SYSTEMATICS OF CUCUJOIDEA & COCCINELLOIDEA (CUCUJIFORMIA: COLEOPTERA) WITH A SPECIAL EMPHASIS ON MONOTOMIDAE

by

THOMAS CHRISTIAN MCELRATH

(Under the Direction of Joseph V. McHugh)

ABSTRACT

Beetles are the most diverse group of life on Earth. However numerous organizational problems remain in describing such a large radiation of life. Small, cryptic, drably colored beetles feeding on rotting organic material are prone to such problems. Two such groups are Cucujoidea and Coccinelloidea. Many members are less than 6 mm long, fungus feeding, and difficult to identify with morphology. To address these issues, I conduct six different projects within these superfamilies addressing basic and higher level questions. First, I use molecular phylogenetic analysis to examine the family and subfamily-level relationships within the “flat bark beetle” lineage. My results demonstrate independent origins of the “flat bark beetle” body type and support the placement of Propalticidae within Laemophloeidae. Second, using traditional morphological methods, I discover a newly adventive species, *Antibothrus morimotoi* (Coleoptera: Bothrideridae) that has become established in the United States and provide identification tools. Third, I address the lack of taxonomic resources for identifying Monotomidae (Coleoptera: Cucujoidea) in the New World by building an interactive identification key and information-rich website, creating a hub for future research into this family. Fourth, I provide the first records of the family Monotomidae in Peru, laying the groundwork for future study of that family in that region. One subfamily, three tribes, three genera, and four species are recorded for the first time. Fifth, I examine the lack of biodiversity knowledge about saproxylic beetle in the southeastern United States by collecting and identifying monotomid beetles in the state of Georgia. With limited resources and funding, I expand the number of species of Monotomidae in Georgia by over 100%, which speaks volumes to the current state of biodiversity knowledge in "well-studied" areas. Finally, I revise the genus *Bactridium* LeConte 1861 for North America north of Mexico, which is plagued by numerous nomenclatural and taxonomic problems. This revision results in one new species, two new generic names, 31 new combinations, and six synonymies. The genus is identifiable without comparison to type material for the first time in over 100 years.

INDEX WORDS: Coleoptera, beetles, evolution, Cucujoidea, Coccinelloidea Monotomidae, new species, distribution, adventive, taxonomy, synonymy, new combination, Georgia, Peru, United States, New World, interactive key, minute clubbed beetles, root eating beetles, flat bark beetles

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B.S., Covenant College, 2010

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2017

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August 2017

Dedication

To my parents, Kenneth and Donna McElrath, for always encouraging and supporting me in my passion for things that crawled, even when I brought them into the car and they got loose.

And to my wife, Karen, who supported and encouraged me throughout the entire writing process, and means more to me even than beetles.

Acknowledgements

I am incredibly grateful for this experience and the generous help that I received from many people along the way. First, my Ph.D. advisor, Joseph V. McHugh, who has been an incredible teacher, advisor, and source of information and wisdom along the way, not to mention a fountain of apt writing critique. I thank the rest of my Ph.D. committee, Kamal J.K. Gandhi, and Kenneth G. Ross for helpful feedback and encouragement of my chapters. I also thank the Department of Entomology and our two deopartment heads, Dr. Ray Noblet and Dr. Kris Braman, for providing an encouraging and supportive learning environment and funding for travel and research.

I am immensely grateful to my coauthors throughout these studies, without whom I could not have completed these projects. Yves Bousquet inspired me to study Monotomidae, as much of his work built the foundations for new research on that family. James Robertson assisted on an almost weekly basis during the course of Chapter 2, and has inspired me to pursue a variety of projects since. Robert Androw provided the initial specimens and infrastructure for Chapter 3. Su Yee Lim and I co-organized an ESA National Meeting symposium on interactive keys in 2013 “Interactive Keys Transforming Identification: Melding Traditional Methods with New Technologies” which initially inspired Chapter 4. Olivia Boyd’s illustrations and humor jump-started my research on Monotomidae, and without her, Chapter 4 would be a shadow of what it is now. Caroline Chaboo initially contacted me for Chapter 5, and started the overall project, but encouraged me to pursue the project on my own. Chapter 6 was the direct result of a 2016 ESA Southeastern Branch Student Symposium “Advances in understanding Southeastern insect biodiversity”, and I would like to thank my co-chairs and organizers: Lina Bernaola, Lindsy Iglesias, and Steven Reyna for support and assistance in organizing the symposium. I also thank all other presenters and contributors to the symposium, who inspired me to continue this project.

Invaluable technical support was provided by many throughout my dissertation. Sam Waychoff helped with technical problems in the UGA Entomology Department on a monthly and sometimes weekly basis. Nancy Jordan assisted with financial matters at UGA. John Shields assisted greatly with SEM during my time at Georgia Electron Microscopy. Zach McElrath wrote much of the Javascript needed for Chapter 4.

I greatly appreciate the many people who contributed to my development professionally over the last seven years, especially James Robertson, Nathan Lord, Nancy Hinkle, Don Champagne, Kris Miller, Michael Ivie, and E. Richard Hoebeke.

Finally, I would like to acknowledge several friends. Andrew Shaughnessy continues to inspire me to be the entomologist he always wrote me to be. I thank William Sunderland for allowing me to cultivate my love for entomology right next to his cubicle in college, even when it smelled weird. The members of the McHugh lab (and extended lab): Brad Hounkpati, Elizabeth Studer, James Murphy, Courtney Brissey, Conor Fair, Tom Sheehan, Kelly Murray, and Brittany Murphy, provided helpful discussions, encouragement, assistance with numerous projects. My fellow Linnaean team members Cheri Abraham, Ishakh Pulakkatuthodi, Joni Blount, Stephanie Weldon, Ian Knight, Brett Nolan, Annie Rich, Laura Kraft and Ruby Harrison inspired me to pursue entomological knowledge. Adam Martinez, Jayce Brandt, Kerri Coon, Clesson

Higashi, Andrew Kafer, Kelsey Coffman, and Matt Doremus provided helpful insights into the distribution of the minute beer beetle.

This work was supported by an NSF PEET grant (#DEB-0329115) to JVM, M.F. Whiting, and K.B. Miller, an N.S.F. ATOL grant DEB-0531768 (to B. Farrell, D. Maddison and M.F. Whiting, subaward JVM), numerous travel grants from the H.H. Ross Fund to TCM, a UGA CURO Research Grant (Olivia F. Boyd & JVM), an Ernst Mayr Travel Grant from Museum of Comparative Zoology at Harvard University (TCM), a CanaColl Foundation Endowment Fund Collections Grant (Y. Bousquet & TCM), an NSF-EPSCoR #66928 grant to C.S. Chaboo (Beetles of Peru project), a Hatch Grant (JVM), and a Coleopterists Society Graduate Student Research Enhancement Award (GSREA) (TCM).

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A SUPPORTING INFORMATION FOR CHAPTER 2

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Insects are the most biodiverse lineage of life on Earth, and if success were equated with numbers of species, then Coleoptera, the beetles, would be the undisputed winner, with an estimated 350,000-400,000 species described and many more yet to be described (Erwin 1982; Grimaldi and Engel 2005). Much of this undescribed diversity lies in the so called “LBBs” or “LBJs”, the “little brown beetles”, or “little brown jobs.” While it is easy to marvel at the diverse colors and large sizes of groups like Buprestidae, Curculionidae, or Scarabaeidae (e.g., Seago et al. 2009; Sharkey et al. 2017), much of the diversity of insects (and life on earth) still remains to be discovered in the less charismatic fauna like small black rove beetles (estimated to have thousands of undescribed species in Australia alone). This is especially true of groups that do not regularly come into contact with humans, or are not noticed except in specific circumstances like scientific studies or if they reach pest status.

Perhaps foremost among these problematic groups are the superfamily lineages of Coccinelloidea and Cucujoidea, which until recently were united in a more broadly defined Cucujoidea, which study after study recovered as non-monophyletic (Robertson *et al.* 2004; Hunt *et al.* 2007; Robertson *et al.* 2008; Lawrence *et al.* 2011; Bocak *et al.* 2014; Robertson et al. 2015; McKenna et al. 2015). These two groups are lineage rich, but species-poor (at least in terms of described diversity), with numerous convergent body types reflected in numerous feeding strategies (McElrath et al. 2015) that have evolved independently, many of which revolve around the tendency of these groups to feed on rotting or decaying materials or other forms of life that accelerate such processes such as fungi, slime mold, or bacteria. Notably, many of these beetles are cryptic, feeding in leaf litter or under tree bark. As a result, their importance in decomposition is underestimated. They have been comparatively little studied, with numerous groups having not been comprehensively revised in dozens or even hundreds of years. As a result, many incredible biological phenomena have gone unnoticed until recent advances in imaging technology, molecular phylogenetics, or sampling methodology have made them more accessible (e.g., Polilov and Beutel 2010; Polilov 2015). Even new families and superfamilies have been discovered within these lineages (e.g., Lord et al. 2010; Robertson et al. 2015).

The beetle family Monotomidae [Coleoptera: Cucujoidea *sensu* (Robertson et al. 2015)], exemplifies many of the problems that plague scientific understanding of Cucujoidea and Coleoptera in general. They are small (1.3-6.0 mm in length), colored in various shades of brown, black, yellow, and red, and for the most part inhabit areas most people never explore (Bousquet 2009). There are 36 genera and 257 described species (before this study), divided into two extant subfamilies, Rhizophaginae and Monotominae, and one extinct incertae sedis genus, *Jurorhizophagus*. Some Holarctic groups, such as *Rhizophagus* and *Monotoma*, have received enough taxonomic attention to be identifiable in that biogeographic region. Most genera, however, have not received comprehensive reviews except in narrowly focused geographic treatments.

Much about the family is changing, assumed, or just plain misleading. Until recently, the family was known as Rhizophagidae until Monotomidae was found to have priority (Pakaluk et al. 1994). The widely used common name "root-eating beetles" is a misnomer, as they feed on other beetles, fungi, or rotting material, but are not root feeders as far as is currently known. The family is cosmopolitan, with some species of *Monotoma* being distributed throughout the world through commerce, perhaps in rotting vegetation (Kuschel 1979; Bousquet & Laplante 1999). Many groups are assumed to be fungivorous, but diverse lifestyles exist. The family includes pollinators (Jenkins et al. 2013; 2015), myrmecophiles (Peacock 1977; Bousquet et al. 1999), melittophiles (Pakaluk & Ślipiński 1993; 1995), and bark beetle predators (Gregoire et al. 1985). Some inhabit the intertidal zone in rotting beach wrack (Bousquet 2009), are vectors of cankers (Hinds 1972), or occur in coffins, and are therefore of forensic paleoentomological significance (Panagiotakopulu and Buckland 2012). Their morphology is also poorly characterized. The assumed tarsal formula of two tribes was recently discovered to be inaccurate, the result of males being poorly collected or unknown within those tribes (McElrath, personal observation).

Finally, the placement of Monotomidae within the larger Cucujoidea and the relationships within the family remain equivocal. Crowson (1955), Sen Gupta (1988), Robertson et al. (2008), Robertson et al. (2015), and McKenna et al. (2015) have all suggested a relationship with Nitidulidae, which is supported by the exposed pygidial segment. However, numerous other studies have recovered conflicting results, most of which suggest a relationship to other Erotylidae-allied groups (Leschen et al. 2005; Hunt et al. 2007; Lawrence et al. 2011; Bocak et al. 2014). In addition, no phylogenetic analysis using molecular or morphological characters, has been conducted to evaluate the relationships of genera, tribes, or subfamilies within Monotomidae, although all larger analyses with multiple exemplars of Monotomidae have recovered it as a monophyletic group.

Therefore, the primary goal of this dissertation was to address several critical issues related to the study of biodiversity at multiple taxonomic levels (alpha, beta) within the superfamilies Cucujoidea and Coccinelloidea, focusing several of my studies on the beetle family Monotomidae, which has critical questions left to address at all levels, while also opportunistically addressing several challenges within the two superfamilies.

In Chapter 2, I conduct a molecular phylogenetic analysis of one of the unexamined potential branches of the Elateriformia tree of life, that of the Cucujidae *sensu lato*. No molecular phylogenetic analysis had been performed on this group before this study. Using modern molecular methods (at the time of sequencing and analysis) I show that the Cucujidae *sensu lato* is indeed a polyphyletic lineage, and actually represents at least two groups of families with various body shapes (each group having convergently evolved the “flat bark beetle” phenotype independently), supporting the current classification that separates families formerly included within the Cucujidae. I also show that the beetle family Propalticidae belongs within the beetle family Laemophloeidae, and take appropriate taxonomic action to subsume it.

In Chapter 3, I report the discovery of a non-native beetle newly found in the United States, *Antibothrus morimotoi* (Coleoptera, Coccinelloidea, Bothrideridae). Such invasive events are poorly reported, especially among groups of small nondescript insects. Not only is this the first adventive insect recorded in the family, but is unique due to the parasitic nature of the beetle. It has potential for biological control of destructive bark beetles. Within, I highlight the "collection to discovery" gap that occurs for most adventive species, and discuss potential reasons and solutions for this problem.

In Chapter 4, I use new identification key making tools to create the first interactive key to Monotomidae using Lucid software. This key uses novel database solutions, plentiful figures, illustrations, and photomicrographs to ease identifications for specialists and amateur users alike. Within, I highlight how interactive keys can solve some of the taxonomic impediment that faces identifiers and taxonomists. For Monotomidae, this key represents an up-to-date, modern attempt to provide identification resources for the New World genera of Monotomidae for all to use in an easy to access and use format (available www.monotomidae.com).

In Chapter 5, I discuss the lack of knowledge of the beetle family Monotomidae in understudied areas of the world, in this case, the country of Peru. I provide the first records of beetles in the family Monotomidae for the entire country, while also highlighting the poor state of biodiversity knowledge within the country.

In Chapter 6, I use a similar approach to Chapter 5 to highlight the lack of biodiversity knowledge for saproxylic beetles in areas we normally consider well-studied, in this case, the state of Georgia in the United States. Using a bare-minimum sampling approach and identifying specimens already in museums, I increase the number of species known from the state by over 100%, and summarize knowledge of Monotomidae within the state using an online data entry portal.

In Chapter 7, I address one of the foremost basic taxonomic problems within the Monotomidae in the New World: the genus *Bactridium* LeConte. I describe new species, redescribe old species, provide identification resources (a key and figures), address nomenclatural issues, clarify generic limits, and designate type material. After this study is published, it will actually be possible for a scientist who encounters these beetles to identify them with some level of certainty for the first time in over 100 years.

Ultimately, this dissertation provides new insights at higher phylogenetic levels using new tools (Chapter 2), addresses threats posed by adventive beetle species to biodiversity and economic security facing modern society (Chapter 3), provides general identification resources and modern tools for a poorly illustrated and known beetle family, the minute clubbed beetles (Chapter 4), gives an example of and helps to address problems in basic biodiversity knowledge in the developing world (Chapter 5), highlights the lack of knowledge about saproxylic beetles in the United States, especially as concerns the fauna in the southern coastal plain and Georgia (Chapter 6), and solves basic taxonomic problems in an inordinately difficult genus (*Bactridium* LeConte 1861) (Chapter 7).

CHAPTER 2

A MOLECULAR PHYLOGENETIC STUDY OF CUCUJIDAE *SENSU LATO* (COLEOPTERA: CUCUJOIDEA) [1]

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[1] McElrath TC, Robertson JA, Thomas MC, Osborne J, Miller KB, McHugh JV, Whiting MF. 2015. *Systematic Entomology* 40: 705-718.

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2.1 Abstract

Of all the superfamilies within the megadiverse order Coleoptera (Insecta), Cucujoidea (Cucujiformia) is arguably the most problematic taxonomically. The families comprising Cucujidae *sensu lato* (Silvanidae, Laemophloeidae, Passandridae and Cucujidae *sensu stricto*) represent a large portion of cucujoid diversity. Herein we presented the results of a rigorous molecular phylogenetic analysis of Cucujidae *s.l.* using maximum likelihood and Bayesian analyses of seven genes. Representatives of over half of the families of Cucujoidea (excluding the cerylonid series) as well as a broad sampling of Silvanidae and Laemophloeidae were analyzed. The monophyly of Cucujidae *s.l.* is rejected but a subgrouping of taxa that may form the core of a natural cucujoid lineage is recovered. This clade consists of two large monophyletic groups including several families each. Relationships among these smaller cucujoid groups are discussed, including several novel phylogenetic hypotheses, while morphological characters considered significant for classification in Cucujidae *s.l.* are evaluated in light of these phylogenetic hypotheses. Silvaninae, Telephanini, Brontini and Brontinae are recovered as monophyletic in the Bayesian analysis, but the former two are weakly supported as paraphyletic in the maximum likelihood analysis. Our results support the placement of *Psammoecus* Latreille within Telephanini and also recover a paraphyletic *Telephanus* Erichson. Silvaninae is divided into three lineages, each representing a potential tribal lineage. Laemophloeidae is rendered paraphyletic in all analyses by Propalticidae and the latter is herein formally transferred to Laemophloeidae **stat. nov**. Several suprageneric laemophloeid clades are recovered and discussed as potential higher-level groups. *Laemophloeus* Dejean is not recovered as monophyletic.

Keywords: multiple sequence alignment, beetles, coleoptera, systematic position, 3 antennomeres, antennal club, mixed models, family, classification, Polyphaga, evolution

2.2 Introduction

Coleoptera (Insecta) represents one of the largest radiations of diversity on Earth. Four suborders, 24 superfamilies, 211 families and over 350,000 described beetle species (Bouchard *et al.* 2011) reflect an astounding breadth of phenotypic diversity, and the order presents numerous taxonomic and classification challenges. One superfamily that retains a disproportionate amount of these problems is Cucujoidea, which currently includes 36 families (Leschen & Ślipiński 2010; Lord *et al.* 2010). Crowson (1955) originally defined this superfamily as 'Clavicornia' using the following features: antennae usually clubbed, front coxae not projecting, tarsi not 5-5-4 in both sexes, ventrites not connate, aedeagus of the ring-type, larvae with distinct prostheca and not obviously belonging to any other well-defined groups of beetles. Today, Cucujoidea is regarded as a taxonomic 'dumping ground' of mostly little brown beetles and has repeatedly been shown to be an artificial group in phylogenetic studies (Robertson *et al.* 2004; Hunt *et al.* 2007; Robertson *et al.* 2008; Lawrence *et al.* 2011; Bocak *et al.* 2014). In light of these findings, efforts have been made to recognize natural subgroupings within Cucujoidea that could form the basis for a new, more natural classification for this clade. Several recent phylogenetic studies have recovered one large, well-supported clade within Cucujoidea, the cerylonid series (Crowson 1955), which includes nine recognized families (Robertson *et al.* 2008; Lord *et al.* 2010). Thus far, the cerylonid series is the only well-supported, large subgrouping of Cucujoidea to emerge; no other large clades have been well supported in phylogenetic studies.

The informal names 'lower Cucujoidea' (sensu Leschen 1996) and 'basal Cucujoidea' (Leschen *et al.* 2005), were coined for cucujoid families that did not belong to the cerylonid series (Table A.1). This grouping, while not formal, has been widely used among the systematics community but there is no consensus as to its membership or monophyly. Several smaller groups within the remaining cucujoids have been proposed, with varying degrees of support, including among others, the nitidulid (Audisio 1994; Leschen 1996; Cline *et al.* 2014), erotylid, silvanid and cucujid-series (Hunt *et al.* 2007; Bocak *et al.* 2014), but there is a need for further evaluation of nearly every proposed group. Numerous taxa remain uncertainly allied with well-supported groups and even families generally thought to be closely related, have received conflicting support depending on the data used.

One such grouping of taxa is 'Cucujidae *sensu lato*' (Figure 2.1), comprising members of what was once the single family (Table A.1). This historically broader family concept contained a heterogeneous assortment of beetles united by a subcortical lifestyle and a flattened body shape, although there has been debate over its membership (Table A.1). However, recent efforts have resulted in the elevation of several subgroups of this larger concept into separate families, including Silvanidae (Crowson 1955), Laemophloeidae (Thomas 1993) and Passandridae (Crowson 1955). Cucujidae *sensu stricto* (Crowson & Sen Gupta 1969) retains comparatively few genera. In addition, it is increasingly evident that other families are allied with this group of cucujoids, such as Phalacridae (Thomas 1984a; Thomas 1993; Gimmel 2013) and

Propalticidae (Thomas 1984a). The taxonomic history of these families is complicated so a brief summary is provided for the current families in Table A.1.

Silvanidae (silvanid flat bark beetles) (Figure 2.1A-C) are thought to form a monophyletic assemblage that includes 58 genera and nearly 500 species worldwide (Thomas & Leschen 2010c). The family is currently split into two subfamilies: Brontinae Lawrence & Newton with 20 genera and Silvaninae Grouvelle with 38 genera. Brontinae is further split into two tribes, Telephanini LeConte and Brontini Erichson, each with ten genera. This tribal split is based mainly on characters of the aedeagus and procoxal cavities (Thomas 2003; Thomas & Nearns 2008). Telephanini are generally associated with plants and plant debris, while Brontini are most often encountered subcortically. Both tribes are thought to be fungivorous. Silvaninae has not been split into tribes, yet a wide variety of lifestyles are represented in the subfamily, including subcortical fungus feeders, leaf litter dwellers, ant inquilines, facultative predators and seed feeders (Thomas & Leschen 2010c). The latter ecological group (e.g., *Oryzaephilus* Ganglbauer, *Nausibius* Redtenbacher, *Cathartus* Reiche and *Ahasverus* Gozis) has received the most taxonomic attention due to their economic importance as pests of stored grains (Thomas & Leschen 2010c). The sister group of Silvanidae remains uncertain. Phylogenetic analyses have suggested Cucujidae *s.s.* (Leschen *et al.* 2005; Bocak *et al.* 2014), Passandridae (Robertson *et al.* 2008), *Hymaea* Pascoe (Hymaeinae: Phloeostichidae) (Lawrence *et al.* 2011) and even the entire superfamily Curculionoidea (Hunt *et al.* 2007).

Laemophloeidae (lined flat bark beetles) (Figure 2.1F) are a family of approximately 430 species arranged in 37 genera (Thomas & Leschen 2010b). The

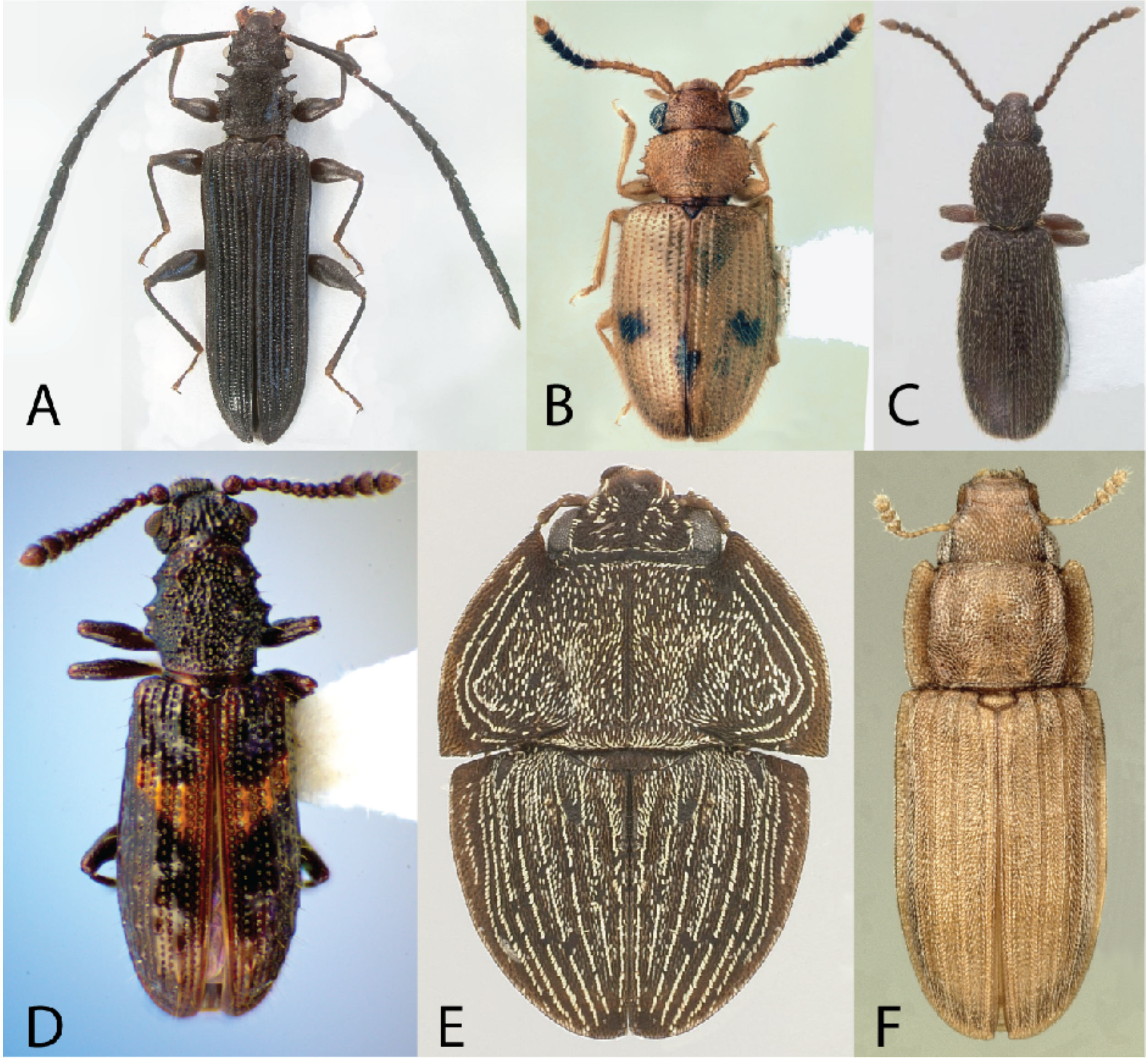

Figure 2.1. Examples showing the diversity of the Cucujidae *sensu lato*, all dorsal habitus images created by focus stacking. Images not to scale. A. *Macrohyliota spinicollis* (Brontinae: Silvanidae) from Malaysia (body length: ~11.0 mm). B. *Psammoecus trimaculatus* (Brontinae:Silvanidae) from Brazil (body length ~3.5 mm). C. *Airaphilus* sp. (Silvaninae:Silvanidae) from the USA (body length: ~3.1 mm). D. *Hymaea magna* (Hymaeinae:Phloeostichidae) from Australia (body length: ~4.0 mm). E. *Slipinskogenia* sp. (Propalticidae) from Central African Republic (body length: ~2.5 mm). F. *Carinophloeus raffrayi* (Laemophloeidae) from Malawi (body length: ~2.2 mm). Fig. 1D by Thomas McElrath, all others by Michael Thomas.

family is widespread in forested regions of the world. Most members are subcortical and are thought to feed on fungi although, some genera are likely predaceous on bark beetles (Curculionidae: Scolytinae) and others on scale insects (Coccoidea) (Thomas & Leschen 2010b). Some members of *Cryptolestes* Ganglbauer are important pests of stored grain. No suprageneric classification has been proposed because a phylogenetic analysis of the family is lacking (Thomas & Leschen 2010b), but a few informal genus-groups have been suggested (Thomas 1984a, d; 1988). A close affinity among Laemophloeidae, Phalacridae, Propalticidae and Passandridae was suggested by Thomas (1984a) and subsequent studies have generally supported this hypothesis (e.g., Leschen *et al.* 2005; Robertson *et al.* 2008; Lawrence *et al.* 2011; Bocak *et al.* 2014), although poor taxon sampling or insufficient data have produced inconsistencies (Leschen *et al.* 2005; Robertson *et al.* 2008; Lawrence *et al.* 2011; Bocak *et al.* 2014).

Passandridae (parasitic flat bark beetles) form a small family of 109 species in nine genera (Burckhardt & Ślipiński 2010). The few known larvae are ectoparasitic on wood-boring beetles or parasitic wasps. Most species are restricted in distribution, although a few are widespread (some through human activities) (Burckhardt & Ślipiński 2010). Due to their unique biology and resulting morphology, the family is widely regarded as monophyletic, an assumption that is supported by a cladistic analysis of morphological data by Burckhardt & Ślipiński (2003).

Cucujidae *sensu stricto* (flat bark beetles) retain only four genera and 48 species (Thomas & Leschen 2010a). *Pediacus* Shuckard and *Cucujus* Fabricius are primarily Holarctic. The remaining two genera, *Palaestes* Perty and *Platisus* Erichson, are restricted to the Neotropics and Australian areas, respectively. Cucujid beetles are usually encountered subcortically. A few species have been reported to be predaceous, but the biology remains unknown for most species (Thomas & Leschen 2010a).

Phalacridae (shining mould beetles) contain 34 genera and 635 species (Gimmel 2013) and have a generally convex body shape that is superficially dissimilar to most other cucujid-type taxa. Many species feed on fungi associated with rotting plants (e.g. smuts, stem rusts, ergots) (Lawrence *et al.* 2010). Several genera contain palynophagous (pollen feeding) species (Gimmel 2013). Also fungivorous, Cyclaxyridae form a small group (two species) of sooty mould feeders endemic to New Zealand that only recently received familial status (Gimmel *et al.* 2009). Its affinities are currently unclear. Although historically they were placed within Phalacridae (Gimmel *et al.* 2009), they have only been recovered as sister to Phalacridae in a recent morphological phylogeny using a limited number of outgroups and this relationship received only weak support (Gimmel 2013). Rather equivocally, *Cyclaxyra* Broun have been placed as the sister taxon to *Lamingtonium* Sen Gupta & Crowson (Lawrence *et al.* 2011), *Tasmosalpingus* Lea (Leschen *et al.* 2005) and *Pediacus* (Bocak *et al.* 2014).

Agapythidae, Priasilphidae, Phloeostichidae (Figure 2.1D), Myraboliidae and Tasmosalpingidae are infrequently collected, primarily austral taxa that were until recently united in a single family Phloeostichidae *sensu lato*. Recent analyses, however, suggest that several of these lineages are of independent origin (Leschen *et al.* 2005; Lawrence *et al.* 2011). The sister-taxa for most of these families are uncertain and few have been included in molecular phylogenetic studies (Bocak *et al.* 2014). Some species have been shown to be mould or fungus-feeders, although information about host and feeding preferences is scarce (Leschen *et al.* 2005).

The family Propalticidae (Figure 2.1E), comprising only two Old World genera (*Propalticus* Sharp and *Slipinskogenia* Gimmel) and forty-three species (Gimmel 2011), has a convoluted taxonomic history, although recent analyses have consistently placed it as either the sister taxon to (Leschen *et al.* 2005; Hunt *et al.* 2007; Lawrence *et al.* 2011), or within, (Bocak *et al.* 2014) Laemophloeidae. The former relationship is consistent with some historical concepts (Thomas 1984a; Lawrence & Newton 1995). Propalticids are thought to feed on lichens or fungi on the surface of living trees, where adults are commonly found (Gimmel 2011).

Cryptophagidae (silken fungus beetles) contain about 600 species in 60 genera (Leschen 2009) which historically has been allied with Languriini (Erotylidae) and several taxa have moved back and forth between the two families due to superficial resemblances (Leschen 1996). Thus, historical affinities of Cryptophagidae were perhaps erroneously thought to be with Erotylidae, but recent phylogenetic analyses have recovered the family as a close relative of several Cucujidae *s.l.* taxa (Hunt *et al.* 2007; Lawrence *et al.* 2011; Bocak *et al.* 2014). Leschen (1996) suggested a close relationship between Cryptophagidae and either Hobartiidae or Cavognathidae, with more distant affinities to Cucujidae *s.l.* Though generally fungivorous, the biology of this family is quite diverse, with numerous inquilinous species and plant-associates (Leschen 1996).

Silvanidae, Laemophloeidae, Passandridae and Cucujidae *s.s.* form the core of Cucujidae *sensu lato*, but the other families mentioned above may be closely related. Several of the sister-group relationships proposed have been based on morphological characters (Crowson & Sen Gupta 1969; Thomas 1984a; Thomas 1993; Leschen *et al.*

2005; Lawrence *et al.* 2011; Gimmel 2013). The most widely used include the state of the procoxal & mesocoxal cavities, the inversion of the aedeagus and the relative lengths of the protibial spurs. Each has been used for phylogenetic inference from the interfamilial to the generic levels within these families, but the polarity of the adjacent character states has never been independently tested.

Given the conflicting phylogenetic estimates frequently based on insufficient gene sampling (Hunt *et al.* 2007; Robertson *et al.* 2008*;* Bocak *et al.* 2014) and historical taxonomic confusion surrounding the Cucujidae *s.l.,* a rigorous molecular phylogenetic analysis of Cucujidae *s.l.* was conducted to test the familial and intrafamilial relationships of this heretofore poorly-sampled group. In addition, the above four anatomical characters proposed as important to the classification of these groups were independently evaluated in light of the phylogenetic hypothesis generated from the molecular data.

2.3 Materials and Methods

Taxon Sampling and DNA sequencing

Taxon sampling focused primarily on Silvanidae (27) and Laemophloeidae (25). This sampling broadly covers both silvanid subfamilies (Brontinae & Silvaninae) as well as both tribes within Brontinae (Telephanini & Brontini). No other families of Cucujidae *s.l.* have a formally proposed suprageneric classification. Within Laemophloeidae, exemplars from numerous hypothesized genus-groups (Thomas 1984a, d; 1988) were selected to represent a broad range of geographical and behavioural diversity. For numerous species-poor groups, only a single exemplar was used to test interfamilial relationships. This was the case for Cucujidae, Myraboliidae, Propalticidae, Phloeostichidae, Agapythidae, Priasilphidae, Monotomidae, Cyclaxyridae and other cucujoid outgroups. For more species-rich or supposed sister-lineages (e.g., Cryptophagidae, Phalacridae, Passandridae and Nitidulidae) multiple exemplars were included. Finally, for more distant outgroups, the following exemplars were included: four cerylonid series taxa (three Coccinellidae, one Latridiidae), four Tenebrionoidea (two Tenebrionidae, two Salpingidae) and one Cleroidea (Cleridae) as the most distant outgroup. In total, 81 taxa were included in the analysis (Table A.2). Specimens used in this study were collected into 100% EtOH and stored at -80ºC. Techniques and protocols associated with specimen dissection, clearing and vouchering follow Robertson *et al.* (2004, 2008, 2013). Genomic DNA was extracted using the Qiagen DNeasy tissue kit (Qiagen, Valencia, CA, U.S.A.). Voucher specimens are deposited in the University of Georgia Collection of Arthropods (UGCA) Coleoptera Tissue Collection, Athens, GA (most) or in the Brigham Young University Insect Genomics Collection (BYU IGC). We sampled seven genes in this study: nuclear 18S rRNA, 28S rRNA, histone subunit 3 (H3) and mitochondrial 12S rRNA, 16S rRNA, cytochrome-c oxidase subunit I (COI) and subunit II (COII). Primers and conditions used follow those detailed in Robertson *et al.* (2013). Product yield, specificity and potential contamination were monitored using agarose gel electrophoresis and UV-light visual verification. PCR products were transferred to GeneMate vacuum plates and subjected to -25 psi vacuum for ten minutes to remove PCR residues. Reaction products were cleaned using Sephadex matrix micro beads and sequenced using BigDye Terminator v3.1 (Applied Biosystems, Foster City, CA, U.S.A.) on an ABI 3730 DNA Analyser (ABI, Foster City, CA, U.S.A.). Assembly and editing of resulting contig sequences was performed in Sequencher 4.2.2 (Genecodes 1999). All resulting nucleotide sequences were cross-referenced using a BLAST search of the GenBank nucleotide database prior to use in this study to check for contamination. Some sequenaces were downloaded from GenBank or provided by collaborators (Table A.2).

Sequence alignment and partitioning

The COI, COII and H3 gene regions required no further adjustment or alignment (since they were length invariant and contained no indels) and were not subjected to the following alignment protocols. Ribosomal markers (12S, 16S, 18S, 28S) were aligned in MAFFT (Katoh & Standley 2013) and refined in Muscle (Edgar 2004). Alignments were visually inspected in Geneious 6.1.4 and corrected for obvious alignment errors. Even after rigorous alignment, these genes included regions of extreme length variation, thus Gblocks 0.91b was used to remove ambiguously aligned regions under the least stringent conditions (Castresana 2000; Talavera & Castresana 2007). Alignments of individual markers were concatenated in Sequence Matrix (Vaidya *et al.* 2011). Partition Finder 1.0.1 was used to select among 13 different partitions (by gene & by codon position for protein-coding genes) using the AICc selection criterion, unlinked branch lengths and a greedy search algorithm (Lanfear *et al.* 2012). The partitioned dataset was subjected to heuristic maximum likelihood analysis using the program RAxML (Stamatakis 2006) hosted on the Cipres Science Gateway (Miller *et al.* 2010) (www.phylo.org) with rapid bootstrap replicates (terminated by the RAxML algorithm) using a GTR + G model. Two independent RAxML analyses were performed to ensure convergence of runs. The topology with the best likelihood score is discussed below when it differed from the Bayesian analysis (Figure 2.S1). The same dataset was subjected to a mixed model Bayesian analysis in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) hosted on the CIPRES Science Gateway. The partitioned Bayesian analysis consisted of four independent runs of 30 million generations, flat priors, unlinked partitions, four chains (one cold, three hot) and trees sampled every 1000 generations. Tracer 1.5 (Rambaut & Drummond 2009) was used to graphically determine stationarity, burn-in and convergence of runs. Trees sampled after the burn-in were used to create a 50% majority-rule consensus tree (Figure 2.2). Each gene was also subjected to an individual RaxML analysis using similar conditions and visually inspected to assess general contributions of each gene to the dataset. Branch lengths proportionally adjusted relative to the gene with the longest branch lengths (histone3) and compared (Figure 2.S2). Individual gene trees are available in the supplementary material (Figure 2.S3-9).

Morphological characters

Four morphological characters (Table A.3) widely used for classification of cucujid group taxa (Thomas 1984a, c, d; 1988; 1993; 2009; Leschen 1996; Leschen & Ślipiński 2010) were mapped onto a cladogram of the 50% majority-rule Bayesian tree (Figure 2.3-4) using maximum likelihood probabilistic ancestral character state reconstruction models in the StotchChar package (Maddison & Maddison 2006) of Mesquite 2.75 (Maddison & Maddison 2011) using the default one-parameter Markov k-state model.

Pie charts were used to show the estimate probability of the likelihood of each state at each node. Ancestral State reconstructions were as follows:

Aedeagus uninverted vs. aedeagus inverted: This character state was scored entirely from the literature, which is described in different ways depending on the source, but the concept used herein is a combination of Lawrence *et. al* (2011) and Thomas (2003). In general, it refers to the orientation of the tegmen relative to the proctiger [segment IX of Lawrence *et al.* (2011)] of the male genitalia, which in the inverted condition is rotated 180°, such that the parameres are located on the ventral aspect of the median lobe (Thomas 2003).

Protibial spurs equal vs. protibial spurs unequal: This character state was scored entirely from the literature (see above) and simply refers to the relative lengths of the two spurs at the end of the protibia. If one is distinctly longer (and sometimes wider) than the other then the character was coded as unequal. Thus the unequal character state may refer to cases in which one of the spurs is not present or highly reduced, or it may refer to cases where it is merely of shorter length.

Procoxal cavities closed vs. procoxal cavities open: This character state was scored entirely from the literature and in this case does not distinguish between narrowly or broadly closed or open. In addition, this feature was only scored for the external condition of the cavity, not the internal condition, which is often scored as a completely separate character. For the purposes of this study, when any extension of the prosternal and/or postcoxal process completely separated the procoxal cavity from the mesoventrites, the character was scored as closed. If this division was not complete, then the character was scored as open.

Mesocoxal cavities closed vs. mesocoxal cavities open: This character state refers to the lateral closure of the mesocoxal cavity (Lawrence *et al.* 2011). If only the mesoventrite and metaventrite were involved in such a lateral closure then the character was scored as mesocoxal cavities closed. If any other sclerites were involved (e.g., mesepimeron, metepimeron), then the character was scored as mesocoxal cavities open. For this character, the condition reported in the literature was confirmed by the authors for *Microlaemus* Lefkovitch, *Propalticus*, *Carinophloeus* Lefkovitch and *Lathropus* Erichson. All other taxa were scored entirely from literature.

2.4 Results

Complete gene coverage was not obtained for all 81 terminals in this study, but was as follows: 18S: 81/81; 28S: 80/81, H3: 54/81, 12S: 77/81; 16S: 75/81; COI: 77/81; COII: 72/81. Sequences generated from this study are deposited on GenBank under the accession numbers KP133861 — KP134301 (Table A.2). The final combined nucleotide dataset comprised 6984 characters, only 543 of which were invariant. Graphical analysis of the trace plots from the Bayesian analyses determined that in two of the four runs convergence and stationarity was reached after three million generations, which were discarded as burn-in and the remainder of the sampled trees from the posterior distribution were used to construct the 50% majority rule consensus tree. The two runs that did not converge were discarded. Examination of individual gene trees (Figure 2.S2) showed that histone subunit three (H3) had the longest branch lengths (most nucleotide substitutions/site) of all genes sampled in this study and 18S had the least. No individual gene tree recovered all the relationships found in the combined analysis, an outcome that is not surprising given that individual genes (especially from different regions) have different histories and evolve at different rates (Liu *et al.* 2009). The results of the Bayesian (Figure 2.2) and RaxML (Figure 2.S1) analyses were largely concordant with few exceptions, which are noted when present. Otherwise all relationships discussed were recovered in both analyses. Important nodes discussed in the text are referenced with letter corresponding to the nodes in Figure 2.2. Posterior probabilities and bootstrap support values are provided in this format: (Node letter in Figure 2.2: Posterior probability, Bootstrap support), for example, (C: 100, 100).

The cerylonid series (100, 90) was recovered as monophyletic with strong support and was weakly supported as sister to the remaining Cucujoidea (A: 87, 56). Several small monophyletic groups were recovered that sequentially form sister-groups to the remaining cucujoid families, including the following: Boganiidae + (*Ericmodes* Reitter + *Protosphindus* Sen Gupta & Crowson); Monotomidae + monophyletic Erotylidae; monophyletic Nitidulidae; and monophyletic Cryptophagidae. Cryptophagidae (D: 100, 90) were recovered as sister (C: 100, 100) to a clade (E: 96, <75) comprised of two large subclades, one containing Silvanidae and a few small families (referred to below as the silvanid-clade) and the other containing Laemophloeidae, Phalacridae and a few small families (referred to below as the laemophloeid-clade). The silvanid-clade (F: 84, <75) consisted of a moderately supported clade (G: 100, 92) of (Phloeostichidae: *Hymaea* + (Agapythidae + Priasilphidae) which was then sister to a well-supported grouping of Cucujidae + monophyletic Silvanidae (H: 100, 93). The laemophloeid-clade (Q: 100, 78) consisted of Myraboliidae + (Cyclaxyridae + monophyletic Passandridae) (R: 82, 58) and formed the

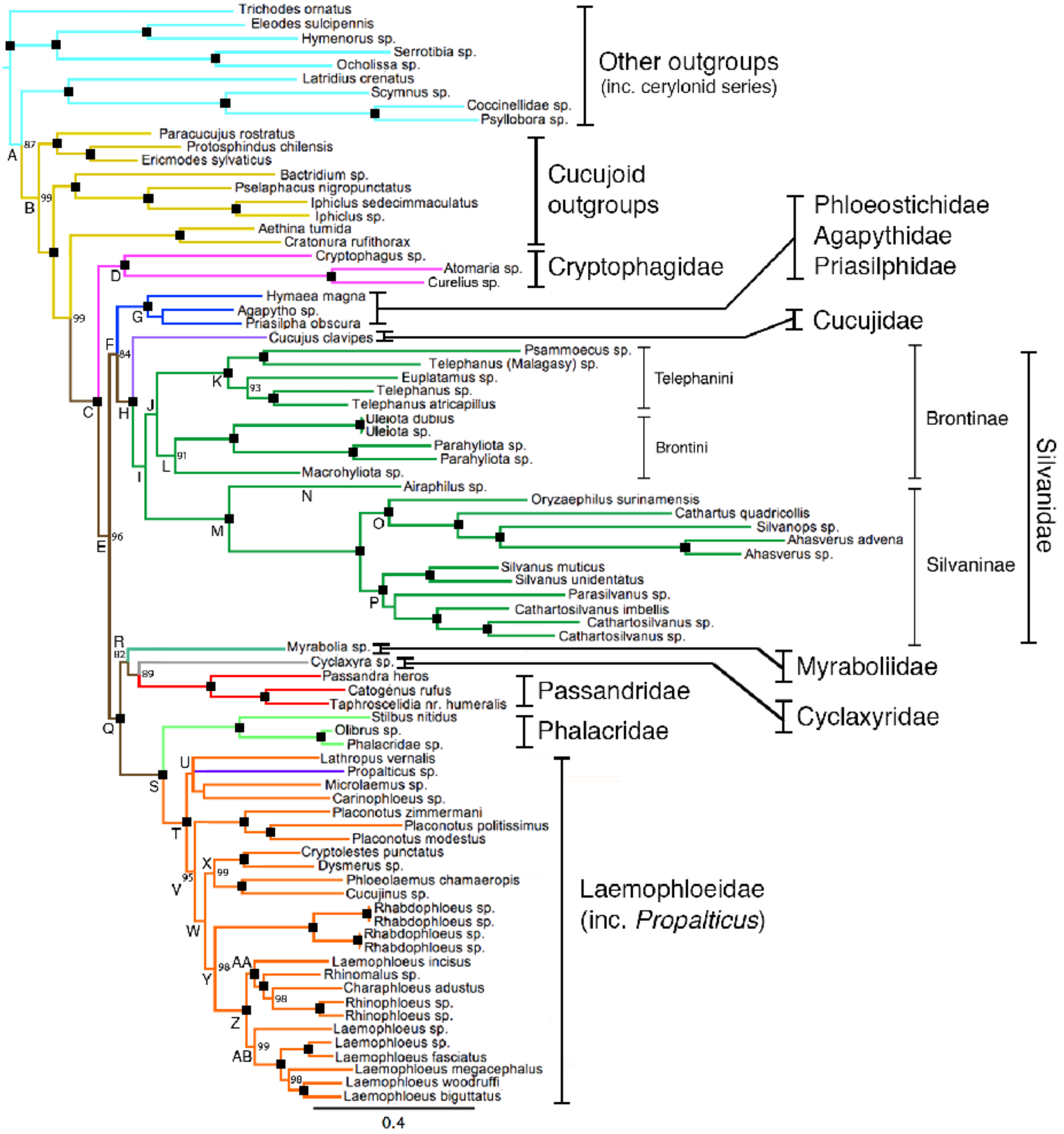

Figure 2.2. Bayesian 50% majority rule consensus tree. Nodes marked with a black square indicate a 100% posterior probability. Support values for nodes of less than 75% posterior probability are not indicated. Branch colours mark family-level clades, unless otherwise indicated. Brown indicates internal branches of uncertain taxonomic affinity.

sister group to a strongly supported clade (S: 100, 100) comprising Phalacridae + paraphyletic Laemophloeidae. Phalacridae (U: 100, 100) were recovered as the sister group to Laemophloeidae. *Propalticus* was recovered within Laemophloeidae (see below). Silvanidae were monophyletic with strong support in both analyses (I: 100, 91). The same was true for Silvaninae (M: 100, 100) and Telephanini (K: 100, 100). In the Bayesian analysis, the subfamily Brontinae (J: PP=55) and the tribe Brontini (L: PP=91) were each recovered as monophyletic, but in the ML analysis (Figure 2.S1), the tribe Brontini was rendered paraphyletic because *Macrohyliota* Thomas was recovered with very weak support (BS<50) as sister to Telephanini in a clade that is sister to the remaining Brontini + Silvaninae (BS=91). In the ML analysis (Figure 2.S1), a monophyletic *Placonotus* Macleay was recovered as sister to the remaining Laemophloeidae (inc. *Propalticus*), with strong support (BS=99). The next diverging laemophloeid lineage was a poorly supported branch (BS=33) comprised of two clades: (*Lathropus* + *Microlaemus*) and (*Propalticus* + *Carinophloeus*). These relationships are reversed in the Bayesian analysis, which recovered a polytomy comprising the latter clade (U: PP=56) that was the sister (T: PP=100) to a monophyletic *Placonotus* + all remaining laemophloeids (V: PP=95). *Dysmerus* Casey*, Cryptolestes, Phloeolaemus* Casey and *Cucujinus* Arrow were recovered as a strongly supported (X: 99, 85) genus-group clade. *Rhabdophloeus* Sharp was recovered as monophyletic (100, 100) and sister (Y: 98, 60) to a clade (Z: 100, 100) containing various species of *Laemophloeus* Dejean, which was rendered paraphyletic with respect to a clade containing *Rhinomalus* Gemminger*, Charaphloeus* Casey and *Rhinophloeus* Sharp (100, 75).

2.5 Discussion

Early diverging cucujoid lineages

The apparent monophyly of Cucujoidea (A: 87, 56) (Figure 2.2) and the non-cerylonid series cucujoids (B: 99, 99) (Figure 2.2) recovered in the present study may seem surprising given the findings of recent studies (e.g., Hunt *et al.* 2007; Robertson *et al.* 2004, 2008; Lawrence *et al.* 2011; Bocak *et al.* 2014; Kergoat *et al.* 2014). Our findings should be regarded with caution, however, because the taxon sampling for the current study was not designed to investigate those higher-level relationships. This study unequivocally rejects the monophyly of Cucujidae *s.l.* (Silvanidae + Passandridae + Laemophloeidae + Cucujidae *s.s.*), which was not recovered as a monophyletic group in any analysis, supporting the current recognition of each as a separate family and corroborates numerous morphological analyses and treatments that suggested they should be classified separately (Crowson 1955; Leschen *et al.* 2005; Lawrence *et al.* 2011; Thomas 1984). Multiple other families were intermixed among the core of Cucujidae *s.l.* Support for this expanded, multi-family clade was mixed (node E: 96, <75) (Figure 2.2) and may include other cucujoid families for which DNA sequences are presently unavailable, such as Cavognathidae, Tasmosalpingidae, Lamingtoniidae and Hobartiidae.

Cryptophagidae

The family Cryptophagidae, represented in the present study by *Cryptophagus* Herbst, *Atomaria* Stephens and *Curelius* Casey, was strongly supported as monophyletic in both analyses (D: 100, 90) and was recovered as the sister-group to the remaining Cucujoidea *s.l.* (C: 100, 100). It has been placed close to silvanids and cucujids in morphological analyses (Leschen *et al.* 2005; Lawrence *et al.* 2011) whereas previous molecular analyses have recovered it near Laemophloeidae + Propalticidae (Hunt *et al.* 2007; Bocak *et al.* 2014). Leschen (1996) considered both Hobartiidae and Cavognathidae to be closely related to Cryptophagidae, yet neither was recovered near Cryptophagidae in the analysis of Leschen *et al.* (2005); these families should be included in future molecular analyses of the Cucujoidea, as they could clarify the placement of Cryptophagidae within Cucujoidea.

Silvanid-clade

The silvanid-clade (F: 84, 52) contained at least the families Silvanidae, Cucujidae, Phloeostichidae (*Hymaea*) (Figure 2.1D), Agapythidae (*Agapytho* Broun) and Priasilphidae (*Priasilpha* Broun). The placement of the latter three families close to Cucujidae + Silvanidae is consistent with the morphological analysis of Lawrence *et al.* (2011), but this sister grouping was not strongly supported in the present study (F: 84, 52). The clade comprising Phloeostichidae, Agapythidae and Priasilphidae was well supported (G: 100, 92). The taxon sampling within this clade was sparse and exemplars representing other presumed closely related taxa (e.g., *Priastichus* Crowson, *Phloeostichus* Redtenbacher and *Tasmosalpingus*) are needed. The grouping of Cucujidae and Silvanidae as sister-taxa was well supported (H: 100, 93) in this analysis as well as several morphological analyses (e.g., Leschen *et al.* 2005; Lawrence *et al.* 2011). Characters supporting this sister-grouping include antennal insertions being concealed by a frontal ridge, procoxae with a long, concealed lateral extension, meso-metaventral junction simple, bases of frontal arms contiguous in larva and larval spiracles annular (Leschen *et al.* 2005).

Silvanidae

Silvanidae formed a well-supported monophyletic group in these analyses (I: 100, 91) and are also supported by the combination of several well-defined adult and larval morphological characters (Leschen *et al.* 2005), including procoxal cavities internally closed, galea at least 2.5 times as wide as lacinia, scutellary striole absent, parameres fused to phallobase, larval pretarsus unisetose and larval abdominal tergum simple (Leschen *et al.* 2005; Thomas & Leschen 2010c). However, the currently defined suprageneric classification of Silvanidae with two subfamilies, Brontinae (Brontini + Telephanini) and Silvaninae (Thomas 2003; Thomas & Nearns 2008), was only supported by the Bayesian analysis. In the RaxML analysis, *Macrohyliota* (Figure 2.1A), a member of the tribe Brontini, was recovered as the sister group to a monophyletic Telephanini, albeit with poor support (BS=<50). In addition, Brontini in part (*Uleiota* Latreille + *Parahyliota* Thomas) were recovered as sister to the subfamily Silvaninae (BS=<50). These relationships rendered both Brontinae and Brontini paraphyletic with respect to Silvaninae. In contrast, the Bayesian analysis was largely concordant with the current internal classification of Silvanidae, though it should be noted that the monophyly of Brontinae was poorly supported (PP=55). Brontinae, unlike Silvaninae, have an inverted aedeagus (a possibly plesiomorphy shared with Cucujidae) (Figure 2.3A). Brontini also have open procoxal cavities, unlike Telephanini and Silvaninae, which have the closed condition (Figure 2.4A), a condition that seems remarkably stable within the family, especially when compared to the number of transitions within Laemophloeidae (see discussion below). Given the weak support for the monophyly of Brontinae and the questionable monophyly of the tribe Brontini recovered here and in the morphological analysis of Thomas & Nearns (2008), it is clear that more attention is needed to clarify the relationships within subfamily. The potential paraphyly of Brontini as observed is caused by the unstable position of *Macrohyliota*. Interestingly, *Macrohyliota* is the only representative of this tribe in the current analyses that has *Dendrophagus*-type tarsi (Thomas 2003).

Our results corroborate the monophyly of Telephanini (K: 100, 100), but the generic limits within the tribe may be artificial. *Psammoecus* Latreille (Figure 2.1B), historically restricted to the Old World, was considered by Pal *et al.* (1984) to be unique enough to warrant it being treated as a monotypic subfamily Psammoecinae Pal. Thomas (1984b) disagreed and this analysis supports the latter hypothesis, as it is consistently recovered embedded within the clade with other telephanines. *Telephanus* Erichson, a mostly Neotropical group with some Old World representatives, was recovered in two clades, thus rendered paraphyletic with respect to *Psammoecus* and *Euplatamus* Sharp. The first was an Old World clade containing the aforementioned *Psammoecus* and a Malagasy species of *Telephanus* that differs from other congeners in having a scutellary striole. The second clade included two typical *Telephanus* (not possessing a scutellary striole) from the New World that are sister to *Euplatamus*. The Malagasy *Telephanus* likely represents a distinct group of telephanines that could possibly be recognized separately pending a thorough revision of the genus.

Silvaninae were strongly supported as monophyletic (M: 100, 100) and comprised three main lineages (Figure 2.2: N, O, P). *Airaphilus* Redtenbacher (N) (Figure 2.1C) formed the sister group to the remaining Silvaninae, which are subtended by a notably longer branch (Figure 2.S2). Indeed, the long-branch separating *Airaphilus* from the remaining silvanines indicates significant molecular distance underlying this bifurcation. This genus is unique from other Silvaninae in possessing a well-developed dorsal mandibular mycangium. The remaining Silvaninae were split into two well-supported clades, one comprised of *Oryzaephilus, Cathartus*, *Silvanops* Grouvelle and *Ahasverus* (O: 100, 94) and the other comprised of *Silvanus* Latreille, *Parasilvanus* Grouvelle and *Cathartosilvanus* Grouvelle (P: 100, 85). The mandibles in both groups have only a weakly incised line and no dorsal mycangium is present. All genera within this subfamily with multiple exemplars (*Cathartosilvanus*, *Silvanus* and *Ahasverus*) were recovered as monophyletic with strong support (100, 100). Except for *Oryzaephilus,* the three genera in the former clade (O) possess lobed or incrassate tarsal segments. The three genera in the latter clade (P) were regarded by Halstead (1973) as being closely related, citing the form of the tarsi, finely denticulate prothoracic sides and a three-segmented club of a particular form (as well as several others not sampled in this study). Further investigation of the potential synapomorphies uniting these genera seems warranted, as each clade represents a potential tribe within Silvaninae.

Laemophloeid-clade

The laemophloeid-clade formed the sister group to the silvanid-clade and comprised Myraboliidae, Cyclaxyridae, Passandridae, Phalacridae, Laemophloeidae and Propalticidae (Q: 100, 78). There remains uncertainty regarding the exact relationships of these families due to the moderate to poor support recovered for several branches. The laemophloeid-clade had a basal split that divides the group into two main lineages. The first clade was only weakly to moderately supported (R: 82, <75) and included Myraboliidae (*Myrabolia* Reitter) as sister to Cyclaxyridae (*Cyclaxyra)* + Passandridae (89, 66). Passandridae were recovered as monophyletic with strong support (100, 100). In preliminary analyses (not including *Cyclaxyra*), Passandridae often formed the sister group to the clade comprising Phalacridae, Laemophloeidae and Propalticidae. Support for this alternative resolution was likely adding to the instability at the base of the laemophloeid-clade. Interestingly, Hunt *et al.* (2007) recovered Passandridae as sister to Cucujidae, whereas in Bocak *et al.* (2014), Passandridae were nested within Nitidulidae. In the morphological analysis of Leschen *et al.* (2005), Myraboliidae, Passandridae, Phalacridae and Laemophloeidae + Propalticidae were interspersed among several cucujoid taxa either not included in the present study (e.g., Lamingtoniidae, Cavognathidae, Tasmosalpingidae and Smicripidae) or far-removed in the tree (e.g., Nitidulidae). No previous analyses have recovered Cyclaxyridae as the sister-group to Passandridae and thus provides putative support for a transition from mycophagy to parasitism in the evolutionary history of Passandridae.

The placement of Myraboliidae as the sister-group to *Cyclaxyra* + Passandridae was a novel finding. Previously, Leschen *et al.* (2005) recovered Myraboliidae as the sister to a much larger clade of ten cucujoid families including Passandridae and *Cyclaxyra*, but also including more distantly related cucujoid families such as Nitidulidae and Smicripidae. Leschen *et al.* (2005) included *Cavognatha* Crowson and

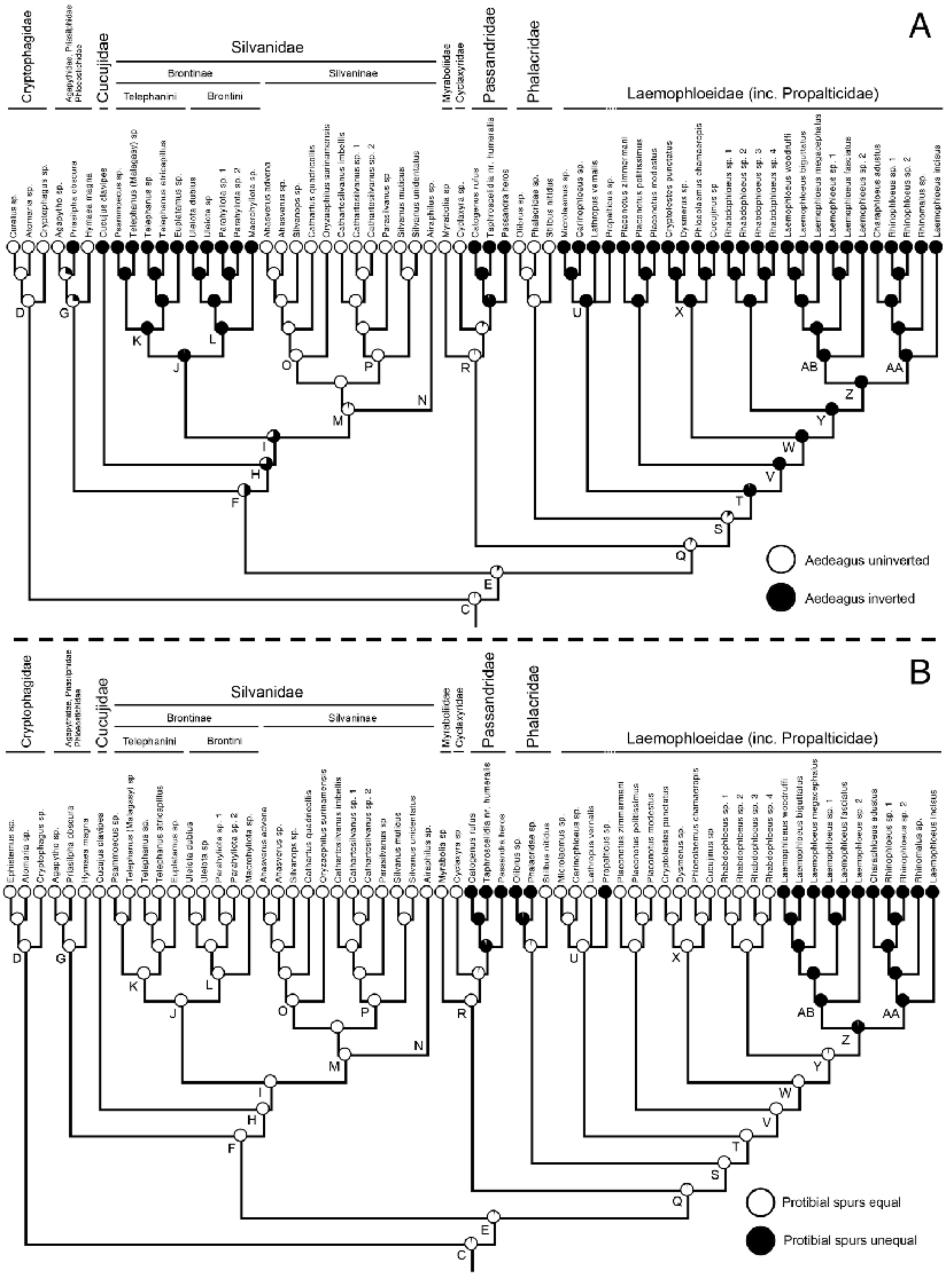

Figure 2.3. Ancestral maximum likelihood character state reconstruction and optimization of characters coded from literature into a matrix and optimized as proportional likelihoods using Mesquite under the Mk1 model, onto the Bayesian 50% majority rule consensus tree. A. 'Aedeagus uninverted (white)' or 'Aedeagus inverted (black)' B. 'Protibial spurs equal (white)' or 'Protibial spurs unequal (black)'.

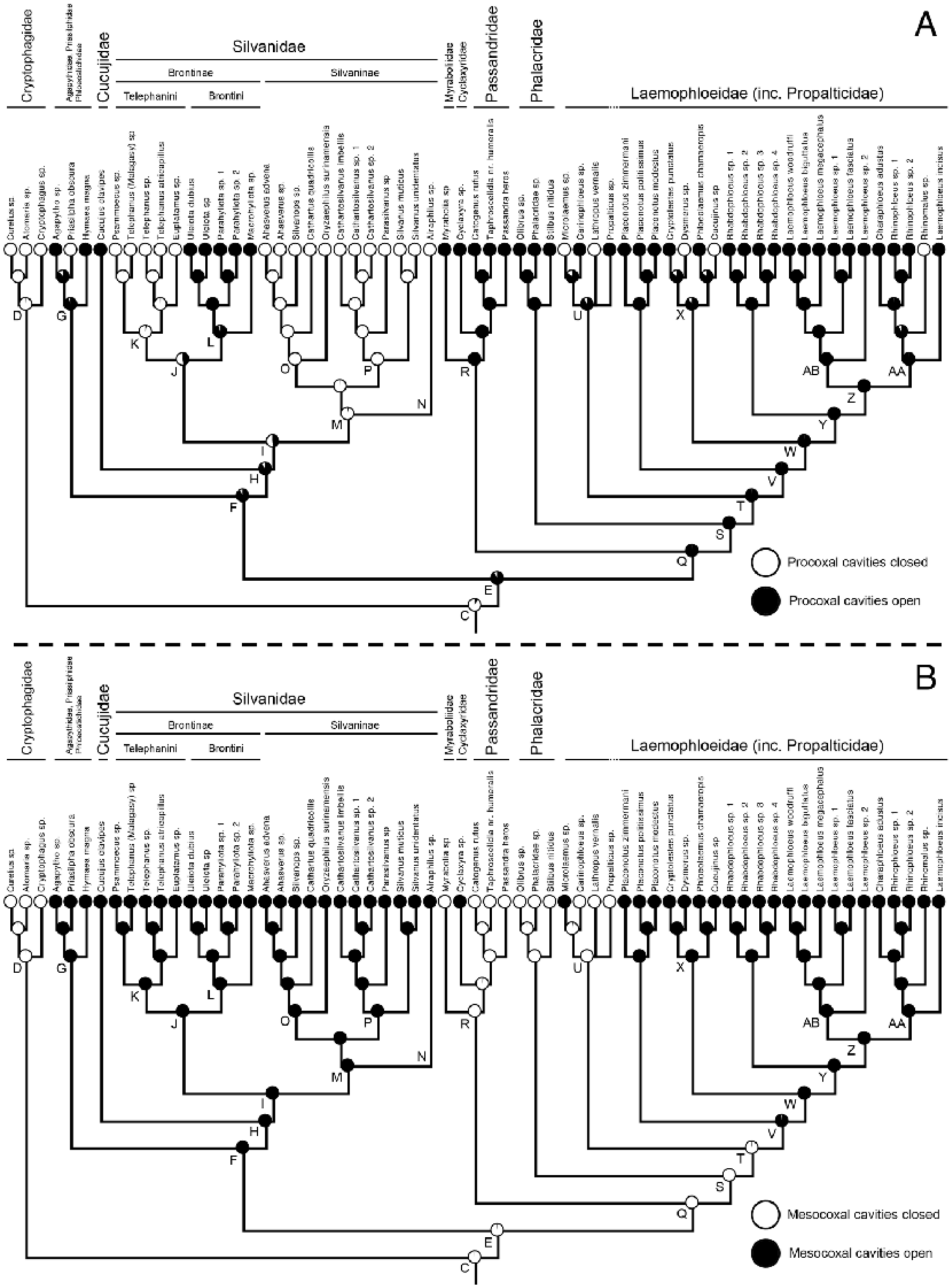

Figure 2.4. Ancestral maximum likelihood character state reconstruction and optimization of characters coded from literature into a matrix and optimized as proportional likelihoods using Mesquite under the Mk1 model, onto the Bayesian 50% majority rule consensus tree. A. ‘Procoxal cavities closed (white)’ or ‘Procoxal cavities open (black)’ B. ‘Mesocoxal cavities closed (white)’ or ‘Mesocoxal cavities open (black)’.

Lamingtonium in their study, which were recovered closer to Passandridae than *Myrabolia*. Lawrence *et al.* (2011) found *Myrabolia* to be sister to *Cavognatha*. Further analyses should include these families, whose placement within the larger context of Cucujoidea remains elusive and whose addition may resolve some of the weak support for the deeper nodes in this area of the tree. In addition, further inquiry into the feeding habits of *Myrabolia* (which are currently unclear) will shed light on the evolution of parasitic habits within this clade. If *Myrabolia* is shown to be mycophagous, this would support a hypothetical mycophagous passandrid ancestor.

The second major clade in the laemophloeid series comprised Phalacridae + Laemophloeidae (inc. Propalticidae) with high support (S: 100, 100), corroborating previous studies suggesting that these families are closely related (Thomas 1984a; Leschen *et al.* 2005; Hunt *et al.* 2007; Robertson *et al.* 2008; Bocak *et al.* 2014). The monophyly of Phalacridae was also supported (100, 100) but broader taxon sampling is needed within this diverse family to address the current suprageneric classification. Thomas (1984a, 1993) suggested that Phalacridae, Laemophloeidae, Propalticidae (Figure 2.1E) and Passandridae form a natural lineage based on a number of morphological features including unequal protibial spurs (Figure 2.3B), structural affinities of the male genitalia (Figure 2.3A) and the presence of pronotal lines and elytral cells. The present study confirmed the close affiliation of Phalacridae, Laemophloeidae and Propalticidae. However, when the tibial spur (Figure 2.3B) and male genitalic characters (Figure 2.3A) were viewed in light of the phylogenetic findings, the topology suggested that these features may represent convergences, especially the unequal protibial spurs (Figure 2.3B). In *Propalticus*, this character may be involved with its unique ability to jump using its forelegs. The inverted aedeagus also seems to be a convergent feature (Figure 2.3A), having only evolved twice within the laemophloeid series (Passandridae & Laemophloeidae). A similar pattern seems to have occurred within the silvanid-series, with at least two independent evolutions of the inverted aedeagus (Cucujidae + Silvanidae & Priasilphidae), although the Silvaninae may have secondarily lost the inversion. This character may be involved in having an end-to-end mating position or a subcortical habitat (Thomas 1984a).

The monophyly of Laemophloeidae was not supported by either analysis due to the nested placement of *Propalticus* within the family. These results were consistent with the molecular analysis of Bocak *et al.* (2014). The clade of Laemophloeidae (inc. *Propalticus*) received nearly maximum support (T: 100, 99) in both analyses, strongly suggesting that the family Propalticidae (incl. *Propalticus* and *Slipinskogenia*) (Figure 2.1E) should be subsumed within Laemophloeidae. Although *Slipinskogenia* was not included in this study, it shares unequivocal synapomorphies with *Propalticus* including a strengthened medial prothoracic endocarina and fore legs modified for saltation (Gimmel 2011). Based on the findings of the present study, *Propalticus* Sharp and *Slipinskogenia* Gimmel are formally transferred to the family Laemophloeidae **stat.nov**. Numerous analyses have previously suggested a sister-grouping of Propalticidae and Laemophloeidae (Leschen *et al.* 2005; Hunt *et al.* 2007; Lawrence *et al.* 2011), but because of the limited sampling strategy, the nested position of Propalticidae within Laemophloeidae remained undetected, or poorly supported (Bocak *et al.* 2014). *Lathropus, Microlaemus* and *Carinophloeus* (Figure 2.1F) are each anatomically odd among laemophloeids (Crowson & Sen Gupta 1969; Thomas 2010) and thus their phylogenetic position has been historically elusive (Thomas 1984a, d; Thomas & Leschen 2010b). When compared to most laemophloeid genera all three are atypical in having a more obvious antennal club and denser setation on the body. In addition, some lack the obvious constriction behind the head and the closure of the procoxal and mesocoxal cavities varies (Figure 2.4). Within Laemophloeidae, *Propalticus* grouped consistently with these three genera*,* albeit with poor support (<75, <75), but it shares many of the unusual characters exhibited by them. Similarly, *Propalticus* and *Slipinskogenia* possess ample setation and a more pronounced (wider) antennal club. *Lathropus, Propalticus* and *Carinophloeus* also possess closed mesocoxal cavities (Figure 2.4B), a character shared with Phalacridae, albeit equivocally, indicating its plesiomorphic nature, since the rest of Laemophloeidae have open mesocoxal cavities (Figure 2.4B). It is also noteworthy that the mesocoxal cavities in *Microlaemus* are only narrowly open, whereas they are widely open in the remaining laemophloeids (not incl. *Lathropus* & *Carinophloeus*) (Figure 2.4B). *Carinophloeus* and *Propalticus* also retain open procoxal cavities (Figure 2.4A) while *Microlaemus* and *Lathropus* have closed procoxal cavities. These morphological features, especially the conditions of the mesocoxal cavities, suggest that this group could represent the earliest diverging lineage of the extant laemophloeids (Thomas 1984a, d) since its likely sister-group, Phalacridae, shares these character states (Thomas & Leschen 2010b). Now that *Propalticus* and *Slipinskogenia* are grouped within Laemophloeidae, a search for derived morphological characters, not just plesiomorphies or secondary losses, should be undertaken. However, it is certainly worth noting that while this hypothesis was supported in the Bayesian analysis, with *Propalticus, Lathropus, Microlaemus* and

Carinophloeus forming the sister group to the remaining Laemophloeidae, it was not supported as such in in the RaxML analysis, where the clade (BS=<75) was recovered one node higher on the laemophloeid tree, with a monophyletic *Placonotus* (100, 100) forming the sister group to the remaining Laemophloeidae. Nonetheless, *Placonotus* retains none of the characters discussed above and has been hypothesized previously to be more closely related to genera such as *Gannes* Lefkovitch, *Parandrita* LeConte & Horn, or *Laemophloeus* (Thomas 1984c).

A clade comprising *Dysmerus* + *Cryptolestes* (100, 100) as sister to the clade *Phloeolaemus* + *Cucujinus* (100, 99) was supported by the current analysis. This larger clade, which was moderately well supported (X: 99, 85) here, is also supported morphologically based on the structure of male genitalia, body shape and modifications to the male antennal scape, which is expanded in both *Dysmerus* and *Cryptolestes* (Thomas 1988; 2009). Thomas (1988b) also included *Leptophloeus* Casey in this informal group. *Dysmerus* and *Cryptolestes* are two of the few laemophloeid genera with predaceous members (feeding on scolytines and scale insects, respectively (Thomas & Leschen 2010b)). *Phloeolaemus* is also commonly collected in areas where scolytine beetles may be found, although no definitive associations have been made.

Our analyses recovered a clade of monophyletic *Rhabdophloeus* Sharp (100, 100) as sister (Y: 98, <75) to a well-supported clade (Z: 100, 100) comprising the *Laemophloeus*-group of genera (see below), which is contrary to previous hypotheses that suggest a close relationship of *Rhabdophloeus* with the *Carinophloeus*-group of genera (Thomas 1984d). However, a close relationship with *Odontophloeus* Thomas has also been suggested (Thomas 1984d) and upon further sampling of that family, as well as other Neotropical genera, it is possible that this clade could be expanded to include these. All share a lengthened terminal antennomere and undulating pronotal margins with several teeth. *Odontophloeus dives* (Sharp) is strikingly similar to members of *Rhabdophloeus* (Thomas 1984b; 1993). Little is known of their biology to suggest that they might share similar habitats or associations.

*Laemophloeus wa*s not recovered as monophyletic in our analyses, as it was rendered paraphyletic by the *Rhinomalus* genus-group; instead, a North American clade (100, 100) of five *Laemophloeus* species was recovered as the sister to a South American representative of the genus (AB: 99, <75). The Nearctic members of this genus are currently being revised (Thomas 2015) and morphological characters may be discovered that support the unique nature of Nearctic *Laemophloeus* as recovered in this analysis. *Laemophloeus incisus*, *Charaphloeus*, *Rhinomalus* and *Rhinophloeus* were recovered in a well-supported clade (AB: 100, 100). The latter-three taxa share a suite of derived characters, including the loss of one or more (of the three) elytral cells, absence of lateral elytral carina and tarsomere one being longer or subequal to the penultimate tarsomere (Thomas 1984a). All of these genera, including *Laemophloeus*, possess an acuminate abdominal intercoxal process (Thomas 2013). *Laemophloeus incisus* and its hypothesized sister-species, *L. mathani* Grouvelle, are unique among congeners in lacking a pronotal antebasal denticle and in possessing atypical genitalia (Thomas 2014). Further examination of these two species seems warranted based on these results.

Further investigations into food preferences and life histories within cucujoids should reveal insights about the apparently numerous historical transitions between parasitism, predation, phytophagy, palynophagy and mycophagy within them. Unfortunately, such information is usually poorly documented or unconfirmed for many Cucujoidea. For most genera of Laemophloeidae, for example, food preferences are completely unknown or represent assumptions that are simply based on associations with a particular habitat. The remarkable diversity of lifestyles shown by the laemophloeid- and silvanid-series, as well as the remaining Cucujoidea, despite low numbers of species relative to other Coleoptera superfamilies, is an interesting evolutionary phenomenon that merits further attention. This group of cucujoids is also well suited for addressing biogeographic patterns, since there are numerous groups with relictual Gondwanan distributions (e.g., Phloeostichidae, Myraboliidae). Expanded taxon sampling to include more members of such families, as well as more genera of Laemophloeidae and Silvanidae and focusing on poorly sampled biogeographic regions with unique and endemic faunas would allow more accurate inferences about such questions. For example, sampling of the remaining genera of Cucujidae and Phloeostichidae (of mostly Austral, Oriental and South American distribution) would allow for the development of a more robust hypothesis regarding the origins of the silvanid-clade. Strikingly, the placement of the only Malagasy specimen included in this analysis suggests that a genus needs revision; undoubtedly further sampling from this region would reveal numerous important insights. Poor sampling of taxa from these areas remains a problem in modern molecular phylogenetic analyses (Bocak *et al.* 2014).

2.6 Acknowledgements

This study was funded by a NSF PEET grant (#DEB-0329115) to JVM, MFW and KBM and N.S.F. ATOL grant DEB-0531768 (to B. Farrell, D. Maddison and MFW). Additional support was provided as travel grants from the H.H. Ross Fund to TCM. The authors would like to thank Duane McKenna (University of Memphis) for providing *Cyclaxyra* sequences. Numerous collaborators from the Beetle Tree of Life Project (BToL) provided valuable specimens and identifications at various phases of the project. R.A.B. Leschen provided helpful comments at a critical point of manuscript development. We also would like to thank the anonymous reviewers for their comments that helped to improve the manuscript. This study was done in partial fulfillment of the Ph.D. dissertation requirements at the University of Georgia. The first author wishes to thank his advisory committee members K.G. Ross, K. Gandhi and J.V. McHugh.

CHAPTER 3

ANTIBOTHRUS MORIMOTOI SASAJI, AN OLD WORLD COCOON-FORMING BEETLE (COLEOPTERA: COCCINELLOIDEA: BOTHRIDERIDAE) NEWLY ESTABLISHED IN NORTH AMERICA [2]

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[2] McElrath TC, Androw RA, McHugh JV. 2016. *Zootaxa* 4154: 323-330.

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3.1 Abstract

Antibothrus morimotoi Sasaji, a cocoon-forming beetle (Coccinelloidea: Bothrideridae) native to the Palearctic region, is newly reported from North America. In 2013 and 2015, several series of specimens were collected during an ongoing USDA/APHIS/PPQ exotic bark beetle survey in Franklin County, Ohio, U.S.A. This is the first confirmed record of the species and genus in the New World. The capture of these specimens suggests that the beetle is established in the greater Columbus, Ohio, metropolitan area.

Keywords: adventive, exotic, biocontrol, new record, dry bark beetle

3.2 Introduction

Beetles in the family Bothrideridae (*sensu* Robertson *et al.* 2015) (Coleoptera: Coccinelloidea) are ectoparasites of wood-boring insects, such as scolytine bark beetles, carpenter bees, wood wasps, long-horned beetles, and others (Ślipiński *et al.* 2010). Adults are most commonly collected under bark in association with such insects. However, bothriderids are uncommonly collected, and often have very little associated biological data; therefore, much remains unknown about their biology. *Antibothrus* Sharp 1885, distributed in Africa, Madagascar, and Asia, is no exception. Recent reviews of the genus (Ślipiński 1982; Ślipiński *et al.* 1989) include numerous species descriptions, most of which are based on singletons or single, small series, and include very little information about hosts and habitat. Three Japanese species were more recently described in three separate papers (Sasaji 1997; Narukawa 2002; Aoki 2009); the most recent included detailed habitat information (e.g., photos of logs with bark removed). Narukawa (2002) mentioned that *Antibothrus ichihashii* Narukawa was found under bark of *Castanopsis sieboldii* (Makino) Hatus [commonly known as Itajii Chinkapin, Itajii, or Japanese Shii (Chang & Kim 2015)]. Nikitsky (1985a, b) claimed that *Antibothrus fatalis* Nikitsky could be found on “alder and quivering aspen in tunnels of ambrosia beetles of the genus *Xyleborus* (Eichhoff).” For most species of *Antibothrus*, nothing is known about biology and life history. Information about host associations and descriptions of larvae and pupae are lacking. It was surprising, therefore, when a monitoring survey targeting bark beetles and other wood-boring insects in the United States recovered a series of *Antibothrus morimotoi* Sasaji 1997. The survey was part of a United States Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS), Plant Pest and Quarantine (PPQ) exotic bark beetle survey. Multiple series, totaling twenty specimens, were recovered from the bycatch of samples taken during two months (April and May) of two years (2013 and 2015) in Columbus, Franklin County, Ohio. This is the first adventive Palearctic species of Bothrideridae to be recorded in North America. A related species, *Anommatus duodecimstriatus* Müller (Coleoptera: Terediidae) (Peck 1972; Robertson *et al.* 2015), is adventive as well, but has been transferred out of Bothrideridae (Robertson *et al.* 2015). These captures of *Antibothrus morimotoi* represent the first records of this genus and species for North America. We provide a diagnosis, a description, and an updated identification key for the bothriderid genera of North America north of Mexico. This key is the first for North American bothriderids after the family was redefined by Robertson *et al.* (2015).

3.3 Materials and Methods

In April and May of 2013 and 2015, as part of a USDA/APHIS/PPQ Exotic Bark Beetle Survey, several Lindgren funnel or cross-vane panel traps were installed and operated for various intervals. The traps were baited with either ethanol, alpha-pinene and ethanol, *Platypus quercivorus* (Murayama) lure and ethanol, or *Megaplatypus* Wood lure. Specimens of non-target taxa obtained through this sampling approach were mounted and set aside for later attention by members of the Biodiversity Services Facility (BSF) at the Carnegie Museum of Natural History (CMNH). In 2015, one of the authors (TCM) received some beetle specimens from this bycatch material as part of a museum loan for a different project. Included in the loaned material were several unusual specimens that were recognized (by TCM and JVM) as a species of Bothrideridae that was not previously known to occur in North America. Subsequent consultation with Nathan Lord determined that they represented the genus *Antibothrus* Sharp, 1885. Using a combination of Nikitsky (1985a, b), Ślipiński (1982), Ślipiński *et al.* (1989), Sasaji (1997), Narukawa (2002), Philips & Ivie (2002), and Aoki (2009), we were able to identify the specimens as *Antibothrus morimotoi* Sasaji. This determination was further confirmed by Natalia Vandenberg at the USDA/Systematic Entomology Laboratory (SEL). Further examination of samples from 2015 led to the discovery of two additional collecting events.

Specimens were examined with Leica MZ8 and Leica M10 Wild Dissecting Microscopes. Specimens for dissection were cleaned and softened in warm soapy water, then cleared in a 10% KOH solution for approximately one hour. Dissected specimens were slide mounted in glycerol and viewed with a Leica Leitz DMRB Compound Microscope.

Habitus images were captured with a Canon EOS-1 digital camera and a Canon Macro Photo MP-E 65mm lens. Lighting consisted of two Yongnuo Digital Speedlite YN560 III speed flashes pointed indirectly at a white “Chinese lantern” diffuser. Sequential images were made of each beetle at different focal depths and combined to create a deep focus image, using Helicon Focus 6.4.2 Pro software. The composite images were edited with Adobe Photoshop CS6 (Adobe Systems, Inc., 2003, San Jose, California).

Voucher specimens of *A. morimotoi* are deposited in the University of Georgia Collection of Arthropods, Athens, GA (UGCA) and the Carnegie Museum of Natural History, Pittsburgh, PA (CMNH). Specimens were georeferenced from label data and the CMNH BSF collecting event database, then mapped with GoogleEarth™ version 7.1.5.1557.

3.4 Results

Antibothrus Sharp 1885

Systematics. *Antibothrus* is a predominantly Old World genus of cocoon-forming beetles with 17 described species (Ślipiński *et al.* 1989). Most of the species occur in Madagascar and Africa (Ślipiński 1982), but three species are known from Japan (Sasaji 1997; Narukawa 2002; Aoki 2009), one from Russia (Nikitsky 1985a, b), and one from Sri Lanka (Sharp 1885).

