0. Number of antennomeres: (0) 11; (1) 10; (2) 9.

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 (Fig. 102) or broad depression that clearly can receive the antennae (Fig. 67-69, 118) is present.

2. Nodule on male femora: (0) absent on all femora; (1) present on at least two pairs of femora. This secondary sexual character (Figs. 79, 80) 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 *Nosoderma*, and some *Sesaspis* but is absent on some or all femora in *Meralius*, some *Sesaspis*, and rarely *Nosoderma*. This character is totally absent in members of *Scoriaderma*, *Zopherus*, and *Zopherosis*.

3. Transverse groove on prosternum: (0) absent; (1) present (Fig. 123). 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. 78); (1) overlapping cuticle (Fig. 130); (2) with empodium (Fig. 129). In *Zopherus* the cuticle overlaps between the tarsal claws enclosing 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. 129) and/or setose empodium that may have a few or a tuft of setae (2). The plesiomorphic condition (0) of simple exposed insertions between the claws is present in most members of the Zopherini (Fig. 78)
6. Epipleuron: (0) tuberculate/smooth; (1) with distinct ridge (Fig. 128).
7. Labial palp insertions: (0) dorsal/lateral (Fig. 76, 77, 119-121); (1) ventral (Fig. 122).
8. Labial palp insertions: (0) exposed; (1) concealed by mentum (Fig. 119).
9. Scutellum: (0) present; (1) absent.

10. Eye: (0) wide, greater than 10 facets at narrowest point; (1) narrow, less than 10 facets at narrowest point.
11. Antennal-club number of apparent segments enlarged: (0) 3 segments (Fig 113); (1) 2 segments (Fig. 115); (2) 1 segment (Fig. 114).
12. Penultimate antennomere with sensillae: (0) on both sides; (1) protruding on lateral sided (Fig. 115); (2) absent. All of the species of Zopherini with 10-segmented antennae have a protruding area that is variably covered in sensilla.
13. Apical antennomere with micro-setose field: (0) covering most of apex (Fig. 126); (1) depressed and emarginate (Fig. 127).
14. Mandibular membraneous prostheca: (0) present (Fig. 101); (1) absent (Figs. 99, 100)
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. 121). 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. 103); (1) strong (Fig. 102).
19. Secondary setose vestiture on pronotum: (0) present; (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 basal 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; (1) broad depression (Fig. 118); (2) complete cavity (Figs. 67, 69); (3) incomplete (Fig. 68); (4) arcuate depression (Fig. 102); (5) with thumb like projection where prosternal suture meets margin (Figs. 103).

22. Ventral surface with: (0) tubercles with single setae (Fig. 124); (1) setose punctures (Fig. 125); (2) only setae.

23. Ligula: (0) with margin evenly setose; (1) with tuft of setae inserted in fossae (Fig. 77).

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 groove; (2) single narrow groove along nearly entire margin.

26. Tarsal strip: (0) absent; (1) weak, usually tufts of golden setae; (2) well developed, (Fig. 71).

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) uniform setose; (1) bi-setose (Fig. 116); (2) glabrous with strip. A bi-setose vestiture consists of setae of two distinctly different lengths.

30. Submentum: (0) with setose pit; (1) without setose pit. The plesiomorphic condition (0) is found in all other tribes of Zopherinae, but its loss in the Zopherini is considered a synapomorphy.

31. Apical and pre-apical antennomeres: (0) distinct and free (Fig. 113); (1) partly or entirely fused together (Figs. 114, 115).

Results -- Phylogenetic Analysis

In the analysis with *Phellopsis porcata* as the outgroup, 4 most parsimonious trees (Length=81, Consistency Index=.56, Retention Index=.80) were found using heuristic search methods in NONA 2.0. Based on these cladograms a strict consensus tree was found using WINCLADA (Fig. 131, L=83, CI=.55, RI=.78). The strict consensus option retains only those monophyletic groups occurring in all input trees (Schuh 2000).

With *Zopherus* as the designated outgroup, 20 most parsimonious tress (L=70, CI=.61, RI=.83) were found using the same heuristic search methods in NONA 2.0. Based on these cladograms a strict consensus tree was found using WINCLADA (Fig. 132, L=78, CI=.58, RI=.81).

Both consensus cladograms support the recognition of 9 genera of Zopherini (Table 4, Fig. 131, 132). The analysis with *Phellopsis* as the outgroup (Fig. 131) is preferred over the analysis with *Zopherus* as the outgroup (Fig. 132) to look at relationships within the Zopherini because the polarization of certain characters (number of antennomeres, presence of complete antennal cavity, etc.) is unclear within *Zopherus*. The characters 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 clade *Zopherus* + *Zopherosis* is supported as basal to the rest of the Zopherini by the synapomorphy of having maxillary palpomere 2 strongly and abruptly expanded at base 17 (1) as it was in the analysis of Ślipiński and Lawrence (1999). In that analysis the *Zopher* + *Noserinus* linage arose within the rest of the Zopherini, but as a distinct group. The present analysis supports *Zopher* as an independent linage from the rest of the Zopherini based on the presence of functional flight wings 4 (1), which also occurs as a homoplasy in *Noserinus dormeanus*. *Zopher* and the independent *Noserinus* clade are shown as basal to the rest of the Zopherini, but are weakly supported. In the analysis with *Zopherus* as the outgroup, this group forms a linage that terminates in a trichotomy, but the group is well supported by several synapomorphies: 5 (2) presence of a setose empodium between the tarsal claws, 6 (1) distinct epipleural ridge, 9 (0) large scutellum, and 10 (0) wider eye. The relationship between *Zopher* and *Noserinus* warrants further investigation. In those genera possessing 10-segmented antennae, the data of Ślipiński and Lawrence (1999) shows the genus *Nosoderma* in varying phylogenetic positions. In two of the consensus cladograms presented, it occurs basally as the sister-group to the rest of the Zopherini, which are defined by the synapomorphy of loss of the membranous mandibular prostheca (14 (1) in this analysis). In the other two cladograms *Nosoderma* is placed within the other Zopherini where the presence of the mandibular prostheca occurs as a homoplasic reversal. The current analysis supports *Nosoderma* as arising within the 10-segmented antennal group, with the reversal of the mandibular prostheca as synapomorphy at the generic level and a homoplasy with basal members of the

Zopherinae. *Nosoderma* is also defined by the synapomorphies of the weak sub-genal ridge 18 (0), and flattened apex of the last maxillary palpomere 16 (1).

Table 4. Character matrix used for phylogenetic analysis.

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**
Zopherus n. haldemani	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
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
Noserus emarginatus	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
Nosoderma 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 n. sp. Tampas.	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
Nosooderma venustus	1	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1	5	0	1	0	2	2	1	0	1	1	1
Noserus 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
Noserus n. sp. Hidalgo	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
Nosoderma inaquale	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
Nosoderma insigne	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
Nosoderma scabrosum	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
Nosoderma exsculptum	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
Nosoderma denticulata	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
Nosoderma lutosus	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
Nosoderma 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
Nosoderma 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
Nosoderma 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
Nosoderma 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
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
Meralius echinatus	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
Meralius n. sp. VENZ	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
Meralius 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 sp. 1	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
Scoriaderma sp. 2	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 ivie	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
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

This clade is supported as the sister-group of *Phloeodes* which together are defined by synapomorphies of tuberculate ventral 22 (0) and dorsal sculpture 28 (0). In the remaining clade defined by the synapomorphy of short arcuate groove on the hypomeron 21 (4), (this character is reversed in *Scoriaderma*) *Meralius* + *Scoriaderma* are supported as the sister group of the *Sesaspis* linage. The sister-group relationship between *Meralius* and *Scoriaderma* was previously supported (Ślipiński and Lawrence) and is supported by the analysis with *Phellopsis* as the outgroup. The hypothesized relationship between is *Sesaspis* and *Meralius* + *Scoriaderma* is not unreasonable based on a geographic proximity and generally similar morphological appearance between *Meralius clavapilus*, from Venezuela, and species of *Sesaspis*. The relationship of *Meralius*, *Noserinus* + *Zopher*, *Sesaspis*, and *Phloeodes* + *Nosoderma* is an unresolved polytomy in the cladograms with *Zopherus* as the outgroup. In that cladogram *Scoriaderma* is basal to the other genera with 10-segmented antennae plus *Zopher*.

The independent status of the genus *Sesaspis* Casey from the *Nosoderma* + *Phloeodes* lineage, where all of its previously described members were placed, is well supported by the arcuate depression on the hypomeron 21(4), patch of setae on the apical margin of the basal antennomeres 20 (2), ventral body surfaces with setose punctures 22 (1), and the weak tarsal strip 26 (1).

The results of the analysis support changing the generic placement of several species that are discussed under the generic headings below. The species within the genera *Sesaspis* and *Nosoderma* are mostly presented as unresolved polytomies (with two separate clades within *Nosoderma*), these are also discussed below.

Key to World Genera -- Zopherini

(modified from Slipinski & Lawrence 1999, and García-París, et. al. 2001)

1. Antennae appearing 9-segemented, club composed of 3 fused segments (Fig. 114); femora and tibia with paired rows of golden setae on inner surface; dorsal

vestiture glabrous (Southwestern U.S., Central America). Figs. 110, 111.
…………………………………………….…………………..*Zopherus* Gray

1’. Antennae 10 or 11-segemented; club variable, weakly 1 segmented to distinctly 3 segmented (Fig. 113, 115); dorsal vestiture densely setose or tomentose..…...…...2

2. (1’). Antennae 11-segmented with weak to strong 3-segmented club……..…..………3

2’. Antennae 10-segmented with 1 or 2-segmented club……………..……..…………4

3. (2). Scutellum partially visible; flight wings absent; hypomeron with complete cavity to contain antennae (Fig. 69); weak 3-segmented antennal club (Fig. 113); dorsal surface glabrous, sculpture strongly nodulate (Australia). Fig. 112.
………………………………………...........................…*Zopherosis* White

3’. Scutellum large and visible; functional flight wings; hypomeron lacking antennal cavity; strong 3-segmented antennal club; dorsal surface with dense patchy pubescence (Penn. Malaysia). Fig. 106. ………….*Zopher* Ślipiński and Lawrence

4. (2’). Scutellum large and visible; epipleural ridge distinct in basal 2/3rd of elytra (Fig. 128); setose empodium present between tarsal claws (Fig. 129) (South America). Figs. 104, 105. ....*Noserinus* Casey NEW SENSE

4’. Scutellum not visible or very small; epipleural ridge totally absent; between tarsal claws simple……………………………………………………......…………...5

5. (4’). Lateral margin of pronotum with distinct teeth or lobes (Fig. 107, 108, 109); prosternum densely setose with transverse groove (Fig. 123).
…………………………………………………………….……...……..……...6

5’. Lateral margin of pronotum without distinct lobes, at most irregularly denticulate;

prosternum densely setose to tuberculate, rarely with broad transverse depression……...7

6. (5). Sensilla area at apex of last antennomere medially constricted, reduced and recessed, not visible laterally (Fig. 127); hypomeron with shallow antennal cavities; labial palps inserted laterally concealed by mentum (Fig. 119); apical portion of pronotum with sinuate channel (Fig. 117); thin ridge connecting suprantennal and sub-genal ridge, enclosing apical margin on antennal insertion (Fig. 118) (Africa, Comoro Islands). Fig. 109 …………………..…...........……………………………..*Scoriaderma* Fairmaire

6'. Micro-setose field at apex of last antennomere large, covering approximately half of antennomere, visible laterally (Fig. 126); labial palps inserted ventrally, visible; pronotal hypomera without antennal cavities; apicolateral portion of pronotum with indistinct arcuate depression; thin ridge between suprantennal and sub-genal ridges absent (Cuba, South America). Figs. 107, 108. …………………………………….……………...…*Meralius* Casey

7. (5'). Ventral surfaces with setose punctures (Fig. 125), setation often very dense obscuring punctures; apical margin of hypomeron with short arcuate depression (Fig. 102); apical margin of at least 1st antennomere, sometimes antennomeres 1-6, with dense tuft of golden setae not present on basal margin (Central America, Texas). Figs. 92-98. ……………………………..*Sesaspis* Casey NEW SENSE

7'. Ventral surfaces with tubercles (Fig. 124); hypomeron variable from small break in margin to complete antennal cavity; apical margin of 1st antennomere usually with only bristle like setae, rarely with patch of short flat golden setae. ……..……….8

8. (7’). Mandible with membraneous prostheca (Fig. 101); hypomeron without large antennal cavity, occassionaly with weak straight depression (Fig. 103); 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. 121) (Central America). Figs. 83-92.

……………………...…………………..……..*Nosoderma* Solier NEW SENSE

8’. Mandible without membraneous prostheca (Figs. 99, 100); hypomeron with complete antennal cavity to weak depression (Figs. 69, 70); 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). ……………………………………..…*Phloeodes* LeConte NEW SENSE

Zopherus Gray

(Figs. 110, 111, 114, 130)

The genus was described by Gray (1832) (Type species *Zopherus mexicanus* Gray 1832, subsequent designation by Casey 1907a). 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: 0 (2) the apparent 9-segmented antennae, 11 (2) with a fused club, 5 (1) the overlapping cuticle between the tarsal claws, 19 (2) glabrous pronotum and 25 (1) ventrite 5 with a sinuate preapical groove.

Diagnosis: The genus can be distinguished from all Zopheridae by having 9-segmented antennae with the club composed of 3 fused segments, and complete antennal cavities on the hypomeron. Key to Species (see Triplehorn 1972).

Synopsis of *Zopherus* Gray Species

Z. chilensis Gray 1832	Central America
Z. insignis Blanchard 1861	
Z. bremei Guerin-Meneville 1844	
Z. moreletii Lucas, 1852	
Z. nervosus Solier 1841	Mexico
Z. pectoralis LeConte 1851	
Z. reticulatus (var.) Champion 1884	
Z. compactus Champion 1884	
Z. marmoratus Casey 1907a	
Z. nodulosus nodulosus Solier 1841	Mexico
Z. variolosus Sturm 1843	
Z. sallaei (var.) Champion 1884	
Z. verrucosus (var.) Champion 1884	
Z. nodulosus haldemani Horn 1870	Texas
Z. jourdani Salle 1849	Central America
Z. mexicanus (auct., nec. Gray)	
Z. costaricensis Champion 1884	
Z. jansoni Champion 1884	Costa Rica, Nicaragua
Z. mexicanus Gray 1832	Mexico
Z. maculatus Champion 1884	
Z. *angulicollis* Champion 1884	Mexico
Z. laevicollis Solier 1841	Mexico
Z. venosus (var.) Champion 1884	
Z. tuberculatus Champion 1884	

Z. limbatus (Casey) 1907a	
Z. xestus Triplehorn 1972	Texas
Z. solieri Triplehorn 1972	Mexico
Z. elegans Champion (nec. Horn) 1892	
Z. championi Triplehorn 1972	Mexico
elegans Champion (nec. Horn) 1892	
Z. tristis LeConte 1851	Arizona, California, Mexico
Z. aequalis (Casey) 1907a	
Z. variabilis (Casey) 1907a	
Z. incrustans (Casey) 1907a	
Z. concolor LeConte 1851	New Mexico, Texas,
Z. guttulatus Horn 1867	
Z. morosus (Casey) 1907a	
Z. gracilis Horn 1867	Arizona, New Mexico, Mexico
Z. pudens (Casey) 1907a	
Z. caudalis (Casey) 1907a	
Z. lugubris (Casey) 1907a	
Z. pruddeni (Casey) 1907a	
Z. luctuosus (Casey) 1907a	
Z. elongatus (Casey) 1907a	
Z. germinatus (Casey) 1907a	
Z. *uteanus* (Casey) 1907a	SW United States
Z. mormon (Casey) 1907a	
Z. granicollis granicollis Horn 1885	Arizona, Nevada, Baja Mexico
Z. induratus (Casey) 1907a	
Z. californicus (Casey) 1907a	
Z. prominens (Casey) 1907a	
Z. granicollis ventriosus (Casey) 1907a	California
Z. parvicollis (Casey) 1907a	
Z. opacus Horn 1867	SW United States
Z. elegans Horn 1870	SW United States
Z. otiosus (Casey) 1907a	
Z. verrucipennis (Casey) 1907a	
Z. circumductus (Casey) 1907a	

Z. woodgatei (Casey) 1907a

Z. sanctaehelenae (Blaisdell) 1931 California (Napa Co.)

Zopherosis White

(Figs. 112, 113)

This monotypic genus was described by White (1859) (Type species *Zopherosis georgei* White 1859). Casey (1907b) described the separate tribe, Zopherosini, for this species 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 unique combination of plesiomorphies (11-segmented antennae 0 (0), scutellum present 9 (0)) as well as apomorphies (groove on prosternum 3 (1) and setose vestiture 22 (1)) that occur as homoplasies higher in the cladograms.

Adults of *Zopherosi 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).

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).

Synopsis of *Zopherosis* White Species

Z. georgei White 1859 Australia, N.S.W

Zopher Ślipiński and Lawrence

(Fig. 106)

Type Material: PARATYPE ♂, intact in MAIC. MALAYA: Cameron; Highlands, Mt.; Brichang, 2-7.I.59/ L. W. Quate; Collector/ blue rectangle Paratype; Zopher; iviei; Slip. & Lawe.

This monotypic genus was described by Ślipiński and Lawrence (1999) (Type species *Zopher iviei* Ślipiński and Lawrence 1999). The relationship with the genus *Noserinus* is unresolved by the cladograms, but in the analysis with *Phellopsis* as the outgroup, *Zopher* lacks the synapomorphy of *Noserinus* (lateral margins of pronotum with distinct teeth or lobes 15 (1)).

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*.

Synopsis of *Zopher* Ślipiński and Lawrence Species

Z. iviei Ślipiński and Lawrence 1999 Peninsular Malaysia

Noserinus Casey

(Figs. 104, 105, 128, 129)

Type Material Examined: COTYPE, *Noserinus dormeanus* ♀, 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 dormenaus.

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 larva of *Noserinus dormeanus* was described by Costa et al. (1988). While only reported in the literature from Brazil, specimens have also been seen from Argentina and Paraguay (NEW COUNTRY RECORDS).

The species *Noserinus dormeanus, Zopher iviei* Ślipiński and Lawrence, and *Meralius furcatus* form a distinct cluster in the phylogenetic analysis. This group shares the presence of a large setose scutellum 9 (0), distinct epipleural ridge 6 (1), empodium between tarsal claw 5 (2) (occurs as a homoplasy with *Zopherosis*), and the wider eye 10 (0). The present phylogenetic data, with *Phellopsis* as the outgroup, supports *Meralius furcatus* as the sister-species to *Noserinus dormenaus*. Therefore, based on the phylogenetic analysis *Meralius furcatus* is moved to *Noserinus*, rather than recognizing a third monotypic genus; NEW COMBINATION. The species *N. furcatus*, differs from

Noserinus dormeanus in lacking functional flight wings and possessing small pits along the basal margin of the pronotum.