Generic diagnosis. In America north of Mexico, this genus can be diagnosed by the following combination of characters (modified from Ślipiński *et al.* 1989) (Fig. 1):

Small (less than 3 mm long), moderately to strongly convex. Head produced, eyes large, protuberant. Antennae 11-segmented with 2-segmented club, with terminal segment smaller than penultimate. Pronotum hexagonal in outline (although only vaguely so in *A. morimotoi*). Elytra with alternate intervals carinate, even intervals usually punctate. Procoxae narrowly separated, intercoxal process produced into single lobe. Metaventrite and abdominal ventrite 1 without postcoxal lines. Tibiae expanded toward apices.

Key to the Nearctic genera of Bothrideridae (*sensu* Robertson *et al.* 2015) (Coleoptera: Coccinelloidea) [modified from Stephan (1989) and Philips & Ivie (2002); see those references for figures of genera other than *Antibothrus*]

1. Procoxae separated by half or more than half the width of one procoxa; greatest width of pronotum less than greatest width of elytra; body generally flattened and wider 2

1”. Procoxae contiguous or nearly so; greatest width of pronotum about equal to greatest width of elytra; body generally subcylindrical, elongate, or narrow 4

2(1). Elytral costae interrupted or notched; each elytron with pair of conspicuous yellow callosities at or near mid length .... *Lithophorus* Sharp

2”. Elytral costae uninterrupted and even; elytra lacking yellow callosities 3

3 (2”). First abdominal ventrite with distinct postcoxal lines extending beyond mid length of ventrite, usually nearly reaching the posterior margin; pronotal disc with pair of large, unusually shaped nodules bordered by deep grooves and separated by narrower groove ……………………………………………………………….. *Prolyctus* Zimmerman

3”. First abdominal ventrite with postcoxal lines at most vaguely indicated; pronotal disc not extremely modified, usually at most with median longitudinal depression … …………………………………………………………………………….*Bothrideres* Dejean

4 (1”). Length greater than 9.0 mm; antennal club weakly 3-segmented; pronotal disc with well-developed, deep, median longitudinal groove, interrupted near middle; Pacific Northwest and California …………………………………………..… *Deretaphrus* Newman

4”. Length less than 6.0 mm; antennal club 2-segmented; pronotal disc variously modified, but if possessing groove never interrupted near middle; eastern and southern US ………………………………………………………………………………………. 5

5 (4”). Procoxae contiguous; scape and pedicel normal, not joined asymmetrically; terminal two antennomeres subequal in width ………………………….. *Sosylus* Erichson

5”. Procoxae narrowly separated; scape and pedicel joined asymmetrically, scape with pointed nodule; terminal antennomere narrower than penultimate (~ 2/3 as wide) (Figure 3.1) ………………………………………………………………… *Antibothrus* Sharp

Antibothrus morimotoi **Sasaji 1997**

(Figure 3.1)

Species diagnosis. In the New World, *A. morimotoi* is the only species of *Antibothrus* currently established. Thus, the generic level diagnostic characters are sufficient to distinguish it from all other species of Bothrideridae that are known to occur in North America.

When compared with similar species of *Antibothrus* in its native range, *A. morimotoi* can be distinguished by the peculiar form of the basal two antennal segments (scape with stout spine protruding asymmetrically; pedicel wider than following segment, inserted asymmetrically into scape); penultimate antennal segment much wider than terminal segment [of similar width in *A. fatalis* (Nikitsky 1985a)]; eyes prominent laterally; pronotal longitudinal furrow barely impressed; lateral edges of pronotum rounded, not carinate; sub-interval carinae of elytra shorter; and short stout setae on apex of elytra lacking [present in *A. hirsutus* Aoki (Aoki 2009)].

Species redescription (modified from Sasaji 1997, additional terminology from Lawrence *et al.* 2010)

Body: somewhat cylindrical-flat, about 3.1× as long as wide, nearly parallel-sided. Uniformly reddish brown or yellowish brown, without any dark or light markings. Surface almost glabrous.

Head: Relatively large, wider than long in dorsal aspect. Eyes strongly prominent laterally and glabrous. Frons finely and sparsely punctate. Fronto-clypeal suture distinct.

Clypeus wider than long, with visible setae near apex. Antenna clearly 11-segmented. Scape (A1) stout, mostly glabrous with small setal fringe preceding A2 insertion, with acute basal spine on outer edge, spine with associated longer seta; pedicel (A2) much smaller than A1 but strongly widened (measured perpendicularly to A1 insertion), inserted asymmetrically on A1 outer lateral edge; A3 subcylindrical, slightly longer than wide; A4–9 each wider than long; A10 strongly widening apically, about twice as wide as long; terminal antennomere (A11) transverse oval, much wider than long, with narrow stem, about 2/3 size of A10. Genal processes expanded into acute points ventrally.

Prothorax: Nearly as long as wide, hexagonal, with weakly angulate sides. Surface of pronotal disc roughly sculptured by large (0.1–0.2 mm), irregular, elongate-oval punctures, each with a single minute, short seta. Pronotal base with a pair of weak and very short admedian elevations bordered laterally by weak depressions and mesally with an additional weak median depression. Lateral pronotal carina weakly present basally, nearly obliterated anteriorly. Prosternal process very narrow, and weakly widening posteriorly with a subtruncate apex, and nearly as long as basisternal length. Postcoxal process of prothoracic hypomeron very narrow.

Pterothorax: Scutellar shield small, wider than long. Mesocoxal cavities closed externally, separated by ~1/2 width of mesocoxal cavity, subcircular. Mesoventrite trapezoidal, roughly punctured, nearly as long as mesocoxal cavity (not including mesoventral process); mesoventral process with gradual elevation anteromedially, reaching level of metaventrite; mesanepisternum distinctly separated from mesoventrite, roughly punctured, subtriangular in lateral view. Meso-metaventral junction straight. Metaventrite longer than first abdominal ventrite, coarsely and more densely punctured,

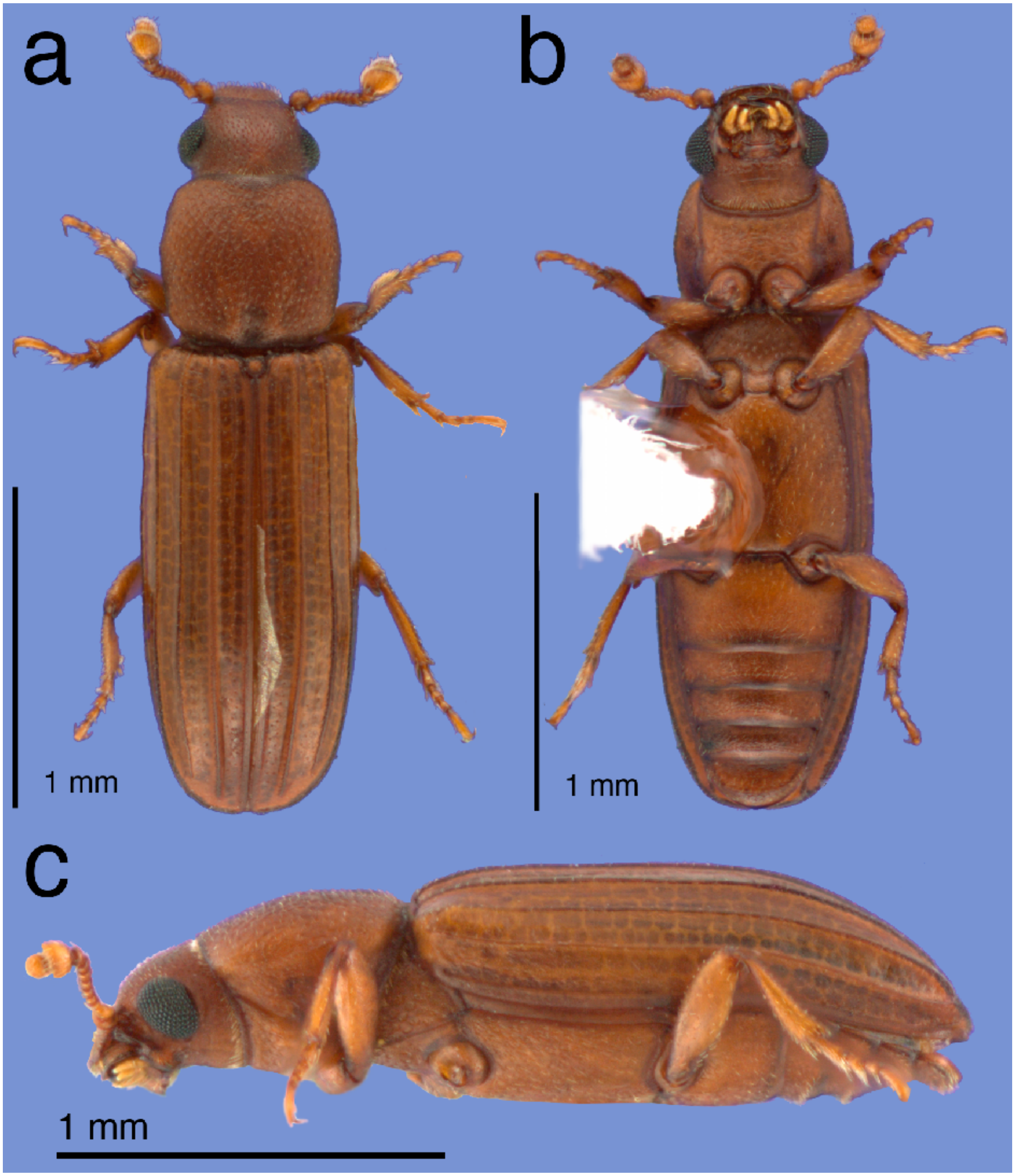

Figure 3.1. *Antibothrus morimotoi* (a) dorsal, (b) ventral, and (c) lateral habitus. Images by TC McElrath.

with some minute setation. Metanepisternum long, thin, not expanded, impunctate.

Elytra: Anteriorly wider than prothorax, widest in anterior third; almost parallel-sided with a short rounded apex. Disc of elytron with three distinct longitudinal carinae, reaching almost to elytral apex; suture also carinate; each of three intervals with a weak longitudinal carina at anterior half or anterior two-thirds. Surface of interstices between carinae very weakly, sparsely punctate, mostly smooth; nearly glabrous, except for minute, sparse setae only visible under high magnification.

Abdomen: Intercoxal process broad, flat, truncate. Ventrite one (V1) longest, about 2–3× as long as each of the remaining ventrites (V2–5). All ventrites somewhat coarsely, densely punctured. V1 mostly flat, curving towards dorsum laterally. V2-4 subequal in length. V2–4 each with median posterior margin with ridge-like expansion away from body, especially V4, so that the posterior edges of V2–4 project more strongly ventrad than the anterior edges. V5 mostly flattened, slightly longer than V4.

Legs: Tarsal formula 4-4-4, basal and terminal tarsomeres longest. Tibial spur formula 1-2-2. Protibia with sharp terminal outward extension forming spine and several small but distinct denticles along outer edge; protibia with one long (nearly reaching apex of first tarsomere), slender, socketed, darkened, apically curved tibial spur. Meso- and metatibia each with a sharp terminal outward extension forming spine and two subequal, straight tibial spurs, each shorter and less robust than protibial spur.

Body length: 2.00–2.35 mm (avg. 2.17 mm) (up to 2.5 mm in native range); width: 0.65–0.75 mm (avg. 0.69 mm) (n = 20, all specimens included).

Distribution: JAPAN (Honshu: Fukui, Mie, Nara and Hyôgo); UNITED STATES (Ohio: Franklin Co.). North American (Figure 3.2)

Biology: *Antibothrus fatalis* is associated with burrows of the scolytine genus *Xyleborus* (Nikitsky 1985a). Two species of *Antibothrus* have been collected beneath the bark of trees: *Antibothrus ichihashii* on *Castanopsis sieboldii* (Narukawa 2002) and *A. hirsutus* on an unidentified tree. The specimens of *A. morimotoi* found in North America were all collected by Lindgren funnel traps baited with various bark beetle attractants, such as alpha-pinene, *Platypus quercivorus* or *Megaplatypus* lure, and ethanol. Considering that most members of Bothrideridae are ectoparasites of wood-boring insect larvae, the capture of *A. morimotoi* in these baited traps suggests that the species is ectoparasitic on larvae of bark beetles, perhaps a species of *Xyleborus*.

Interestingly, the specimens collected in 2013 were slightly shorter ($\bar{x}$ = 2.14 mm, n = 15) than those collected in 2015 ($\bar{x}$ = 2.27 mm, n = 5). While this difference is not statistically significant, it was readily visible and easily measurable. This may be due to changes in the host species utilized, or the health (and nutritional value) of the host species between the two years, or alternatively, to the number of individuals utilizing a single host larva or pupa.

New North American Records

Specimens examined:

2013 SPECIMENS: UNITED STATES: Ohio: Franklin County, 2.6 km SE Riverlea, 271 m, E. Larue, collector: BSF# 50618, 40.0711°N, 82.9986°W, 30 April–14

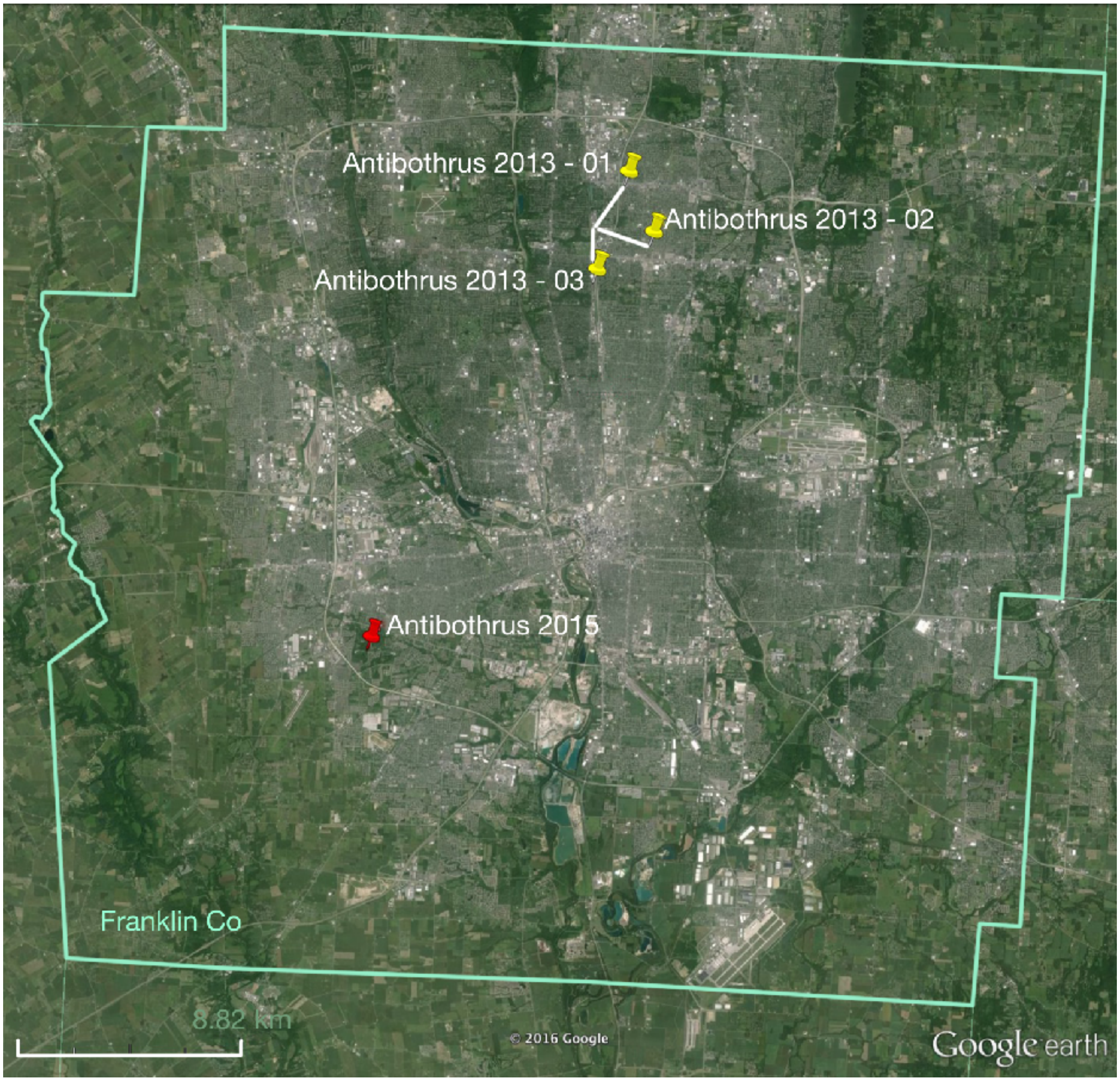

Figure 3.2. Map of *Antibothrus morimotoi* specimen collecting events reported in this work. Yellow and red pins are 2013 and 2015 collection points, respectively. Image created with GoogleEarth™ version 7.1.5.1557. Interactive KML file available: "https://archive.org/download/Antibothrus/Antibothrus.kml"

May 2013, Lindgren funnel trap with alpha-pinene + EtOH (3 specimens); BSF# 50619, 40.0711ºN, 82.9986ºW, 14–29 May 2013, Lindgren funnel trap with alpha-pinene + EtOH (2 specimens); BSF# 50632, 40.0713ºN, 82.9993ºW, 30 April–14 May 2013, Lindgren funnel trap with EtOH (6 specimens); BSF# 50633, 40.0713ºN, 82.9993ºW, 14–29 May 2013, Lindgren funnel trap with EtOH (3 specimens); BSF# 50640, 40.0709ºN, 82.9996ºW, 14–29 May 2013, Lindgren funnel trap with *Platypus quercivorus* lure (1 specimen).

2015 SPECIMENS: UNITED STATES: Ohio: Franklin County, 3.1 km NW Urbancrest, Big Run Park, 39.92197ºN, 83.10441ºW, 258m, cross-vane panel trap with *Megaplatypus* lure, E. Larue, collector: BSF# 63656, 16 April–12 May 2015 (4 specimens); BSF# 63657, 12–26 May 2015 (1 specimen).

3.5 Discussion

During the identification and redescription of this species, it was discovered that *Antibothrus morimotoi* lacks one of the two protibial spurs that typically occur in Bothrideridae (Ślipiński *et al.* 2010). The single protibial spur is longer, darker, more apically recurved, and more robust than the meso- and metatibial spurs. This condition is unusual within this family; other species have a second protibial spur that is reduced dramatically, but very few have completely lost the second spur. In the original description, Sasaji (1997) claimed that the protibia has “a long slender and a short spurs”, but these were not well illustrated or described in detail. Other *Antibothrus* such as the Japanese species *A. ichihashii* and *A. hirsutus* both possess the full complement of two protibial spurs (Aoki 2009). Interestingly, *A. ichihashii* has a reduced second protibial spur (Naraukawa 2002). The Palearctic species *A. fatalis* has no second protibial spur illustrated in its description (Nikitsky 1985b). At least one African species is known to have reduced second protibial spurs (SA Ślipiński, pers. comm.). This character merits further investigation in Bothrideridae.

Since *Antibothrus morimotoi* has been collected in two different years over a three year period, and in two different localities in Ohio, it seems likely that it has become established in North America. While the 2013 collections occurred at a commercial site, a potential point of introduction, the subsequent collection of the species two years later in a suburban park, over ten miles distant, surrounded primarily by residential areas, lends additional support to this hypothesis. Some bothriderids, however, live up to three years in the adult stage (Togashi & Itabashi 2005), so further sampling is necessary to verify establishment and monitor the spread of these beetles.

The exact mode of introduction for *Antibothrus morimotoi* is not yet clear, but some speculation can be made. The USDA/APHIS/PPQ monitoring project targeted areas where imported goods are stored or transferred within the United States, including ports, distributors, shipping areas, and business parks. The traps that recovered *A. morimotoi* in 2013 were set at a commercial location in Columbus, Ohio that provides a variety of ceramic and stone products. This type of business frequently ships and receives products using wooden pallets, crating or supports. There are numerous distributors and import businesses near that location, and several nearby patches of local undeveloped woods might support populations of wood-boring scolytines that *A. morimotoi* would need to reproduce. Any resampling efforts should target those local forested areas as well as the local distributors.

The establishment of *A. morimotoi* seems innocuous, especially considering the numerous other insects that are already causing millions of dollars in damage (Aukema *et al.* 2010). This may be one adventive species that will not cause alarming tree deaths, as it is likely to be an ectoparasite of wood-dwelling insects, but its effects on the forest ecosystem are yet to be seen. Its potential association with *Xyleborus* species may be of some potential use in biocontrol efforts, but until the biology of this species is better known, its use as a biocontrol agent cannot be pursued.

This discovery highlights the "collection to identification" time gap that exists for specimens collected from biological monitoring projects. From the time of first collection of *A. morimotoi* in April, 2013, to the definitive identification in early January of 2016, there was a time gap of over 2.5 years. It is entirely possible that the introduction of this species occurred earlier than April 2013, as the likelihood is low that just one trap caught the only established population (Wheeler & Hoebeke 2009). Considering the obscure habits of the family Bothrideridae and the nondescript appearance of *A. morimotoi*, it is possible that specimens taken during other projects may have gone unrecognized and the actual distribution is greater than currently documented.

Were it not for the exotic bark beetle monitoring projects undertaken by USDA/APHIS/PPQ, as well as numerous other monitoring programs across the United States, we would have no knowledge of the diverse insect pests becoming established within our borders. Unfortunately, monitoring projects are often overworked, understaffed, underpaid, and at continual risk of defunding. Many projects only target particular taxa of interest or of potential risk to economic industries within the United States. The "by-catch", or extra insects that are caught, are usually discarded or stored in a much less accessible preservation medium (e.g. bulk trap samples in jars of ethanol, numerous poorly labeled vials), because there is no funding or time for proper curation of such material. The fact that non-target specimens of *A. morimotoi* were detected, deemed unusual enough for further examination, then properly curated, labeled, and made available to specialists, is a testament to the foresight of staff at the museum from which they originated (CMNH). When establishing the *Biodiversity Services Facility* at CMNH, the museum stipulated that only raw, unsullied samples would be accepted so that all taxa, not just target taxa, would be potentially available for examination and documentation. Such worthy efforts are currently underfunded, or not funded at all. Future monitoring projects should include extra time and funding for the processing, curation, and identification of such non-target catches, not only to intercept new invasive or adventive species, but to bolster the natural history data of many under-caught or rare species that such trapping and monitoring efforts recover.

3.6 Acknowledgements

E. Richard Hoebeke (UGCA) provided helpful comments and encouragement with this project. James Robertson and Adam Ślipiński reviewed the manuscript and provided helpful comments. Nathan Lord (Brigham Young University) & Natalia Vandenberg (USDA/SEL) assisted with the species determination and confirmation. Robert Davidson (CMNH) arranged the initial loan of specimens that led to this project. Avraham Eitam and Stephen Bullington (USDA/PPQ/APHIS) helped with processing and upcoming trap surveys. Two impeccable translations of Russian taxonomic literature were done by Tatiana Kiselyova (Monroe, GA).

CHAPTER 4

MONOTOMIDGEN — A MATRIX-BASED INTERACTIVE KEY TO THE NEW WORLD GENERA OF MONOTOMIDAE (COLEOPTERA, CUCUJOIDEA) [3]

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[3] McElrath TC, Boyd OF, McHugh JV. 2016. *Zookeys* 634: 47-55.

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4.1 Abstract

A matrix-based Lucid™ key is presented for the twelve genera of Monotomidae (Coleoptera: Cucujoidea) represented in the New World. A general overview is given for the features and technical specifications of an original interactive key for the identification of these genera. The list of terminal taxa included with the key provides a current summary of monotomid generic diversity for the Nearctic and Neotropical regions.

Keywords: interactive key, data matrix, identification, morphology, LUCID, minute clubbed beetles

4.2 Introduction

Matrix-based (also known as interactive, multi-access, multi-entry, or filter-style) keys offer vast advantages over traditional dichotomous identification keys. Some advantages include: freedom to follow more than a single path, ability to use only subsets of characters, integration of non-traditional (e.g., biology, distribution) and overlapping characters, effective use of multi-state characters, and inclusion of numerous graphics (Penev et al. 2009; 2012). These keys have been used successfully to overcome the challenges of identification of many groups of organisms, including various flies (Lyons & Dikow 2010; Cerretti et al. 2012), thrips (Mound et al. 2012), aphids (Favret & Miller 2012), and beetles (Lawrence et al. 2010; Lord et al. 2011; Nearns et al. 2016). However, many other challenging groups could use such powerful identification tools.

With 117 described species in twelve genera, the New World Monotomidae (also known as the “minute clubbed beetles”) are a small group of mostly mycophagous and predaceous beetles within the superfamily Cucujoidea. The worldwide generic diversity was last reviewed by Sen Gupta (1988). Since that review, nine new genera have been described, including one from the New World (Pakaluk & Ślipiński 1993; Pal 1996; Sen Gupta & Pal 1995). The North American genera were briefly reviewed and an identification key was provided by Bousquet (2002a). Many Nearctic genera have been reviewed relatively recently (Bousquet 1990; 2002b; 2003a, b, c; Bousquet & Laplante 1999). Despite these reviews, identification remains difficult, especially to non-specialists who are unfamiliar with the diagnostic characters. Since Monotomidae are important components of forest ecosystems as predators of scolytine bark beetles (Gregoire et al. 1985), vectors of fungal pathogens in trees (Hinds 1972), and pollinators (Jenkins et al. 2013; 2015), non-specialists frequently encounter them and need to make confident determinations. In addition, some monotomids, such as *Rhizophagus parallelocollis, Monotoma longicollis, M. spinicollis, M. johnsoni, M. picipes*, and others (Kuschel 1979; Bousquet 1990; Bousquet & Laplante 1999; Jelinek 2007), are being spread worldwide through human commerce or expanding their native range (Peck & Thomas 1998), and their effects on ecosystems will remain undocumented until they are identified. However, monotomid identifications have been complicated by the inaccessibility of taxonomic literature, lack of a recent, synthetic, genus-level treatment, and inadequacy of available graphics (habitus photographs, electron micrographs, and illustrations) to interpret many diagnostic features.

To address these issues, an interactive matrix-based identification key was developed for the twelve described genera of New World Monotomidae. This key is based on a matrix of 46 characters derived from morphometrics, discrete anatomical features, distributional data, and ecology. Included are illustrations of diagnostic features and dorsal and ventral photomicrographs of reliably determined representatives of each genus. Complete taxonomic coverage was possible for some genera, allowing inclusion of photomicrographs and morphometric data for all known species.

4.3 Project description

Taxonomic coverage

This key covers 12 of the 12 genera belonging to the family Monotomidae that are currently known to occur in the New World (Bousquet 2009).

List of the terminal taxa included in the current version of the identification key (last update November 2016)

Aneurops Sharp, 1900; ***Bactridium*** LeConte, 1861; ***Crowsonius*** Pakaluk & Ślipiński, 1993; ***Europs*** Wollaston, 1854; ***Hesperobaenus*** LeConte, 1861; ***Leptipsius*** Casey, 1916; ***Macreurops*** Casey, 1916; ***Monotoma*** Herbst, 1793; ***Phyconomus*** LeConte, 1861; ***Pycnotomina*** Casey, 1916; ***Rhizophagus*** Herbst, 1793; ***Thione*** Sharp, 1899.

Photomicrographs of terminal taxa

Each genus included in the key has at least one associated dorsal and ventral photomicrograph. For most genera, multiple photomicrographs were provided in order to illustrate the range of intrageneric diversity. All photomicrographs represent either type specimens, authoritatively identified museum material, or material determined by the first author (TCM). Illustrative shots of important characters are provided within the key, and larger dorsal and ventral habitus photographs are included within the Fact Sheets section of the website.

Characters used in the key

General features

Characters used for identification were derived from existing literature (Sen Gupta 1988; Bousquet 2009) but then confirmed and scored from specimens in the University of Georgia Collection of Arthropods (UGCA) and the Smithsonian Institution National Museum of Natural History (NMNH). Anatomical terminology follows that of Bousquet (2009) and Sen Gupta (1988), the most comprehensive morphological treatments of Monotomidae to date.

The data matrix forming the foundation for this key is based on 46 anatomical, distributional, and ecological characters. These features are encoded into characters with a range of two to eight possible states. Most characters refer to external anatomical features of the adult form that are easily visible without preparation or dissection. Because multi-access keys provide users with greater flexibility than dichotomous keys, hard-to-view and rarely available features also are included. For example, ecological characters are provided for unusual cases when such information is available. The key includes several hind wing characters, usually visible only after dissection and preparation, because they are very valuable for separating genera. In addition, five morphometric characters are included. The diagnostic range values for these characters were based on measurements of multiple species within each genus, including measurements from as many reliably identified specimens as was reasonable. By measuring many diverse individuals representing each genus, more accurate estimates of the range in sizes was possible for these morphometric characters. The morphological characters are sorted by body part (head, mouthparts, thorax, scutellum, legs, hind wing, and abdomen; available via the "Subsets" button on the Lucid Player control bar, and sorted by default) allowing the user to easily focus on particular regions or preparations of a specimen. To quickly narrow some identifications, distributional characters are included.

Most characters are accompanied by supporting images and clarifying explanations within the key, as well as in the "Glossary of Terms" section (see below) of the website.

List of the characters used in the key

GENERAL: length (mm); ratio of body length: greatest body width; body shape (lateral view); dorsal surface of the body (setation); elytral color; biology (habitat, known host associations, etc.); geographic distribution

HEAD: ratio of head length: greatest head width (including eyes); head constriction (presence/absence); ratio of temple length: longitudinal length of eye;

antennal cavity on ventral side of head (presence/absence); eyes (number of facets); antennal club (number of apparent segments); antennal club (whether distinct)

MOUTHPARTS: maxillary palps (size of second segment); labial palps (size of second segment); mandibular dentation (number of teeth); mandibular cavity (presence/absence)

THORAX: ratio of pronotal length along midline: greatest pronotal width; pronotal disc (vestiture); pronotal disc (shape); lateral margin of pronotum (smooth/crenulate); pronotal disc (impressions); pronotal microsculpture (presence/absence); pronotal puncture density (center of disc only); anterior angles of pronotum (whether projecting); procoxal cavities externally (shape); procoxal cavities (degree of separation); procoxal trochantins (exposure); scutellar microsculpture (presence/absence); scutellar setation (presence/absence); mesocoxal cavities (degree of separation)

LEGS: number of metatarsomeres of male

WINGS: elytral setigerous punctures (arrangement); setigerous punctures on epipleural fold (number of rows); hind wing (presence/absence); number of anal veins; r-m cross (degree of development); subcubital fleck (presence/absence)

ABDOMEN: intercoxal process of abdominal ventrite (shape); metacoxal bead or femoral line (presence/absence); metacoxal bead or femoral line (length of production); first abdominal ventrite of male (special modifications); puncture rows on abdominal ventrites two-four (presence/absence); number of rows of punctures on abdominal ventrites two-four; punctures on abdominal ventrites two-four (size/shape)

Software technical specifications

Application: Lucid Builder 3.5 (available at www.lucidcentral.org, see website for exact technical specifications and features list)

Key version: 1.0

Requirements for use: Java-enabled browser and internet connectivity

License for use of the key: Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited

Web location: http://www.monotomidae.com/MonotomidGen.html

Data resources

The data underpinning the Lucid Key (Lucid Key files) reported in this paper are deposited in the Dryad Data Repository at **http://dx.doi.org/10.5061/dryad.q9p4j**.

Website features

Genus fact sheets (http://monotomidae.com/facts.html):

Each of the twelve genera represented in the key are treated and figured with dorsal and ventral habitus images. For each genus, informational sections about the following subjects are provided to assist identifications: Taxonomy, Diagnosis, Biology, Distribution, List of Species (photographed and not-photographed), and Suggested References.

Resources (http://monotomidae.com/resources.html)

An anatomical atlas, glossary of terms, and guide to diagnosing the beetle family Monotomidae are included here. The anatomical atlas illustrates many of the characters used in the identification key and includes an illustration of the dorsal and ventral habitus of *Monotoma producta*, as well as a wing illustration of *Rhizophagus sayi*. The glossary of terms (http://monotomidae.com/glossary.html) provides clarifiying definitions and explanations of all terms included in the interactive key, listed alphabetically, drawn from Nichols (1989), Lawrence et al. (2011), and Nearns et al. (2016). The diagnosis page (http://monotomidae.com/whatis.html) discusses characters that could diagnose a beetle as belonging to Monotomidae. It also provides photographs of taxa that are commonly misidentified as Monotomidae.

References (http://monotomidae.com/references.html)

A list of useful monotomid references is given. Links are provided to available PDFs or websites of these references when not in violation of copyright restrictions.

4.4 Conclusions and future work

During development of this identification resource, several problems became apparent. First and foremost, nearly all monotomid genera included herein require modest or extensive taxonomic work. For the Nearctic region, the problem is not as serious because most genera, with the exception of *Bactridium*, have been at least partially treated within the last 25 years (e.g., Bousquet 1990; 2002a, b; 2003a, b; 2003c; Bousquet & Laplante 1999). *Bactridium* requires extensive work and is currently undergoing revision by TCM. In addition, most other genera represented in the Nearctic harbor some undescribed species (e.g., *Monotoma, Aneurops,* and *Rhizophagus*). As new types of data are examined, some currently recognized polymorphic species may be recognized as species complexes. The Neotropical fauna has been far less studied; numerous undescribed species and potentially even genera exist. Species identification in this region almost always requires comparison with type material. Even genus-level identifications of Neotropical specimens should be confirmed by a specialist, though this key will narrow down options for tentative determinations considerably.

Second, the relationships between monotomid genera are poorly understood. No phylogenetic analyses of any kind have been performed for this family. Thus, some morphological characters currently used to delimit genera require investigation to test their success in characterizing monophyletic groups. Some monotypic North America genera (e.g., *Pycnotomina*, *Macreurops*, and *Phyconomus*) should especially be targeted, as they may represent highly autapomorphic lineages nested within other genus-level clades.

Pending completion of a number of alpha taxonomic studies and phylogenetic analyses of the family, it will be possible to update this key to include species as the terminal units, and to more rigorously define the genera, as supported by additional characters. In the meantime, the numerous habitus images and illustrations should provide enough resources for confident genus-group determinations, and the other resources provided within MonotomidGen should facilitate approximate species identification.

This key provides a flexible, powerful, and media-rich information resource for any scientist or non-professional who needs to identify monotomid beetles. In addition, it provides a framework upon which to build future identification resources for this family. Eventually, a worldwide resource for identification of monotomid beetles should be completed to identify the species being transported around the world through human activities. This will allow for quicker identifications and therefore, quicker documentation of the spread of newly adventive species. Taxonomic resources of broader scope such as MonotomidGen can assist those tasked with discovering and identifying these anthropogenic species introductions.

4.5 Acknowledgements

This study was supported by a UGA CURO Research Grant (OFB & JVM), H.H. Ross Memorial Fund Grant (TCM), Ernst Mayr Travel Grant from Museum of Comparative Zoology at Harvard University (TCM), and CanaColl Foundation Endowment Fund Collections Grant (Y Bousquet & TCM).

We thank Darren Pollock (Eastern N.M. Univ.), Zach Falin (Univ. Kansas), Bob Turnbow (Enterprise, AL), the late Chuck Bellamy (CDFA), and Andy Cline (CDFA) for providing critical specimens for this study. Yves Bousquet, Nathan Lord, and Michael Thomas reviewed this manuscript and provided valuable comments and revisions. In addition, Lynette Elliott, Insect Images (Bugwood.org), Nathan Lord, Chris Mallory, the Pest and Disease Images library (PaDIL), Udo Schmidt, and Michael C. Thomas generously allowed their photos to be used for the Monotomidae diagnosis page. We would like to thank Floyd Shockley and David Furth (NMNH) for their assistance and

hospitality, Gene Wright (UGA Lamar Dodd School of Art) for technical assistance, Zach McElrath for extensive coding and CSS support, and the UGA Department of Entomology for supporting this project.

CHAPTER 5

BEETLES (COLEOPTERA) OF PERU: A SURVEY OF THE FAMILIES.

MONOTOMIDAE LAPORTE, 1840 [4]

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[4] McElrath TC. Accepted by *Peruvian Journal of Biology*.

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5.1 Abstract/Resumen

The diversity of the beetle family Monotomidae is summarized for the country of Peru. One subfamily, three tribes, three genera, and four species are recorded. This paper presents the first record of this family in Peru, as part of the 'Beetles of Peru' project. Diagnostic characters for the family are given. This is only a preliminary checklist; many specimens were not identifiable past genus with current literature. The diversity of Monotomidae will expand considerably with additional surveys and sampling work within the country.

La diversidad de la familia Monotomidae se resume para el país de Perú. Una subfamilia, tres tribus, tres géneros y cuatro especies son registrados. Este trabajo presenta el primer registro de esta familia en Perú, como parte del proyecto 'Escarabajos de Perú'. En adición, se presentan los caracteres diagnósticos para la familia. Este listado representa uno solamente preliminar, ya que muchos especímenes no eran identificables con la literatura actual a más halla de género. La diversidad de Monotomidae se expandirá considerablemente con más trabajos de muestreos dentro del país.

Keywords: taxonomy; Neotropical; minute clubbed beetles; South American biodiversity; checklist

Palabras clave: taxonomía; Neotrópico; escarabajos minúsculos de antenas capitadas; biodiversidad de Sudamérica; listado de especies

5.2 Introduction

The family Monotomidae (the minute clubbed beetles) comprises two extant subfamilies, Rhizophaginae Redtenbacher and Monotominae Laporte, of which only the latter is known from Peru (Bousquet 2009). The sister group of the family is, as yet, unknown, but may be the Nitidulid-series (Nitidulidae+Kateretidae+Smicripidae) (McElrath et al. 2015; McKenna et al. 2015; Robertson et. al 2015) or various families allied to Erotylidae (Helotidae, Erotylidae, others) (Leschen et al. 2005; Hunt et. al 2007; Lawrence et al. 2011; Bocak et al. 2014). The family is thought to be monophyletic, although this has yet to be rigorously tested. Monotominae is divided into four tribes: Europini Sen Gupta, Lenacini Crowson (endemic to New Zealand), Monotomini Laporte, and Thionini Crowson. There are about 250 species described worldwide, nearly half of which are placed in three genera: *Europs* Wollaston (53 spp.), *Monotoma* Herbst (40 spp.), and *Rhizophagus* Herbst (53 spp.).

Below is the first checklist of the Monotomidae of Peru, which comprises 1 subfamily, 3 tribes, 3 genera, and 4 confirmed species. This report is another installment in the ‘Beetles of Peru’ project (see Chaboo 2015). Beyond the confirmed species mentioned below, there are many Peruvian specimens that are unidentifiable past genus until comparisons with type material are possible, or until the respective genera are revised. Following the format used for other contributions to the Beetles of Peru Project, a summary is given of information on the recognition, habitat, biology and collecting methods of Monotomidae to advance research on this family, especially by Peruvians.

Recognition

Adults can be reliably identified with the following combination of characters (Bousquet 2009; McElrath et al. 2012; McElrath et al. 2016): 1) antennae appearing ten-segmented, with a one- or two-segmented antennal club, the terminal segment actually representing a fusion of the true 11th and 10th antennal segments; 2) procoxal cavities broadly closed; 3) one (females and *Thione* Sharp) or two (males of most genera have a small sixth abdominal segment) abdominal tergites exposed beyond elytral apices; 4) first and fifth abdominal ventrites longer than any of ventrites 2-4 individually; and 5) tarsal formula 5-5-5 (females and Thionini) or 5-5-4 (males of most genera) (this character can be difficult to see as the first tarsal segment is small and somewhat hidden within the apex of the hind tibia).

Other characters helpful for recognition include: small body size (1-6 mm long from clypeus to elytral apex); body generally elongate-cylindrical to elongate-flattened, subglabrous to setaceous; head prognathous, exposed from above; antennae usually not concealed from above, widely separated, usually with an abrupt 1-2 segmented antennal club (not abrupt in *Crowsonius* Pakaluk & Ślipiński and some *Leptipsius* Casey), never 3 segmented; pronotum variable; mesocoxal cavities open; elytra with strong puncture rows or with dense, confused punctation; abdominal ventrite 1 usually as long as 2-4 combined; and pygidium well-sclerotized, punctured (Bousquet 2009; McElrath et al. 2012; McElrath et al. 2016).

Biology, Habitat, and Collecting Methods

Monotomids can be collected in a wide variety of habitats, though much is still to be learned about their biology. Passive collecting devices like flight intercept traps (FIT) and Lindgren funnel traps have proven effective in catching large numbers of Monotomidae. The specimens reported below were collected by FIT, Malaise, colored pans, and from fungus and tree sap.

Monotoma, especially the cosmopolitan species *M. longicollis* Gyllenhal and *M. picipes* Herbst, can be collected by sifting decaying vegetable matter such as decaying grass or compost heaps (Bousquet & Laplante 1999). Some *Monotoma* species can also be collected in refuse piles of ants (e.g., *Atta* F. or *Formica* L.), although no myrmecophilous taxa are known from Peru as of yet. Other species can be collected by sifting leaf litter or small mammal nests.

Thione species are thought to feed on scolytine and platypodine Curculionidae, or on their fungal crops; although this assumption is based on very limited data. They can be collected by examining the host galleries closely, peeling bark, or by using extraction methods that target these microhabitats such as emergence traps. Very little association or host data exists, but the three New World species have variously been collected from fungi: e.g. *Polyporus* (Micheli ex. Adanson), or from plants (probably under bark): *Lecythis corrugata* (Poiteau)*, Persea borbonia* (L.)*, Pouteria egregia* (Sandwith)*, Toulicia pulvinata* (Radlkofer)*,* and *Vismia guianensis* (Aublet).

Europs species, and especially *Europs bilineatus* Sharp, can be collected in great numbers under bamboo sheaths, especially those beginning to decay. Other species of *Europs* are associated with various rotting microhabitats, such as mammal nest detritus, rotting fruits, and fungus. *Europs fervidus* Blatchley, known from Florida and the Caribbean Islands, is a pollinator of the tropical hybrid fruit atemoya (*Annona x atemoya*). It is possible that other species may function in pollinator roles through the tropics (Jenkins et al. 2013; 2015). In the United States, *Europs pallipennis* LeConte and some other monotomids can be collected in great numbers using elevated flight intercept traps in old growth temperate forests (Ulyshen & Hanula 2007). This is the most diverse genus of tropical monotomids. It may well be collected in microhabitats that are currently undocumented.

Additional genera that may be found in Peru include *Leptipsius*, *Bactridium* LeConte, *Aneurops* Sharp, and *Hesperobaenus* LeConte, all of which are usually collected under bark in association with ascomycete fungi such as *Hypoxylon* Bulliard (Lawrence 1977; Bousquet 2009). Searching the subcortical microhabitat and other types of decaying vegetative material may yield new genus or species records of Monotomidae in Peru. The enigmatic genus *Crowsonius* is known only from a few collecting events in the nearby state of Pará, Brazil, and only from the nests of *Trigona* bees (Pakaluk & Ślipiński 1993; 1995). As *Trigona* bees are known to occur throughout the tropics, it is possible that *Crowsonius* also occurs in Peru. To collect this genus, direct examination of host bee nests is required, as all known *Crowsonius* species are flightless.

Identification

Peruvian monotomid genera can be identified using the filter key of McElrath *et al.* (2016) or Sen Gupta (1988). However, it should be noted that additional undescribed taxa may be present, and identifications should be confirmed with a specialist. Species identification in this region, with the exception of a few well-characterized species, is extremely difficult, and usually requires comparison with type material.

5.3 Materials and Methods

Data presented here are based on examination of 361 adult specimens assembled from the following collections:

CAS — California Academy of Sciences, San Francisco, CA, USA — David Kavanaugh, Rachel Diaz Bastin

FMNH — Field Museum of Natural History, Chicago, IL, USA — Crystal Meier

FSCA — Florida States Collection of Arthropods, Gainesville, FL, USA — Kyle Schepp, Paul Skelley

NCSU — North Carolina State University Insect Museum, Raleigh, NC, USA — Bob Blinn

SEMC — Snow Entomological Museum, University of Kansas Biodiversity Institute — Zackary Falin

Specimens collected for the Beetles of Peru Project were obtained under Peruvian research permits No. 506-2011-AG-DGFFS-DGEFFS and No. 0159-2010-AGDGFFS-DGEFFS (PI C.S. Chaboo). Types, uniques and 50% of all other specimens from that project are to be repatriated to the Museum of Natural History, University of San Marcos, Lima, Peru.

5.4 Results

Because no monotomid species have been reported from Peru before (e.g. Blackwelder 1945), those identified below represent **NEW COUNTRY RECORDS**. However, many species not recorded herein are known from surrounding countries, so this preliminary checklist is expected to expand greatly given sufficient time and collecting effort (Blackwelder 1945, McElrath unpublished data). Furthermore, there are additional species known from Peru, especially in the genera *Bactridium*, *Europs,* and *Monotoma*, that will be recorded from the country once these genera are revised. Peruvian specimens of the genus *Monotoma* were studied, but could not be confidently identified with current literature. It also is likely that the cosmopolitan species *Monotoma longicollis* and *Monotoma picipes*, recorded from neighboring countries, eventually will be found in Peru too.

Checklist of Monotomidae of Peru

Monotomidae Laporte, 1840

Monotominae Laporte, 1840

Europini Sen Gupta, 1988

Europs Wollaston, 1854

Europs bilineatus Sharp, 1900 (Fig. 5.1A)

Monotomini Laporte, 1840

Monotoma Herbst, 1793 (Fig. 5.1B)

Monotoma species undetermined

Thionini Crowson, 1952

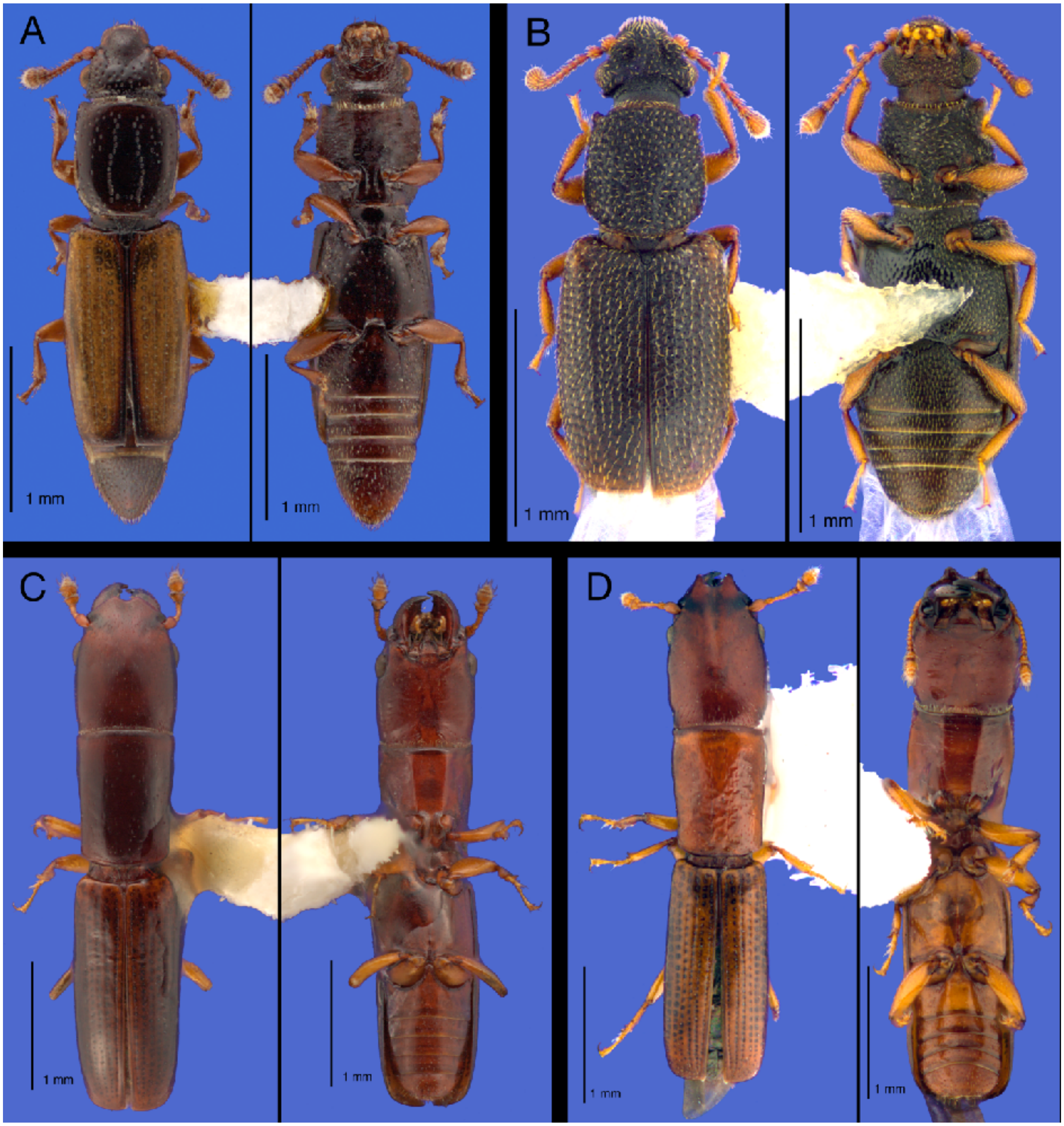

Figure 5.1. Monotomidae species occuring in or near Peru. Dorsal and ventral habitus images taken by TC McElrath: A) *Europs bilineatus* Sharp, 1900; B) *Monotoma picipes* Herbst, 1793; C) *Thione cephalotes* Sharp, 1899; D) *Thione championi* Sharp, 1899.

Thione Sharp, 1899

Thione cephalotes Sharp, 1899 (Fig. 5.1C)

Thione championi Sharp, 1899 (Fig. 5.1D)

Thione puncticeps Sharp, 1899

Rhizophaginae Redtenbacher, 1845

None represented

5.5 New Country Records

For each new record the label data are quoted directly below, with "/" dividing separate lines of data on the labels, and quotes surrounding the entirety of each unique collecting event. Multiple similar collecting events are separated by "//", with the first event containing all label data and the remaining events with only the changes listed. The number of specimens and the repository are given at the end of each record.

Europs bilineatus

"Peru: Torrentoy / Canyon, base of / Machu Picchu, 2000 / m. 20.VI.1964 / leg. B. Malkin / under bark Inst. Zool. P.A.N. / Warszawa / 68/67 (325, FMNH)"

"Peru: Madre de Dios / Coche Cashu Bio. Stn. / Manu National Park, 350 m / 11º53'45"S,71º24'24"W / 17-19 OCT 2000, R. Brooks / PERU1B00 042 / ex. flight intercept trap (8, SEMC)"

"Peru: Tambopata Prov. / Madre de Dios Dpte. / 15km NE Puerto / Maldonado Reserva / Cuzco Amazónico / 12º33'S, 69º03'W / 200m, camp / 3 July 1989, J. S. Ashe, / R. A. Leschen #377 / ex. under bark with / fermenting sap (1, SEMC)"

Thione cephalotes

“PERU: / Monson Valley / Tingo Maria / X-19-1954 / E.I.Schlinger / & E.S.Ross / collectors (1, CAS) // same, except X-10-1954 (2 specimens, CAS) // same, except X-26-1954 (4, CAS) // same, except XI-10-1954 (1, CAS) // same, except XII-9-1954 (1, CAS) // same, except XII-23-1954 (1, CAS)”

“PERU: Tambopata Prov. / Madre de Dios Dpte. / 15km NE Puerto / Maldonado Reserva / Cuzco Amazónico / 12º33’S, 69º03’W / 200m, camp / 21 June 1989, J. S. Ashe, / R. A. Leschen #213 / ex. at light (1, SEMC) // same except, 30 June 1989 #348 ex. under bark with fermenting sap (1, SEMC) // same except, 12 July 1989 / #493 ex. *Favolus hexagonalis* (1, SEMC)”

“PERU: Jauja Prov. / Junín Dept., 840m. / Sani Beni (8km.E. / Satipo) Oct-Nov 1935 / Felix Woytkowski (1, SEMC)”

“PERU: Madre de Dios: / CICRA Field Station, / Exp. Plot, South Transect / 12.55261ºS 70.11008ºW, 295m / 11-13.VII.2010 Chaboo team / ex. Malaise trap / PER-10-07-MaT-4 (1, SEMC) // same, except trail 6, rsrch / plot, 12.55207ºS 70.10962ºW / 11-13.VI.2011 / PER-11-MAT-021 (1, SEMC // same, except PER-11-MAT-029 (1, SEMC)”

Thione championi

“PERU: / Monson Valley / Tingo Maria / X-19-1954 / E.I.Schlinger / & E.S.Ross / collectors / *Thione championi /* Sharp 1899 / det TC McElrath 2015 (1, CAS)”

“PERU: Tambopata Prov. / Madre de Dios Dpte. / 15km NE Puerto / Maldonado Reserva / Cuzco Amazónico / 12º33’S, 69º03’W / 200m, camp / 9 June 1989, J. S. Ashe, / R. A. Leschen #009 / ex. at light (1, SEMC)”

“PERU: Madre de Dios: / CICRA Field Stn., garden / 12.56940°S 70.10100°W / 260m 26.VIII-2.IX.2010 / MJ Endara, malaise trap / PER10-08-MAT-013 (1, SEMC)”

“PERU: Madre de Dios, / Puerto Maldonado / 17-XII-2013, 267 m / 12.56104°S, 71.10645°W / T. Perez, Malaise Trap (1, FSCA)”

“PERU:Loreto: 160 km / NE Iquitos, 3 mi.N.Rio / Sucusari on Rio Napo, / Lk. Shimigay; 29-VIII- / 1992; P.E. Skelley (1, FSCA)”

Thione puncticeps

“PERU: / 15 mi.NEof / Tingo Maria, / 700 m XI-11-54 / E.I.Schlinger / & E.S.Ross / collectors (1, CAS)”

“PERU: Madre de Dios / Dept. Tambopata / 25-X-1982 / FMHD #82-391, L. E. / Watrous & G. Mazurek (1, FMNH)”

“PERU: Madre de Dios: / CICRA Field Station, / Exp. Plot, North Transect / 12.55261°S 70.11008°W, 295m / 13-15.VII.2010 Chaboo team / ex. flight intercept trap / PER-10-07-FIT-009 (1, SEMC)”

“PERU: Madre de Dios: / CICRA Field Station, / Exp. Plot, South Transect / 12.55261°S 70.11008°W, 295m / 11-13.VII.2010 Chaboo team / ex. blue pan trap / PER-10-07-DJB-020 (1, SEMC)”

“PERU Madre De Dios / nr.PuertoMaldonado / Explorer’s Inn / 22 Aug.1985 / J.F.Cornell / under bark & logs (1, NCSU)”

5.6 Acknowledgements

The author thanks Caroline Chaboo for the invitation to write this paper and for her comments on an earlier draft. Joseph McHugh, Roberto Carrera-Martínez and Emmanuel Arriaga Varela assisted greatly with comments on earlier versions of the manuscript and Spanish translation. The author acknowledges NSF-EPSCoR #66928 (PI: CS Chaboo) for supporting the 'Beetles of Peru' project and thanks all curators and collections managers for access to specimens. The Department of Entomology and the H.H. Ross Fund at the University of Georgia supported the author's research on Monotomidae.

CHAPTER 6

THE MONOTOMIDAE OF GEORGIA: A CASE STUDY OF UNDOCUMENTED BEETLE DIVERSITY IN THE SOUTHEASTERN UNITED STATES

6.1 Abstract

Studies of the small beetle family Monotomidae (Coleoptera: Cucujoidea) in the southeastern USA, increased the known diversity for the family in the state of Georgia by one genus and nine species. This work highlights the lack of basic diversity information about small beetles that inhabit wood, leaf litter, and other decaying plant matter in this region.

Keywords: biodiversity; new state records; saproxylic; Georgia; Monotomidae; minute clubbed beetles; biodiversity hotspot; southeastern coastal plain

6.2 Introduction

The state of Georgia, USA, comprises 59,425 square miles, spanning five major ecoregions: Southwestern Appalachians, Ridge and Valley (Great Valley), Blue Ridge, Piedmont, and Coastal Plain (Griffith et al. 2001). Approximately 60% of the state falls in the North American Coastal Plain (NACP) (Seabrook 2016), an area that recently was designated as the world's 36th biodiversity hotspot (Noss et al. 2015). Since Georgia represents an ecological transition zone between multiple biodiversity-rich regions, one might expect it to rank highly in terms of insect biodiversity; however, the published literature often fails to support that expectation. In fact, the state often appears as part of a conspicuous southeastern blank area on the distribution maps of insect species, an artifact of the low rate of taxonomic research activity in the area historically.

Few surveys of the entomofauna of Georgia have been published. For Coleoptera, the most speciose order of life on Earth (Grove and Stork 2000; Ślipiński et al. 2011), there are some species lists that were compiled for conspicuous economically or ecologically significant taxa (e.g., Fattig 1935; 1936; 1937; 1944; 1947; 1948; 1949; 1951; Franklin and Lund 1956; Turnbow and Smith 1983). Digitization of data from museum specimens is beginning to provide a vast amount of new occurrence information to researchers through aggregators like iDigBio and GBIF. Both traditionally published and digitally available records are possible, however, only if material was collected and identified first. For many groups of small, detritus-inhabiting and saproxylic beetles from poorly sampled regions like Georgia, few occurrence records have been generated.

Monotomidae (Coleoptera, Cucujoidea), the “minute clubbed beetles,” are nondescript, drably colored, and small (1.5 - 6.0 mm) beetles that are detritivorous, mycophagous or predaceous on wood-inhabiting insects. Adults generally occur under the bark of fungus-infested trees, or in galleries of scolytine beetles, compost piles, or other habitats with fungus-infested plant material. Myrmecophilous and melittophilous species are known (Pakaluk and Ślipiński 1993, Sen Gupta 1988). Some monotomids are effective predators of bark beetles and have been used in biocontrol efforts (Gregoire et al. 1985). Other species are known to be pollinators (Jenkins et al. 2013; 2015), vectors of pathogenic fungi (Hinds 1972), or valuable indicators in forensic paleoentomology (Panagiotakopulu and Buckland 2012). A few species are cosmopolitan, but most have more restricted distributions. Worldwide, there are 36 genera and 257 described species, with many more undescribed.

Monotomidae present an ideal group to examine the state of knowledge about detritus-inhabiting and saproxylic beetles occurring in Georgia. Like many groups of small, cryptic beetles, this family suffers from an historic lack of study in the region. Some revisionary work has been done recently on North American monotomids (Bousquet 1990; Bousquet and Laplante 1999; Bousquet 2002; Bousquet 2003a;b;c), so there already was a strong taxonomic foundation upon which to work. In addition, the group has a modest number of described species known from the eastern half of the U.S.

Prior to this study, seven monotomid species were known to occur in the state of Georgia. All of these existing records were traditionally published. Not a single digitized specimen record existed on the data aggregators GBIF and iDigBio for the family in the state. Even informal citizen science projects (such as Bugguide.net) contained no identified records for Georgia prior to this study. Herein, we present a preliminary survey of the fauna of Monotomidae in the state of Georgia (United States of America).

6.3 Methods

Monotomid specimens collected in Georgia were documented from museum holdings and identified to the lowest level possible using available resources (e.g., Bousquet 1990; 2002a; b; 2003a; b; c; d; 2009; Bousquet and Laplante 1999; McElrath et al. 2016). In addition, the authors collected extensively in a few locations around the state of Georgia from 2010-2016, targeting the northwestern (Walker Co.), northeastern (Lumpkin Co.), central (Athens-Clarke Co.), and southeast coastal (McIntosh Co.: Sapelo Island) parts of the state. These newly collected specimens were prepared, identified, and deposited in the University of Georgia Collection of Arthropods (UGCA).

Species-level identification was possible for most of the material studied, with the exception of some *Bactridium* and *Monotoma* specimens. The senior author is currently conducting a revision of the genus *Bactridium* which will include additional species and collection records for Georgia. A preliminary checklist of monotomid species known from Georgia was created using the existing literature (see cited) and label data from specimens borrowed from the collections listed below. An updated version of the checklist was generated by the addition of data from the newly collected material.

Museum holdings

(Note: many other museums were checked, but did not reveal new records of Georgia specimen; those listed here are the only ones that had holdings not already mentioned in the literature)

CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, United States (Robert Davidson)
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, United States (Kyle Schnepp, Paul Skelley)
UGCA	University of Georgia Collection of Arthropods, Athens, Georgia, United States (E. Richard Hoebeke, Joseph V. McHugh)

UTIC	University of Tennessee at Chattanooga Insect Collection, Chattanooga, Tennessee, United States (Stylianos Chatzimanolis)

All specimen records for this study were digitized and submitted to iDigBio via the SCAN (Symbiota Collections of Arthropods Network) portal (Gries et al. 2014; http://symbiota4.acis.ufl.edu/scan/portal/index.php). Specimen collection records were mapped using the SCAN Map Search tool, Google Maps, and Google Earth v. 7.1.8.3036.

6.4 Results

Sixteen species of Monotomidae, representing six genera, are now reported from the state of Georgia. One genus and nine species are new state records. Three of the newly reported species (*Monotoma bicolor, M. johnsoni*, and *M. longicollis*) are known adventive species in North America (the date of introduction to the United States and Georgia specifically is uncertain). The remaining six (including the newly recorded genus) are native species that had never been recorded previously in the state. Data were digitized and submitted to iDigBio for a total of 857 monotomid specimens from Georgia.

Checklist of Monotomidae of Georgia, U.S.A.

Rhizophaginae:

1. *Rhizophagus (Anomophagus) brunneus brunneus* **(NEW STATE RECORD)** (Fig. 6.1A, D)
2. *R. (Rhizophagus) cylindricus* (Bousquet 1990) (Fig. 6.1B, D)

3. *R. (R.) sayi* **(NEW STATE RECORD)** (Fig. 6.1C, D)

Monotominae:

4. *Bactridium ephippigerum* (Lawrence 1973) (Fig. 6.4A, D)
5. *B. striolatum* **(NEW STATE RECORD)** (Fig. 6.4B, D)
6. *Europs pallipennis* (Bousquet 2003) (Fig. 6.5A, D)
7. *Hesperobaenus rufipes* (Bousquet 2002) (Fig. 6.5B, D)
8. *Monotoma americana* **(NEW STATE RECORD)** (Figs. 6.2A, 6.3)
9. *M. arida* (Bousquet and Laplante 1999) (Figs. 6.2B, 6.3)
10. *M. bicolor* **(NEW STATE RECORD)** (Figs. 6.2C, 6.3)
11. *M. emarginata* **(NEW STATE RECORD)** (Figs. 6.2D, 6.3)
12. *M. johnsoni* **(NEW STATE RECORD)** (Figs. 6.2E, 6.3)
13. *M. longicollis* **(NEW STATE RECORD)** (Figs. 6.2F, 6.3)
14. *M. picipes* (Fattig, 1937) (Figs. 6.2G, 6.3)
15. *M. producta* (Bousquet and Laplante 1999) (Figs. 6.2H, 6.3)
16. *Pycnotomina cavicolle* **(NEW STATE RECORD)** (Fig. 6.5C, D)

Rhizophagus Herbst, 1793

R. (Anomophagus) brunneus brunneus Horn 1879 **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Fig. 6.1A, D)

Habitat and Biology: These beetles are known to vector aspen cankers in the western United States (Hinds 1972). They are found under bark of pine and spruce and are active in the spring, summer, and fall months in Georgia. They may be bark beetle predators. Lindgren funnel traps baited with ethanol and ultraviolet lights will attract them in small numbers.

R. (R.) cylindricus LeConte 1866 (Fattig 1937; Bousquet 1990)

Records: SYMBIOTA**,** CSV, KML (Fig. 6.1B, D)

Habitat and Biology: This species can be found under bark of freshly fallen or dead standing pine trees, usually in association with bark beetles (including southern pine beetle). They are active in the fall, winter, and spring months in Georgia and across the eastern United States, and may be passively caught with Lindgren funnel traps.

R. (R.) sayi Schaeffer 1913 **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Fig. 6.1C, D)

Habitat and Biology: A winter-active species, it can be found under the bark of deciduous or coniferous trees (Bousquet 1990, Thomas and Lundgren 1992). It may also be associated with bark beetle galleries. Passive traps, especially Lindgren funnel or windowpane traps baited with ethanol, may collect adult beetles on warmer days in the winter months in Georgia.

Monotoma Herbst, 1793

M. americana Aube 1837 **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Figs. 6.2A, 6.3)

Habitat and Biology: A widespread species native to North America, it can be collected in association with rotting plant material, such as grass clippings, *Magnolia* leaf litter,

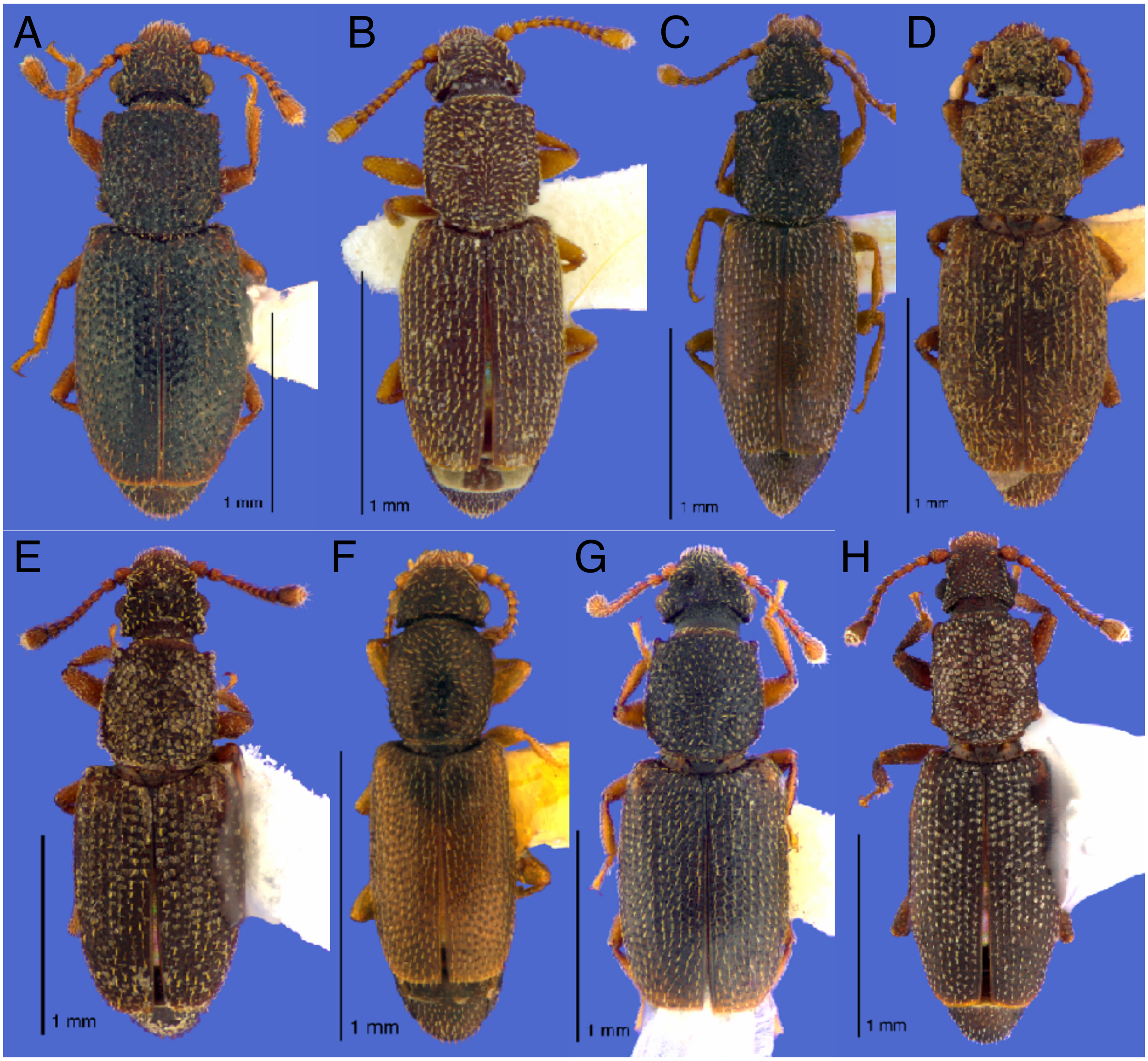

Figure 6.2. Dorsal habitus images of *Monotoma* occurring in Georgia. A) *M. americana,* B) *M. arida,* C) *M. bicolor,* D) *M. emarginata,* E) *M. johnsoni*, F) *M. longicollis*, G) *M. picipes* H) *M. producta*.

compost, moldy flooring, or moldy bark chips. It may be passively trapped with pitfalls, Lindgren funnels baited with ethanol, and berlese extractions of moldy plant matter.

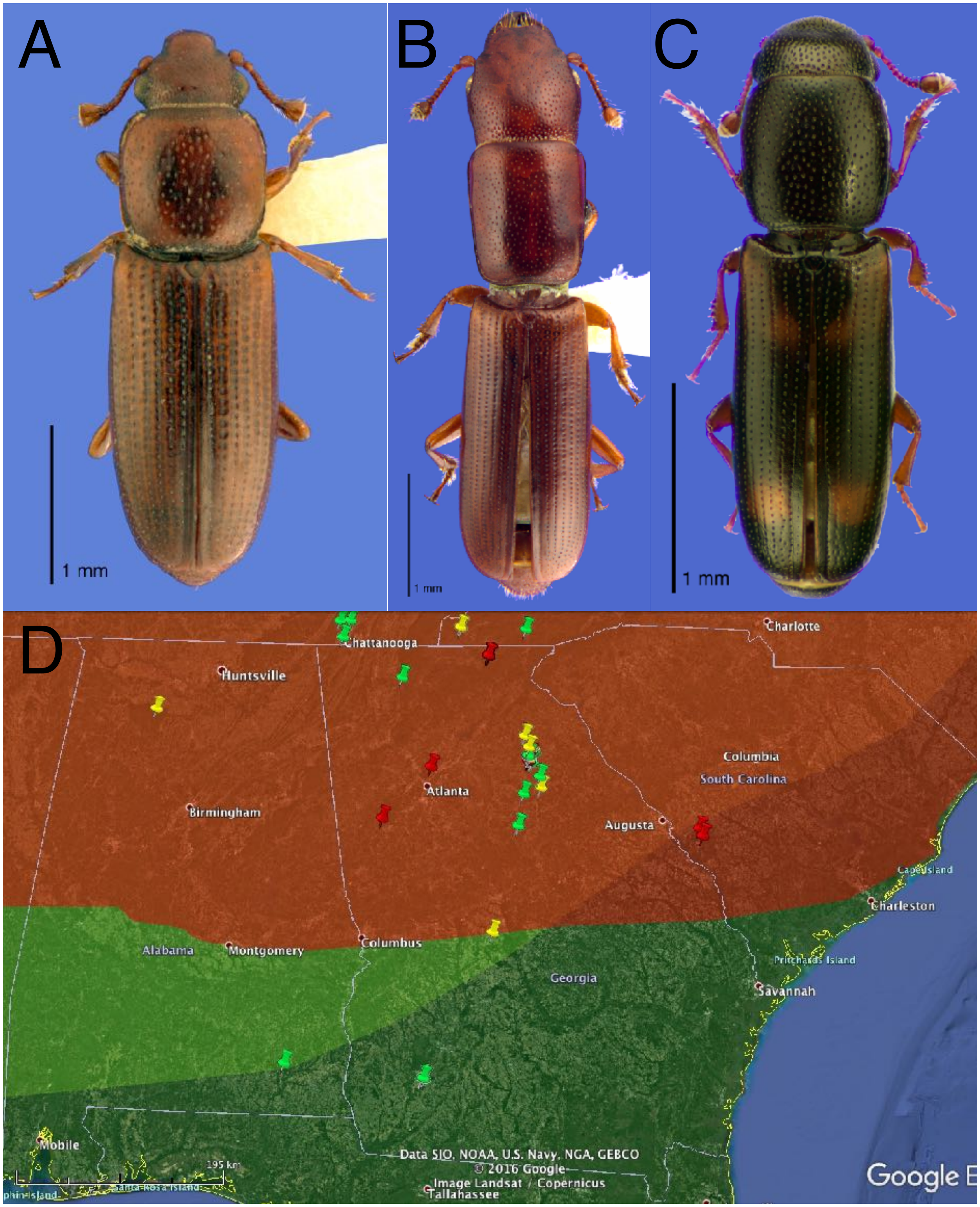

Figure 6.1. Dorsal habitus images and occurrence map of *Rhizophagus* in Georgia and surrounding states. A) *R. brunneus brunneus*, dorsal habitus. B) *R. cylindricus* (male) dorsal habitus. C) *R. sayi*, dorsal habitus. D) Distribution map of three species of *Rhizophagus* known to occur in Georgia. Yellow pins & yellow-green region) = *R. b. brunneus*, Red pins & region = *R. cylindricus*, green pins and region (distributed over all visible area) = *R. sayi*.

M. arida Casey 1916 (Bousquet and Laplante 1999)

Records: SYMBIOTA**,** CSV, KML (Figs. 6.2B, 6.3)

Habitat and Biology: Not much is known about this species. It can be found in many of the same habitats as *Monotoma americana* and *M. emarginata*.

M. bicolor Villa & Villa 1835 **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Figs. 6.2C, 6.3)

Habitat and Biology: An adventive species in North America, likely native to Europe, it can be collected by Berlese extraction from rotting vegetable or animal matter.

M. emarginata Bousquet and Laplante 1999 **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Figs. 6.2D, 6.3)

Habitat and Biology: This species may be collected in rotting or moldy plant matter, and passively sampled with ethanol baited Lindgren funnel traps.

M. johnsoni Bousquet and Laplante 1999 **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Figs. 6.2E, 6.3)

Habitat and Biology: An adventive species, likely native to the Palearctic. *Monotoma johnsoni* can be collected with ethanol-baited Lindgren funnel traps, or found in rotting plant matter. It has been collected only rarely in Georgia.

M. longicollis (Gyllenhal 1827) **(NEW STATE RECORD)** “minute beer beetle”

Records: SYMBIOTA**,** CSV, KML (Figs. 6.2F, 6.3)

Habitat and Biology: An adventive, locally common species that is thought to feed on decaying plant matter, *M. longicollis* is very attracted to fermented products as evidenced by the numerous specimens caught around breweries and caught by Lindgren funnel traps baited with ethanol. It is regarded as cosmopolitan, but its lifecycle and distribution remains poorly known.

M. picipes Herbst 1793 (Fattig 1937)

Records: SYMBIOTA, CSV, KML (Figs. 6.2G, 6.3)

Habitat and Biology: An adventive species originally native to the Palearctic, this species can be collected in decaying plant matter such as compost heaps, *Fuligo septica* infested bark chips, and grass piles. It also can be passively trapped with Lindgren funnel traps baited with ethanol.

M. producta LeConte 1855 (Bousquet and Laplante 1999)

Records: SYMBIOTA, CSV, KML (Figs. 6.2H, 6.3)

Habitat and Biology: A species endemic to the eastern North American seashore, *M. producta* can be collected in rotting beach wrack. In Georgia, this species can be found in large numbers if the correct conditions occur. The ideal wrack for this species may be the large piles of sea vegetation that are deposited on the north ends of the coastal barrier islands.

Bactridium LeConte 1861

B. ephippigerum (Guerin-Meneville 1837) (Lawrence 1977)

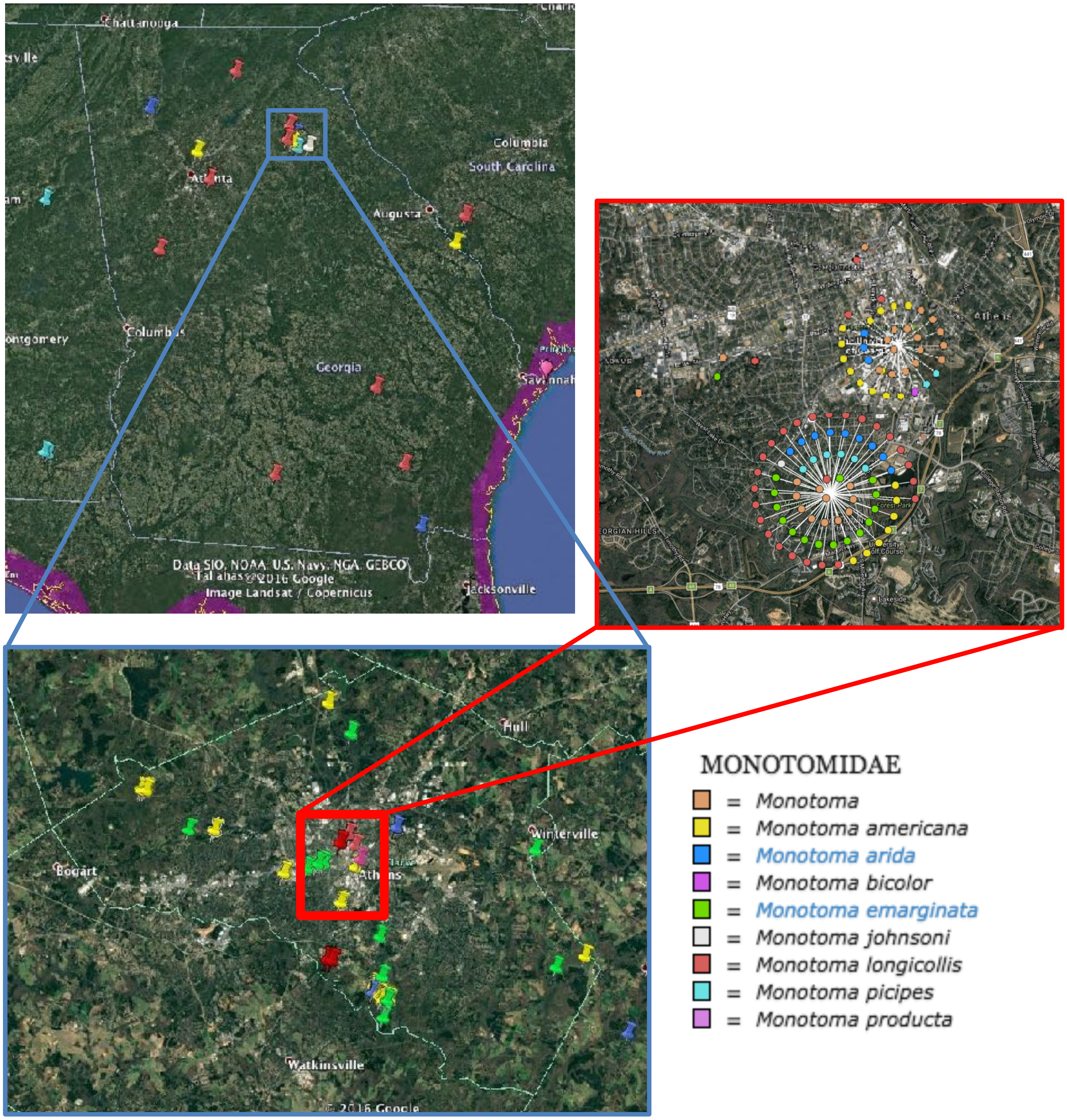

Figure 6.3. Map of *Monotoma* species of Georgia. Colors of each pin correspond with legend. A) Map of Georgia, Purple shaded area = distribution of *Monotoma producta*. Other species did not have enough points are either widespread in the state (e.g. *M. longicollis*) or have too few points to make an accurate distribution map. B) Zoom-in on Athens-Clarke County. c) Zoom-in on University of Georgia and surrounding residential areas. Expanded spiral of points indicate records from a single GPS locality, showing the effects of prolonged sampling in a single location.

Records: SYMBIOTA**,** CSV, KML (Fig. 6.4A, D)

Localities and biological information to be summarized in upcoming revision.

B. striolatum (Reitter 1872) **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Fig. 6.4B, D)

Localities and biological information to be summarized in upcoming revision.

Europs Wollaston 1854

E. pallipennis (LeConte 1861) (Fattig 1937)

Records: SYMBIOTA**,** CSV, KML (Fig. 6.5A, D)

Habitat and Biology: While little is known about the biology of this species, a congener is often found in flowers of Atemoya in Puerto Rico (Jenkins et al. 2015). *Europs pallipennis* can be collected in large numbers in elevated traps (traps placed in the canopy) of hardwood forests (Ulyshen and Hanula 2007). There are scattered host records for this species, reporting them from flowers of *Calycanthus* spp., old codling moth borings, flowers of *Rhododendron nudiflorum*, *Exobasidium* galls on azalea, and *Exobasidium symploci* galls on *Symplocos tinctoria.* Various singletons were taken by beating, sweeping, and extractions. Most records are from summer months, but the species seems to be active from spring to late fall. There is much that remains unknown about the biology of this species.

Hesperobaenus LeConte 1861

Hesperobaenus rufipes LeConte 1863 (Fattig 1937; Bousquet 2002b)

Records: SYMBIOTA**,** CSV, KML (Fig. 6.5B, D)

Habitat and Biology: *H. rufipes* is found under bark (*Quercus, Acer,* other hardwoods) where it eats fungal hyphae, probably mostly Fungi Imperfecti (*bugguide.net*). Most records are from the winter months, so it is possible the adults are only active in the winter months.

Pycnotomina Casey 1916

Pycnotomina cavicolle (Horn 1879) **(NEW STATE RECORD)**

Records: SYMBIOTA**,** CSV, KML (Fig. 6.5C, D)

Habitat and Biology: A rarely collected species in Georgia, it is supposed attracted to molasses traps. The two specimens caught in Georgia were collected in an ethanol-baited Lindgren funnel trap. Most non-Georgian records indicate the adult is active in spring and summer months.

6.5 Discussion

This survey raises the total number of monotomid species known to occur in Georgia from seven to sixteen (a 129% increase), not including several undescribed or unidentified species of *Bactridium* and *Monotoma* that were excluded from this study. That the known diversity for this family increased so much following a survey that was neither systematic nor extensive, is symptomatic of the poor level of knowledge that exists for the diversity of beetles inhabiting dead wood, leaf litter, and other types of decaying plant matter in the region.

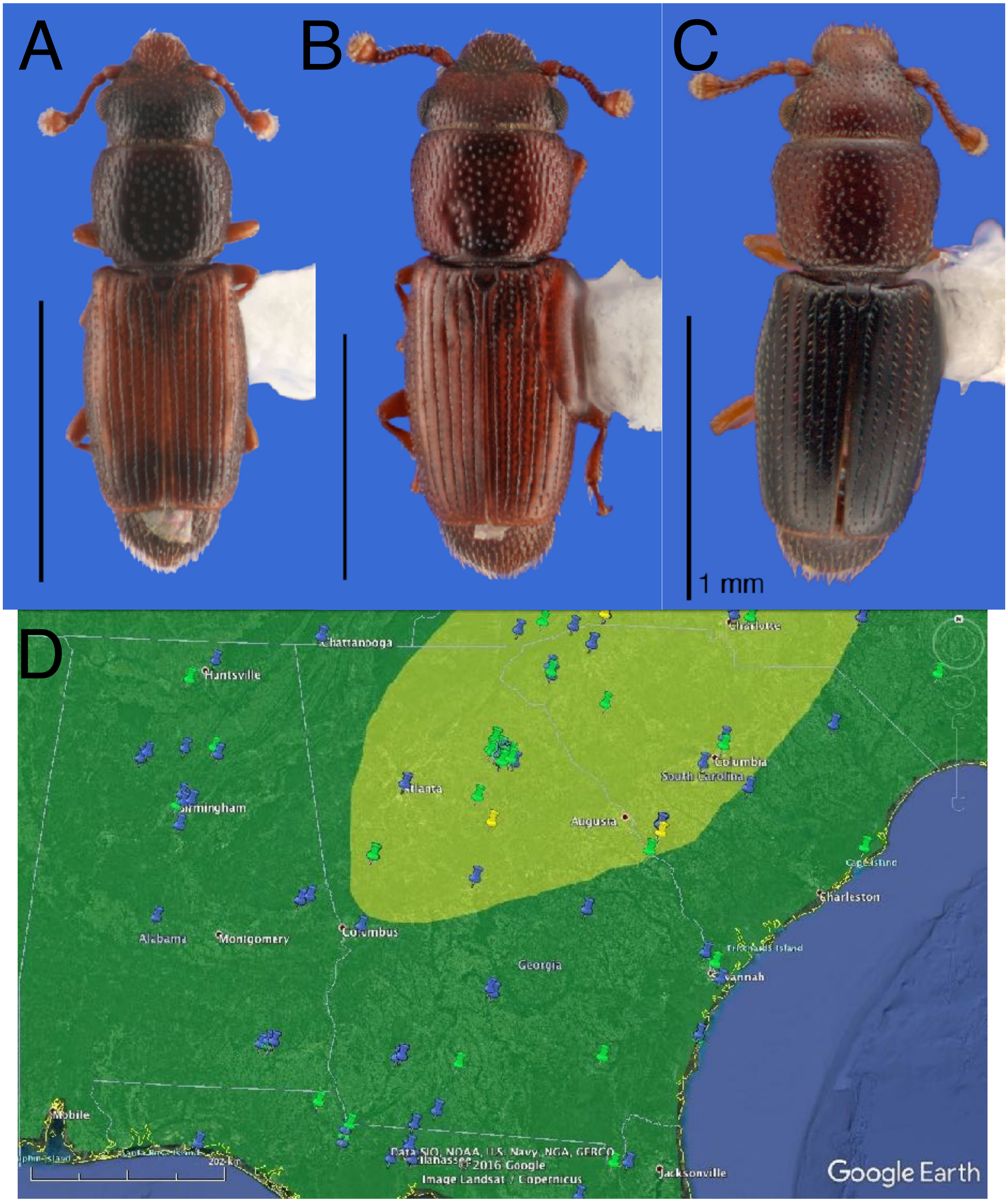

Figure 6.4. Dorsal habitus images and occurrence map of *Bactridium* in Georgia and surrounding states. A) *Bactridium ephippigerum*, dorsal habitus. B) *B. striolatum*, dorsal habitus. C) *Bactridium* n. sp., dorsal habitus. D) Distribution map of three species of *Bactridium* known to occur in Georgia. Green pins = *B. ephippigerum,* blue pins = *B. striolatum*, yellow pins and region = *Bactridium* n. sp. Blue-green area (covering whole map) = distribution of *B. ephippigerum* and *B. striolatum*. Shaded regions based on published records and records in this study, author's best hypothesis for distribution, made manually in Google Earth.

Saproxylic insects represent a major component of arthropod biodiversity in forest ecosystems (Speight 1989; Grove 2002). This assemblage is credited with providing important ecosystem services and includes some of the most threatened taxa in many regions due to loss and alteration of habitats (Ulyshen 2013). As a result, saproxylic insects are of increasing interest to land managers and conservation biologists.

Coleoptera is the most diverse order of life on Earth (Grove and Stork 2000), and a large percentage of that diversity is comprised of saproxylic beetle species (Grove 2002). Beetles that inhabit dead wood and other decaying plant matter are often small and drably colored, attributes leading them to be overlooked. Often the taxonomy of these groups is not as mature as that of larger and more charismatic taxa, making it more difficult to incorporate them into studies. As a result, there exists a disappointing lack of basic biological information available about these taxa and their distributional records are often woefully incomplete.

In light of the newly reported records, the most diverse monotomid genus in the state is *Monotoma*, with species that feed mainly on decaying plant matter or the molds therein. Most *Monotoma* species in Georgia were introduced from the Old World (e.g., *M. bicolor, M. johnsoni, M. longicollis, M. picipes*). Georgia has historically and recently been the point of origin for many introduced species, a trend that will likely continue with increased commerce and shipping in the state (Cartwright 1938; Eger et al. 2010). In addition to those adventive species, there are several undescribed species located in the southeast that seem closely related to *M. americana* and *M. emarginata* (Bousquet and Laplante 1999). *Rhizophagus* and *Bactridium* are the next two most diverse

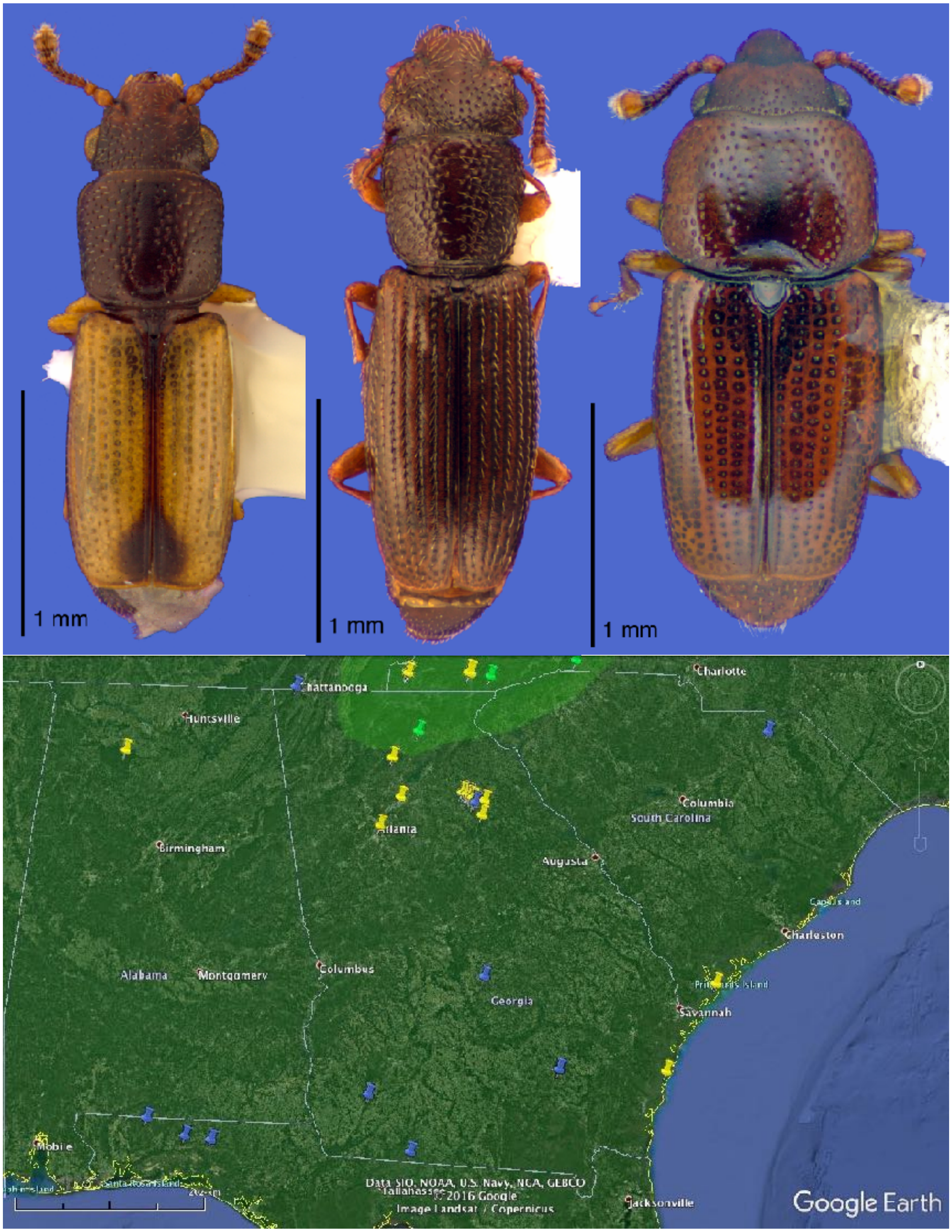

Figure 6.5. Dorsal habitus images and occurrence map of *Europs*, *Hesperobaenus*, and *Pycnotomina* in Georgia and surrounding states. A) *E. pallipennis*, dorsal habitus. B) *H. rufipes*, dorsal habitus. C) *P. cavicolle* dorsal habitus. D) Distribution map of above species: Yellow pins = *E. pallipennis,* blue pins = *H. rufipes*, green pins and light green shaded region = *P. cavicolle*. *E. pallipennis* and *H. rufipes* widely distributed, indicated with darker green shaded region. Shaded regions based on records in this study, author's best hypothesis for distribution, made manually in Google Earth.

monotomid genera in Georgia, but both are expected to increase in numbers after focused sampling and revisionary taxonomy is done.

Clarke County, in the Piedmont Region, appears as the most species-rich area in the state, an apparent example of “expert bias” or “sampling bias” in biodiversity estimation. (Figure 6.2B-C). This county is the location of the University of Georgia and home to some coleopteran taxonomists (e.g., TCM, JVM, E.R. Hoebeke) who conducted year-round sampling locally. While concentrated collecting in one location leads to many new records of widespread species, such as the adventive *Monotoma* species, it cannot capture the full diversity of the state. If year-long sampling had been made in other parts of Georgia, utilizing various collecting techniques, more monotomid species would almost certainly have been found. Targeted long-term sampling in different ecoregions such as the southern coastal plain, sand hills, and Appalachian Foothills, would certainly increase the known diversity of the family in the state.

Sampling efforts being made in southern Tennessee (see UTIC holdings), are beginning to reveal the beetle fauna that occurs in the Tennessee River Gorge and Lookout Mountain areas around Chattanooga, TN, part of the Ridge and Valley ecoregion which extends into northwestern Georgia as well. It is quite possible that four additional species of *Rhizophagus* (*R. dimidiatus, R. parallelocollis, R. remotus,* and *R. pusillus*) occur in Georgia in the southern Appalachian Mountains, as there are records of these taxa occurring in that ecozone in neighboring states (Bousquet 1990). In addition, some species currently known from Florida may be found in the southern coastal plains or sand hills of Georgia, including *Europs fervidus* and *E. frugivorous* (Bousquet 2003) and the enigmatic *Thione championi* (Peck and Thomas 1998). Finally, it should be noted that this study revealed a rarely collected, undescribed species of *Bactridium* (TCM, in prep) (Fig. 6.4C, D) that occurs around the Fall Line in Georgia and South Carolina.

While Monotomidae does not rank highly in terms of economic significance, even this small family has representatives that are considered beneficial or pest species. *Rhizophagus grandis* is an effective, augmentative biological control agent of *Dendroctonus micans* in Europe (Gregoire et al. 1985), and recently was introduced into China to control *Dendroctonus valens* (Yang et al. 2014). *Rhizophagus brunneus* has been implicated as a vector of a *Ceratocystis* fungus species that causes aspen cankers in the western U.S.A. (Hinds 1972). Some monotomid species occasionally appear in stored products and have proven that they are well adapted for accidental, human-mediated introductions. For example, *Monotoma longicollis* and *Monotoma picipes* have been spread around the world, almost always being detected long after their introduction (Bousquet and Laplante 1999; McElrath pers. observation).

Prior to this study, Georgia was about equal to several other southeastern states in terms of known monotomid diversity, with a species total that was quite low. However, once existing museum specimens were identified and some modest collecting effort was undertaken, this number quickly increased until now, when the state is ranked among the top regions in North America for diversity of the family. In addition, given the above information about species that may occur here once adequate sampling is undertaken, the diversity estimate given herein is likely an underestimate.

This study reveals that well over half of the monotomid species occurring in Georgia were not previously known to exist there and serves as an example illustrating a much broader problem. The same lack of information certainly exists for many other groups of small and inconspicuous insects. Such inaccurate and incomplete records of distributions has many ramifications. Conservation biologists, ecologists, foresters, landcare agents, port inspectors, and politicians cannot make informed decisions if the existing biota in an area is so poorly known. This widespread problem can only be resolved through increased attention and funding to regional collections and surveys.

6.6 Acknowledgements

The authors thank individuals who collected monotomids in Georgia and made them available to us, especially D.R. Miller, R.H. Turnbow, Jr., M.D. Ulyshen, and W.B. Sikora. We thank the following undergraduate interns and persons who assisted with mounting, labeling, and databasing efforts: Brandon Cochran, Shelby Ford, Thuy Le, Karen McElrath, Terry McHugh, Kelsey McShane, and Jennifer Parelli. This project was supported by the UGCA, H.O. Lund Club, and UGA Department of Entomology, and by funding from a Hatch Grant (to JVM), an H.H. Ross Grant (to TCM), and an Ernst Mayr Travel Grant from the Museum of Comparative Zoology (to TCM). The authors appreciate technical assistance with Symbiota and SCAN provided by N.M. Franz. This study was done in partial fulfillment of Ph.D. dissertation requirements at the University of Georgia. The first author thanks his advisory committee members K.J.K. Gandhi, J.V. McHugh, and K.G. Ross.

CHAPTER 7

REVISION OF *NEOBACTRIDIUM* OF NORTH AMERICA, NORTH OF MEXICO, WITH DIAGNOSES OF CLOSELY RELATED NEW WORLD GENERA AND A REVISED CLASSIFICATION OF THE SPECIES OF *CRINE*, *NEOBACTRIDIUM*, AND *PYCNOTOMINA*

7.1 Abstract

Neobactridium McElrath, replacement name, is provided for *Bactridium* LeConte 1861, junior homonym of Bactridium Reusse, 1848. The genus is revised for North America, north of Mexico, all current species are redescribed and *Neobactridium hopkinsi* **new species**, is described. The following species are placed in synonymy: *Neobactridium ephippigerum* Guerin-Meneville 1837 senior synonym (= *Rhizophagus erythropterus* Melsheimer, 1844, junior synonym, **new combination;** = *Bactridium curtipenne* Casey, 1916, junior synonym, **new combination**), *Neobactridium striolatum* Reitter 1872 senior synonym (= *Rhizophagus corpulentus* Reitter, 1872, junior synonym, **new combination**; = *Bactridium convexulum* Casey, 1916, junior synonym, **new combination**; = *Bactridium hudsoni* Casey, 1916, junior synonym, **new combination**; = *Bactridium obscurum* Casey, 1916, junior synonym, **new combination**)**.** The generic limits of *Neobactridium* are more narrowly defined, resulting in many species being moved to *Leptipsius* Casey, including *Crine cephalotes* Pascoe, resulting in a **new status** for *Crine* Pascoe 1863, senior synonym of *Leptipsius* Casey 1916. The following

combinations are a result of redefined generic limits and the aforementioned name changes: *Crine adustus* (Reitter 1872) **new combination**, *Crine angulicollis* (Reitter 1872) **new combination**, *Crine angustus* (Sharp 1900) **new combination**, *Crine brevicornis* (Sharp 1900) **new combination**, *Crine cephalotes* Pascoe 1863 **restored status**, C*rine cubensis* (Chevrolat 1863) **new combination**, *Crine crassus* (Sharp 1900) **new combination**, *Crine dilutus* (Casey 1916) **new combination**, *Crine eumorphus* (Sharp 1900) **new combination**, *Crine exiguus* (Grouvelle & Raffray 1908) **new combination**, *Crine imberbis* (Bousquet 2003) **new combination**, *Crine insularis* (Van Dyke 1953) **new combination**, *Crine germanus* (Sharp 1900) **new combination,** *Crine quadricollis* (Reitter 1872) **new combination**, *Crine rudis* (Sharp 1900) **new combination**, *Crine striatus* (LeConte 1858) **new combination**, *Mimemodes humilis* (Grouvelle 1906) **new combination**, *Mimemodes orientalis* (Reitter 1872) **new combination**, *Mimemodes parvus* (Grouvelle 1906) **new combination**, *Neobactridium atratum* (Reitter 1876) **new combination**, *Neobactridium brevicolle* (Reitter 1876) **new combination**, *Neobactridium californicum* (Fall 1917) **new combination,** *Neobactridium divisum* (Sharp 1900) **new combination,** *Neobactridium ephippigerum* (Guérin-Méneville 1837) **new combination,** *Neobactridium flohri* (Sharp 1900) **new combination,** *Neobactridium fryi* (Horn 1879) **new combination**, *Neobactridium heydeni* (Reitter 1872) **new combination,** *Neobactridium subtile* (Reitter 1872) **new combination**, *Neobactridium striolatum* (Reitter 1872) **new combination**. Lectotypes are defined and figured for many species. An identification key for *Neobactridium* and *Pycnotomina* in North America, north of Mexico is provided, and we comment on the relationships of these genera.

Keywords: *Bactridium*; *Neobactridium*; *Leptipsius*; *Crine*; *Mimemodes*; new combination; new species; biodiversity; replacement name

7.2 Introduction

Monotomidae Laporte, 1840 (Coleoptera: Cucujoidea), is a small but economically important family of beetles. Despite their small body size (~1-6 mm) and low species diversity (~ 250 spp.) the Monotomidae exhibit a wide range of lifestyles including predation, fungivory, inquilinism, and pollination (McElrath *et al.* 2012; Jenkins *et al.* 2015). Studies of monotomid evolution and ecology, however, remain complicated by the poor state of alpha taxonomy in the family. Additionally, the current subfamilial and tribal classifications of Sen Gupta (1988) were not based on any phylogenetic analysis, and it is unknown whether many genera are artificially constructed. Except for a few well-characterized European and North America taxa, nearly every genus within the family includes undescribed species in existing museum holdings. Many of those genera have not been revised recently or ever, making identifications very difficult.

The New World genus *Bactridium* LeConte 1861 is one of these difficult genera. With its hidden subcortical habitat, small size (~ 2-3 mm), cryptic coloration, and likely fungivorous lifestyle, it has received little attention over the past century (Bousquet 2002a). Despite being regularly encountered in forest ecosystem studies (e.g., Ulyshen and Hanula 2007; 2010), discrimination of the thirty described species is impossible with currently available literature. The last treatment of the genus was by Casey (1916) who described several new taxa for North America but did not provide resources for identifying those previously described, the majority of which were Neotropical species described by Sharp (1900). In fact, *Bactridium*, in its 155 year history, has never been comprehensively revised.

To make matters worse, the nomenclature of this genus has a few problems. Foremost, *Bactridium* LeConte 1861 is a junior homonym of *Bactridium* Reuss 1848, a genus of extinct sponge described 13 years earlier. The only other available generic name for *Bactridium* LeConte 1861 is *Crine* Pascoe 1863, but this name actually refers to *Leptipsius* Casey 1916 (discussed in more detail herein). Thus, the name *Bactridium* cannot continue to be used for the concept of *Bactridium* LeConte 1861.

Current morphological characters used for delimitation and identification of species within this genus are poor at best, confusing and misleading at worst. Relative size-ratios (e.g., “a bit wider than the others”) (Casey 1916), color patterning (e.g., “surface dark ferruginous” vs. “color black, elytra ferruginous throughout”) (Casey 1916), strial patterns, (e.g., “Elytral striae present on sides, finer …” vs. “elytral striae on sides semiobsolete…”) (Downie & Arnett 1996), and many other unillustrated, relative characters are all that is available to distinguish between species.

In addition, genera that are hypothesized to be closely related to *Crine* (*Leptipsius* Casey & *Pycnotomina* Casey) are nearly as poorly known. Sen Gupta’s (1988) review of monotomid genera was cursory, sparing with illustrations, and did not rigorously examine the species representing each genus. No photomicrographs or SEMs were provided, and the figures were often diagrammatic. Bousquet (2003b) described a new species of *Leptipsius* from the United States, but did not review the species or provide keys for their discrimination. Most of the characters were not represented by illustrations or photomicrographs. Detailed morphological examination of the above genera would greatly advance the systematic knowledge of Monotomidae.

In response to these taxonomic problems, we provide a replacement name *Bactridium* LeConte 1861 (STAT NOV): *Neobactridium* McElrath 2017 (NOM NOV), and *Crine* Pascoe 1863 (STAT NOV) is resurrected from synonymy to take the place of *Leptipsius* Casey 1916 (subjective junior synonym of *Crine* Pascoe 1863)(STAT NOV). Next, we redescribe *Neobactridium, Crine,* and *Pycnotomina*, and provide a checklist of all species according to current generic limits. In addition, we revise *Neobactridium* for North America North of Mexico, and provide a key to the described species of *Neobactridium* and *Pycnotomina.*

7.3 Materials and Methods

Material Examined. Most of the world's holdings of *Neobactridium* were examined and acquired in order to conduct a revision of this genus. About 2000 specimens were examined or borrowed from the following 58 collections around the world, focusing on major North American museums and European institutions with significant type or historical holdings. Museum codons follow those given by museums or when unknown, Arnett et al. (1993) and Evenhuis (2017), available (http://hbs.bishopmuseum.org/codens/). Persons of contact follow collection names.

AMDC	Anthony M. Deczynski Personal Collection, Clemson, SC, USA — Anthony Deczynski
AMNH	American Museum of Natural History, New York, NY, USA — Sarfraz Lodhi

BBEC	Brad Barnd Entomology Collection, IN, USA — Brad Barnd
BBPC	Brian Baldwin Personal Collection, Jessieville, AR, USA — Brian Baldwin
BBRC	Bobby Brown Personal Collection, KS, USA — Bobby Brown
BMNH	British Museum of Natural History, London, UK — Roger Booth, Max Barclay
BYUC	Monte L. Bean Life Science Museum Arthropod Collection - Brigham Young University, Provo, UT, USA — Shawn Clark
CAS	California Academy of Sciences, San Francisco, CA, USA — David Kavanaugh, Rachel Diaz-Bastin
CIDA	Orma J. Smith Museum of Natural History - The College of Idaho, Caldwell, ID, USA — Alan Gillogly
CMNC	Canadian Museum of Nature Collection, Ontario, Ottawa, CAN — Francois Genier
CMNH	Carnegie Museum of Natural History, Pittsburgh, PA, USA — Robert Davidson, Robert Androw
CNC	Canadian National Collection, Ontario, Ottawa, CAN — Yves Bousquet
CSCA	California State Collection of Arthropods, Sacramento, CA, USA — Andrew Cline
CUAC	Clemson University Arthropod Collection, Clemson, SC, USA — Michael Caterino
CUIC	Cornell University Insect Collection, Ithaca, NY, USA — Jason Dombrowskie
DAPC	Darren A. Pollock Collection, Portales, NM, USA — Darren Pollock
EGRC	Edward G. Riley Personal Collection, College Station, TX, USA — Edward Riley

EMEC	Essig Museum of Entomology Collection, UC Berkeley, Berkeley, CA, USA — Peter Oboyski
FMNH	Field Museum of Natural History, Chicago, IL, USA — Crystal Meier
FSCA	Florida State Collection of Arthropods, Gainesville, FL, USA — Kyle Schnepp, Paul Skelley
GPPC	Gareth Powell Personal Collection, West Lafayette, IN, USA — Gareth Powell
JGCC	Jeff Gruber Coleoptera Collection, Madison, WI, USA — Jeff Gruber
INHS	Illinois Natural History Survey, Champaign, IL, USA — Christopher Grinter
INPA	Instituto Nacional de Pesquisas da Amazonia, Colecão Sistemática da Entomologia, Manaus, Amazonas, Brazil — Marcio Oliviera
KSPC	Kyle Schnepp Personal Collection, Gainesville, FL, USA — Kyle Schnepp
LACM	Los Angeles County Museum, Los Angeles, CA, USA — Weiping Xie
LSAM	Louisiana State Arthropod Museum, Louisiana State University, Baton Rouge, LA, USA — Victoria Bayless
MAIC	Michael A. Ivie Collection, Bozeman, MT, USA — Michael Ivie
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA — Philip Perkins
MNHN	Muséum National d'Histoire Naturelle, Paris, France — Azadeh Tagavian
MSUC	A.J. Cook Arthropod Research Collection, Michigan State University, East Lansing, MI, USA — Gary Parsons
MTEC	Montana Entomology Collection, Bozeman, MT, USA — Michael Ivie
NHMW	Naturhistorisches Museum Wien, Wien, Austria — Harald Schillhammer

OSAC	Oregon State University Arthropod Collection, Corvallis, OR, USA — Christopher Marshall
OSUC	Charles A. Triplehorn Insect Collection, Columbus, OH, USA — Luciana Musetti
PERC	Purdue Entomology Research Collection, West Lafayette, IN, USA — Gino Nearns
RMNH	National Musuem of Natural History, Naturalis Biodiversity Center, Leiden, Netherlands, — Pasquale Ciliberti
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, CA, USA — Matthew Gimmel
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany — Stephan Blank
SEMC	Snow Entomological Museum, Kansas Museum of Natural History, Lawrence, KS, USA — Zachary Falin
TAMU	Texas A&M University Insect Collection, College Station, TX, USA — Edward Riley
UAIC	University of Arizona Insect Collection, Tuscon, AZ, USA — Gene Hall
UBCZ	Spencer Entomological Museum, Dept. of Zoology, University of British Columbia, Vancouver, British Columbia, CAN — Karen Needham
UCFC	Stuart Fullerton Collection of Arthropods, U. of Central Florida, Orlando, FL, USA — Shawn Kelly
UCRC	University of California Riverside Collection, Riverside, CA, USA — Doug Yanega

UGCA	University of Georgia Collection of Arthropods, Athens, GA, USA — E. Richard Hoebeke
UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan — Mark O’Brien
UMRM	Enns Entomology Museum, University of Missouri, Columbia, MO, USA — Kristin Simpson
UMSP	University of Minnesota Insect Collection, St. Paul, MN, USA — Robin Thompson
UNHC	University of New Hampshire Insect Collection, Durham, NH, USA — Donald Chandler
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA — Floyd Shockley
UVCC	University of Vermont Invertebrate Collection, Burlington, VT, USA — Sohath Zamira Yusseff Vanegas
UTCI	University of Tennessee at Chattanooga Insect Collection, Chattanooga, TN, USA — Stylianos Chatzimanolis
WFBM	William F. Barr Entomological Museum, University of Idaho, Moscow, ID, USA — Luc Leblanc Merickel
WIRC	Wisconsin Insect Research Collection, Madison, WI, USA — Steven Krauth
WSUC	James Entomology Collection, Washington State University, Pullman, WA — Richard Zack
ZMHB	Museum für Naturkunde Berlin, Humboldt Universitat, Berlin, Germany — Bernd Jäger

ZSMC Zoologische Staatssammlung at München, Munich, Germany — Michael Balke

Specimen preparation. Specimen prep closely mirrored that of Lord & McHugh (2013). Dried specimens were placed into just boiled distilled water (with ~ one drop of detergent for every two liters of distilled water) and allowed to relax for 5-10 minutes. Some specimens were also placed into a Branson 1210 ultrasonic cleaner in order to dislodge grease or dirt. Specimens were disarticulated and cleared in 10% KOH solution at room temperature. Dissected parts were washed in dilute acetic acid/water solution and stored in glycerin. In some cases only the abdomen was removed, cleared, and slide mounted in this manner. The abdomen was subsequently glued to a card, and the genitalia and other dissected parts were placed in glycerin in a genitalia vial, which was pinned beneath the specimen, above the labels.

Imaging and Illustrations. Dorsal, ventral, and occasionally lateral color habitus images were captured using a Microptics ML-1000 Digital Imaging system (Microptics, Inc., Ashland, VA, USA), using a Canon EOS-1 camera, MP-E 65 mm lens, white Chinese lantern diffuser, and two speed flashes. Genitalia were imaged on a Leitz DMRB microscope and imaged with a Sony HD Handycam with a Martin Microscope MM99 Adapter. Image stacks were montaged in Helicon Focus 6.5.0 (Helicon Soft Ltd., Kharkov, Ukraine) or Zerene Stacker v. 1.04 (Zerene Systems LLC, Richland, WA, USA). SEM images were captured using a Leica 1450 EP Environmental Scanning Electron Microscope at Georgia Electron Microscopy (Barrow Hall, University of Georgia). Images were edited in Adobe Photoshop CS6 v.13.0.6 (Adobe Systems, Inc., San Jose, CA, USA).

Measurements. Images of specimens were captured with a Sony HD Handycam with a Martin Microscope MM99 Adapter camera attached to a Leica WILD M10, and calibrated using a stage micrometer. Morphometric data were then generated in AutoMontage Pro, v. 5.01 (Synoptics, Ltd., Frederick, MD, USA).

Unique Specimen Identification Numbers. For each unique locality for *Neobactridium ephippigerum* & *N. striolatum,* and for every specimen for *N. californicum, N. hopkinsi,* and *Pycnotomina cavicolle*, a unique specimen identification number was assigned and databased within the ARTSYS collection on Symbiota [SCAN Collection of Externally Processed Specimens (Arthropod Systematics Research) (SCAN-ARTSYS)] (see **http://symbiota4.acis.ufl.edu/scan/portal/collections/misc/collprofiles.php?collid=114**) for more details (Gries et al. 2014; Seltmann et al. 2017). The number itself is arbitrary. The numbers in this study fall between ARTSYS0001576 and ARTSYS0003150. Specimens from the University of Georgia Collection of Arthropods were each given GUIDs following the format of that collection, and databased for the purposes of this study within the GMNH-UGCA collection on Symbiota [**http://symbiota4.acis.ufl.edu/scan/portal/collections/misc/collprofiles.php?collid=56**].

Label Data. Transcribed labels in this study are formatted as follows. All data per specimen is captured within quotation marks. Each individual label on a specimen is separated by two slash marks (e.g. “//“). Each line on a label is separated by a single slash (e.g. “/“). Any remarks about conditions of the label (such as handwritten or typed) are placed in brackets (e.g. “[typed]”).

All label data captured in this study is available on the Symbiota SCAN Data Portal, available at **http://symbiota4.acis.ufl.edu/scan/portal/index.php**.

Type specimens. Primary type specimens for all species in this study were examined, with the exception of *Neobactridium ephippigerum*, which is explained in more detail below. Red labels were affixed to holotypes, lectotypes, and neotypes. Yellow labels were affixed to paratypes and paralectotypes. In the case of card mounted specimens on a single card, where one was designated the lectotype, and the others paralectotypes, a red label was affixed with both lectotype and paralectotype, with care taken to differentiate between them on the label (see Fig. 7.72F). Images of type labels, including those affixed by the authors, are included herein (Figs. 7.71—7.85).

The International Code of Zoological Nomenclature (ICZN 1999) requires that designations of lectotypes post-1999 must "contain an express statement of the taxonomic purpose of the designation" (74.7.3) (Jameson and Smith 2002). Herein, we designate lectotypes in order to link the original descriptions with the specimens used by original authors in order to serve as a reference for that taxon. All label data is included with lectotype designations, as well as figures of type labels. Lectotypes are designated for the following species: *Rhizophagus adustus* Reitter, *R. angulicollis* Reitter, *Bactridium angustus* Sharp, *B. brevicornis* Sharp, *Crine cephalotes* Pascoe, *Rhizophagus cubensis* Chevrolat*,* *B. crassum* Sharp, *B. eumorphum* Sharp, *Bactridium exiguum* Grouvelle & Raffray, *B. germanum* Sharp, *R. quadricollis* Reitter, *B. rude* Sharp, *B. humile* Grouvelle, *R. orientalis* Reitter, *B. parvum* Grouvelle, *B. atratum* Reitter, *B. brevicolle* Reitter, *B. californicum* Fall, *B. divisum* Sharp, *B. flohri* Sharp, *B. fryi* Horn, *R. heydeni* Reitter, and *R. striolatus* Reitter 1872.

The International Code of Zoological Nomenclature (ICZN 1999) stipulates that neotypes are “validly designated when there is an exceptional need and only when that need is stated expressly" (75.3). The neotype designated herein serves to tie the published name to an actual physical specimen and to serve as a reference specimen. We designate a neotype for *Rhizophagus ephippiger* Guerin-Meneville because the original specimen(s) are either lost or destroyed. See discussion of this species for more details.

Species Concept. We apply the phylogenetic species concept *sensu* Wheeler and Platnick (2000) e.g. “ the smallest aggregation of (sexual) populations or (asexual) lineages diagnosable by a unique combination of character states.” *Neobactridium* and *Pycnotomina* are assumed to reproduce sexually (both male and females are known, and easily diagnosable by external and internal morphology). Character states are morphological characters that are heritable and fixed across the populations observed.

Georeferencing and Mapping. All informative collection localities that could be reliably identified and were informative (e.g. “10 km NW Washington DC” or “Athens GA”, not “Canada” or “boreal America”) were georeferenced either from the labels (when GPS data was included), using the GEOLocate (GEOLocate, Tulane University Biodiversity Research Institute, Belle Chasse, LA, USA) plug-in within Symbiota (http://www.museum.tulane.edu/geolocate/), GoogleMaps, GoogleEarth, or a variety of internet searches. The mapping of localities was done within the MapSearch function on Symbiota.

Morphometrics. Head length was measured from imaginary line connecting posterior margin of eyes to tip of clypeus. Head width was measured from widest point (including eyes). Eye length was measured from anterior to posterior extremity. Eye width was measured at a perpendicular angle to eye length at the widest point. Pronotum width was measured at widest point, usually just in front of middle. Pronotum length was measured at midline. Elytron length was measured from posterior extremity of scutellum to apex of elytra along midline of elytra. Elytron width measured from innermost edge of elytron at midline of body to widest point, usually around middle of body.

Antennal segments lengths were measured relative to the shortest antennal segment (segment five). Lengths were measured on the midline.

7.4 Results & Taxonomy

***Neobactridium* McElrath, 2017.** Type species: *Rhizophagus ephippiger* Guérin-Méneville, 1837 (Figs. 7.1 - 7.5)

= *Bactridium* LeConte, 1861: 86. Type species: *Rhizophagus nanus* Erichson, 1843: 360.

Anatomical terminology follows systems of Sen Gupta (1988); McHugh et al. (1997); Bousquet (2009); Lawrence et al. (2011); & Lord & McHugh (2013).

Adult Diagnosis. Within the Monotomidae, *Neobactridium* is characterized by the following character states: antennal club 2-segmented (seemingly 1-segmented) (Figs. 7.20-7.22); head lacking a constriction behind the eyes (and therefore lacking a distinct temple) (Figs. 7.16-7.19); head without antennal grooves (Figs. 7.25-7.27); males possessing a modified pore on the boundary of the subgenal brace and the submental suture bearing longer, closely packed setae (Figs. 7.25-7.27); procoxal and mesocoxal cavities moderately widely separated (Figs. 7.35, 7.36, 7.40, 7.41); elytral disc with punctures arranged in longitudinal rows (Figs. 7.52, 7.53); coxal bead on first abdominal ventrite triangularly produced, reaching past mid-point of ventrite (Figs. 7.62, 7.63); first abdominal ventrite lacking of sexual modification (Figs. 7.62, 7.63); abdominal ventrites II-IV with small-large punctures arranged in distinct rows (Figs. 7.64-7.65); aedeagus with symmetrical, chiral, sclerotized sperm pump (Fig. 7.69). Several keys for separating Monotomidae genera are available: McElrath et al. (2016) (New World), Bousquet (2002a) (North America), Sen Gupta (1988) (worldwide but not including genera described after 1988), Nikitsky (1986) (Soviet Far East), Peacock (1977) (Britain), and several others of more regional focus.

Redescription: Length 1.3-3.9 mm. Width 0.3-1.0 mm. Body approx. 2-3 times as long (measured from tip of elytra to tip of frons) as wide (measured approx. midpoint of elytra at widest point), approx. 1.5-2.5 times as wide as deep (measured from top of pronotum to bottom of pronotum in lateral view). Body flattened-subcylindrical, subparallel, pale yellow to reddish-orange to brown to black. Subglabrous, except for minute hairs visible under high magnification arising from punctures. Surface dull - shiny. Visible sclerites of adults well-sclerotized.

Head. Dorsal surface: Subtriangular, transverse, widest at eyes, maximum width slightly less wide than pronotum. Basal subsinuate depressed area forming line connecting eyes posteriorly. Labrum (Fig. 7.6) reduced, small, mostly membranous, not visible dorsally. Labral surface (when viewed head-on) with numerous longer setae that project forward over mandibles. Lateral supraocular ridge present, but not much expanded. Most, if not all, of antennal insertion visible from above. Clypeus narrowed to ~0.5x width of head between antennal bases (not including eyes). Frontoclypeal suture absent. Anterior margin of clypeus usually broadly rounded, sometimes truncate or slightly emarginate.

Ventral surface: Gular region absent. Tentorial pits arise at the posterior margin of head capsule. Subgenal brace with two regions, one anterolateral, extending medially opposite mandible, forming outer brace and rest for mandible. Second region paramedial, lateral of cardo, forming short acute finger-like protrusion. Vague gular sutures arising and slightly converging towards anterior portion of head. Pregula sparsely setose, with very few minute pits and setae, though with abundant microsculpture. Transverse lateral depression present, forming a line arising from just behind posterior eye margin, forms articulation point of a ball-and-socket joint for head. Posterior portion of head behind this line not usually visible, concealed beneath pronotum. Pregular region sub-trapezoidal, with lateral edges converging slightly anteriorly, about 2x as wide as deep. Submental suture concave. Submentum about 4x as wide as deep, with slightly convex posterior edge and straight anterior edge forming mental suture. Medially with 5-6 long, erect setae 2-3x length of normal medial seta. Posterior portion of subgenal brace bearing densely setose pit 10-20 μm wide, but only in males.

Lateral surface: Beneath eye, subgenal brace and postgenal expanded down to form lateral expansion with a slightly concave surface, where the antenna may rest when not extended. The size and amount of the expansion varies among individuals, but is largest in males. The lateral face bears a few scattered setae, pores. Usually the setose pit of the subgenal brace is visible in males.

Eyes. Eyes prominent, protuberant, coarsely faceted. Interfacetal setae of length less than one ommatidium present.

Antennae. Scape longest segment, about twice as long as wide; terminal groove present that extends about half of the circumference of the scape, usually with 1 or more associated setae; pedicel about half as long as scape, also bearing similar terminal groove; third segment a little more than half as long as pedicel, with a few scattered setae. all segments except club, scape, and pedicel with single circumferential row of setae (about 4-10 per segment); fourth, fifth, sixth segments subequal, seventh and eighth slightly wider than each previous; ninth segment slightly wider than eighth, a little over half as wide as tenth. 10th segment begins antennal club; longer than broad. Club segment sub-spherical, with lines separating true antennal segments approximately circular. 10th segment appearing one-segmented, but actually bearing somewhat withdrawn true 11th segment; 10th segment with 1-several circumferential rows of setae, but always with one apical row of closely approximate setae; true 11th segment bearing many circular rows of fine, closely packed sensory setae, most of 11th segment not visible, withdrawn into tenth or covered with setae.

Mouthparts. Labrum (Fig. 7.6A) concealed beneath clypeus, transverse, apical section about 4x as wide as long, broadly rounded, with a row of strong stiff setae projecting away from body (visible from above), two paramedian sclerotized plates present on anterior labral edge; posterior labral edge narrows at about 1/4 of width to median fused tormae, which extend about 2-3x as long as anterior of labrum to mouth retractor muscle articulations, fused tormae with large oblique medial oval raised sclerotized plate (potentially the epipharyngeal impression [Lord and McHugh 2013]).

Labium (Fig. 7.6B)**:** In dorsal view mentum truncate posteriorly, with broadly rounded anterior edge before descending towards ligula; about 2x as wide as long, with numerous median setae; mentum narrows to broadly concave anterior edge, encompassing ligula and labial palp base. Ligula more membranous, still lightly sclerotized, with dense setal area between palps, apically broadly rounded, with serrate edge, numerous setae. Paraglossae membranous, lightly sclerotized, coming to median emargination. Ligula ventrally with dense brush of lateral setae, lateral ligular edges roughly sclerotized. Palpiger present ventrally. Labial palpi three-segmented, first minute and barely visible, second longer, third largest, longer than wide, fusiform.

Mandible (Fig. 7.6C) about as wide as long, triangular; Unidentate apically, with small subapical obtuse point. Apex varies in length and curvature. Prostheca present, but reduced, with only a short fringe of hairs. Well-developed mola present, with numerous ridges. Incisor edge with ventral projection, forming oval callosity. Median ventral surface with elongate ridge. Outer edge of mandible simple, straight or broadly rounded to mandibular apex. Dorsal lateral edge with row of long stout setae. Outer basal articulation with two smooth rounded knobs. Inner basal articulation with muscle attachment about 1/3 of width.

Maxilla (Fig. 6D) with distinct galea and lacinia. Galea elongate, thin, with apical setae. Lacinia fan-like, with outer dense row of setae extending to broad, flat widened apical portion. Palpifer elongate, with broad apical portion that wraps around to ventral surface, encompassing most of width of maxilla, with rough, subserrate outer edge, narrow basally, forming opposite side of wide basal basistipes. Mediostipes small, elongate triangular, lightly sclerotized, visible only ventrally. Maxillary palp 4-segmented. Apical segment fusiform, longer than wide. Cardo widest apically, about as wide as basal portion of basistipes, which it abuts; narrows quickly on outside edge and slightly on inside edge then widens again to form flat basal edge that abuts submental suture.

Prothorax. Variable in length and width, much longer than wide, subquadrate, or slightly longer than wide. Sides broadly rounded, arcuate, slightly sinuate, or subparallel. Widest anteriorly to just in front of middle. Anterior edge narrowly rounded, straight, or slightly emarginate. Posterior edge broadly rounded or with area behind posterior angles concave. Pronotum usually narrowly converging posteriorly. Narrow median impunctate zone present, ranging from small thin strip medially to large semicircular to oval zone. Subglabrous, with numerous small punctures present on pronotal disc each bearing a seta (rarely glabrous). Base of pronotum with slightly depressed zone loosely bordered with punctures. Pronotal lateral carinae usually minutely crenulate with three minute denticles posteriorly, or smooth. Disc usually with microsculpture.

Ventral surface: Underside of pronotum gently convex. Anterior margin of prosternum with row of long, stout setae resting parallel to body forming a “neck fringe”. Prosternum anteriorly with a row of minute punctures extending laterally, each with setae much longer than width of puncture extending away from body. Prosternum medially sparsely punctured, wrinkled, formed by elongated, sparse punctures with small setae, that are wider than long. Laterally to hypomeron, cuticle forms irregular net-like sculpturing (most well-developed in *N. ephippigerum*) containing some scattered setae and individual punctures. Hypomeron with extension posteriorly broadly closing procoxal cavity. Prosternal process with two grooves sublaterally. Process between procoxal cavities approx. subequal to width of single coxal cavity at narrowest point, gradually expanded towards apophysis of process, broadly rounded or truncate, sometimes minutely angulate. Prosternal apophysis irregularly punctured and wrinkled, with or without microsculpture. Apophysis and margin of pronotum posteriorly minutely crenulate, with row of fine setae. Sharp drop-off laterally to hypomeral-process suture. Procoxal cavities subcircular, of approx. same width as height, with thin apical lateral extension (perhaps a remnant of the notosternal suture); prothoracic trochantin not visible externally. Notosternal suture absent. Lateral posterior margin sometimes forming minute denticles with associated seta.

Pterothorax. Scutellar shield wider (measured from widest point) than long (measured from basal tip to the drop off to mesoscutum), with microsculpture; broadly rounded, subtriangular. Large punctures and setae absent. Mesoscutum and most mesothoracic parts not visible dorsally, withdrawn into prothorax. Mesoscutum slightly emarginate anteriorly, with two anterolateral arms forming complex junction with elytral interlocking joint. Mesoscutal plate with rough microsculpture, and a few scattered setae and punctures. Mesoscutum narrows to scutellar elevation, where it widens slightly to join the scutellar shield.

Mesoventrite wider than long. Anterior edge smooth, straight. Hidden portion of mesoventrite smooth, without microsculpture or punctation. Exposed mesointercoxal process with irregular, rough sculpturing, small seta, and microsculpture. Large paired setae present just anterior to posterior edge of meso-metaventral junction. Posterior edge of mesoventrite concave, fitting against convex, broadly rounded edge of metaventrite. Laterally mesoventrite extending just short of lateral edge of mesocoxal cavity, joining mesanepisternum and mesanepimeron; mesepimeron with suture separating mesanepisternum and mesanepimeron, but not fully impressed; mesepimeron roughly sculptured; mesocoxal cavities open laterally to mesanepimeron; subcircular, separated by approx. the width of one mesocoxal cavity. Mesothoracic trochantin not visible externally.

Metaventrite variously punctured, generally less so medially, becoming more densely punctured laterally. Less than half as long as wide. Anterior edge below mesocoxal cavity with raised bead extending approx. from middle of coxal cavity medially towards meso-metaventral junction, joining or not joining medially. Metaventral discrimen poorly impressed, terminating approx. 2/3 of length of metaventrite. Metakatepisternal sutures reduced, represented by weak groove and fused punctures, not extending to midline. Metepisternum long narrow, subparallel, usually with 1-2 rows of punctures; extending to abdominal ventrite (past metacoxal cavity). Metacoxal cavities wider than long, extending laterally to meet metepisternum.

Elytra. Elytron 2-3x as long as wide (length from tip of scutellum to apex of elytron)(width at maximum width). 9-12 rows punctures on each elytron (including inflexed edge) with five rows on the main portion of the elytral disc before the inflexed elytral epipleuron begins; rows forming either connected slight grooves in elytra or aligned rows of punctures that do not connect; scutellary striole absent. 1st row curves laterally in basal section, avoiding intersection with scutellum; interior edge slightly raised, forming part of elytral sutural bead. Puncture rows more confused laterally, starting with sixth row of punctures on inflexed part of elytron. Elytral interstices smooth, with isodiametric microsculpture until the lateral edges. Apex of elytra usually with punctures confused, not forming rows. Elytral epipleural fold with 3-7 rows of confused punctures. Punctures with associated seta of varying length. Elytra expose 1-2 abdominal tergites beyond elytra.

Hind Wing (Fig. 7.10). Hind wing venation reduced. Costa (C) present only at base before fusing with wing margin. Subcosta (Sc) fused with Radius (R) about 1/8 of length of wing. RA extending about 1/4 length of wing radius. R3 vein with small extension past anterior cross that fades into wing area quickly. Only small basal radial cell present. Small row of setae present anterior to R-M cross, about 10 setae. Median anterior vein absent. R-M cross poorly developed. One anal vein present as a fold or very lightly sclerotized.

Legs. Prothoracic coxa round, tapered laterally, slightly wider than long, with one median seta. Protrochanter of the cucujoid-type. Femur robust, narrower distally and basally, widest in the middle. Distally slightly modified for reception of tibia. Tibia approx. same length as femur, gradually expanded, widest distally and asymmetrically, with minute, widely spaced hairs. Two subequal straight tibial spurs present on each leg. Tibia with additional spur-like socketed denticles forming a row of spurs on outer edge. Five tarsomeres present; first small, somewhat withdrawn into tibia, above as wide as long, smaller than second and third; tarsomeres 2-3 often with longer more dense setal brush on underside, about as wide as long, subequal; four smaller than 1-3, conspicuous setae absent; five longest, approx. subequal to length of 2-4 combined, with simple paired pretarsal claws. Mesothoracic legs similar to prothoracic but with less robust (less wide) femur. Mesocoxa round, countersunk. Metathoracic legs similar to above, but with only 4 tarsomeres in male. Reduction causes only tarsomere 2 to have setal pad. Tarsal formula 5-5-5 in female, 5-5-4 in male.

Abdomen. Dorsal view: Tergite VI sometimes exposed, membranous, with rough velcro-like wing binding patches; Tergite VII always exposed by elytra, forming strongly sclerotized pygidium; densely punctured, with longer setae (approx. 1.5-3x as long as punctures); in males, Tergite VIII forming exposed genital capsule, with apical row of elongate setae.

Ventral view: Ventrite 1 longer than 2-4 combined. Ventrite 5 2-3x longer than 4. Ventrite 1 with well-developed post-coxal lines extending subtriangularly towards the posterior edge of V1, reaching past mid-point V1. V1 variously punctured, but without median sexually dimorphic setae or setal patches. Abdominal intercoxal process broad, truncate to broadly rounded. V1 upturned laterally. Lateroposterior margins of V1-3 with gradually widening groove approaching tergites, V4-5 without such a groove. V2-4 short, anterior and posterior edges mostly straight medially, upturned laterally (laterosternites); with single row of punctures with setae, varying from large oval-shaped to small circular punctures. V5 oblong semi-circular, densely punctured. Anterior edge subparallel to previous ventrites; posterior edge laterally upturned, wrapping around dorsal tergites. Apical posterior margin with groove bearing larger setae. In males, posterior margin arcuate, accommodating genital capsule; inner margin with dense with row of dense flattened setae covering anterior edge of genital capsule.

Male genitalia (Figs. 7.7B, 7.9, 7.68, 7.69)**.** Tegmen cucujiform. Dorsal piece of tegmen hood-shaped, longer than wide, bordered laterally with row of small spine-like spicules; thin piece arising from each basal corner and extending ventro-apically around median lobe, joining on ventral side, forming cucujiform ring. Tegmen with median paired setae at widest point. Median lobe smaller, but also hood like, fitting through and into tegminal ring and tegmen. Median struts of penis arising from two knob-like points of articulation laterally, dorsolaterally forming lateral edge of endophallus, touching posteriorly about 3-4x length of dorsal piece of tegmen. Complex sperm pump or sclerotized endophallic tergite present immediately posterior and lying parallel to median lobe. Rotationally symmetrical spiral-shaped, with two-trumpet-like openings on either end, with portion of ejaculatory duct running through center; sperm duct surrounded by slightly sclerotized “envelope” of tissue extending to one side in a “hill-like” projection. Endophallus mostly membranous, widest medially, holding long, curled ejaculatory duct with apical sclerotized knob. Male genitalia vary little, and are not useful for species discrimination.

Female terminalia, genitalia, and ovipositor (Figs. 7.7A, 7.8). Sternite VIII translucent, divided at middle both dorsally and ventrally, most well sclerotized in the laterotergal sides, lightly sclerotized, bearing one pair of long setae on posterolateral margin, another pair on posterointerior margin, attached to spiculum ventrale anterolaterally. Spiculum ventrale with pair of arms attached to anterior corners of sternite VIII; S.V. joining together medially with long thin extension extending about 1.5x length of sternite VIII. Tergite VIII attached with thin membrane to sternite VIII, weakly sclerotized, about third of width of sternite VIII, broadly rounded. Sternite IX anteriorly with scaly, finger-like sclerotized formations projecting anteriorly; posteriorly lightly sclerotized, mostly membranous, margin sinuate, attaching to baculi paramedially. Tergite X (proctiger) broadly rounded or truncate with rounded corners, or obtusely angulate apically, varying slightly in width (about 1/3 width of tergite IX [paraprocts]). Tergite IX lightly sclerotized anteriorly, medially becoming more densely sclerotized, wrapping around gonocoxites laterally. Paraprocts a little longer than wide, with posterior edge varying slightly in shape (broadly rounded, emarginate, subsinuate, with median lobe that varies in width). Gonocoxite two-segmented, divided into proximal lobe (=valvifer) and distal lobe (=coxite) bearing very short gonostylus. Proximal lobe subcylindrical with median triangular invagination and lateral lobe bearing two short finger-like processes. Distal lobe finger like, elongate, subequal in length to proximal lobe. Gonostylus with long seta about 1/2 length distal lobe.

Larvae. Larvae have been illustrated for one species, *Bactridium ephippigerum* (Lawrence 1977; Lawrence and Britton 1991), but otherwise have been little studied.

Taxonomic History. When LeConte described the genus *Bactridium* in 1861, he included two species: *Monotoma striatum* LeConte 1858, and *Rhizophagus nanus* Erichson, and in doing so created one of the oldest generic concepts in the currently defined Monotomidae Laporte 1840 (fourth, after *Rhizophagus* and *Monotoma* Herbst 1793 and *Europs* Wollaston 1854). He was unaware, however, of the genus *Bactridium* Reuss 1848 (an extinct sponge genus), and thus created a junior homonym that would last uncorrected until this paper. Furthermore, he was not aware of two species already described, *Rhizophagus ephippiger* Guerin-Meneville 1837 and *Rhizophagus erythropterus* Melsheimer 1844, that would later be placed in *Bactridium* LeConte.

In 1863, Pascoe described *Crine cephalotes* Pascoe 1863, apparently unaware of LeConte's paper describing *Bactridium.* Both Reitter and Horn would recognize *Crine* as a junior synonym of *Bactridium* (Reitter 1874, 1876; Horn 1879a; b).

Edmund Reitter was one of the more important earlier workers on this genus and on Monotomidae in general. Reitter (1872) described numerous new species from around the world, placing most of them in *Rhizophagus* Herbst. Soon after, however, Reitter began to follow LeConte's system, though differing slightly in interpretations of his genera. Reitter (1874) pulled some East Asian species from *Rhizophagus* and placed them in *Bactridium*, creating a genus of Nearctic and Asian distribution. In 1876, following more closely the definition of the genus as laid down by LeConte he removed some of the more remarkable and divergent species from Asia into a new genus *Mimemodes* Reitter 1876, while also placing many of his newly described species (mostly Neotropical and Nearctic) in LeConte's *Bactridium*. Notable among these new species was *Bactridium striolatum* (Reitter 1872), a new North American species.

Simultaneously, George Horn began to examine the limits of this genus, though focused mainly on the North American species, and never saw Reitter's (1876) revision before publishing his "Synopsis of the North American Monotomidae" (Horn 1879b). He also placed *Rhizophagus striolatus* Reitter 1872 into *Bactridium*, and synonymized *Rhizophagus ephippiger, Rhizophagus nanus,* and *Rhizophagus erythropterum* under *Bactridium ephippigerum* (Guerin-Meneville 1837), reversing Reitter's somewhat arbitrary synonymy of all of these species under the erroneously transferred *Rhizophagus minutus* Mannerheim 1853 (as *Bactridium minutum*). Horn (1879b) also described *Bactridium cavicolle* Horn 1879 and *Bactridium fryi* Horn 1879 from Brazil, confirming Reitter's views that the genus was distributed as far as South America.

For the next thirty-seven years, *Bactridium* expanded, mostly due to the efforts of David Sharp in the Biologica Centrali-Americana (Sharp 1900) and a few others (Grouvelle 1906; Grouvelle & Raffray 1908). Sharp pointed out the difference in form among the numerous species he described from Central America, but did not erect any new genera.

Casey (1916), however, had no such qualms about new generic names, and created two new genera based on species formerly placed in *Bactridium*: *Leptipsius* Casey 1916 for *Monotoma striatum* and a new species *Leptipsius dilutus* Casey 1916, and *Pycnotomina* Casey 1916 for *Bactridium cavicolle* Horn. *Leptipsius* was defined as possessing a constricted head behind the eyes, while *Bactridium* lacked the constriction. *Pycnotomina* was erected based on the general lack of microsculpture on the body and a large central pronotal impression.

Casey also described four new species of *Bactridium* from the United States: *Bactridium convexulum, B. hudsoni, B. obscurum, and B. curtipenne*, while also resurrecting *Bactridium erythropterum* from synonymy with *Bactridium ephippigerum,* bringing the total number of North American species to seven. Casey failed to include any of the Central or South American species in his definitions of genera or species, and did not examine European types, especially that of *B. striolatum*, which he differentiated from his new species simply from Reitter's descriptions. No keys were provided for any taxa outside of the United States, and *B. striolatum* was not included.

Before Sen Gupta (1988) and Bousquet (2003b), there were only two more species described within *Bactridium.* Fall described *Bactridium californicum* from California (Fall 1917), and Van Dyke described *Bactridium insularis* from the Galapagos Islands in 1953 (Van Dyke 1953).

Crowson (1955) placed *Bactridium, Leptipsius, Mimemodes* and *Pycnotomina* in the subfamily Monotominae, and Sen Gupta (1988) placed them within his new tribe Europini within the Monotominae (with a separate tribe Monotomini for the genus *Monotoma*). However, none of these authors performed any phylogenetic analysis, and Sen Gupta provided no characters to unite the genera within Europini.

Bousquet (2003) discussed *Leptipsius* in North America, redescrbiing *Leptipsius striatus* and a new species from Arizona and New Mexico, *Leptipsius imberbis*. He also included comments on *L. dilutus*, but not redescribe or give definitive diagnostic characters for that species. He did provided more diagnostic characters for the genus and moved three species of *Bactridium* within.

Thus, before this study, the genus *Bactridium* LeConte 1861 is a junior homonym of *Bactridium* Reuss 1848, has never been exhaustively revised for any region, and has uncertain affinities to at least two, if not three other genera of Monotomidae. There are currently 27 species within the genus, and many may actually belong within the current limits of *Leptipsius* sensu Casey, Sen Gupta, and Bousquet*,* not *Bactridium* (Bousquet 2003b). The 27 species are all small (1-4.5mm), mostly brown, brownish-red, brownish-yellow, or black, and have cryptic habits. They are thought to feed subcortically on ascomycete fungi (Lawrence 1977), but this is based on only one definitive association, that of *Bactridium ephippigerum* with *Hypoxylon* Bulliard. Other species may not feed on fungi, as is common in other Monotomidae genera (e.g. *Rhizophagus*).

Species accounts

***Neobactridium californicum* (Fall, 1917)** (Figs. 7.1A, 7.2A, 7.71A-F)

Bactridium californicum Fall, 1917:169. Type locality: "Southern California, Ojai Valley". Type repository: MCZ[1]. Fall, 1917: 169-170.

Diagnosis. The distribution (southern California, Arizona, possibly New Mexico, western Texas), other generic characters, coloration, lack of distinct lateral elytral united puncture striae (Fig. 7.56A), and elongate subcontiguous punctures on ventrite 5 (Fig. 7.66A) will readily distinguish this southwestern species.

Description.

Redescription: **General**. Length 1.8-2.6 mm. Width 0.55-0.80 mm. Body approx. 2.75 times as long (measured from tip of elytra to tip of frons) as wide (measured approx. midpoint of elytra at widest point). Body flattened, subparallel. Head, pronotum, scutellum (area around scutellum on elytra), pygidium dark reddish-brown or dark brown, elytra orange-brown with tips (1/3 of elytron) infuscate. Dorsal surface subglabrous, moderately shiny; minute hairs visible under high magnification arising from punctures.

Head (Figs. 7.16A, 7.18A, 7.20A): Dorsal surface: Head maximum width varies, but less wide than pronotum. Head length/width ratio avg. 0.74 (male), 0.73 (female), range (0.69-0.79). Vertex with separated punctures (greater than width one puncture) smaller than those closest to eyes, which are larger and closely approximate. Most punctures longer than wide, somewhat oval, teardrop-shaped posteriorly. Setae arising from punctures approx. equal to width of puncture on vertex, length gradually increasing towards distal end with a corresponding decrease in puncture size. Punctures least dense, at middle of head, between eyes. Teardrop-shaped punctures dense posteriorly, extending laterally across head behind vertex. Clypeal area with numerous long setae and correspondingly smaller punctures than those on vertex. Row of subcontiguous punctures present proximal to eyes. Eyes prominent, protuberant, about 0.45 (males), 0.45 (females) length/width ratio (range 0.38-0.57). Longitudinal length ~1.8-1.9x scape length. Eye width about 0.75 width of scape. Anterior margin of clypeus broadly rounded.

Ventral surface (Figs. 7.25A, 7.27A, 7.28A): Pregular punctured and setose, with some visible microsculpture between punctures. Anterior region with united punctures forming shallow groove posterior to submentum. Pregular region densely punctured, with numerous setae of increasing length laterally. 5-7 wide, subcircular punctures bordering lateral edge of pregular region. Male subgenal pore present, located latero-posteriad of mandibular articulation. Submentum about 3x as wide as deep, with slightly convex posterior edge and straight anterior edge forming mental suture. Two larger paramedian setae present, with four smaller anterior setae present. Posterior portion with microsculpture.

Lateral surface (Fig. 7. 23A): Lateral genal expansion with scattered posterior setae. Not as laterally expanded as in other species. Area under eye with rugose sculpturing.

Antennae (Figs. 7.20A, 7.22A): Ratio of segment length: 4.2 : 2.3: 1.3 : 1 : 1 : 1 : 1.2: 1.2 : 1.3 : 4.5 ; terminal club segment longer than broad (~1.1). Yellow-orange, slightly paler than elytra. Extending about 1/3-1/4th past anterior of thorax when posteriorly extended.

Thorax. Dorsal surface (Figs. 7.30A, 7.33A): Wider than long, subquadrate. Males avg. 0.87 L/W (range 0.82-0.91). Females avg. 0.88 L/W (range 0.85-0.93). Widest just in front of middle. Anterior edge straight, with slight median emargination. Posterior edge with area behind posterior angles slightly concave. Pronotum narrowly converging posteriorly. Narrow median impunctate zone present, widest in posterior third. Median half of pronotum (disc) with widely scattered subcircular punctures (separated by greater than width of one puncture). Laterally punctures longer, becoming more closely approximate, but still separated by about 1/2 width one puncture. Base of pronotum with slightly depressed zone loosely bordered with punctures. Pronotal lateral carinae smooth with five-six minute denticles posteriorly, each with long seta. Outer border of disc, just proximal to more densely punctured lateral edges of pronotum with oval-circular impunctate zone. Disc with abundant median and paramedian isodiametric microsculpture.

Ventral surface (Figs. 7.35A, 7.38A): Prosternum medially sparsely punctured (well-separated by >width 1 puncture), elongated, sparse punctures with small setae, wider than long. Lateral irregular net-like sculpturing poorly developed, more individual punctures visible, but still with some area of rugose sculpturing. Intercoxal process broadly rounded at posterior corners. Prosternal apophysis with about 15-20 minute setae, and with some median and lateral microsculpture. Prosternum and prosternal apophysis length subequal (apophysis slightly longer, measured from anterior edge of coxal cavity). Apophysis and margin of pronotum posteriorly minutely crenulate, with row of fine setae. Procoxal cavities subcircular, of approx. same width as height, with thin apical lateral extension (perhaps a remnant of the notosternal suture).

Pterothorax: Scutellar shield (Fig. 7.50A) about as long as wide, with isodiametric microsculpture; broadly rounded, subtriangular; bearing about 13 minute punctures. Mesoscutal plate not examined.

Mesoventrite (Fig. 7.40A) about twice as long as wide (measured from middle mesoventrite and from widest lateral points of mesoventrite. Exposed mesointercoxal process with slightly rectangular (wider than long) microsculpturing; two large paramedian lateral setae present. Area hidden under pronotum not examined. Mesepimeron roughly sculptured. Mesanepimeron with several large punctures and setae, also surrounded by rough sculpturing.

Metaventrite (Fig. 7.42A) brown, with posterior medially reddish-brown area vaguely triangle shaped. Medially lightly punctured, punctures (longer than wide) small, widely separated. Anterior area between mesocoxae nearly impunctate, with microsculpture. Anterior edge below mesocoxal cavity with raised bead extending approx. from middle of coxal cavity medially towards meso-metaventral junction, joining medially. Medially with microsculpture. Laterally large, well-separated punctures present (avg. separated by greater than 1/2 width puncture or more). Exposed portion of metepisternum with 1-2 rows of oblong (longer than wide) punctures, which become smaller posteriorly.

Elytra (Figs. 7.50A, 7.52A, 7.54A, 7.56A): 0.37 avg. W/L (males), 0.39 (females) (0.34-0.40 males, 0.35-0.43 females)(L from tip of scutellum to apex of elytron)(W at maximum width). 10 rows punctures on each elytron (including inflexed edge) with five rows on the main portion of the elytral disc before the inflexed elytral epipleuron begins; elytral epipleural fold with 5 rows of confused punctures; 1st five rows on disc forming connected slight grooves in elytra; all five rows contiguous anteriorly before scutellum. Elytral interstices smooth, with isodiametric microsculpture throughout. Apex of elytra usually with punctures confused, not completely reaching apex, except for first row. Rows become slightly wider laterally. Punctures on elytra with associated seta that become longer laterally. Puncture rows more confused laterally, starting with sixth row of punctures on inflexed part of elytron, which does not start connected basally, but becomes connected until apex of elytra. Rows 7-9 forming series of confused vaguely aligned puncture rows. Row 10 present just proximal to elytral edge, not forming deep groove or united puncture row, but simply loosely aligned row of smaller punctures and associate setae.

Legs (Figs. 7.44A, 7.46A, 7.48A): Rust-light orange-brown, slightly paler than orange coloration of elytra.

Abdomen. Dorsal view: (Figs. 7.58A, 7.60A): Tergite VII (pygidium) densely punctured, with large, circular-oval punctures, especially apico-laterally, grouped nearly subcontiguously (separated by 1/2 width of a single puncture); antero-medially with some smaller oblong punctures; all punctures with long associated setae (approx. 1.5-3x as long as punctures).

Ventral view (7.60A, 7.62A, 7.64A, 7.66A): Ventrites dark reddish-brown. Intercoxal process broadly truncate. V1 with microsculpture throughout. Medially with random, subequally spaced subcircular, small, barely impressed punctures and associated short setae, separated by greater than 1-2 puncture widths. Post coxal lines extending nearly to posterior edge of V1, stopping about 1-2 puncture widths before edge; somewhat roughly sculptured anteriorly, but with more obvious microsculpture medially, with 2-5 punctures and associated setae. Interior line extending at about 10-15° angle to body line; outer angle with a gentle 35-45° curve approaching interior line. Punctures laterally on V1 larger, more oval, more dense, separated by 1/2 - 1 puncture width on average. V2-V4 with single row of large oblong, oval punctures with associated long setae, occupying about 1/3-2/3rds length of ventrite; punctures smaller, subcircular medially, occupying ~1/3rd ventrite, laterally oval, occupying 2/3 ventrite length. V5 with dense oval-elongate punctures, but not blending together (except rarely). Separated on average 1/2 - 1 length puncture width, nearly subcontiguous laterally. Several long, heavy setae present on posterior margin of ventrite around abdominal opening.

Male genitalia. Fitting generic description (Fig. 7.9A)

Female terminalia, genitalia, and ovipositor. Posterior edge of paraproct tergite IX straight across. Tergite IX (paraproct) with truncate apex, broadly rounded corners (Fig. 7.8A).

Type material. Fall's Collection in the MCZ contains two females and two males matching the description of the locality in the description. One of them, a female (Fig. 7.71A-D), bears a label: "TYPE [typed] // *californi- / cus*. [handwritten]" (Fig. 7.71E). Fall did not designate a type in his original description, but because of the additional type label, I am **here designating the LECTOTYPE** as that specimen, and have attached an additional red label designating it as such. The original publication mentions “a good series of this species taken by the writer”, so all specimens with identical label data to the lectotype (e.g. “Ojai Cal / 3.8.92 // H.C. FALL / COLLECTION”) are **DESIGNATED AS PARALECTOTYPES** (Fig. 7.71F).

Distribution. Fig. 7.11. United States: Arizona, California, Texas. Likely in New Mexico & N. Mexico. All databased records available here:

http://symbiota4.acis.ufl.edu/scan/portal/collections/list.php?taxa=Bactridium%20californicum&thes=1&type=1&db=114;&page=1

Life history and collecting. This species is rarely collected, and little is known about its life history. Adults (from the type series) were collected under bark of *Platanus racemosa* Nuttall. Some specimens have been collected with Lindgren funnel traps, or at lights at night, suggesting some nocturnal component of their lifecycle. The species may be confined to higher-elevation areas of the southwest and southern California, such as the Sky Islands, but this is still uncertain.

Discussion. *Neobactridium californicum* is the only species in the genus currently known from the southwestern United States. It has a similar coloration to *N. ephippigerum* but in many characters it is similar to *N. striolatum*. In that region, it may be confused with *Leptipsius striatus*, which also has infuscate elytra, but can be differentiated using generic-level characters.

***Neobactridium ephippigerum* (Guérin-Méneville, 1837)** (Figs. 7.1X, 7.2X, 7.71G-I, 7.72, 7.73A-B)

Rhizophagus ephippiger Guérin-Méneville, 1837:190. Neotype locality: “New York” (original description: “l’Amerique boréale”). Neotype repository: MCZ

= *Rhizophagus nanus* Erichson, 1843: 360. Type locality: “Carolina”. Type repository: ZMHB

= *Rhizophagus erythropterus* Melsheimer, 1844: 109. Type locality: “Pennsylvania. Bank of the Susquehanna”. Type repository: MCZ. NEW COMBINATION.

= *Bactridium curtipenne* Casey, 1916:99. Type locality: “Arkansas”. Type repository: USNM. NEW COMBINATION

Diagnosis. This species is most readily diagnosed by the heavy punctures forming lines on the sides of elytra (Fig. 7.56B). This character is best seen in side-lit harsh lighting or under diffusion. In addition, the densely punctured and subcontiguous punctures laterally on the pronotum and head will also diagnose this species (Figs. 7.18B, 7.33B). They are also usually bicolored, with the apex of elytra, pronotum, and head a dark reddish brown, while the anterior 3/4 of the elytra are a lighter reddish-brown.

Redescription: General. Length 1.3-2.6 mm. Width 0.45-0.80 mm. Body approx. 2.6 times as long (measured from tip of elytra to tip of frons) as wide (measured approx. midpoint of elytra at widest point), approx. 2.1 times as wide as deep (measured from top of pronotum to bottom of pronotum in lateral view). Body flattened, subparallel. Head, pronotum, and pygidium dark reddish-brown or dark brown, elytra orange-brown with tips (1/3rd-1/4th of elytron) infuscate. Dorsal surface subglabrous, moderately shiny; minute hairs visible under high magnification arising from punctures, longer laterally,

Head. Dorsal surface (Figs. 7.16B, 7.18B, 7.20B): Head maximum width varies, but slightly less wide than pronotum. Head length/width ratio avg. 0.75 (male), 0.73 (female), range (0.69-0.80). Vertex with disconnected punctures smaller than those closest to eyes, which are larger and subcontiguous. Most punctures longer than wide, somewhat oval. Setae arising from punctures approx. equal to width of puncture on vertex, length gradually increasing towards distal end with a corresponding decrease in puncture size. Punctures least dense posteriorly, at middle of head, between eyes. Clypeal area with numerous long setae and correspondingly smaller punctures than those on vertex. Eyes prominent, protuberant, about 0.44 (males), 0.47 (females) length/width ratio (range 0.34-0.56). Longitudinal length ~1.6-1.7x scape length. Eye width about same length as scape. Interfacetal setae of length less than one ommatidium present. Anterior margin of clypeus broadly rounded.

Ventral surface (Figs. 7.25B, 7.27B, 7.28B): Pregular area punctured and setose, with some visible microsculpture between punctures. Anterior region with united punctures forming shallow groove posterior to submentum. Pregular region densely punctured, with numerous setae of increasing length laterally. Subgenal brace with two regions, one anterolateral, extending medially on mandible, forming outer brace and rest for mandible. Second region paramedial, lateral of cardo, forming short acute finger-like protrusion. Male subgenal pore present, located latero-posteriad of mandibular articulation. Submentum about 3x as wide as deep, with slightly convex posterior edge and straight anterior edge forming mental suture. Posterior portion with microsculpture.

Lateral surface (Fig. 7.23B): Lateral genal expansion with scattered posterior setae. Area under eye with rugose sculpturing.

Antenna (Figs. 7.20B, 7.22B): Ratio of segment length: 3.5 : 2.9 : 1.2 : 1.1 : 0.226 : 1 : 1.1 : 1.1 : 1.2 : 5.1 ; terminal club segment longer than broad (~1.1). Yellow-orange, slightly paler than elytra. Extending about 1/3-1/4th past anterior of thorax when posteriorly extended.

Thorax. Dorsal surface (Figs. 7.30B, 7.33B): Wider than long, subquadrate. Males avg. 0.85 L/W (range 0.82-0.89). Females avg. 0.85 L/W (range 0.80-0.90). Widest just in front of middle. Anterior edge straight, with slight median emargination. Posterior edge with area behind posterior angles concave. Pronotum narrowly converging posteriorly. Narrow median impunctate zone present, widest in posterior third. Median half of pronotum (disc) with widely scattered mostly oval punctures (separated by greater than width of one puncture). Laterally punctures longer, becoming subcontiguous and united to form loose longitudinal striae. Base of pronotum with slightly depressed zone loosely bordered with punctures. Pronotal lateral carinae smooth with three-four minute denticles posteriorly, each with long seta. Disc with microsculpture.

Ventral surface (Figs. 7.35B, 7.38B): Prosternum medially sparsely punctured (well-separated by >width 1 puncture), elongated, sparse punctures with small setae, wider than long. Lateral irregular net-like sculpturing well-developed, course, individual punctures obliterated. Intercoxal process minutely angulate at posterior corners. Prosternal apophysis with about 20-25 minute setae, but without microsculpture. Prosternum and prosternal apophysis length subequal (apophysis slightly longer, measured from anterior edge of coxal cavity). Apophysis and margin of pronotum posteriorly minutely crenulate, with row of fine setae. Procoxal cavities subcircular, of approx. same width as height, with thin apical lateral extension (perhaps a remnant of the notosternal suture).

Pterothorax. Scutellar shield (Fig. 7.50B) wider (measured from widest point) than long (measured from basal tip to the drop off to mesoscutum) (~1.2x W/L), with isodiametric microsculpture; broadly rounded, subtriangular. About 15 minute punctures. Mesoscutal plate with rough microsclpture, broken by ~6 punctures with longer setae posteriorly.

Mesoventrite (Fig. 7.40B) about twice as long as wide (measured from middle mesoventrite and from widest lateral points of mesoventrite. Exposed mesointercoxal process with irregular, rough sculpturing, four smaller paramedian lateral seta, no microsculpture. Mesepimeron covered in rough scale-like sculpturing. Antero-proximally, large puncture forms corner of ridge that extends diagonally across mesanepisternum, intersecting elytral ridge around midline; Mesanepimeron with several large punctures and setae, also surrounded by rough sculpturing.

Metaventrite (Fig. 7.42B) brown, with posterior medially reddish-brown area vaguely triangular. Medially lightly punctured, punctures (longer than wide) small, widely separated. Anterior area between mesocoxae nearly impunctate, without microsculpture. Anterior edge below mesocoxal cavity with raised bead extending approx. from middle of coxal cavity medially towards meso-metaventral junction, not joining medially. Medially with poorly impressed microsculpture (somewhat forming sinuous microlines, but also isodiametric). Laterally large, nearly subcontiguous (but separated more than lateral portions of pronotum). Exposed portion of metepisternum with 1-2 rows of oblong (longer than wide) punctures, which become smaller posteriorly (about 30 punctures).

Elytra (Figs. 7.50B, 7.52B, 7.54B, 7.56B): 0.38 avg. W/L (males and females) (0.35-0.44 males, 0.36-0.41 females)(L from tip of scutellum to apex of elytron)(W at maximum width). 12 rows punctures on each elytron (including inflexed edge) with five rows on the main portion of the elytral disc before the inflexed elytral epipleuron begins; elytral epipleural fold with 7 rows of confused punctures; 1st five rows on disc forming connected slight grooves in elytra; all five rows contiguous anteriorly before scutellum. Elytral interstices smooth, with isodiametric microsculpture until the lateral edges. Apex of elytra usually with punctures confused, not completely reaching apex, except for first row. Rows become wider laterally. Punctures on elytra with associated seta that become longer laterally. Puncture rows more confused laterally, starting with sixth row of punctures on inflexed part of elytron, which does not start connected basally, but becomes connected and confused with other rows apically. Rows 7-11 forming series of confusing fused puncture rows visible under diffuse light. Row 12 present just proximal to elytral edge, not forming deep groove or united puncture row, but simply loosely aligned row of smaller punctures and associate setae.

Legs (Figs. 7.44B, 7.46B, 7.48B): Rust-orange-brown, paler than underside of body.

Abdomen. Dorsal view (Figs. 7.58B, 7.60B): Tergite VII (pygidium) densely punctured, with large, circular-oval punctures, especially apico-laterally, grouped nearly subcontiguously (separated by less than 1/3 width of a single puncture); postero-medially with some smaller oblong punctures; punctures with long associated setae (approx. 1.5-3x as long as punctures).

Ventral view (7.60B, 7.62B, 7.64B, 7.66B): Ventrites dark reddish-brown. Intercoxal process broadly truncate. V1 without microsculpture except at posterior margin. Medially with scattered oval, small, barely impressed punctures and associated short setae, separated by greater than one puncture width. Post coxal lines extending nearly to posterior edge of V1; roughly sculptured, with 3-4 setae. Interior line extending at about 10-15° angle to body line; outer angle with a gentle 35-45° curve approaching interior line. Punctures laterally on V1 larger, more deeply impressed, more oval, densely packed, separated by about 1/2 puncture width on average. V2-V4 with single row of large oblong, oval punctures with associated long setae, occupying about 1/2-2/3rds length of ventrite. V5 with extremely dense punctures, often blending together, but not forming lines. Separated on average <1/2 length puncture with, often not separated. With several long, heavy setae on posterior margin of ventrite around abdominal opening.

Male genitalia. Fitting generic description (Figs. 7.7B, 7.9B, 7.68A-B, 7.69A-B)

Female terminalia, genitalia, and ovipositor. Posterior edge of paraproct tergite IX doubly emarginate, forming two small paramedian depressions with median broadly obtuse curve, about as wide as apex of tergite VIII. Tergite IX (paraproct) broadly rounded (Fig. 7.8B).

Type material. *Rhizophagus ephippiger* Guerin-Meneville. The author did not mention where the type of this species was deposited (Guerin-Meneville, 1837), but the MNHN should have all of Guerin-Meneville's type specimens, at least those identifiable as such (Horn et al. 1990; Jameson and Smith 2002). The specimens were requested from the MNHN but could not be located. We searched other museums for the specimens (see Specimens and Taxonomic Material) but could not locate his types. The original description of *Rhizophagus ephippiger* did not mention how many specimens were used, and the locality ("l'Amerique boréale") was not found labeled on any specimens that could have been seen or used by Guerin-Meneville to describe this species. Therefore, despite extensive searching, we feel it is appropriate to designate a neotype for this species. **NEOTYPE HERE DESIGNATED**. We chose a specimen in LeConte's collection, one that matched the original type locality best, and fit the original description. This is the most distinct and common *Neobactridium* species in the North American fauna, and so it seems appropriate to designate a specimen from LeConte's collection at the MCZ. The specimen, a male (Fig. 7.71G-I), is labeled "N. Y [typed]" pinned through the center between the N. and Y, and I have attached a red NEOTYPE typed label "**NEOTYPE** /*Rhizophagus ephippiger* / Guérin-Méneville 1837 ♂ / det TC McElrath 2017", pinned through the right side of the label between the year and the male symbol (Fig. 7.72A). The specimen is mounted with the head facing away from the pin itself. The tarsi are missing on the front fore leg, but it is otherwise in good condition.

Rhizophagus nanus Erichson. Erichson (1843) described this species from an uncertain amount of specimens that were sent to him by "Zimmermann" from Carolina. Part of Zimmerman's collection was given or sold to George Lewis and G. R. Crotch at the Academy of Natural Sciences in Philadelphia, but which was then transferred to the Museum of Comparative Zoology by LeConte in their historical exchange of material (see Horn et al. 1990; Bousquet 2016). However, the specimens seen by Erichson are not among this material (which was never well-labeled, and can only be identified as Zimmerman's material with difficulty). However, Erichson's collection was deposited in the Museum für Naturkunde in Berlin. This museum has two specimens on a single pin, each point-mounted, that is labeled "Süd-Carolina Zim." (Fig. 7.72B-F) This label, while not added by Zimmermann or Erichson, was added by the former collection manager who arranged and wrote the inventory of the collection between 1855 and 1880 (Jäger, pers. comm.). Both specimens (male) match Erichson's description, and are conspecific with *N. ephippigerum*. **LECTOTYPES here designated.** I have attached a red lectotype label to this pin "**LECTOTYPE ♂ (T.)** [meaning top specimen] / **PARALECTOTYPE ♂ (B.)** [meaning bottom specimen] / *Rhizophagus nanus* / Erichson 1843 / det TC McElrath 2017". Because Erichson did not highlight, illustrate, or otherwise designate either specimen as a type, I chose the top as the lectotype and the bottom as the paralectotype.

Rhizophagus erythropterus Melsheimer. The MCZ contains four specimens on three pins labeled as "Melsh." and in the Melsheimer collection that were in the series labeled as *Rhizophagus erythropterus*. This label was likely attached by Henry Hagen (Hagen 1884).The first pin holds one specimen, a cut-off old-style steel pin (no pin head) a “short common pin…” of Fredereich Valentine Melsheimer - this specimen is actually *Europs pallipennis* LeConte, and may be one of the earliest records of this species. The second pin holds two specimens, on an older style German pin “from Carlsbad” (Hagen 1884), approx. 3.6 cm in length. These two specimens, however, were likely collected by Fredereich Ernst Melsheimer, of Melsheimer (1844). The outermost specimen is conspecific with *Neobactridium striolatum* (Reitter), and the innermost specimen is conspecific with *Neobactridium ephippigerum* (Guerin-Meneville). The locality and date of collection of these two specimens is unknown. The point bears no writing and may have been part of Melsheimer’s type series. The third pin holds one specimen on an older style German pin “from Carlsbad” (Hagen 1884), approx. 3.6 cm in length (Fig. 7.72G). The point itself bears faded handwriting that says “Pa” just before reaching the pin, and something that could be “Na” or “Ma” just below/after the pin (Fig. 7.72H). The one specimen is conspecific with *Neobactridium ephippigerum* (Guerin-Meneville). Because the writing on the point matches Melsheimer’s original type locality (Pennsylvania), a **LECTOTPYE is here designated** for *Rhizophagus erythropterus*. I have attached a red lectotype label saying “**LECTOTYPE** / *Rhizophagus erythropterus* / Melsheimer 1844 / det TC McElrath 2017**”** (Fig. 7.72G). The remaining specimens are not herein designated as paralectotypes, as they cannot be linked to the original type locality or description.

Bactridium curtipenne Casey. Casey’s collection in the USNM contains a single specimen, a male from Arkansas (Figs. 7.72I, 7.72A-B), that bears his determination label. Because Casey only mentioned one specimen, this must be the holotype of *B.*

curtipenne Casey. While smaller and slightly more pale than most specimens of *Neobactridium ephippigerum*, it is nevertheless conspecific with *N. ephippigerum*. While imaging the labels, the locality label "Ark." was slightly damaged and could not be re-pinned, so it was affixed to a card and re-pinned beneath the specimen.

Distribution. Fig. 7.12. Widespread in eastern United States and southern Canada, one or two records from northern Mexico. Records from the following states and provinces: Canada: ONT, QUE; Honduras; Mexico: Nuevo Leon; United States: AL, AR, CT, DE, DC, GA, FL, IA, IL, IN, KS, KY, LA, MA, MD, ME, MI, MO, MN, MS, NC, NH, NJ, NY, PA, OH, RI, SC, TN, OK, TX, WI, WV, VA. All databased records available here:

http://symbiota4.acis.ufl.edu/scan/portal/collections/list.php?taxa=Bactridium%20ephippigerum&thes=1&type=1&db=114;&page=1

Life history and collecting. This species is the only one in the genus and related genera with more than one life-stage figured or identified (Lawrence 1977), and thus much of the biology of the genus is extrapolated from this species. The larvae and adults feed on stromatic tissue and some hyphae and conidia of a *Hypoxylon* species found occurring under bark of fallen *Quercus virginiana* Miller. The larvae were reared from the fungal and bark samples taken back to the lab. Other label data supports this conclusion; adults have been taken under bark of various hardwood trees, likely in (unwritten or unidentified) ascomycete associations. Plant and fungal associations also include: *Acer saccharum* Marshall, *Carya illinoinensis* (Wangenheim), *Celtis occidentalis* L., *Citrullus* Schrader, *Fagus* L., *Fraxinus americana* L., *Gymnocladus dioicus* (L.), *Liquidambar styraciflua* L., *Morus* L., *Rhus* L., *Pinus taeda* L., *Platanus occidentalis*, *Populus* L., *Quercus laevis* Walter, *Quercus macrocarpa* Michaux, *Quercus nigra* L., *Quercus stellata* Wangenheim, *Quercus virginiana, Ulmus* L., and *Zea mays* L. The largest series of specimens often come from under bark of oaks. Large series of specimens may be found under the bark of fallen oaks of various species in Georgia, usually trees that had died within the last two years (TCM, pers. obs.).

This species may be collected throughout the year, especially in the southern United States, although this may require active collecting in the fall, spring, and especially winter months. They do not seem to fly readily in the winter. Peak collecting at passive traps seems to occur in the summer months, with smaller numbers collected during the rest of the year.

Neobactridium ephippigerum can be collected with passive traps, especially those that target the subcortical microhabitat, such as Lindgren funnel/windowpane traps baited with ethanol or other chemicals mimicking the fermenting stage of rotten logs. They are often collected with blacklights/traps or at mercury vapor lights/traps and may be nocturnally active. Emergence traps or Berlese extractions of their host material may also yield large series of specimens. They are rarely collected with methods such as pitfalls, malaise, elevated or non-elevated FITs, moth traps, beating, or yellow pans.

Discussion. This is the most commonly collected species of *Neobactridium* in North America. It is one of the most readily recognizable in North America as well, although abnormal or teneral specimens may be confused with *N. striolatum.* It is most readily confused with *N. californicum*, but distribution and the elytral striae can quickly separate those two species. It may also be confused with the orange-elytra color morph of *N. striolatum*, but can be distinguished by the presence of fused punctures on the side of the elytra in *N. ephippigerum*, which are lacking in *N. striolatum*.