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

With the inclusion of *Noserinus furcatus*, the generic description of *Noserinus* should be slightly modified as follows from Ślipiński and Lawrence (1999). Description (male): 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.

Key to Species of *Noserinus* Casey

1. Functional flight wings present; apical margin of elytral smooth. South America. Fig. 104. …………………………………………….…… *N. dormeanus* (Fairmaire)

1'. Functional flight wings absent; apical margin of elytra with strongly projecting conical nodules. Venezuela. Fig. 105. …………..……………*N. furcatus* (Kirsch)

Synopsis of *Noserinus* Casey Species

N. dormeanus (Fairmaire) 1889	South America
N. annulatipes Casey 1907	
N. furcatus (Kirsch) 1866, NEW COMBINATION	South America

Scoriaderma Fairmaire

(Figs. 109, 117, 118, 119, 127)

Type Material Examined: *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.

Scoriaderma comoriense: 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.

This genus was described by Fairmaire (1894a) for the African species *S. comoriense* Fairmaire 1894 (Type species *S. comoriense* by monotypy). The type species is incorrectly identified by Gebien (1936) as *Nosoderma cordicolle* Waterhouse 1880. Gebien (1936) also moved *Nosoderma cordicolle* into *Scoriaderma* after it was mentioned by Fairmaire (1894b) along with the description of *S. congolense*.

Based on the examination of the type of *Scoriaderma congolense*, it is clear that the locality information was either misinterpreted or incorrect. The information on the specimen is simply handwritten “Congo”, but the specimen is actually an identical match, of the opposite sex, to the type of *Nosoderma scabrosum* Solier and clearly not congeneric with *S. comoriense*. One possible cause of the error could be that there is a town of El Congo (25° 58’ N, 105° 12’ W) in the Mexican state of Durango, and could explain why no additional specimens from the Congo region have been discovered. This scenario also makes considerably more sense biogeographically, rather than a genus that occurs in both tropical forests of Western Africa as well as drier upland forests of Eastern Africa, the genus is restricted to the later and the Comoro Islands (this confirms suspicions held by M. A. Ivie on the distribution of the genus). Whatever the reason for the misidentification, *Scoriaderma congolense* Fairmaire 1894b is proposed as a junior synonym of *Nosoderma scabrosum* Solier 1841, NEW SYNONYMY.

In the analysis with *Phellopsis* as the outgroup, *Scoriaderma* is defined by several synapomorphies that are homoplastic with one or both of the basal *Zopherus* + *Zopherosis* clade. These characters include; 2 (0) absence of femoral nodules on all femora in the male (also homoplasy in *Sesaspis emarginatus* and *Nosoderma aequalis*, 8 (1) labial palp insertions concealed by the mentum, 13 (1) sensilla area at apex of last antennomere in recessed and emarginate area and 24 (1) antennomere 3 transverse (also occurs as a homoplasy in *Sesaspis emarginatus*. The hypomeron with a broad distinct depression (21 (1)) is a synapomorphy that does not occur elsewhere. The lateral bridge between the suprantennal ridge and subgenal ridge that encloses the antennal insertion apically (Fig. 107) is probably also a synapomorphy, but was not included in the phylogenetic analysis. The characters that are shared with the *Zopherus* + *Zopherosis* clade, result in *Scoriaderma* occurring as basal to the rest of the Zopherini in the analysis with Zopherus as the outgroup.

Diagnosis: Similar in general appearance to *Meralius echinatus*, but distinguished from that genus by having a sinuate channel near the apical margin of the pronotum (Fig. 117), lateral bridge between the suprantennal ridge and subgenal ridge that encloses the antennal insertion apically (Fig. 118), the labial palp insertions concealed by the mentum (Fig. 119), the micros-setose field of the last antennomere depressed and emarginate at the apex (Fig. 127), well developed but incomplete antennal cavity on the hypomeron, and lack of femoral nodules in the male.

Synopsis of *Scoriaderma* Fairmaire Species

S. *cordicolle* (Waterhouse) 1880	Africa
S. *comoriense* Fairmaire 1894a	Comoro Islands

Meralius Casey

(Figs. 107, 108, 116, 123, 126)

The genus *Meralius* was described by Casey (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 type species was later synonomized with *Nosoderma echinatus* Guérin-Méneville 1838 (Gebien 1936).

The species *Nosoderma furcatus* Kirsch (1866) from Venezuela has been 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) and is incorrectly placed. It differs from true *Meralius* species most obviously in having a large scutellum and lacking a groove on the prosternum which is only broadly depressed. Coincidentally, there is an undescribed species of *Meralius* from Venezuela that was represented in Gebien's collection (label data- "Sammlung H. Gebien") and probably assumed to be *Meralius furcatus*. Gebien could have based his placement of *Nosoderma furcatus* in *Meralius* based on this specimen. There was nothing done with the 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 these 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 *Nosoderma*, have the nodules occurring asymmetrically, present on one leg but not the other in a single individual.

This genus is defined by the synapomorphy of 7 (1) ventrally inserted labial palps (homoplasy with *Nosoderma*). The presence of very narrow channel at least along the apical third of the lateral margin of the pronotum occurs nowhere else in the Zopherini and is probably a synapomorphy, but was not included in the analysis because similar pronotal channels occur in different position in *Scoriaderma*, *Noserinus* and *Zopher* and the charcter states could not be clearly defined except in *Scoriaderma*.

Diagnosis: The combination of the transverse groove on the prosternum (Fig. 123), 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 mentum, sensilla at apex of last antennomere covering the apical half of the segment (Fig. 126), presence of nodules on the femora of the male, and a very narrow channel at least along the apical third of the lateral margin of the pronotum.

Key to Species of *Meralius*

1. Apical half of elytra, excluding lateral margin, with 5 or 6 small nodules all similar in size; secondary setation on legs, uniformly thickened and apressed; apex of elytra along suture smooth to weakly emarginate. Cuba. Fig. 108. ……………………………………………*M. echinatus* (Guérin-Méneville)

1’. Apical half of elytra, excluding lateral margin, with single large median nodule, and 2 or 3 weak elevations; secondary setation on legs, very long, projecting, and club shaped (Fig. 116); apex of elytra along suture strongly emarginate. Venezuela. Fig. 107. ……………………..…………*Meralius clavapilus* NEW SPECIES

Synopsis of *Meralius* Casey Species

M. echinatus (Guérin-Méneville) 1838	Cuba
M. duponchelii (Solier) 1841	

M. turquinensis Garrido 2004,	NEW SYNONYMY	Cuba
M. montanus Garrido 2004,	NEW SYNONYMY	Cuba
Meralius clavapilus Foley and Ivie,	NEW SPECIES	Venezuela

Meralius clavapilus Foley and Ivie NEW SPECIES

Description (of male): 17.5 mm. Fig. 107. Brachypterous. Dorsal vestiture multicolored tomentose, consisting of short, appressed 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.

Female: Unknown

Type Material: HOLOTYPE 1 ♂ - Handwritten on green rectangle N. Grenada; underside same label 246/ Meralius; furcatus; unknown character/ Sammlung; H. Gebien (NHMB-Frey Collection).

Distribution: The only known specimen is from the locality N. Grenada. Undoubtedly more specimens occur in collections, probably in the AMNH (Garrido 2004).

Biology: No biological data is present on the label of the holotyope.

Etymology: The name refers to the setae that are strongly club-shaped and present on the body surfaces. It is a combination of the Latin clava=club and pilus=hair.

Diagnosis: This species is distinguished from all mainland American species of Zopherini without a visible scutellum by the distinct transverse groove on the prosternum. It is distinguished from *Meralius echinatus* by the elongate form, large elytral nodules, and long club shaped secondary setose vestiture (Fig. 116). 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 presence of the distinct prosternal groove.

Notes: The holotype bears a label identifying the specimen as *Meralius furcatus*, as well as a label that places it in the collection of Gebien. This is strong evidence to suggest that when Gebien (1936) moved *Nosoderma furcatus* Kirsch to *Meralius*, he was in fact examining the new species described here which is true member of *Meralius*. The species name moved by Gebien (1936) is supported as more closely related to *Noserinus dormeanus*, and is now placed in that genus.

Sesaspis Casey NEW SENSE

(Figs. 75, 92-98, 100, 102, 115, 120, 125)

This genus was described by Casey without examining actual specimens and was based on the published description of *Nosoderma denticulata* Solier (Type species *Nosoderma denticulata* Solier 1841 by original designation). The genus was later synonymized with *Nosoderma* Solier by Doyen and Lawrence (1979). The current phylogenetic analysis supports the recognition of *Sesaspis* as a distinct genus that occurs from Mesoamerica to Texas. The four described species placed in this genus were most recently placed in the genera *Nosoderma* (*S. denticulata* and *S. lutosus*) and *Phloeodes* (=*Noserus*) (*S. emarginatus* 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* (Ślipiński 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. 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 *Nosoderma*. For example, *Noserus emarginatus* was described in 1878 from Texas. This species has been reported from a relatively wide geographic area in Southern Texas, some of which are highly populated, but relatively few specimens (very few when compared to *Phloeodes*) have been collected. The rarity of specimens (Casey never saw any 1907a, 1907b) during a time of questionable taxonomy, saved the genus from the accumulation of synonyms that have plagued the related genera. Almost all of the type material from which the three new species are described has been collected since 1980, and is the result of relatively recent collecting efforts in Central Mexico and Central America.

The species of the genus *Sesaspis* appear as a totally unresolved polytomy in the strict consensus cladograms. However, general patterns can be identified based on morphology. The species *Sesaspis doyeni* and *Sesaspis ashei*, *Sesaspis emarginatus* and *Sesaspis denticulata*, and *Sesaspis lutosus* and *Sesaspis adami* are all probably sibling species. This leaves the species *Sesaspis triplehorni* relatively isolated in Central America and sharing general sculptural patterns with four of the other species (*S. emarginatus*, *S. denticulata*, *S. lutosus* and *S. adami*) 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.

Diagnosis: This genus is defined by having the ventral body surfaces covered with punctures with single inserted setae (tubercles in *Phloeodes* and *Nosoderma*) and the presence of a short arcuate cavity on the hypomeron (also present in *Meralius*, 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. 100) 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.

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 coaxal 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. Aedeagus without basal stop.

Female: Similar to male except lacking nodules on femora. When the nodules are absent in male (*S. emarginatus*), there is no distinguishable difference.

Larva: Unknown

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 and have led to the formation of several allopatric species.

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

1’. 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. (1). Elytra with faint elevation in 5th interval; lateral margin of apical declivity smooth. Mexico, Nuevo Leon. Fig. 94……………………..…*S. doyeni* (García-París et al.)

2’. Elytra with faint elevation in 3rd interval; lateral margin of apical declivity weakly serrate. Mexico, Hidalgo. Fig. 93…………..…………..…..*S. ashei* NEW SPECIES

3. (1’). 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. Fig. 96 ……….*S. emarginatus* (Horn)

3’. 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. (3’). Elytra 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. 92. ……………………..…………………………....*S. denticulata* (Solier)

4’. 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. (4’) 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. 95.

…………………………………………………*S. triplehorni* NEW SPECIES

5’. 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. (5’) 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. 97.

……………………………………………………………*S. lutosus* (Champion)

6’. 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. 98.

……………………………………………………...*S. adami* NEW SPECIES

Biology: At least two species have been collected from Oak (*Quercus* sp.), and *Sesapis doyeni* was described from under loose bark of dead pine stumps (García-París et al. 2001).

Synopsis of *Sesaspis* Casey Species

S. denticulata (Solier) 1841,	NEW COMBINATION	Mexico
S. emarginatus (Horn) 1878,	NEW COMBINATION	Texas
S. triplehorni Foley and Ivie,	NEW SPECIES	Central America
S. lutosus (Champion) 1884,	NEW COMBINATION	Mexico
S. adami Foley and Ivie,	NEW SPECIES	Mexico
S. doyeni (García-París et al. 2001),	NEW COMBINATION	Mexico
S. ashei Foley and Ivie,	NEW SPECIES	Mexico

Sesaspis denticulata (Solier) NEW COMBINATION

(Fig. 92)

Type Material Examined: *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.).

Fig. 4. The known distribution of the genus *Sesaspis* Casey. *S. emarginatus* Texas, green squares. *S. denticulata* Mexico, Nuevo Leon, white circles. *S. doyeni* Mexico, Nuevo Leon, orange square. *S. adami* Mexico, Tampaulipas, Hidalgo, and Queretaro, blue circles. *S. ashei* Mexico, Hidalgo, yellow square. *S. lutosus* Mexico, Hidalgo red square. *S. triplehorni* Mexico, Chiapas, and Belize, Guatemala, Honduras, and Nicaragua, orange circles.

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

Sesaspis emarginatus (Horn) NEW COMBINATION

(Fig. 96)

Type Material: 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.

Diagnosis: Distinguished by very dense bristle like setose vestiture, antennomere 3 transverse 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 *Nosoderma aequalis* Champion).

Sesaspis doyeni (García-París, Coca-Abia, & Parra-Olea) NEW COMBINATION

(Fig. 94)

Type Material: *Noserus doyeni*: 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/ Red Rectangle *Noserus doyeni* García-París, Coca-Abia, & Parra-Olea 2000, Paratipo.

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 elytrl interval.

Sesaspis lutosus (Champion) NEW COMBINATION

(Fig. 97)

Type Material: *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.

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

Notes: Only a single specimen besides the types has been examined. This specimen from Mexico, Oaxaca (MAIC), differs slightly from the types in the intensity of the sculpture but shows the same pattern.

Sesaspis adami Foley and Ivie NEW SPECIES

(Figs. 98, 100, 102, 115, 120)

Description (male): Length 16-20 mm. Black to dark brown appearing furry when in natural state, cleaned specimens have a mottled dark red to black pattern. Dorsal vestiture of very short bristle like setae, not scales, secondary vestiture of longer golden setae. Anterior clypeal margin distinctly concave. Antennomere 3 approximatley 1.20 X longer than 4; antennomeres 1 and 2 with distinct tuft of golden setae. Labium with tufts of setae inserted in fossae. Pronotum with weak arcuate lateral ridges; lateral margin slightly serrate; hind angles strongly produced into acute angles. Elytral sculpture with weak elevation at base of 3rd interval; strong sinuate ridge from base to start on ventrite 2 in 5th interval terminating in nodule; arcuate nodule at start of declivity tapering into 3rd interval; area around suture swollen with nodule at apex. Femoral nodules always large and distinct on pro and mesofemora, almost always absent on metafemora, rarely smaller nodule. Ventrites 1-3 flattened medially. Parameres dorsally not fused; apex strongly emarginate and pointed, knob like.

Female: Same as male except lacking femoral nodules.

Type Material: HOLOTYPE 1 ♂ intact in IEXA. MEXICO: Tamaulipas,; El Cielo. 1080m. Tronco-; *Quercus* . 28-IV-82.; M. A. Morón, col.

PARATYPES: 1 ♂, 1♀ same data as Holotype (IEXA). 1 ♂ - MEXICO: Rancho del; Cielo, Gomez Farias, Edo.; Tampas. 8-II-1980.; Bosq. mexifilo de montaña; P. Reyes-C. col. (IEXA). 1 ♂ - MEXICO: Rancho del; Cielo, Gomez Farias, Edo.; Tampas. Mayo.1981; P. Reyes-C. col. (IEXA). 1 ♂ - MEXICO: Rancho del Cielo,; Mpio.

Ģ.Farias, Tampas.; 7-V-81; Alt. 1188m; Bosque Mesofilo.; M.L. Castillo (IEXA). 1 ♂ - MEXICO: Tamaulipas,; El Cielo.1080m.col.divrna; 26-V-82; R. Terrón, col.; M. Hist. N. Cd. Méx. (IEXA). 1 ♂, 1 ♀ - MEXICO: Tamaulipas, Gómez; Farías, Ranch El Cielo.; 11-X-2002, Alt. 1200 m.; L. Cervantes y L. Delgado cols. (IEXA). 1 ♂ - MEXICO: Hidalgo; 48.5 km S Tamazunchale; Hwy.85, 10 July 1990; 1030 m, J.S. Ashe, K.J.; Ahn, R.Leschen #141; ex: Polyporales (SEMC). 1 ♀ - MEXICO: Queretaro; Hy. 120- El Madroño; D. Brzoska 21-VII-1991 (SEMC). 1 ♀ - MEXICO: Queretaro; 8.3 km W San Luis; Potosi/Queratero border; Hwy.120, 8 July 1990/ 1560m, J.S.Ashe, K.J.; Ahn, R.Leschen #87; ex: under bark (SEMC). 2 ♂ - MEXICO: Tampas., El; Cielo, Ejido San Jose, 7.4 km W Gomez; Farias, 1400 m/ VII-21-1994; Wm. Godwin (TXAM). 1 ♀ - MEXICO: Tampaulipas, Mpio.; Gomez Farias nr. Rancho; deCielo, 1200m.; III-19-1992. R. Jones; T. Carlow, & W. Godwin (TXAM). 1 ♀ - MEXICO: Tampaulipas, Ejido San José, 7.5 km.; W. Gomez Farias, 1400 m; VII-20-1994, Wm.; Godwin, rotten log pile (TXAM). 20 ♂, 6 ♀ - MEXICO: Tamps., El Canindo; nr. Ejido San José,; 7.5 km.W. Gomez Farias,; 1400 m., VII-28-30-;1993, J.C. Schaffner (TXAM).

Distribution: Known from the Mexican provinces of Tamaulipas, Queretaro, and Hidalgo, where the species apparently occurs at elevations between 1000-1400 m in the Sierra Madre Oriental.

Biology: Three specimens were associated with Oak (*Quercus* sp.) and several others were collected in “mesófilos”, mountain forests or cloud forests.

Etymology: This species is named in honor of Stanisław Adam Ślipiński, who along with John F. Lawrence, recently reviewed the genera of Zopherinae (Ślipiński and

Lawrence 1999) and provided an excellent framework to address the Zopheridae at the species level.

Diagnosis: The species is closely related to *S. lutosus*, 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 bi-fid large nodule at the apex in *S. lutosus* and strongly serrate lateral margin of the pronotum.

Notes: *Sesaspis lutosus* apparently replaces *S. adami* in more southern Mexican locales such as Oaxaca.

Sesaspis ashei Foley and Ivie NEW SPECIES

(Fig. 93)

Description (male): Length 17.5-22.5 mm. Black to dark brown; in natural state covered in greasy exudates and environmental debris; cleaned specimens have the cuticle uniformly 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 approximatley 1.25 X longer than 4; antennomere 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 apex, sides not strongly projecting forward.

Type Material: HOLOTYPE: 1 ♂, MEXICO: Hidalgo; 4.4 km N Tlanchinol; Hwy. 105, 8 July 1992; 1420 m, J. S. Ashe #31; ex: misc. collecting (SEMC). PARATYPES: 1 ♂, 1 ♀, MEXICO, Hgo.,; La Mojonera,; 28.X.1992,; leg. J. Pál (HNHM).

Distribution: Known only from the Mexican state of Hidalgo.

Biology: 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 Pine-Oak forest ecosystem.