The head and genal process varies considerably in size within the species, as in *N. striolatum*. However, it is not necessarily sex-specific, although males are usually larger, females may also have expanded genal processes.

Neobactridium hopkinsi **McElrath NEW SPECIES** (Figs. 7.1C, 7.2C, 7.73C-E)

Diagnosis. This species can be distinguished by the lack of united lateral elytral puncture rows forming striae (separates from *N. ephippigerum*); the wider than long pronotum (Males avg. 0.80 L/W (range 0.82-0.91), females avg. 0.80 L/W (range 0.85-0.93) (Table 1); the thorax (or sometimes just head) being red-brown, with a distinctly darker body, usually dark brown-black; convex body; and having very small punctures on ventrites 2-4, occupying at most 1/2 of length of ventrite, usually much smaller.

Description. **General**. Length 1.9-2.2 mm. Width 0.55-0.75 mm. Body approx. 2.75 times as long (measured from tip of elytra to tip of frons) as wide (measured approx. midpoint of elytra at widest point). Body flattened-subcylindrical, subparallel. Head and pronotum reddish-brown, pygidium and elytra dark blackish-brown, antennae and legs light orange-brown. Dorsal surface subglabrous, moderately shiny; minute hairs visible arising from punctures.

Head. Dorsal surface (Figs. 7.16C, 7.18C, 7.20C): Head maximum width varies, but slightly less wide than pronotum. Head length/width ratio avg. 0.74 (male), 0.71 (female), range (0.68-0.76). Vertex with separated punctures (greater than width one puncture) smaller than those closest to eyes, which are larger and closely approximate. Most punctures on vertex and behind longer than wide, larger, more closely approximate laterally. Vertex with poorly impressed or absent microsculpture. Setae arising from punctures approx. equal to width of puncture on vertex, length gradually increasing towards distal end with a corresponding decrease in puncture size. Punctures least dense, at middle of head, between eyes. Posteriorly, extending laterally across head behind vertex, more dense puncture area, punctures sub-circular to oval. Clypeal area with numerous long setae and correspondingly smaller, circular punctures than those on vertex. Row of subcontiguous punctures present proximal to eyes. Eyes prominent, protuberant, about 0.44 (males), 0.43 (females) length/width ratio (range 0.38-0.48). Longitudinal length ~1.3-1.4x scape length. Eye width about 0.9 width of scape. Anterior margin of clypeus broadly rounded.

Ventral surface (Figs. 7.25C, 7.27C, 7.28C): Pregular area punctured and setose, with some visible, but poorly impressed microsculpture between punctures. Anterior region with united punctures forming shallow groove posterior to submentum. Pregular region sparsely, evenly punctured. Punctures evenly spaced, only increasing in size by about two-fold laterally. 5-6 subcircular punctures loosely bordering lateral edge of pregular region. Male subgenal pore present, located latero-posteriad of mandibular articulation. Submentum about 2.5-3x as wide as deep, with slightly convex posterior edge and straight anterior edge forming mental suture. Ten smaller anterior setae present. Posterior portion with poorly impressed microsculpture.

Lateral surface (Fig. 7. 23C): Lateral genal expansion lined posteriorly with posterior setae. Area under eye with numerous punctures and setae.

Antennae (Figs. 7.20C, 7.22C): Ratio of segment length: 4.1 : 2.6 : 1.5 : 1 : 1 : 1 : 1.2 : 1.2 : 1.5 : 4.5; terminal club segment longer than broad (~1.1). Yellow-orange, slightly paler than elytra. Extending about 1/2 - 1/3 past anterior of thorax when posteriorly extended.

Prothorax. Dorsal surface (Figs. 7.30C, 7.33C): Wider than long, subquadrate. Males avg. 0.80 L/W (range 0.82-0.91). Females avg. 0.80 L/W (range 0.85-0.93). Widest just in front of middle. Anterior edge straight, with slight median emargination. Posterior edge with area behind posterior angles slightly concave. Pronotum narrowly converging posteriorly. Narrow median impunctate zone present, widest in posterior third. Median half of pronotum (disc) with widely scattered subcircular punctures (separated by greater than width of one puncture). Laterally punctures longer, becoming more closely approximate, but still separated by about 1/2 width one puncture, associated hairs longest laterally. Base of pronotum with slightly depressed zone loosely bordered with punctures. Pronotal lateral carinae smooth with three minute denticles posteriorly, each with long seta. Outer border of disc, just proximal to more densely punctured lateral edges of pronotum with narrow oval-circular impunctate zone. Disc with absent or poorly impressed isodiametric microsculpture, but with abundant minute punctures.

Ventral surface (Figs. 7.35C, 7.38C): Prosternum medially sparsely punctured (well-separated by >width 1 puncture), elongated, sparse punctures with small setae, wider than long. Lateral irregular net-like sculpturing somewhat-developed, more individual punctures visible, but still with areas of rough sculpturing laterally. Medio-lateral area smooth, lacking punctures and rough sculpturing. Small area of large wider punctures present anterior of procoxal cavities; Intercoxal process minutely angulate at posterior corners. Prosternal apophysis with about 15-20 minute setae, with sublateral, postero-medial microsculpture. Prosternum and prosternal apophysis length subequal (apophysis slightly longer, measured from anterior edge of coxal cavity). Apophysis and margin of pronotum posteriorly minutely crenulate, with row of fine setae. Procoxal cavities subcircular, of approx. same width as height, with thin apical lateral extension (perhaps a remnant of the notosternal suture).

Pterothorax. Scutellar shield (Fig. 7.50C) wider than long, with poorly impressed isodiametric microsculpture; broadly rounded, subtriangular. About 12 minute punctures present. Mesoscutal plate with area of large punctures surrounded by rough sculpturing just anterior to scutellar shield.

Mesoventrite (Fig. 7.40C) about twice as long as wide (measured from middle mesoventrite and from widest lateral points of mesoventrite. Exposed mesointercoxal process with isodiametric microsculpturing forming irregular lateral lines; two large paramedian sublateral setae present; sublateral rough sculpturing forming aligned groove present, bordered anteriorly by four setaceous punctures. Area hidden under pronotum not examined. Mesepimeron roughly sculptured. Mesanepimeron with several large punctures and setae, also surrounded by rough sculpturing.

Metaventrite (Fig. 7.42C) brown throughout. Medially lightly punctured, punctures small, subcircular, widely separated. Anterior area between mesocoxae nearly impunctate, without microsculpture. Anterior edge below mesocoxal cavity with raised bead extending approx. from middle of coxal cavity medially towards meso-metaventral junction, not joining medially. Medially with poorly impressed microsculpture.

Anterolaterally large, approximate punctures present (avg. separated by less than 1/2 width puncture or nearly subcontiguous), becoming smaller and more widely separated posterolaterally. Exposed portion of metepisternum with 1-2 rows of oblong (longer than wide) punctures, which become smaller posteriorly (about 24 punctures).

Elytra. (Figs. 7.50C, 7.52C, 7.54C, 7.56C): 0.38 avg. W/L (males), 0.39 (females)(0.35-0.42 males, 0.36-0.42 females)(L from tip of scutellum to apex of elytron)(W at maximum width). 10 rows punctures on each elytron (including inflexed edge) with five rows on the main portion of the elytral disc before the inflexed elytral epipleuron begins; elytral epipleural fold with 5 rows of aligned punctures; 1st five rows on disc forming connected slight grooves in elytra; all five rows contiguous starting at the lateral level of scutellum. Elytral interstices smooth, with isodiametric microsculpture throughout (poorly impressed). Apex of elytra usually with punctures confused, not completely reaching apex, except for first row. Rows become slightly wider laterally. Punctures on elytra with associated seta that become longer laterally. Puncture rows more confused laterally, starting with sixth row of punctures on inflexed part of elytron, which are not connected at all during their length. Rows 7-9 forming series of aligned puncture rows. Row 8 begins about around 1/3 of length of elytron, disappears before apical third. Row 10 present just proximal to elytral edge, not forming deep groove or united puncture row, but simply loosely aligned row of smaller punctures and associated setae.

Legs. (Figs. 7.44C, 7.46C, 7.48C): Rust-light orange-brown, slightly paler than orange coloration of elytra.

Abdomen. Dorsal view (Figs. 7.58C, 7.60C): Tergite VII (pygidium) densely punctured, with large, circular-suboval punctures, especially apico-laterally, grouped nearly subcontiguously (separated by 1/2 width of a single puncture), mostly evenly spaced; antero-medially with some smaller punctures; all punctures with long associated setae (approx. 1.5-3x as long as punctures).

Ventral view (7.60C, 7.62C, 7.64C, 7.66C): Ventrites dark reddish-brown. Intercoxal process broadly truncate. V1 with microsculpture anteromedially & anterolaterally, but poorly impressed or absent elsewhere. Medially with random, subequally spaced subcircular, small punctures and associated short setae, separated by 1-2 puncture widths. Post coxal lines extending nearly to posterior edge of V1, stopping about two-three puncture widths before edge; somewhat roughly sculptured anteriorly (forming small irregular groove just posterior to coxal cavity), but with more obvious microsculpture medially, with 2-5 punctures and associated setae. Interior line extending at about 10-15° angle to body line; outer angle with a gentle 35-45° curve approaching interior line. Punctures laterally on V1 slightly larger, more oval, more dense, separated by 1/2 - 1 puncture width on average, but with punctures not occupying anterolateral and posterior edges of latero-triangular area set off by coxal lines. Posterior edge V1 with impunctate zone also without microsculpture medially and poorly impressed microsculpture laterally. V2-V4 with single row of large subcircular punctures with associated long setae, occupying about 1/3 length of ventrite; punctures slightly smaller medially, occupying ~1/3rd ventrite, laterally only slightly larger. V5 with dense punctation, but only subcontiguous and slightly oval in two obvious areas just laterad of middle, not blending together. Remaining areas of V5 with smaller, subcircular punctures becoming more widely separated laterally and posteriorly. Separated on average 1/2 - 1 length puncture width. Several long, heavy setae present on posterior margin of ventrite around abdominal opening.

Male genitalia. Fitting generic description (Figs. 7.9C, 7.69C)

Female terminalia, genitalia, and ovipositor. Posterior edge of paraproct tergite IX straight across. Tergite IX (paraproct) with truncate apex, broadly rounded corners. (Fig. 7.8C)

Type material. The holotype, a male, is deposited in the UGCA (Fig. 7.73C-E), along with a paratype female collected in the same location, both by Michael D. Ulyshen. Two other paratypes, collected by Daniel Miller, are deposited in the UGCA. All other 14 specimens of this species have been labeled as paratypes, and are from the following museums: 1 CMNH, 1 UMRM, 2 FSCA, 1 NCSU, 4 USNM, 5 TAMU. Detailed locality records available here: **http://symbiota4.acis.ufl.edu/scan/portal/collections/list.php?taxa=Bactridium%20sp.%20a&thes=1&type=1&db=56,114;&page=1**.

Etymology. This species is a patronym in honor of Andrew Delmar Hopkins, whose associate collectors provided the earliest records and some of the only biological information concerning these specimens. It is also intended to honor, in general, the US Forest Service, which has employed A.D. Hopkins, W.F. Fiske, D.R. Miller, and M.D. Ulyshen, who collected and deposited voucher specimens of this species, and without whom there would be almost no specimens or biological information available for this rarely collected species. In addition, many of the few specimens of this species were collected in designated United States National Forests, which promote and preserve biodiversity and biodiversity research in the United States.

Distribution. Fig. 13. Primarily southern United States, perhaps greater, known from the following states: United States: GA, LA, MO, NC, OK, SC, TX All databased records available here:

http://symbiota4.acis.ufl.edu/scan/portal/collections/list.php?taxa=Bactridium%20sp.%20a&thes=1&type=1&db=56,114;&page=1

Life history and collecting. Little is known of this, the rarest of North American *Neobactridium* species. The holotype and one paratype were collected from an emergence trap of *Pinus taeda* logs that had been recently burned. Four specimens (part of the Hopkins collection at the USNM) were hand collected from galleries of *Scolytus* Geoffroy under hickory and chestnut bark that had been burned by fire. It's notable that these two series were both collected from logs that had been recently burned (albeit lightly). One specimen was collected at a blacklight, and two more were collected via berlese extraction from forest leaf litter and dead wood. This beetle may be fungivorous or predaceous based on the above information, and may be linked with burned wood, possibly making this a threatened species in areas that are not under conservation fire regimes.

Discussion. This species is likely most closely related to *N. striolatum*, but its exact affinities are uncertain. The distribution is so far limited to the southern United States, but may be larger when more specimens are collected.

***Neobactridium striolatum* (Reitter, 1872)** (Figs. 7.1D, 7.2D, 7.73F-I, 7.74, 7.75)

Rhizophagus striolatus Reitter, 1872:38. Type locality: none given. Type repository: MNHN. Reitter 1872: 38.

= *Rhizophagus corpulentus* Reitter, 1872:35. Type locality: “America boreale”. Type repository: BMNH. NEW COMBINATION

= *Bactridium convexulum* Casey, 1916:97. Type locality: “Michigan”. Type repository: USNM. NEW COMBINATION

= *Bactridium hudsoni* Casey, 1916:98. Type locality: “Catskill Mountains, New York”. Type repository: USNM. NEW COMBINATION

= *Bactridium obscurum* Casey, 1916:99. Type locality: “Indiana”. Type repository: USNM. NEW COMBINATION

Diagnosis. The lack of lateral elytral striae formed from united punctures (Fig. 7.57A-C); head, pronotum, and elytra concolorous or with elytra lighter than head and pronotum; incomplete mesocoxal bead (Fig. 7.43A-C); and longer than wide, subcontiguous punctures on ventrite V (not as long as *N. californicum*) (Fig. 7.67A-C) will serve to distinguish this species. This is the most variable of North American *Neobactridium*, and varies considerably in head and pronotal width.

Redescription. **General**. Length 1.5-2.6 mm. Width 0.50-0.80 mm. Body approx. 2.80 times as long (measured from tip of elytra to tip of frons) as wide (measured approx. midpoint of elytra at widest point). Body flattened-subcylindrical, subparallel. Body color varies from yellow to reddish-brown, orange-brown, to dark brown, although usually a dark red-brown (as in lectotype). Body usually unicolorous, although some biotypes have the elytra paler than pronotum and head (but never the reverse). Dorsal surface subglabrous, moderately shiny; minute hairs visible arising from punctures, some specimens slightly more hairy.

Head. Dorsal surface (Figs. 7.17A-C, 7.19A-C, 7.21A-C, 7.86A-C): Head maximum width varies, but slightly less wide than pronotum. Head length/width ratio avg. 0.75 (male), 0.75 (female), range (0.69-0.84). Vertex with separated punctures (greater than width one puncture) smaller than those closest to eyes, which are larger and closely approximate or separated by half a puncture width. Most punctures on vertex and behind longer than wide, larger, more closely approximate laterally. Vertex with isodiametric microsculpture. Setae arising from punctures approx. equal to width of puncture on vertex, length gradually increasing towards distal end with a corresponding decrease in puncture size. Punctures least dense, at middle of head, between eyes. Posteriorly, extending laterally across head behind vertex, more dense puncture area present, punctures sub-circular. Clypeal area with numerous long setae and correspondingly smaller, circular punctures than those on vertex. Row of subcontiguous punctures present proximal to eyes. Eyes prominent, protuberant, about 0.44 (males), 0.47 (females) length/width ratio (range 0.36-0.64). Longitudinal length ~1.6-1.7x scape length. Eye width about 0.9-1.0 width of scape. Anterior margin of clypeus broadly rounded.

Ventral surface (Figs. 7.26A-C, 7.29A-C): Pregular area punctured and setose, with some visible, but poorly impressed microsculpture between punctures. Anterior region with united punctures forming shallow groove posterior to submentum. Pregular region sparsely, evenly punctured. Punctures evenly spaced, only increasing in size slightly laterally. No punctures loosely bordering lateral edge of pregular region. Male subgenal pore present, located latero-posteriad of mandibular articulation. Submentum about 2.5-3x as wide as deep, with slightly convex posterior edge and straight anterior edge forming mental suture; two large paramedian setae present on submentum, surrounded by 10 smaller setae. Posterior portion with poorly impressed microsculpture.

Lateral surface (Fig. 7. 24A-C): Lateral genal expansion lined posteriorly with subcircular setae, smaller closer to antennae, larger closer to eye.

Antennae (Figs. 7.21A-C, 7.86A-C): Ratio of segment length: 4.5 : 2.4 : 1.6 : 1.1 : 1.0 : 1.0 : 1.1 : 1.2 : 1.6 : 5.0; terminal club segment longer than broad (~1.1). Red-brown, slightly paler than head. Extending about 1/4-1/3rd past anterior of thorax when posteriorly extended.

Prothorax. Dorsal surface (Figs. 7.31A-C, 7.32A-C, 7.34A-C): Wider than long, subquadrate. Males avg. 0.85 L/W (range 0.76-0.92). Females avg. 0.85 L/W (range 0.73-0.91). Widest just in front of middle. Anterior edge straight, with slight median emargination. Posterior edge with area behind posterior angles slightly concave. Pronotum narrowly converging posteriorly. Narrow median impunctate zone present, widest in posterior third. Median half of pronotum (disc) with widely scattered subcircular punctures (separated by greater than width of one puncture). Laterally punctures longer than wide, becoming more closely approximate, but still separated by about 1/2 width one puncture, until lateral-most 1/4, where punctures subcontiguous; associated hairs longest laterally. Base of pronotum with slightly depressed zone. Pronotal lateral carinae smooth with four-five minute denticles posteriorly, each with long seta. Outer border of disc, just proximal to more densely punctured lateral edges of pronotum with narrow oval-circular impunctate zone. Disc with isodiametric microsculpture, and with abundant minute punctures.

Ventral surface (Figs. 7.36A-C, 7.37A-C, 7.39A-C): Prosternum medially very sparsely punctured (only about 6-8 minute punctures present on median prosternum (well-separated by >width 1 puncture); small area of slightly larger (than median) and wider than long punctures present anterior of procoxal cavities (about 10-13 punctures). Lateral irregular net-like sculpturing somewhat-developed, more individual punctures visible, but still with areas of rough sculpturing laterally, not extending posteriorly much past procoxal cavity. Intercoxal process rounded at posterior corners. Prosternal apophysis with about 15-20 minute setae, with sublateral, poorly impressed postero-medial microsculpture. Prosternum and prosternal apophysis length subequal (apophysis slightly longer, measured from anterior edge of coxal cavity). Apophysis and margin of pronotum posteriorly minutely crenulate, with row of fine setae. Procoxal cavities subcircular, of approx. same width as height, with thin apical lateral extension (perhaps a remnant of the notosternal suture). Procoxal cavity bead without punctures above cavity.

Pterothorax. Scutellar shield (Fig. 7.51A-C) wider than long, with isodiametric microsculpture; broadly rounded, subtriangular. About 12 minute punctures present. Mesoscutal plate with area of large punctures surrounded by rough sculpturing just anterior to scutellar shield.

Mesoventrite (Fig. 7.41A-C) about twice as long as wide (measured from middle mesoventrite and from widest lateral points of mesoventrite. Exposed mesointercoxal process with isodiametric microsculpture forming irregular lateral lines, present anteriorly and posteriorly, although poorly impressed in some larger specimens; two large paramedian sublateral setae present; sublateral rough sculpturing forming aligned groove present anterior to coxal cavities and medially. Medial area of rough sculpturing containing several setaceous punctures. Area hidden under pronotum not examined. Mesepimeron roughly sculptured. Mesanepimeron with several large punctures and setae, also surrounded by rough sculpturing.

Metaventrite (Fig. 7.43A-C) brown throughout. Medially lightly punctured, punctures small, subcircular, widely separated. Anterior area between mesocoxae nearly impunctate, without microsculpture. Anterior edge below mesocoxal cavity with raised bead extending approx. from middle of coxal cavity medially towards meso-metaventral junction, not joining medially. Medially metaventrite with isodiametric microsculpture. Anterolaterally large, subcircular, approximate punctures present (avg. separated by 1/2 - 1 width puncture), becoming smaller and more widely separated posterolaterally. Exposed portion of metepisternum with 1-2 rows of oblong (longer than wide) punctures, which become smaller posteriorly (about 23-29 punctures).

Elytra (Figs. 7.51A-C, 7.53A-C, 7.55A-C, 7.57A-C): 0.37 avg. W/L (males), 0.37 (females)(0.35-0.42 males, 0.36-0.42 females)(L from tip of scutellum to apex of elytron)(W at maximum width). 10-11 rows punctures on each elytron (including inflexed edge) with five rows on the main portion of the elytral disc before the inflexed elytral epipleuron begins; elytral epipleural fold with 5 rows of aligned punctures; 1st five rows on disc forming connected slight grooves in elytra; all five rows contiguous starting at the lateral level of scutellum, except for some occasional breaks lasting less than 2 puncture widths. Elytral interstices smooth, occasionally with one or two interstitial puncture(s), also with isodiametric microsculpture throughout. Apex of elytra usually with punctures confused, not completely reaching apex, except for first row. Rows become slightly wider laterally. Punctures on elytra with associated seta that become longer laterally. Puncture rows more confused laterally, starting with sixth row of punctures on inflexed part of elytron, which may be connected from about 1/3rd length of elytra to apex, or only during apical 1/3 of length. Rows 7-9 (or 7-10) forming series of aligned puncture rows. Row 8 (or 8 and 9) begins about around 1/3 of length of elytron, disappears before apical third. Row 10/11 present just proximal to elytral edge, not forming deep groove or united puncture row, but simply loosely aligned row of smaller punctures and associate setae.

Legs (Figs. 7.45A-C, 7.47A-C, 7.49A-C): Legs concolorous with antennae.

Abdomen. Dorsal view (Figs. 7.59A-C, 7.61A-C): Tergite VII (pygidium) densely punctured, with large, circular-suboval punctures, especially apico-laterally, grouped nearly subcontiguously (separated by 1/2 width of a single puncture), mostly evenly spaced; antero-medially with some smaller punctures; all punctures with long associated setae (approx. 1-3x as long as punctures). Some microsculpture present between punctures.

Ventral view (7.61A-C, 7.63A-C, 7.65A-C, 7.67A-C, 7.68C): Intercoxal process broadly truncate. V1 with microsculpture anteromedially & anterolaterally, sometimes poorly impressed medially. Medially with random, subequally spaced elongate, small punctures and associated short setae, separated by 1-3 puncture widths. Post coxal lines extending nearly to posterior edge of V1, stopping about 1-2 puncture widths before edge; somewhat roughly sculptured throughout (still forming small irregular groove just posterior to coxal cavity), but with some microsculpture medially, with 2-5 punctures and associated setae integrated into rough sculpturing on postcoxal bead.

Interior line of bead extending at about 10-15° angle to body line; outer angle with a gentle 35-45° curve approaching interior line. Punctures laterally on V1 larger (about 2x as large as medially), more oval, more dense, separated by 1/2 - 1 puncture width on average, but with punctures not occupying anterolateral and posterior edges of latero-triangular area set off by coxal lines. Posterior edge V1 with impunctate zone also without microsculpture medially and poorly impressed microsculpture laterally. V2-V4 with single row of large subcircular punctures with associated long setae, occupying about 1/3-2/3rds length of ventrite; punctures slightly smaller medially, occupying ~1/3rd ventrite, laterally about twice as long. V5 with dense punctation, but not blending together. Medially with more smaller, subcircular punctures, laterally with oblong, larger (about 2x as large as medially) punctures; separated on average 1/2 - 1 length puncture width. Several long, heavy setae present on posterior margin of ventrite around abdominal opening.

Male genitalia. Fitting generic description (Figs. 7.9D, 7.68C)

Female terminalia, genitalia, and ovipositor. Posterior edge of paraproct doubly emarginate, forming two small paramedian depressions with median narrowly obtuse curve, about half as wide as apex of tergite VIII, or, the same, but median area not pointed, more broadly flat, about as wide as apex of tergite VIII, or not emarginate, broadly rounded, curve encompassing about half of width of tergite VIII. Posterior edge of paraproct tergite IX straight across (Figs. 7.7A, 7.8D)

Type material. *Rhizophagus striolatus* Reitter, 1872. Reitter (1872) described two species from North America. One, *Rhizophagus striolatus* Reitter, 1872, was described without a locality, but Reitter (1876) mentioned that the speices was from

"Canada, Carol. m." The MNHN has a single specimen of this species in Reitter's collection, mounted on a card that is thinly black-bordered (Fig. 7.73F-G). The label of "Texas" matches Grouvelle's handwriting, not Reitter's, but this may have been a specimen seen or determined by Reitter and kept by Grouvelle in his collection, who acquired many of Reitter's specimens (Horn et al. 1990). This specimen has been designated a lectotype, as it is the only specimen found that could be linked to Reitter, and was likely determined by him. It matches his original description, and is **HERE DESIGNATED AS THE LECTOTYPE** for the name *Rhizophagus striolatus* Reitter 1872.

Rhizophagus corpulentus Reitter, 1872. The second species described by Reitter in 1872, *Rhizophagus corpulentus*, was from "America boreale". He attributed the name to Motschulsky "in litt.", but this was never described by Motschulsky, and the name was later attributed to himself (Reitter 1876). The specimen(s) used were from Andrew Murray, whose collection is integrated into the general holdings of the British Museum. The BMNH has two specimens, labeled "corpulentus" and "N. Amer." with the same accession number of 68-106 (Figs. 7.73 H-I, 7.74A-B). The first also has a typical Murray label (Fig. 7.73I, top) (see Horn et al. 1990, Tafel 38:5) that says, handwritten "corpulentus Motsch [crossed out in pencil and written underneath, also in pencil "Reitt."] / nov. spec. / N. America". This specimen, which also has an additional BMNH blue "Syntype" label and is point mounted the body parallel to the point, is **HERE DESIGNATED AS THE LECTOTYPE**. The second specimen, mounted on a black card of unknown material, but without a larger Murray label like the lectotype, is **HERE DESIGNATED AS THE PARALECTOTYPE**. The specimen, a female, is mostly embedded in some sort of glue. Both are conspecific with *Neobactridium striolatum* as defined herein.

These names of *Rhizophagus striolatus* Reitter 1872 and *Rhizophagus corpulentus* Reitter 1872 were simultaneously published, so we invoke the principle of first reviewer (ICZN Article 24.2) and choose *Rhizophagus striolatus* as the senior synonym, making *Rhizophagus corpulentus* Reitter 1872 a junior synonym (NEW COMBINATION) of *Rhizophagus striolatus* Reitter 1872. *Rhizophagus striolatus* Reitter has been used more frequently than *R. corpulentus*, and I prefer to use the more commonly referred to name.

Bactridium convexulum Casey, 1916. Casey's collection in the USNM contains two specimens, both males, both matching his descriptions and the locality (Michigan). The first (Fig. 7.74C-E), is labeled as a holotype (USNM 49193), but this was added later, but it also bears Casey's determination label. It is **HERE DESIGNATED AS THE LECTOTYPE**. The second specimen (Fig. 7.74F-H), bearing a USNM paratype label (convexulum-2 paratype USNM 49193), is **HERE DESIGNATED AS THE PARALECTOTYPE**. I have attached type labels to both.

Bactridium hudsoni Casey, 1916. Casey's collection in the USNM contains a single specimen, a male (Figs. 7.74I, 7.75A), and is considered the holotype since the original description mentions a single male specimen collected in New York (Casey 1916). During the course of study the specimen and point were damaged. The specimen has been remounted on a card, glued with shellac, with the scutellum and left elytron mounted separately from the head, thorax, and remaining body. The original point is included in a genitalia vial beneath the specimen.

Bactridium obscurum Casey, 1916. Casey's collection in the USNM contains a single specimen, a female (Fig. 7.75B-D), that matches the original description and locality, and bears Casey's determination label. The specimen is considered the holotype since a single female specimen was used to describe the species (Casey 1916).

Distribution. Fig. 7.14. Widespread in eastern United States and southern Canada, west to Montana and eastern Texas, south as far south as Guatemala. Records from the following countries, states, and provinces: Canada: British Columbia, Ontario, Quebec; Guatemala: Zacapa; Mexico: Campeche, Yucatan, Tamaulipas; United States: AL, AR, CT, DE, DC, GA, FL, IA, IL, IN, KS, KY, LA, MA, MD, ME, MI, MO, MN, MT, MS, NC, ND, NE, NH, NJ, NY, PA, OH, SC, TN, OK, TX, VA, VT, WI, WV. All databased records available here:

http://symbiota4.acis.ufl.edu/scan/portal/collections/list.php?taxa=Bactridium%20striolatum&thes=1&type=1&db=56,114;&page=1

Life history and collecting. Often collected in the same locality, sometimes even the same series, as *N. ephippigerum*, this species is more rarely collected. However, it too is likely a fungus feeder. Gut dissections of some specimens from Montana revealed the presence of stromatic tissue and spores. It is usually collected under bark in association with rotting hardwood logs, similarly to *N. ephippigerum*. It may feed on a different group or ecotype of fungus, or specialize in some other way. More investigation is warranted.

Specimens have been collected directly from under bark, but also passively using UV and mercury vapor lights, bottle traps with fermenting fruit, fermenting sugar traps, Lindgren funnel traps, flight intercept traps, sifting leaf litter, berlese extraction, malaise traps, canopy traps, molasses traps, pitfall traps, banana trap, fogging fungusy logs, and rearing traps.

Specimens have been collected from or in association with the following taxa: *Acer saccharum*, *Carya, Castanea dentata* (Marshall)*, Celtis occidentalis, Fagus, Gymnocladus dioicus, Kretzschmaria deusta* (Hoffmann) (Bertone, personal communication)*, Morus, Platanus occidentalis, Polyporus squamosus* (Hudson)*, Quercus alba* L.*, Q. macrocarpa, Salix* L.*, Ulmus.*

One of specimens imaged in ESEM had an abundant covering of mites (Fig. 7.70), which occasionally occurs on specimens of this genus. The mites are not identified, so it is unknown if they are parasitic or commensal, but the dense covering suggests they may be harming the host, if simply from the weight and numbers attached to this specific specimen.

Discussion. This species is the second most commonly collected in North America, and the most difficult to characterize morphologically. This species may yet represent a species complex, as several different biotypes of it seem to exist. However, even with SEM, genitalia dissections, and external morphology, reliable species-level diagnostic characters to separate them were not found. Many putative characters turned out to be extreme ends of variable characters. The amount of variation in body ratios is comparable to that of *N. ephippigerum*, so it is not unreasonable to expect a similar amount of intraspecific variation. *N. striolatum* exhibits similar amounts of pronotal and head width variation, and like *N. ephippigerum*, this could be subject to diet-related expression or sexual selection.

The color patterns in this species are highly deceptive. While many specimens are typically unicolorous, some are much darker in the head and pronotum, with lighter elytra, which have variable degrees of coloration and infuscation. The midwestern United States, in particular, has many examples of atypical coloration. One particular morph of this species, which I call the “Montana” biotype, has a dark brown head and pronotum with reddish-orange elytra, some of which even having a hint of infuscation on the apices of the elytra, mimicking the coloration of *N. ephippigerum*. It also differs in some minor ways, but overall falls within the normal variation of this species.

The species described by Casey (1916) seem to be extreme examples of this species. *B. obscurum* is a good example of a narrow specimen, without the wider head and prothorax. *B. convexulum* is the opposite extreme, possessing a wide head and pronotum and slightly more pronounced and fused punctures.

Possible new species. We also discovered a morphotype that we hesitate to assign to any currently assigned species or describe as a new species due to lack of additional material. Only a few specimens were found, and they may lie within extreme intraspecific variation. We refer to this as *Neobactridium* morphotype 1, and SEMs taken can be found on the same plates as *N. striolatum*. (e.g. Fig. 7.67D)

Morphotype 1. United States: Maryland: Montgomery Co.: Potomac: 25 Sept. 1973: W. E. Steiner (4 USNM); United States: Vermont: Bennington: Manchester: evening flight (1 UVCC); United States: Vermont: Bennington: East Dorset: fungus etc. at base of dead tree; Berlese funnel (1 UVCC).

***Crine* Pascoe 1863** - type species *Crine cephalotes* Pascoe 1863

= *Leptipsius* Casey 1916 - type species *Monotoma striata* LeConte 1858 NEW COMBINATION

Adult Diagnosis. Within the Monotomidae, *Crine* is characterized by the following character states (Bousquet 2003; this paper): antennal club 2-segmented (seemingly 1-segmented); heading with a constriction behind the eyes (and therefore with a distinct temple) (Figs. 7.80 - 7.85); head without antennal grooves; in males, possessing a modified pore on the boundary of the subgenal brace and the submental suture bearing longer, closely packed setae; procoxal and mesocoxal cavities moderately-widely separated; elytral disc with punctures arranged in longitudinal rows; coxal bead on first abdominal ventrite triangularly produced, reaching past mid-point of ventrite; first abdominal ventrite with two paramedian pores bearing cluster of much longer, stouter setae (Fig. 7.85E), or not sexually modified; abdominal ventrites II-IV with small irregularly placed punctures or with single row of regular punctures.

The currently described species of *Neobactridium* and *Leptipsius* were studied and reassigned to genus considering the definition of *Leptipsius* provided by Bousquet (2003) and Sen Gupta (1988). However, in reassigning *Crine cephalotes* Pascoe 1863 to *Leptipsius*, the generic name *Crine* became the oldest available name for species previously placed in *Leptipsius*. Therefore, *Leptipsius* Casey 1916 is a junior synonym NEW STATUS of *Crine* Pascoe 1863 NEW STATUS, resulting in the combinations listed below.

***Pycnotomina* Casey 1916** - type species *Bactridium cavicolle* Horn, 1879:267

Distribution: Fig. 7.15

Adult Diagnosis. Within the Monotomidae, *Pycnotomina* is characterized by the following character states: antennal club 2-segmented (seemingly 1-segmented); heading lacking a constriction behind the eyes (and therefore lacking a distinct temple); head without antennal grooves; in males, possessing a modified pore on the boundary of the subgenal brace and the submental suture bearing longer, closely packed setae; pronotum transverse (avg. 0.75, range: 0.72-0.80), with central depressed region and lacking microsculpture (Fig. 7.30D); procoxal and mesocoxal cavities moderately-widely separated; elytral disc with punctures arranged in longitudinal rows; coxal bead on first abdominal ventrite triangularly produced, reaching past mid-point of ventrite; first abdominal ventrite lacking of sexual modification; abdominal ventrites II-IV with a single row small circular punctures arranged in distinct rows (Fig. 7.66D).

Pycnotomina is currently a monotypic genus, with only a few characters that separate it from the currently defined limits of *Neobactridium*. It may belong in that genus, but without a rigorous phylogenetic analysis or concrete apomorphies, subsuming *Pycnotomina* within *Neobactridium* cannot be justified.

7.5 Discussion of phylogenetic relationships

Following the redescription of the species above, a discussion of the relationships of *Neobactridium* and putatively related taxa is warranted. Firstly, within *Neobactridium*, the North American species seem to form a monophyletic unit; they share the following synapomorphy: first five elytral striae with united punctures from scutellum to just prior to apex of elytra. The Neotropical species of *Neobactridium* not covered in this revision vary in the form of their elytral striae, either some with no united puncture striae, some with only partial united puncture striae, and some with only one striae not formed from united punctures. Interestingly, *Pycnotomina cavicolle* has many features of that Neotropical group, as it lacks the united puncture striae on the elytral disc. The North American species have not been subjected to a phylogenetic analysis yet, and genetic information would add tremendously to the knowledge of this group, especially informing about species boundaries and sister-group relationships.

Based on a preliminary morphological phylogenetic analysis of Monotomidae (McElrath, unpublished data), the genera of *Crine*, *Neobactridium*, and *Pycnotomina* form a monophyletic unit within the Europini. Supporting this monophyly were a few characters: two-segmented antennal club (appearing one-segmented), widely separated procoxal and mesocoxal cavities, and a broadly truncate or broadly rounded abdominal intercoxal process. During the course of this study, we discovered another unifying character: males of *Leptipsius, Neobactridium,* and *Pycnotomina* all possess a lateral subgenal pore filled with long, densely packed setae (Figs. 7.25-7.27). These characters are also true of Neotropical representatives for each of these genera. This character was previously unknown prior to ESEM imaging conducted during the course of this study. Numerous other North American genera, such as *Europs*, *Rhizophagus*, and *Monotoma* lack this character. Studies of non-North American genera may reveal that the subgenal pore delimits a larger clade of genera, potentially recognizable as a new tribe.

Other Old World genera may also be related to the above three taxa. *Mimemodes*, an Old World genus, closely resembles *Neobactridium* and *Crine* in many ways, sharing the two-segmented antennal club (appearing one-segmented), while still maintaining its own synapomorphies, such as a post-antennal ridge and a row of sexual setae in males (Sen Gupta 1976). Several other Indian genera have been proposed by Sen Gupta and others to be closely related to *Neobactridium* and *Crine* (Sen Gupta 1976, 1988; Sen Gupta & Pal 1995; Pal 1996), such as *Indoleptipsius* Pal, *Malabica* Sen Gupta, and would add to that several other genera, such as *Tarunius* Sen Gupta, *Kakamodes* Sen Gupta and Pal, and *Barunius* Sen Gupta and Pal. The Indo-Malaysian tropics also harbor numerous monotypic groups, or undescribed species that look superficially similar to *Neobactridium* (Fig. 7.79H-I). All are potentially related to *Neobactridium*, *Crine*, and *Pycnotomina,* and should be represented in any phylogenetic analyses.

7.6 Key to *Neobactridium* and *Pycnotomina* of North America, north of Mexico

1 — First five elytral puncture rows (those on elytral disc) forming distinct linear striae formed from the union of punctures (Figs. 7.52 A-C, 7.53), pronotal disc without large central depression (Figs. 7.30A-C, 7.31) 2

1” — None of first five elytral puncture rows (those on elytral disc) forming distinct striae (Fig. 7.52D), pronotal disc with large central depression (Fig. 7.30D) .... *Pycnotomina cavicolle*

2 (1) — Elytral epipleural fold with 6-7 rows of contiguous punctures, forming sinuous lines that look like wrinkles (Fig. 7.56B). All punctures subcontiguous, epipleural

fold highly sculptured; head and thorax dark red-brown; elytra orange-brown with infuscate tip (Figs. 7.1B, 7.2B) ……………….. *Neobactridium ephippigerum*

2” — Elytral epipleural fold with maximum 4-5 rows of punctures, some of which are highly reduced and only present medially (Figs. 7.56A&C, 7.57); maximum one puncture row (one on fold inflection) forming a stria, but not complete, and not formed from wide, subcontiguous punctures; coloration variable, either unicolorous or as above (Fig. 7.1A&C-D) …………………………………………. 3

3 (2”) — Punctures on ventrites 2-4, small, circular, occupying at most 1/2 of length of ventrite in length, usually only about 1/3rd (Fig. 7.64C). Thorax and head (or sometimes just head) red-brown, with dark brown-black elytra; body strongly convex (Figs. 7.1C, 7.2C)………………..………………..…………….. *N. hopkinsi*

3” — Punctures on ventrites 2-4, larger, circular-oblong, occupying at least 1/2 of length of ventrite, usually about 2/3rds (Figs. 7.64A-B, 7.65) Thorax and head either unicolorous with elytra or darker than elytra, never with elytra darker than head and pronotum; body convex-flattened ………………………………………. 4

4 (3”) — Head and thorax lighter red-brown, elytra orange-brown with infuscate tip (Fig. 7.1A); poorly developed sculpturing on hypomeron (Fig. 7.35A); complete mesocoxal bead (Fig. 7.40A); elongate subcontiguous punctures on ventrite 5 (Fig. 7.66A); southwestern United States and northwestern Mexico, east to western Texas ..………….……………..…………….……..………… *N. californicum*

4” — Usually whole body concolorous; occasionally (in midwest and northwest portion of distribution) as above (Figs. 7.1D, 7.75B-I; hypomeron strongly sculptured (Fig. 7.36A-C); incomplete mesocoxal bead (Fig. 7.41A-C); longer than wide, subcontiguous punctures on ventrite 5, but not as elongate as above (Fig. 7.67A-C); eastern North America, w, west to Kansas and Montana, south to eastern & southeastern Mexico, Guatemala ……………………… *N. striolatum*

7.7 Catalogue of *Crine*, *Neobactridium*, and *Pycnotomina* of the world

List of the described species of *Neobactridium*, *Crine*, and *Pycnotomina* of the world

Crine Pascoe 1863, restored status

(=_Leptipsius_ Casey 1916, new status)

C. adustus (Reitter 1872) **new combination**

C. angulicollis (Reitter 1872) **new combination**

C. angustus (Sharp 1900) **new combination**

C. brevicornis (Sharp 1900) **new combination**

C. *cephalotes* Pascoe 1863 **restored status**

C. cubensis (Chevrolat 1863) **new combination**

C. crassus (Sharp 1900) **new combination**

C. dilutus (Casey 1916) **new combination**

C. eumorphus (Sharp 1900) **new combination**

C. exiguus (Grouvelle & Raffray 1908) **new combination**

C. imberbis (Bousquet 2003) **new combination**

C. insularis (Van Dyke 1953) **new combination**

C. germanus (Sharp 1900) **new combination**

C. quadricollis (Reitter 1872) **new combination**

C. rudis (Sharp 1900) **new combination**

C. striatus (LeConte 1858) **new combination**

***Mimemodes* Reitter 1876**

M. humilis (Grouvelle 1906) **new combination**

M. orientalis (Reitter 1872) **new combination**

M. parvus (Grouvelle 1906) **new combination**

***Neobactridium* McElrath 2017 (replacement name)**

(=*Bactridium* LeConte 1861)

N. atratum (Reitter 1876) **new combination**

N. brevicolle (Reitter 1876) **new combination**

N. californicum (Fall 1917) **new combination**

N. divisum (Sharp 1900) **new combination**

N. ephippigerum (Guérin-Méneville 1837) **new combination**

N. flohri (Sharp 1900) **new combination**

N. fryi (Horn 1879) **new combination**

N. heydeni (Reitter 1872) **new combination**

N. hopkinsi **new species**

N. subtile (Reitter 1872) **new combination**

N. striolatum (Reitter 1872) **new combination**

***Pycnotomina* Casey 1916**

P. cavicolle (Horn 1879)

Catalogue of *Crine*, *Neobactridium*, and *Pycnotomina* of the world

genus *Crine* Pascoe 1863:7 - type species *Crine cephalotes* Pascoe 1863

= *Leptipsius* Casey 1916:93 - type species *Monotoma striata* LeConte 1858

***Crine adustus* (Reitter, 1872)** (Fig. 7.80A-C), NEW COMBINATION

Rhizophagus adustus Reitter, 1872:39. Type locality: “America [Teapa, Mexico (Reitter, 1876)]”. Type repository: MNHN, **LECTOTYPE AND PARALECTOTYPE (Fig. 7.80A-C) HERE DESIGNATED**. Reitter 1872:39-40; Reitter 1876: 299; Horn 1879:265; Sharp 1900: 575; Casey 1916: 93; Bousquet 2003: 133-137.

***Crine angulicollis* (Reitter, 1872)** (Fig. 7.80D-F), NEW COMBINATION

Rhizophagus angulicollis Reitter, 1872:36. Type locality: “Columbia”. Type repository: NHMW, **LECTOTYPE (Fig. 7.80D-F) HERE DESIGNATED**. Reitter, 1872: 36; Reitter 1876: 299; Sharp: 1900: 575.

***Crine angustus* (Sharp, 1900)** (Fig. 7.80G-I), NEW COMBINATION

Bactridium angustum Sharp, 1900:576. Type locality: “Guatemala, Senahu in Vera Paz, Guatemala city”. Type repository: BMNH, **LECTOTYPE AND PARALECTOTYPE (Fig. 7.80G-I) HERE DESIGNATED**. Sharp: 1900: 575; Bousquet 2003: 134.

***Crine brevicornis* (Sharp, 1900)**, NEW COMBINATION

Bactridium brevicorne Sharp, 1900:575. Type locality: “Panama, Bugaba”. Type repository: BMNH. Sharp 1900: 575; Bousquet 2003: 134.

***Crine cephalotes* Pascoe, 1863** (Fig. 7.81A-E), RESTORED STATUS

Crine cephalotes Pascoe, 1863:9. Type locality: “Ega (Amazons) [Brazil]”. Type repository: BMNH, **LECTOTYPE AND PARALECTOTYPE (Fig. 7.81A-E) HERE DESIGNATED**. Reitter 1876: 299; Horn 1879:265-266; Casey 1916: 93-94.

***Crine cubensis* (Chevrolat, 1863)** (Fig. 7.81F-H), NEW COMBINATION

Rhizophagus cubensis Chevrolat, 1863:604. Type locality: “Cuba: Havane”. Type repository: MNHN, **LECTOTYPE AND PARALECTOTYPE (Fig. 7.80A-C) HERE DESIGNATED**. Chevrolat, 1863: 604; Reitter 1876: 299; Horn 1879:265-266.

***Crine crassus* (Sharp, 1900)**, NEW COMBINATION

Bactridium crassum Sharp, 1900:575. Type locality: “Guatemala, Capetillo”. Type repository: BMNH. Sharp 1900: 575-576; Bousquet 2003: 134.

***Crine dilutus* (Casey, 1916)** (Figs. 7.81I, 7.82A-F), NEW COMBINATION

Leptipsius dilutus Casey, 1916:93. Type locality: “Illinois”. Type repository: USNM, **LECTOTYPE AND PARALECTOTYPE (Figs. 7.81I, 7.82A-G) HERE DESIGNATED**. Casey 1916: 93-94; Bousquet 2003: 137.

***Crine eumorphus* (Sharp, 1900)**, NEW COMBINATION

Bactridium eumorphum Sharp, 1900:577. Type locality: “Guatemala, Capetillo, Zapote, Cerro Zunil, Panajachel”. Type repository: BMNH. Sharp 1900: 577; Bousquet 2003: 134.

***Crine exiguus* (Grouvelle & Raffray 1908)** (Fig. 7.82H-I), NEW COMBINATION

Bactridium exiguum Grouvelle & Raffray 1908:58. Type locality: “Trois-Riviéres [Guadeloupe]”. Type repository: MNHN, **LECTOTYPE (Fig. 7.82H-I) HERE DESIGNATED**. Grouvelle & Raffray, 1908:58.

***Crine imberbis* (Bousquet, 2003)** (Fig. 7.83E-F), NEW COMBINATION

Leptipsius imberbis Bousquet, 2003:137. Type locality: “N.Mex: Lincoln Co. Valley of Fire 10 mi. E Carrizozo.” Type repository: CDAE. Bousquet 2003: 137-139.

***Crine insularis* (Van Dyke, 1953)** (Figs. 7.83G-I, 7.84A-C), NEW COMBINATION

Bactridium insularis Van Dyke, 1953:63. Type locality: “Indefatigable Island (Galapagos Islands)”. Type repository: CAS. Van Dyke 1953:63-64.

***Crine germanus* (Sharp, 1900)** (Fig. 7.83A-D), NEW COMBINATION

Bactridium germanum Sharp, 1900:577. Type locality: “Guatemala, Mirandilla”. Type repository: BMNH, **LECTOTYPE AND PARALECTOTYPE (Fig. 7.83A-D) HERE DESIGNATED**. Sharp 1900: 577-578; Bousquet 2003: 134.

Crine quadricollis **(Reitter, 1872)** (Fig. 7.84D-H), NEW COMBINATION

Rhizophagus quadricollis Reitter, 1872:36. Type locality: “Columbia”. Type repository: NHMW, **LECTOTYPE AND PARALECTOTYPE (Fig. 7.84D-H) HERE DESIGNATED**. Reitter 1876: 299.

Crine rudis **(Sharp, 1900)** (Figs. 7.84I, 7.84A-C), NEW COMBINATION

Bactridium rude Sharp, 1900:576. Type locality: “Guatemala, Cubilguitz; Panama, David”. Type repository: BMNH, **LECTOTYPE AND PARALECTOTYPE (Figs. 7.84I, 7.85A-B) HERE DESIGNATED**. Sharp 1900: 576-577.

Crine striatus **(LeConte, 1858)** (Fig. 7.85D-I), NEW COMBINATION

Monotoma striata LeConte, 1858):65 (*Monotoma*). Type locality: “Colorado River, at Fort Yuma”. Type repository: MCZ. LeConte 1861: 86; Reitter 1876: 299; Horn 1879:265-266; Casey 1916: 93-94; Bousquet 2003: 133-137.

Mimemodes **Reitter 1876**

***Mimemodes humilis* (Grouvelle, 1906)** (Fig. 7.79C-E), NEW COMBINATION

Bactridium humile Grouvelle, 1906:122. Type locality: “Ile Key prés Céram [Seram Island, Indonesia]”. Type repository: MNHN, **LECTOTYPE AND PARALECTOTYPE (Fig. 7.79C-E) HERE DESIGNATED.** Grouvelle, 1906:122.

***Mimemodes orientalis* (Reitter, 1872)**, NEW COMBINATION

Rhizophagus orientalis Reitter, 1872:38. Type locality: “Waigow [Waigeo Island, Indonesia]”. Type repository: BMNH. Reitter 1872:38-39; Reitter 1876: 299.

***Mimemodes parvus* (Grouvelle, 1906)** (Fig. 7.79F-G), NEW COMBINATION

Bactridium parvum Grouvelle, 1906:123. Type locality: “Sumatra, Deli [Medan, Indonesia]”. Type repository: MNHN, **LECTOTYPE (Fig. 7.79F-G) HERE DESIGNATED.** Grouvelle, 1906:123.

***Neobactridium* McElrath 2017. Type species *Rhizophagus ephippiger* Guerin-Meneville 1837.**

= *Bactridium* LeConte 1861:86. Type species *Rhizophagus ephippiger* Guerin-Meneville 1837.

***Neobactridium atratum* (Reitter, 1876)** (Fig. 7.76A-B), NEW COMBINATION

Bactridium atratum Reitter, 1876:300. Type locality: “Brasilia”. Type repository: MNHN, **LECTOTYPE (Fig. 7.76A-B) HERE DESIGNATED**. Reitter 1876: 299-300.

***Neobactridium brevicolle* (Reitter, 1876)** (Fig. 7.76C-H), NEW COMBINATION

Bactridium brevicolle (Reitter, 1876):300. Type locality: “Brasilia”. Type repository: MNHN, **LECTOTYPE (Fig. 7.76C-D) HERE DESIGNATED**. Reitter 1876: 299-300.

***Neobactridium californicum* (Fall, 1917)** (Fig. 7.71A-F), NEW COMBINATION

Bactridium californicum Fall, 1917:169. Type locality: “Southern California, Ojai Valley”. Type repository: MCZ. Fall, 1917: 169-170.

***Neobactridium divisum* (Sharp, 1900)** (Figs. 7.76I, 7.77A), NEW COMBINATION

Bactridium divisum Sharp, 1900:574. Type locality: “Guatemala, Zapote”. Type repository: BMNH, **LECTOTYPE (Figs. 7.76I, 7.77A) HERE DESIGNATED**. Sharp, 1900: 574.

***Neobactridium ephippigerum* (Guérin-Méneville, 1837)** (Figs. 7.71G-I, 7.72, 7.73A-B), NEW COMBINATION

Rhizophagus ephippiger Guérin-Méneville, 1837:190. Type locality: “New York (original description: l’Amerique boréale)”. Type repository: MCZ , Neotype (Figs. 7.71G-I, 7.72A).

= *Rhizophagus nanus* Erichson, 1843: 360. Type locality: “Carolina”. Type repository: ZMHB, Lectotype and paralectotype (Fig. 7.72B-F)

= *Rhizophagus erythropterus* Melsheimer, 1844: 109. Type locality: “Pennsylvania. Bank of the Susquehanna”. Type repository: MCZ, Lectotype labels (Fig. 7.72G-H). NEW COMBINATION.

= *Bactridium curtipenne* Casey, 1916:99. Type locality: “Arkansas”. Type repository: USNM. Holotype (Figs. 7.72I, 7.73A-B) NEW COMBINATION

***Neobactridium flohri* (Sharp, 1900)** (Fig. 7.77B-C), NEW COMBINATION

Bactridium flohri Sharp, 1900:576. Type locality: “Mexico, Motzorongo in Vera Cruz”. Type repository: BMNH. Sharp, 1900: 576.

***Neobactridium fryi* (Horn, 1879)** (Fig. 7.77D-H), NEW COMBINATION

Bactridium fryi Horn, 1879:266. Type locality: “Brazil, Rio de Janeiro”. Type repository: MCZ[1], **LECTOTYPE (Fig. 7.77D-H) HERE DESIGNATED**. Horn, 1879: 265-266.

***Neobactridium heydeni* (Reitter, 1872)** (Figs. 7.77I, 7.78A), NEW COMBINATION

Rhizophagus heydeni Reitter, 1872:37. Type locality: “Cuba”. Type repository: MNHN, **LECTOTYPE (Figs. 7.77I, 7.78A) HERE DESIGNATED**. Reitter 1876: 37.

***Neobactridium hopkinsi* new species** (Fig. 7.73C-E)

Neobactridium McElrath. Type locality: “USA, South Carolina, Savannah River Site”. Type repository: holotype: UGCA, paratypes: 3 UGCA, 4 USNM, 1 NCSU, 1 CMNH, 2 FSCA, 1 UMRM, 5 TAMU.

***Neobactridium subtile* (Reitter, 1872)** (Fig. 7.78B-D), NEW COMBINATION

Rhizophagus subtilis Reitter, 1872: 39. Type locality: “Columbia”. Type repository: NHMW, **LECTOTYPE (Fig. 7.78B-D) HERE DESIGNATED**. Reitter 1872: 39.

Neobactridium striolatum **(Reitter, 1872)** (Figs. 7.73F - 7.75I) NEW COMBINATION

Rhizophagus striolatus Reitter, 1872:38. Type locality: none given. Type repository: MNHN, Lectotype (Fig. 7.73 F-G), Reitter 1872: 38.

= *Rhizophagus corpulentus* Reitter, 1872:35. Type locality: “America boreale”. Type repository: BMNH, lectotype (Fig. 7.73 H-I), paralectotype (Fig. 7.74 A-B) NEW COMBINATION

= *Bactridium convexulum* Casey, 1916:97. Type locality: “Michigan”. Type repository: USNM. Lectotype (Fig. 7.74 C-E), paralectotype (Fig. 7.74 F-H) NEW COMBINATION

= *Bactridium hudsoni* Casey, 1916:98. Type locality: “Catskill Mountains, New York”. Type repository: USNM, holotype (Figs. 7.74 I, 7.75 A) NEW COMBINATION

= *Bactridium obscurum* Casey, 1916:99. Type locality: “Indiana”. Type repository: USNM, holotype (Fig. 7.75 B-D) NEW COMBINATION

Pycnotomina **Casey 1916:100. Type species *Bactridium cavicolle* Horn, 1879.**

Pycnotomina cavicolle **(Horn, 1879)** (Figs. 7.4D, 7.5D, 7.7.78E-I, 7.79A-B)

Bactridium cavicolle Horn, 1879:267. Type locality: “Pennsylvania”. Type repository: MCZ. Horn 1879:265-267; Casey 1916: 100-101; Bousquet 2003: 134.

7.8 Acknowledgements

This study was supported by a UGA CURO Research Grant (Olivia F. Boyd & JVM), H.H. Ross Memorial Fund Grant (TCM), Ernst Mayr Travel Grant from Museum of Comparative Zoology at Harvard University (TCM), CanaColl Foundation Endowment

Fund Collections Grant (Y Bousquet & TCM), and a Coleopterists Society Graduate Student Research Enhancement Award (GSREA) (TCM).

Olivia Boyd provided morphometric and illustration assistance in the early days of this project. The authors thanks all of the curators and collection managers who sent specimens for this study from the museums listed above, but would especially like to thank Floyd Shockley, David Furth, Jason Dombroskie, Philip Perkins, Yves Bousquet, Sarfraz Lodhi, Crystal Maier, Luciana Musetti, Norman Johnson, Roger Booth, Michael Geiser, and Max Barclay for their hospitality during collection visits.

Karen McElrath and Terrence McHugh provided databasing and labeling assistance at a critical juncture of this project. John Shields and Georgia Electron Microscopy (UGA) provided invaluable instruction and assistance with the ESEM imaging sessions.

The first author thanks his Ph.D. advisory committee members K.J.K. Gandhi, J.V. McHugh, and K.G. Ross for feedback on this section.

7.9 Tables and Figures

Table 7.1. Morphometrics of *Neobactridium* and *Pycnotomina* species in North America north of Mexico.

Species (sex)	n	Head length/ width ratio	Range	Eye length/ width ratio	Range	Pronotum length/ width ratio	Range	Elytron width/ length ratio	Range
Neobactridium striolatum ♂	22	0.75	0.69 — 0.84	0.44	0.36 — 0.54	0.85	0.76 — 0.92	0.37	0.34 — 0.42
N. striolatum ♀	25	0.73	0.69 — 0.81	0.47	0.41 — 0.64	0.85	0.73 — 0.91	0.37	0.34 — 0.41
N. ephippigerum ♂	25	0.75	0.69 — 0.80	0.44	0.34 — 0.56	0.85	0.82 — 0.89	0.38	0.35 — 0.44
N. ephippigerum ♀	20	0.73	0.69 — 0.78	0.47	0.39 — 0.54	0.85	0.80 — 0.90	0.38	0.36 — 0.41
N. californicum ♂	22	0.74	0.69 — 0.78	0.45	0.39 — 0.53	0.87	0.82 — 0.91	0.37	0.34 — 0.40
N. californicum ♀	31	0.73	0.69 — 0.79	0.45	0.38 — 0.57	0.88	0.85 — 0.93	0.39	0.35 — 0.43
N. hopkinsi ♂	8	0.74	0.71 — 0.76	0.44	0.41 — 0.48	0.80	0.77 — 0.83	0.38	0.35 — 0.42
N. hopkinsi ♀	10	0.71	0.68 — 0.74	0.43	0.38 — 0.48	0.81	0.79 — 0.85	0.39	0.36 — 0.42
Pycnotomina cavicolle ♂	25	0.69	0.66 — 0.74	0.47	0.42 — 0.55	0.76	0.72 — 0.80	0.41	0.38 — 0.44
P. cavicolle ♀	20	0.73	0.69 — 0.77	0.47	0.41 — 0.56	0.74	0.72 — 0.77	0.42	0.39 — 0.45

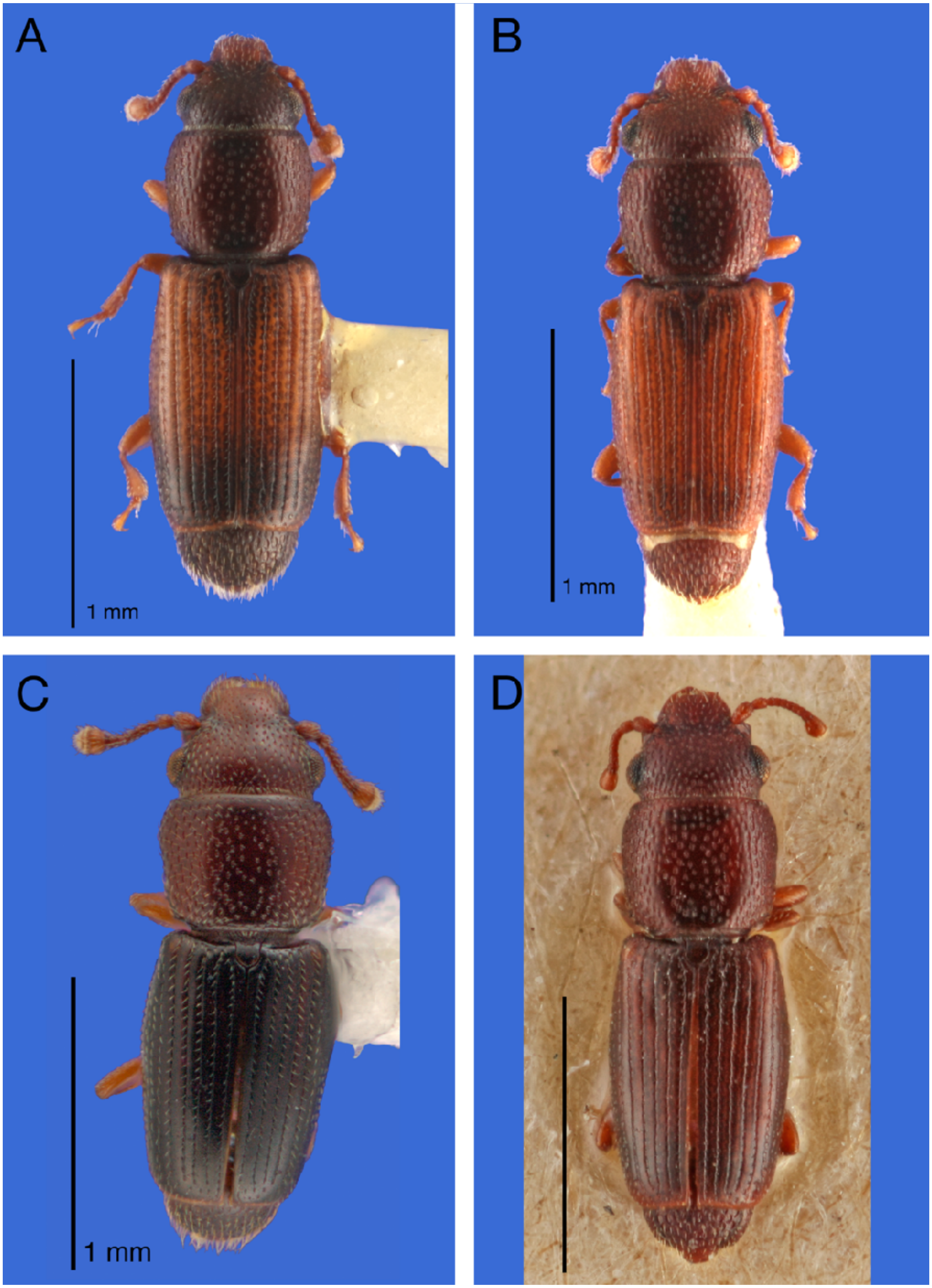

Figure 7.1. Dorsal habitus figures of *Neobactridium* species in North American north of Mexico. A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *N. striolatum*.

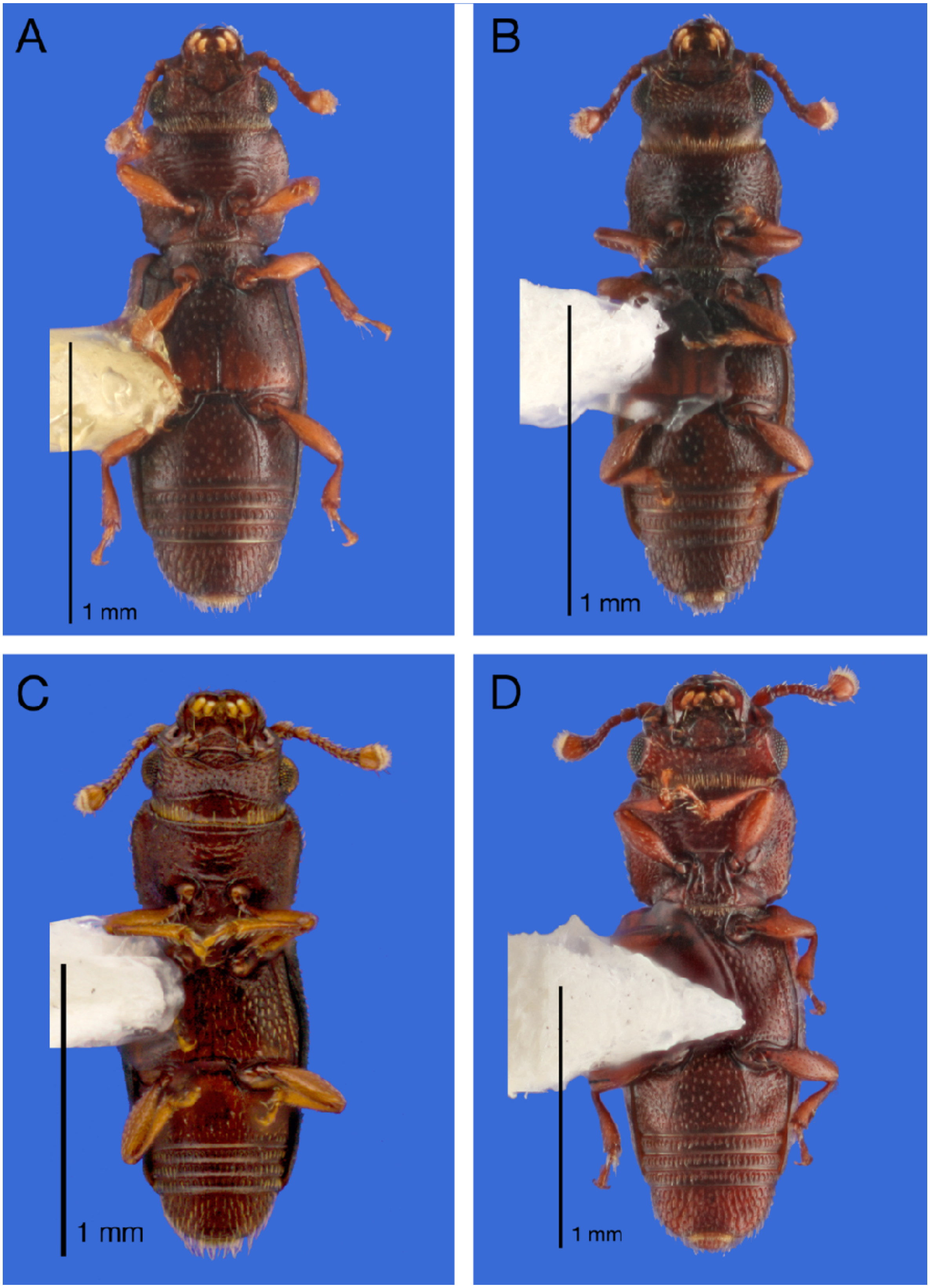

Figure 7.2. Ventral habitus figures of *Neobactridium* species in North American north of Mexico. A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *N. striolatum*.

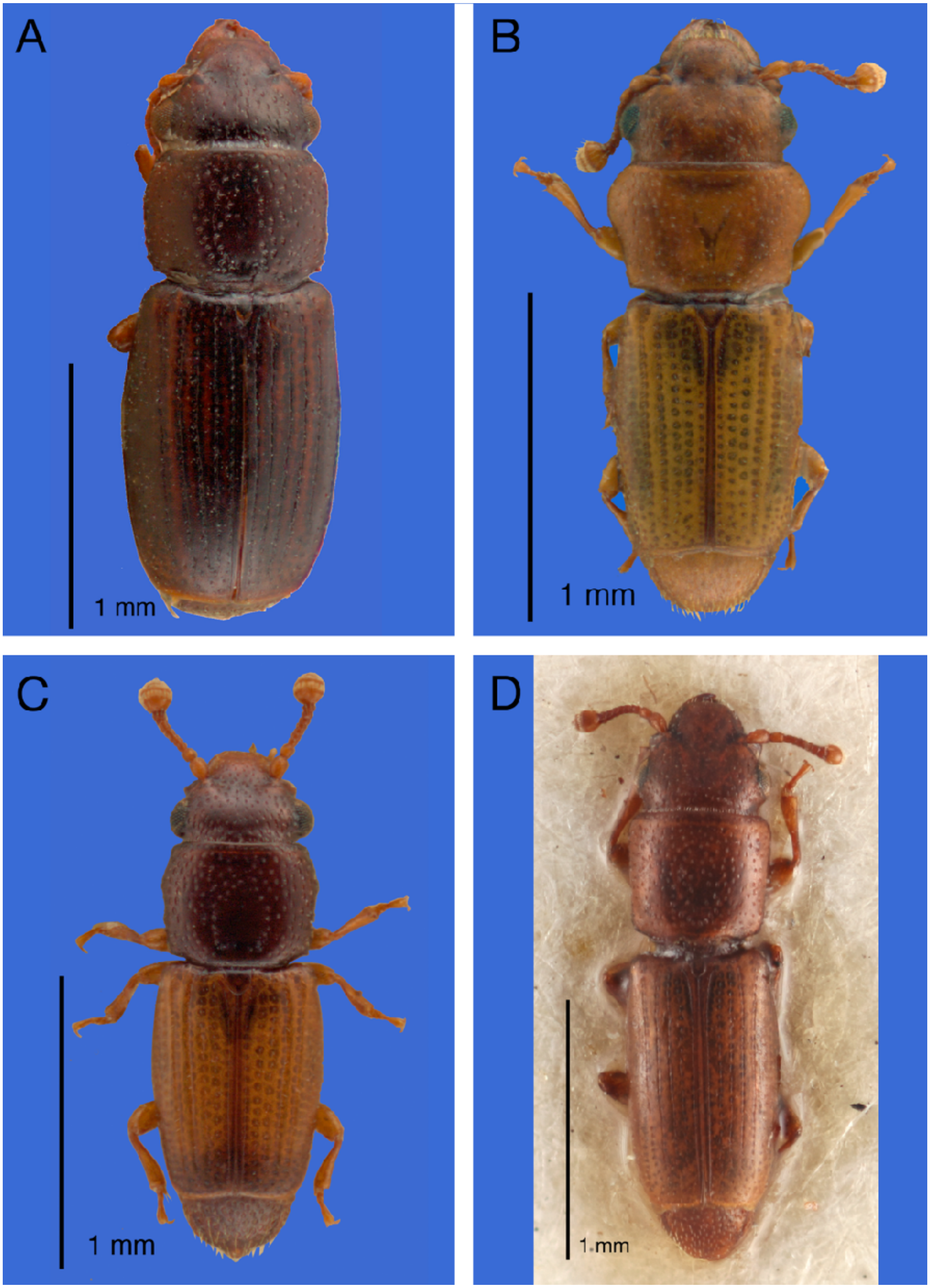

Figure 7.3. Dorsal habitus figures of *Neobactridium* species. A) *N. atratum*, B) *N. brevicolle*, C) *N. divisum*, D) *N. flohri*.

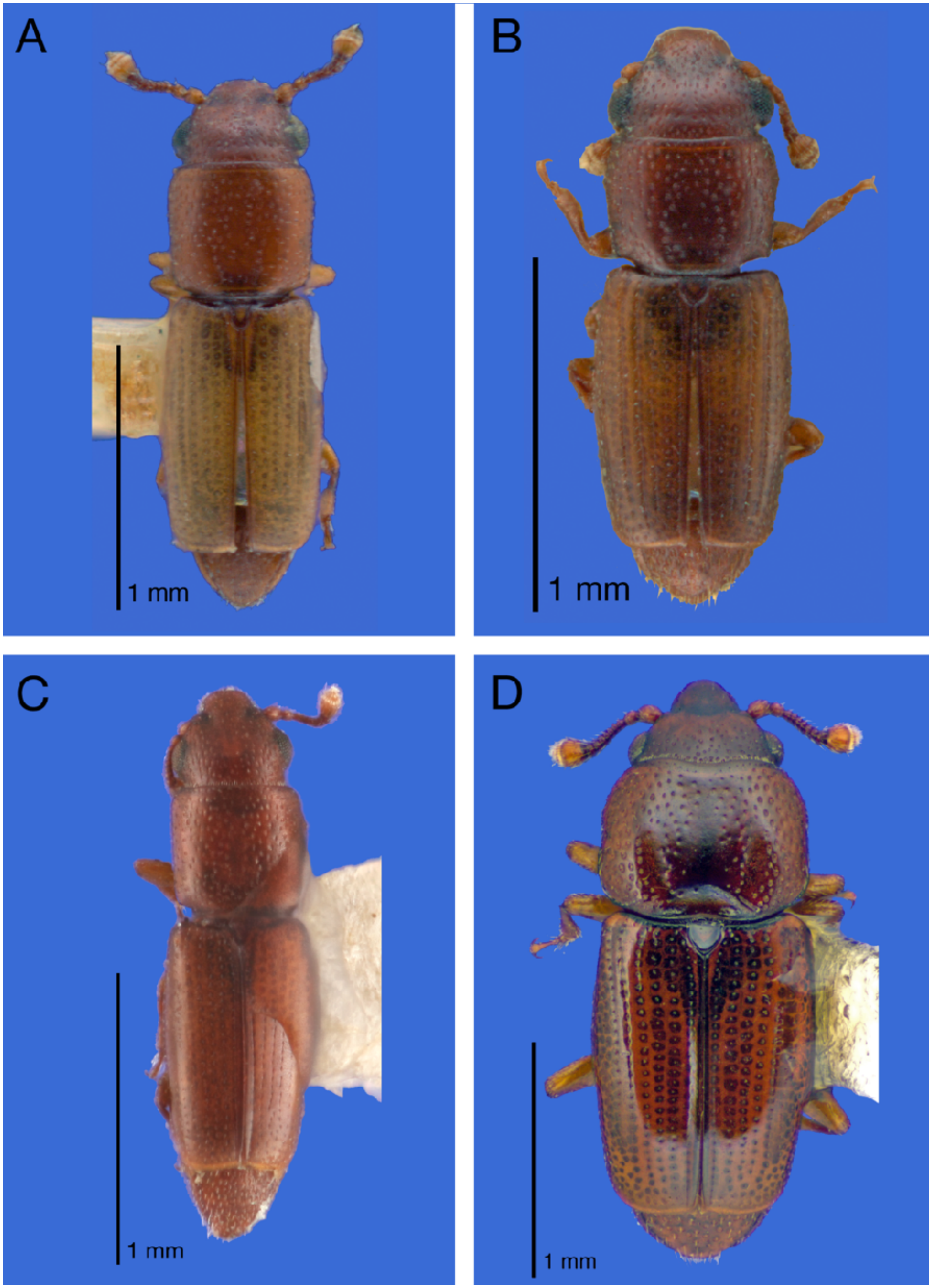

Figure 7.4 Dorsal habitus figures of *Neobactridium* and *Pycnotomina* A) *N. fryi*, B) *N. heydeni*, C) *N. subtilis*, D) *P. cavicolle*.

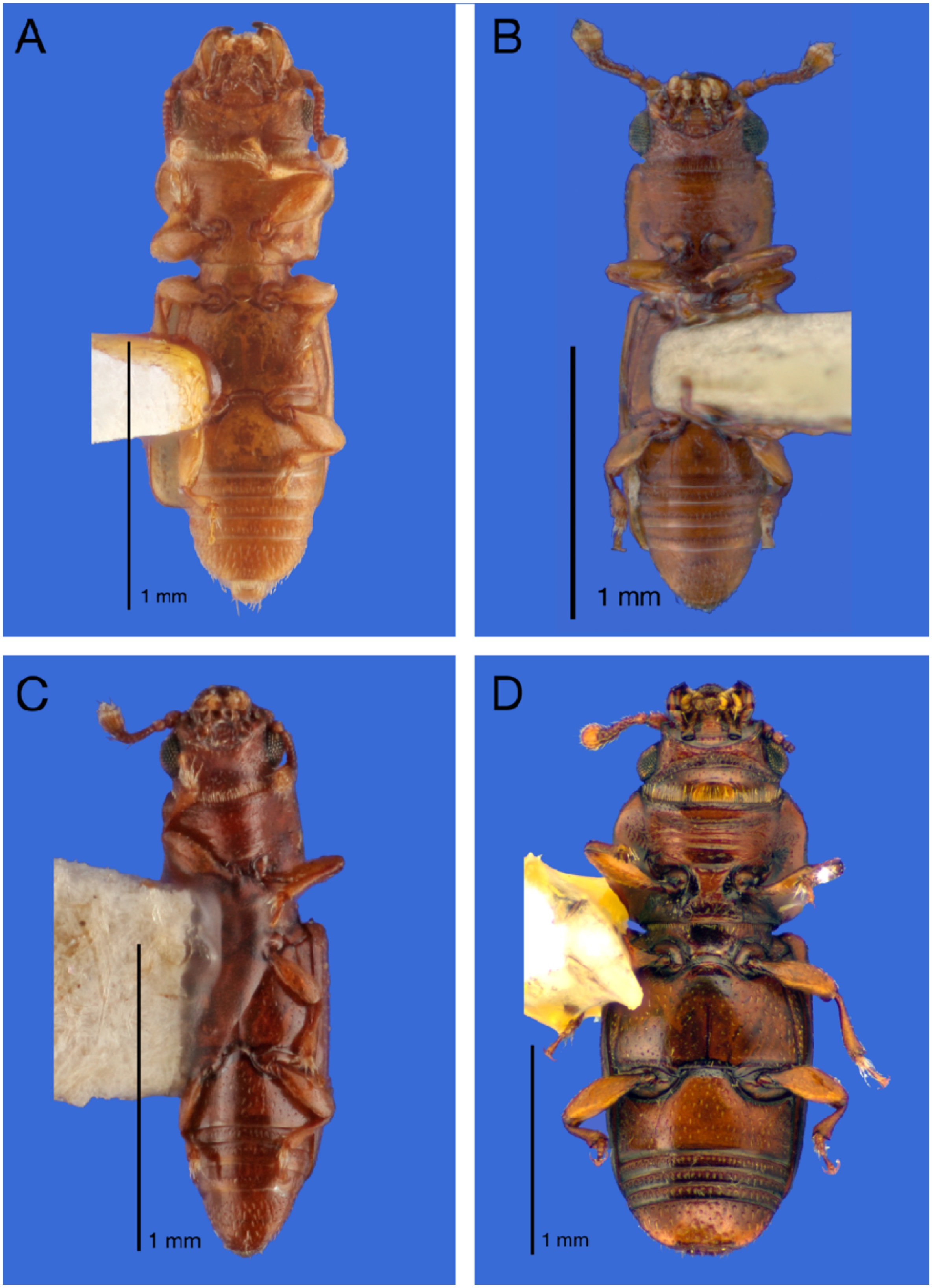

Figure 7.5. Ventral habitus images of *Neobactridium* and *Pycnotomina*. A) *N. brevicolle*, B) *N. fryi*, C) *N. subtilis*, D) *P. cavicolle.*

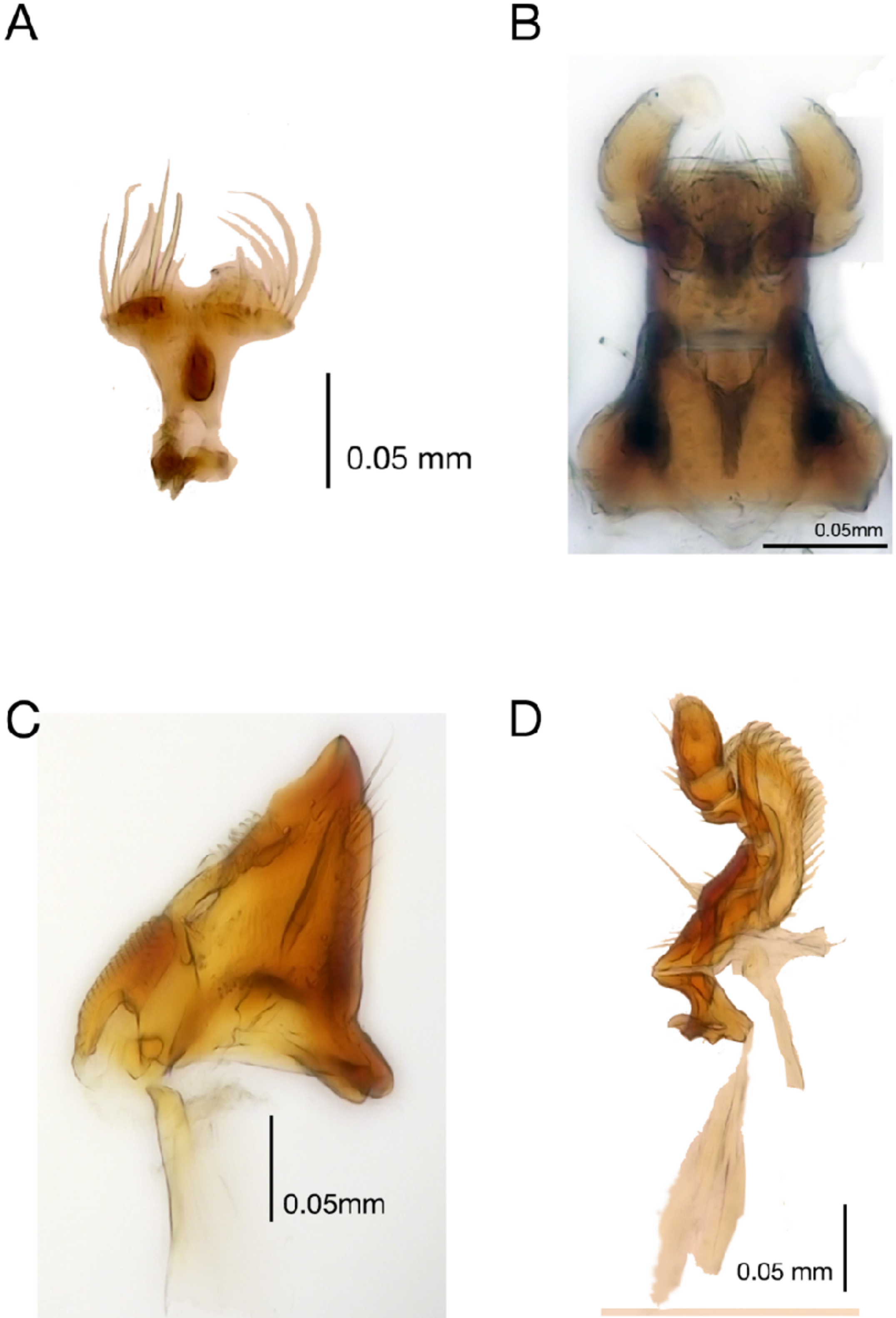

Figure 7.6. Mouthparts of *Neobactridium ephippigerum* A) labrum ventral, slightly damaged, B) labium, ventral, C) Mandible, ventral, D) Right maxilla.

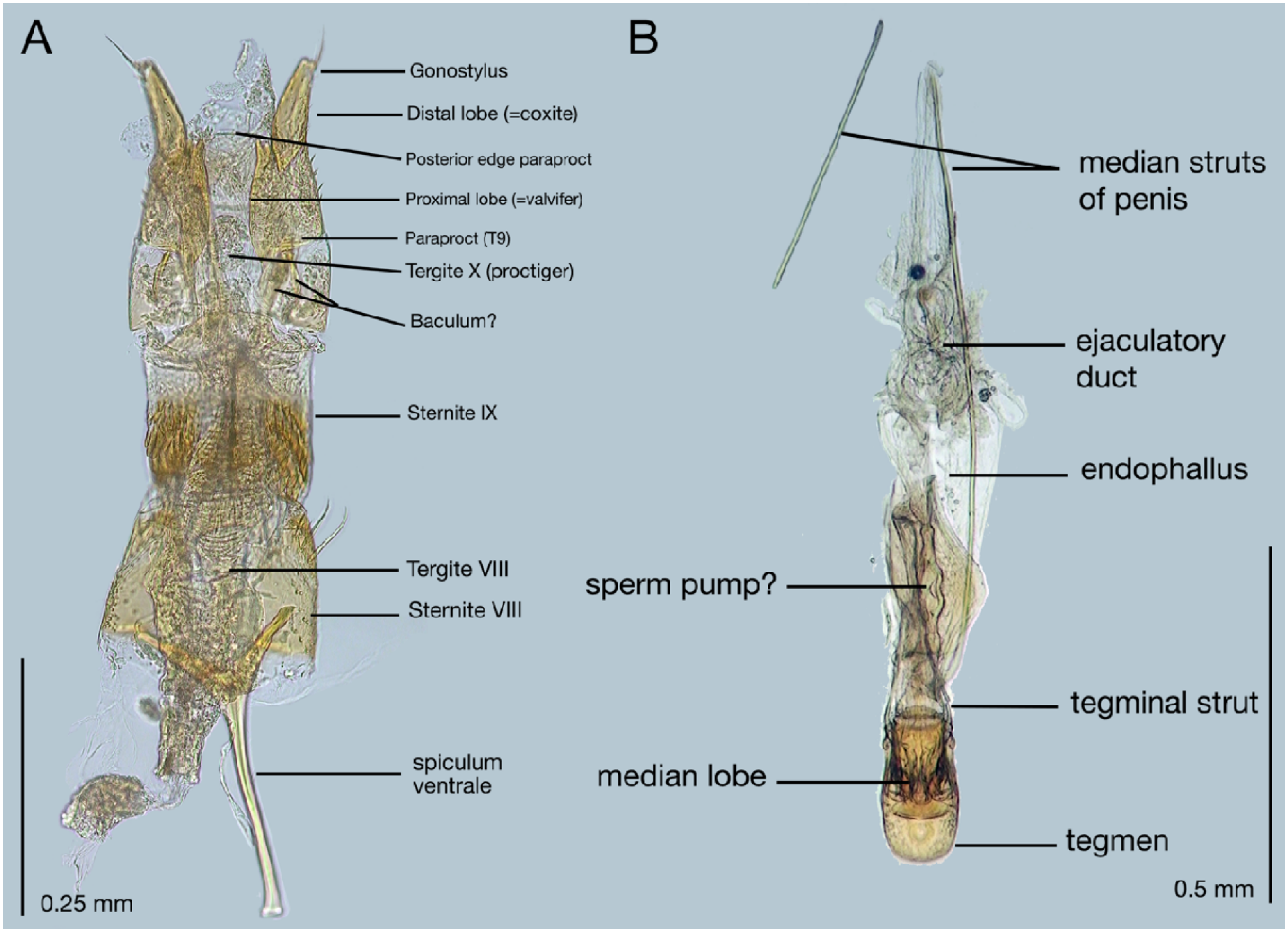

Figure 7.7. Representative genitalia of *Neobactridium*. A) Female genitalia,everted, *N. striolatum* (USA: NE), everted, B) Male genitalia, *N. ephippigerum* (left median strut broken, floating to left)

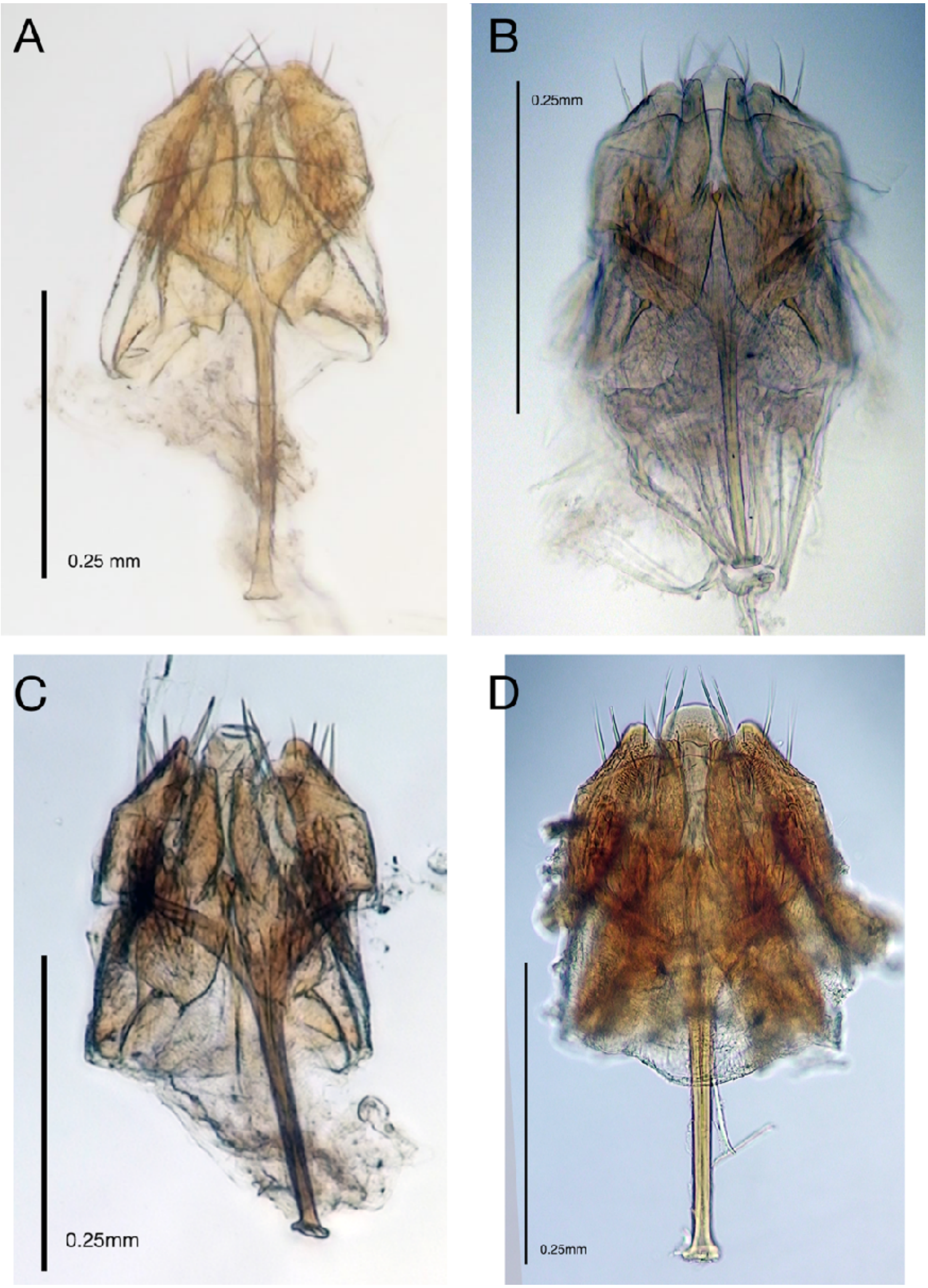

Figure 7.8. Female genitalia (withdrawn): *Neobactridium* species in N. America north of Mexico A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *N. striolatum* (USA:GA).

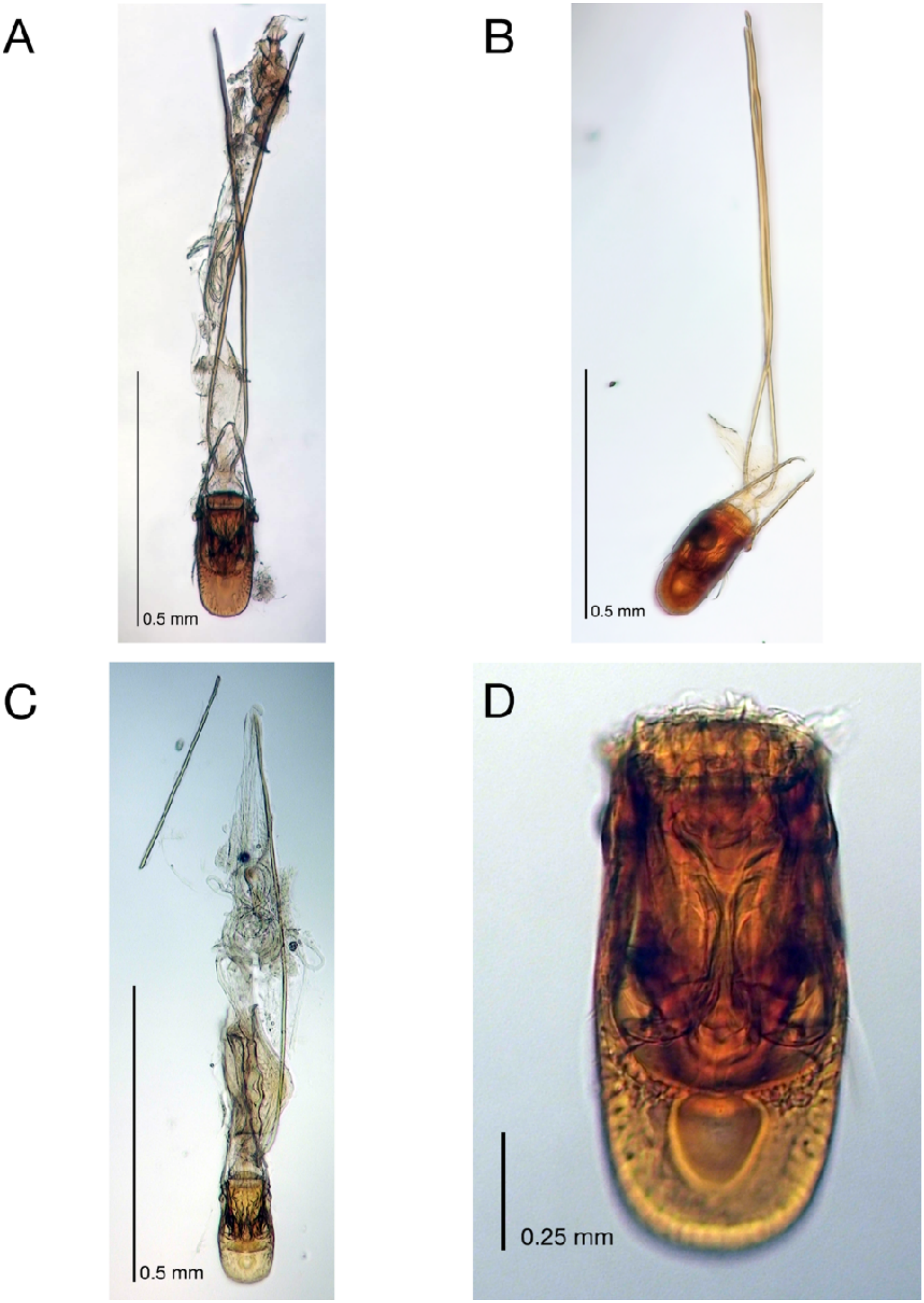

Figure 7.9. Male genitalia (dorsal view): A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *N. striolatum* (just dorsal lobe and tegmen) (USA:GA).

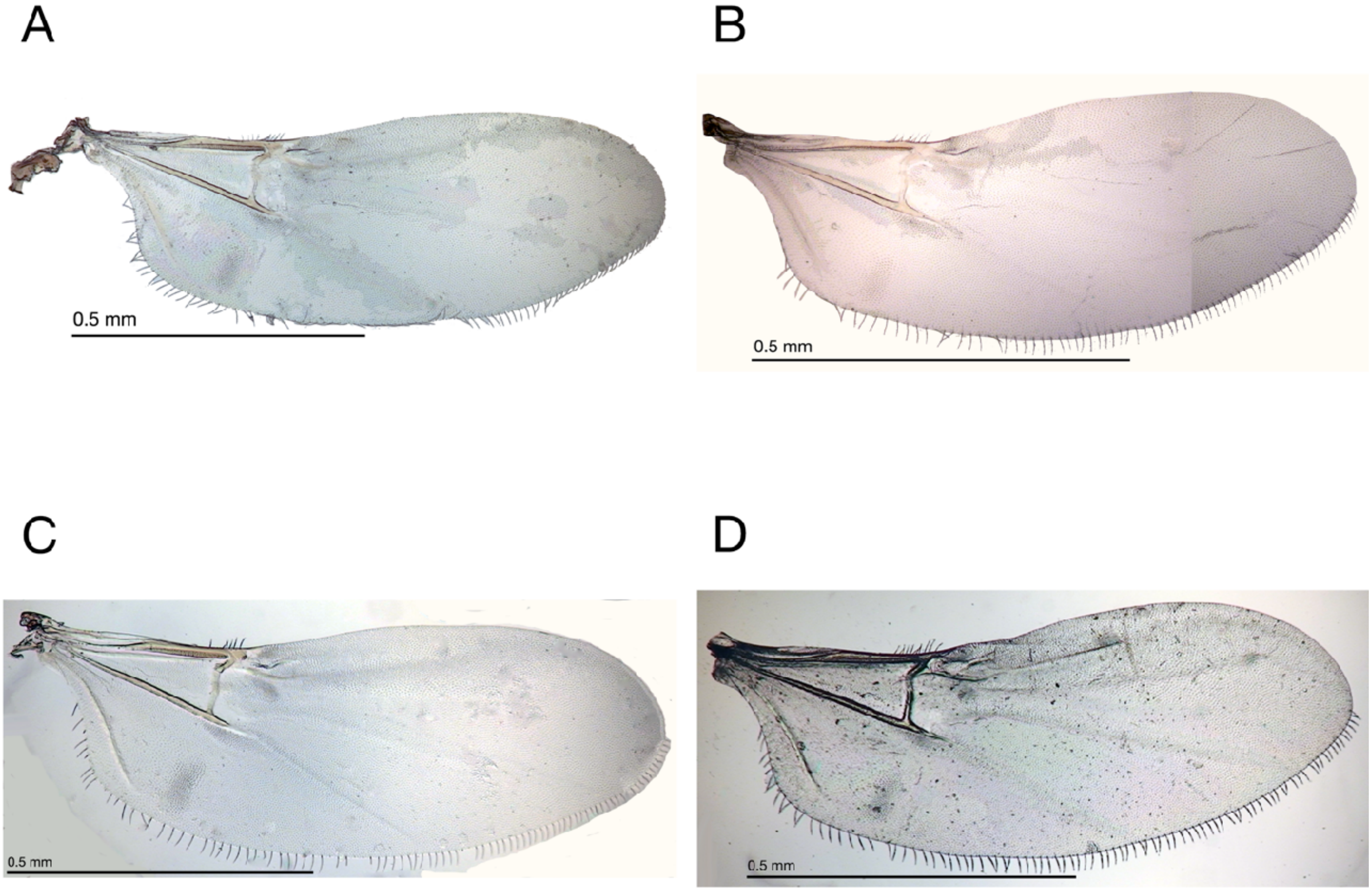

Figure 7.10. Hind wings: *Neobactridium* species in N. America north of Mexico A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *N. striolatum*

Figure 7.11. Distribution map of *Neobactridium californicum* (Fall). Orange dots represent unique localities, and are not indicative of number of records from each locality. Created using GoogleEarth(TM). Species ranges from California east to Texas, where it co-occurs in a narrow area with *Neobactridium ephippigerum*. Specimen records available: SYMBIOTA, KML, CSV.

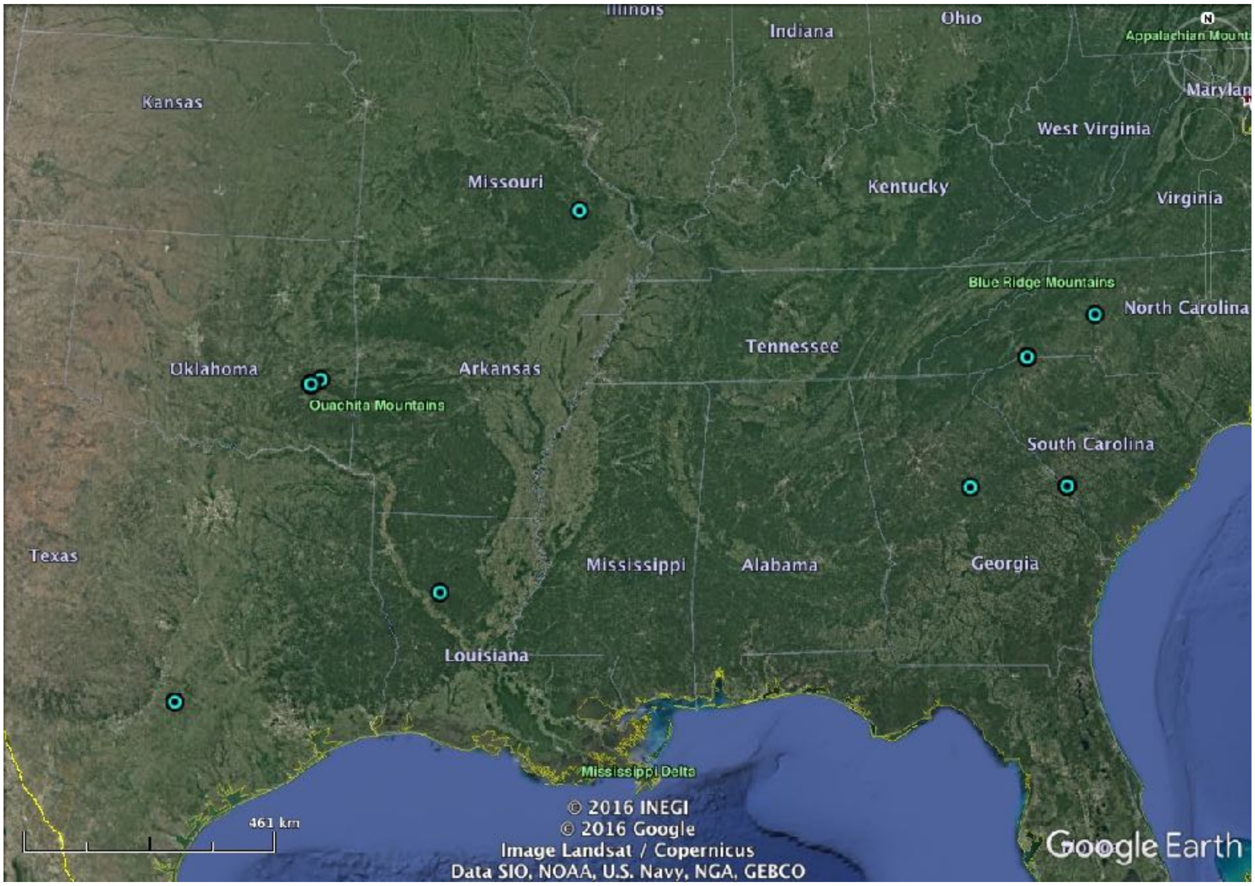

Figure 7.13. Distribution map of *Neobactridium hopkinsi* new species. Blue dots represent unique localities, and are not indicative of number of records from each locality. Created using GoogleEarth(TM). Species occurs in the southern United States (as far north as Missouri), with lots of gaps in distribution. Specimen records available: SYMBIOTA, KML, CSV.

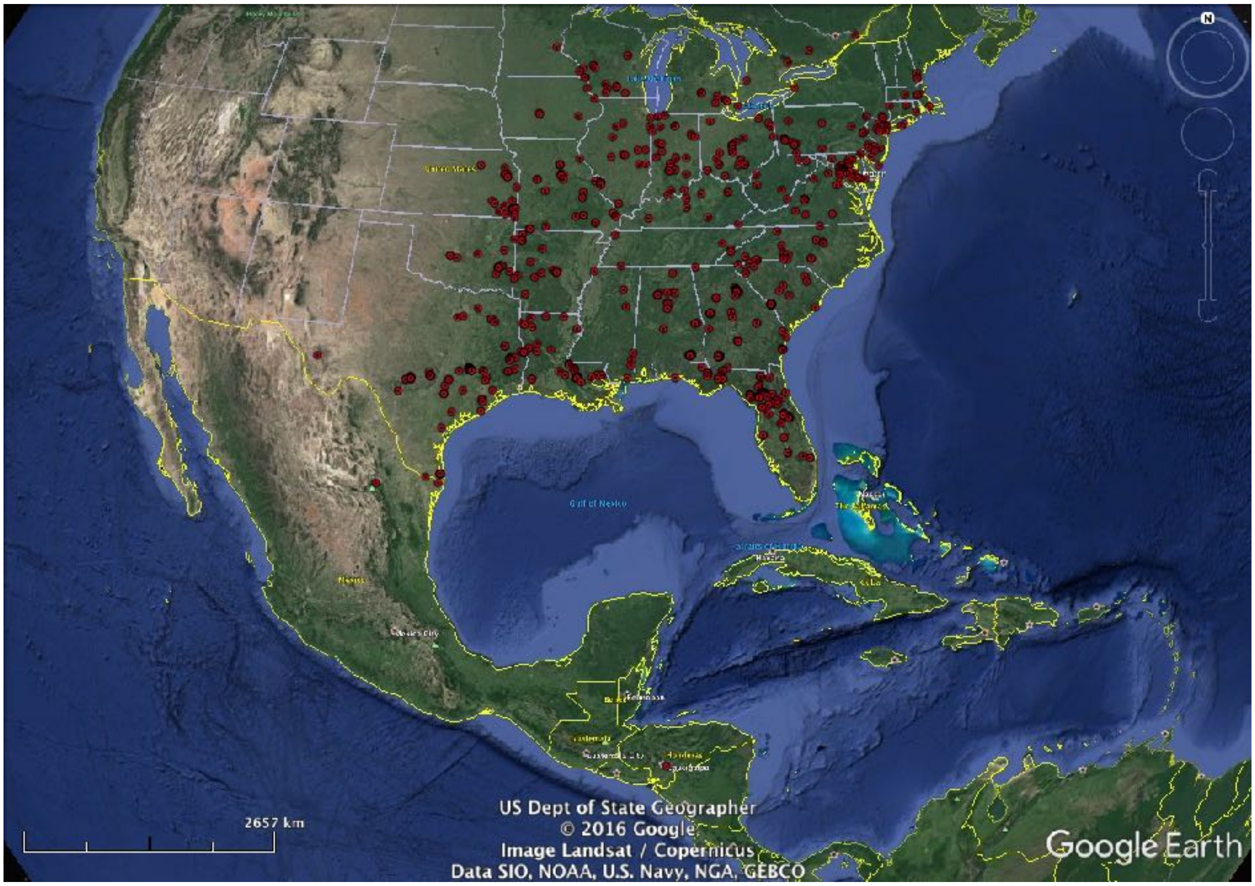

Figure 7.12. Distribution map of *Neobactridium ephippigerum* (Guerin-Meneville). Red dots represent unique localities, and are not indicative of number of records from each locality. Created using GoogleEarth(TM). Species ranges north to southern Canada south to at least southern Texas and Florida, into northern Mexico and perhaps as far south as Honduras (one isolated record from Honduras). From the east coast it ranges west as far as Minnesota in the north to western Texas, where where it co-occurs in a narrow area with *Neobactridium californicum*. Specimen records available: SYMBIOTA, KML, CSV.

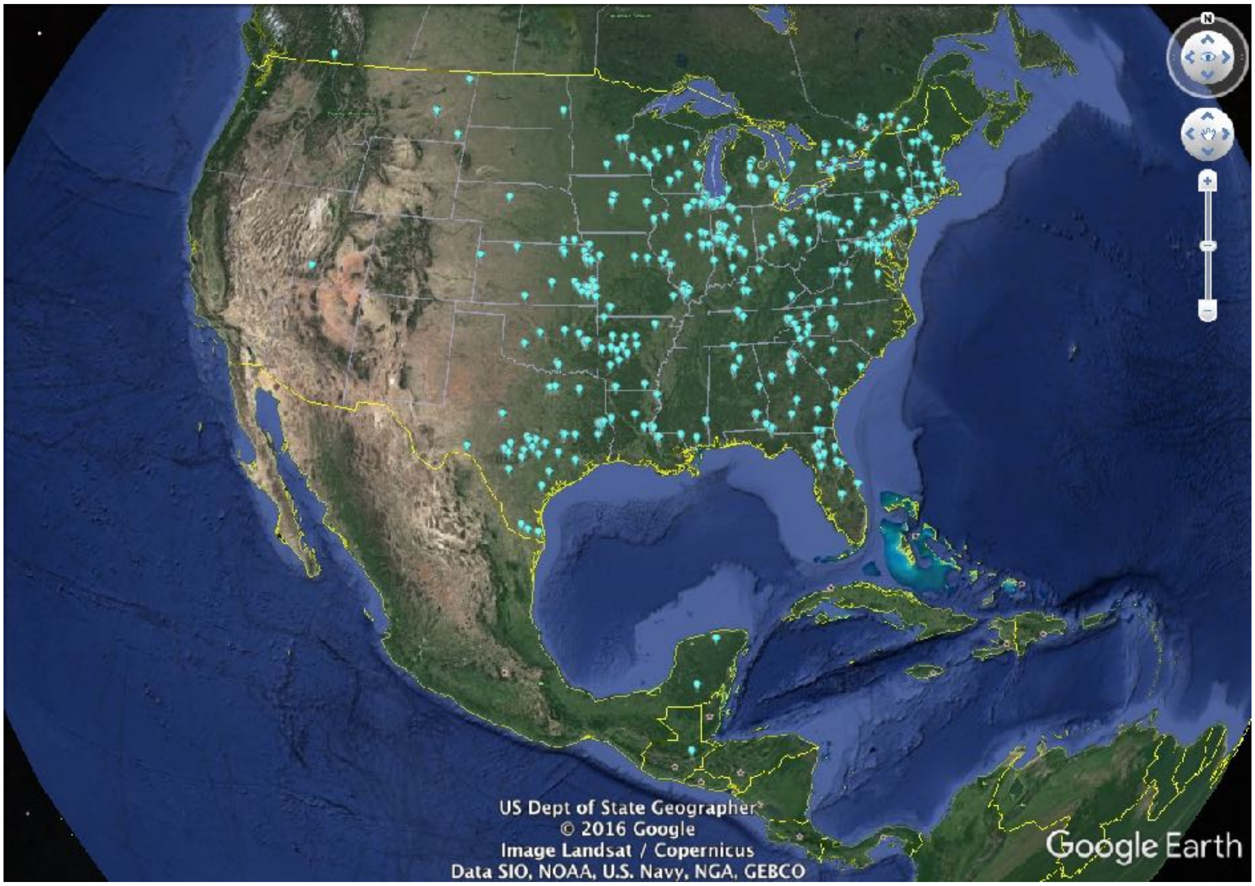

Figure 7.14. Distribution map of *Neobactridium striolatum* (Reitter). Blue pointers represent unique localities, and are not indicative of number of records from each locality. Created using GoogleEarth(TM). Species ranges north to southern Canada south to at least southern Texas and middle Florida, and perhaps as far south as the Yucatan Peninsula and Guatemala (three records). From the east coast it ranges west as far as British Columbia in the north to western Texas, co-occuring with in a narrow area with *Neobactridium californicum.* Broadly co-occurs with *N. ephippigerum* except in its western range. Specimen records available: SYMBIOTA, KML, CSV.

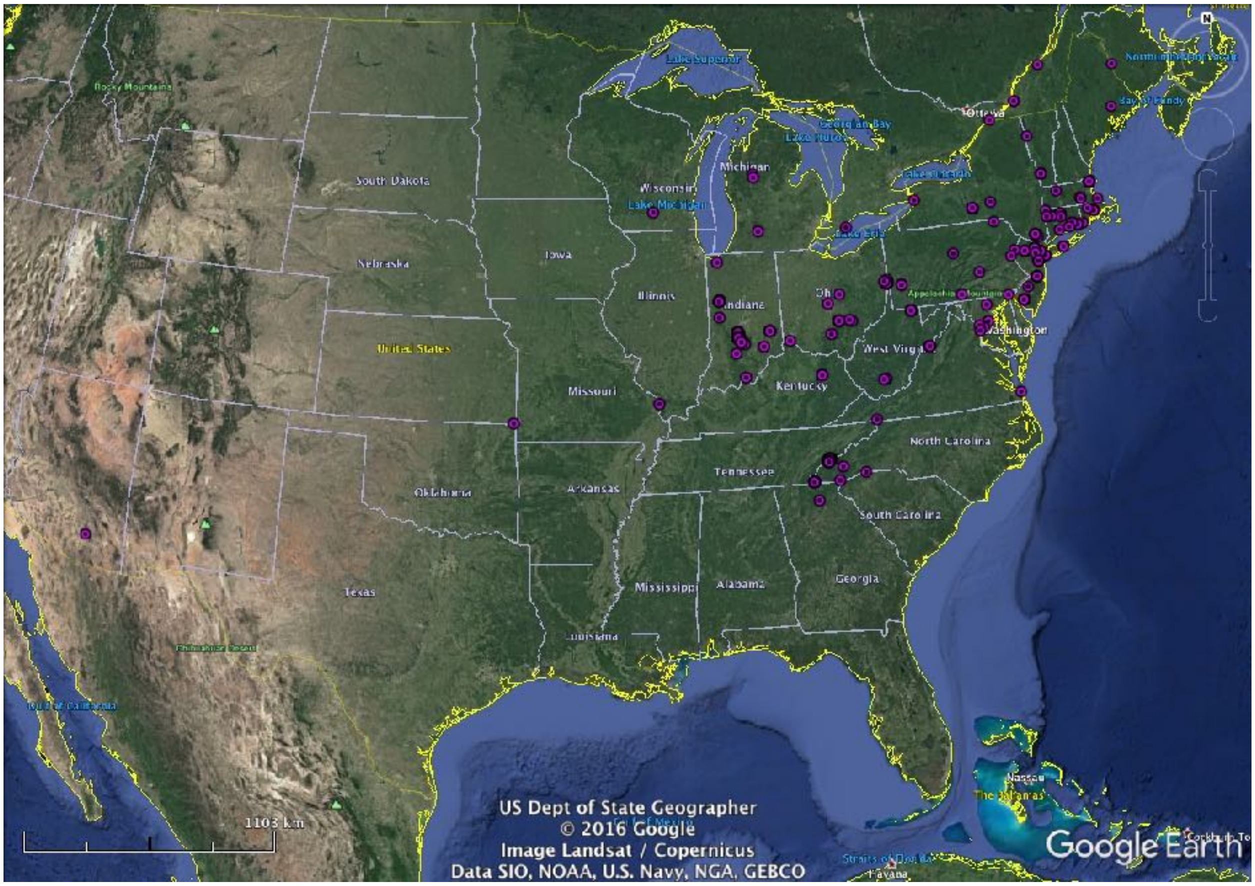

Figure 7.15. Distribution map of *Pycnotomina cavicolle* (Horn). Purple dots represent unique localities, and are not indicative of number of records from each locality. Created using GoogleEarth(TM). Species ranges north to southern Canada southwest to Kansas and north Georgia, and perhaps as far west as Arizona (one record). Specimen records available: SYMBIOTA, KML, CSV.

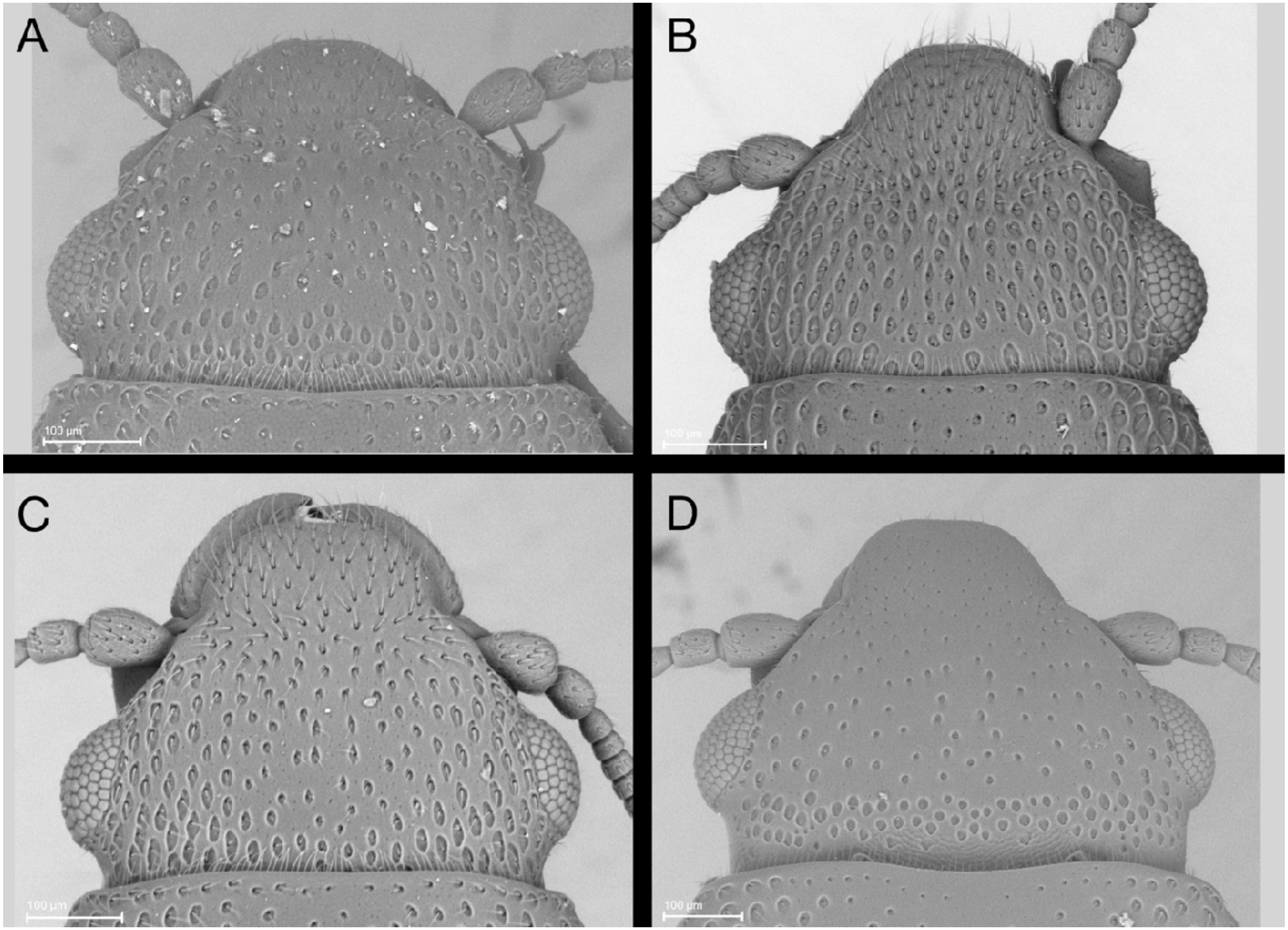

Figure 7.16. ESEM head dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

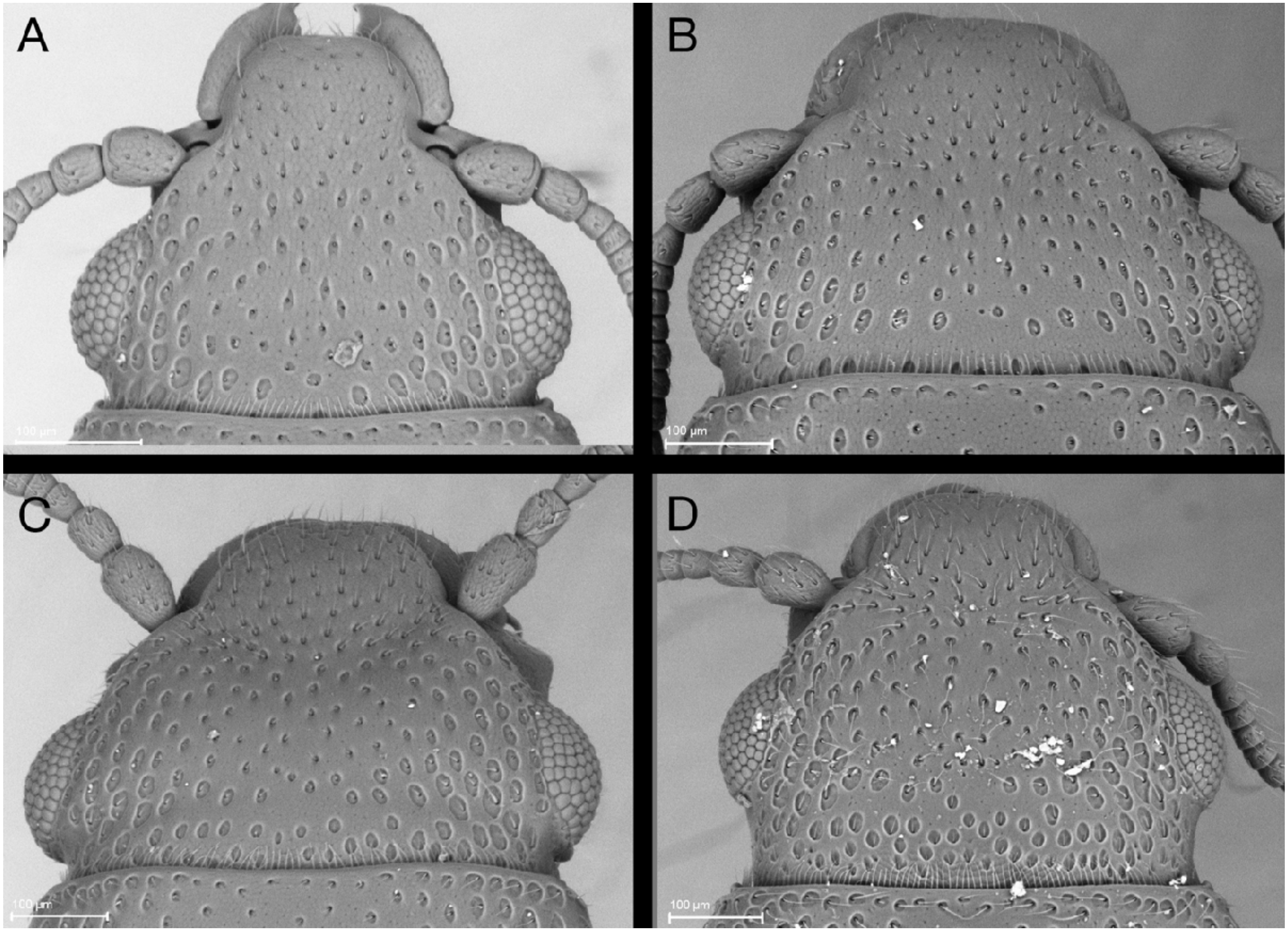

Figure 7.17. ESEM head dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

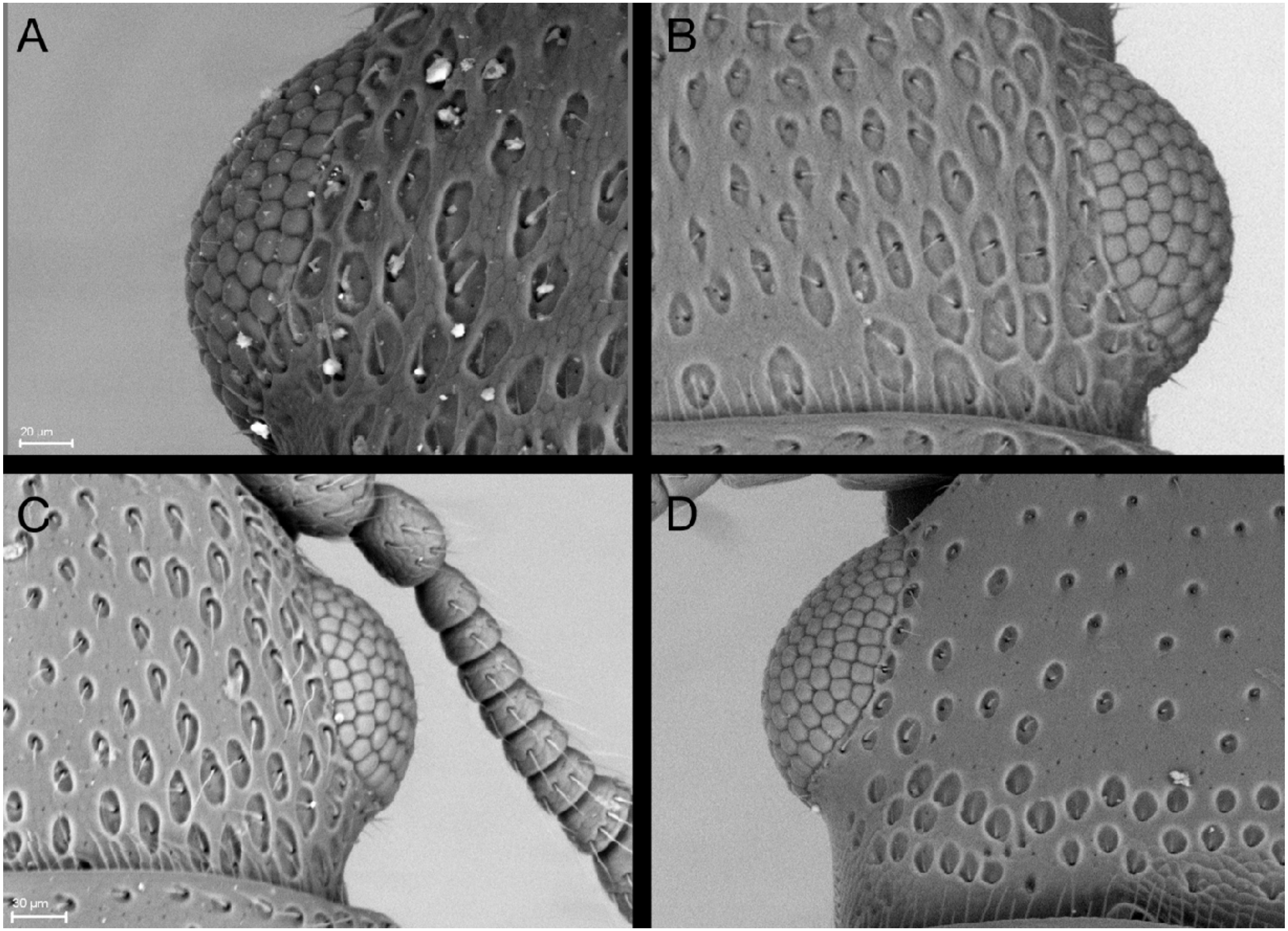

Figure 7.18. ESEM eye dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

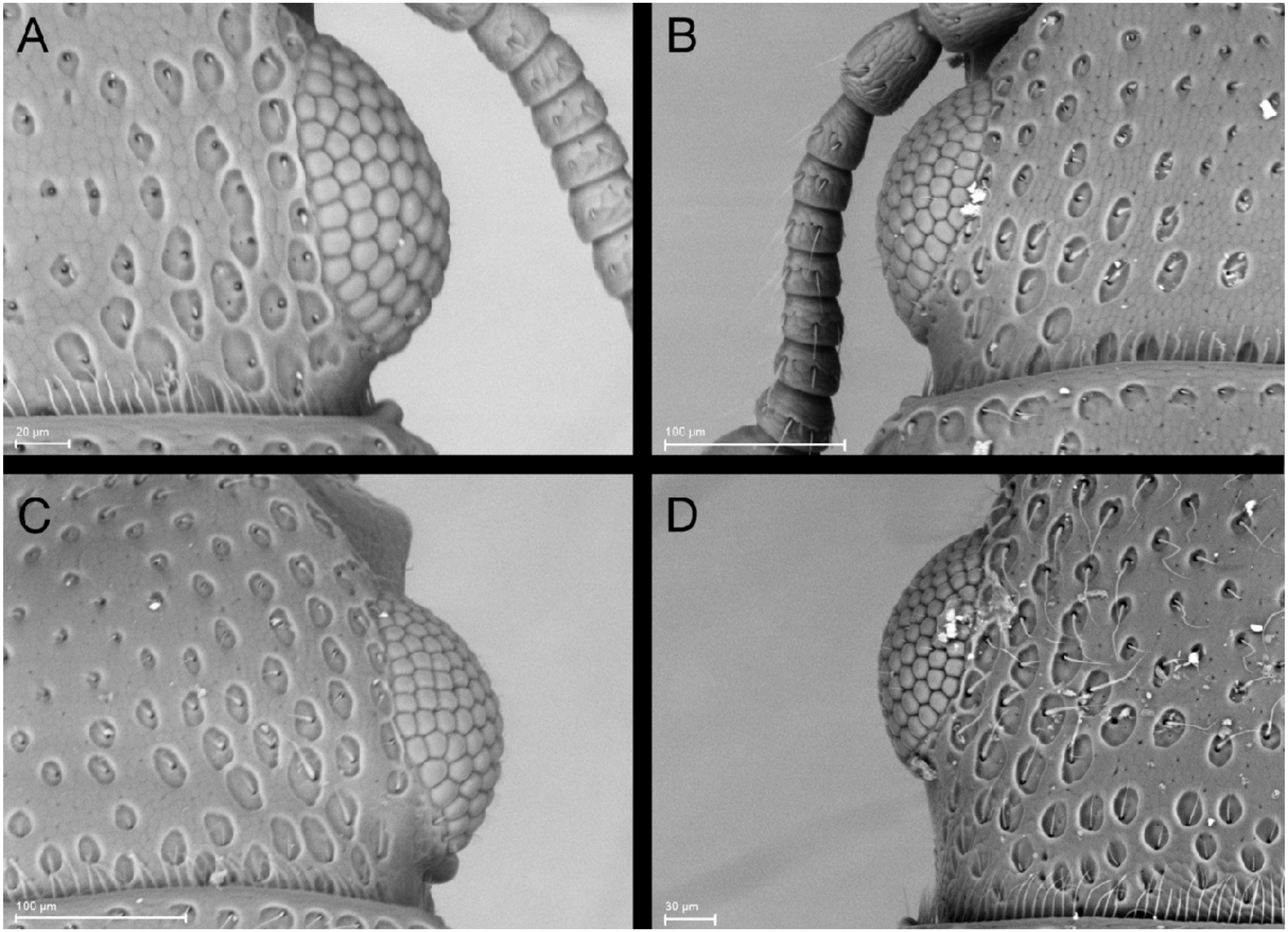

Figure 7.19 ESEM eye dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

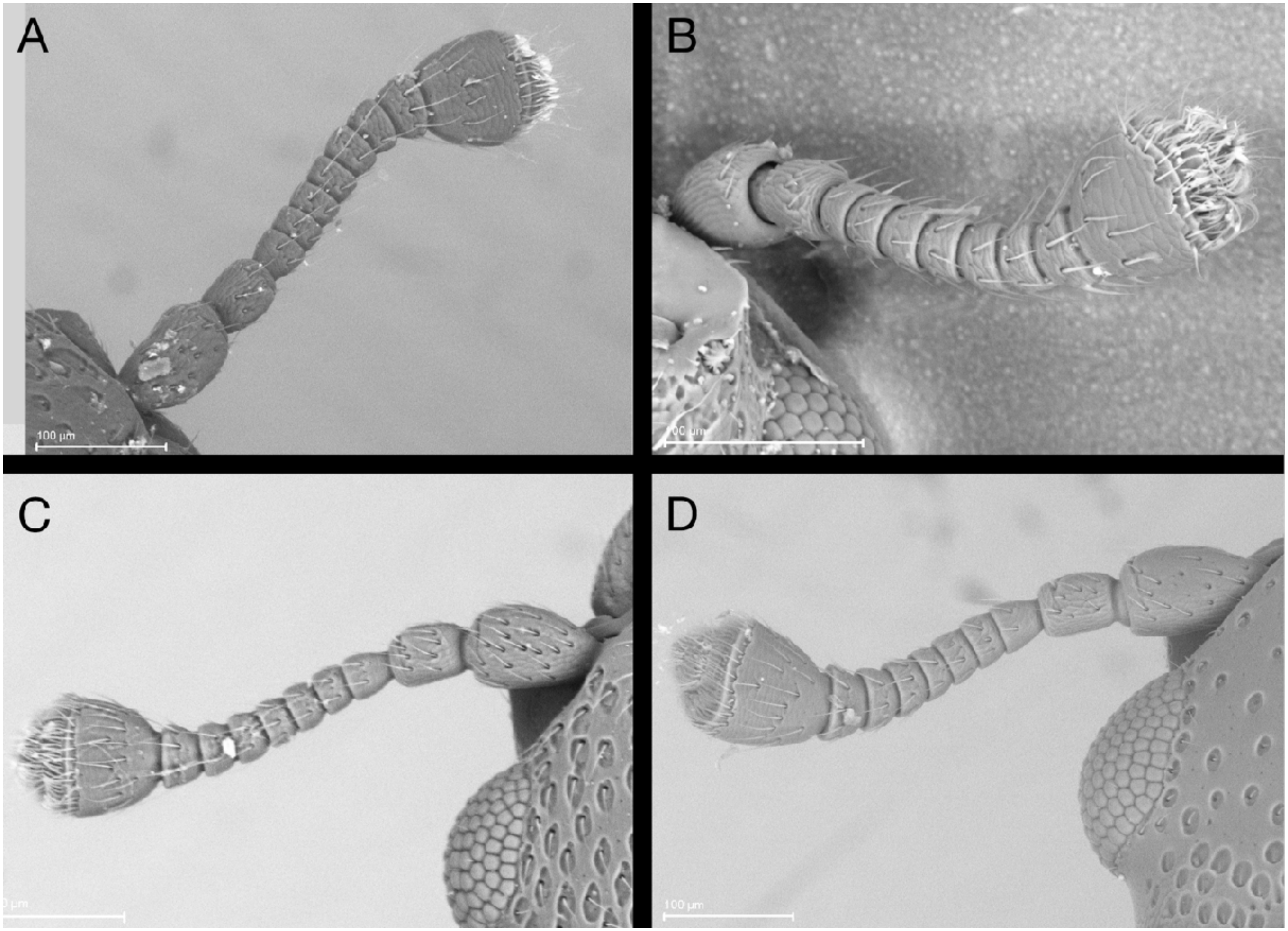

Figure 7.20. ESEM antenna dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

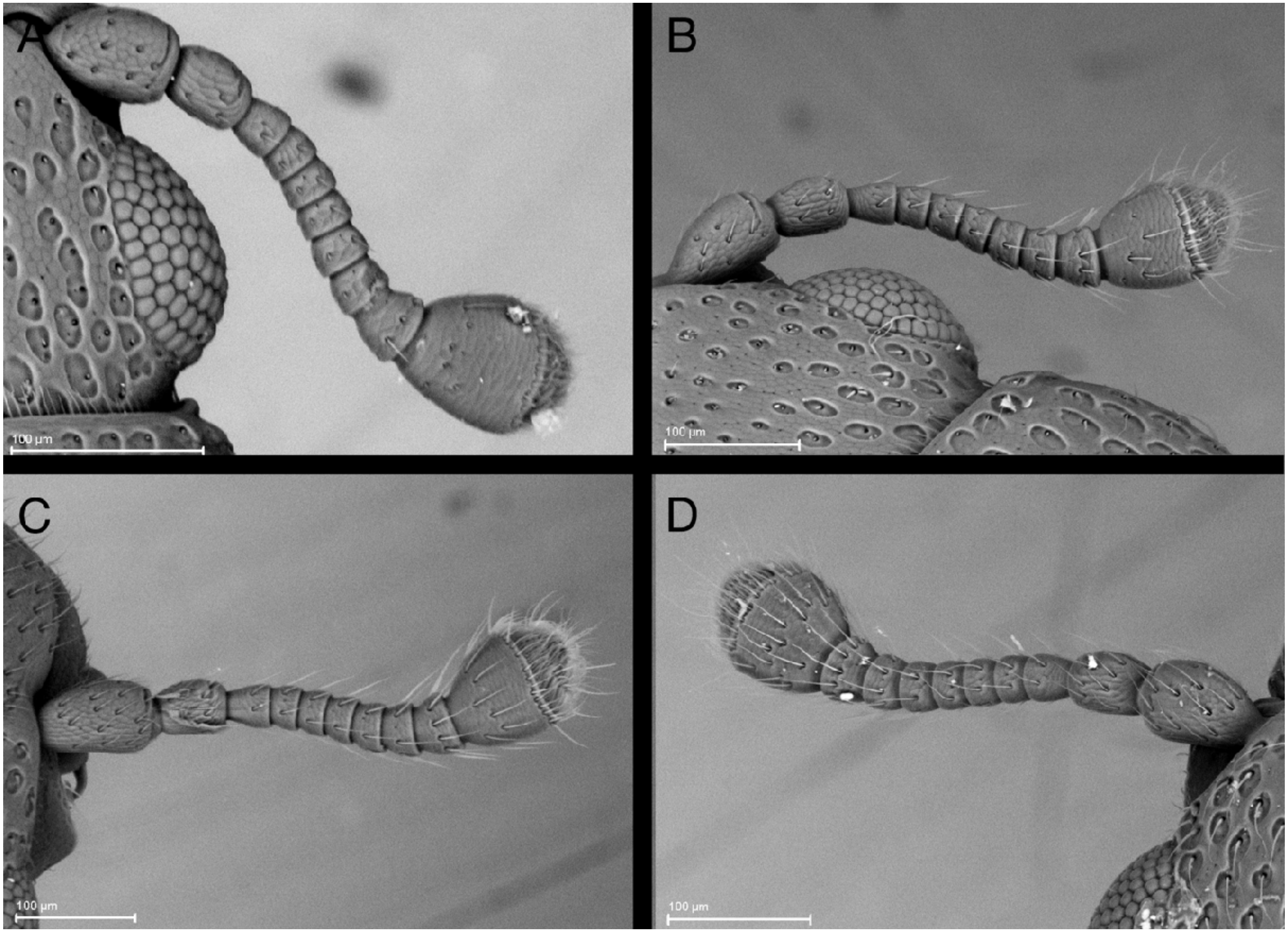

Figure 7.21. ESEM antenna dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) *N. striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

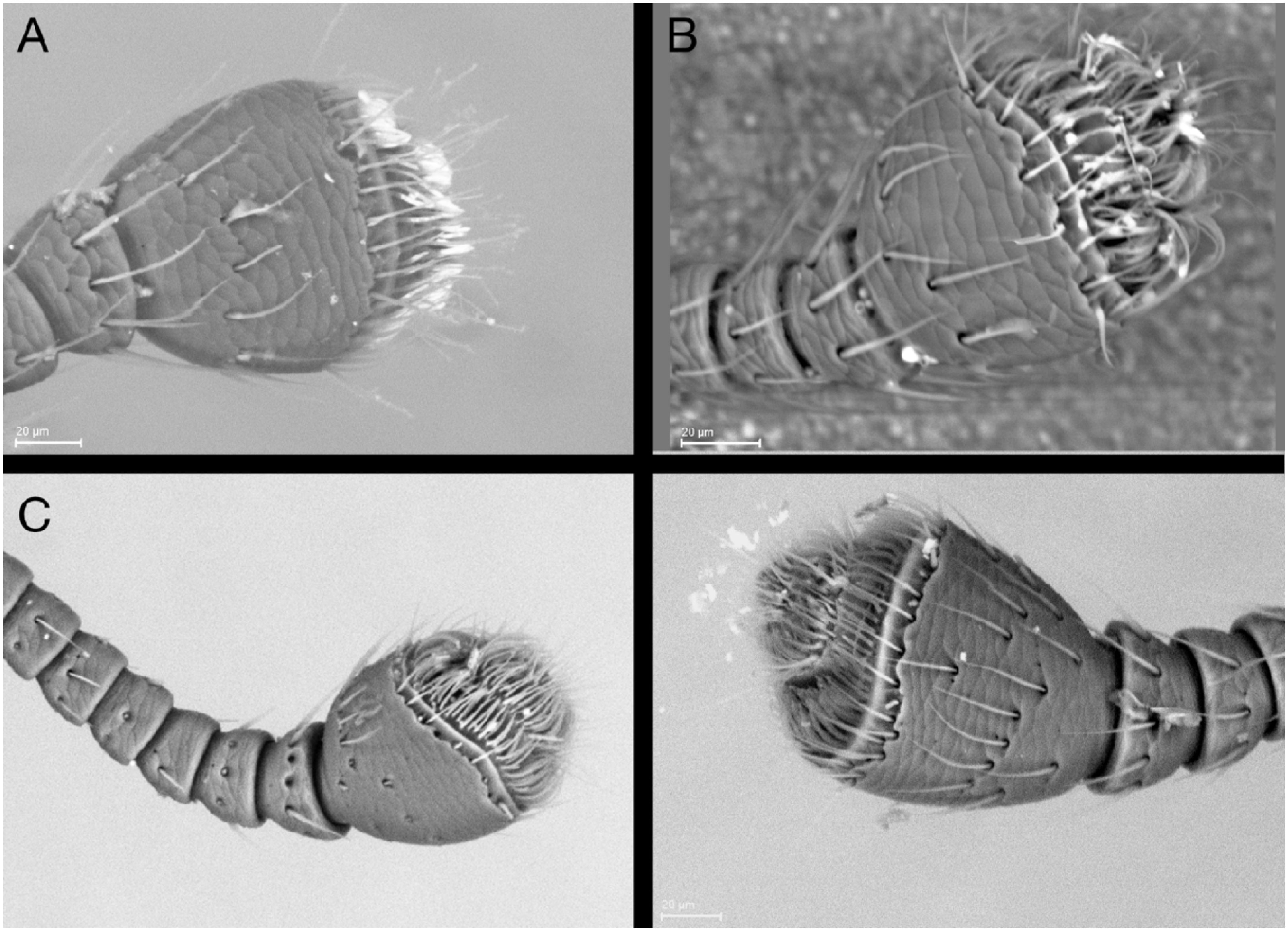

Figure 7.22. ESEM antennal club ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

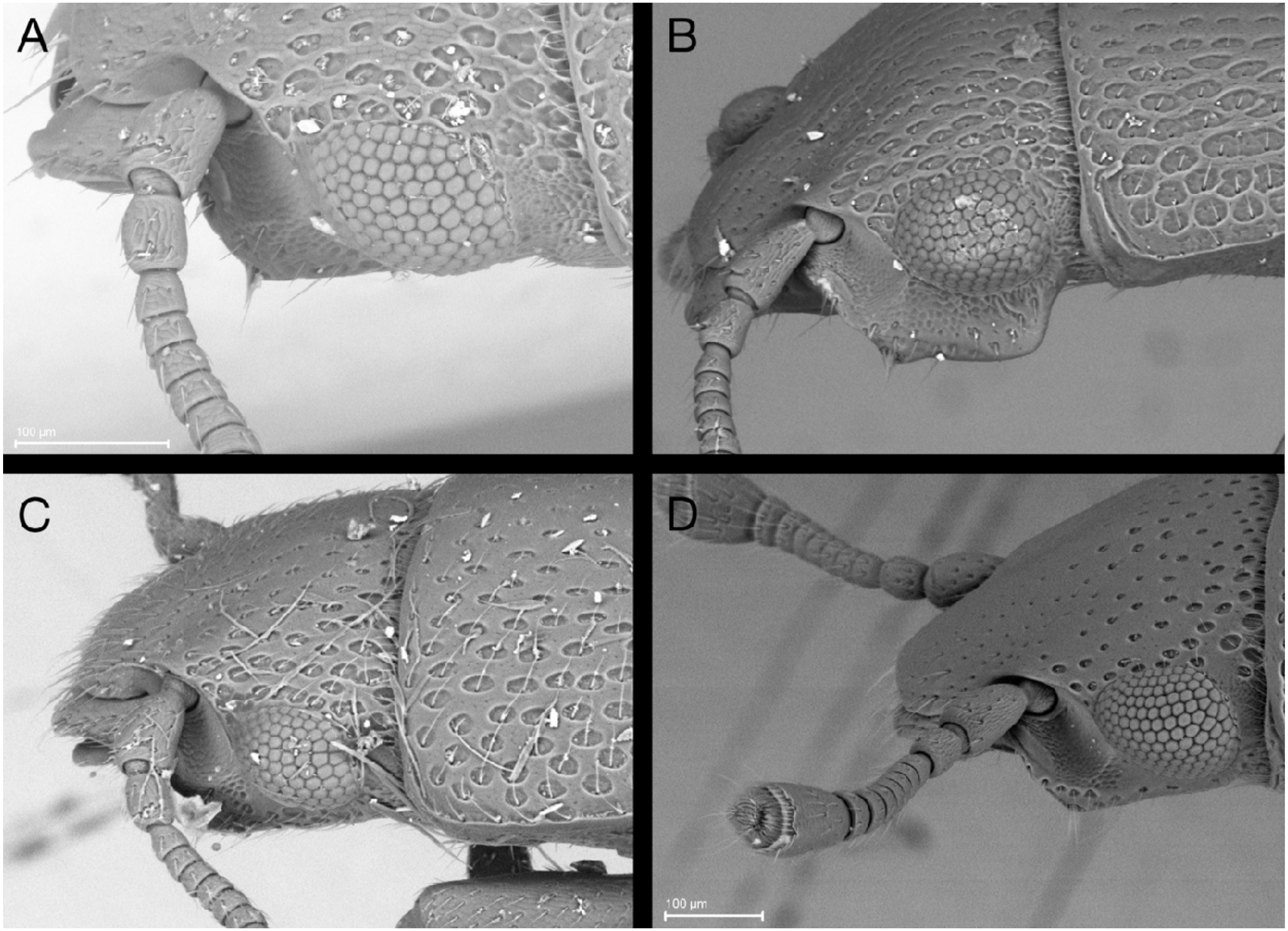

Figure 7.23. ESEM head, lateral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

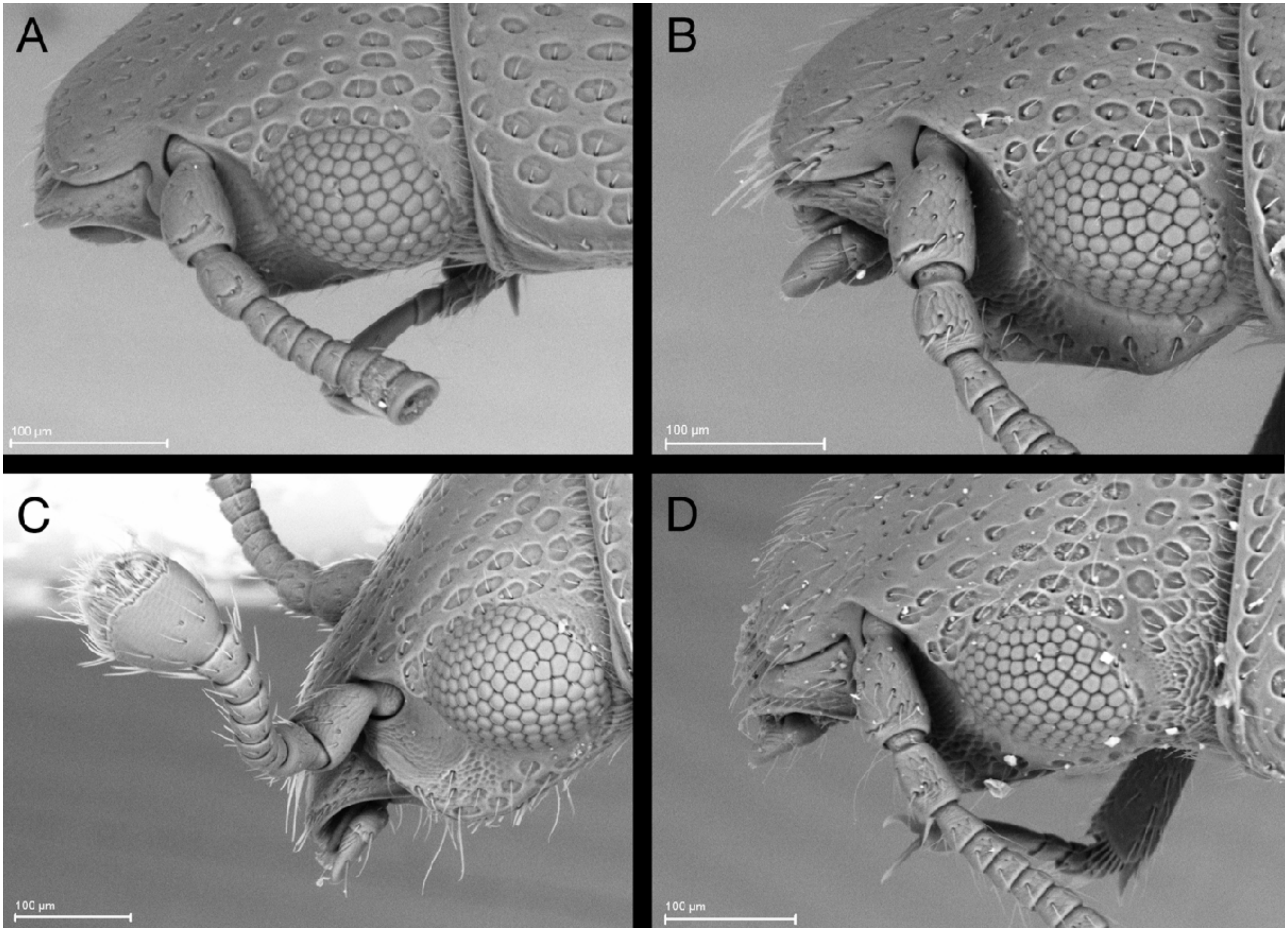

Figure 7.24. ESEM head, lateral *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

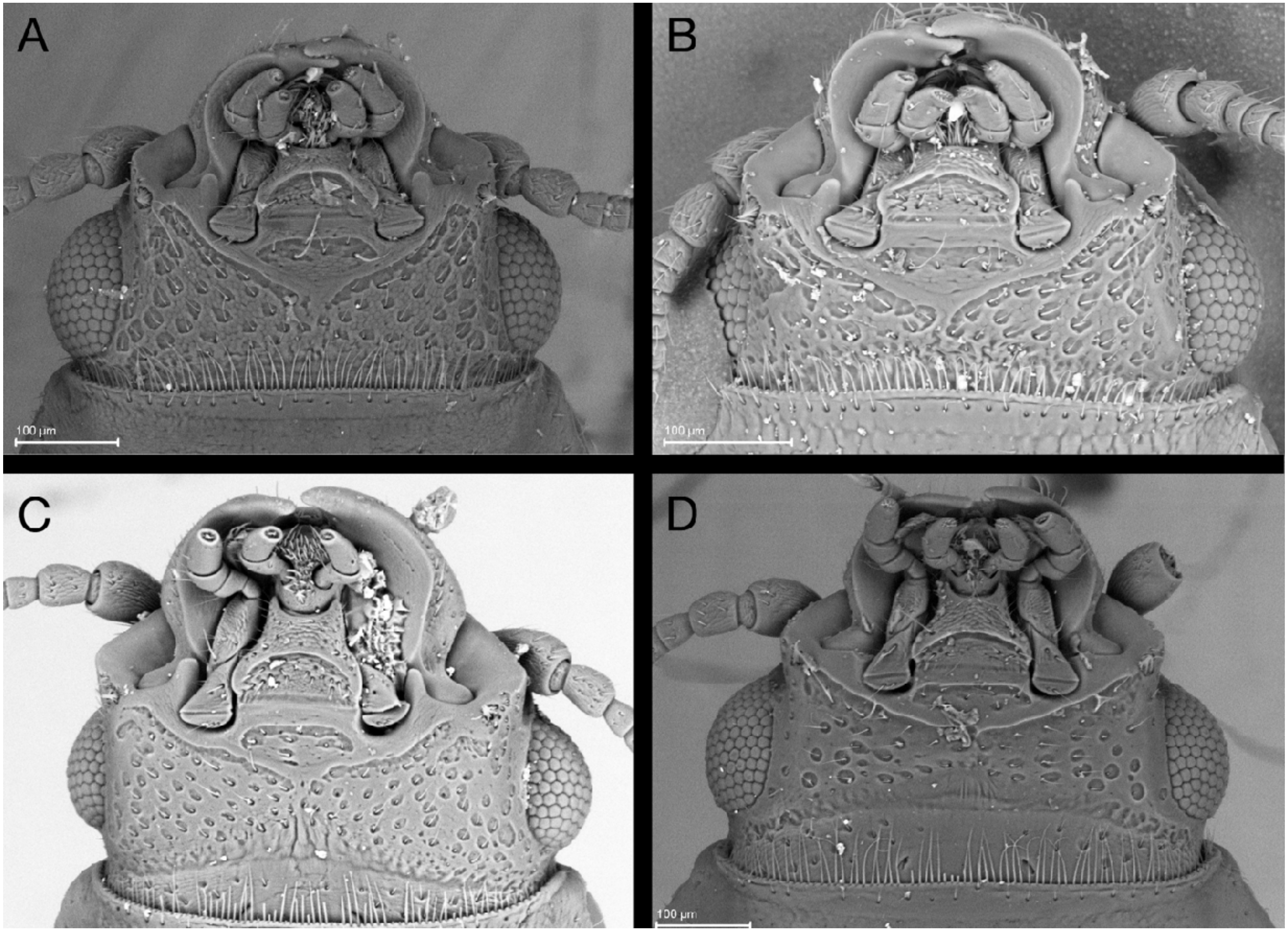

Figure 7.25 ESEM head ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

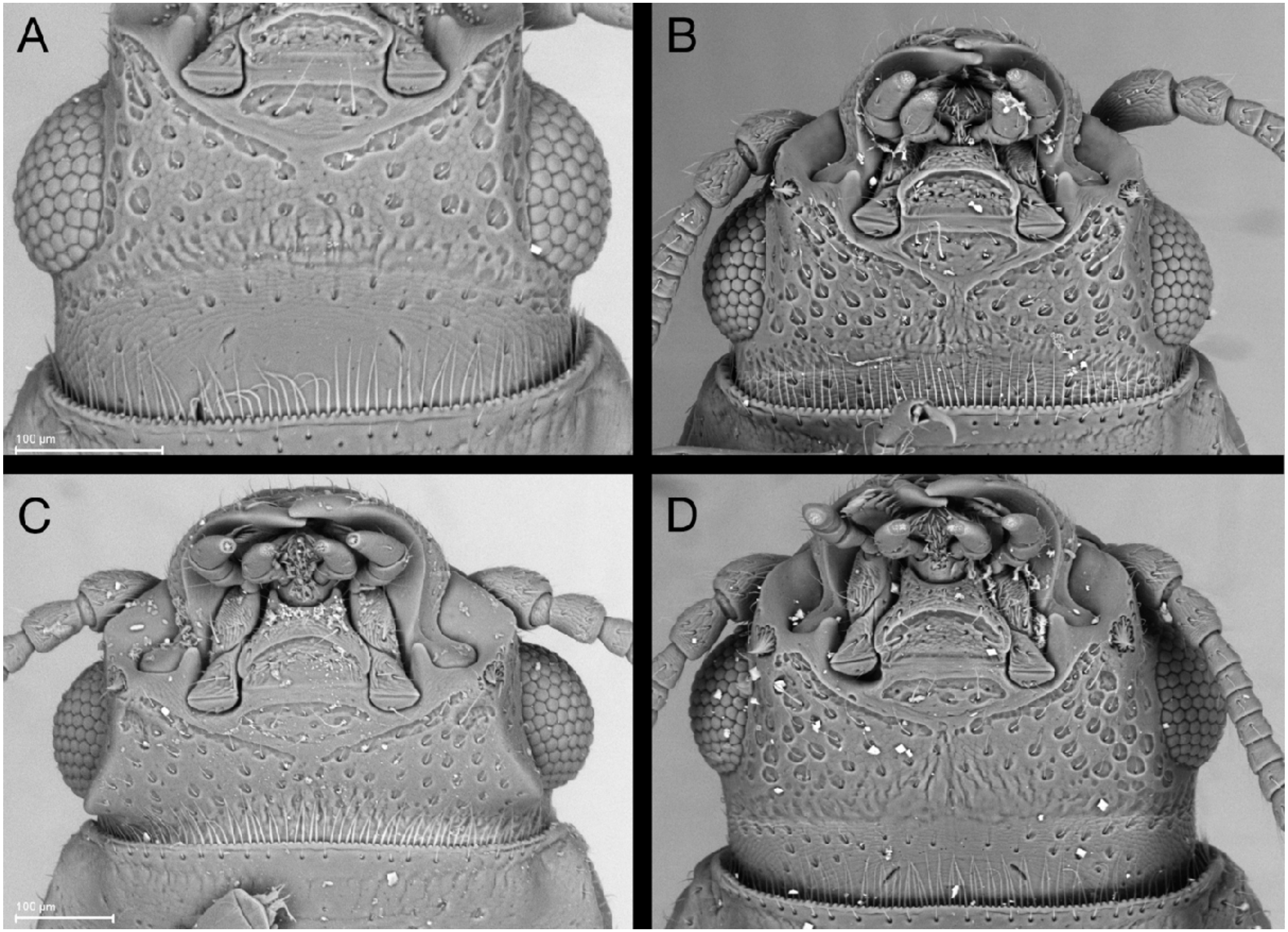

Figure 7.26. ESEM head ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

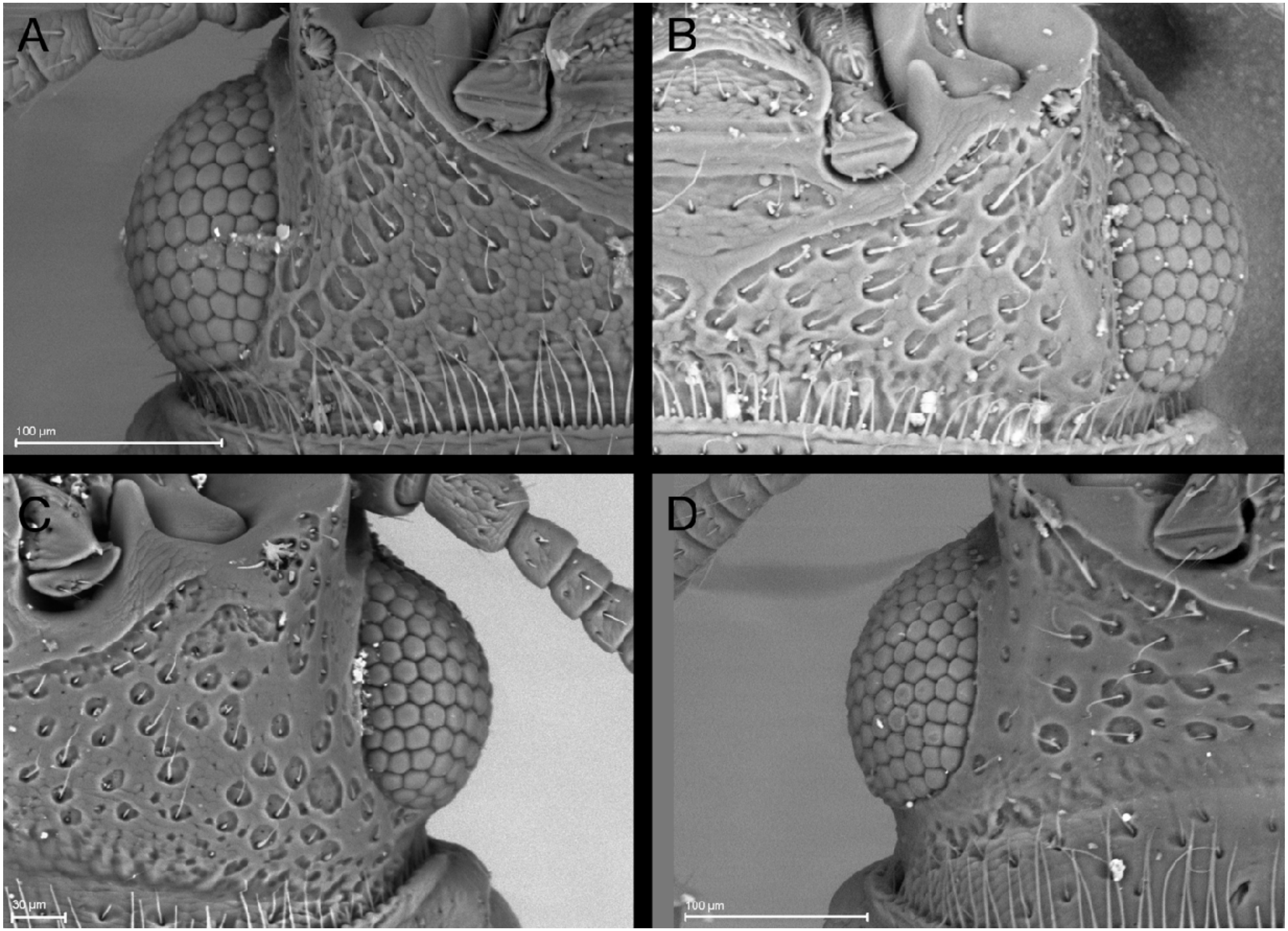

Figure 7.27. ESEM eye ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

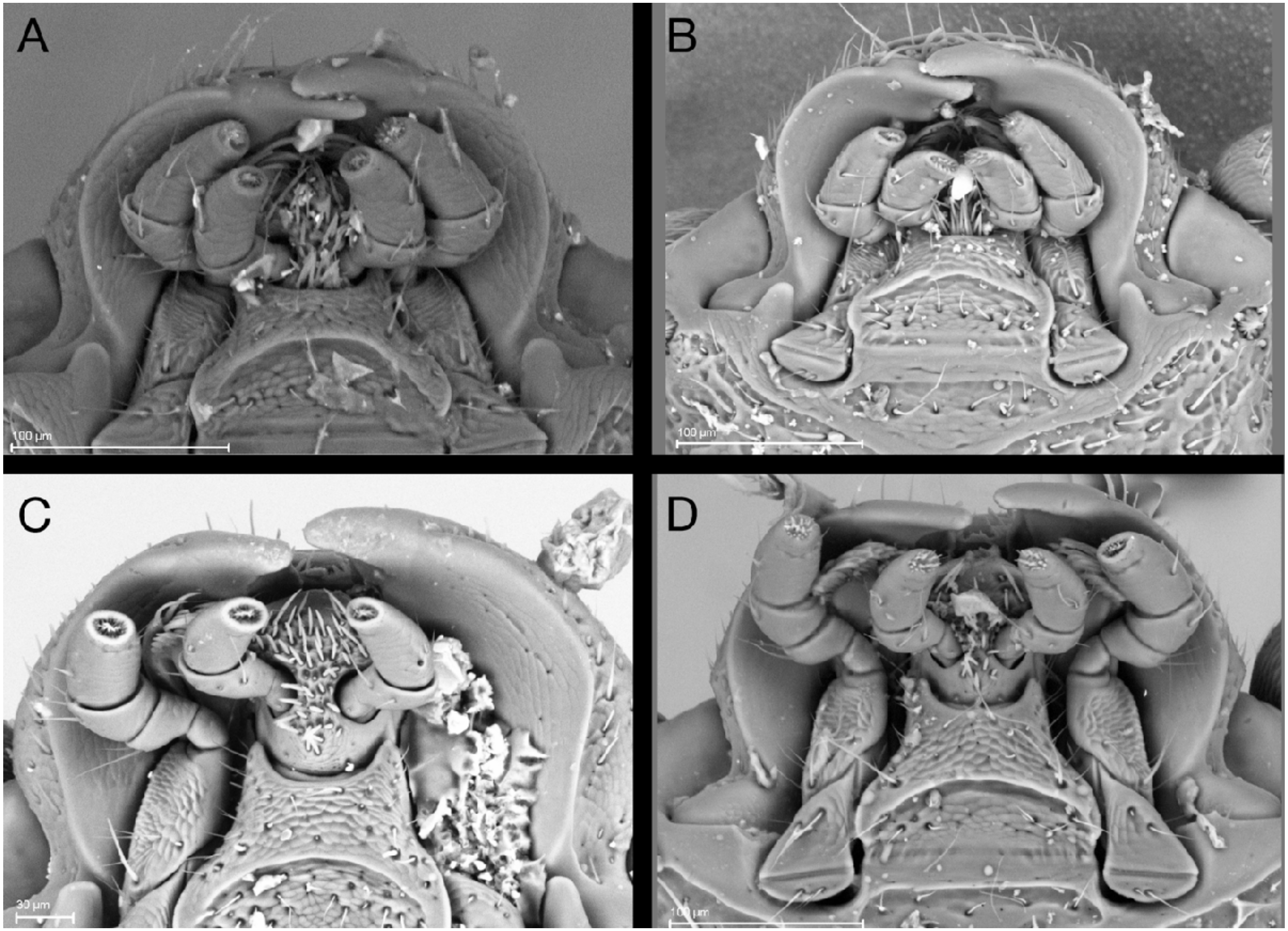

Figure 7.28. ESEM mouthparts ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

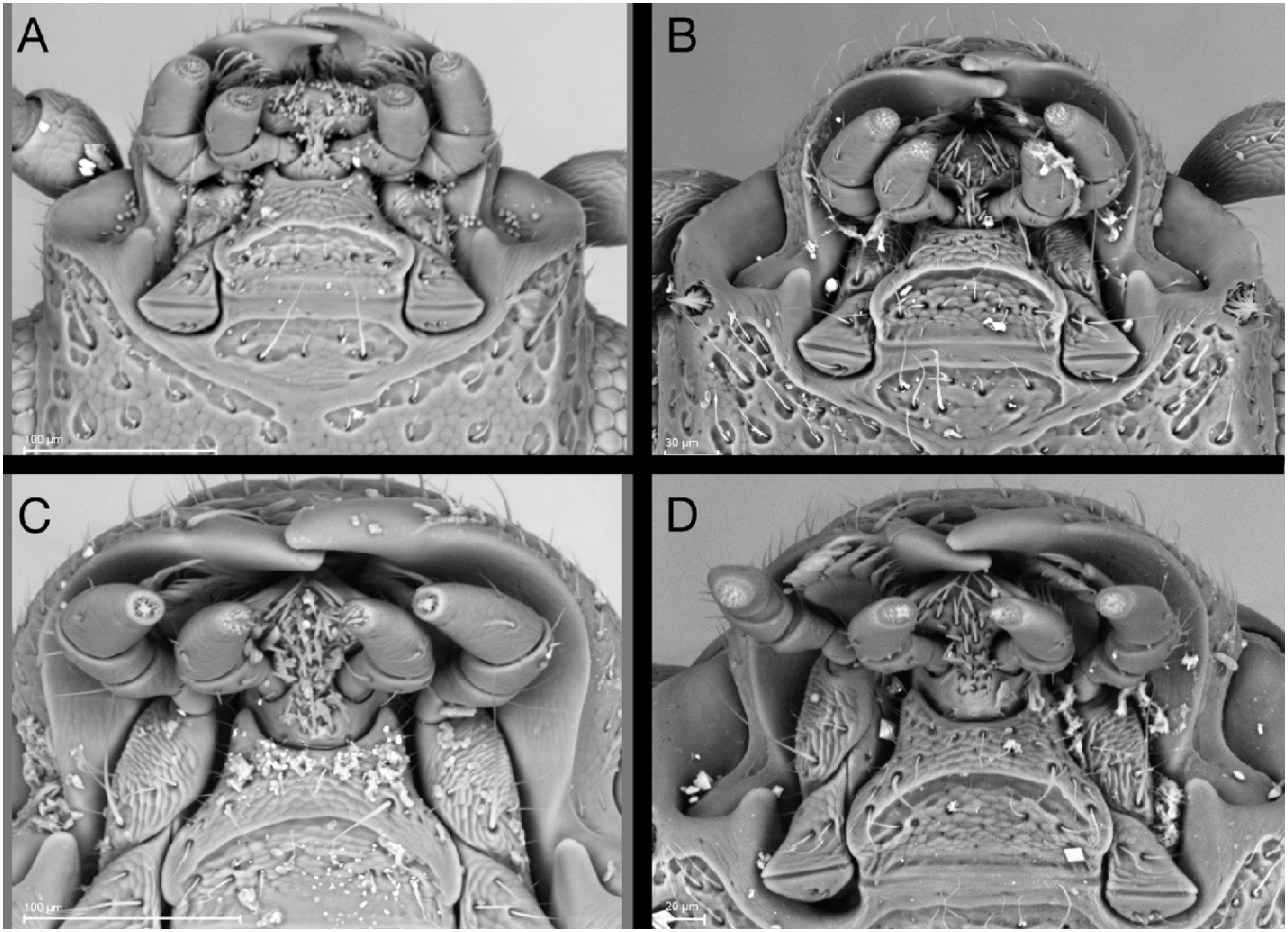

Figure 7.29. ESEM head dorsal view *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1..