Etymology: This species is named in honor of the late Dr. J. Steve Ashe, who was the collector of the holotype and a significant number of other Central American Zopherini.

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.

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.

Sesaspis triplehorni Foley and Ivie NEW SPECIES

(Fig. 75, 95)

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; antennomere 1-6 with short dense golden setae on apical margin. Labium with two lateral tufts and median few 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 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 (Fig. 75).

Type Material: HOLOTYPE: 1 ♂ - BELIZE: Toledo Dist.; Blue Creek Village; 16 June 1981; W. E. Steiner/ EARTHWATCH Belize; Expedition 1981; D. H. Messersmith,; W. E. Steiner, et al. (USNM). PARATYPES: 7 ♂, 5 ♀ - same data as Holotype (USNM). 3 ♂, 3 ♀ - same data as Holotype, except 1 July 1981 (USNM). 1 ♂ - BELIZE: Orange Walk District; Rio Bravo Conservation Area; Mahogony 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 dung; coll. D. Inward; BMNH{E}; 2005-78 (BMNH). 1 ♀ - BELIZE: Orange Walk Dist.; Rio Bravo Conserv. Area; Mahogany Trail, 2-3.IX.1995, P. W. Kovarik, coll.; taken on logs at night (MAIC). 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). 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 (TXAM). 1 ♂ - GUATEMALA: Tikal; 20-22.VII.1970; J. & M. Sedlacek (BISH). 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).

Distribution: Far southern Mexico through Central America.

Biology: Specimen data reports 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.

Etymology: This species is named in honor of Dr. Charles A. Triplehorn, whose excellent species level revision of *Zopherus* was motivation to understand the other genera of the tribe, and for considerable additional unpublished observations on the group which were kindly shared with M. A. Ivie.

Diagnosis: Resembles the species *S. emarginatus* (Texas) and *S. denticulata* (Mexico), in the dense setose vestiture, but is quite distinct in sculpture. The pronotum has sub-parallel ridges beside the midline that have weakly divided elevations at the apex and base (not quite as strong as *S. emarginatus*), 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.

Phloeodes LeConte

(Figs. 63-74, 76-82, 99, 124)

This genus is revised in the following chapter, and only a diagnosis and species synopsis of the genus is provided here.

Diagnosis: This genus is separated from all others of the tribe with 10-segmented antennae, by having tubercles on the ventral surface and lacking a membranous mandibular prostheca.

Synopsis of *Phloeodes* LeConte Species

P. diabolicus LeConte 1851	California, BAJA MEXICO, possibly Arizona
P. pustulosus LeConte 1859,	NEW SYNONYMY

P. latipennis Casey 1907a	
P. ovipennis Casey 1907a,	NEW SYNONYMY
P. elongatus Casey 1907a,	NEW SYNONYMY
P. scaber Casey 1907a,	NEW SYNONYMY
P. angustus Casey 1907a,	NEW SYNONYMY
P. remotus Casey 1907b,	NEW SYNONYMY
P. plicatus (LeConte) 1859	California, BAJA MEXICO, possibly Arizona
Noserus torvus (Casey) 1907a,	NEW SYNONYMY
N. collaris (Casey) 1907a,	NEW SYNONYMY
N. corrosus (Casey) 1907b,	NEW SYNONYMY
N. convexulus (Casey) 1907b,	NEW SYNONYMY
P. venustus (Champion) 1884	NEW COMBINATION Central America

Nosoderma Solier NEW SENSE

(Figs. 83-91, 101, 103, 121-122)

The genus *Nosoderma* is the second largest in the tribe behind *Zopherus*, and at the beginning of the study contained 23 valid named species. *Nosoderma* was described by Solier into which he placed 5 species (*Nosoderma denticulatum*, *Nosoderma duponchelii*, *Nosoderma scabrosum*, *Nosoderma morbillosum,* and *Nosoderma vicinium*) without designating a type species. Casey (1907b) incorrectly designated the type species as *Eurychora inaequlais* Say, which was not one of the species included in the genus at the time of its description by Solier, this designation was followed by Doyen and Lawrence (1979). The type species was subsequently correctly identified as *Nosoderma morbillosum* Solier by Gebien (1936) who synonymized it and *Nosoderma vicinium* with

Nosoderma inaequale (Say), this designation was followed by Ślipiński and Lawrence (1999).

Champion (1884) in his Biologia Centrali-Americana described 13 new species of *Nosoderma* and Casey (1907b) added an additional 7. After Casey's revision of the zopherids, the 23 named *Nosoderma* species were placed in the genera *Sesaspis*, *Noserodes* Casey, and *Verodes* Casey. This placement was followed by Gebien (1936), but the three genera were all later synonymized with *Nosoderma* (Doyen and Lawrence 1979).

Phylogenetic analysis of this group suggests that as currently constituted it is not monophyletic. The species group centered on *Nosoderma denticulata* forms a distinct group and is here recognized as the reconstituted Casey genus *Sesaspis* NEW SENSE. When *Sesaspis* is recognized as a genus, *Nosoderma*, *Phloeodes*, and *Sesaspis* all form monophyletic genera with the only remaining problem being the placement of *Nosoderma venustus*. This species does not fit the definition of either *Nosoderma* or *Sesaspis*. It is excluded from *Nosoderma* because it lacks a membranous mandibular prostheca, and from *Sesaspis* because the ventral surface is covered with tubercles and it lacks an arcuate groove on the hypomeron. The phylogenetic analysis of the tribe supports *Nosoderma venustus* at the base of a monophyletic lineage containing the two California species *Phloeodes diabolicus* and *Phloeodes plicatus*. Based on this evidence, *Nosoderma venustus* is moved to *Phloeodes*, and becomes the only member of that genus to occur outside the California Floristic Province.

The genus *Nosoderma* as here defined contains nine species in two separate clades, that both appear as polytomies in the consensus cladogram. A group of five species occurs generally from Oaxaca, Mexico, north possibly into the United States (there are unconfirmed localities of *Nosoderma exsculptum* in Texas with simply state data), and another group containing four species that generally occur from Oaxaca, Mexico, south into Central America.

The species-group occurring northwards from Oaxaca is generally restricted to high-elevation cloud forests and contains the two most widespread species of *Nosoderma*, *Nosoderma inaequalis* and *Nosoderma exsculptum*, and three that are quite rare. *Nosoderma scabrosum* and *Nosoderma asperatum* appear to be sister-species that are isolated to high elevation cloud forests, only *Nosoderma scabrosum* was included in the phylogenetic analysis because the two species are coded exactly the same in the character matrix. These species were presumed to be synonymous until the types of *Nosoderma scabrosum* was examined. The type specimens are the only representatives of this species that have been examined. *Nosoderma insigne* is the other rare species that is known only from the state of Oaxaca. The elytral sculpture of this species, consisting of ridges that are hooked at the apex is unique in *Nosoderma*.

The linage occurring in more southern locales in Central America contains the species that Casey placed into the genera *Noserodes* (*Nosoderma zunilensis*, *Nosoderma guatemalensis*, and *Nosoderma sparsus*) and *Verodes* (*Nosoderma aequalis*). The three species previously placed in *Noserodes* are closely allied, and *Nosoderma zunilensis* and *Nosoderma guatemalensis* are probably sister-species. The species previously placed in

Verodes is distinct among species of *Nosoderma* in having the elytral sculpture completely reduced, even more so than *Sesaspis doyeni*, and lacking nodules on all femora of the male, but these characters do not warrant generic distinction based on the current analysis.

Diagnosis: The true core *Nosoderma* group is supported by the presence of a distinct membranous prostheca on the mandible (Fig. 101), ventrally inserted labial palps (Fig. 122), lack of any hint of an antennal cavity on the hypomeron, and the presence of tubercles on the ventral surface (also in *Phloeodes*).

Type Material Examined: *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.

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.

Nosoderma exsculptum: 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 %, intact and % left meta leg missing, left meso tarsus missing 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 two ♂, intact in BMNH. Same data as LECTOTYPE

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.

Nosoderma interruptum: LECTOTYPE ♀, missing left antennae, 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; Garcia-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.

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 ♀, same data as above/Paralectotipo M. Garcia-Paris et al det. 2002.

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.

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.

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.

Nosoderma aequale: HOLOTYPE ♀, left antennae broken, left pro and meso tarsus broken, right meso and meta tarsus 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.

Synopsis of *Nosoderma* Solier Species

N. inaequale (Say) 1835 Mexico

- *N. morbillosum* Solier 1841
- *N. vicinum* Solier 1841
- *N. championi* Casey 1907b, NEW SYNONYMY
- *N. prominens* Casey 1907b, NEW SYNONYMY
- *N. senex* Casey 1907b, NEW SYNONYMY
- *N. brevicolle* Casey 1907b, NEW SYNONYMY
- *N. subglabrum* Casey 1907b, NEW SYNONYMY

N. insigne Champion 1884 Mexico

- *N. interruptum* Champion 1884, NEW SYNONYMY

N. scabrosum Solier, 1841 Mexico

- *Scoriaderma congolense* Fairmaire 1894b, NEW SYNONYMY

5

6

Figs. 5 and 6. 5. Wide angle distribution of specific localities of examined specimens of *Nosoderma*. 6. Closer view of distribution of specimens of Nosoderma centered about Mexico City, MEXICO. *N. inaequalis*, blue squares. *N. insigne*, yellow circles. *N. asperatum*, green square. *N. exsculptum*, red squares. *N. scabrosum*, white circles. *N. aequalis*, blue squares. *N. guatemalensis*, white squares. *N. sparsus*, yellow square. *N. zunilensis*, red circles.

N. asperatum Champion 1884	Mexico
N. exsculptum Champion 1884	Mexico, possibly Texas
N. carinatum Champion 1884,	NEW SYNONYMY
N. anceps Champion 1884,	NEW SYNONYMY

N. impressum Champion, 1884,	NEW SYNONYMY
N. longipennis Casey 1907b,	NEW SYNONYMY
N. zunilensis Champion 1884	Central America
N. guatemalensis Champion 1884	Central America
N. squalidus Casey 1907b,	NEW SYNONYMY
N. sparsus Champion 1884	Guatemala
N. aequalis Champion 1884	Mexico

Key to the Species of *Nosoderma* Solier

1. Dorsal surface of pronotum with all setae singly inserted at the base of tubercles; tubercles on pronotum uniformly distributed………………………………….…………2

1’. Dorsal surface of pronotum with dense setae between tubercles inserted directly on surface; tubercles on pronotum more dense on ridges, and absent in intervening areas……………….………………………………………………………………5

2. (1). Pronotal and elytral surface smooth with dense flattened tubercles lacking any distinct ridges or nodules; male femoral nodules absent. Mexico, Oaxaca. Fig. 91. ………………..................……………………………..…… *N. aequalis* Champion

2’. Pronotal and elytral surfaces with distinct ridges and nodules; male femoral nodules present on at least meso and metafemora…………..…….………………………..…3

3. (2’). Metepisternum irregularly foveolate; elytra elongate, 1.95-2.05X longer than widest point; elytral smooth at apex. Guatemala. Fig. 88.

………………………………………………………...……….*N. sparsus* Champion

3’. Metepisternum tuberculate; elytra more stout, 1.60-1.75 X longer than widest point; elytra very shallowly to deeply emargiate at apex. Mexico and Central America………… ……………..……………………..4

4. (3’). Elytra shallowly emarginate at apex, rounded; 5th elytral interval with weak ridge. Mexico and Central America. Fig. 90. ……………………………………………………. *N. guatemalensis* Champion

4’. Elytra deeply emarginate at apex, sharply pointed; 5th elytral interval containing three large disconnected nodules. Mexico and Central America. Fig. 89. ………..…..*N. zunilensis* Champion

5. (1’). Base of elytra with two broad shallow transverse depression across suture; posterior angles of pronotum weakly to moderately expanded; prosternum anterior of procoxae flat; 5th elytral interval with straight ridge starting at base; apical third of elytron with 4 small nodules. Mexico. Fig. 84. ....……… *N. exsculptum* Champion

5’. Base of elytra without transverse depressions; posterior angles of pronotum strongly expanded; prosternum anterior of procoxae with broad depression; 5th elytral interval with arcuate ridge starting at base, beyond level of mesocoxal cavity, or only nodules; apical third of elytron with less than 4 nodules…..…………………...6

6. (5’). Third elytral interval with subapical ridge distinctly hook at apex; apex of elytra with swollen ridge around suture; 5th elytral interval with arcuate ridge starting at base. Mexico. Fig. 87. ………...… *N. insigne* Champion

6’. Third elytral interval with short ridge at base, only nodules, or combination of both; apex of elytra flat around suture; 5th elytral interval simple at base.......................7

7. (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. 83. ………………………………….....…………….……. *N. inaequalis* Say

7’. (6’). Third elytral interval with nodule at base; 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, subapical very large, much larger than one near apex. Mexico ………………...……………………………………………………8

8. (7’). Apical margin of elytra weakly serrate; male nodule present on all femora. Mexico. Fig. 86. ……………………………………………..*N. scabrosum* Solier

8’. (7’). Apical margin of elytra with strongly projecting conical nodules, appearing very strongly serrate; male nodule present only on meso and metafemora. Mexico, Hidalgo. Fig. 85. ……………………………………….*N. asperatum* Champion

Future Research

More data are needed on the Zopherini in all areas where they occur. Many species are highly restricted in their habits and require specific collecting efforts to discover specimens. The known distributions for most Central American species are probably incomplete and represent only a portion of the actual populations that exist. The collection of additional specimens preserved for molecular study would bring an entirely knew data set into the phylogenetic analysis of the tribe. Even representative samples of the genera are not currently available for molecular analysis. Obtaining specimens of the genera *Meralius*, *Sesaspis*, and *Nosoderma* for molecular analysis would add characters that could go a long way to support or reject the current hypothesis on the classification of the described species.

The larvae of several genera remain undescribed, and those that are described are usually only based on a single species. A more complete representation of larvae in the Zopherini would add significant characters to future phylogenetic analyses.

It is also possible that new species are yet to be discovered in isolated high elevation forests and/or lowland tropical forests throughout Central America. Only the genus *Zopherus* has been recorded from El Salvador, but other genera of the tribe almost certainly occur in that country.

The relationship between *Zopher* and *Noserinus* needs further investigation as to whether the group forms a single monophyletic genus, or is in fact two distinct genera. New species could also be discovered in Southeastern Asia, and South America.

The very large body-sized monotypic genus *Zopherosis* would be interesting to examine at the population level. This genus is predicted to be relatively old and highly fragmented. It would be interesting to examine the intraspecific population structure to see if it indicates low level of gene flow between distinct identifiable populations.

The species level taxonomy of the genus *Scoriaderma* has yet to be resolved, due to a lack of specimens. It is possible that only one relatively widespread species exists in Eastern Africa and on the Comoro Islands. Molecular data from this genus would also offer insight into its relationship within the Zopherini, as to whether it is more closely related to *Zopherus* + *Zopherosis*, or to *Meralius* and the American genera, or if it is possibly intermediate between the two clades.

Many members of the Zopherini are quite rare in collections, especially considering their large size, and future collecting efforts will be important to continuing to advance our knowledge of this diverse assemblage of remarkable beetles.

CHAPTER 4

REVISION OF THE GENUS *PHLOEODES*

Introduction

Phloeodes is closely related to the other large flightless “ironclad” beetles with 10-segmented antennae and closed procoxal cavities. It is one of eight recognized genera in the apparently monophyletic tribe Zopherini (*sensu* Ślipiński & Lawrence 1999). While the genera have recently been redescribed (Ślipiński & Lawrence 1999), the species are poorly defined and their placement is unresolved. I examined the species of *Phloeodes* LeConte 1862 (=*Noserus* LeConte 1862, *sensu* Ślipiński & Lawrence 1999, Ivie 2002c) to evaluate the many names available for the group (Doyen and Lawrence 1979, Ivie 2002c). There are currently 14 names available but they have not been evaluated since Casey (1907a and 1907b). The surplus of available names in this genus makes it difficult to achieve accurate determinations for individual specimens. The desperate need for a species-level revision of this group was pointed out by Ivie (2002c), and was undertaken with the explicit purpose of clearing up the nomenclature of the genus. I have revised the species, redefined the genus based on a phylogenetic analysis of the tribe, provided descriptions, illustrations, a key, as well as documented the distribution of the species.

Taxonomic History

The genera *Phloeodes* LeConte and *Noserus* LeConte were originally described for species described in *Nosoderma* Solier 1841. The taxonomic histories of the 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 (2002c) restored it to synonymy following Ślipiński and Lawrence (1999), but little actual analysis of this question has been conducted.

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. The genus *Nosoderma* Solier, occurring in Central America, was not included in LeContes' 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 (*Noserus*, *Nosoderma*, and *Phloeodes*).

The only attempted revision of the components of *Phloeodes* was conducted by Casey (1907a, 1907b). In these two papers Casey described 6 new species of California *Phloeodes*: *P. latipennis* 1907a, *P. ovipennis* 1907a, *P. elongatus* 1907a, *P. scaber* 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 in *Phloeodes*. 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, therfore Casey (1907b) designated *Phloeodes diabolicus* as the type species. To date, only one of the Casey names, *Phloeodes latipennis*, has been synonymized. It was listed as junior synonym of *Phloeodes pustulosus* by Gebien (1936).

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 decribed 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 very useful in defining species limits.

The most recent species addition to the genus was *Noserus doyeni* García-París et al. (2001) from Nuevo Leon, Mexico. The confusion surrounding the valid names in California *Noserus* species has been noted by García-París et al. (2001), who published a key to species of adult *Noserus* without including the Casey species. They stated that these species are a "group of poorly defined forms allied to *Noserus plicatus*, which do not deserve a specific taxonomic status because most of their diagnostic characters are variable features widespread along the geographic range" (García-París et al 2001). However, they never formally synonymized the names, leaving them in limbo.

This group has proven to be a perfect example of Casey's approach to species description, where he describes individual specimens rather than true species. Triplehorn (1972) gave an excellent critical review of the genus *Zopherus*, in which he retained only one of the 23 species described by Casey, recognizing a maximum of seven synonyms for a single previously-described species (*Zopherus gracilis* Horn).

At the generic level, I have found that two of four valid species (*Noserus* *emarginatus* and *Noserus doyeni*) do not belong to either available generic name, but rather belong to a genus mistakenly synonymized elsewhere. Thus, at the beginning of this study the genus *Phloeodes* (=*Noserus*) contained 14 validated species names with only one published synonym. Virtually all of these names are unused in collections and the literature, and no available resources existed that provided any characteristics by which species-level decisions could be made. In their genera of Zopherinae (*sensu lato*), Doyen and Lawrence (1979) stated there were only eight valid names in this group, two in *Phloeodes* and six in the old *Noserus*, but they published no synonymies and did not indicate which species names were in fact valid.