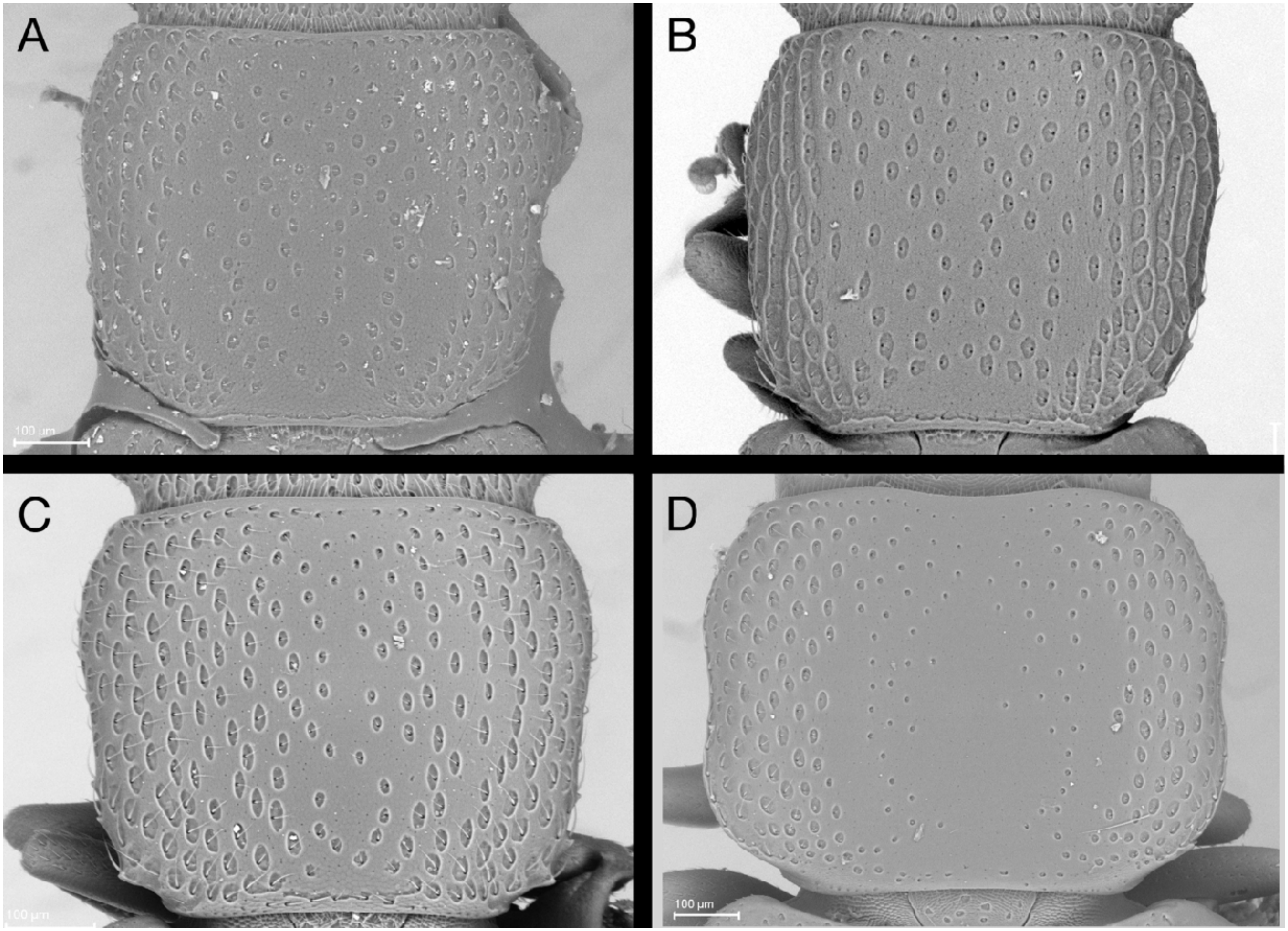

Figure 7.30. ESEM pronotum dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

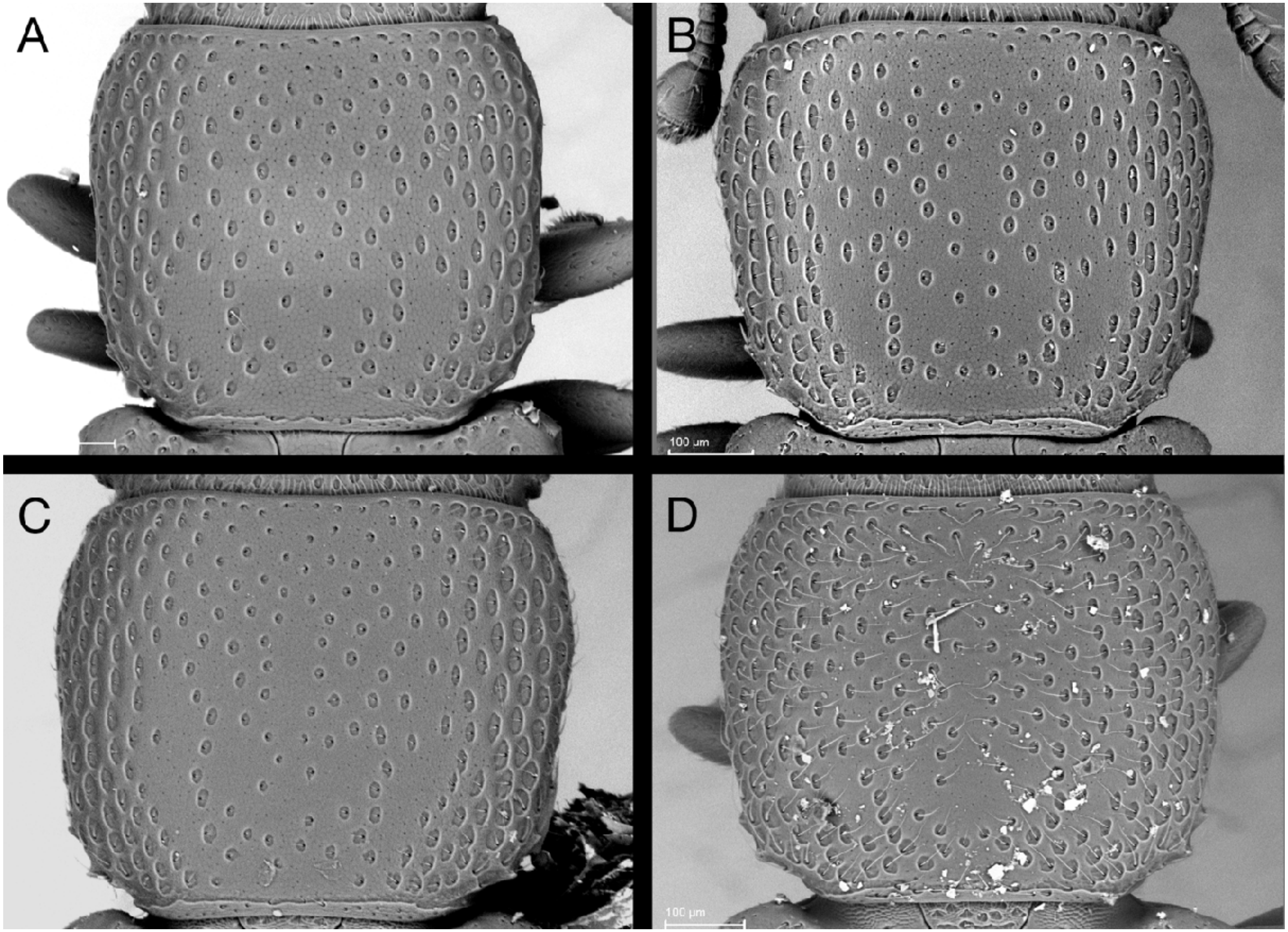

Figure 7.31. ESEM pronotum dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

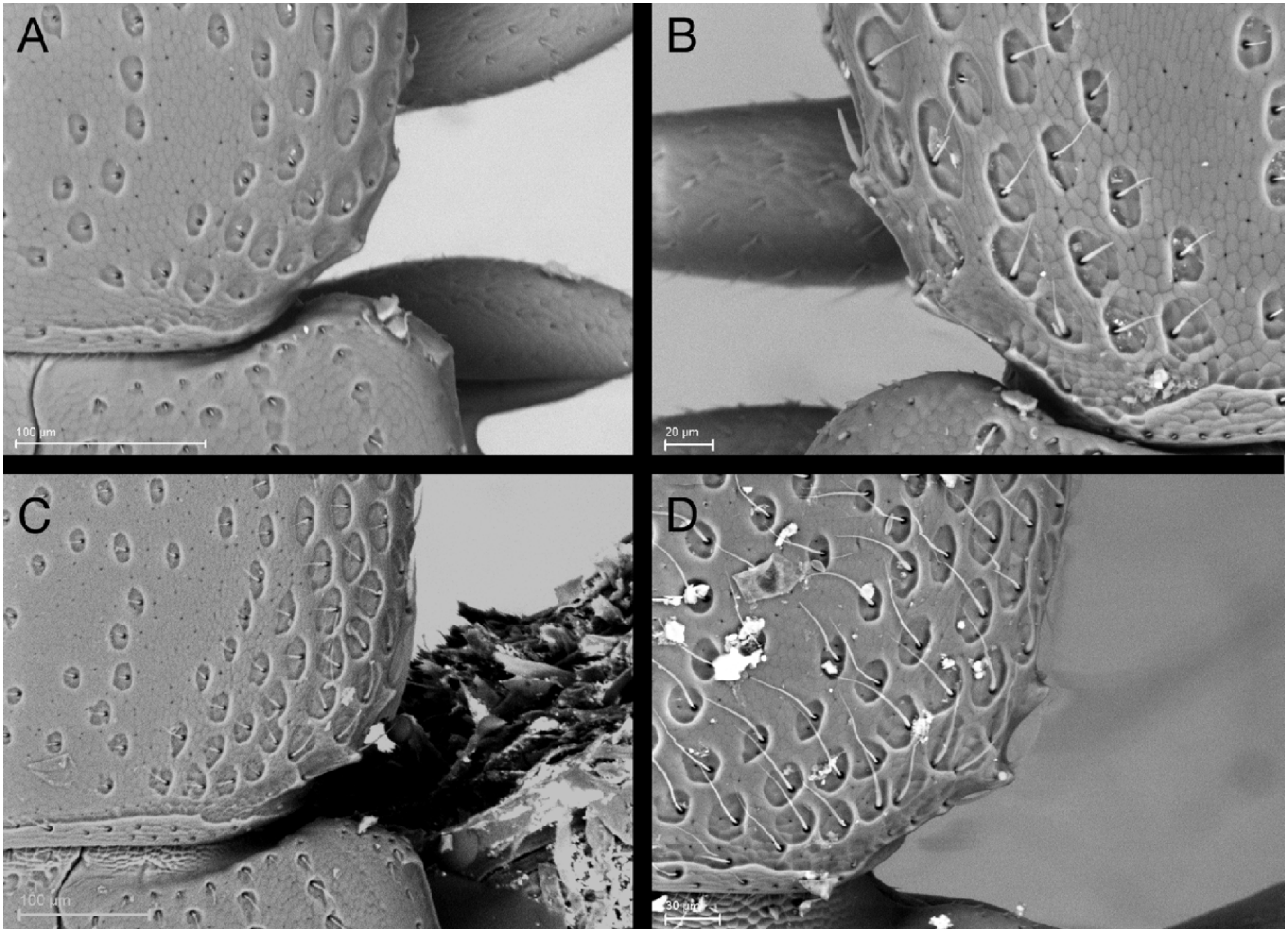

Figure 7.32. ESEM pronotal lateroposterior angle dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

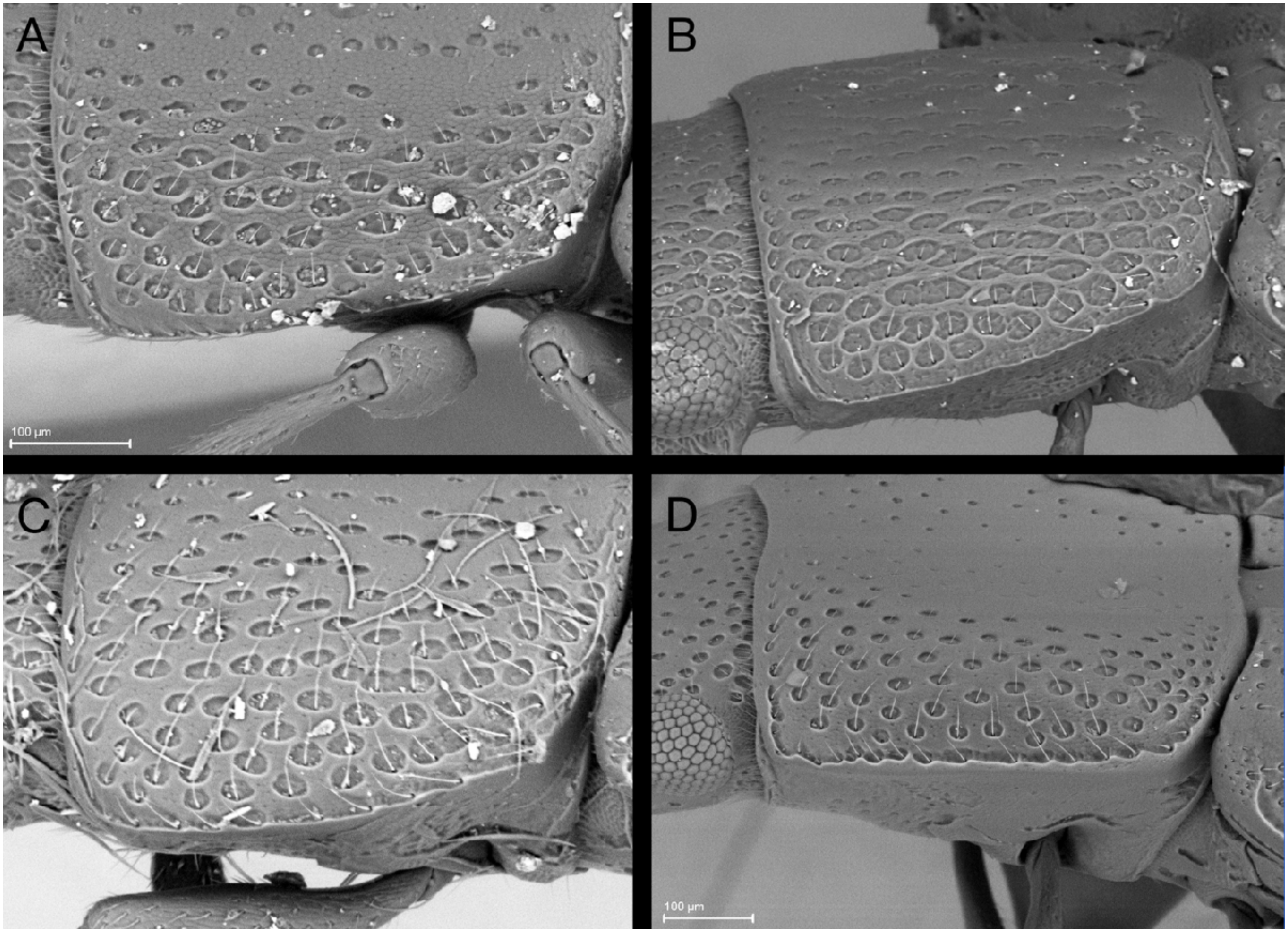

Figure 7.33. ESEM pronotum lateral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

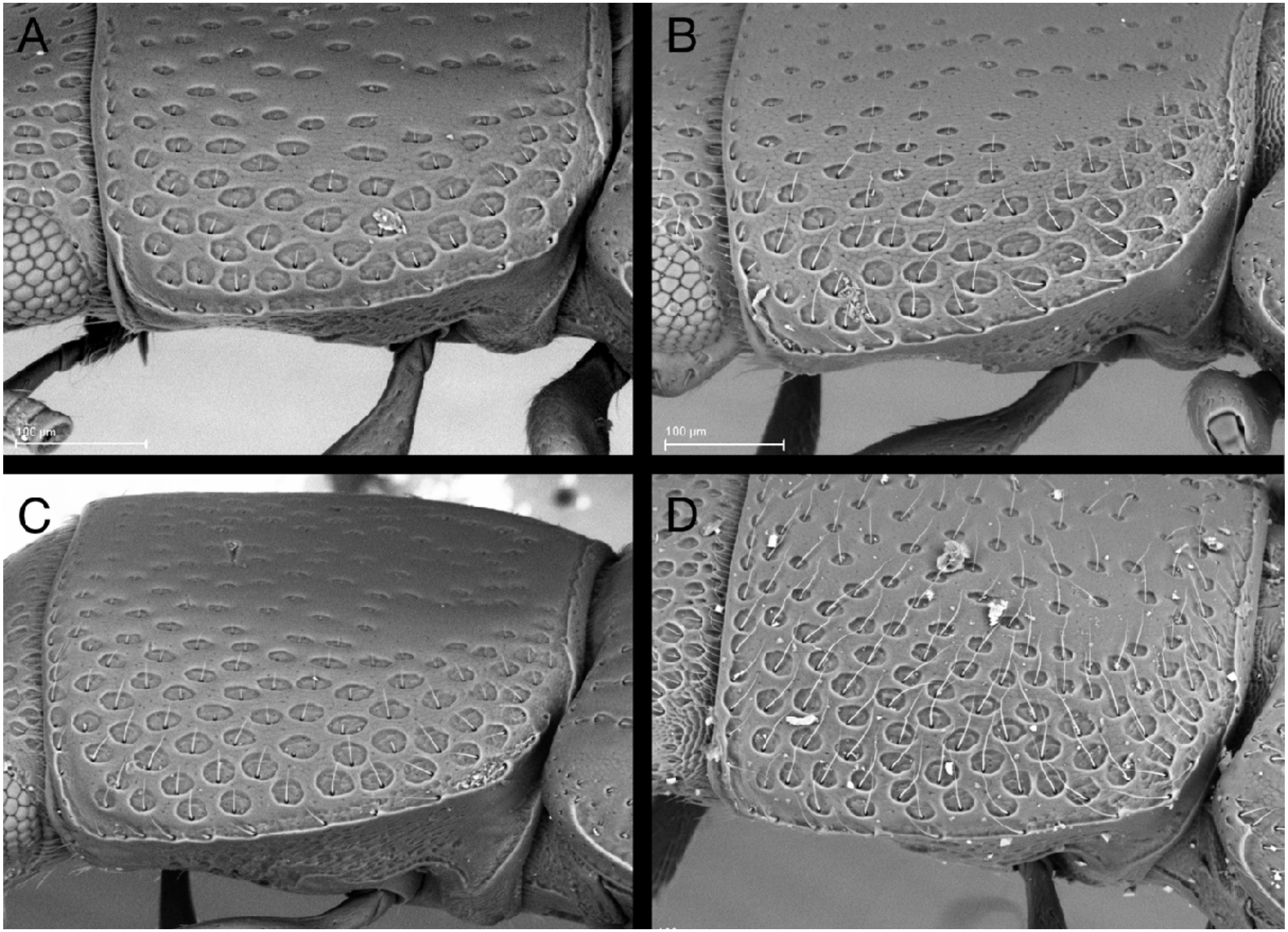

Figure 7.34. ESEM pronotum lateral *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

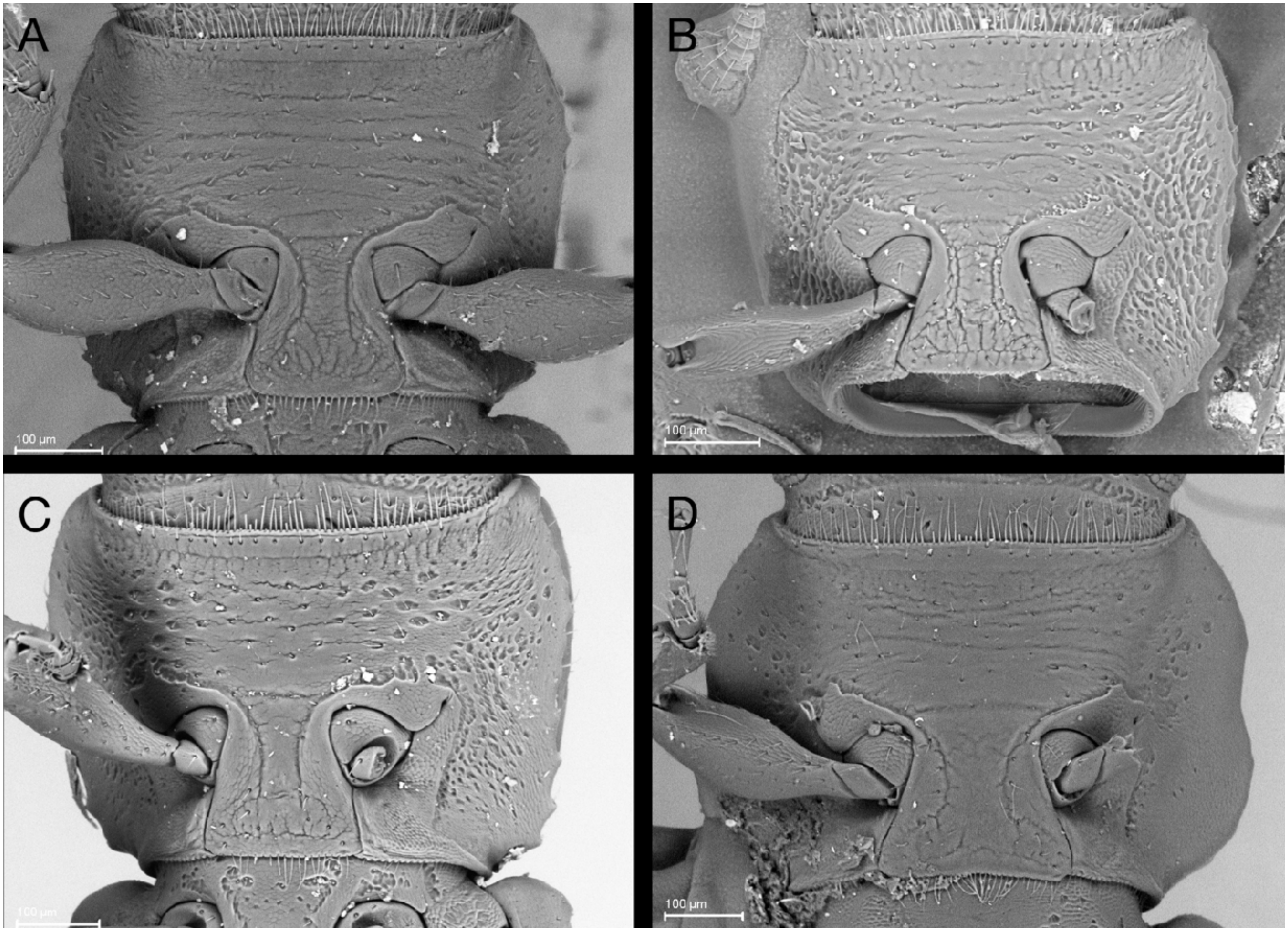

Figure 7.35 ESEM pronotum, ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

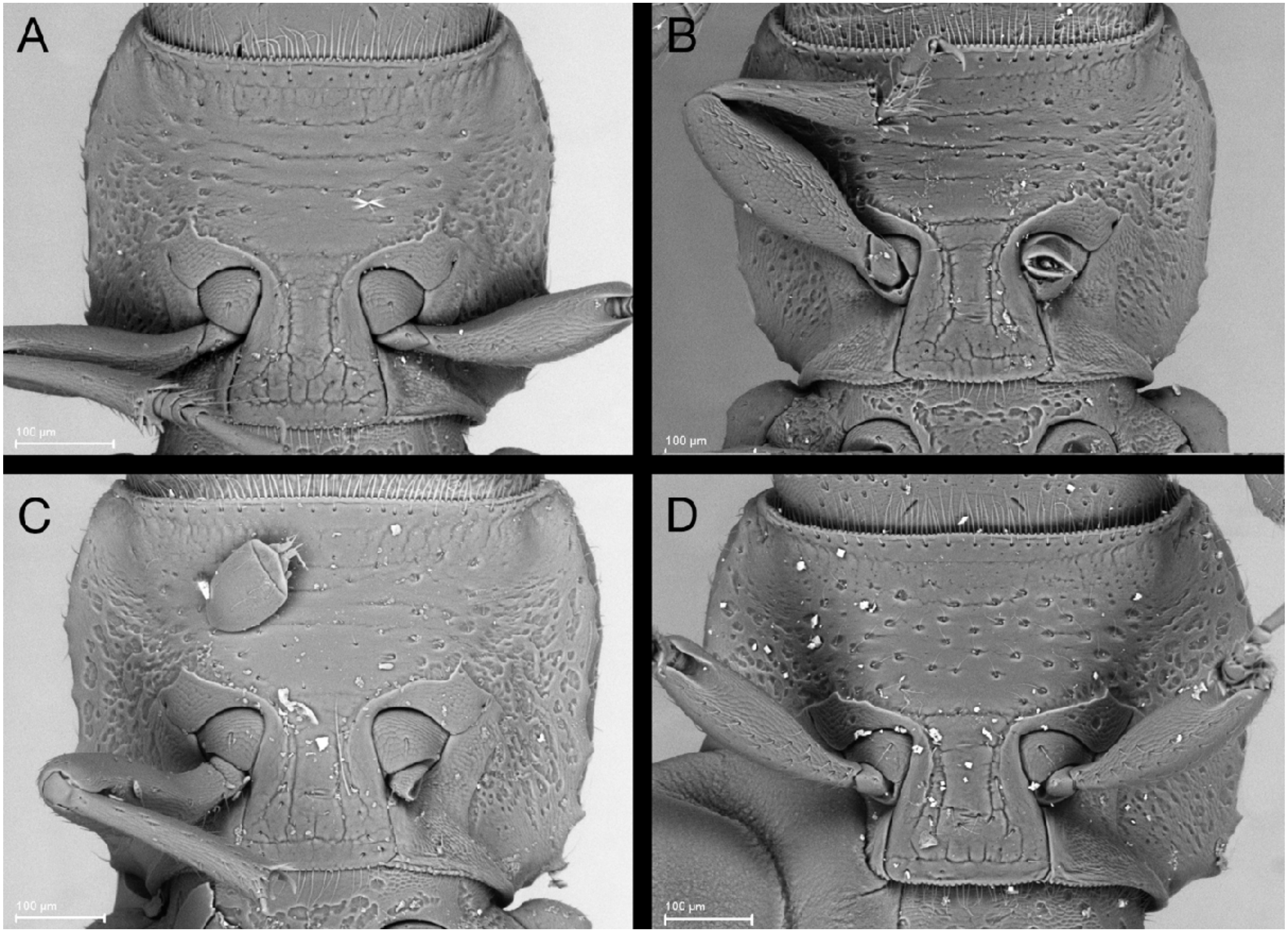

Figure 7.36. ESEM pronotum, ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

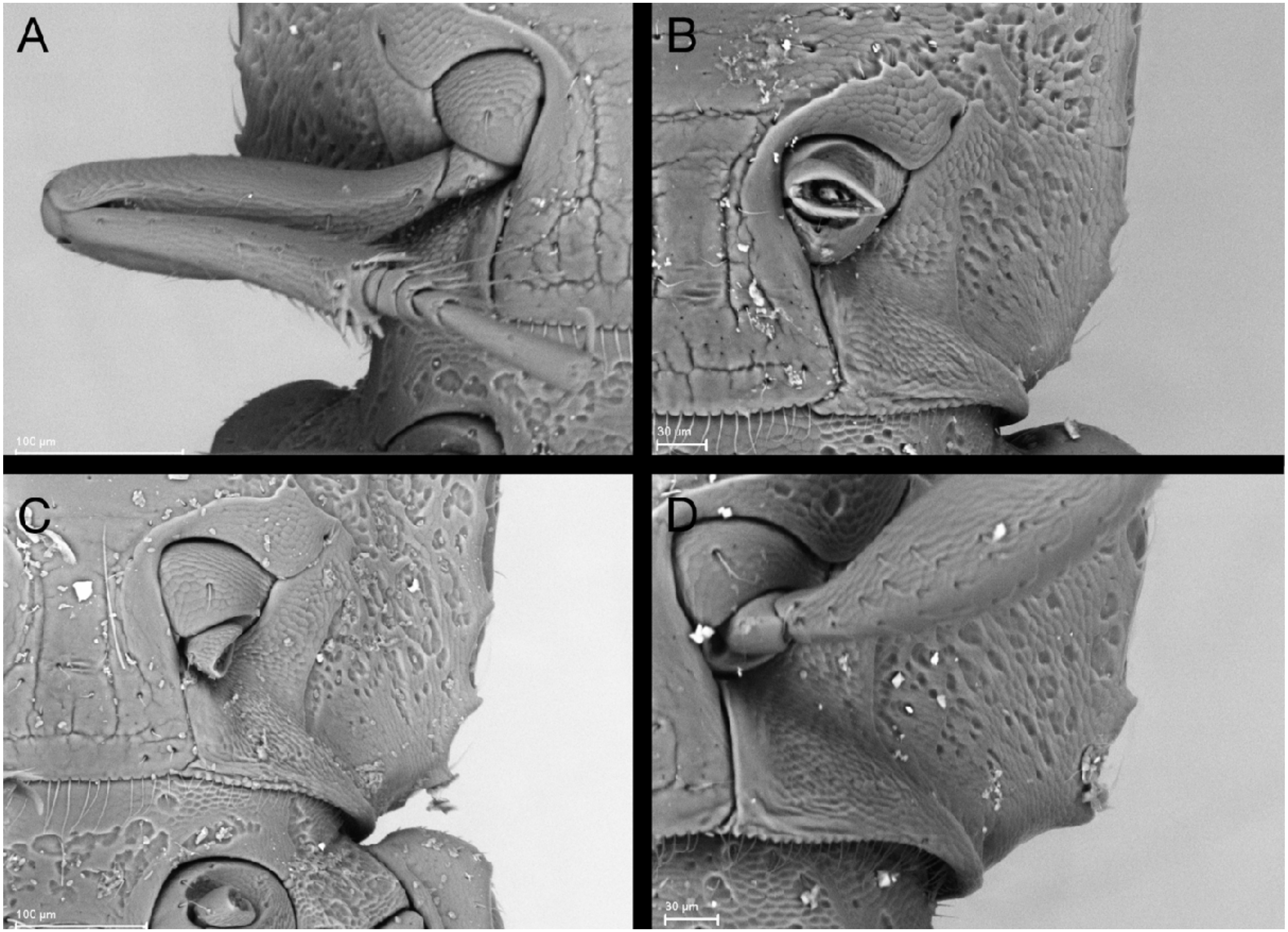

Figure 7.37. ESEM procoxal cavity, ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

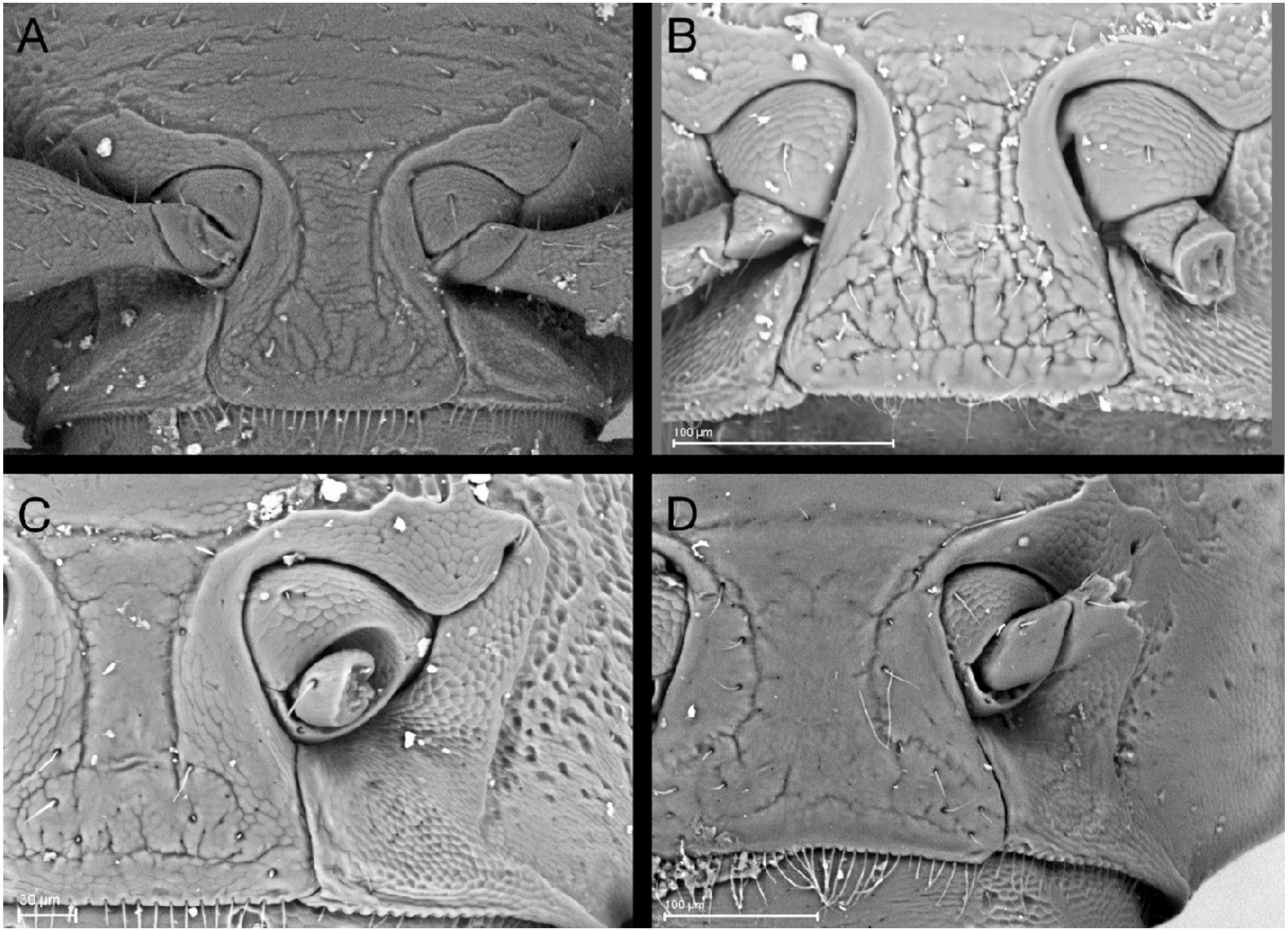

Figure 7.38. ESEM prosternal epiphysis, ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

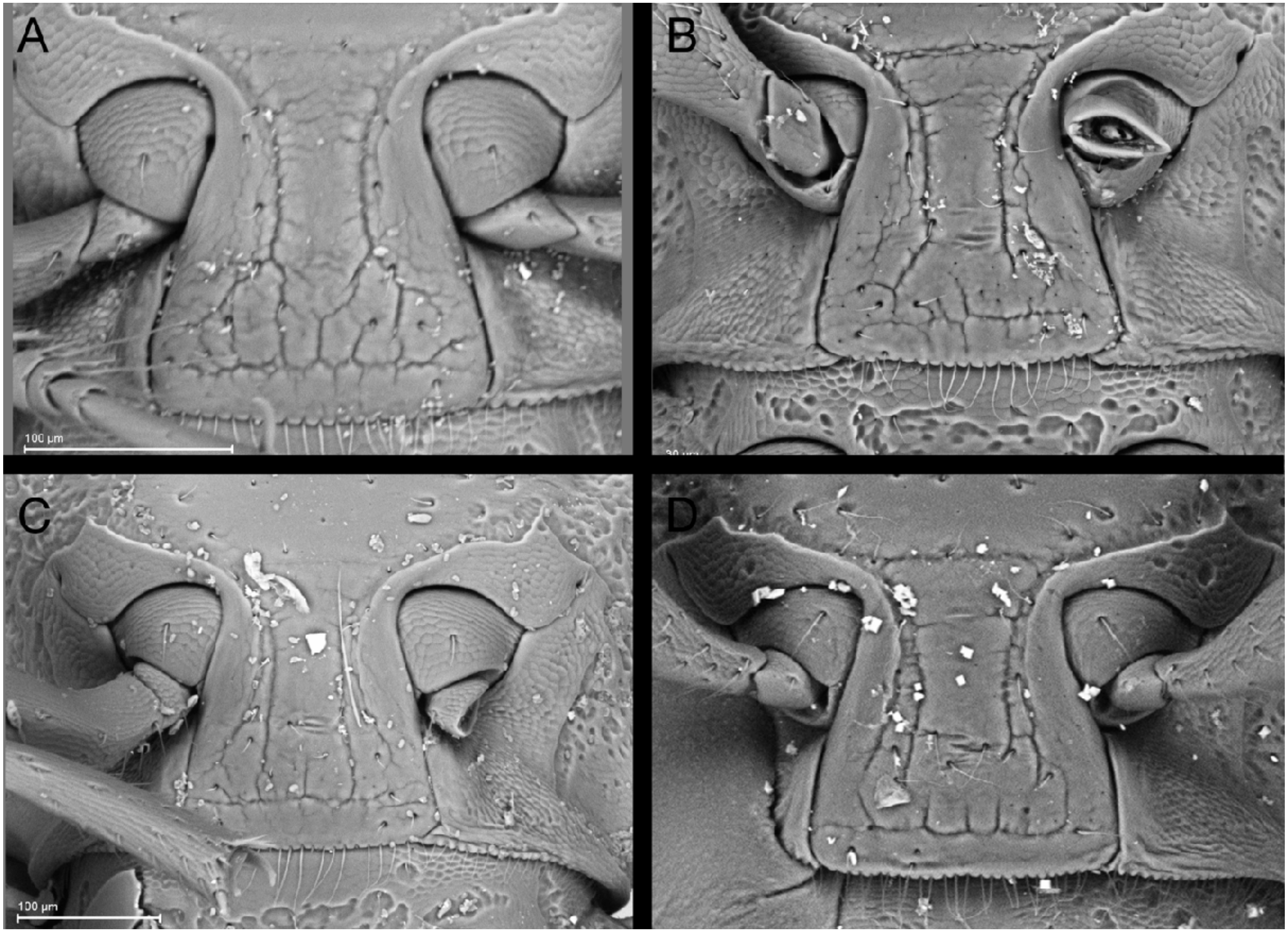

Figure 7.39. ESEM prosternal epiphysis, ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

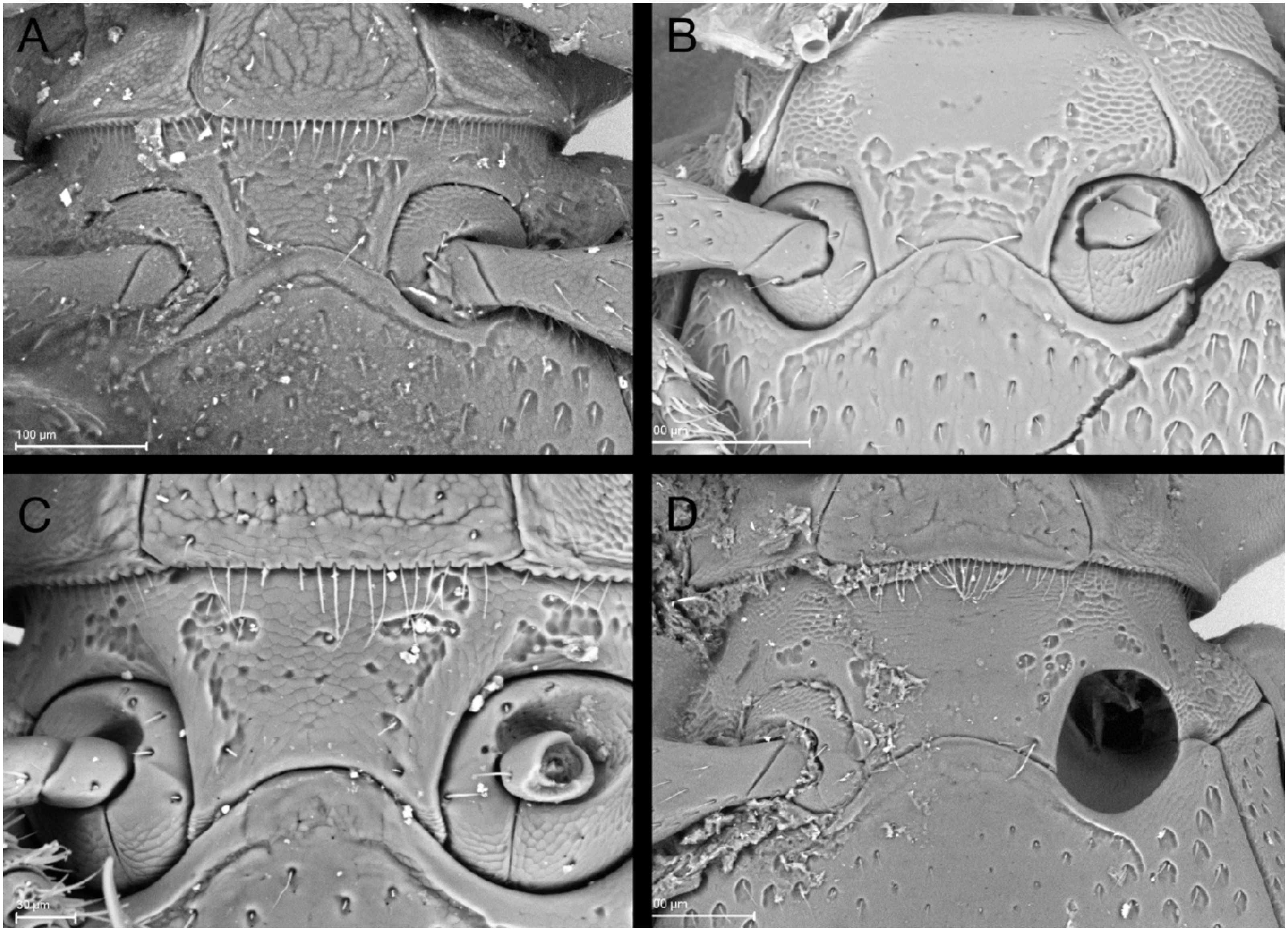

Figure 7.40. ESEM mesoventrite, ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

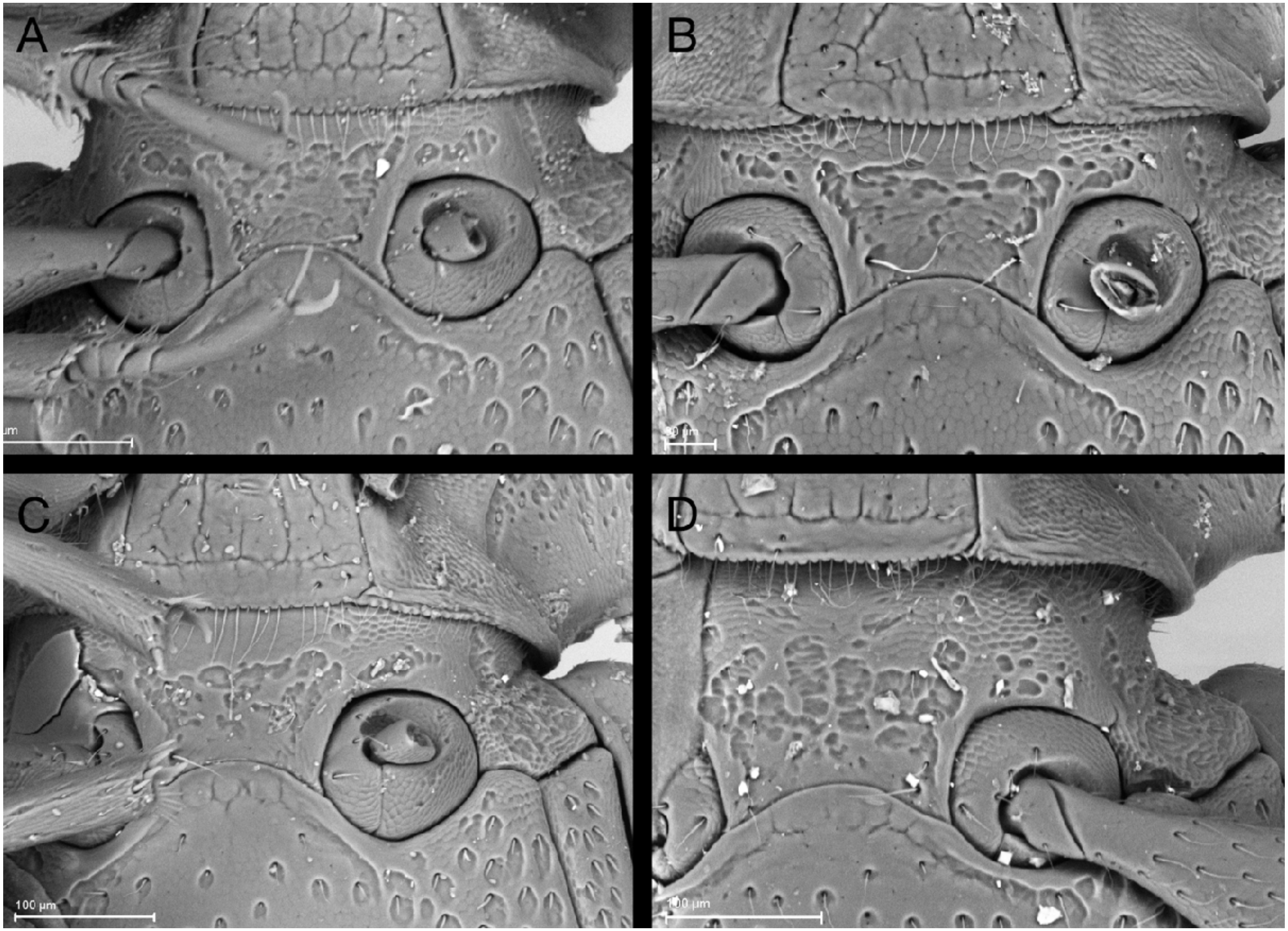

Figure 7.41. ESEM mesoventrite, ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

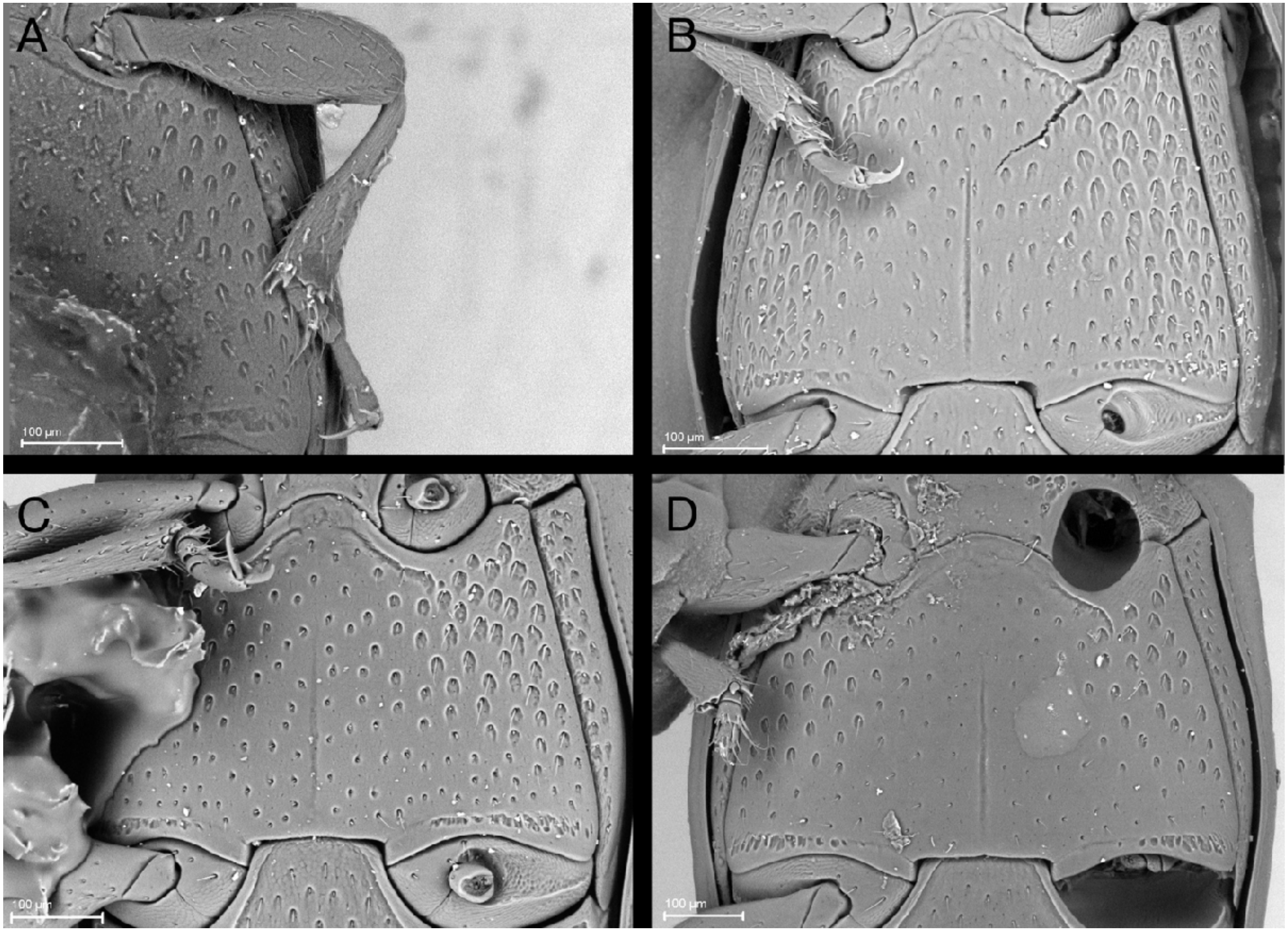

Figure 7.42. ESEM metaventrite, ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

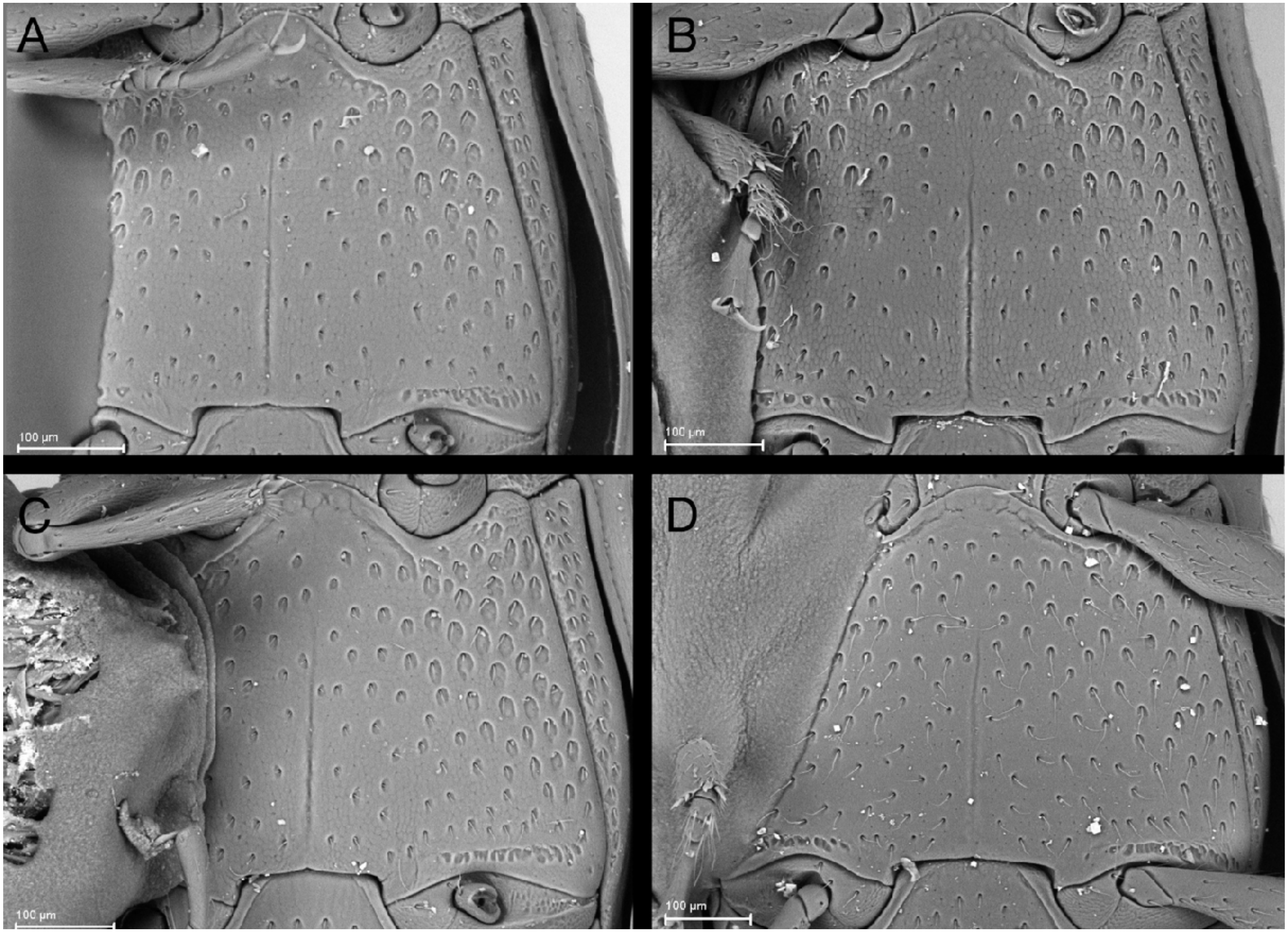

Figure 7.43. ESEM metaventrite, ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

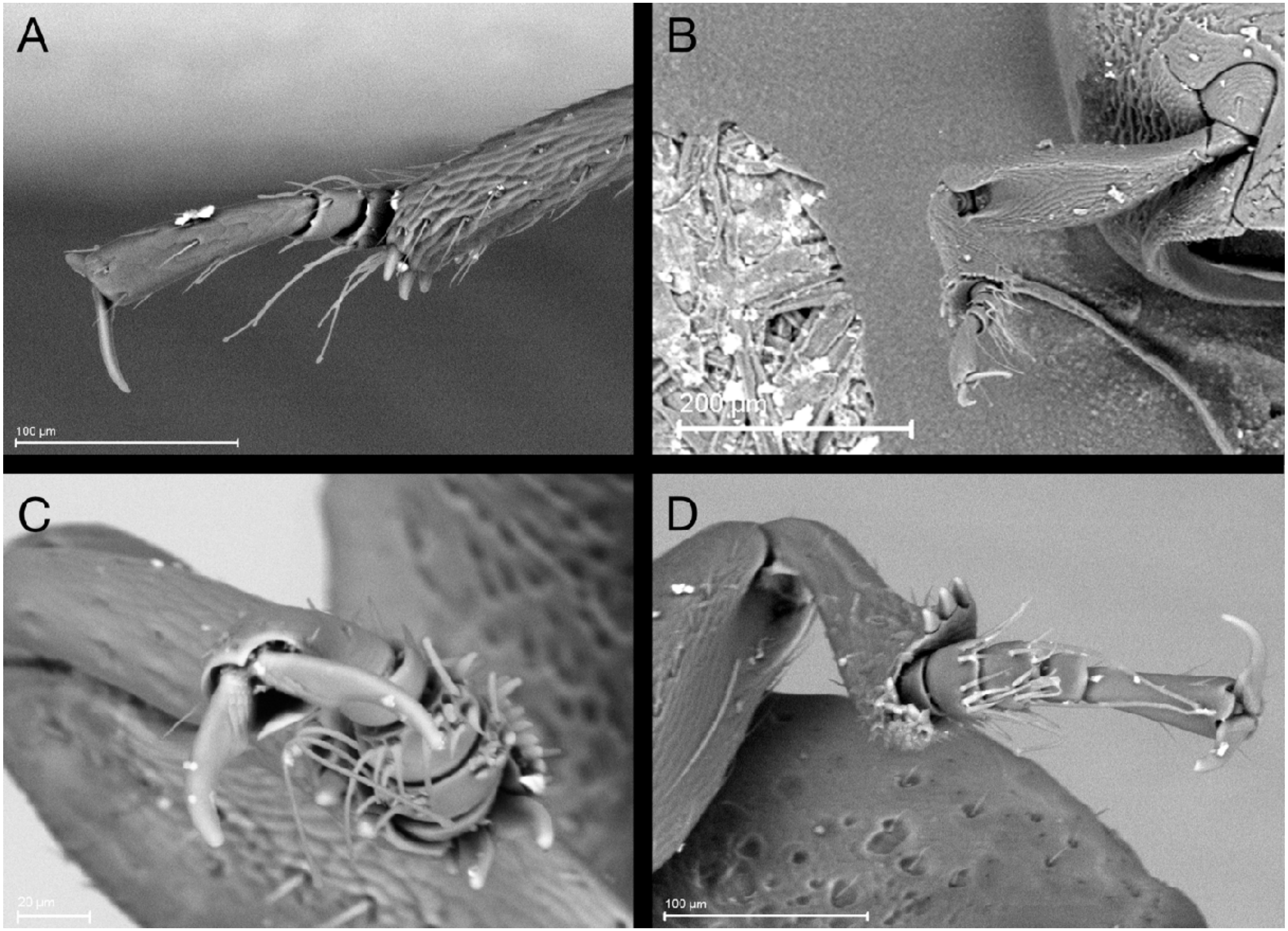

Figure 7.44. ESEM protarsus (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

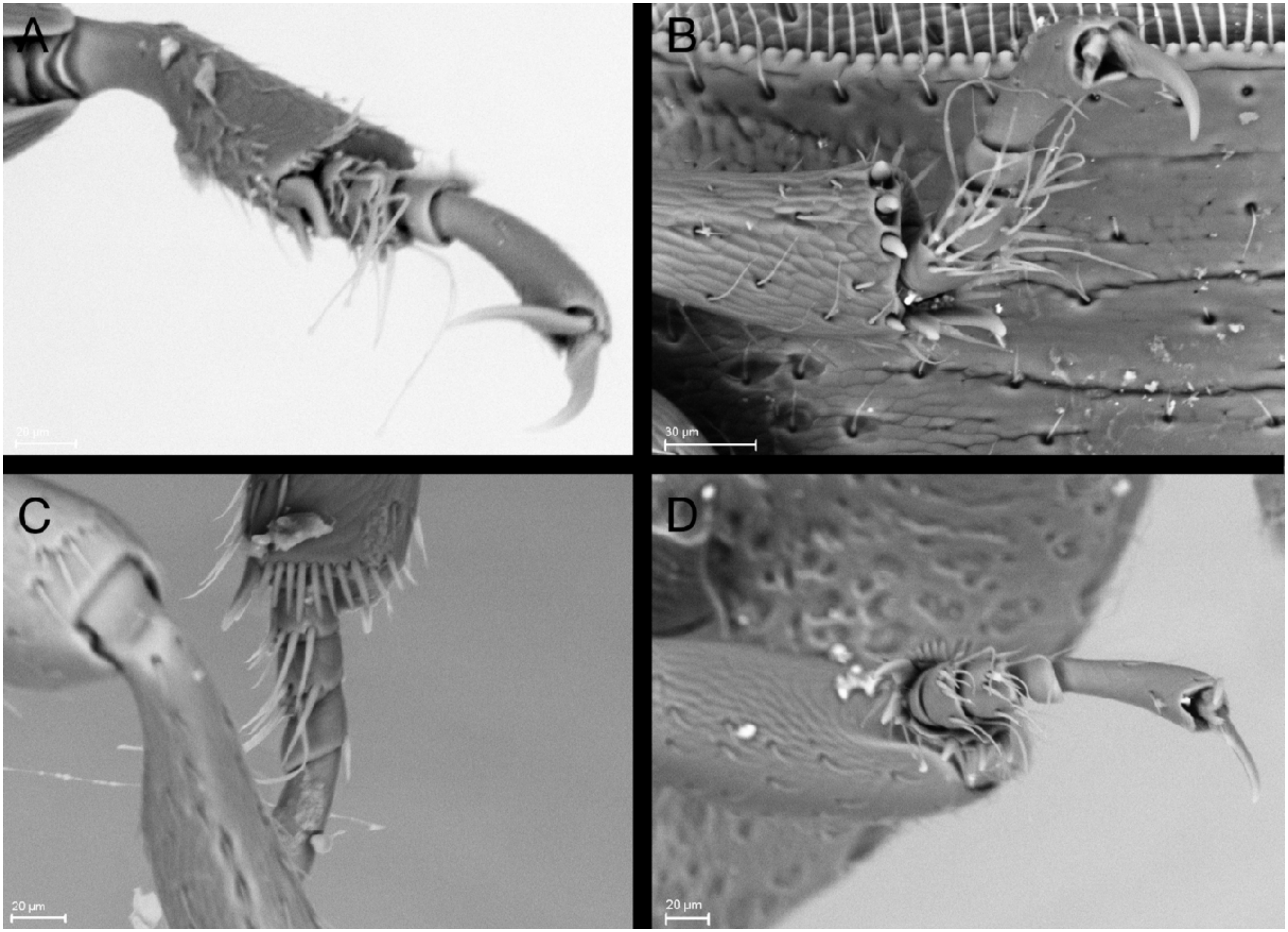

Figure 7.45. ESEM protarsus *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

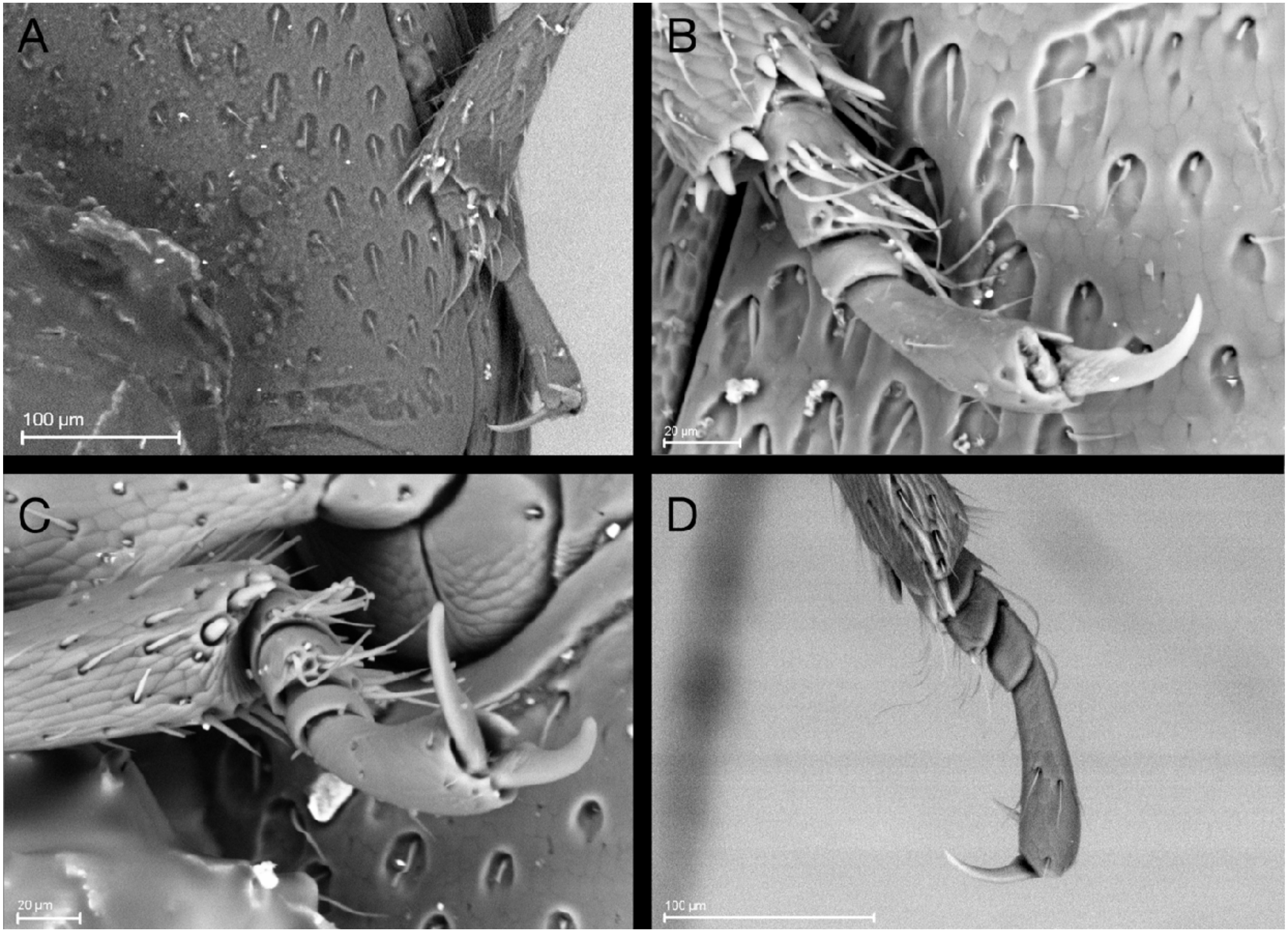

Figure 7.46. ESEM mesotarsus (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

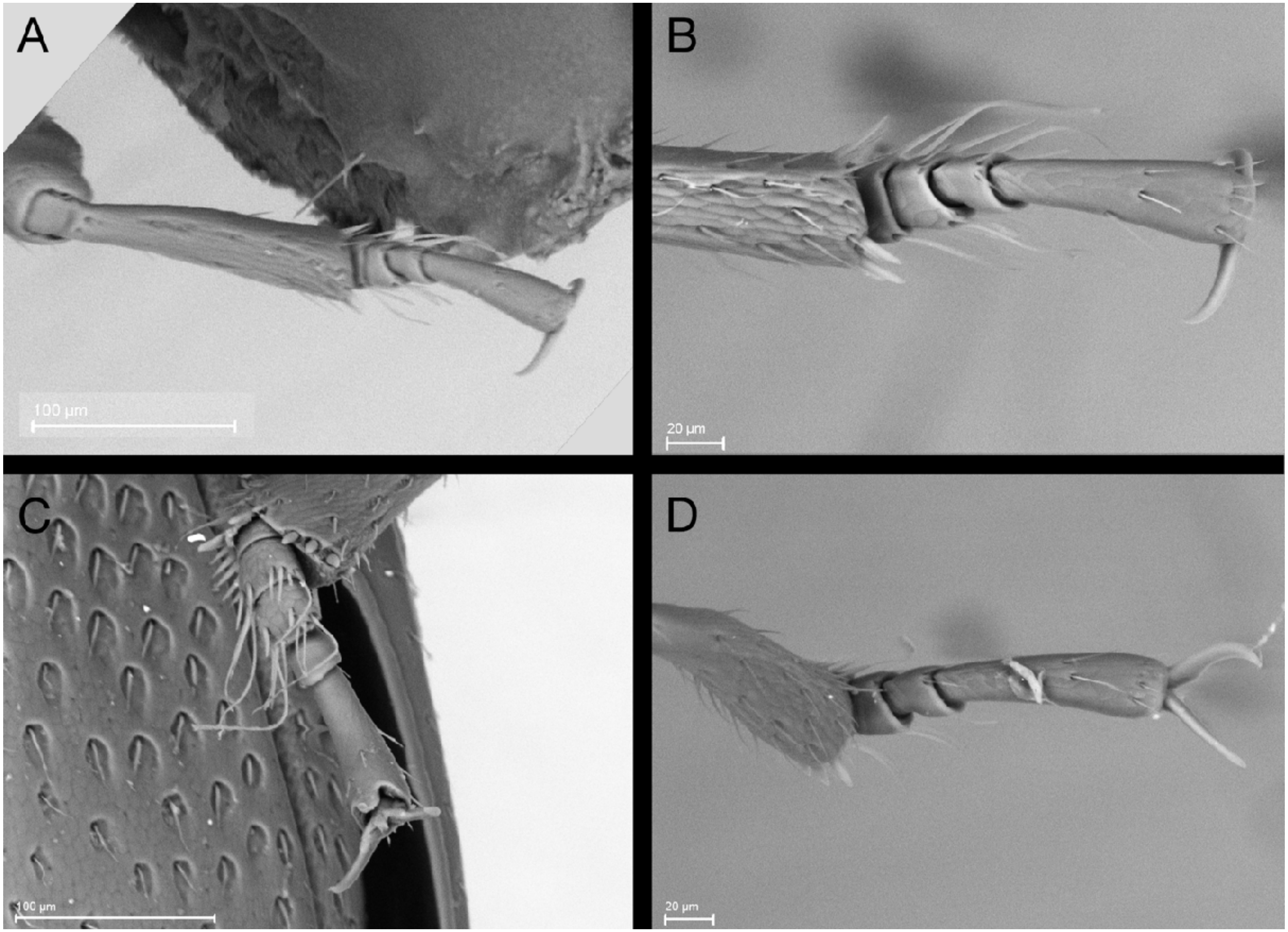

Figure 7.47. ESEM mesotarsus *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

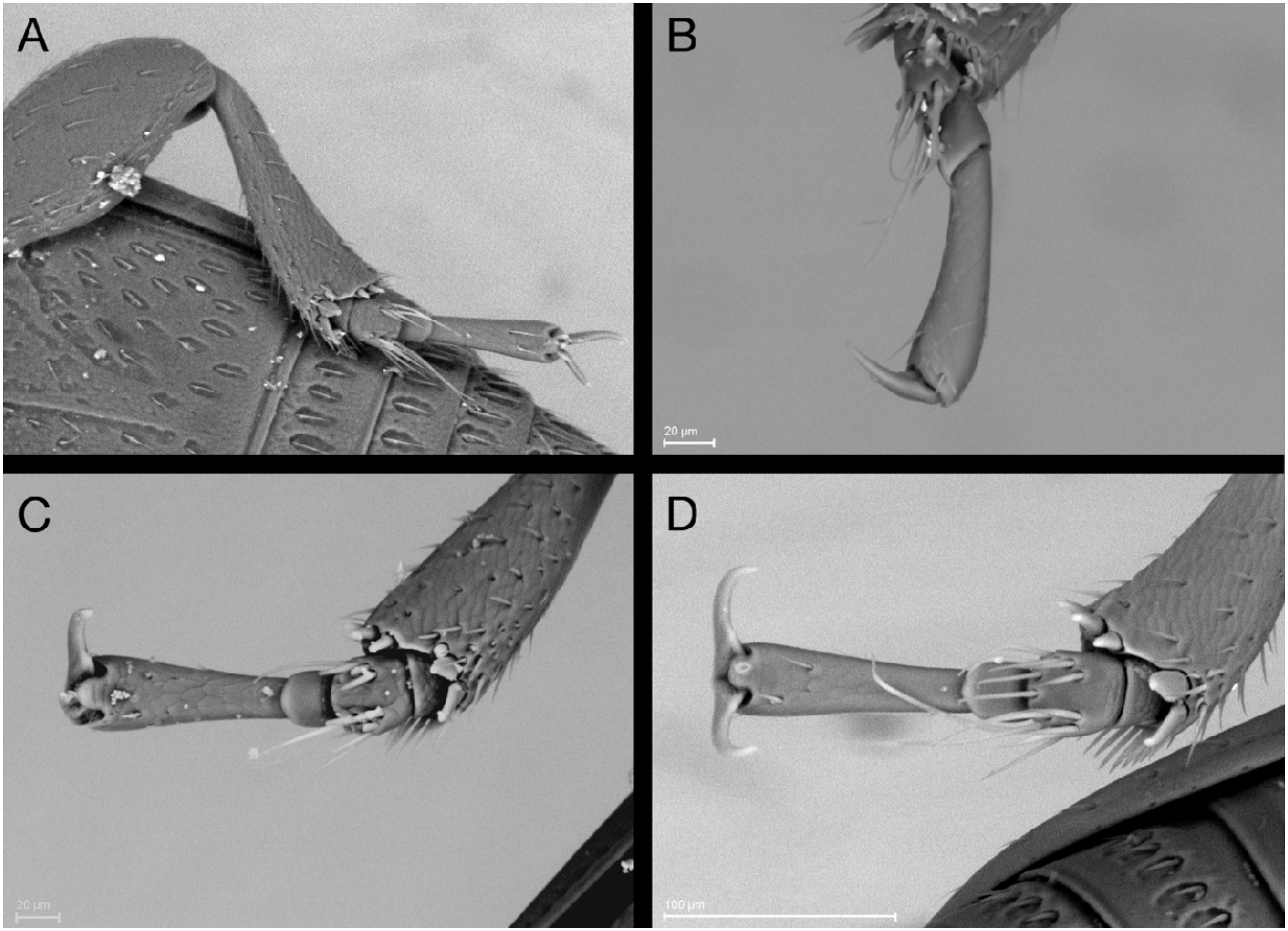

Figure 7.48 ESEM metatarsus (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

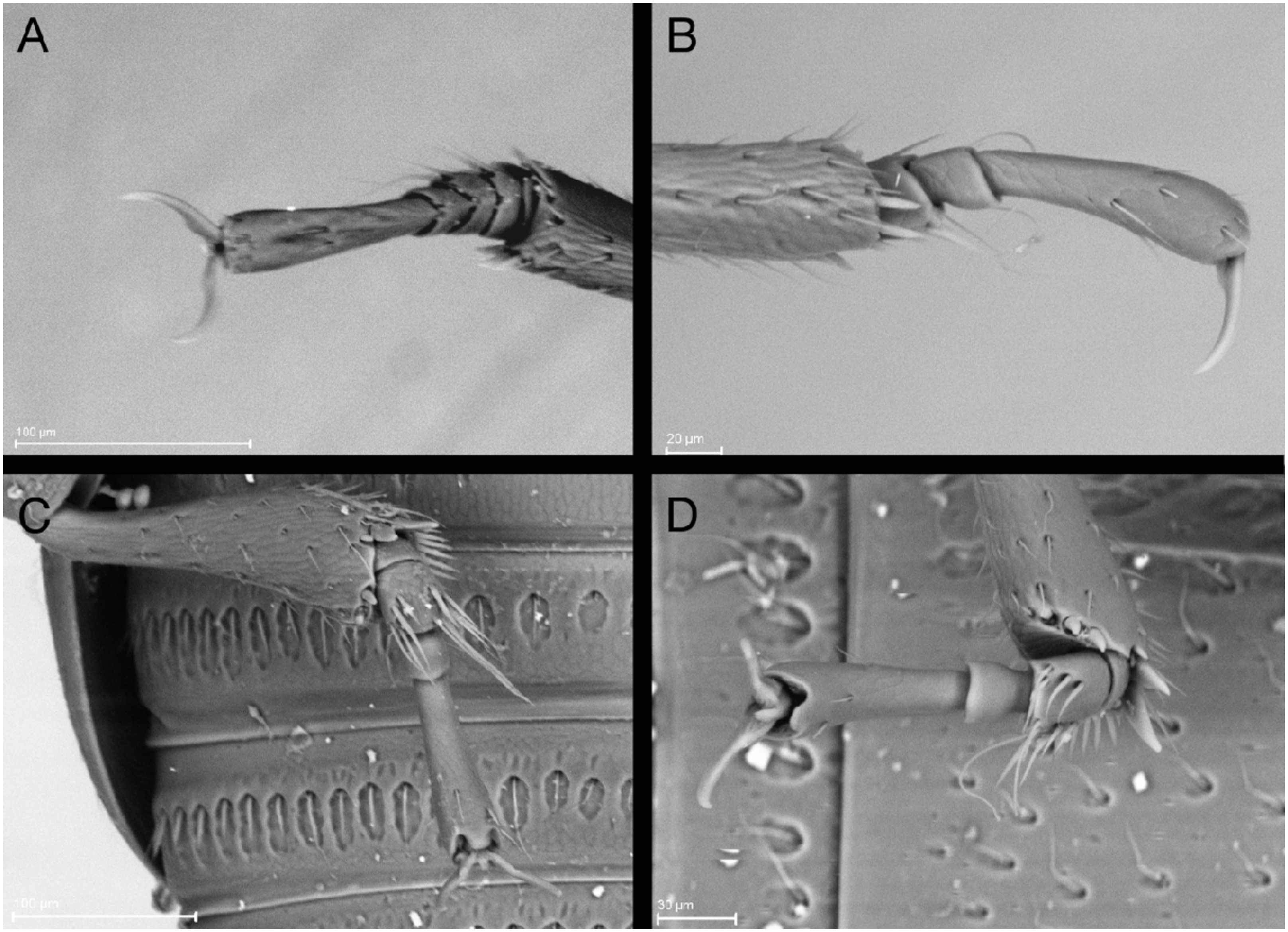

Figure 7.49. ESEM metatarsus *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

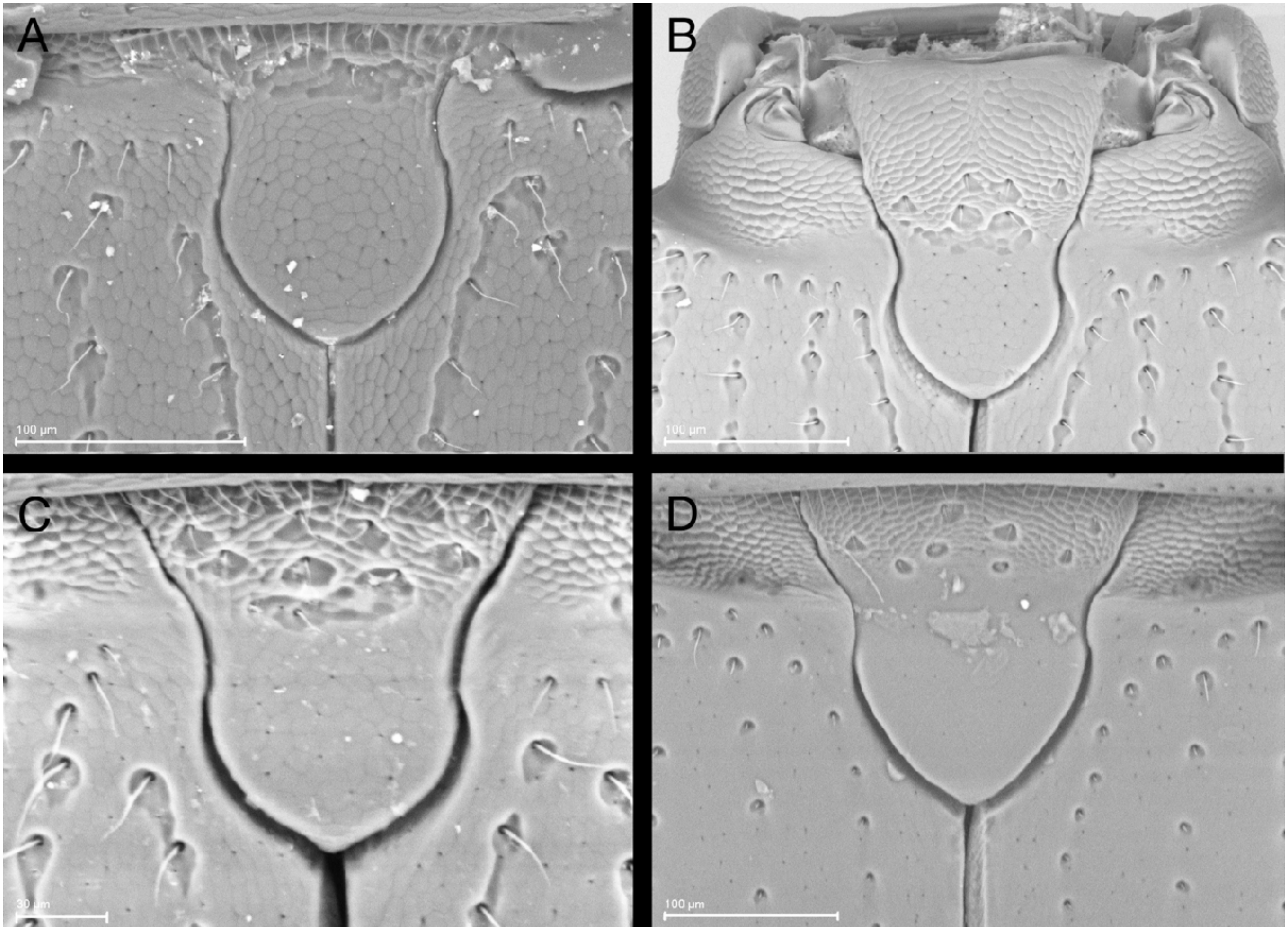

Figure 7.50. ESEM scutellum, dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

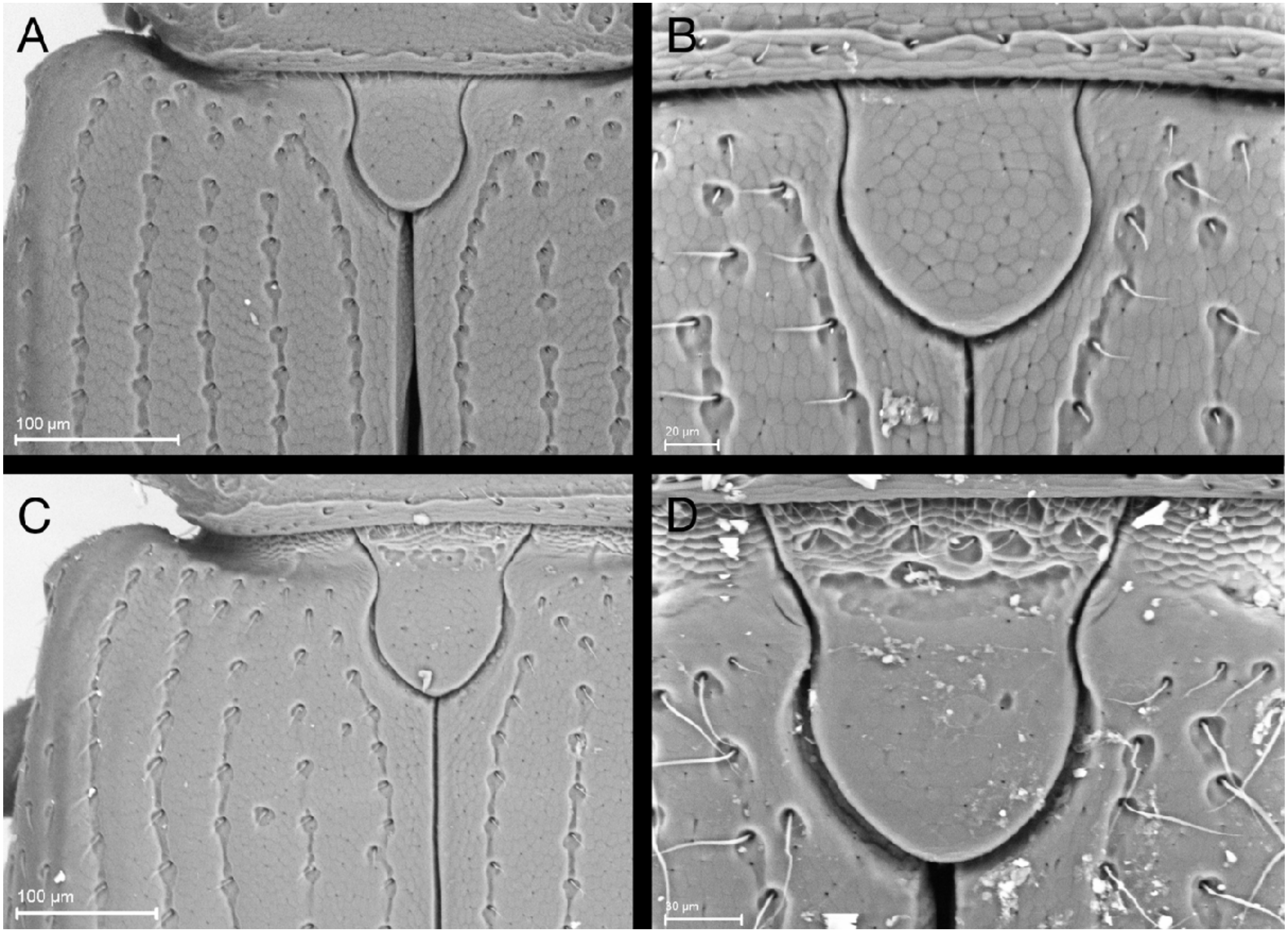

Figure 7.51. ESEM scutellum, dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