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 two described species that occur outside of California, *Noserus emarginatus* from Texas [possibly Northern Mexico (García-París et al. 2000)] and *Noserus doyeni*, 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 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 of Central America. The placement of the eastern species in *Noserus* has recently been questioned (García-París et al. 2000), and some similarities with species of *Nosoderma* have been acknowledged but without action. Horn (1878) mentioned a general similarity in sculpture between *Noserus emarginatus* and *Meralius echinatus* (Guérin-Méneville) from Cuba but did not suggest any actual relationship between these species, but probably recognized differences from the California species.

These two species of "*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 *Nosoderma* 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* Casey NEW SENSE as *Sesaspis emarginatus* (Horn) NEW COMBINATION and *Sesaspis doyeni* (García-París et al.) NEW COMBINATION (see previous chapter for further discussion). In the process of resolving this quandary, the species currently placed in *Nosoderma* were examined, and unexpectedly an additional species belonging to *Phloeodes* was discovered. *Nosoderma venustus* was described from Guatemala by Champion (1884), and is here recognized as a member of *Phloeodes*.

The results of a phylogenetic analysis of the Zopherini (Chapter 2, above) have led to significant changes in the membership of *Phloeodes* proposed here. The two *Phloeodes* species from the Gulf of Mexico region (*emarginatus* and *doyeni*) were found to belong to a group with members in *Nosoderma*, but that cluster together as a separate linage. Those species are now to be placed in a reconstituted *Sesaspis* Casey.

Phloeodes (*sensu strictu*) 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 to be 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*, was called the "finest and most distinct" of all the Central American species (Champion 1884), so it is also readily identifiable. Limiting the valid species names in California to two, while synonymizing nine of Casey's names and one of LeConte's, will hopefully clear up some of the confusion surrounding these large and very interesting beetles.

The reader is referred to Chapter 2 for methods and detailed results of the phylogenetic analysis and rationale for these actions.

Materials

The current study was based on the examination of over 5,000 adult specimens including all types of the genus *Phloeodes*, as well as an equal number of related genera. Adults of the two California species recognized here are relatively common and are very well represented in museum collections. In contrast, the Texan, Mexican, and Central American species are far less collected. The following numbers of adults of each species were examined: *Phloeodes diabolicus* (n=3,875), *Phloeodes plicatus* (n=1035), *Phloeodes venustus* (n=21), *Sesaspis doyeni* (n=113), *Sesaspis emarginatus* (n=70). The availability of adult specimens was sufficient to complete a thorough examination of morphology and delimit each species.

The material for this investigation was obtained on loan from most of the North American entomological collections, as well as many collections in Europe, and a few Central American collections. Specimens were obtained from the following institutions and collections (the curator responsible for the loan is listed in parenthesis):

AAPC - Albert Allen Personal Collection, Boise, Idaho (Albert Allen).
ASUT - Arizona State University, Tempe, Arizona (David Pearson).
BMNH - The Natural History Museum, London, United Kingdom (Maxwell V. L. Barclay).
BPBM - Bernice P. Bishop Museum, Honolulu, Hawaii (Alistair S. Ramsdale).
BYUC - Brigham Young University, Provo, Utah (Shawn M. Clark)
CASC- California Academy of Sciences, San Francisco, California (Norm Penny and David H. Kavanaugh).
CHICO - Chico State University, Chico, California (Donald Miller).
CMNC - Canadian Museum of Nature, Ottawa, Ontario (François Génier).
CNCI - Canadian National Collections of Insects, Ottawa, Ontario (Patrice Bouchard).
CSCA - California State Collection of Arthropods, Sacramento, California (Chuck Bellamy).
CSUC - Colorado State University, Fort Collins, Colorado (Boris C. Kondratieff).

DBTC - Donald B. Thomas Personal Collection, Weslaco, Texas (Donald Thomas).

DEI-ZALF - Deutsches Entomologisches Institut (DEI) in Leibniz-Zentrums für Agrarlandschaftsforschung (ZALF), Müncheberg, Germany.

DKYC - Daniel K. Young Personal Collection, Madison, Wisconsin (Daniel K. Young).

EMEC - University of California, Berkeley, California (Cheryl Barr).

ENMU - Eastern New Mexico University, Portales, New Mexico (Darren A. Pollock).

FMNH - Field Museum, Chicago, Illinois (James H. Boone)

FSCA - Florida State Collection of Arthropods, Gainesville, Florida (Paul E. Skelley).

HNHM - Hungarian Natural History Museum, Budapest, Hungary (Otto Merkl).

HUMB - Humboldt State University, Arcata, California (Michael Camann).

IEXA- Instituto De Ecología, A.C., Xalapa, Veracruz, Mexico (Miguel Angel Morón Ríos).

INBC - Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica (Angel Solís).

INHS - Illinois Natural History Survey, Champaign (Colin Favret).

IRCW - University of Wisconsin, Madison, Wisconsin (Steven Krauth).

JEWC - James E. Wappes Personal Collection, Bulverde, Texas (James E. Wappes).

LACM - Natural History Museum of Los Angeles County, Los Angeles, California (Weiping Xie).

LSAM - Louisiana State Arthropod Museum, Baton Rouge, Louisiana (Victoria Bayless).

LUND - Lund University, Lund, Sweden (Roy Danielsson).

MAIC - Michael A. Ivie Private Collection, Bozeman, Montana (Michael. A. Ivie).

MCPM - Milwaukee Public Museum, Milwaukee, Wisconsin (Susan Borkin).

MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (Philip D. Perkins).

MNHN - Museum National d'Histoire Naturelle, Paris, France.

MIZ - Museum and Institute of Zoology, Polish Academy of Sciences, Warszawa, Poland (Wioleta Tomaszewska).

MSUC - Michigan State University, East Lansing, Michigan (Gary L. Parsons).

MTEC - Montana Entomology Collection, Montana State University Bozeman (Michael A. Ivie).

NHMB - Natural History Museum Basel, Switzerland (Michael Brancucci and Eva Sprecher).

NHMW - Naturhistorisches Museum Wien, Vienna, Austria (Heinrich Schönmann).

NMPC - National Museum of Natural History, Prague, Czech Republic (Svatopluk Bílý).

OSAC - Oregon State Arthropod Collection, Oregon State University, Corvallis (Andrew Brower).

RLAC - Rolf L. Aalbu Personal Collection, Sacramento, California (Rolf L. Aalbu).

ROME - Royal Ontario Museum, Toronto, Ontario (Brad Hubely).

SBMN - Santa Barbara Museum of Natural History, California (Michael S. Caterino).

SEMC - Snow Entomological Collections, University of Kansas, Lawrence (Zachary H. Falin).

SMDV - Spencer Entomological Museum, University of British Columbia, Vancouver (Karen M. Needham).

TAMU - Texas A&M University, College Station (Edward G. Riley).

UTSC -Utah State University, Logan (Colin Brammer).

UCDC - Bohart Museum of Entomology, University of California-Davis (Steve L. Heydon).

UCMC - University of Colorado Museum, Boulder (Virginia Scott).

UCRC - University of California-Riverside (Douglas Yanega).

UGCA - Georgia Museum of Natural History, Athens (Cecil L. Smith).

NMNH - National Museum of Natural History, Washington D.C. (Warren E. Steiner)

WFBM - William F. Barr Entomological Museum, Univ. of Idaho, Moscow (Frank W. Merickel).

WSUC - Washington State University, Pullman (Richard Zack).

ZIN - Russian Academy of Sciences, St. Petersburg (Mark G. Volkovitsh).

Methods -- Morphology

This revision was based on morphological characters primarily of adult specimens following the operational species concept of Whitehead (1972). This concept hypothesizes that unique morphological characters have a genetic basis. These unique characters can be inherited, and therefore used to delimit species. The California species of *Phloeodes* are better defined and morphologically quite distinct when compared to other members of the subfamily, so initial sorting of the “species” was done based on general gestalt, and then specific characters were examined to delimit the species and generate a character set for phylogenetic analysis.

Frequently specimens of the tribe are encrusted with a greasy exudate as well as accumulated environment debris, such as sand and soil. 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. Dissection and disarticulation were used to study certain morphological characters (i.e. mouthparts, genitalia) of relaxed specimens.

Specimens were studied on 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 AutoMontage® 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 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 a single inserted setae, I use setose punctures to refer to these features following Harris (1979). Other sculpture terms 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).

Taxonomy of the Genus *Phloeodes* LeConte

(Figs. 63-74, 76-82, 99, 124)

Phloeodes LeConte 1862: 216. (Type species: *Nosoderma diabolicum* LeConte, 1851, designated by Casey 1907b). 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. Essig 1934: 110. 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 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 2002c: 458-461. Caterino 2004: 7.

Noserus LeConte 1862: 216. (Type species: *Nosoderma plicatum* LeConte, 1859, by monotypy). Synonymy by Ślipiński and Lawrence (1999). 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 1981: 145. Arnett 1985: 350. Ślipiński & Lawrence 1999: 19. García-París et al. 2000: 473. García-París et al. 2001: 151-153. Ivie 2002: 461.

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

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

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

Noserodes [in part] Gebien 1936: 670.

Diagnosis: The current phylogenetic analysis supports this group based on the synapomorphy of a well-developed glabrous tarsal strip (Fig. 71), this character also occurs as a homoplasy in the distantly related *Zopherus*, and weakly in some *Nosoderma*, but *Zopherus* has 9-segmented antennae (10 in *Phloeodes*) and *Nosoderma* has no hint of an antennal cavity (well developed in *Phloeodes,* Figs. 67-70). This genus is very closely related to the genus *Nosoderma* Solier, 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. The third member of the genus, *Phloeodes plicatus* is uniformly colored, but has a unique antennal cavity structure that is distinct but not clearly limited in the posterior margin (Fig. 68).

Description (male): 9.5-29 mm. Body elongate and subcylindrical, dark brown, gray to black, often with whitish vestiture on portions or majority of elytra. Dorsal surface densely granulose, covered with small black tubercles bearing single laterally inserted golden setae; secondary vestiture consisting of short appressed setae dark to white; arcuate velvety spots often present; elevated ridges and tubercles distinct to absent.

Head inserted into prothorax to subgenal ridge; not constricted behind eyes; eyes transverse, slightly emarginate; interfacetal setae absent; occiput with median longitudinal ridge; frontal ridges clearly raised above antennal insertions; subgenal ridge strong. Antenna 10-segmented; relatively short, not extending beyond middle of pronotum; antennomere 2 transverse, shorter than 1 or 3; antennomere 3 quadrate, longer than wide; antennomere 9 with anterior slightly protruding smooth area; weakly developed 1- or 2- segmented club; antennomere 10 with micro-setose field covering entire apex, visible laterally; antennomeres with regularly spaced bristles. Gular suture arcuate; tentorial pits near base along suture, small rounded to slightly elongate; gular incisions u-shaped; mentum narrowed anteriorly, anterior edge sharply emarginate; ventrally setose; submentum without setose pit. Labrum transverse, margin rounded, fringed with golden setae; labial palps inserted laterally (Fig. 76-77); maxillae with lacinia and galea densely covered with golden setae; mandible bidentate, without membranous prostheca, more than half of basal portion strongly punctured laterally, apex smooth.

Pronotum with anterior edges produced forwards; lateral margins arcuate; disc with shallow depressions, and weak arcuate ridges; prothoracic hypomera with distinct antennal cavities or shallow depression, complete or not (Fig. 67-70); prosternum with deep pits to shallow depression along inner margin on prosternal suture; prosternal process concave; procoxal cavities externally closed (Fig. 67-68).

Flight wings absent; suture distinct but elytra fused; scutellum not externally visible; dorsum of elytra with irregular punctures and small black tubercles, often with paired velvety patches or elevated ridges; tip of elytra at most slightly emarginate.

Femora with small black tubercles covering surface; tibia with moderate to weak setose ridges, with slightly too strongly expanded distal nodule containing tuft of golden setae extending between paired apical spurs; setose nodules on inner surface of all femora (Fig. 79-82); tarsal formula 5-5-4; tarsi with all segments bearing rows of golden setae with median area with glabrous strip (Fig. 71); last segment with simple but strong claws (Fig. 78).

Metasternum sub-equal in length to abdominal V1; intercoxal process of abdominal V1 broad; abdomen with ventrites 1 to 4 connate, 5 free; all with irregular small black tubercles on surface; V5 with irregular semicircular preapical groove. Male genitalia (Figs. 72-74) with basal piece scoop shaped; parameres fused basally, strongly to weakly emarginate at tip, with tufts of setae. Median lobe narrow, acute.

Female: Differs from male in lacking nodules near base on the ventral surface of the femora.

Larva: (see description of the larva of *Phloeodes diabolicus* below).

Notes: The inclusion of *Phloeodes venustus* in this genus is based on the absence of a membranous mandibular prostheca (which excludes it from *Nosoderma*), presence of tubercles on all body surfaces (which excludes if 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.

Synoptic Catalog of *Phloeodes* Species

Phloeodes LeConte *1862*
        Ageonoma Pascoe *1866*
        Noserus LeConte 1862
    P. diabolicus (LeConte) 1851
        P. pustulosus (LeConte) 1859, NEW SYNONYMY
        P. latipennis Casey 1907a, synonomy by Gebien 1936
        P. ovipennis Casey 1907a, NEW SYNONYMY
        P. elongatus Casey 1907a, NEW SYNONYMY

P. scaber Casey 1907a, NEW SYNONYMY

P. angustus Casey 1907a, NEW SYNONYMY

P. remotus Casey 1907b, NEW SYNONYMY

P. plicatus (LeConte) 1859

Noserus torvus Casey 1907a, NEW SYNONYMY

Noserus collaris Casey 1907a, NEW SYNONYMY

Noserus corrosus Casey 1907b, NEW SYNONYMY

Noserus convexulus Casey 1907b, NEW SYNONYMY

P. venustus (Champion) 1884, NEW COMBINATION

Biology

A general evolutionary trend towards wood boring larvae has been suggested in the Zopherini (Triplehorn 1972, Doyen and Lawrence 1979, Doyen 1976, Ślipiński and Lawrence 1999, Ivie 2002c). 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*) and was suggested as a nonspecific decomposer that probably 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. with M. A. Ivie).

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. 81-82). 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 feigndeath (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).

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. 67, 69); 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. 63, 64. ……………………………………………………...……..*P. diabolicus* (LeConte)

1'. Prothoracic hypomera with deep antennal cavities that are incomplete and not limited posteriorly (Fig. 68), or broad shallow depression (Fig. 70); elytral vestiture variable; elytra with three distinct nodules at start of declivity, two offset medially, and one laterally. ……….……………………………………………..2

2\. (1'). Prothoracic hypomera with deep antennal cavity that is not limited posteriorly (Fig. 68); 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. 65. ……………………………………...…....*P. plicatus* (LeConte)

2’. (1’). Prothoracic hypomera with shallow depression, lacking distinct cavity (Fig. 70); 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 over 20mm. Central America. Fig. 66……...……*P. venustus* (Champion)

Species Descriptions

Phloeodes diabolicus (LeConte)

(Figs. 7, 63-64, 67, 69, 72, 76, 79, 81, 99)

Nosoderma diabolicum LeConte 1851: 130. LeConte 1853: 235. LeConte 1857: 49; pl. 2. LeConte 1859: 77. Pascoe 1866: 487. Heyden 1885: 307.

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.

Type Material: LECTOTYPE here designated: ♂ intact. Hand written *Phloeodes* diabolicus (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 LeConte 1859: 77.

Phloeodes pustulosus: Horn 1870: 273. Casey 1907a: 43. Leng 1920: 223. Essig1926: 428. Gebien 1936: 668. Doyen 1980: 3. Arnett 1983: 16. White 1983: 250. Hogue 1993: 296, 298. Ivie 2002c: 461. NEW SYNONYMY.

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

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

Phloeodes ovipennis Casey 1907a: 42. Casey 1907b: 472. Leng 1920: 223. Gebien 1936: 667. Arnett 1983: 16. NEW SYNONYMY.

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

Phloeodes elongatus Casey 1907a: 42. Casey 1907b: 472. Leng 1920: 223. Gebien 1936: 668. NEW SYNONYMY.

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

Phloeodes scaber Casey 1907a: 43. Casey 1907b: 472. Leng 1920: 223. Gebien 1936: 668. Arnett 1983: 16. NEW SYNONYMY.

Type Material: LECTOTYPE, here designated: ♂, intact in USNM. 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 Casey 1907a: 43. Casey 1907b: 472. Leng 1920: 223. Gebien 1936: 668. Arnett 1983: 16. NEW SYNONYMY.

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

Phloeodes remotus Casey 1907b: 472. Leng 1920: 223. Gebien 1936: 668. Arnett 1983: 16. NEW SYNONYMY.

Type material: LECTOTYPE, here designated: ♂, right meta-tarsus missing in USNM. 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 show the following variation: *Phloeodes remotus* is densely clothed through out with a gray-brown vestiture, the velvety spots of the elytra 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, *Phloeodes scaber* the prothorax is narrower than the elytra, the pronotum is strongly elevated along median third, the slopes of the median elevation on the prothorax slightly concave and devoid of tubercles, *Phloeodes elongatus* the prothorax is elongate, the finer tubercles are aggregated slightly stronger arcuate ridges, the elytral velvety spots are large and distinct, *Phloeodes ovipennis* with paler grayish vestiture, the central velvety spot slightly arcuate and oblique, the basal short, the dorsal surface of the head with smaller tubercles.

Diagnosis: The presence of large antennal cavities that are clearly limited posteriorly and completely contain the antennae while in repose (Fig. 69), 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 (male): Length 12.5-24 mm. Dark gray to black; usually black, occasionally with whitish vestiture on elytral humeri, coxae, apical ventrites and lateral portions of apical declivity. Pronotum .80-.95 X as long as broad, sides arcuate, widest slightly anterior of midline, anterior angles produced forward and rounded, margin narrowed towards base, hind angles obtuse; prothoracic hypomeron with large distinct antennal cavities that completely contain the antennae. Elytra 1.50-1.85 X as long as broad, and 1.7-2.0 X as long as pronotum; dorsal profile of elytra rounded; base of elytra frequently with depressed area containing black velvety vestiture, and variable series of black velvety patches along length of elytra; dorsal surface densely granulose; usually without distinct elevations or ridges; rarely with single raised tubercle at start of apical declivity. Ridges of dark setae usually visible on tibia; tibial setae inserted in tubercles dark in color. Male nodules present on all femora (Fig. 79, 81). Parameres strongly emarginate at tip, sides produced forward and slightly sharpened, tuft of setae long (Fig. 72).

Larva: (modified from Doyen 1976). Body elongate up to 51mm when extended, white or creamy in color; head, pronotum, asperities, and legs lightly sclerotized; tarsal claws, urogomphi, and mouthparts heavily sclerotized.

Head subquadrate, dorsoventrally flattened, prognathus, with sparse patches of short setae, stemmata absent, frontal arms V-shaped. Antennae 3-segmented anterolaterally inserted. Mandibles large, prognathus, apical tip bidentate, incisor lobe multidentate, mola distinct with series of ridges on lateral surface. Maxilla thick and fleshy, with apical setae; cardo bifid.

Prothorax enlarged, partly containing head when retracted. Meso and metathorax with arcuate rows of asperites; spiracles annular-biforous.

Abdominal segments rounded; first 2 segments with rows of asperities; 9 with short recurved urogomphi. Legs short, 5 segmented; coxae large and transverse, claw basally thickened.

Notes: Gebien (1936) listed a single Casey species, *Phloeodes latipennis*, as a synonym of *Phloeodes pustulosus* (LeConte), but did not address any of the other species in this genus. The remaining Casey species are all 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 than 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*.

The only non-Casey synonymy proposed is that of *Phloeodes pustulosus*. When LeConte described this species (1859) 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. 64) or absence (Fig. 63) of the whitish vestiture on the elytral humeri, apical declivity, and on the apical ventrites. 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 south in Mexico have a greater proportion of the dorsal surface black (Triplehorn 1972).

Fig. 7. The distribution of *Phloeodes diabolicus*.

Distribution: California Floristic Province as far north as Shasta Co, east possibly all the way to the edge of Arizona (6 specimens: 4 AZ label only, 1-Yuma, 1-“Grand Canon”/VII-1924; Van Dyke), and south into Baja Mexico, Norte. 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.

Phloeodes plicatus (LeConte)

(Figs. 8, 65, 68, 73, 77, 78, 80, 82)

Nosoderma plicatum LeConte 1859: 77. LeConte 1862: 216. LeConte and Horn 1883: 365.

Noserus plicatus: Horn 1870: 273. Casey 1907a: 44. Leng 1920: 223. Gebien 1936: 668. Doyen 1980: 3. Arnett 1981: 145. Arnett 1983: 16. Arnett 1985: 350. Ślipiński and Lawrence 1999: 19. García-París et al. 2000: 473. Milne 2000: 585, pl. 224 (excepting plate of *Phellopsis porcata* LeConte). García-París et al. 2001: 151-153. Ivie 2002: 461.

Phloeodes plicatus: Ivie 2002c: 461.

Type Material: 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 Casey 1907a: 44. Leng 1920: 223. Gebien 1936: 668. Arnett 1983: 16. NEW SYNONYMY.

Type Material: LECTOTYPE, here designated: ♀, intact in USNM. 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.

Noserus collaris Casey 1907a: 44. Leng 1920: 223. Gebien 1936: 668. Arnett 1983: 17. NEW SYNONYMY.

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

Noserus corrosus Casey 1907b: 474. Leng 1920: 223. Gebien 1936: 668. Arnett 1983: 17. NEW SYNONYMY.

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

PARALECTOTYPE *Noserus*; ♀ *corrosus*; Casey 1907; designated; I.A. Foley 2006.

Noserus convexulus Casey 1907b: 474. Leng 1920: 223. Gebien 1936: 668. Arnett 1983: 17. NEW SYNONYMY.

Type Material: HOLOTYPE ♀, missing several tarsi in USNMM. Cal(ifornia)/ Casey; bequest; 1925/ orange rectangle Type USNM; 46383/ hand written convexulus Csy./ red square HOLOOTYPE *Noserus*; ♀ *convexulus*; Casey 1907; designated; I.A. Foley 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 (male): 9.5-19mm. Uniformly dark reddish brown, gray to black; usually grayish, never with any whitish vestiture, rarely light area around scutellum. Pronotum .90-.95 X as long as broad; lateral margins of pronotum with dense tubercles. Elytra 1.45-1.65 X as long as broad, 1.7-1.9 X as long as pronotum; sculpture distinct, consisting of arcuate ridges and tubercles, especially strong in apical third and laterally; short ridge in 3rd elytral interval; longer arcuate ridge in 5th, pointing at v-shaped nodule; three distinct nodules at apical declivity. Dorsal profile of elytral apical declivity, square shaped. Antennal cavities present but not complete, large depression along prosternal suture. Ridges of dark setae on tibia usually indistinct; tibial setae inserted on tubercles golden in color. Mentum, labium (Fig. 77). Male femoral nodules (Fig. 80, 82). Parameres weakly and shallowly emarginate at tip, sides not produced forward, tuft of setae moderately short (Fig. 73).

Female: Similar to male except lacking nodule on femora.

Larva: Unknown.

Notes: 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 *Phloeodes 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.*

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

Fig. 8. The distribution of *Phloeodes plicatus*.

Phloeodes venustus (Champion) NEW COMBINATION

(Figs. 66, 70, 71, 74)

Nosoderma venustus Champion 1884: 45.

Noserodes venusta: Casey 1907b: 481. Gebien 1936: 670. Blackwelder 1945: 515. Arnett 1983: 16.

Type material examined: *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.

Diagnosis: Large elongate species is distinguished from all Zopherini with 10-segmented antennae by lacking a scutellum, having tubercles on the ventral 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.

Description (male): Length 22-29 mm. Dorsal vestiture mottled tomentose, whitish to black, with granulate tubercles with single inserted setae. Pronotum 1.00-1.10 X as long as broad, sides arcuate, widest slightly anterior of midline, anterior angles produced forward and rounded, margin weakly narrowed towards base, hind angles obtuse. Prothoracic hypomeron with large shallow depressions (Fig. 70); tuberculation absent or obviously reduced in depression. Elytra elongate, 1.89-2.15 X as long as broad, and 1.75-2.0 X as long as pronotum; dorsal profile of elytra slightly flattened; area along suture and/or elevated ridges with irregular dark brown to black velvety patches. Tibia with weak ridges with golden setae; setae of legs inserted in very small tubercles; vestiture on legs consisting of mottled dark and light patches. Male nodules present on all femora, with only a few inserted setae; tibia with strongly expanded distal nodule with median depression containing tuft of golden setae extending between paired apical spurs.

Parameres strongly emarginate at tip, sides strongly produced forwards and rounded, setose tuft long.

Female: Similar to male except lacking nodule on femora.

Larva: Unknown

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 distinct species.

Fig. 9. The distribution of *Phloeodes venustus*.

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

Biogeography

The genus *Phloeodes* as currently defined occupies two disjunct geographic areas; the California Floristic Province (CFP), where it occurs from northern California (as far north as Shasta County) south into northwestern Mexico (Baja California, Norte) and Central America. In the CFP, specimens have been recorded from the Coastal, Transverse, and Peninsular ranges, as well as the Central Valley, Sierra Nevada and Channel Islands (*Phloeodes plicatus*). In California species are most commonly associated with oak woodlands.

The uniqueness and biodiversity value of CFP is without question (Mittermeier et al. 2004). It encompasses a biologically rich and threatened eco-region defined by its Mediterranean-type vegetation and climate (Dallman 1998, Mittermeier et al. 2004). The climate type consists of mild, wet winters and hot, dry summers (Dallman 1998). The distinctive climate and topography of the area support a region that is home to over 30% of the known insect species north of Mexico (Calsbeek et al. 2003).

Due to the habitat complexity of the CFP, a variety of phylogeographic studies have been conducted on the genetic structure of animal populations to determine if broad biogeographic patterns can be applied to the region (Calsbeek et al. 2003). These studies indicate that there have been three significant topographic barriers that have influenced population structure and variation: the Plio-Pliestocene inundation of the Monterey delta, the uplift of the Transverse ridge, and elevation of the Sierra Nevada (Maldonado et al. 2001, Calsbeek et al. 2003). While these barriers have not usually been significant enough to induce speciation events, they have influenced the genetic and morphological structure of some populations of animals. The Monterrey delta was probably a vast enough embayment to prevent the dispersal of large flightless beetles such as *Phloeodes*, as it has been suggested to have done in small vertebrates (Peabody & Savage 1958). Several vertebrate species show specific phylogeographic clades associated with the different northern and southern sub-regions (Wake 1997, Maldonado et al. 2001, Calsbeek et al. 2003).

Since species of *Phloeodes* exhibit a high degree of morphological diversity, patterns are difficult to decipher. The only significant variation that appears reasonably consistent is the presence of a dense whitish vestiture on portions of the elytra in Northern California populations of *Phloeodes diabolicus*. This coloration is certainly influenced by the activity of the animal, and can be found weakly in central California populations, and certainly does not merit species-level distinction. But the distribution of the variation could be an indication of a historical vicariance between populations divided by the Monterey delta. This pattern of distinction between northern and southern populations by the delta has been documented in the genetic structure of several vertebrates: the ornate shrew, *Sorex ornatus* (Maldonado et al. 2001), California Newt, *Taricha torosa* (Tan & Wake 1995), the plethodontid salamander, *Batrachoseps* (Yanev 1980), the California mouse, *Peromyscus californicus* (Smith 1978), the pocket gopher, *Thomomys bottae* (Patton & Smith 1994), and the California mountain kingsnake, *Lampropeltis zonata*, (Rodríguez-Robles et al. 1999). It is possible that a similar population structure could be seen in *Phloeodes diabolicus*, and research on the phylogeography of this species has recently been undertaken (M. S. Caterino pers. comm.).

In morphological phylogenetic analyses (Fig. 119, 120) *Phloeodes diabolicus* and *Phloeodes plicatus* come out supported as sister-species and it is interesting that they occur sympatrically throughout their range, despite being very distinct morphologically. The only area where the species are not known to co-occur is the slightly extended far northern edge of the range in *Phloeodes diabolicus,* and on the California, Channel Islands (Santa Cruz and Santa Catalina) where only *Phloeodes plicatus* is known. The presence of *Phloeodes plicatus* on the Channel Islands could be the result of recent colonization/introduction or historic isolation.

The inclusion of *Phloeodes venustus* in this genus significantly increases the known range of the genus. In the phylogenetic analysis of the genus, this species comes out as basal to the California clade. It is somewhat intermediate between the genus *Nosoderma*, and *Phloeodes*, but shares more characters with the later. The only observed character difference between the Central American *Phloeodes venustus* and the California species is the strength of the antennal cavity of which *Phloeodes plicatus* is intermediate between *Phloeodes venustus* (broad depression) and *Phloeodes diabolicus* (complete cavity). The taxonomy of this genus hopefully has been resolved, and the species here retained within the genus well defined.

Future Research

The California species of *Phloeodes* are one part of a group of beetles being investigated for general phylogeographic patterns in the California Floristic Province (M. S. Caterino pers. comm.). This project is based on molecular characters, and *Phloeodes diabolicus* and *Phloeodes plicatus* have both been sequenced for the mitochondrial gene cytochrome oxidase 1 (COI). Obtaining specimens of *Phloeodes venustus* for molecular analysis would be a huge step towards supporting, or rejection the morphologically supported hypothesis of its placement within *Phloeodes*.

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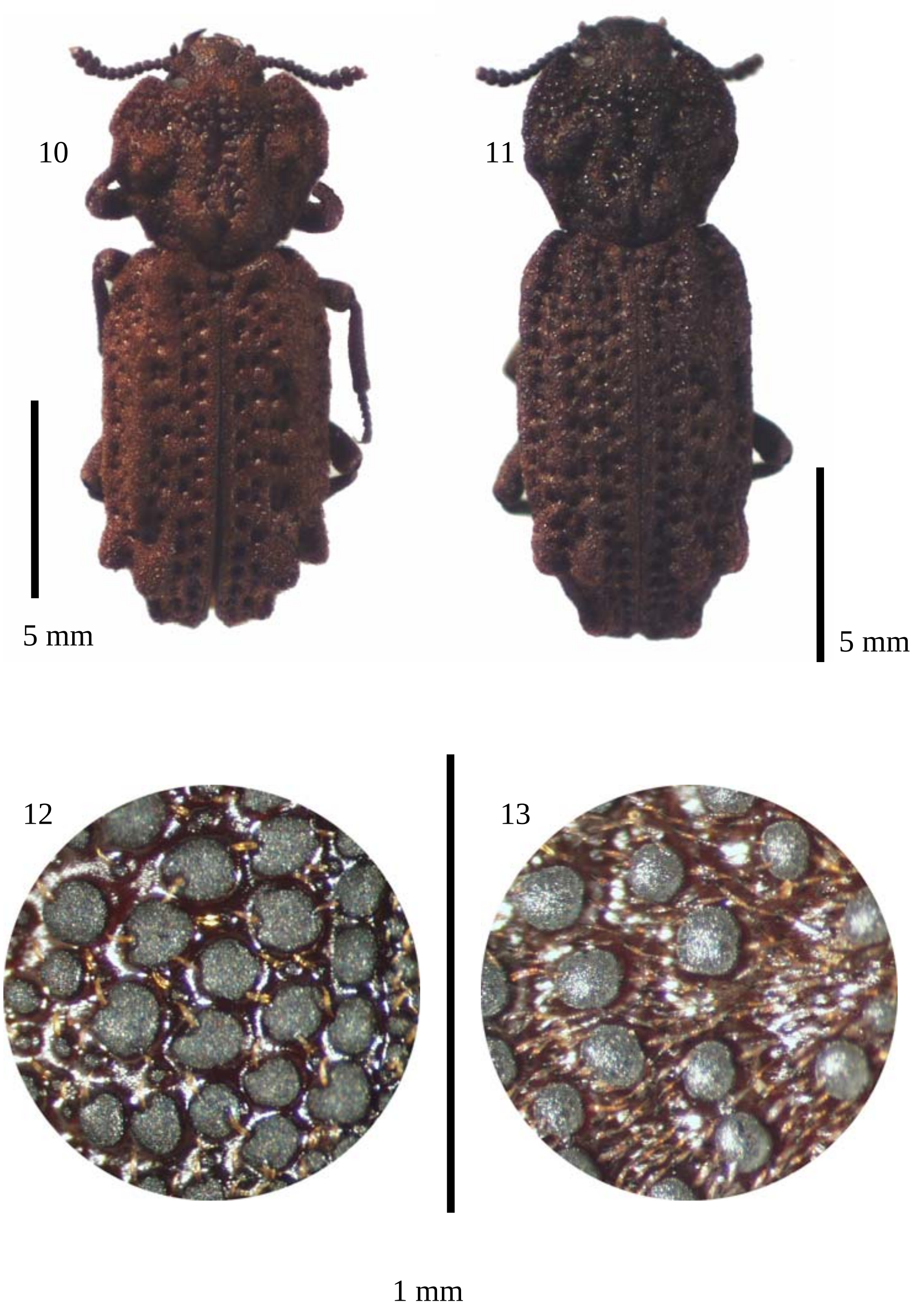

10. *P. obcordata* (Kirby) habitus, Canada, Quebec. 11. *P. porcata* (LeConte) habitus, Claifornia, Shasta Co. 12. *P. obcordata* hypomeron. 13. *P. porcata* hypomeron.

14. *P. amurensis* (Heyden) habitus, Russia. 15. *P. suberea* Lewis habitus, Japan, Honshu, Tochigi Pref. 16. *P. chinensis* (Semenow) habitus, China, Gansu Prov. 17. *P. yulongensis* Foley and Ivie habitus, China, Yunnan Prov.

18

19

18. *P. suberea* dorsal view of head. 19. *P. yulongensis* dorsal view of head.

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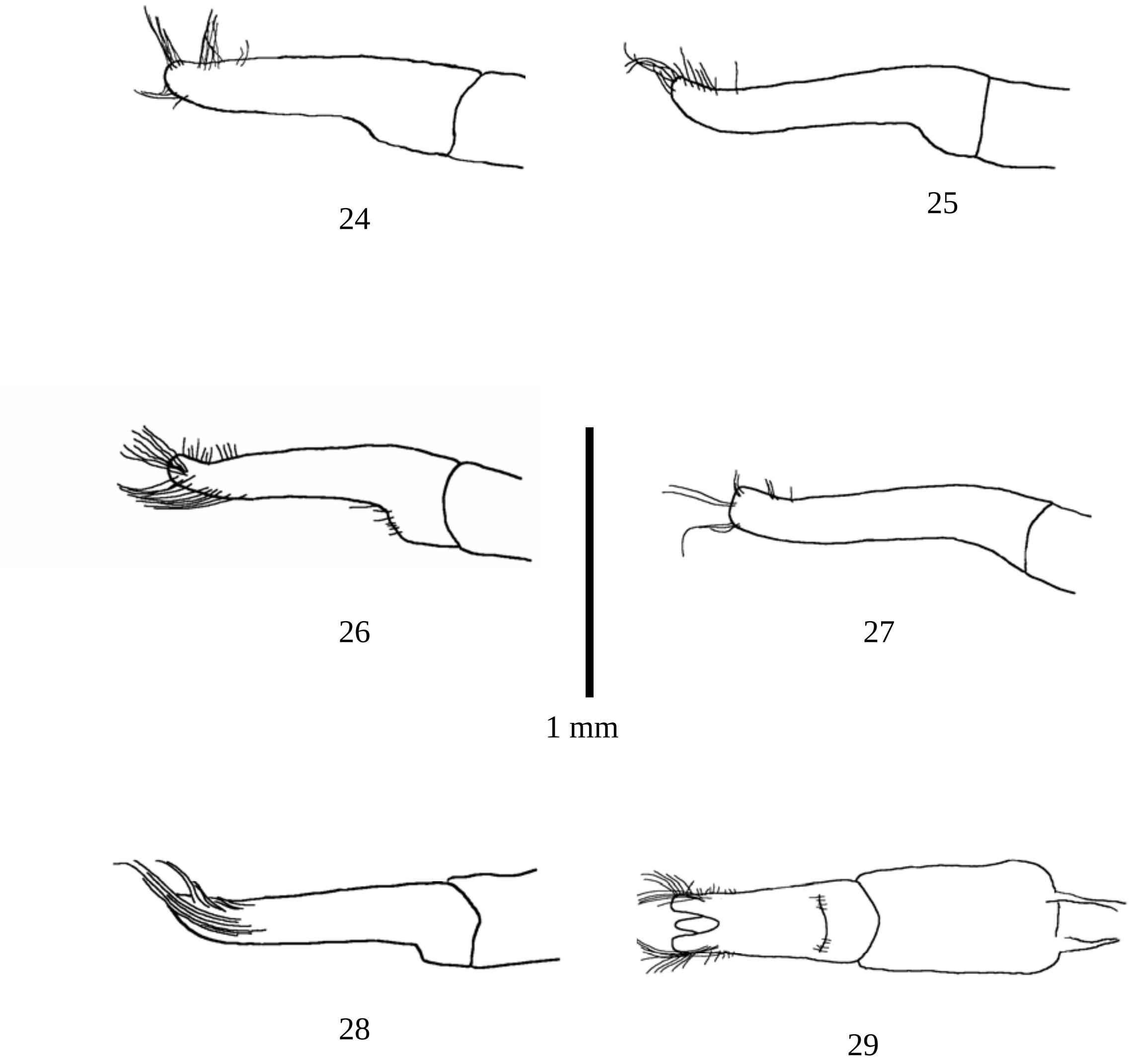
21

20. *P. amurensis* dorsal view of head. 21. *P. chinensis* dorsal view of head.

22. *P. obcordata* dorsal view of head. 23. *P. porcata* dorsal view of head.