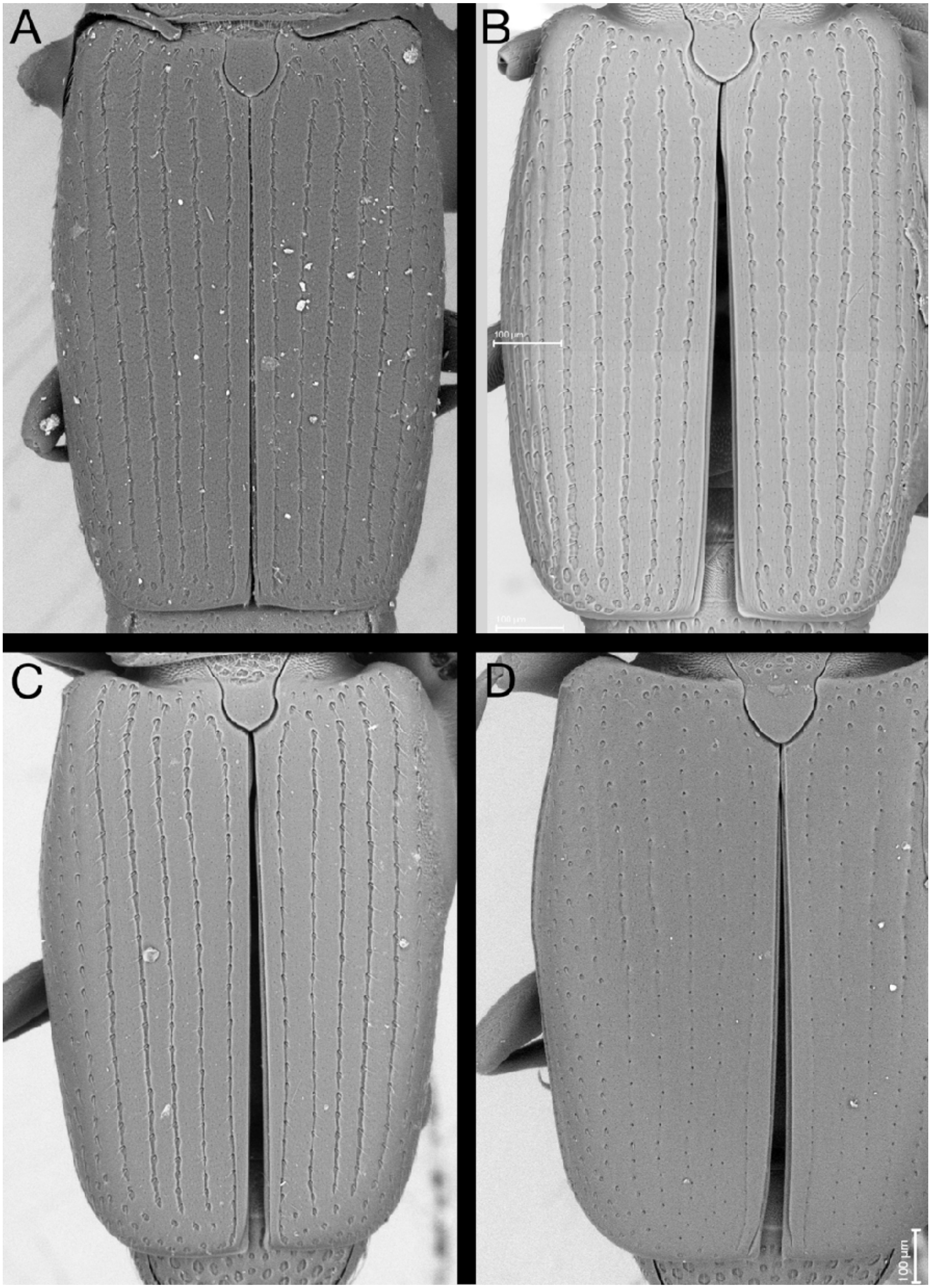

Figure 7.52. ESEM elytra dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

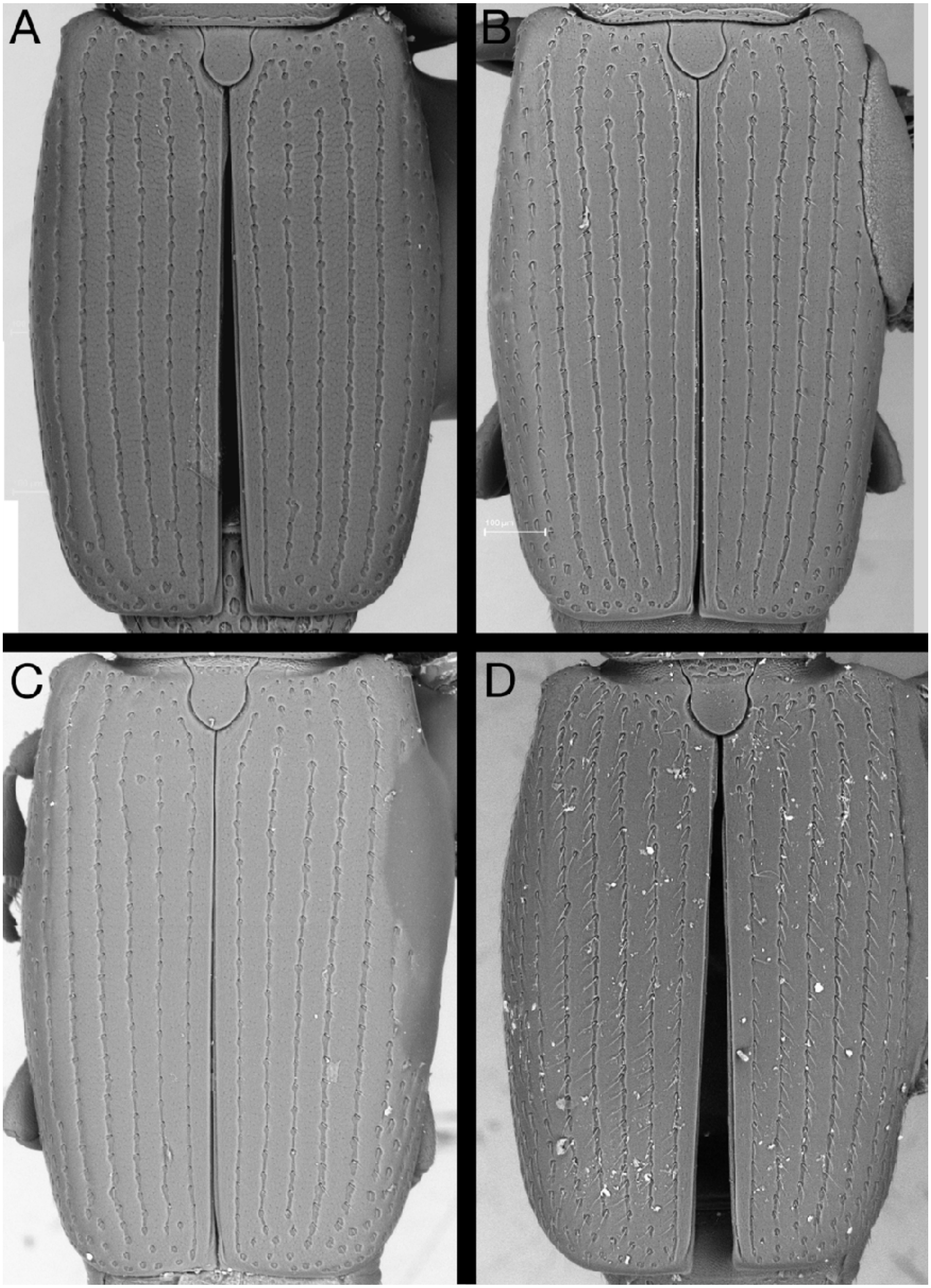

Figure 7.53. ESEM elytra, dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) *N. striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

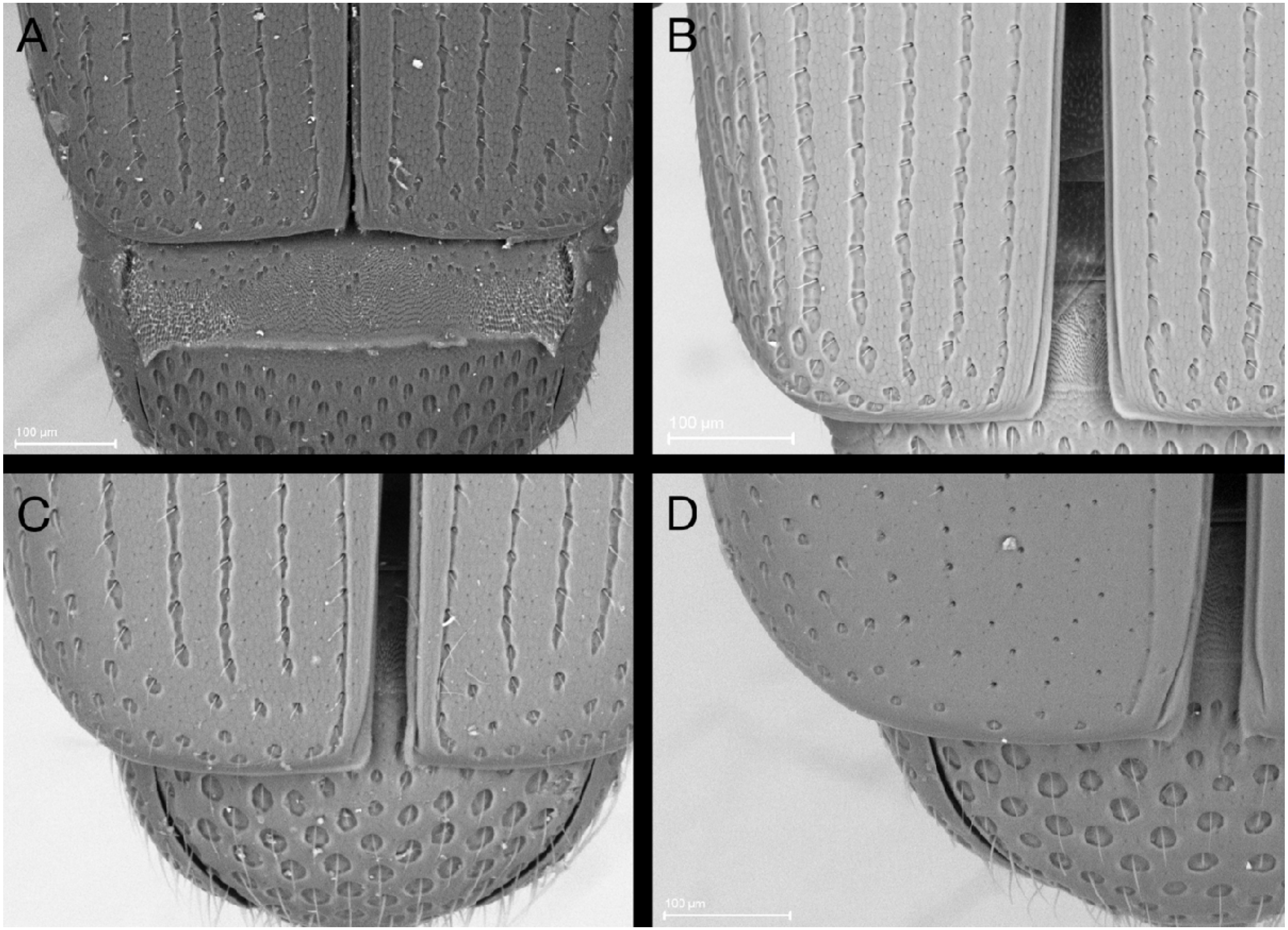

Figure 7.54. ESEM elytral apex dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

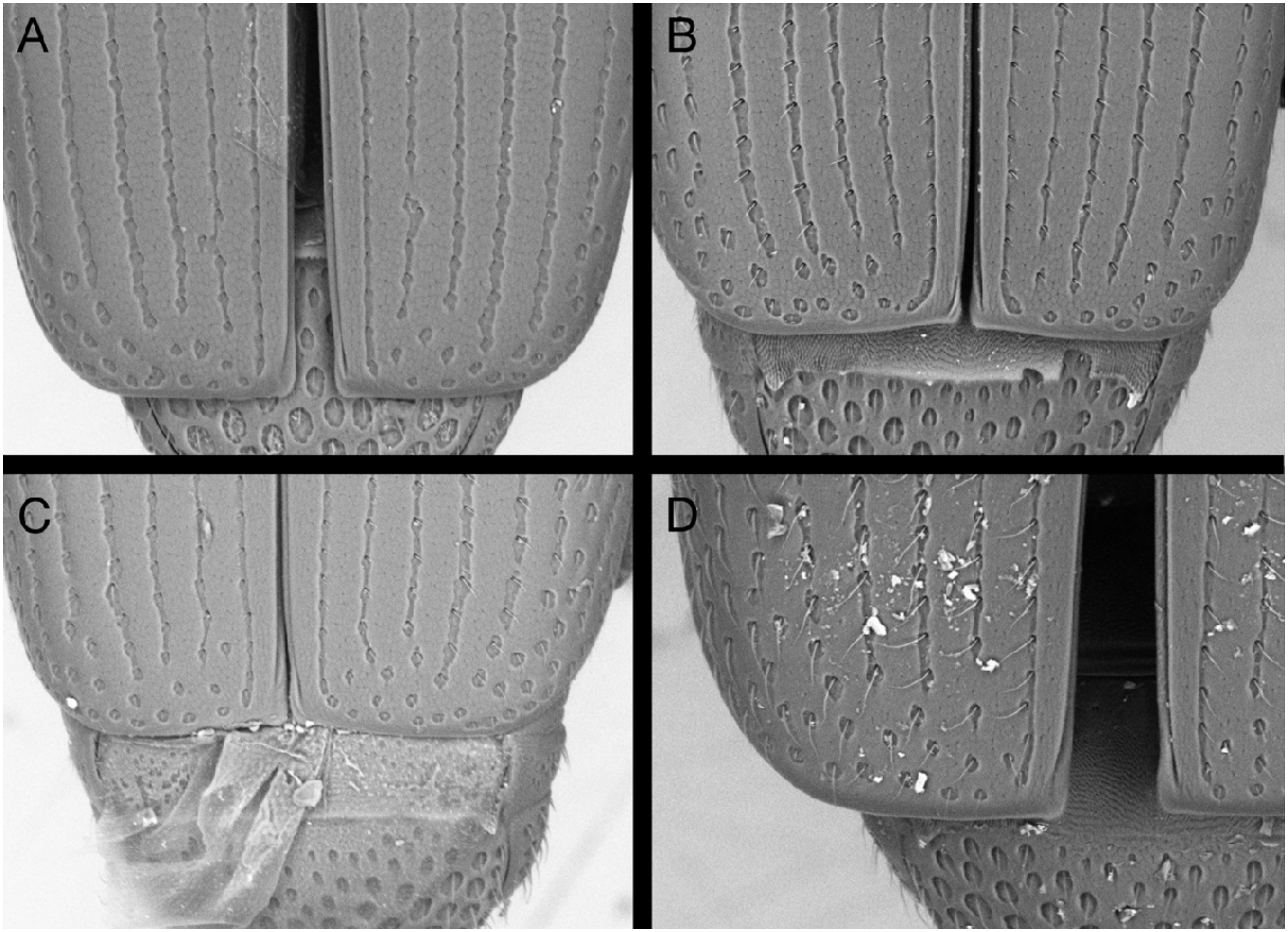

Figure 7.55. ESEM elytral apex, dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

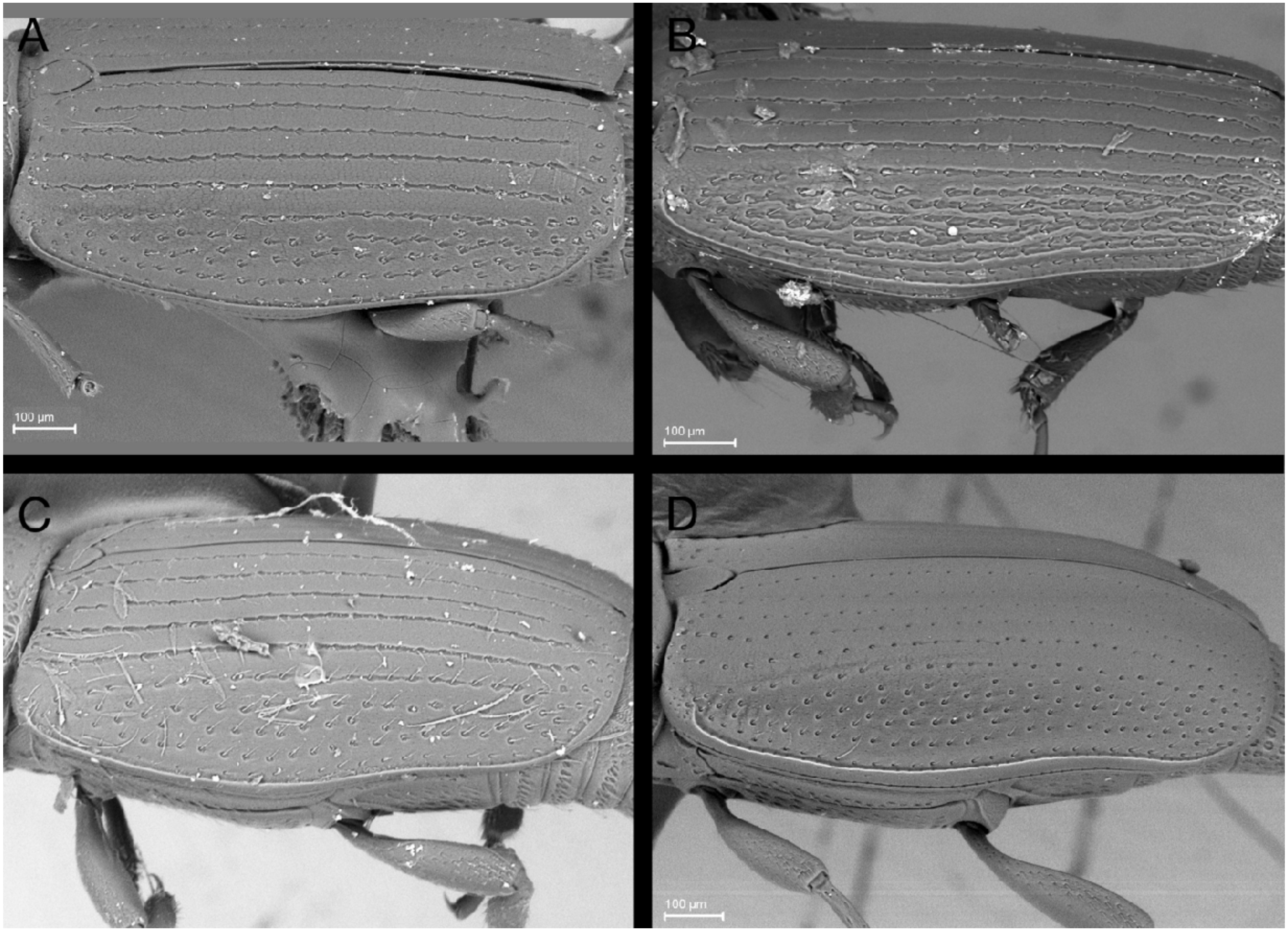

Figure 7.56. ESEM elytra, lateral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

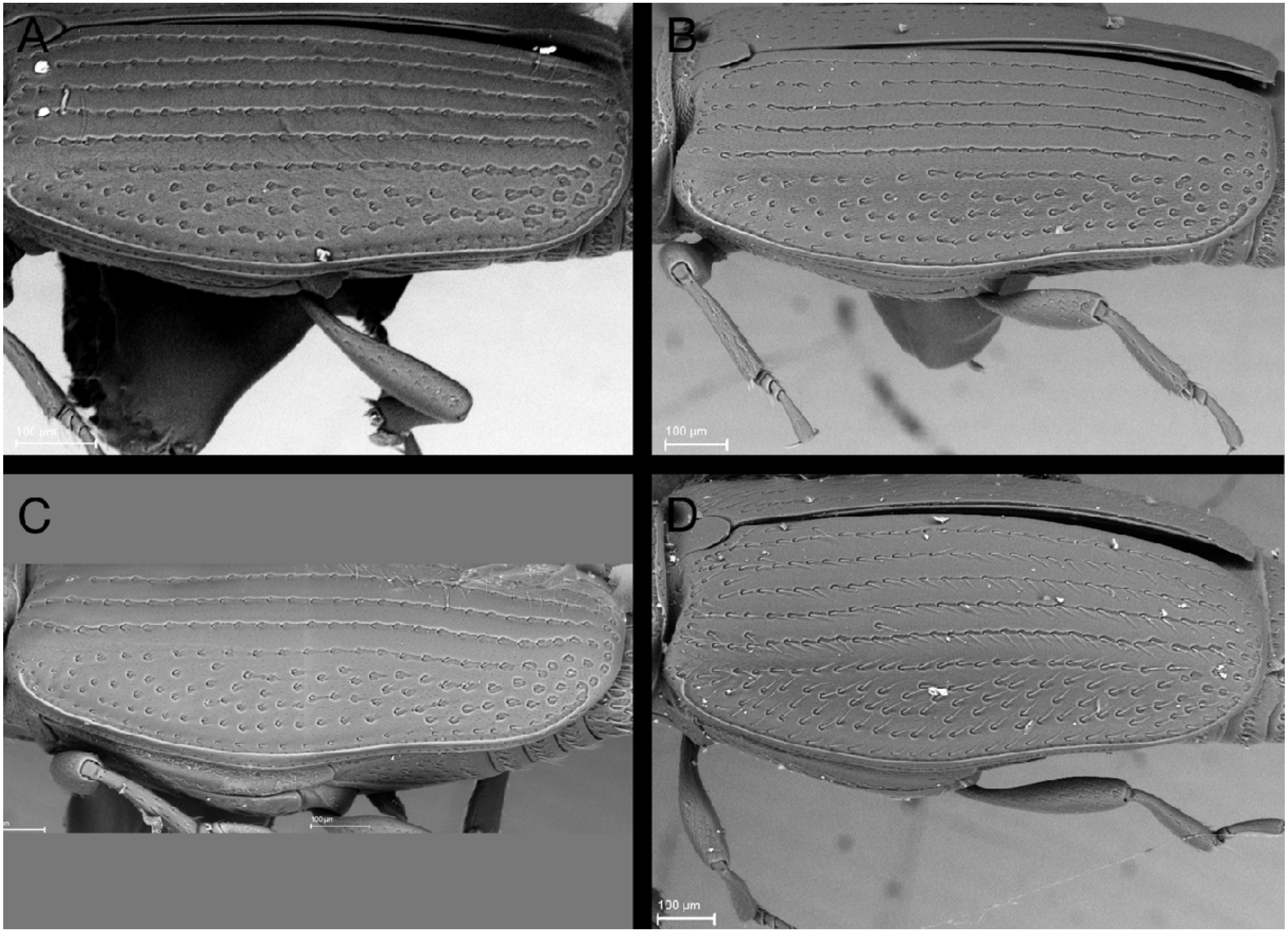

Figure 7.57. ESEM elytra, lateral *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

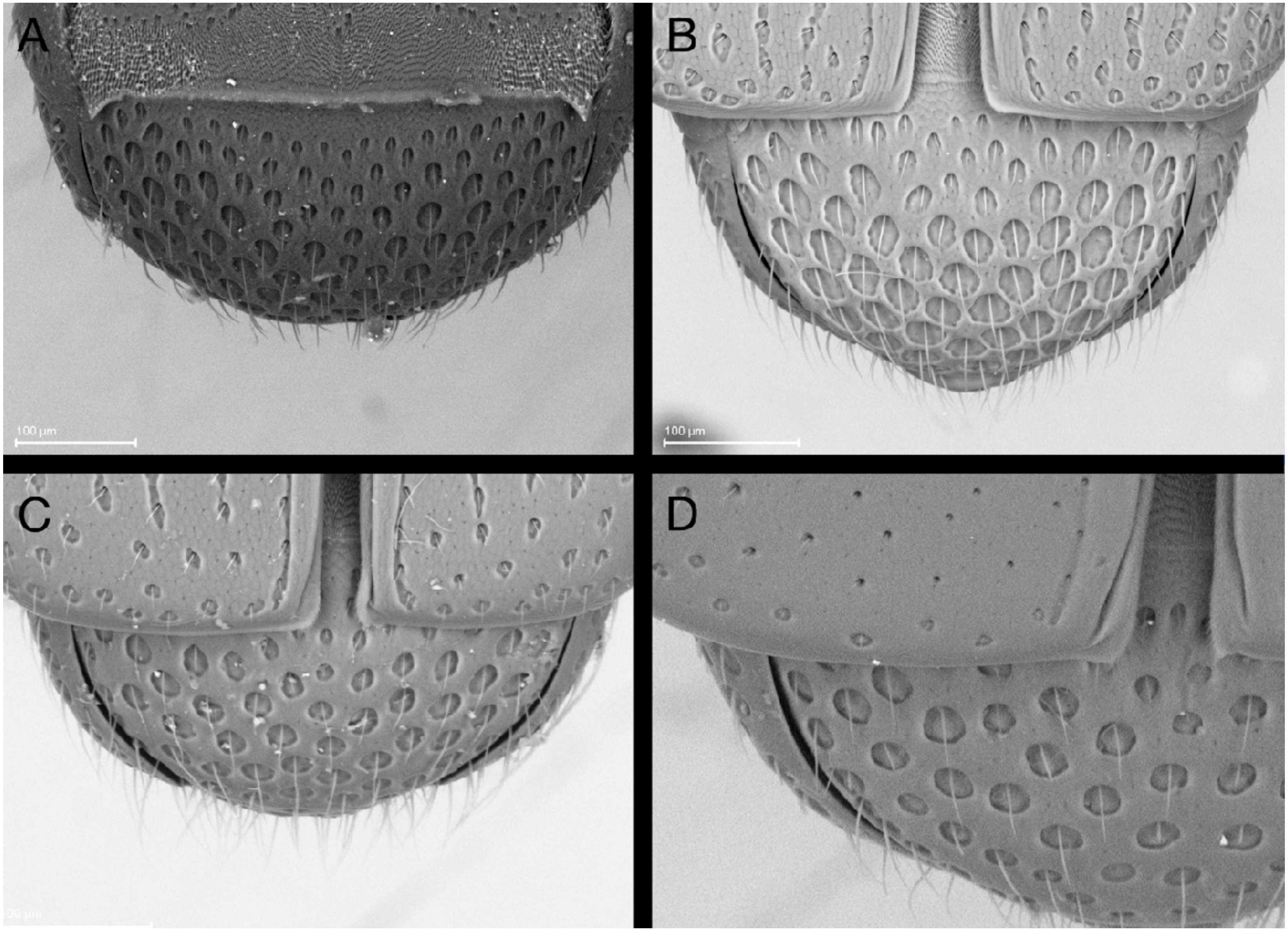

Figure 7.58. ESEM pygidium, dorsal (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

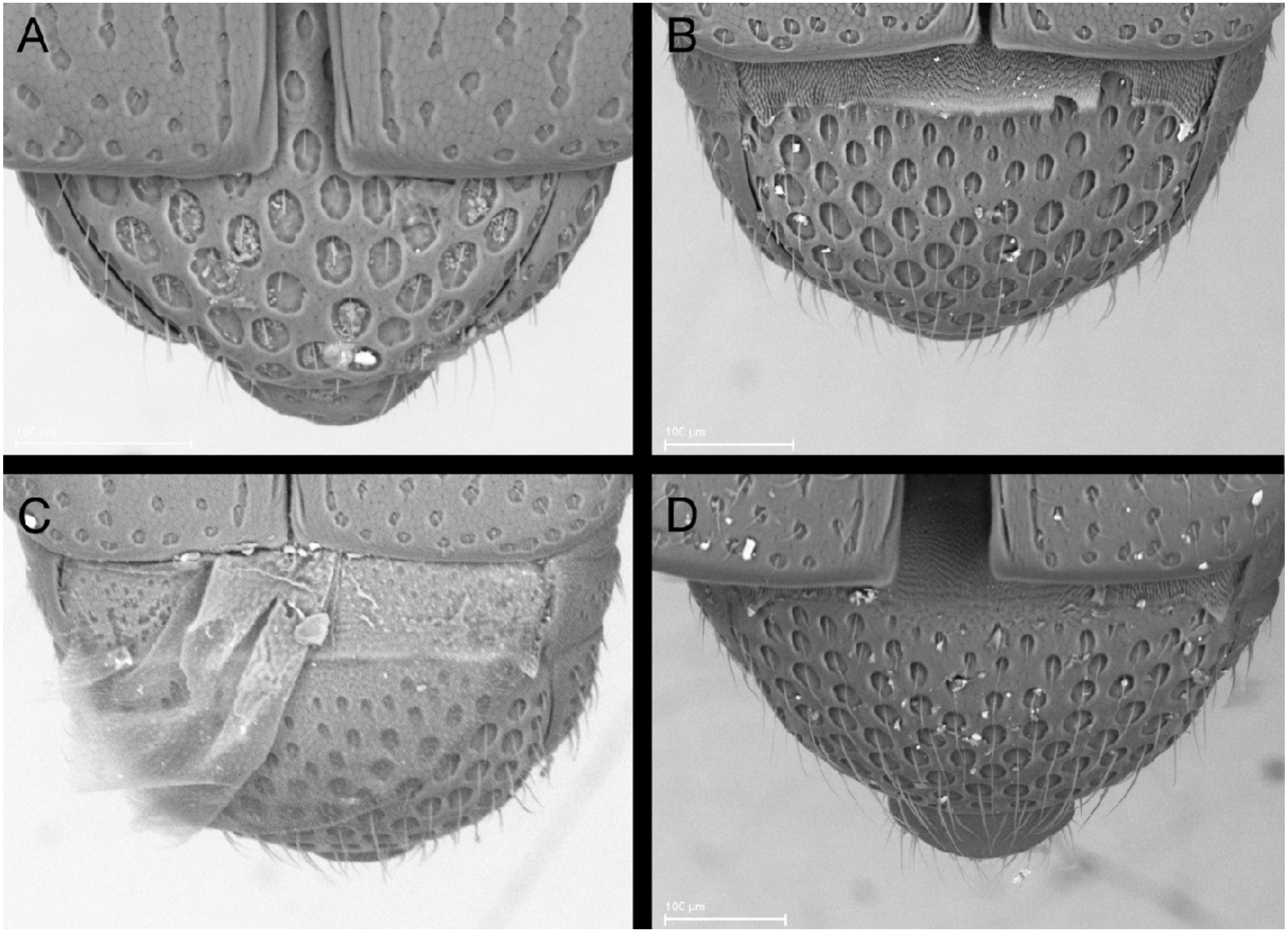

Figure 7.59. ESEM pygidium, dorsal *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

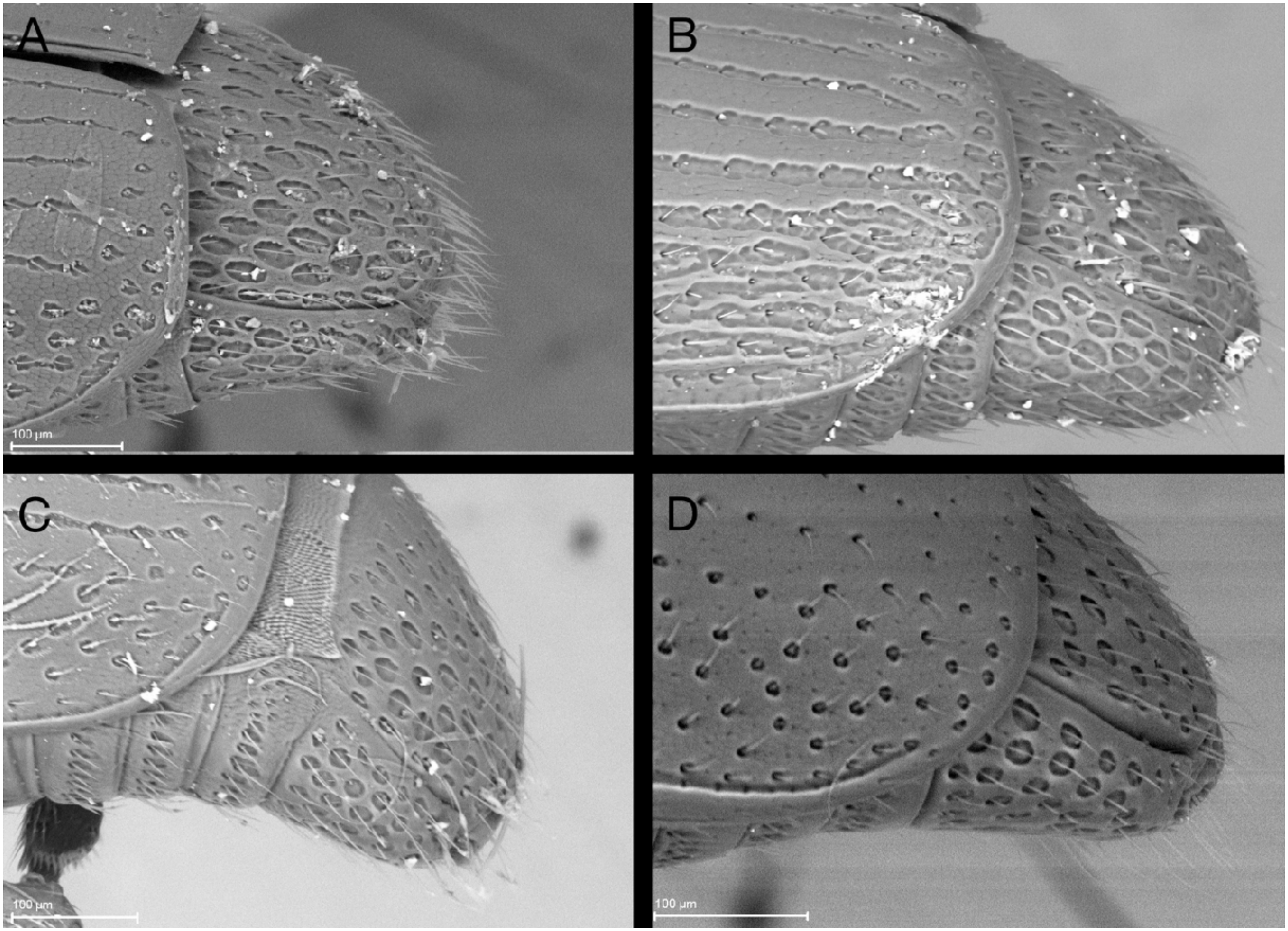

Figure 7.60. ESEM abdominal apex, lateral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

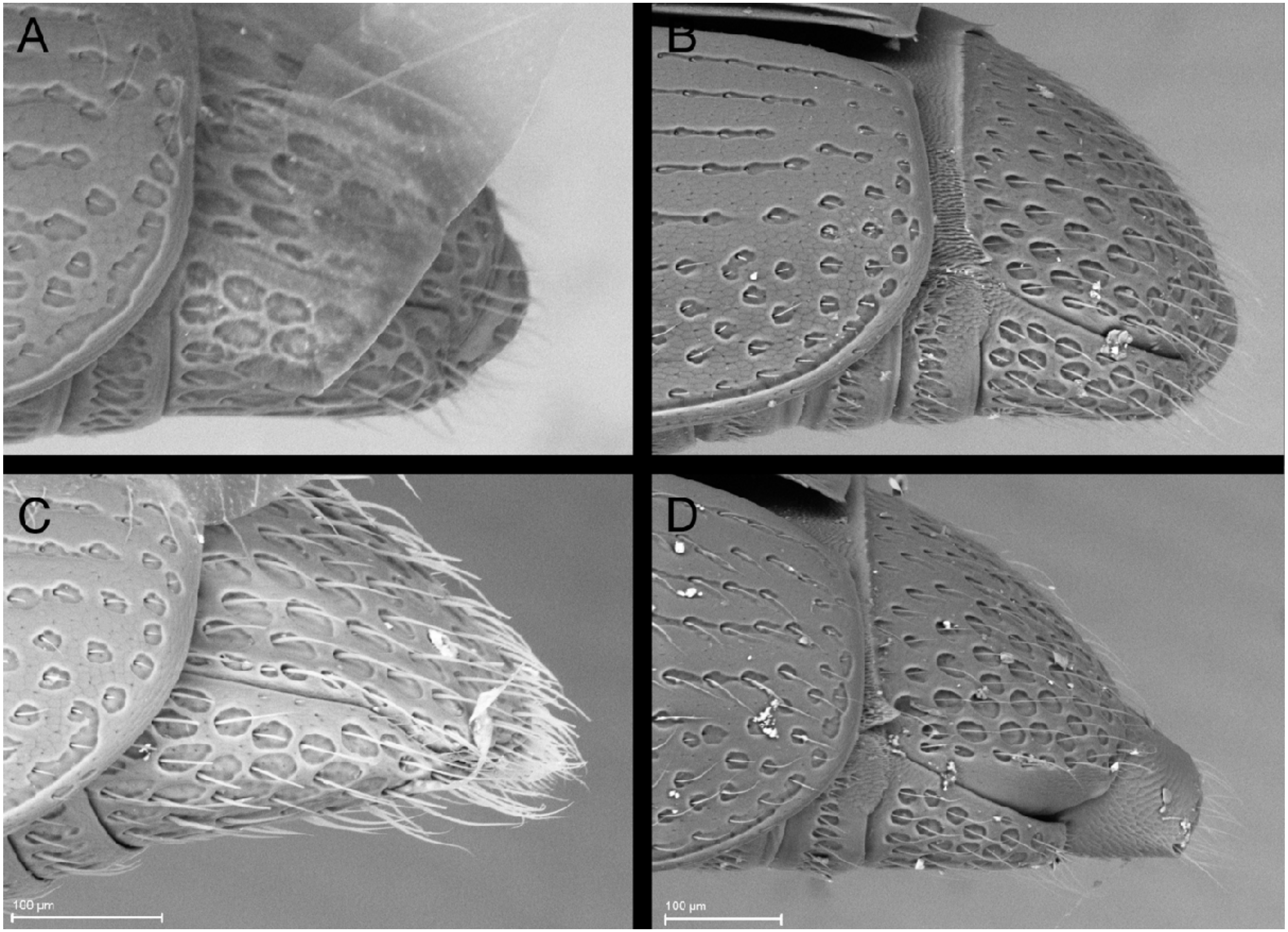

Figure 7.61. ESEM abdominal apex, lateral *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

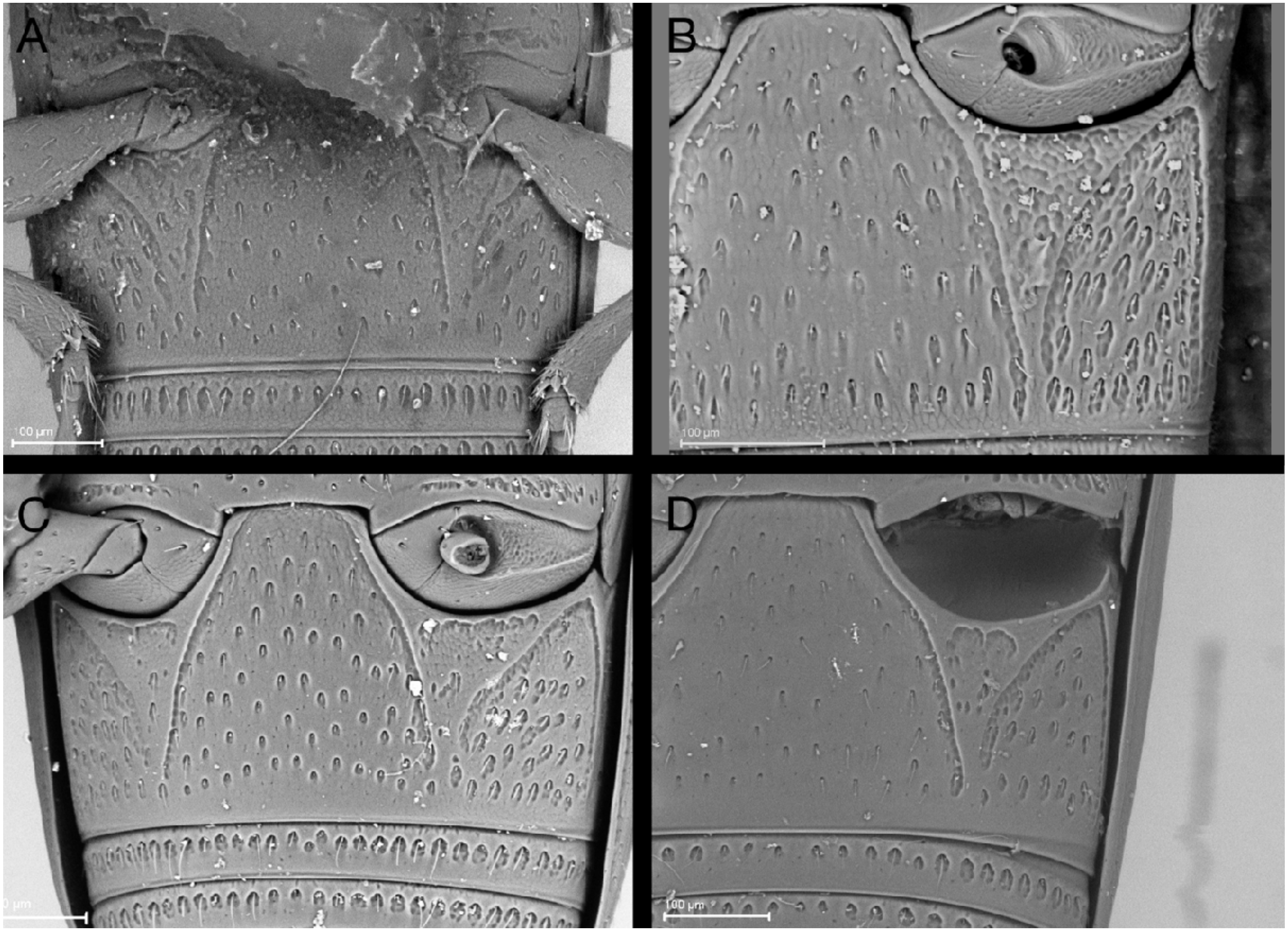

Figure 7.62. ESEM ventrite I, ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

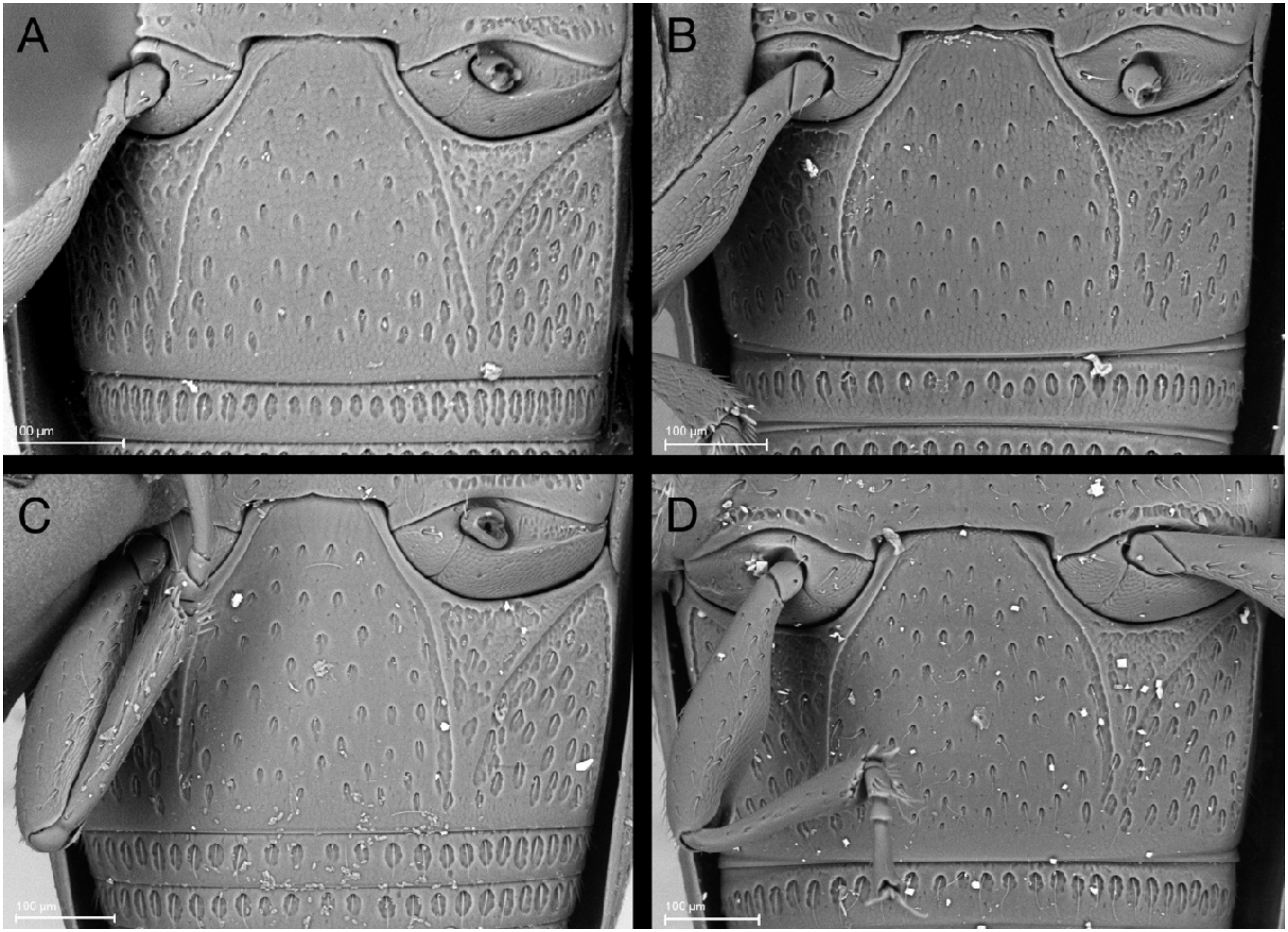

Figure 7.63. ESEM ventrite I, ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

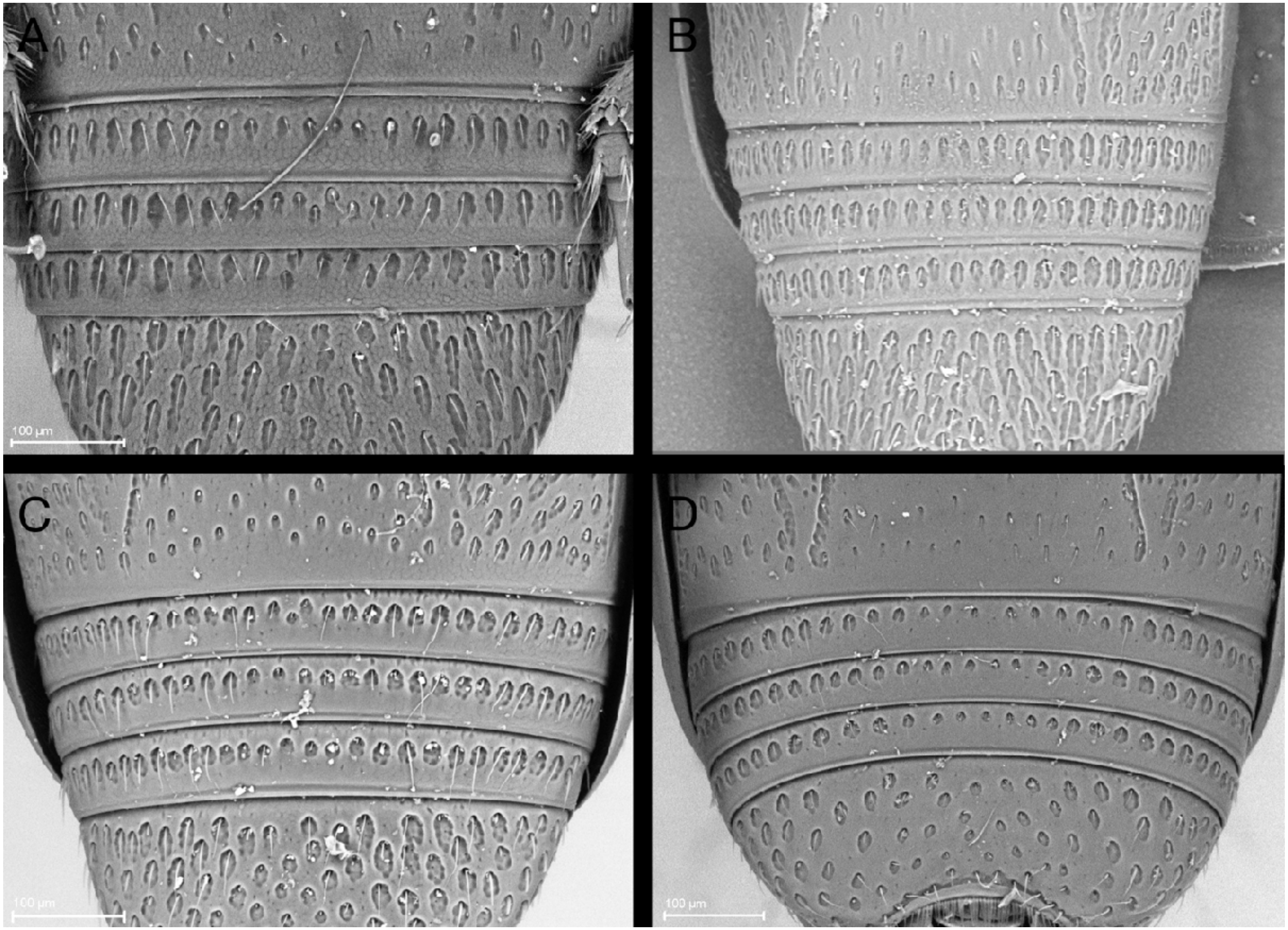

Figure 7.64. ESEM abdominal ventrites II-IV, ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

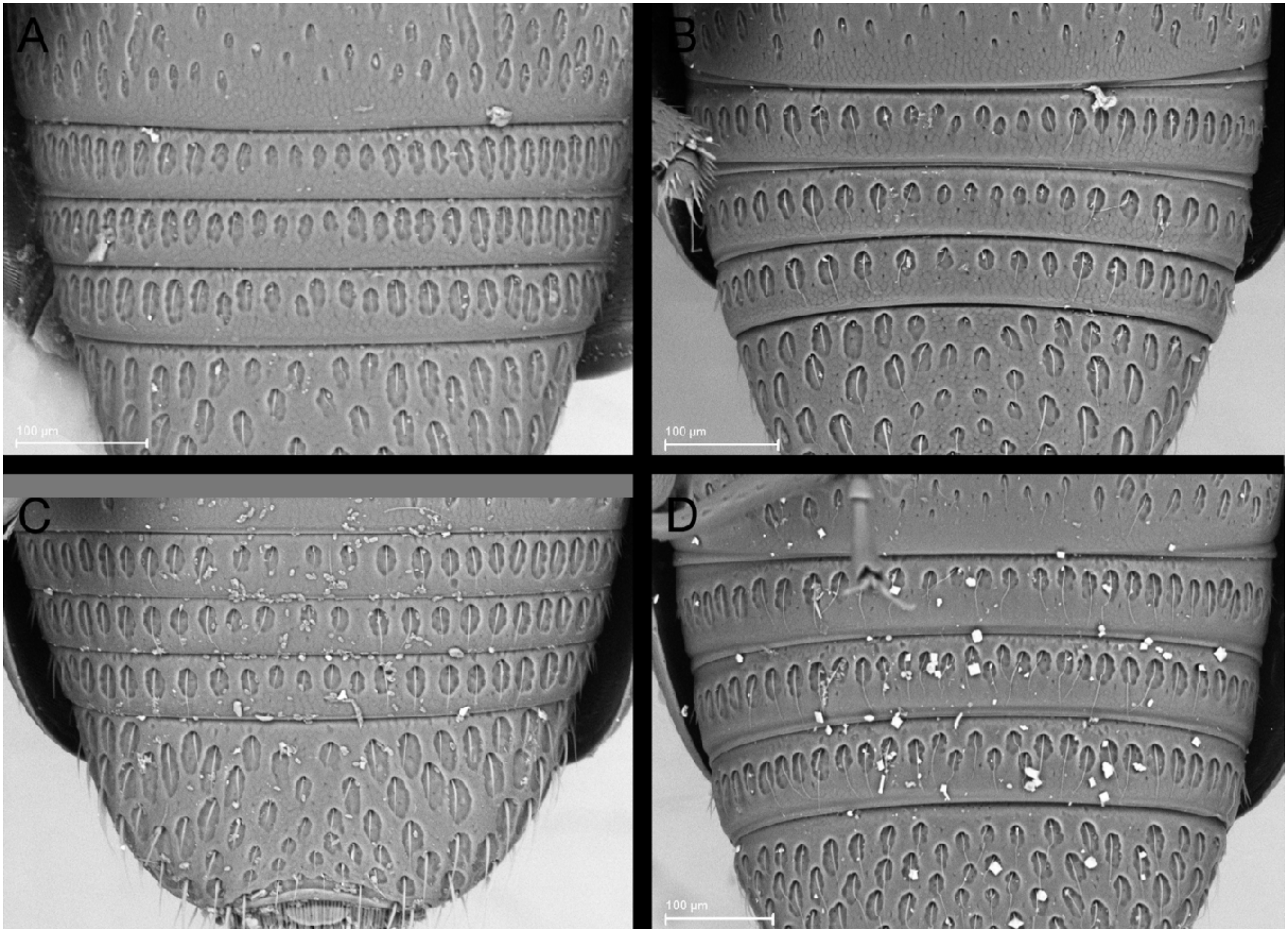

Figure 7.65. ESEM abdominal ventrites II-IV, ventral *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

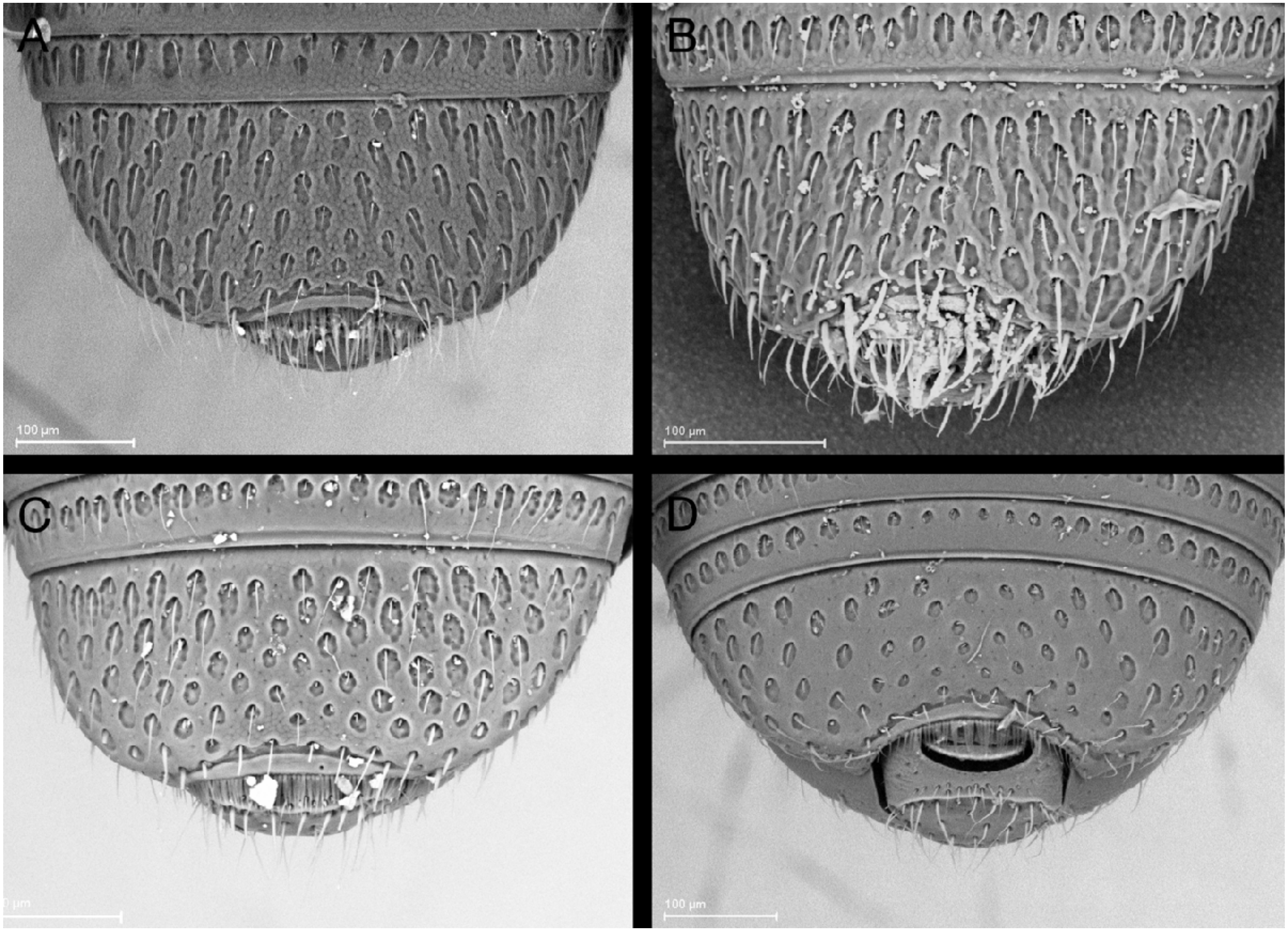

Figure 7.66. ESEM abdominal ventrite V, ventral (males) A) *N. californicum*, B) *N. ephippigerum*, C) *N. hopkinsi*, D) *Pycnotomina cavicolle*

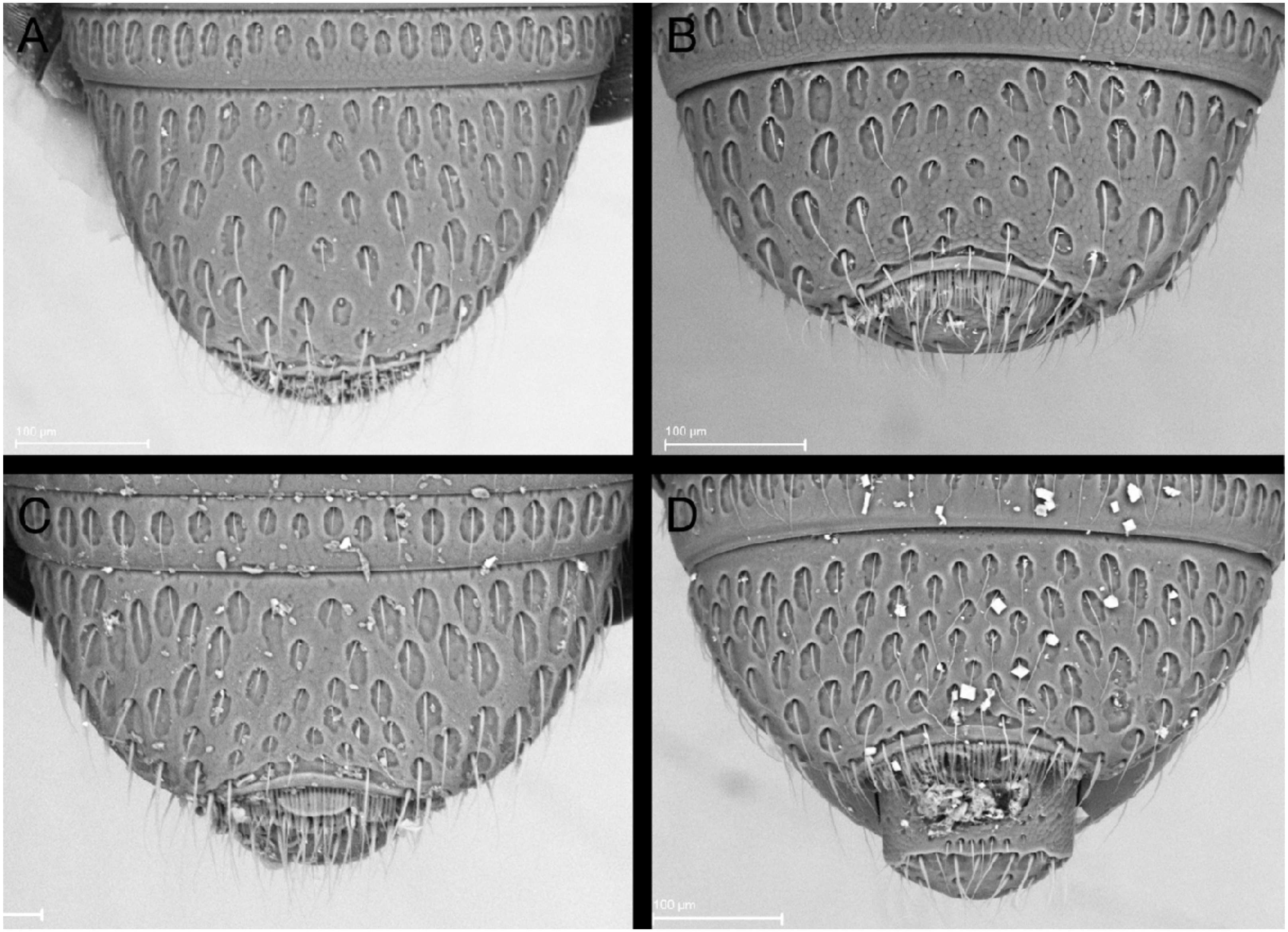

Figure 7.67. ESEM abdominal ventrite V, *Neobactridium striolatum* morphs (male, except A), A) *N. striolatum* GA (female), B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

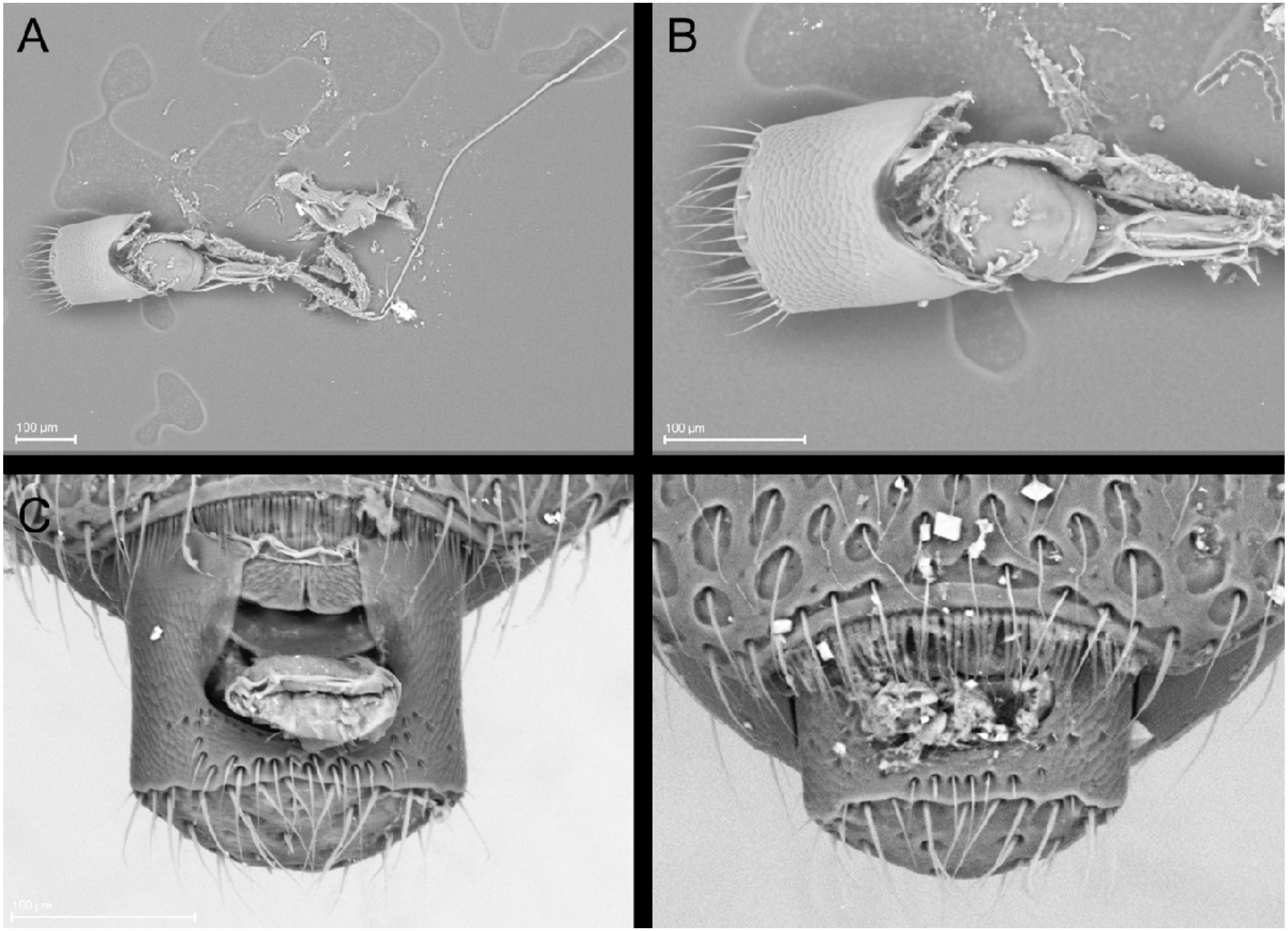

Figure 7.68. ESEM male terminalia A) *N. ephippigerum* genital capsule and aedeagus B) same as A, C) *N. striolatum* terminalia with protruding aedeagus, ventral D) *N. morphotype* genital capsule, ventral.

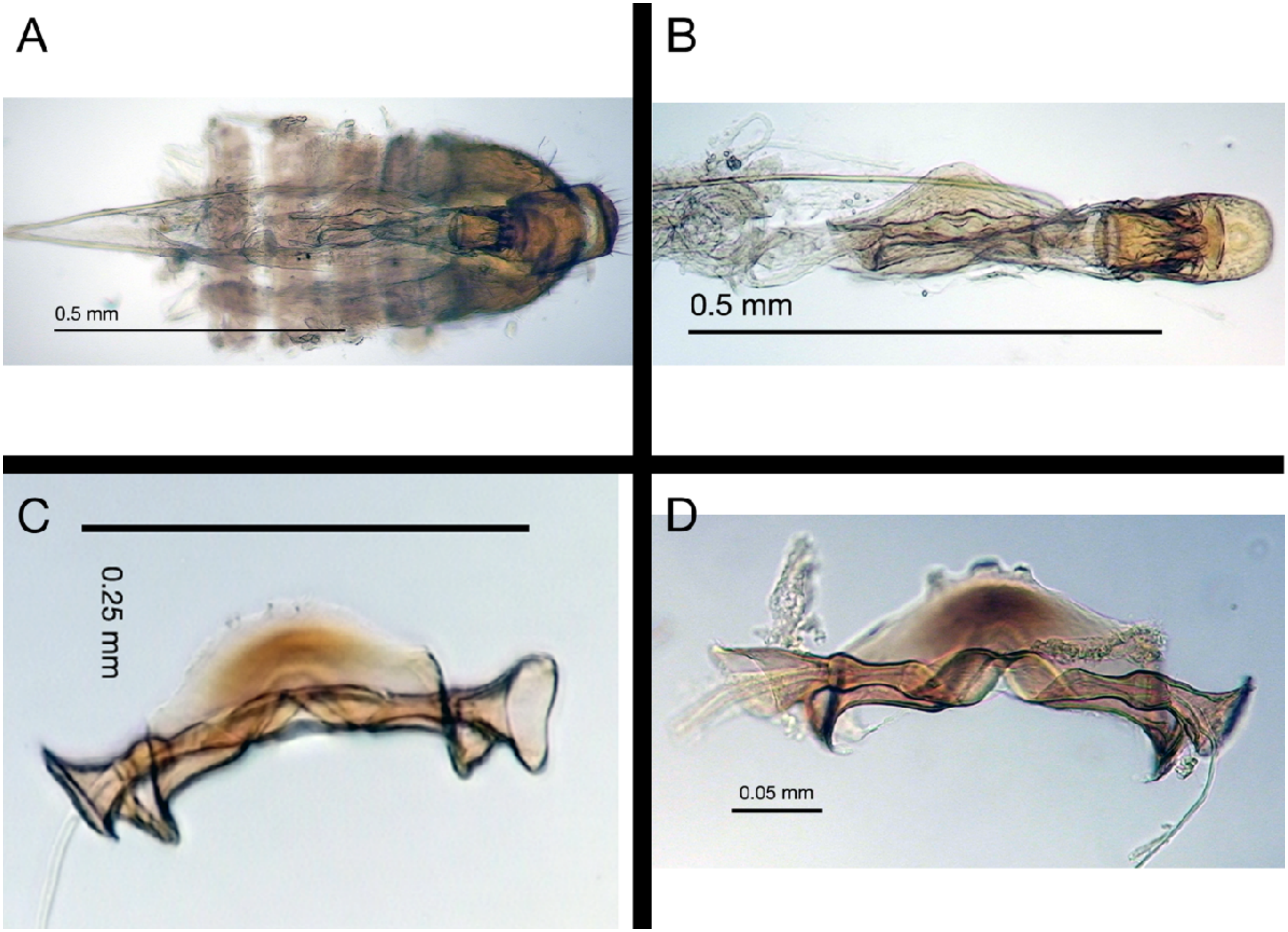

Figure 7.69. Compound light micrographs of sperm pump structure A) + B) N. ephippigerum sperm pump in situ, progressively exposed C) *N. hopkinsi* sperm pump D) *Pycnotomina cavicolle*, sperm pump

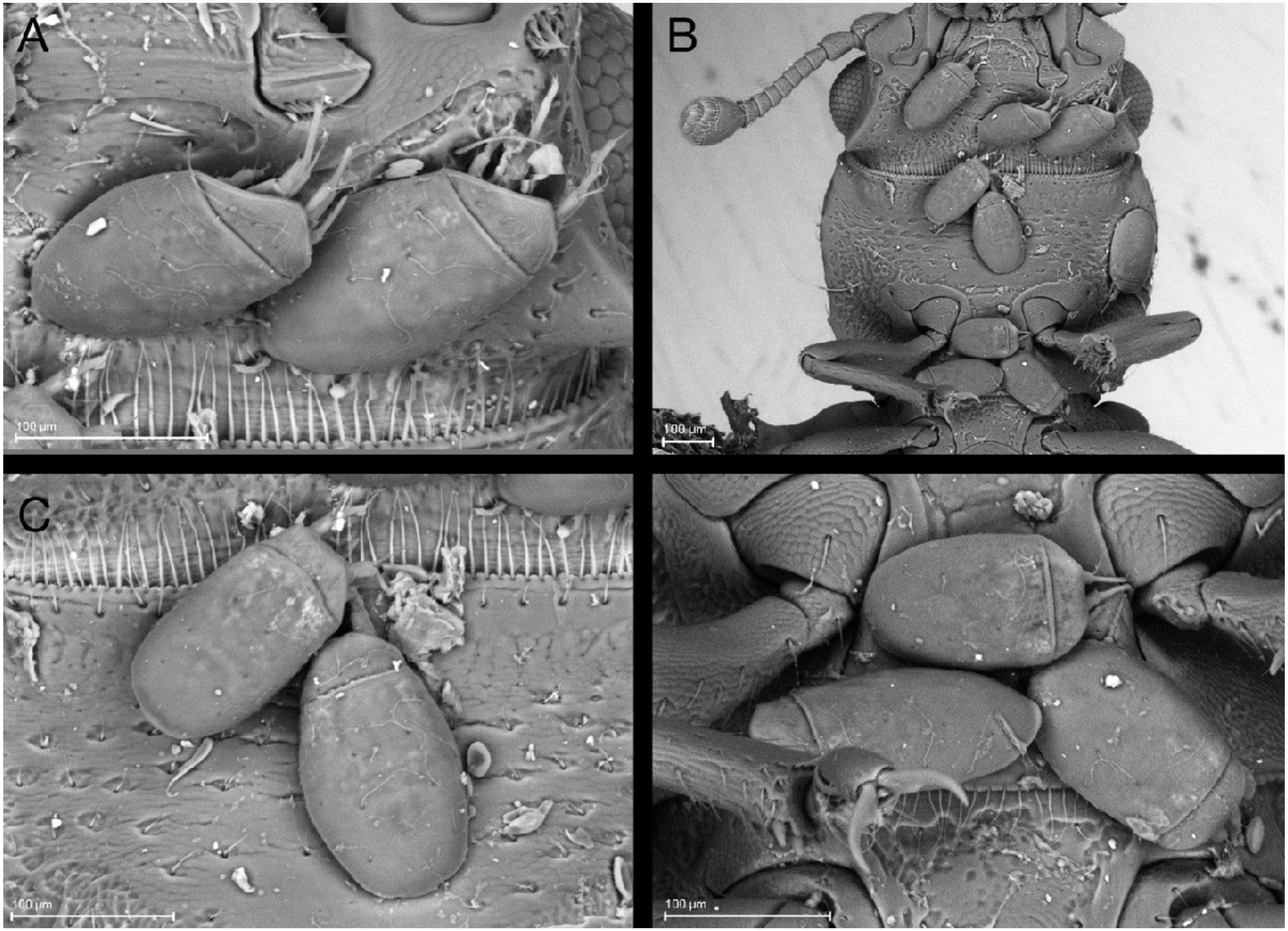

Figure 7.70. ESEM mite infestation of various areas on *N. striolatum*, USA:GA, A) mouthparts, B) head and pronotum, C) prothorax, D) mesoventrite.

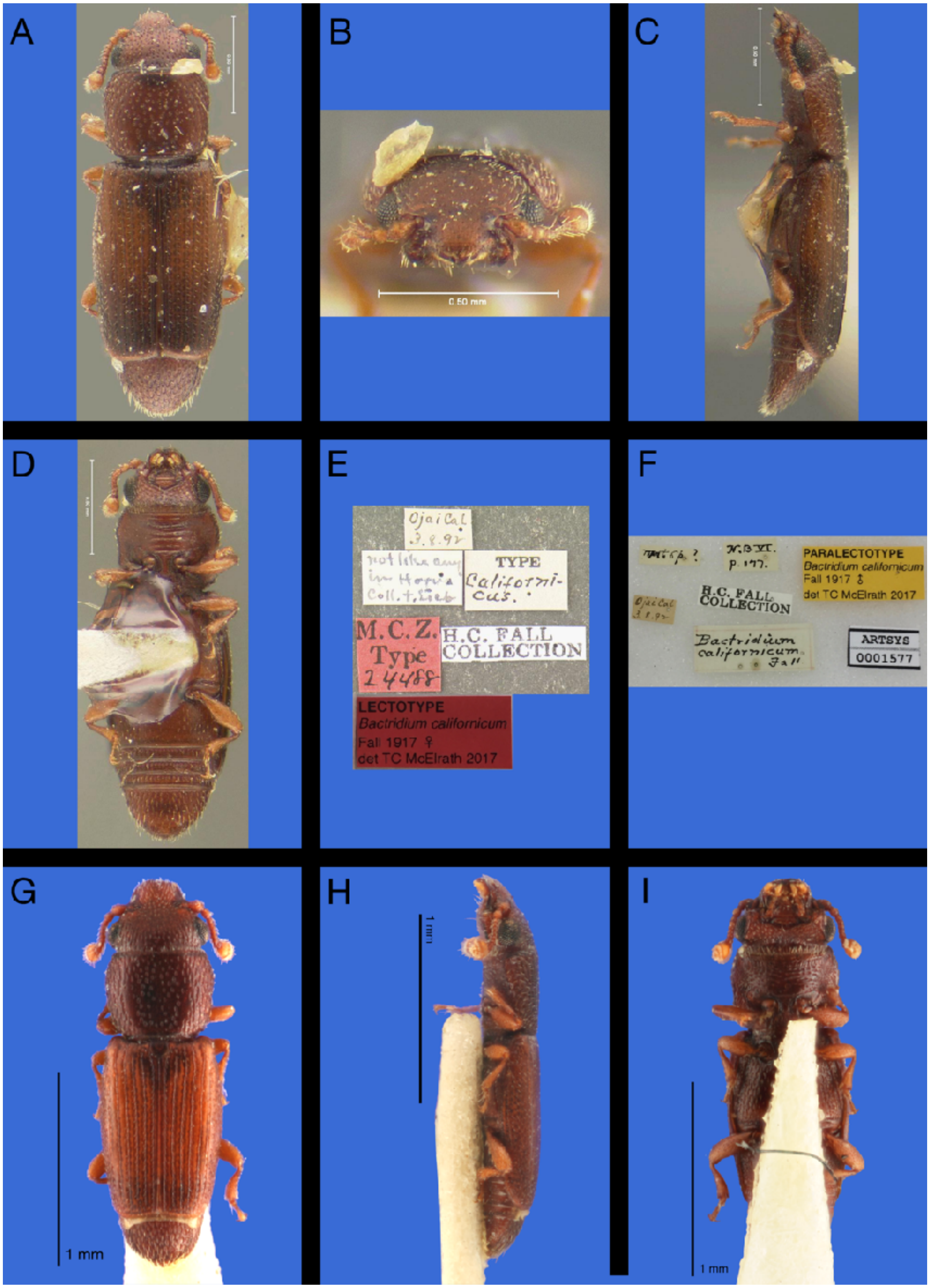

Figure 7.71. A) *Bactridium californicum* Fall lectotype dorsal habitus, B) same, head, C) same, lateral habitus, D)same, ventral habitus, E) same, labels. F) *B. californicum* Fall paralectotype (not figured), labels. G) *Rhizophagus ephippiger* Guerin-Meneville neotype, dorsal habitus H) same, lateral habitus, I) same, ventral habitus. A-E © MCZ.

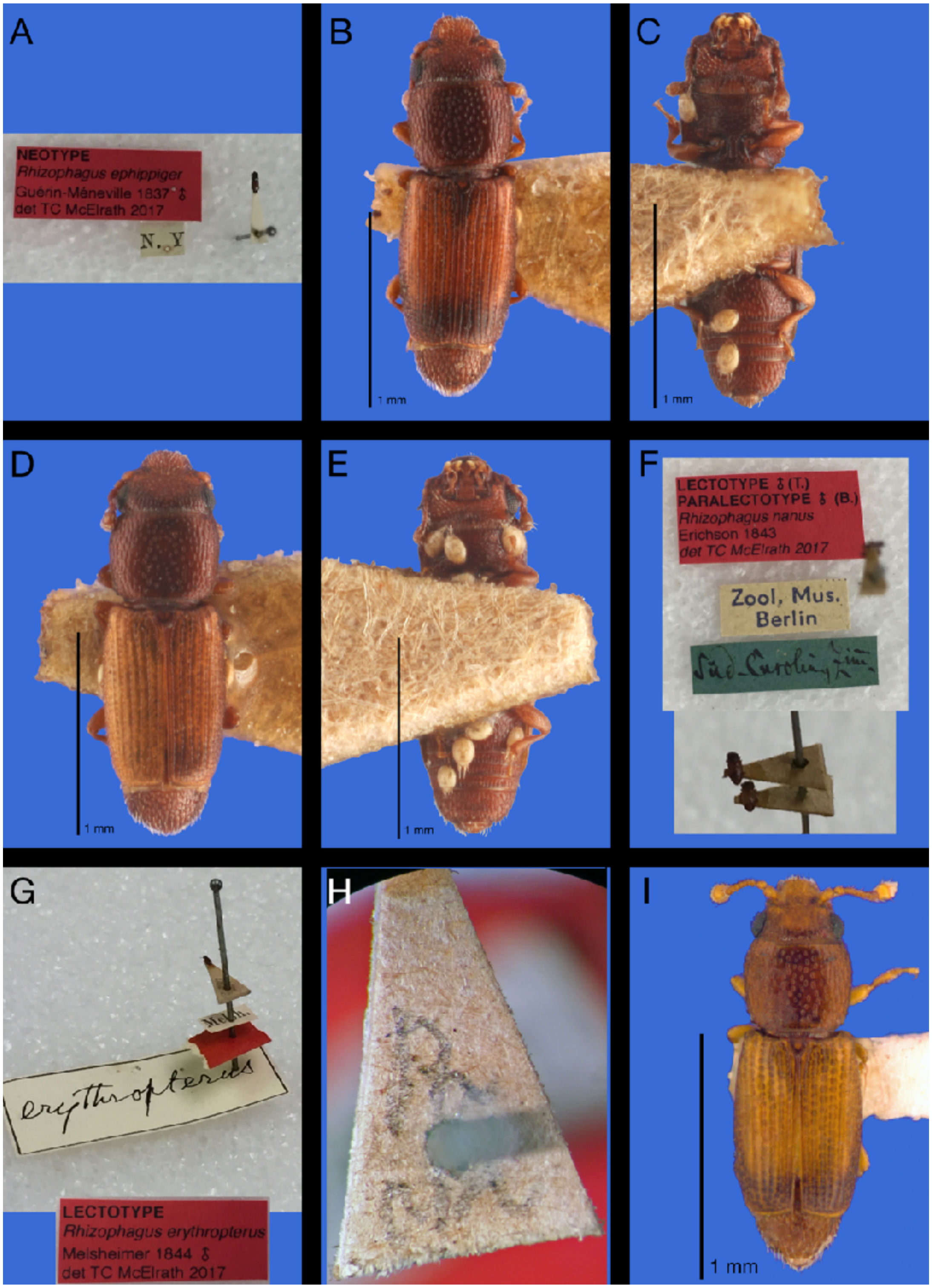

Figure 7.72. A) *Rhizophagus ephippiger* Guerin-Meneville neotype, labels. B) *Rhizophagus nanus* Erichson lectotype, dorsal habitus C) same, ventral habitus, D) *Rhizophagus nanus* Erichson paralectotype, dorsal habitus E) same, ventral habitus F) *R. nanus* lectotype and paralectotype labels and pin condition. G) *Rhizophagus erythropterus* Melsheimer lectotype labels, pin condition, H) same, writing on point. I) *Bactridium curtipenne* Casey, holotype dorsal habitus.

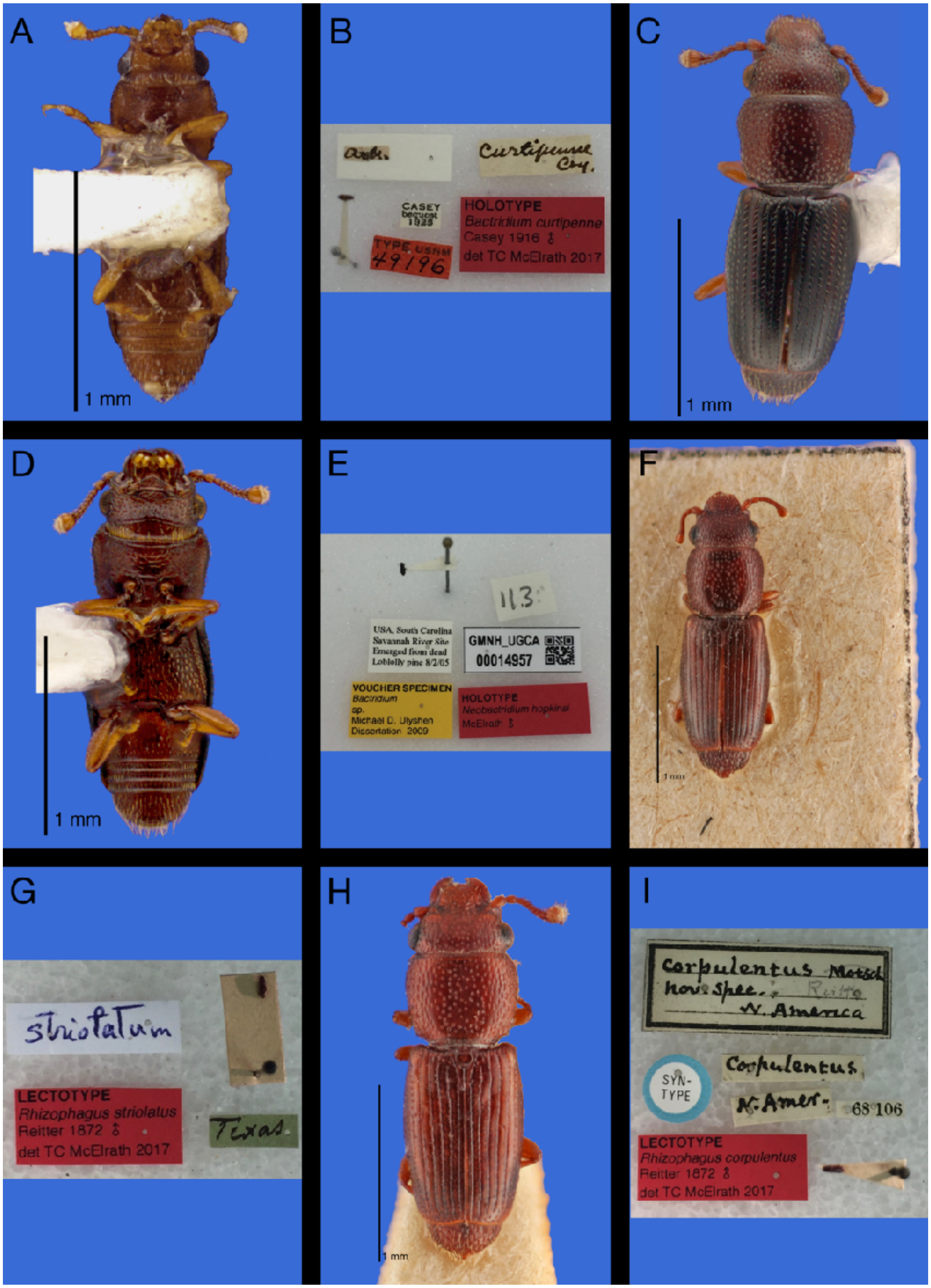

Figure 7.73. A) *Bactridium curtipenne* Casey, holotype ventral habitus, B) same, labels. C) *Neobactridium hopkinsi* holotype, dorsal habitus, D) same, ventral E) same, labels. F) *Rhizophagus striolatus* Reitter, 1872 lectotype, dorsal habitus G) same, labels. H) *Rhizophagus corpulentus* Reitter, 1872 lectotype dorsal habitus, I) same, labels.