24-29. 24-28, lateral views of male parameres. 24. *P. obcordata*, 25. *P. porcata*, 26. *P. yulongensis*, 27. *P. chinensis*, 28. *P. suberea.* 29. Ventral view of male parameres *P. yulongensis.*

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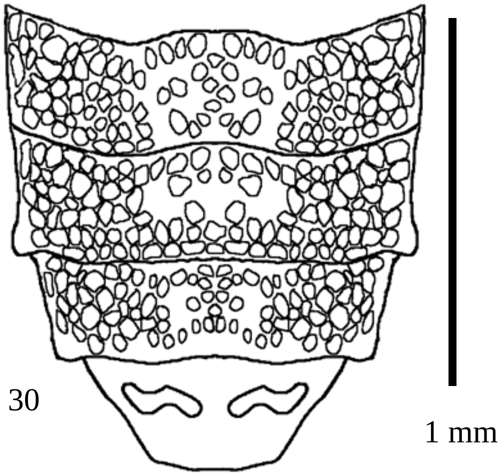

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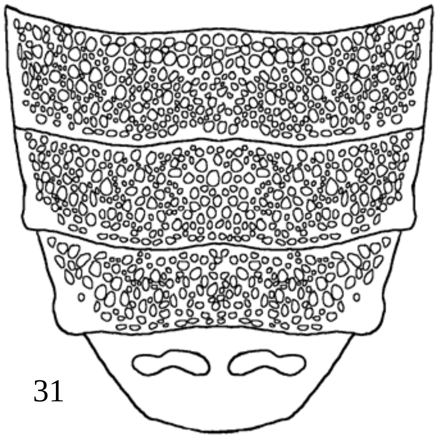

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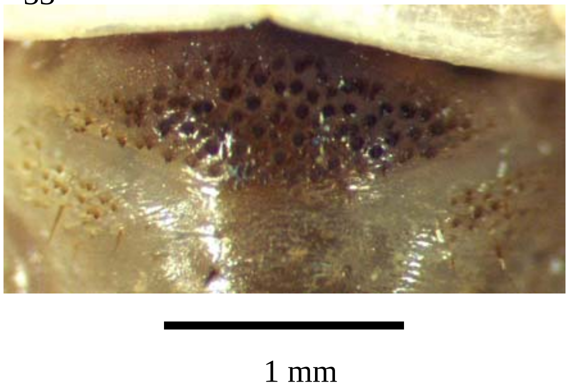
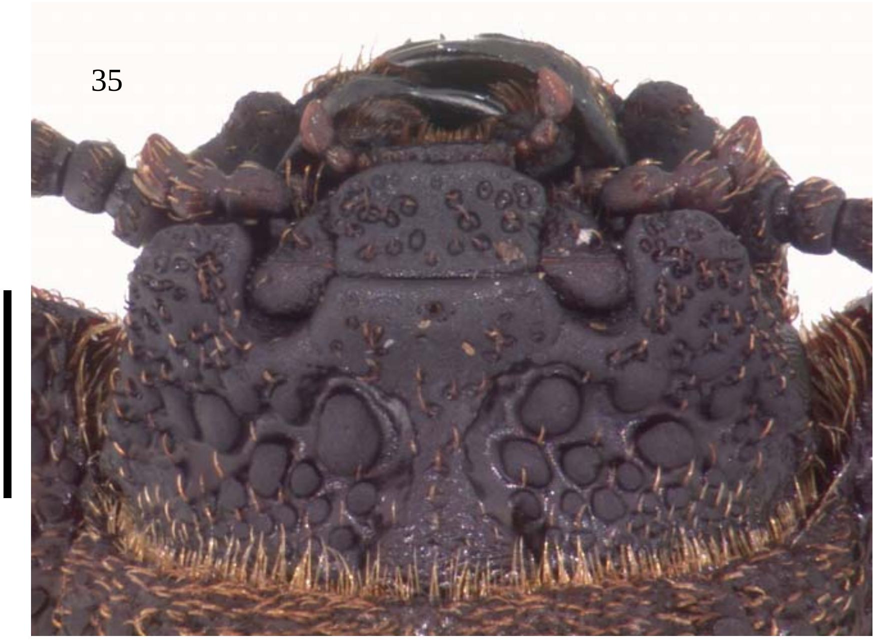


30. *P. chinensis* ventrites 2-5. 31. *P. yulongensis* ventrites 2-5. 32. *P. obcordata* ventral view of larval A8. 33. *P. porcata* ventral view of larval A8.



34. *P. yulongensis* ventral view of head. 35. *P. suberea* ventral view of head.

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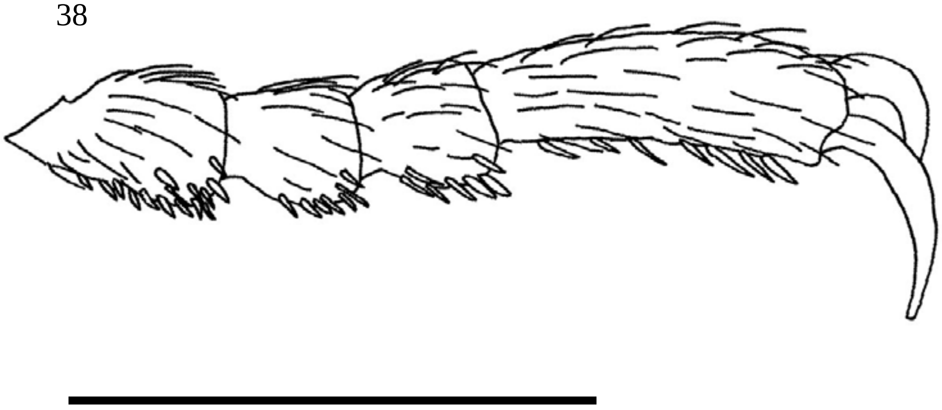
36. *P. chinensis* ventral view of head. 37. *Usechus lacerta* Motschulsky ventral view of head.

38



38. *P. chinensis* metatarsus.

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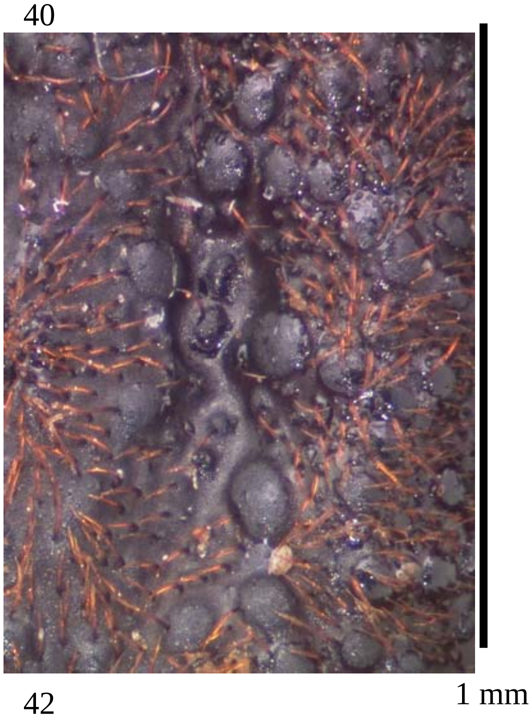

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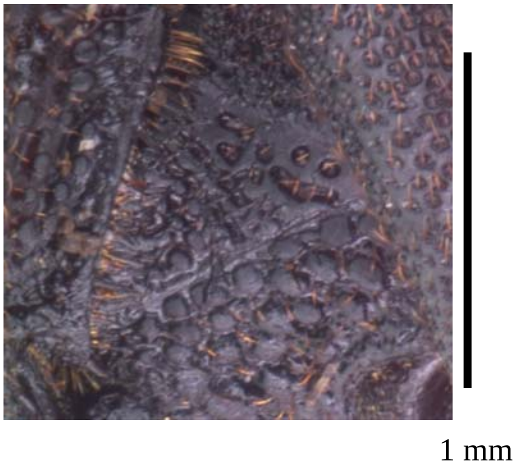
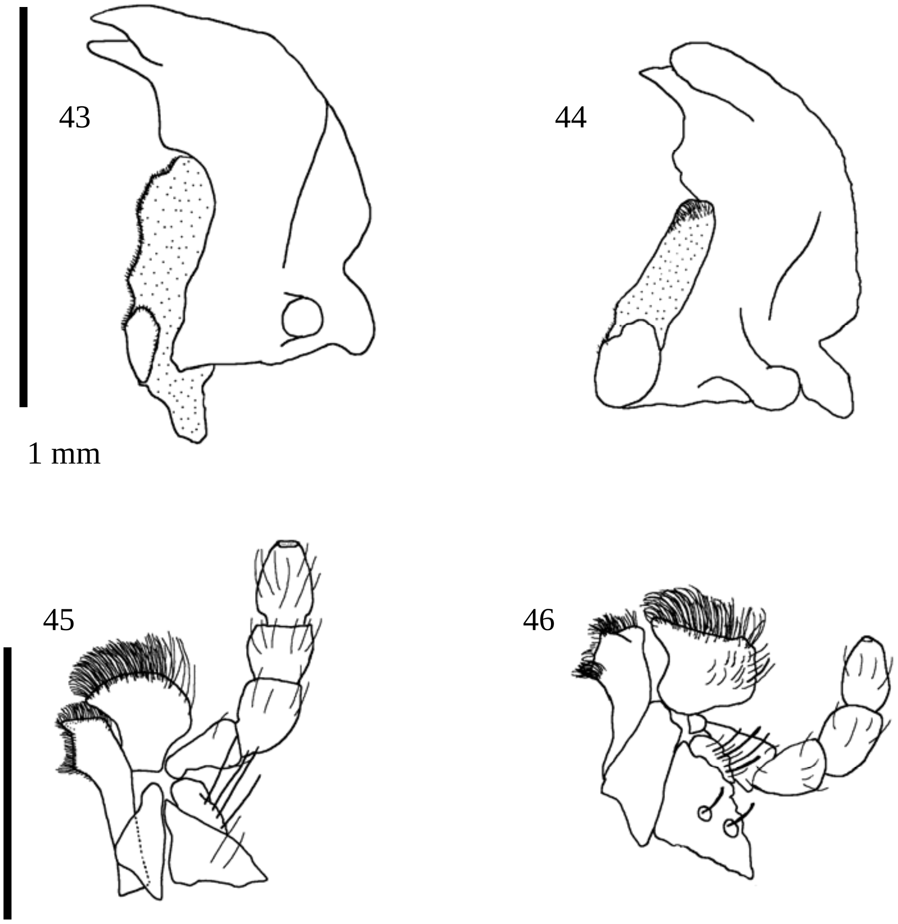


39. *P. chinensis* pronotal scale-like setae. 40. *P. yulongensis* pronotal hair-like setae. 41. *P. amurensis* mesepimeron. 42. *P. yulongensis* mesepimeron.



43. *P. yulongensis* mandible. 44. *P. suberea* mandible. 45. *P. yulongensis* maxilla. 46. *P. suberea* maxilla.

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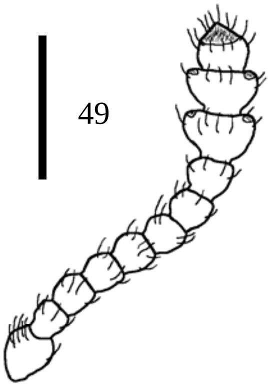


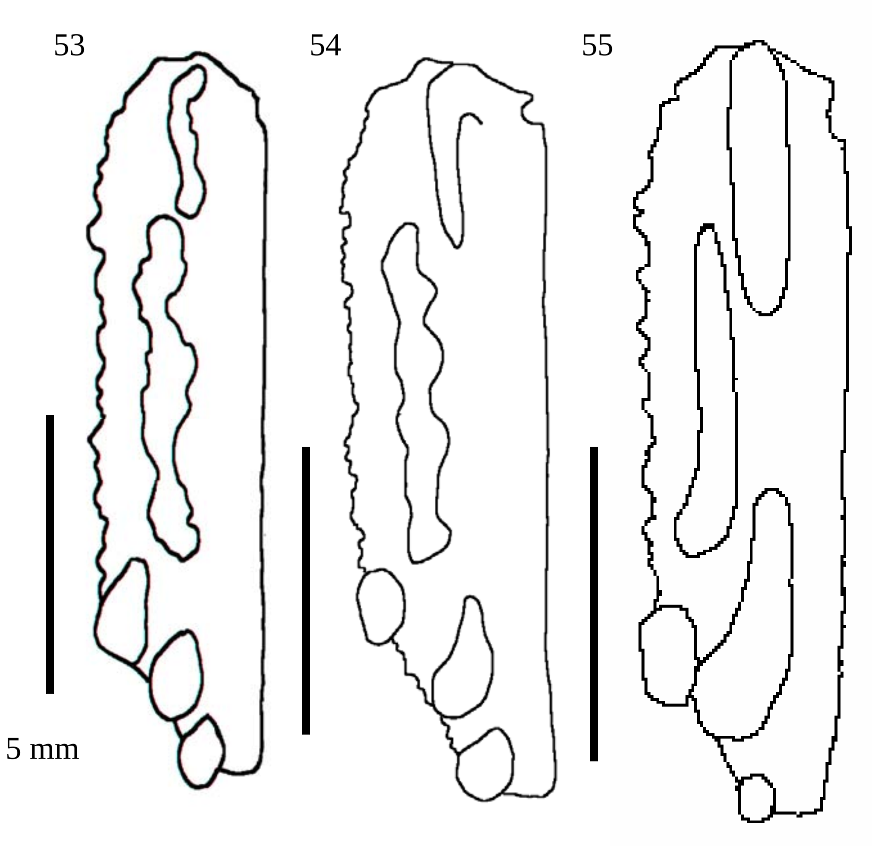
50

47. *P. chinensis* metasternum behind mesocoxa. 48. *P. obcordata* metasternum behind mesocoxa. 49. *P. yulongensis* antennae. 50. *P. porcata* female genitalia.

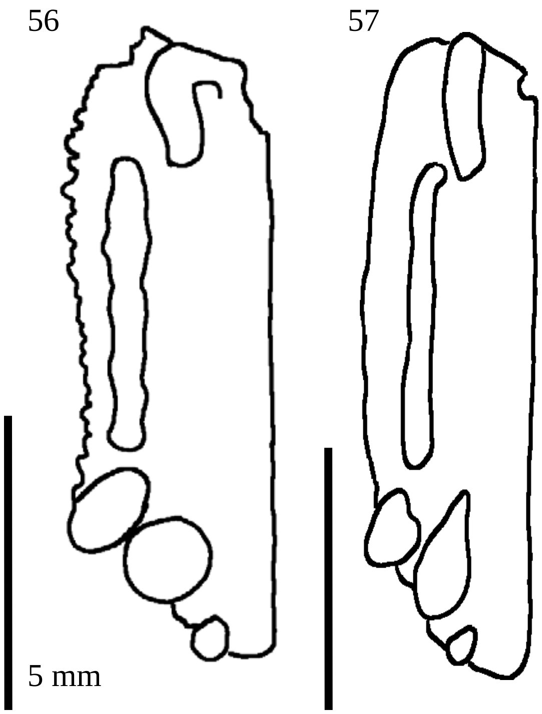
51

52

51. *P. obcordata* prosternal process. 52. *P. yulongensis* prosternal process.

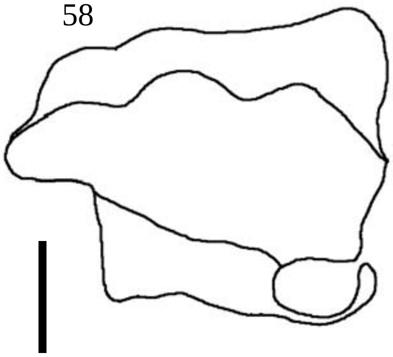


53-55, elytra showing ridges and nodules. 53. *P. chinensis*. 54. *P. yulongensis*. 55. *P. suberea*.



56-57, elytra showing ridges and nodules. 56. *P. amurensis*. 57. *P. obcordata.*

58



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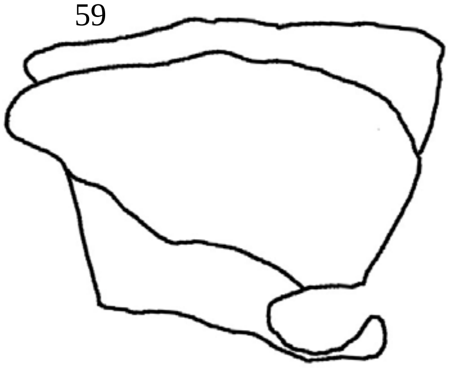

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61

58. *P. obcordata* lateral pronotal margin. 59. *P. porcata* lateral pronotal margin. 60. *Usechus lacerta* habitus California, Monterey Co. 61. *Hyporagus* sp. habitus B.W.I, Montserrat.

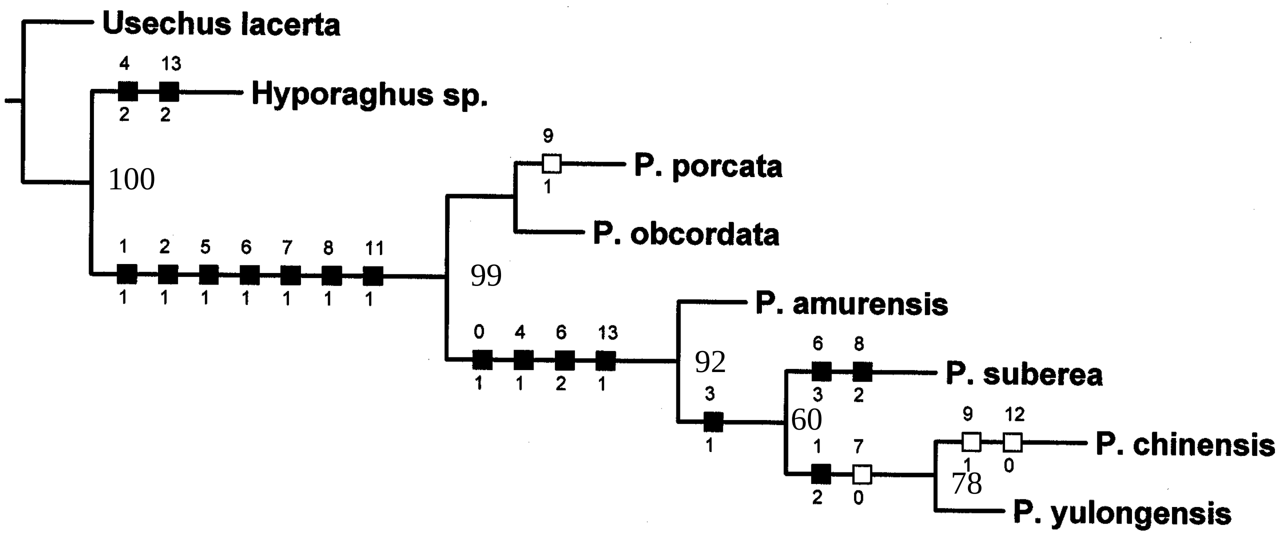


Fig. 62. Single most parsimonious tree found in NONA/WINCLADA (Length 23, CI .86, RI .87), bootstrap support values are shown at all well (>50) supported nodes.

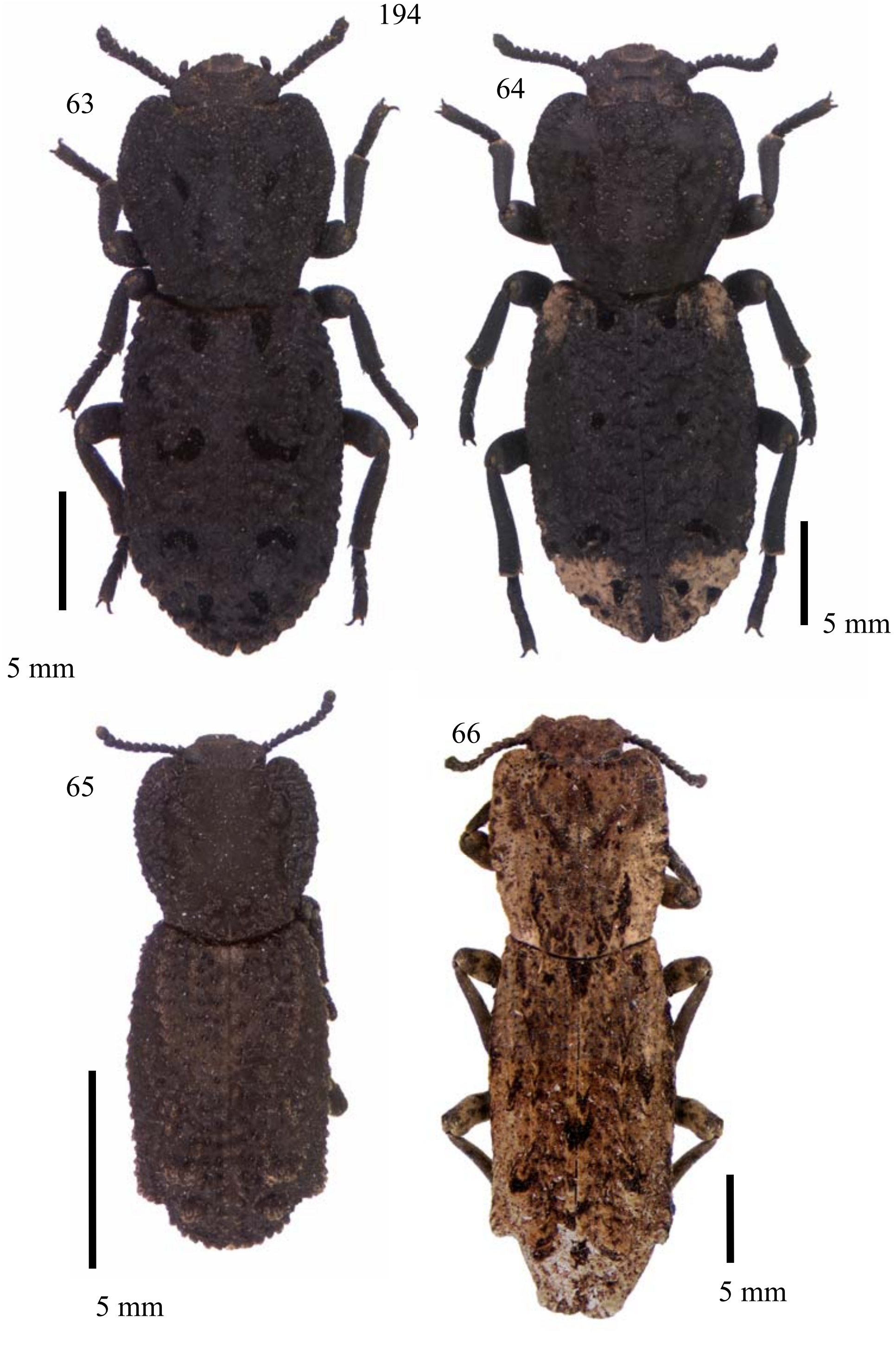
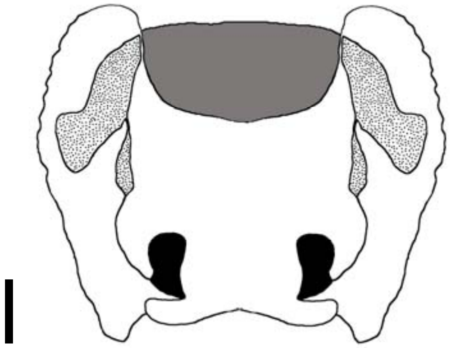


Fig. 63. *Phloeodes diabolicus* habitus, California, San Diego Co. 64. *P. diabolicus* habitus, California, Napa Co. 65. *P. plicatus* habitus, California, Los Angeles Co. 66. *P. venustus* habitus, Costa Rica/

67



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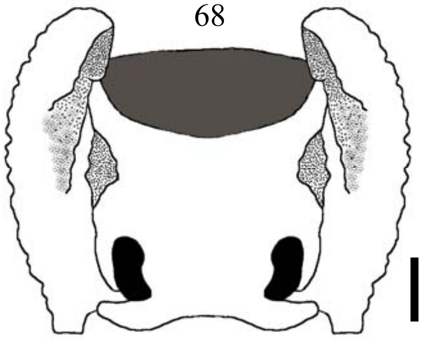


69

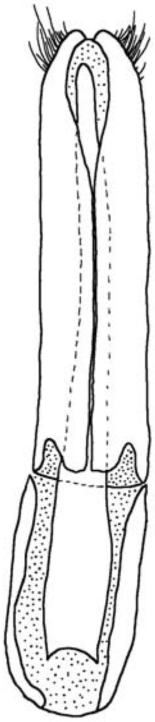
67. *P. diabolicus* prothorax. 68. *P. plicatus* prothorax. 69. *P. diabolicus* antennal cavity.

70

71

70. *P. venustus* prothoracic hypomeron. 71. *P. venustus* tarsal strip.

72



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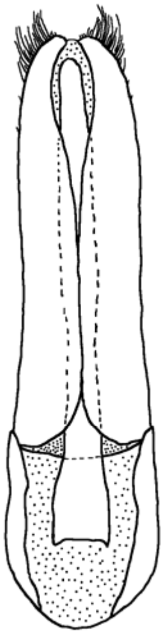

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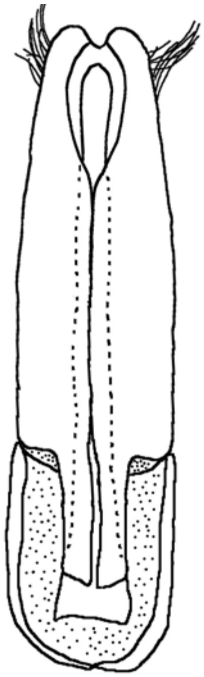
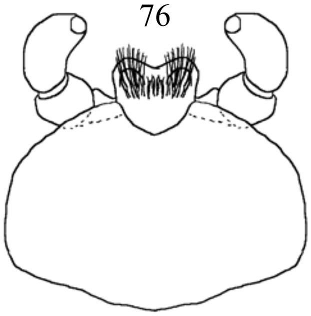


75

Fig. 72. *P. diabolicus* male genitalia. 73. *P. plicatus* male genitalia. 74. *P. venustus* male genitalia. 75. *Sesaspis triplehorni* male genitalia.

76



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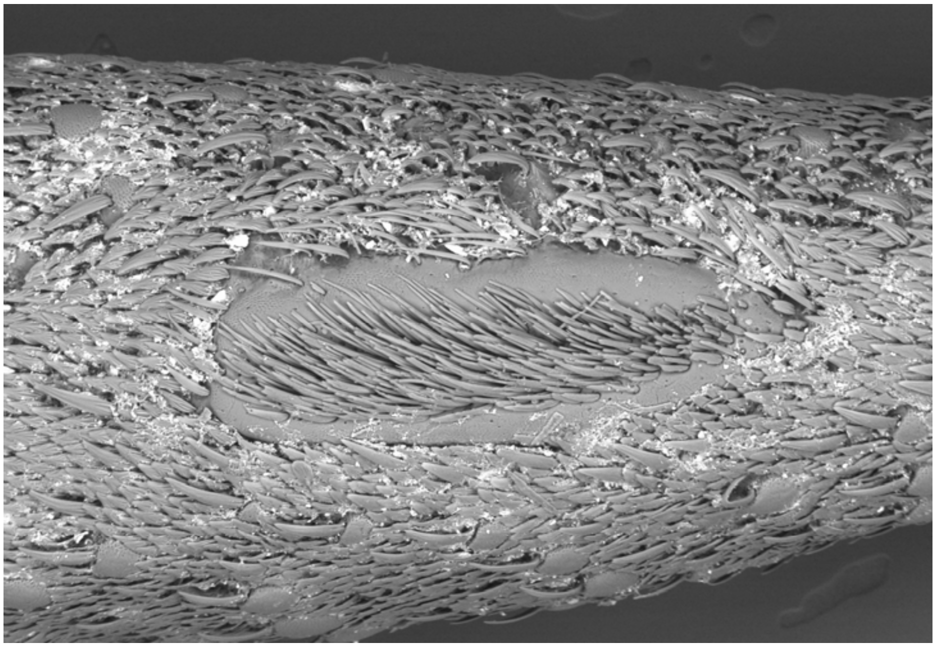
76. *P. diabolicus* labium. 77. *P. plicatus* labium. 78. *P. plicatus* tarsus SEM.

79



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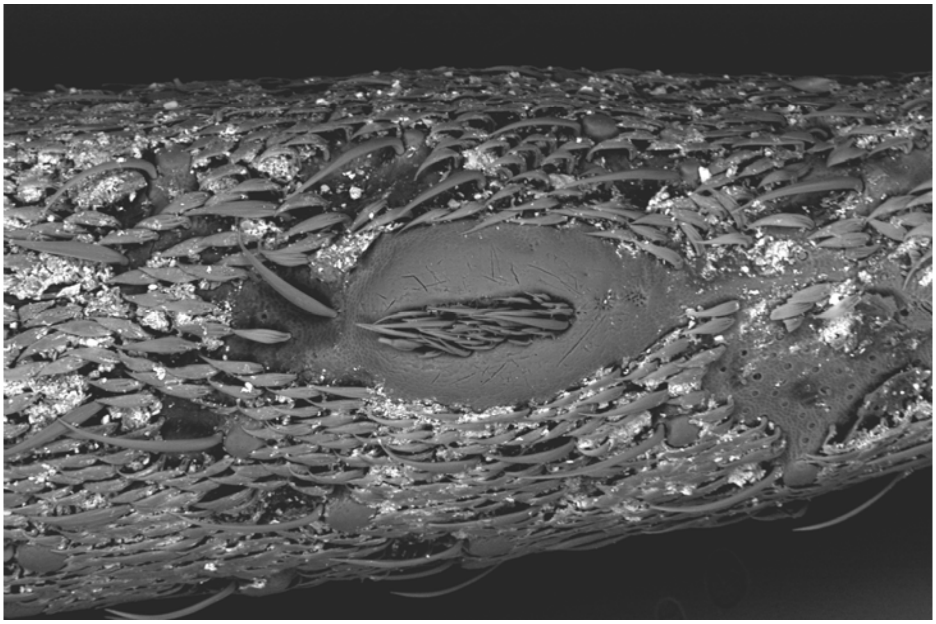
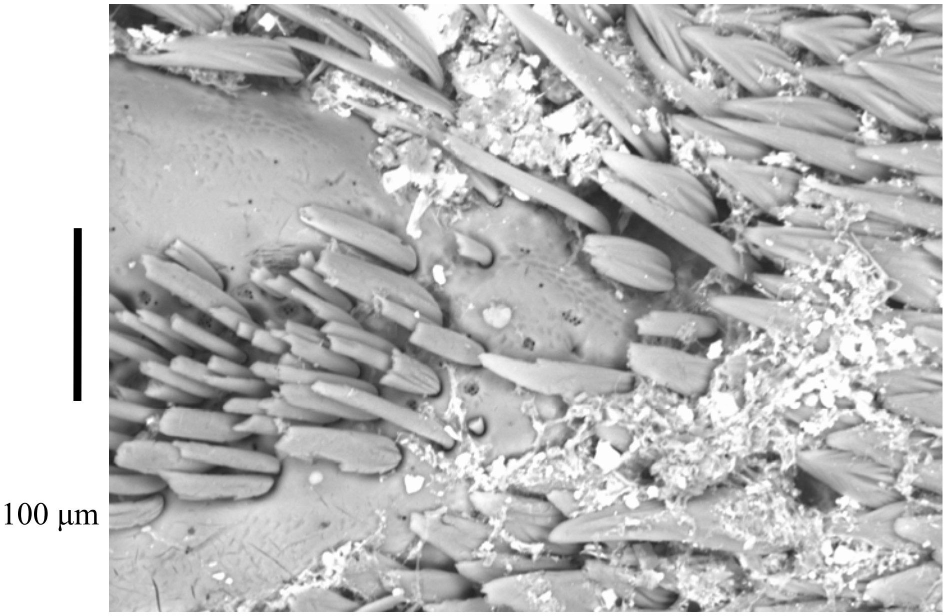
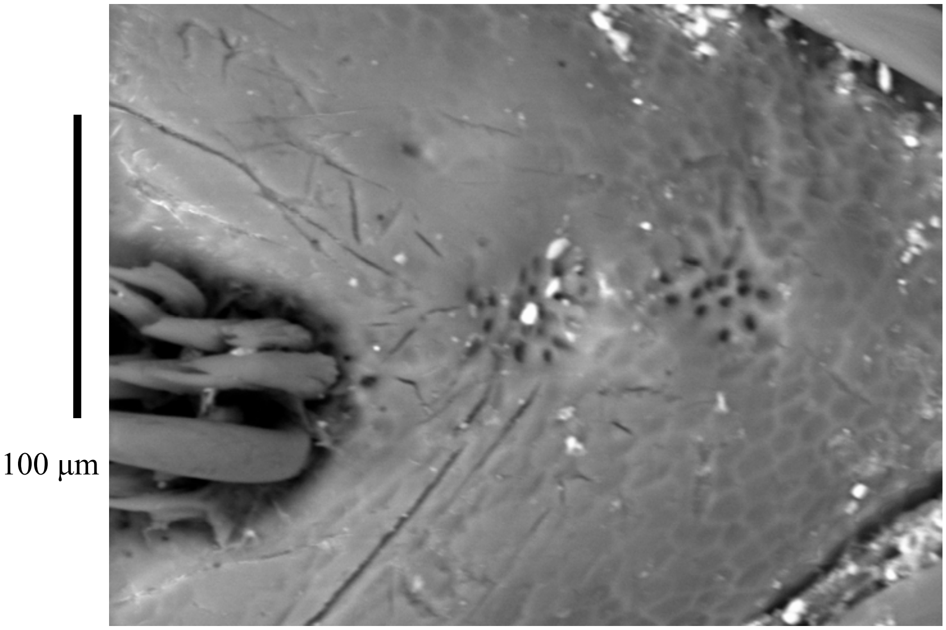


79. *P. diabolicus* male femoral nodule SEM. 80. *P. plicatus* male femoral nodule SEM.

81



82



81. *P. diabolicus* male femoral nodule, apical edge SEM. 82. *P. plicatus* male femoral nodule, apical edge SEM.

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83. *Nosoderma inaequalis* habitus, Mexico, Puebla. 84. *N. exsculptum* habitus, Mexico, Oaxaca. 85. *N. asperatum* habitus, Mexico, Hidalgo. 86. *N. scabrosum* habitus, Mexico.

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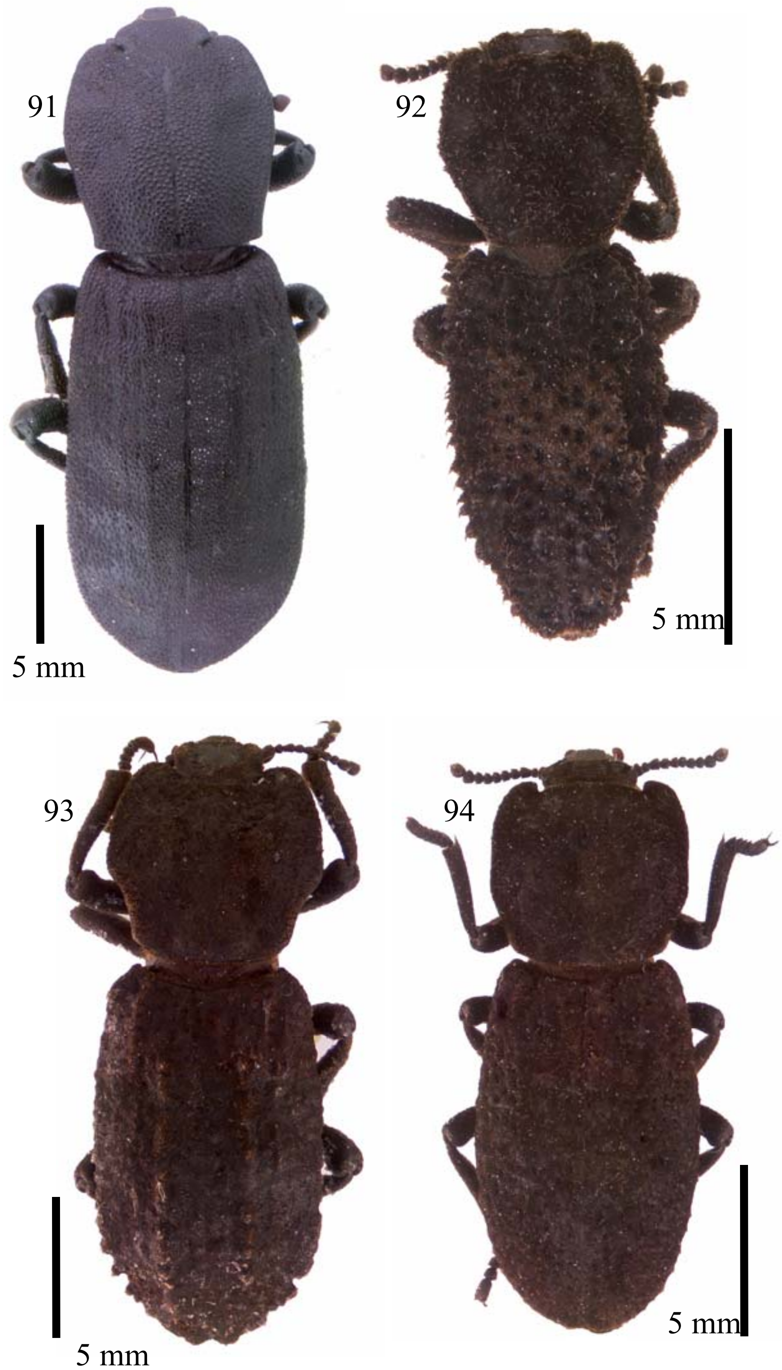
Fig. 87. *N. insigne* habitus, Mexico, Oaxaca. 88. *N. sparsus* habitus , Gutaemala. 89. *N. zunilensis* habitus, Mexico, Chiapas. 90. *N. guatemalensis* habitus, Mexico, Chiapas.



91. *N. aequalis* habitus, Mexico, Oaxaca. 92. *S. denticulata* habitus, Mexico, Nuevo Leon. 93. *S. ashei* NEW SPECIES habitus, Mexico, Hidalgo. 94. *S. doyeni* habitus , Mexico, Nuevo Leon.

95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98


95. *S. triplehorni* NEW SPECIES habitus, Belize. 96. *S. emarginatus* habitus, Texas, Comal Co. 97. *S. lutosus* habitus, Mexico, Oaxaca. 98. *S. adami* NEW SPECIES habitus, Mexico, Tamaulipas.

99

100

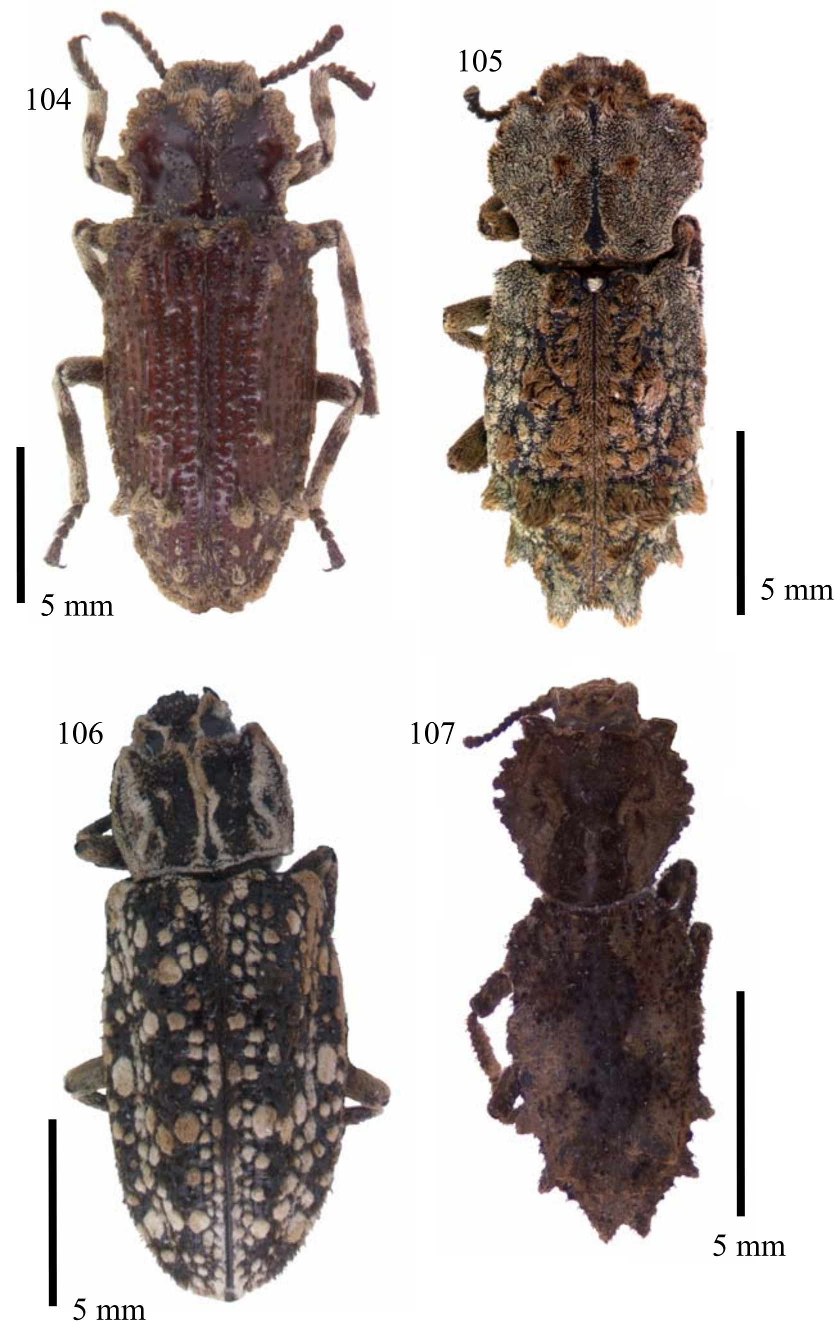
101

99. *Phloeodes diabolicus* mandible. 100. *Sesaspis adami* mandible. 101. *Nosoderma aequalis* mandible.

102

103

102. *Sesaspis adami* prothorax. 103. *Nosoderma exsculptum* prothorax.



104. *Noserinus dormeanus* habitus, Brazil. 105. *Noserinus furcatus* NEW COMBINATION habitus, Venezuela. 106. *Zopher iviei* habitus, Penn. Mayalysia. 107. *Meralius clavapilus* NEW SPECIES habitus, Venezuela.

108. *M. echinatus* habitus, Cuba. 109. *Scoriaderma* sp. Habitus, Tanzania. 110. *Zopherus championi* habitus, Mexico, Nuevo Leon. 111. *Z. jansoni* habitus, Costa Rica.

112

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114

115

112. *Zopherosis georgei* habitus, Australia, N.S.W. 113. *Zopherosis* antennal club. 114. *Zopherus* antennal club. 115. *Sesaspis* antennal club.

116

117

116. *Meralius clavapilus* NEW SPECIES, tibia. 117. *Scoriaderma* sp. pronotum, sinuate groove.

118

119

118. *Scoriaderma* sp. prothoracic hypomeron. 119. *Scoriderma* sp. ventral view of head.

120

121

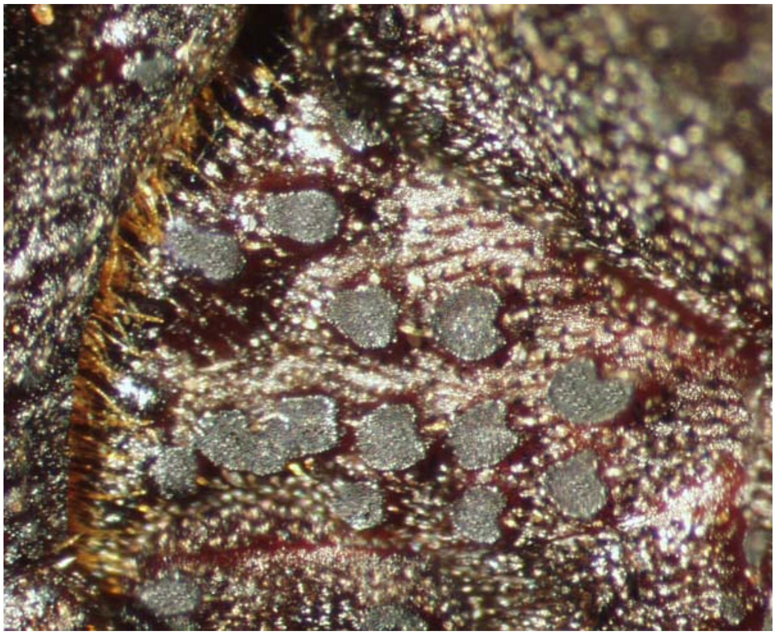
120. *Sesaspis adami* ventral view of head. 121. *Nosoderma aequalis* ventral view of head.

122

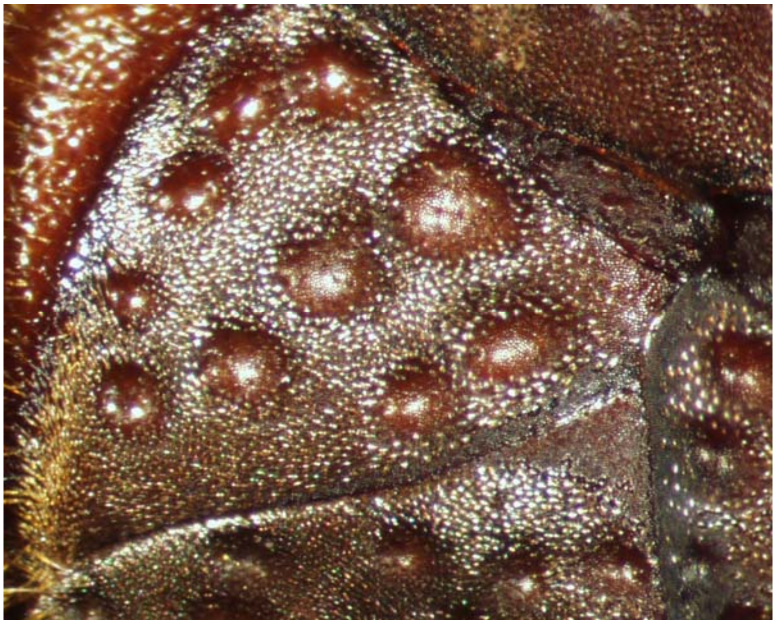
123

122. *Nosoderma inaequalis* ventral view of head. 123. *Meralius echinatus* ventral view of prothorax.

124

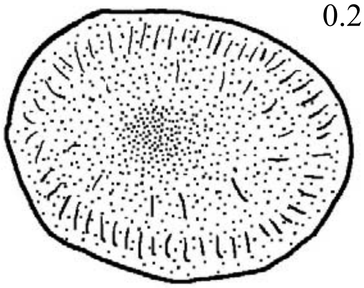


125



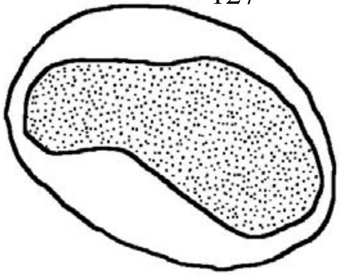
124. Mesepimeron tubercles. 125. Mesepimeron setose punctures.

126



0.25 mm

127

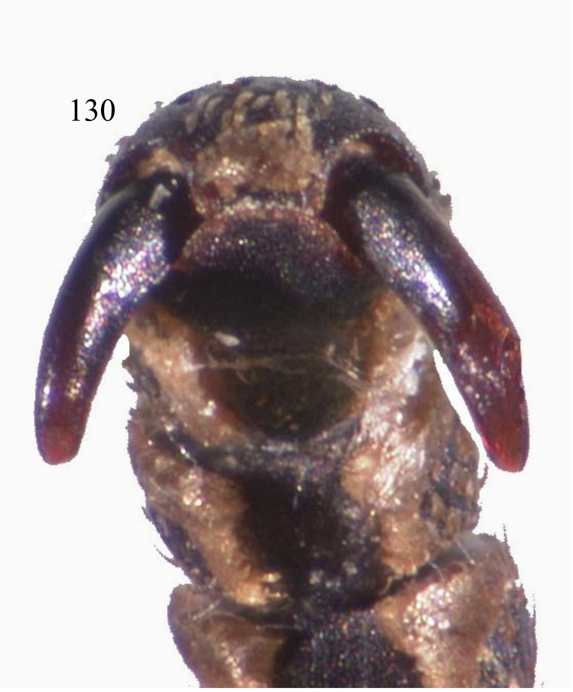


128

126. *Meralius* apex of last antennomere. 127. *Scoriaderma* apex of last antennomere. 128. *Noserinus furcatus* epipleuron.

129

130



129. *Noserinus furcatus* tarsal claw. 130. *Zopherus championi* tarsal claw.

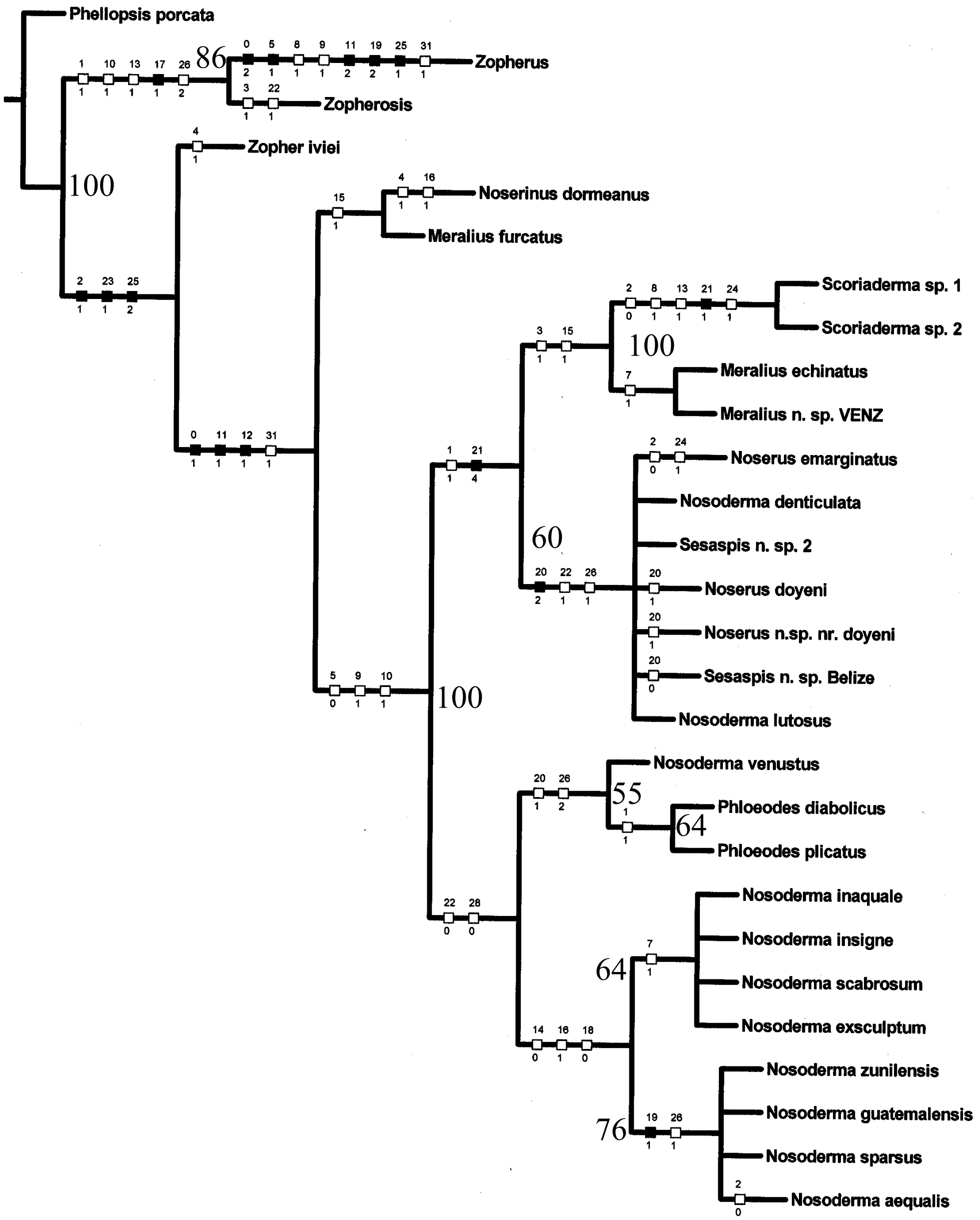


Fig. 131. Strict consensus of 4 MPT with *Phellopsis* as the outgroup found in NONA/WINCLADA (Length 83, CI .55, RI .78). Bootstrap support values are shown at all well (>50) supported nodes.

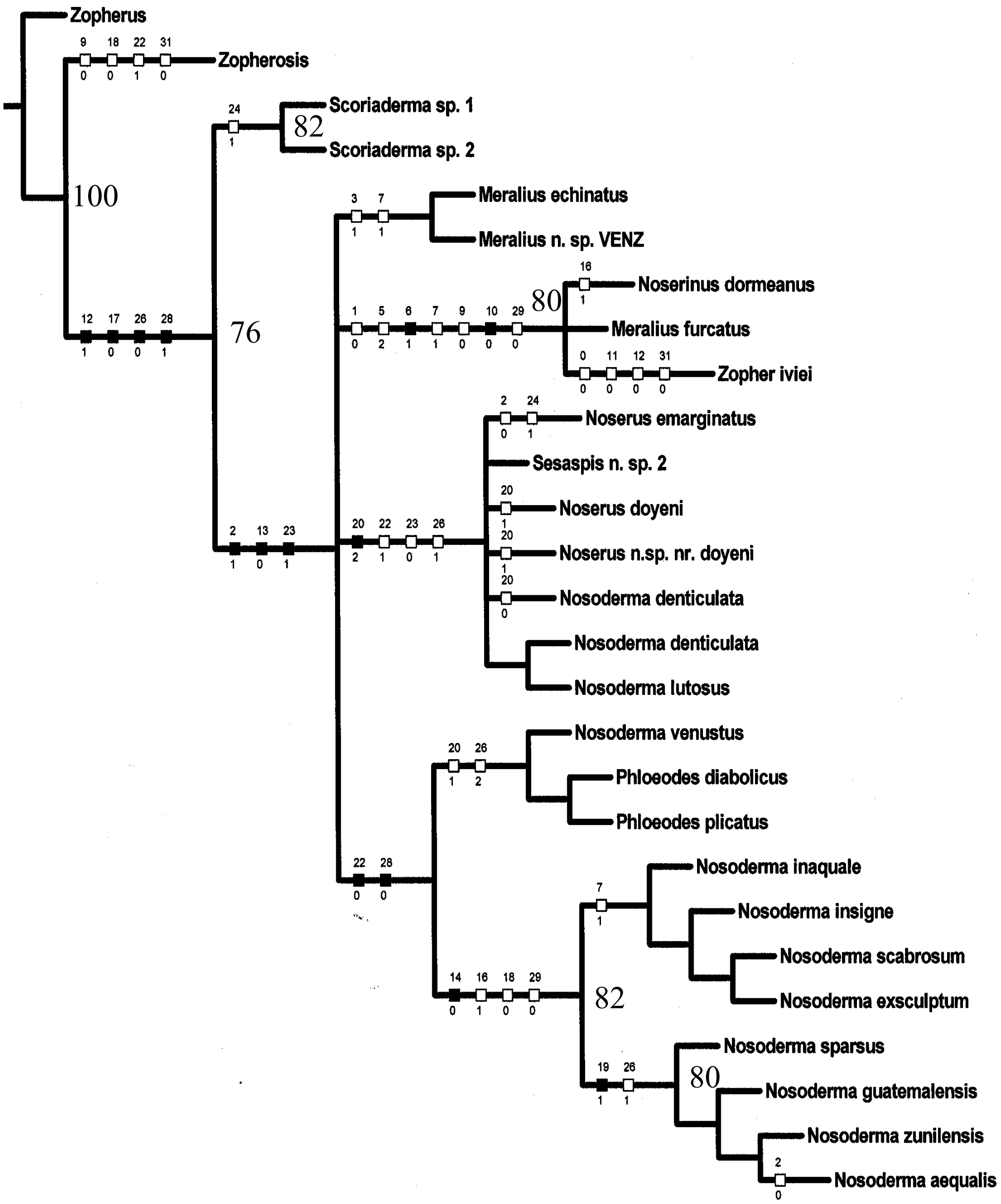


Fig. 132. Strict consensus of 20 MPT with *Zopherus* as the outgroup (Length 78, CI .58, RI .81).