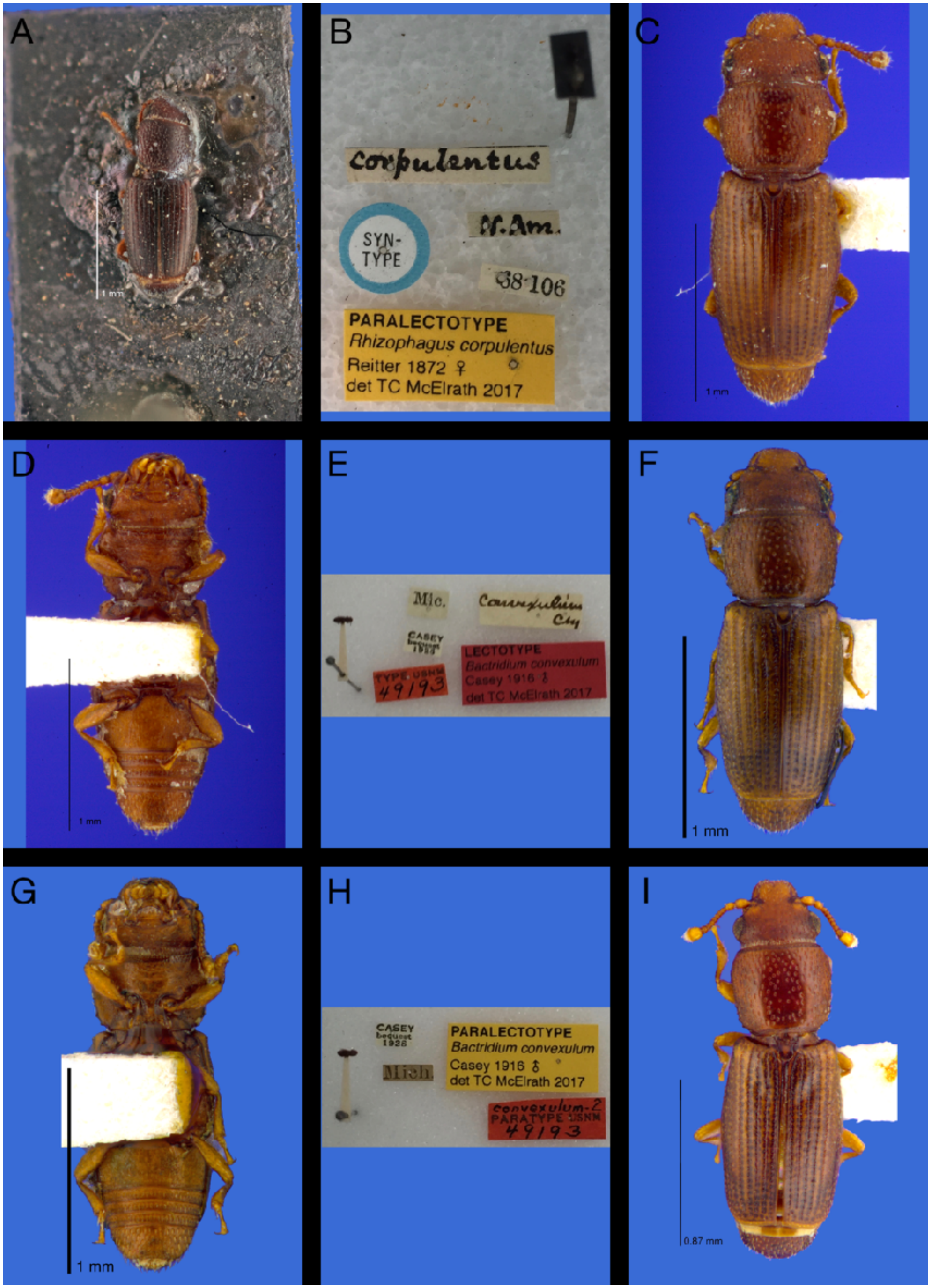

Figure 7.74. A) *Rhizophagus corpulentus* Reitter, 1872 paralectotype dorsal habitus, B) same, labels. C) *Bactridium convexulum* Casey lectotype, dorsal habitus, D) same, ventral habitus, E) same, labels. F) *Bactridium convexulum* Casey paralectotype, dorsal habitus, G) same, ventral habitus H) same, labels. I) *Bactridium hudsoni* Casey holotype, dorsal habitus.

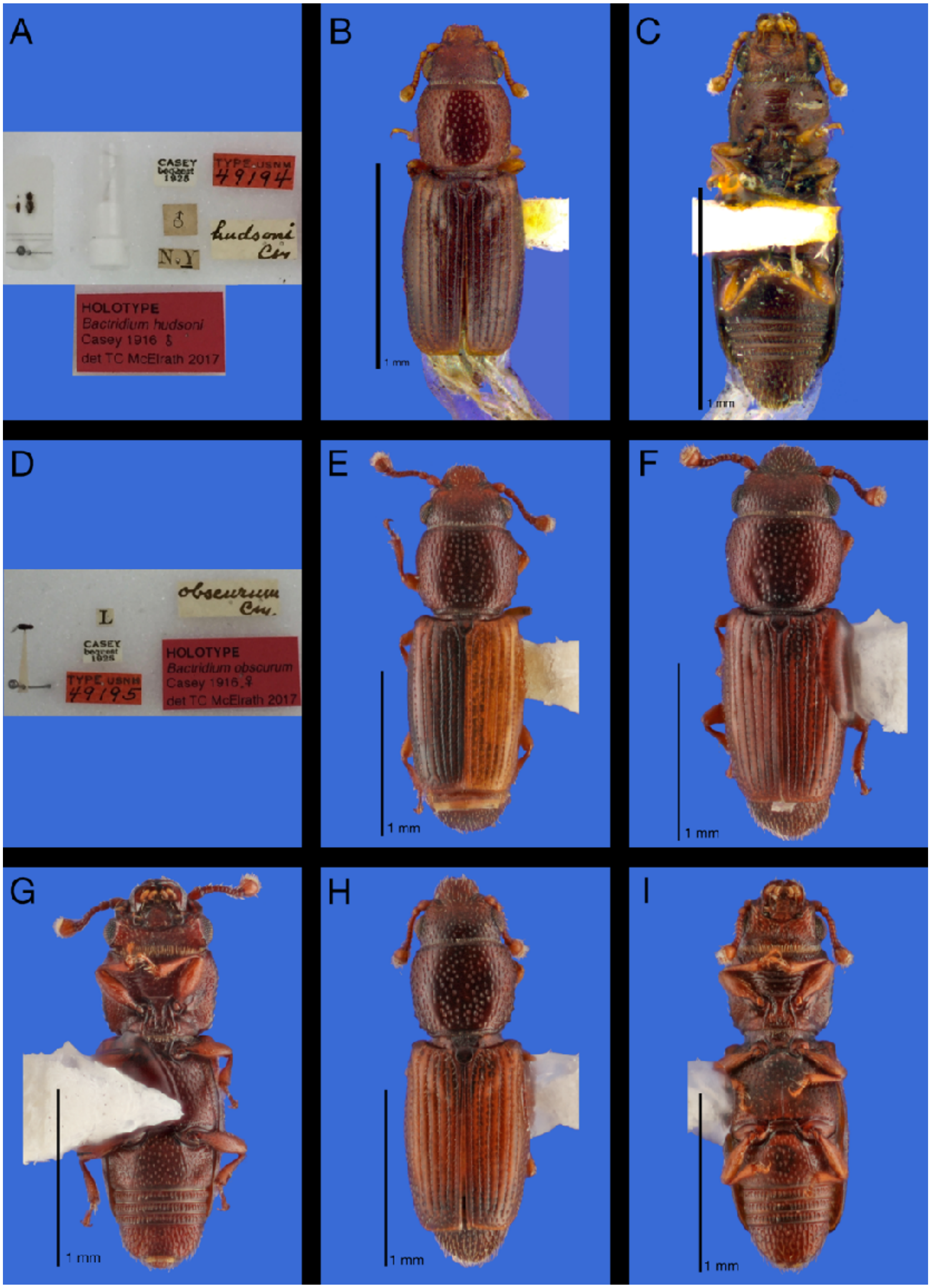

Figure 7.75. A) *Bactridium hudsoni* Casey holotype, labels. B) *Bactridium obscurum* Casey holotype, dorsal habitus. C) same, ventral habitus D) same, labels. E) *Neobactridium striolatum* deformity, with bicolored elytra. F) *N. striolatum* male, from USA: Georgia, dorsal habitus, G) same, ventral habitus. H) *N. striolatum* female, from USA: Montana, dorsal habitus, I) same, ventral habitus.

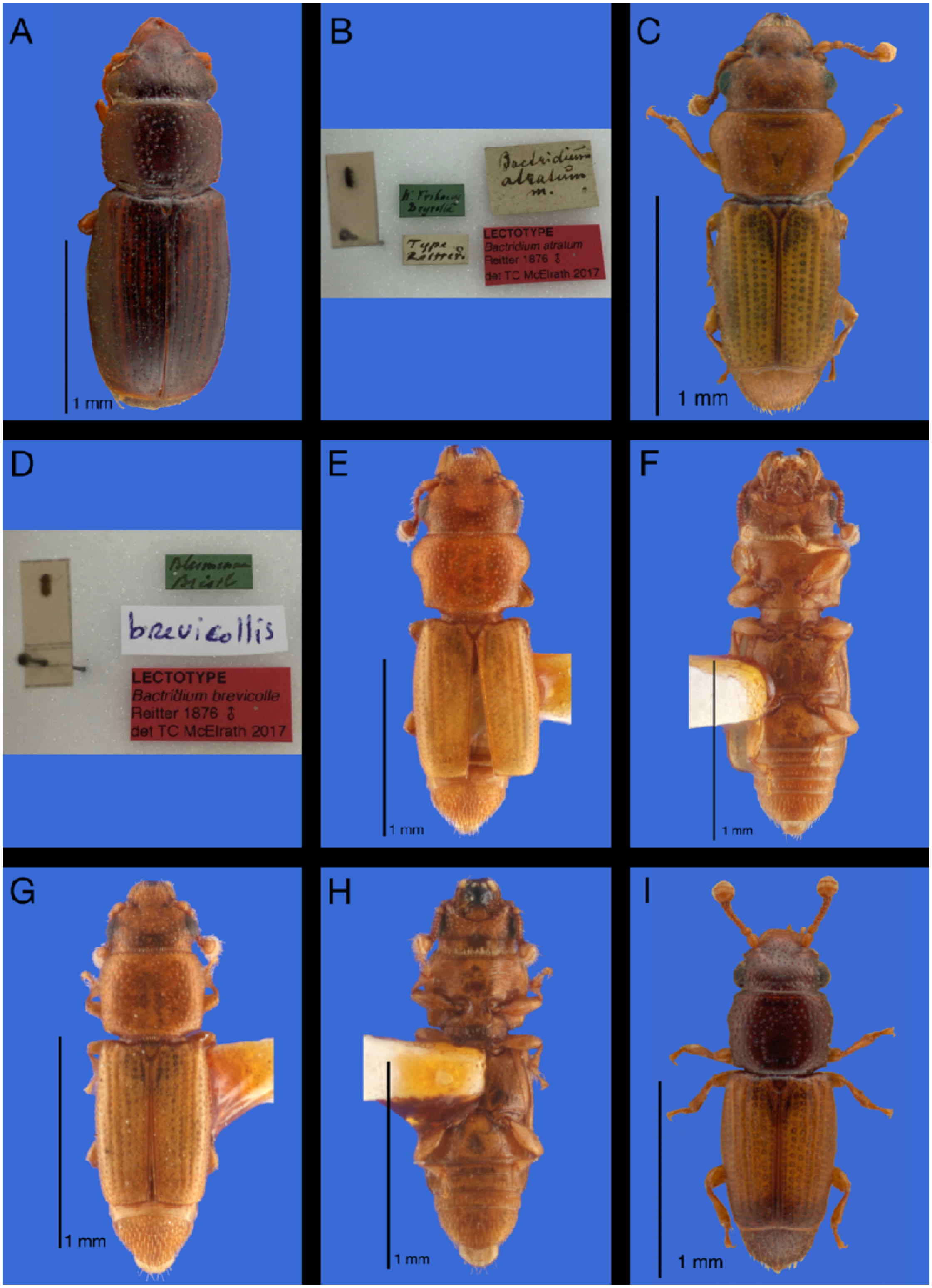

Figure 7.76. A) *Bactridium atratum* Reitter lectotype, dorsal habitus, B) same, labels. C) *Bactridium brevicolle* Reitter lectotype, dorsal habitus, D) same, labels. E) *Neobactridium brevicolle* male, Brazil, dorsal habitus, F) same, ventral habitus. G) same, female, dorsal habitus H) same, female, ventral habitus. I) *Bactridium divisum* Sharp lectotype, dorsal habitus.

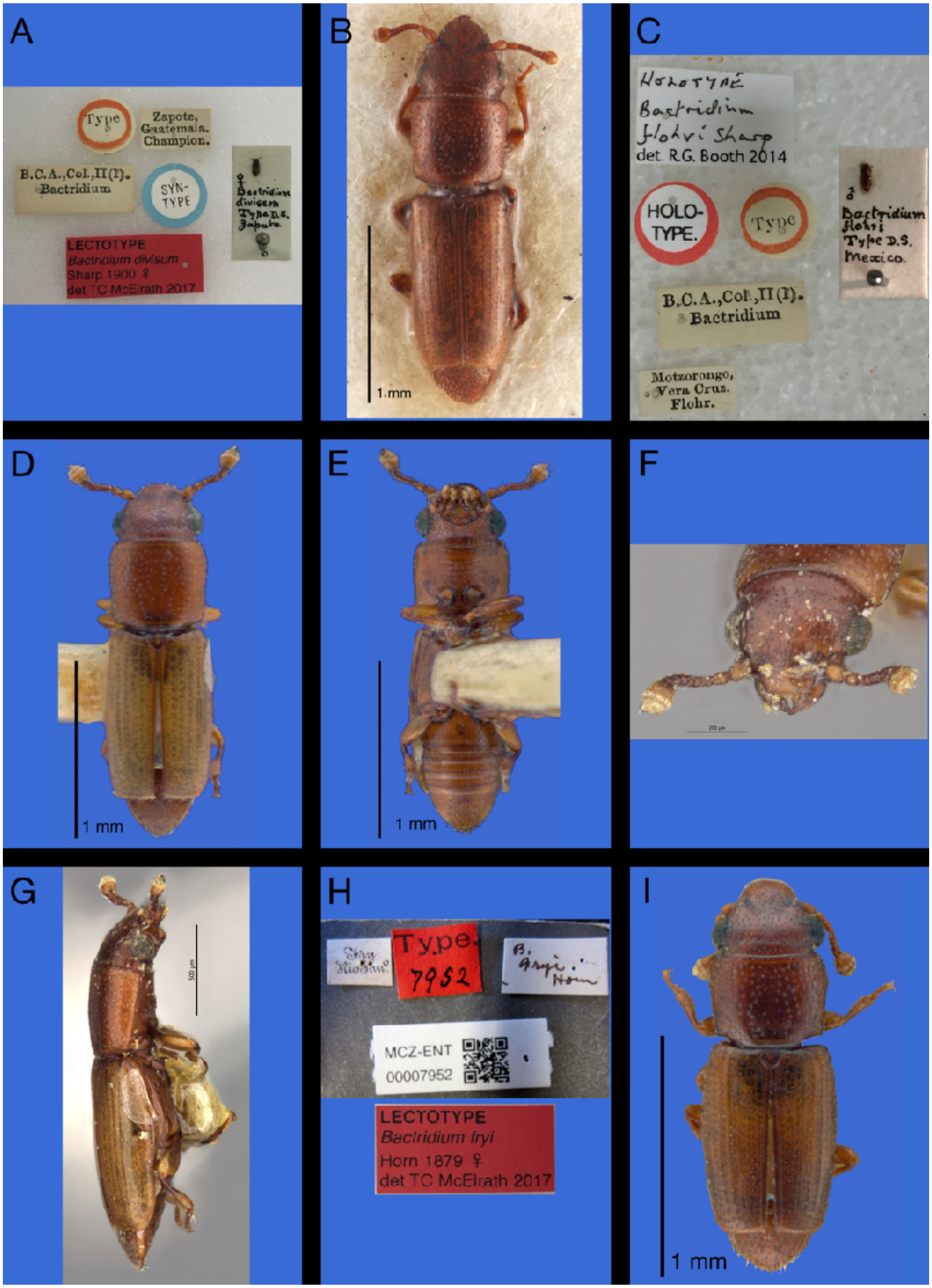

Figure 7.77. A) *Bactridium divisum* Sharp lectotype, labels. B) *B. flohri* Sharp lectotype, dorsal habitus, C) same, labels. D) *B. fryi* Horn, lectotype, dorsal habitus, E) same, ventral habitus, F) same, head. G) same, lateral habitus H) same, labels. I) *Rhizophagus heydeni* Reitter 1872 lectotype, dorsal habitus.

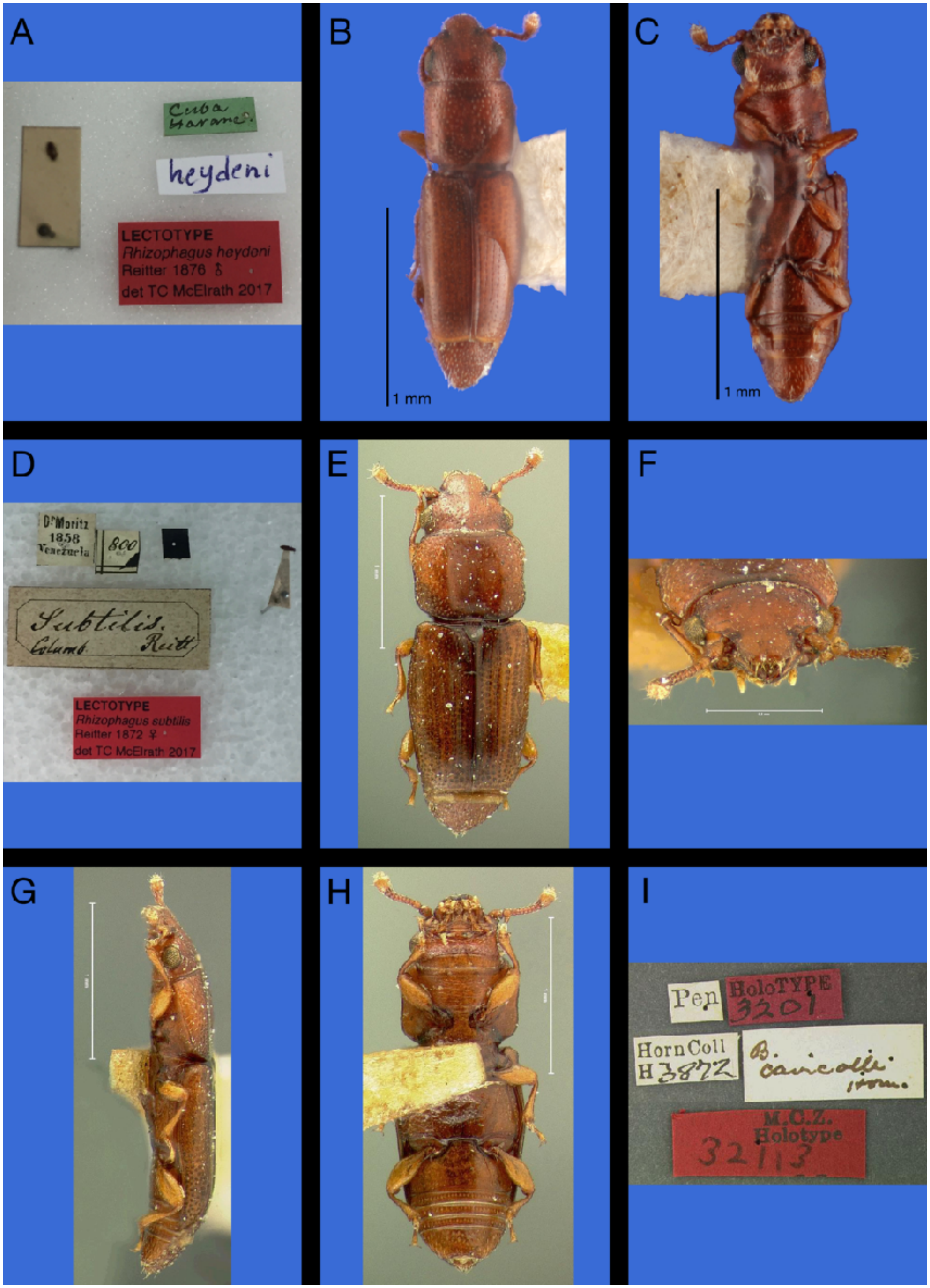

Figure 7.78. A) *Rhizophagus heydeni* Reitter 1872 lectotype, labels. B) *R. subtilis* Reitter 1872 lectotype, dorsal habitus, C) same, ventral habitus, D) same, labels. E) *Bactridium cavicolle* holotype Horn, dorsal habitus, F) same, head, G) same, lateral habitus H) same, ventral habitus, I) same, labels. E-I © MCZ.

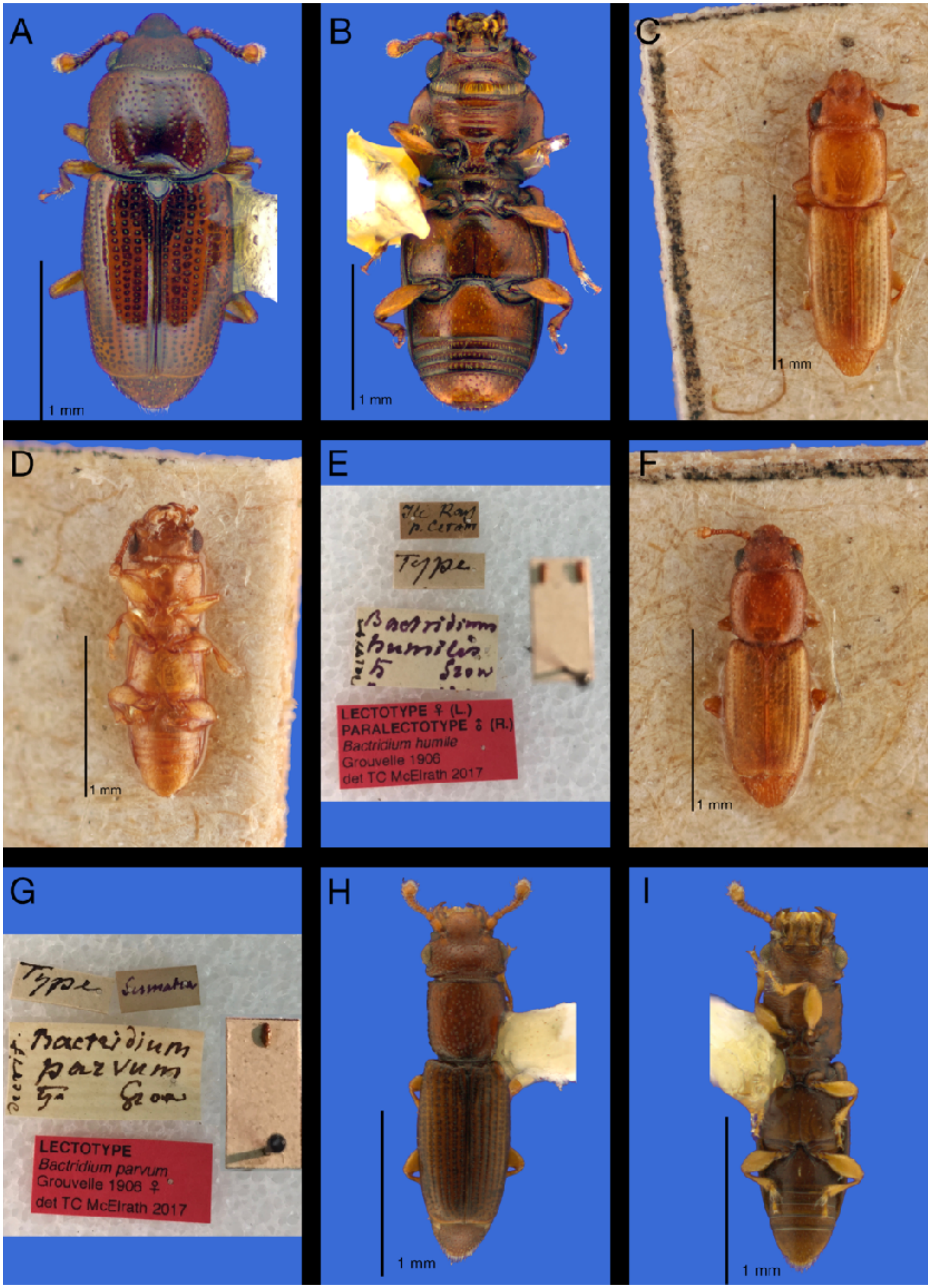

Figure 7.79. A) *Pycnotomina cavicolle*, male, dorsal habitus, B) same, ventral habitus. C) *Bactridium humile* Grouvelle lectotype, dorsal habitus, D) same, paralectotype, ventral habitus, E) same, labels, lectotype and paralectotype. F) *B. parvum* Grouvelle lectotype, dorsal habitus, G) same, labels. H) unknown genus, Okinawa, dorsal habitus I) same, ventral habitus.

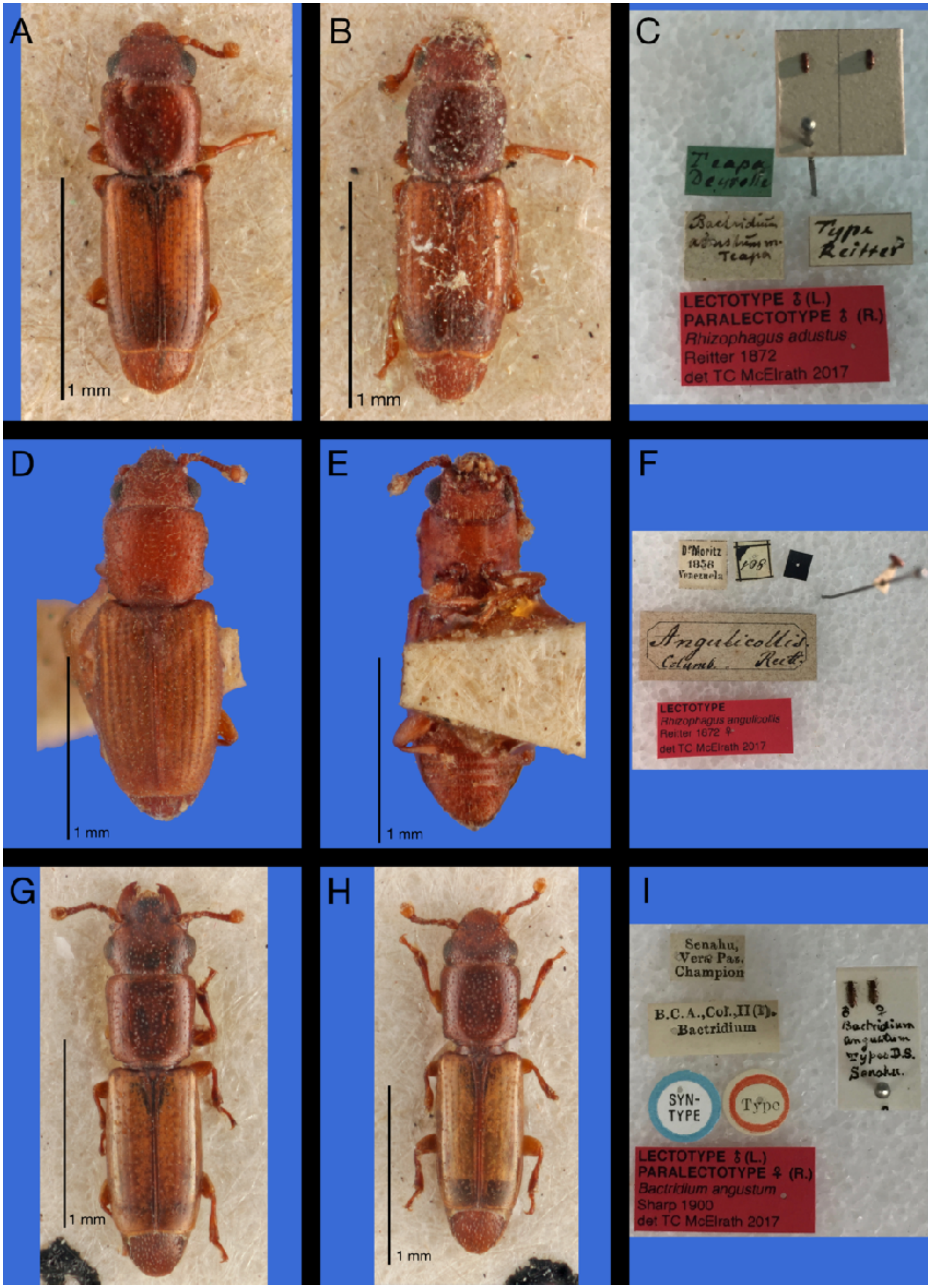

Figure 7.80. A) *Rhizophagus adustus* Reitter, lectotype, dorsal habitus, B) same, paralectotype, C) same, labels, lectotype & paralectotype. D) *R. angulicollis* Reitter lectotype, dorsal habitus E) same, ventral habitus, F) same, labels. G) *Bactridium angustum* Sharp lectotype, dorsal habitus H) same, paralectotype I) same, labels lecto & paralectotype.

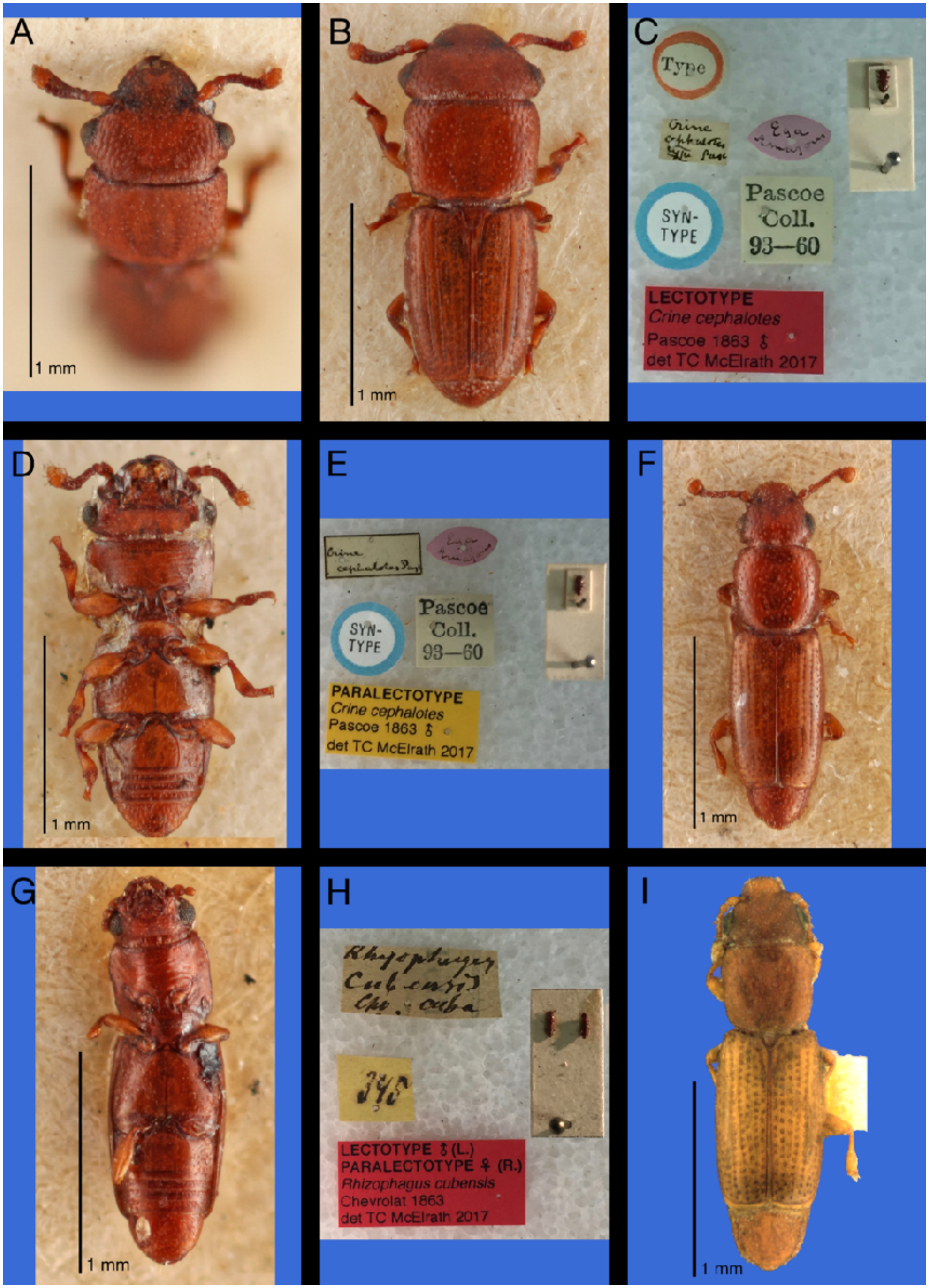

Figure 7.81. A) *Crine cephalotes* Pascoe, lectotype, head, dorsal habitus, B) same, dorsal habitus, C) same, labels, D) same paralectotype, ventral habitus E) same, paralectotype labels. F) *Rhizophagus cubensis* Chevrolat lectotype, dorsal habitus G) same, paralectotype, ventral habitus, H) same, labels. I) *Leptipsius dilutus* Casey lectotype, dorsal habitus.

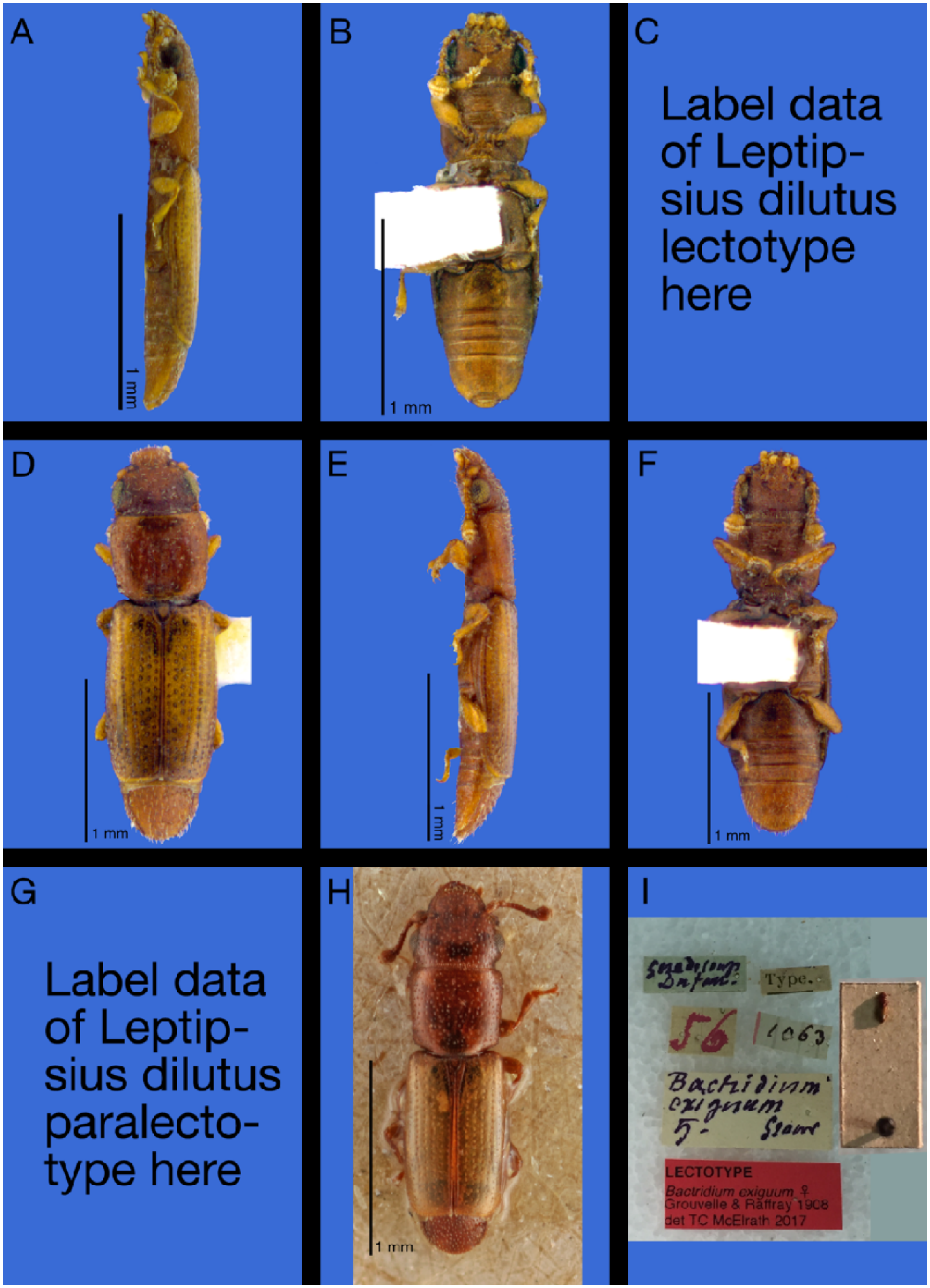

Figure 7.82. A) *Leptipsius dilutus* Casey lectotype, lateral habitus B) same, ventral habitus C) same, labels. D) same, paralectotype, dorsal habitus E) same, lateral habitus F) same, ventral habitus. G) same, labels H) *Bactridium exiguum* Grouvelle & Raffray lectotype, dorsal habitus. I) same, labels.

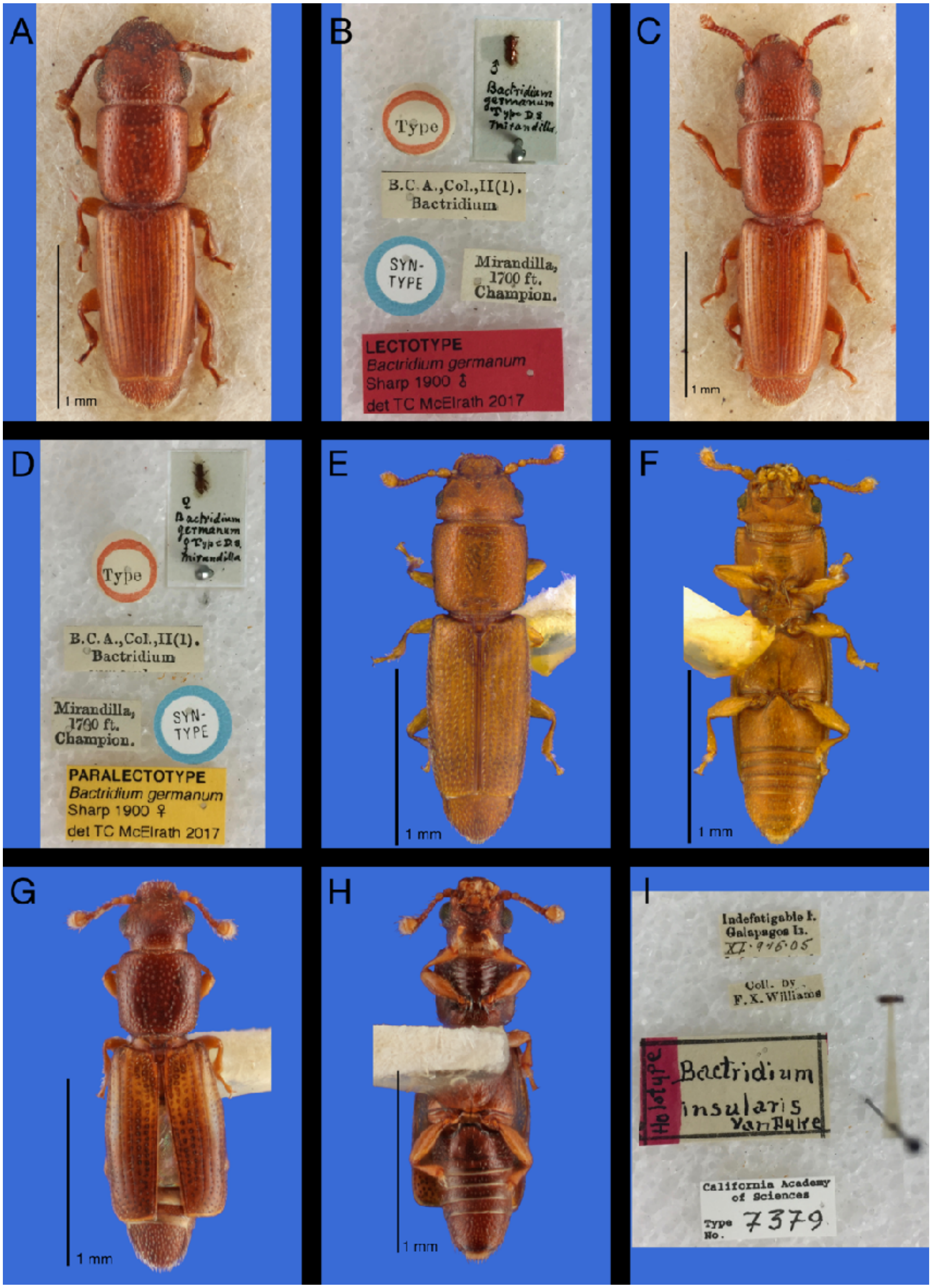

Figure 7.83. A) *Bactridium germanum* Sharp lectotype, dorsal habitus. B) same, labels. C) same, paralectotype, dorsal habitus D) same, paralectotype, labels E) *Leptipsius imberbis* Bousquet paratype, dorsal habitus, F) same, ventral habitus. G) *B. insularis* Van Dyke holotype, dorsal habitus, H) same, ventral habitus I) same, labels.

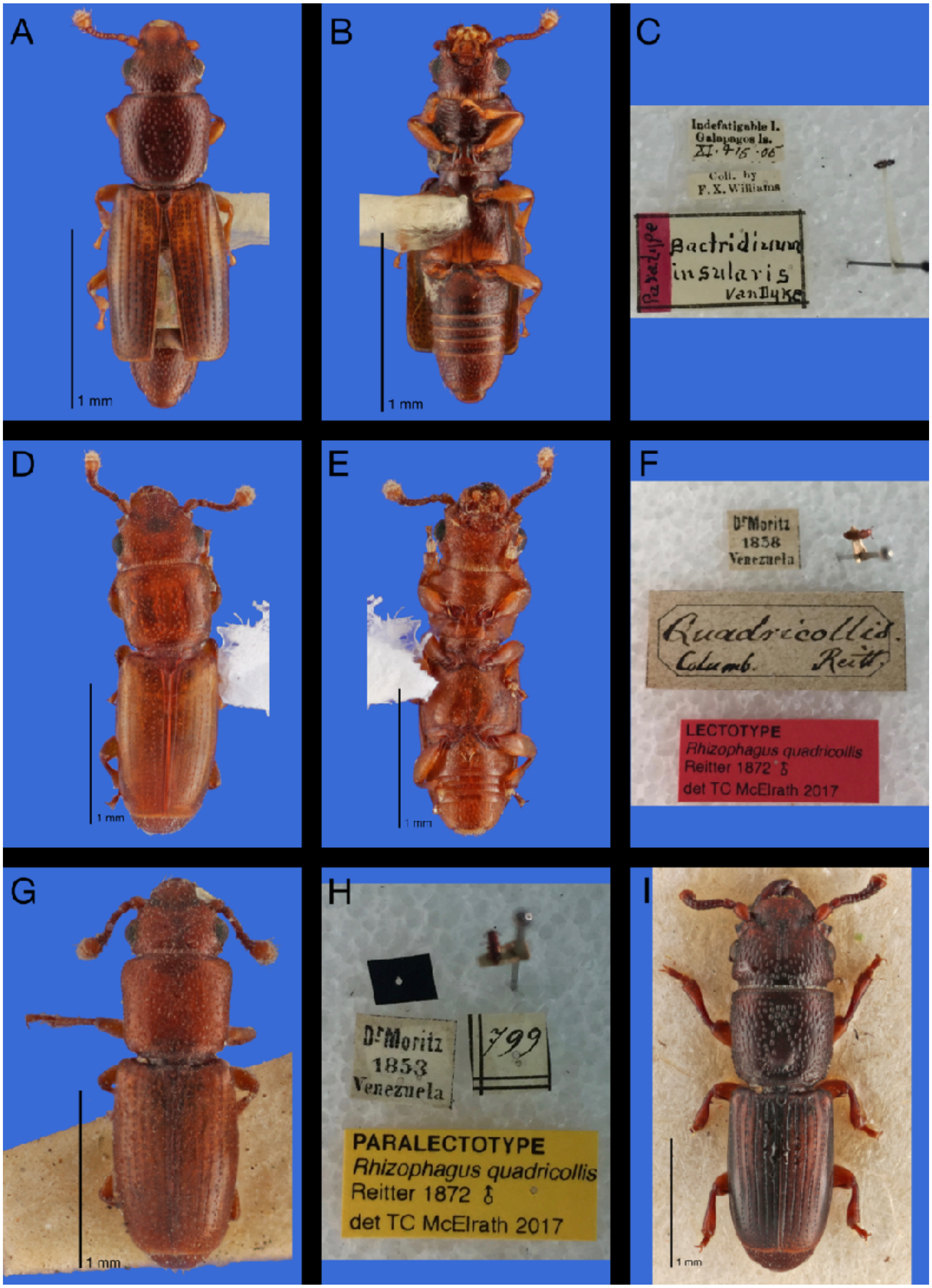

Figure 7.84. A) *Bactridium insularis* Van Dyke paratype, dorsal habitus. B) same, ventral habitus C) same, labels. D) *Rhizophagus quadricollis* Reitter lectotype, dorsal habitus E) same, ventral habitus, F) same, labels, G) same, paralectotype, dorsal habitus H) same, paralectotype, labels. I) *Bactridium rude* Sharp lectotype, dorsal habitus.

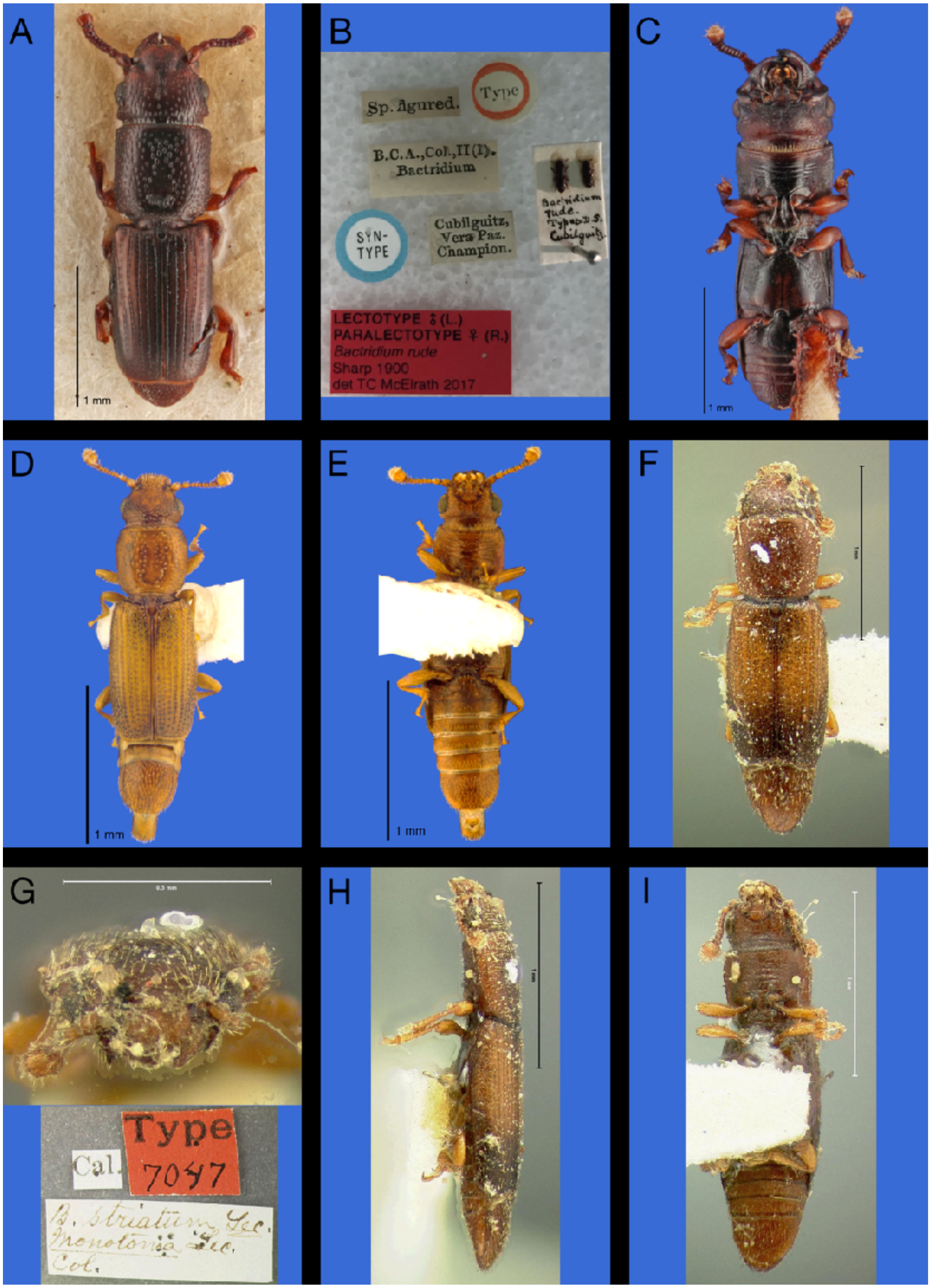

Figure 7.85. A) *Bactridium rude* Sharp paralectotype, dorsal habitus. B) same, labels, lectotype & paralectotype C) *Crine rudis* (Sharp) from Costa Rica, Nevermann coll., ventral habitus. D) *Crine striatus* (LeConte) from Idaho, UGCA, dorsal habitus E) same, ventral habitus, F) *Monotoma striata* LeConte holotype, dorsal habitus, G) same, head and labels, H) same, lateral habitus, I) same, ventral habitus.

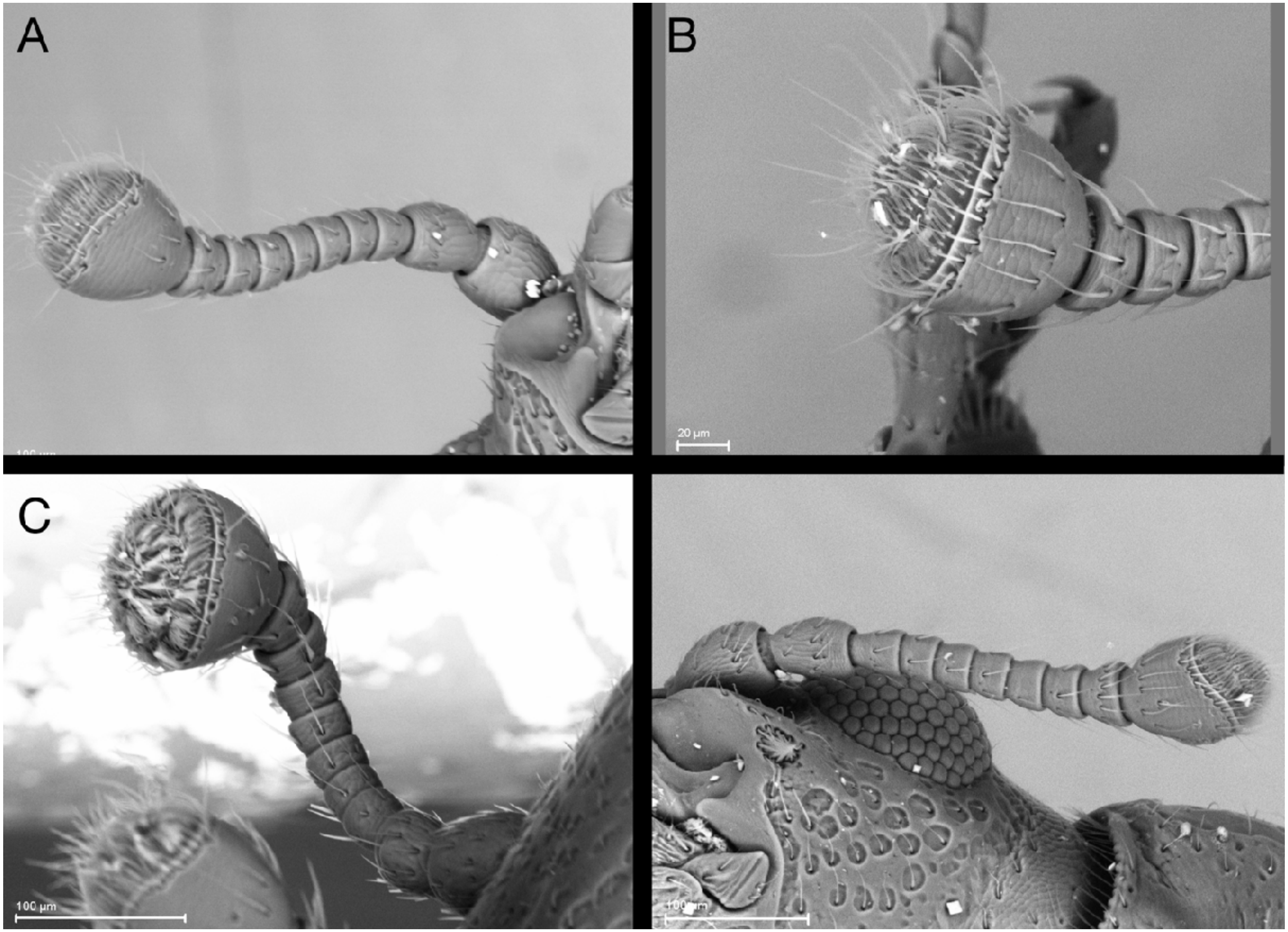

Figure 7.86. ESEM antenna ventral *Neobactridium striolatum* morphs (male), A) *N. striolatum* GA, B) *N. striolatum* MT, C) N. *striolatum* GA (wide head), and D) *Neobactridium* morphotype 1.

A.1 Supplementary Tables

Table A.1. Abbreviated history of relevant Cucujidae *s.l.* classification schemes.

Current accepted extant cucujoid family groups[1]	**Cucujidae *sensu lato***[2]	**Cucujidae *s.l.***[3]	**Cucujidae *s.l.***[4]	**Phloeostichidae *s.l.***[5]
Agapythidae		X	X	X
Biphyllidae				
Boganiidae				
Byturidae				
Cavognathidae				
Cryptophagidae				
Cucujidae *sensu stricto*	X	X	X	
Cybocephalidae				
Cyclaxyridae				
Erotylidae				
Helotidae				
Hobartiidae				
Kateretidae				
Laemophloeidae	X	X	X	
Lamingtoniidae				
Monotomidae	X		X	
Myraboliidae	X	X	X	X
Nitidulidae				
Passandridae	X		X	
Phalacridae				
Phloeostichidae *s.s.*	X	X	X	X
Priasilphidae		X	X	X
Propalticidae				
Protocucujidae				
Silvanidae	X		X	
Smicripidae	X		X	
Sphindidae				
Tasmosalpingidae				X

[1]Bouchard *et. al* (2011), Cline *et. al* (2014), [2]pre-Crowson (1955), [3]pre-Sen Gupta & Crowson (1969), [4]the broadest historical sense of Cucujidae *s.l.*, includes groups elevated by Crowson (1955) as well as groups moved to Phloeostichidae by Sen Gupta & Crowson (1969) and later authors, [5]includes groups placed in this family until Leschen *et. al* (2005)

Table A.2. Taxa, associated genes amplified, and accession numbers in this study. Cells left blank were not successfully amplified.

Superfamily	Family	*Genus*	*species*	Code	Voucher Location	18S	28S	12S	16S	H3	COI	COII
Outgroups												
Cleroidea	Cleridae	*Trichodes*	*ornatus*	CO048	UGCA	AF423775	EU145663, EU145713	KP133863	KP133932	KP134257	KP134124	KP134191
Tenebrionoidea	Tenebrionidae	*Eleodes*	*sulcipennis*	CO031	UGCA	AY310606	AY310667	KP133862	KP133931	KP134256	KP134123	KP134190
Tenebrionoidea	Tenebrionidae	*Hymenorus*	sp.	CO172	UGCA	KP134003	KP134066	KP133871	KP133938	KP134263	KP134132	KP134198
Tenebrionoidea	Salpingidae	*Ocholissa*	sp.	CO404	UGCA	EU145650	EU145708, EU145719	KP133878	KP133944		KP134139	KP134205
Tenebrionoidea	Salpingidae	*Serrotibia*	sp.	CO1009	UGCA	KP829218	KP829347	KP828984		KP829923	KP829644	KP829791
Cerylonid Series	Latridiidae	*Latridius*	*crenatus*	CO483	UGCA	EU164623	EU164654	EU164574	EU164607	EU164749	EU164685	EU164717
Cerylonid Series	Coccinellidae			CO287	UGCA	KP134005	KP134068	KP133873		KP134265	KP134134	KP134200
Cerylonid Series	Coccinellidae	*Scymnus*	sp.	CO303	UGCA	KP134006	KP134069	KP133874	KP133940	KP134266	KP134135	KP134201
Cerylonid Series	Coccinellidae	*Psyllobora*	sp.	CO304	UGCA	KP134007	KP134070	KP133875	KP133941	KP134267	KP134136	KP134202
Ingroups												
Cucujoidea	Cucujidae	*Cucujus*	*clavipes*	CO026	BYUC	AF423767	AY310660	KP133861	KP133930	KP134255	KP134122	KP134189
Cucujoidea	Phalacridae	*Olibrus*	sp.	CO074	UGCA	EU145652	KP134059	KP133864	KP133933	KP134258	KP134125	KP134192
Cucujoidea	Erotylidae	*Iphiclus*	*sedecimmaculatus*	CO101	BYUC	KP133997	KP134060	KP133865	KP133934	KP134259	KP134126	
Cucujoidea	Myraboliidae	*Myrabolia*	sp.	CO1018	UGCA	KP829214	KP829344	KP828981			KP829639	KP829787
Cucujoidea	Silvanidae	*Psammoecus*	sp.	CO1024	UGCA	KP133998	KP134061	KP133866			KP134127	KP134193
Cucujoidea	Cryptophagidae	*Curelius*	sp.	CO144	UGCA	KP133999	KP134062	KP133867	KP133935	KP134260	KP134128	KP134194
Cucujoidea	Cryptophagidae	*Atomaria*	sp.	CO145	UGCA	KP134000	KP134063	KP133868	KP133936	KP134261	KP134129	KP134195
Cucujoidea	Cryptophagidae	*Cryptophagus*	sp.	CO146	UGCA	KP134001	KP134064	KP133869	KP133937	KP134262	KP134130	KP134196
Cucujoidea	Erotylidae	*Iphiclus*	sp.	CO152	UGCA	KP134002	KP134065	KP133870			KP134131	KP134197
Cucujoidea	Phalacridae			CO258	BYUC	KP134004	KP134067	KP133872	KP133939	KP134264	KP134133	KP134199
Cucujoidea	Nitidulidae	*Aethina*	*tumida*	CO352	UGCA	KP134008	KP134071	KP133876	KP133942	KP134268	KP134137	KP134203
Cucujoidea	Nitidulidae	*Cratonura*	*rufithorax*	CO375	UGCA	KP134009	KP134072	KP133877	KP133943	KP134269	KP134138	KP134204
Cucujoidea	Erotylidae	*Pselaphacus*	*nigropunctatu*	CO515	UGCA	EU164627	EU164657	EU164568,	EU164590	EU164744	EU164678	EU164712
Cucujoidea	Silvanidae	*Uleiota*	*dubius*	CO609	UGCA	EU145653	EU145710	KP133879	KP133945	KP134270	KP134140	KP134206
Cucujoidea	Silvanidae	*Ahasverus*	*advena*	CO610	UGCA	KP134010	KP134073	KP133880	KP133946	KP134271	KP134141	KP134207
Cucujoidea	Passandridae	*Catogenus*	*rufus*	CO613	UGCA	EU145651	EU145709	KP133881	KP133947	KP134272	KP134142	KP134208
Cucujoidea	Priasilphidae	*Priasilpha*	*obscura*	CO684	various	AY748179		EU877952	EU877952		EU877952	EU877952
Cucujoidea	Laemophloeidae	*Microlaemus*	sp.	CO739	UGCA	KP134011	KP134074	KP133882	KP133948		KP134143	KP134209
Cucujoidea	Laemophloeidae	*Laemophloeus*	*woodruffi*	CO740	UGCA	KP134012	KP134075	KP133883	KP133949	KP134273	KP134144	KP134210
Cucujoidea	Laemophloeidae	*Cryptolestes*	*punctatus*	CO741	UGCA	KP134013	KP134076	KP133884	KP133950	KP134274	KP134145	KP134211
Cucujoidea	Laemophloeidae	*Rhabdophloeus*	sp.	CO742	UGCA	KP134014	KP134077	KP133885	KP133951	KP134275	KP134146	KP134212
Cucujoidea	Laemophloeidae	*Dysmerus*	sp.	CO743	UGCA	KP134015	KP134078	KP133886	KP133952	KP134276	KP134147	KP134213
Cucujoidea	Laemophloeidae	*Rhabdophloeus*	sp.	CO744	UGCA	KP134016	KP134079	KP133887	KP133953	KP134277	KP134148	KP134214
Cucujoidea	Laemophloeidae	*Placonotus*	*zimmermani*	CO745	UGCA	KP134017	KP134080	KP133888	KP133954	KP134278	KP134149	KP134215
Cucujoidea	Laemophloeidae	*Charaphloeus*	*adustus*	CO746	UGCA	KP134018	KP134081	KP133889	KP133955		KP134150	KP134216
Cucujoidea	Laemophloeidae	*Phloeolaemus*	*chamaeropis*	CO747	UGCA	KP134019	KP134082	KP133890	KP133956	KP134279	KP134151	KP134217
Cucujoidea	Laemophloeidae	*Lathropus*	*vernalis*	CO748	UGCA	KP134020	KP134083	KP133891	KP133957		KP134152	KP134218
Cucujoidea	Laemophloeidae	*Rhinophloeus*	sp.	CO749	UGCA	KP134021	KP134084	KP133892	KP133958	KP134280	KP134153	KP134219
Cucujoidea	Laemophloeidae	*Placonotus*	*politissimus*	CO750	UGCA	KP134022	KP134085	KP133893	KP133959	KP134281	KP134154	KP134220
Cucujoidea	Laemophloeidae	*Rhabdophloeus*	sp.	CO751	UGCA	KP134023	KP134086	KP133894	KP133960	KP134282	KP134155	KP134221
Cucujoidea	Laemophloeidae	*Laemophloeus*	sp.	CO752	UGCA	KP134024	KP134087	KP133895	KP133961	KP134283	KP134156	KP134222
Cucujoidea	Laemophloeidae	*Laemophloeus*	sp.	CO753	UGCA	KP134025	KP134088	KP133896	KP133962		KP134157	KP134223
Cucujoidea	Laemophloeidae	*Placonotus*	*modestus*	CO754	UGCA	KP134026	KP134089	KP133897	KP133963	KP134284	KP134158	KP134224
Cucujoidea	Laemophloeidae	*Laemophloeus*	*biguttatus*	CO755	UGCA	KP134027	KP134090	KP133898	KP133964		KP134159	KP134225

Table A.2. (continued)

Superfamily	Family	*Genus*	*species*	Code	Voucher Location	18S	28S	12S	16S	H3	COI	COII
Ingroups												
Cucujoidea	Laemophloeidae	*Laemophloeus*	*megacephalus*	CO756	UGCA	KP134028	KP134091	KP133899	KP133965		KP134160	KP134226
Cucujoidea	Laemophloeidae	*Laemophloeus*	*fasciatus*	CO757	UGCA	KP134029	KP134092	KP133900	KP133966	KP134286	KP134161	KP134227
Cucujoidea	Silvanidae	*Telephanus*	sp.	CO758	UGCA	KP134030	KP134093	KP133901	KP133967	KP134287	KP134162	KP134228
Cucujoidea	Silvanidae	*Cathartosilvanus*	*imbellis*	CO759	UGCA	KP134031	KP134094	KP133902	KP133968		KP134163	KP134229
Cucujoidea	Silvanidae	*Euplatamus*	sp.	CO760	UGCA	KP134032	KP134095	KP133903	KP133969		KP134164	KP134230
Cucujoidea	Silvanidae	*Sivanops*	sp.	CO761	UGCA	KP134033	KP134096	KP133904	KP133970		KP134165	KP134231
Cucujoidea	Silvanidae	*Cathartosilvanus*	sp.	CO762	UGCA	KP134034	KP134097	KP133905	KP133971	KP134288	KP134166	KP134232
Cucujoidea	Silvanidae	*Telephanus*	*atricapillus*	CO763	UGCA	KP134035	KP134098	KP133906	KP133972	KP134289	KP134167	KP134233
Cucujoidea	Silvanidae	*Silvanus*	*muticus*	CO764	UGCA	KP134036	KP134099	KP133907	KP133973		KP134168	KP134234
Cucujoidea	Silvanidae	*Cathartus*	*quadricollis*	CO767	UGCA	KP134037	KP134100	KP133908	KP133974	KP134290	KP134169	KP134235
Cucujoidea	Silvanidae	*Cathartosilvanus*	sp.	CO768	UGCA	KP134038	KP134101	KP133909	KP133975	KP134291	KP134170	KP134236
Cucujoidea	Silvanidae	*Uleiota*	sp.	CO769	UGCA	KP134039	KP134102	KP133910	KP133976		KP134171	KP134237
Cucujoidea	Silvanidae	*Parasilvanus*	sp.	CO770	UGCA	KP134040	KP134103	KP133911	KP133977			KP134238
Cucujoidea	Silvanidae	*Ahasverus*	sp.	CO771	UGCA	KP134041	KP134104	KP133912	KP133978		KP134172	KP134239
Cucujoidea	Silvanidae	*Airaphilus*	sp.	CO772	UGCA	KP134042	KP134105	KP133913	KP133979		KP134173	
Cucujoidea	Silvanidae	*Macrohyliota*	sp.	CO773	UGCA	KP134043	KP134106	KP133914	KP133980	KP134292	KP134174	KP134240
Cucujoidea	Silvanidae	*Oryzaephilus*	*surinamensis*	CO774	UGCA	KP134044	KP134107	KP133915	KP133981		KP134175	KP134241
Cucujoidea	Silvanidae	*Telephanus*	(Malagasy) sp.	CO846	UGCA	KP134045	KP134108	KP133916	KP133982	KP134293	KP134176	KP134242
Cucujoidea	Laemophloeidae	*Rhabdophloeus*	sp.	CO848	UGCA	KP134046	KP134109	KP133917	KP133983	KP134294	KP134177	KP134243
Cucujoidea	Laemophloeidae	*Rhinomalus*	sp.	CO849	UGCA	KP134047	KP134110	KP133918	KP133984		KP134178	KP134244
Cucujoidea	Laemophloeidae	*Laemophloeus*	*incisus*	CO850	UGCA	KP134048	KP134111	KP133919	KP133985	KP134295	KP134179	KP134245
Cucujoidea	Laemophloeidae	*Rhinoploeus*	sp.	CO851	UGCA	KP134049	KP134112	KP133920	KP133986		KP134180	KP134246
Cucujoidea	Silvanidae	*Parahyliota*	sp.	CO852	UGCA	KP134050	KP134113	KP133921	KP133987	KP134296	KP134181	KP134247
Cucujoidea	Laemophloeidae	*Cucujinus*	sp.	CO853	UGCA	KP134051	KP134114	KP133922	KP133988	KP134297	KP134182	KP134248
Cucujoidea	Passandridae	*Taphroscelidia*	*nr. humeralis*	CO854	UGCA	KP134052	KP134115	KP133923	KP133989		KP134183	
Cucujoidea	Silvanidae	*Parahyliota*	sp.	CO855	UGCA	KP134053	KP134116	KP133924	KP133990	KP134298	KP134184	KP134249
Cucujoidea	Boganiidae	*Paracucujus*	*rostratus*	CO875	UGCA	KP829125	KP829234	KP828840	KP828997	KP829806		
Cucujoidea	Agapythidae	*Agapytho*	sp.	CO880	UGCA	KP829118	KP829226	KP828836	KP828993	KP829797	KP829492	KP829649
Cucujoidea	Phloeostichidae	*Hymaea*	*magna*	CO881	UGCA	KP829215	KP829345			KP829922		
Cucujoidea	Sphindidae	*Protosphindus*	*chilensis*	CO883	UGCA	KP829220	KP829349	KP828987	KP829114	KP829924	KP829646	
Cucujoidea	Laemophloeidae	*Carinophloeus*	sp.	CO893	UGCA	KP134054	KP134117	KP133925	KP133991		KP134184	KP134250
Cucujoidea	Passandridae	*Passandra*	*heros*	CO894	UGCA	KP134055	KP134118	KP133926	KP133992			KP134251
Cucujoidea	Phalacridae	*Stilbus*	*nitidus*	CO895	UGCA	KP134056	KP134119	KP133927	KP133993	KP134299	KP134186	KP134252
Cucujoidea	Propalticidae	*Propalticus*	sp.	CO896	UGCA	KP134057	KP134120	KP133928	KP133994	KP134300	KP134187	KP134253
Cucujoidea	Monotomidae	*Bactridium*	sp.	CO898	UGCA	KP134058	KP134121	KP133929	KP133995	KP134301	KP134188	KP134254
Cucujoidea	Protocucujidae	*Ericmodes*	*sylvaticus*	GENBANK	various	AJ850051	FJ867681		DQ202617.1		DQ222021	
Cucujoidea	Silvanidae	*Silvanus*	*unidentatus*	GENBANK	various	AY748181	DQ20202626		DQ202526		HQ165230	
Cucujoidea	Cyclaxyridae	*Cyclaxyra*	sp.	N/A	various	KP419066	KP419419		DQ202566.1			

Table A.3. Nexus file of four morphological characters scored in text. Only taxa depicted in Figures 2.2-2.4 were scored for these characters.

```
#NEXUS
[written Thu Jun 26 15:31:52 EDT 2014 by Mesquite  version 2.75 (build 566) at
s172-20-220-h145.paws.uga.edu/172.20.220.145]

BEGIN TAXA;
        TITLE Taxa;
        DIMENSIONS NTAX=81;
        TAXLABELS
                CO048_Cle_Trichodes_ornatus CO031_Ten_Eleodes_sulcipennis
CO172_Ten_Hymenorus_sp CO1009_Sal_Serrotibia_sp CO404_Sal_Ocholissa_sp
Cucujus_clavipes Psammoecus_sp. 'Telephanus (Malagasy) sp' Telephanus_sp.
Telephanus_atricapillus Euplatamus_sp. Uleiota_dubius Uleiota_sp Parahyliota_sp._1
Parahyliota_sp._2 Macrohyliota_sp. Ahasverus_advena Ahasverus_sp. Silvanops_sp.
Cathartus_quadricollis Oryzaephilus_surinamensis Cathartosilvanus_imbellis
Cathartosilvanus_sp._1 Cathartosilvanus_sp._2 Parasilvanus_sp Silvanus_muticus
Silvanus_unidentatus Airaphilus_sp. Agapytho_sp. Priasilpha_obscura Hymaea_magna
Olibrus_sp. Phalacridae_sp. Stilbus_nitidus Microlaemus_sp. Carinophloeus_sp.
Lathropus_vernalis Propalticus_sp. Laemophloeus_woodruffi Laemophloeus_biguttatus
Laemophloeus_megacephalus Laemophloeus_sp._1 Laemophloeus_fasciatus
Laemophloeus_sp._2 Charaphloeus_adustus Rhinophloeus_sp._1 Rhinophloeus_sp._2
Rhinomalus_sp. Laemophloeus_incisus Rhabdophloeus_sp._1 Rhabdophloeus_sp._2
Rhabdophloeus_sp._3 Rhabdophloeus_sp._4 Cryptolestes_punctatus Dysmerus_sp.
Phloeolaemus_chamaeropis Cucujinus_sp Placonotus_zimmermani
Placonotus_politissimus Placonotus_modestus Myrabolia_sp Catogenus_rufus
Taphroscelidia_nr._humeralis Passandra_heros Cyclaxyra_sp. Ephistemus_sp.
Atomaria_sp. Cryptophagus_sp. CO352_Nit_Aethina_tumida
CO375_Nit_Cratonura_rufithorax
        ;

END;


BEGIN CHARACTERS;
        TITLE  'Matrix in file "bayes_optimized_characters.tre"';
        LINK TAXA = Taxa;
        DIMENSIONS  NCHAR=4;
        FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = "  0 1 2
3 4 5 6 7 8 9 A B C D E F G H J K M N P Q R S T U V W X Y Z a b c d e f g h j k m n p q
r s t u v w x y z";
        MATRIX
        CO048_Cle_Trichodes_ornatus           ????
        CO031_Ten_Eleodes_sulcipennis         ????
        CO172_Ten_Hymenorus_sp                ????
```

Table A.3. (continued)

CO1009_Sal_Serrotibia_sp	????
CO404_Sal_Ocholissa_sp	????
Cucujus_clavipes	1110
Psammoecus_sp.	1010
'Telephanus (Malagasy) sp'	1010
Telephanus_sp.	1010
Telephanus_atricapillus	1010
Euplatamus_sp.	1010
Uleiota_dubius	1110
Uleiota_sp	1110
Parahyliota_sp._1	1110
Parahyliota_sp._2	1110
Macrohyliota_sp.	1110
Ahasverus_advena	0010
Ahasverus_sp.	0010
Silvanops_sp.	0010
Cathartus_quadricollis	0010
Oryzaephilus_surinamensis	0010
Cathartosilvanus_imbellis	0010
Cathartosilvanus_sp._1	0010
Cathartosilvanus_sp._2	0010
Parasilvanus_sp	0010
Silvanus_muticus	0010
Silvanus_unidentatus	0010
Airaphilus_sp.	0010
Agapytho_sp.	0110
Priasilpha_obscura	1010
Hymaea_magna	0110
Olibrus_sp.	0101
Phalacridae_sp.	0101
Stilbus_nitidus	0100
Microlaemus_sp.	1010
Carinophloeus_sp.	1100
Lathropus_vernalis	1000
Propalticus_sp.	1101
Laemophloeus_woodruffi	1111
Laemophloeus_biguttatus	1111
Laemophloeus_megacephalus	1111
Laemophloeus_sp._1	1111
Laemophloeus_fasciatus	1111
Laemophloeus_sp._2	1111
Charaphloeus_adustus	1111
Rhinophloeus_sp._1	1111
Rhinophloeus_sp._2	1111

Table A.3. (continued)

```
        Rhinomalus_sp.                      1011
        Laemophloeus_incisus                1111
        Rhabdophloeus_sp._1                 1110
        Rhabdophloeus_sp._2                 1110
        Rhabdophloeus_sp._3                 1110
        Rhabdophloeus_sp._4                 1110
        Cryptolestes_punctatus              1110
        Dysmerus_sp.                        1010
        Phloeolaemus_chamaeropis            1110
        Cucujinus_sp                        1010
        Placonotus_zimmermani               1110
        Placonotus_politissimus             1110
        Placonotus_modestus                 1110
        Myrabolia_sp                        0100
        Catogenus_rufus                     1101
        Taphroscelidia_nr._humeralis        1101
        Passandra_heros                     1101
        Cyclaxyra_sp.                       0110
        Ephistemus_sp.                      0000
        Atomaria_sp.                        0000
        Cryptophagus_sp.                    0000
        CO352_Nit_Aethina_tumida            0001
        CO375_Nit_Cratonura_rufithorax      0001

;

END;
BEGIN ASSUMPTIONS;
        TYPESET * UNTITLED   =  unord:  1 -  4;

END;

BEGIN MESQUITECHARMODELS;
        ProbModelSet * UNTITLED  (CHARACTERS = 'Matrix in file
"bayes_optimized_characters.tre"')  =  'Mk1 (est.)':  1 -  4;
END;
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A.2 Supplementary Figures

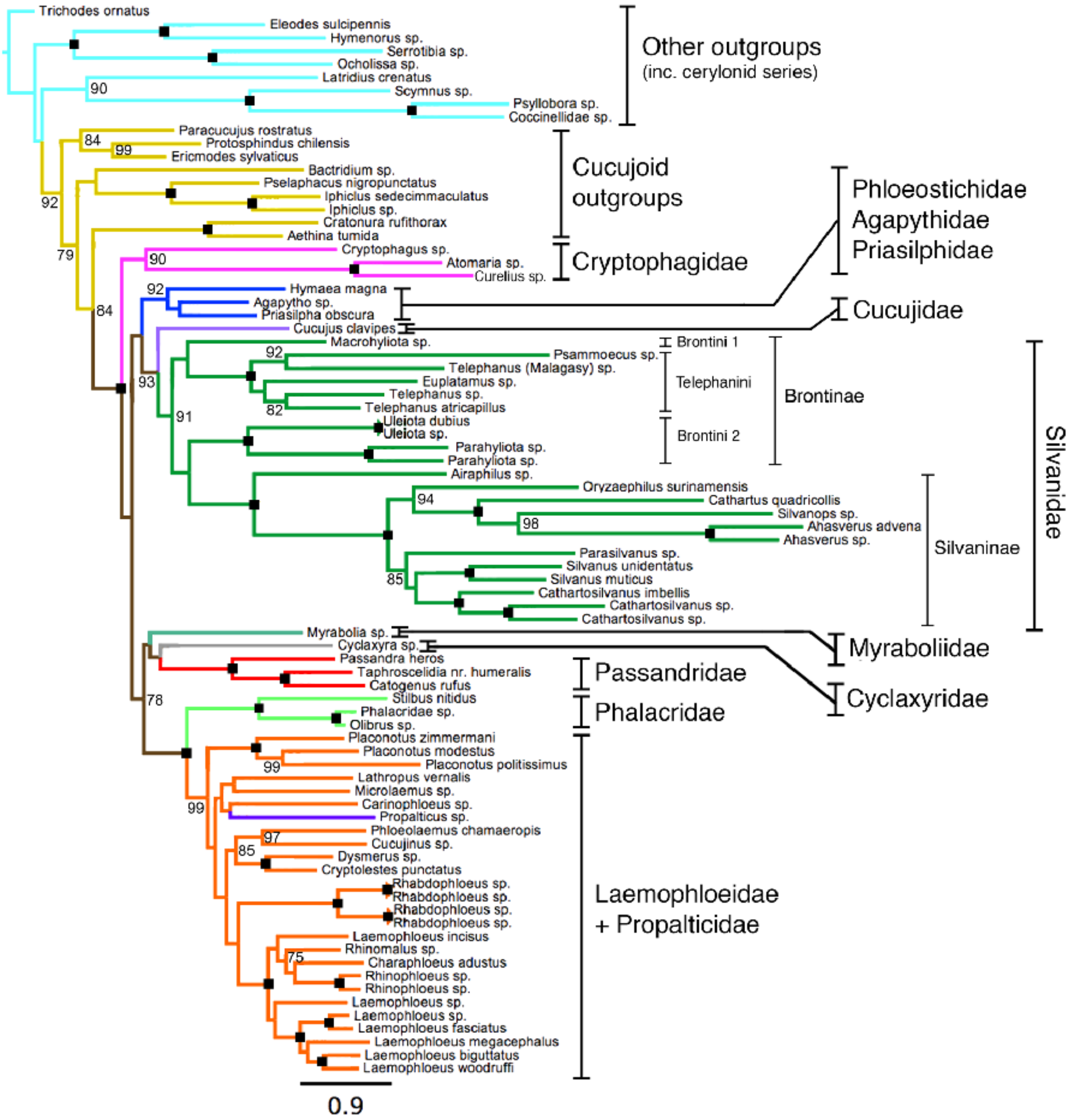

Figure A.1. RaxML most likely tree. Nodes marked with a black square indicate bootstrap support of 100%. Support values for nodes of less than 75% bootstrap are not indicated. Branch colours mark family-level clades, unless otherwise indicated. Brown indicates internal branches of uncertain taxonomic affinity.

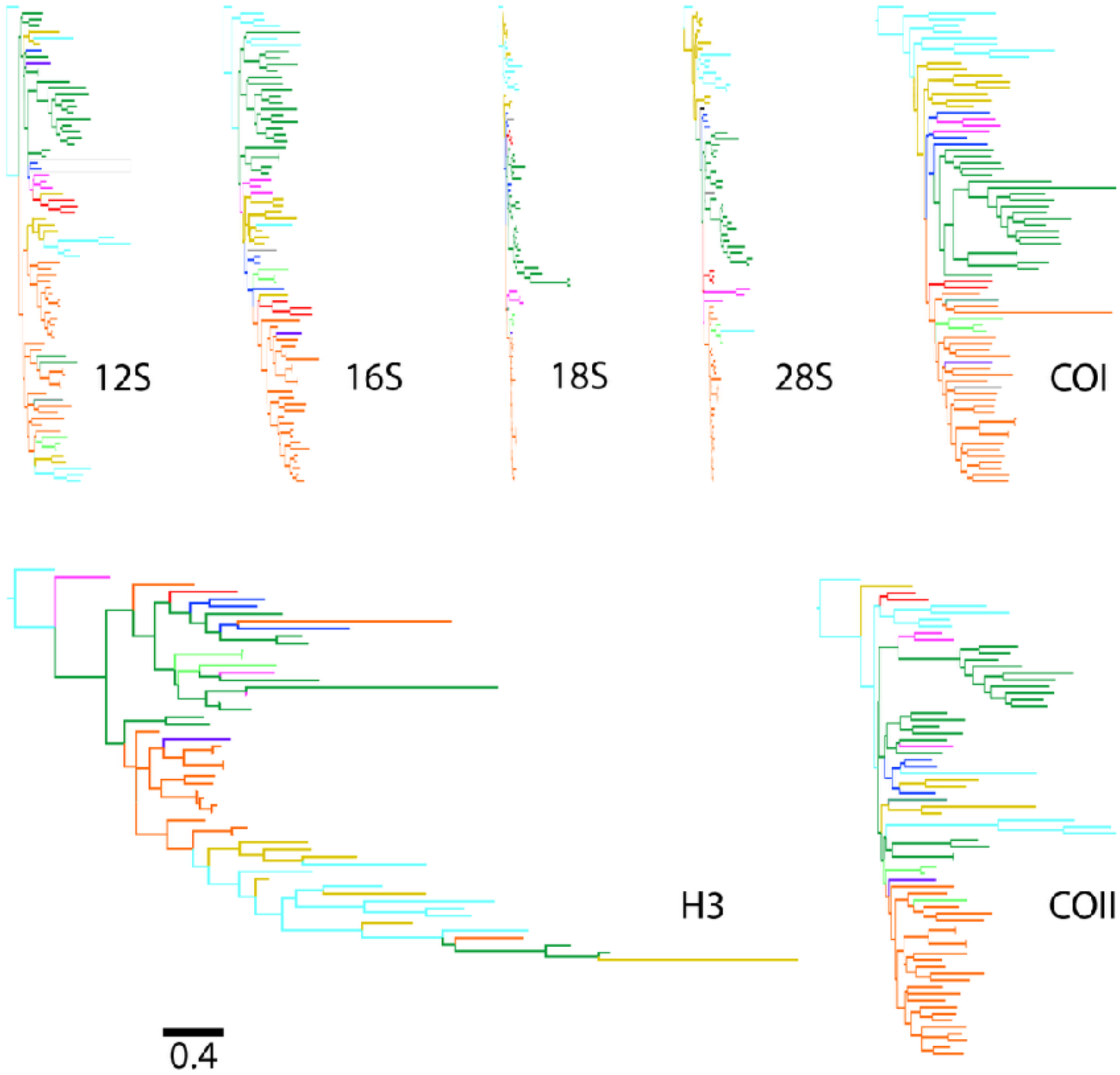

Figure A.2. Scaled RaxML most likely gene trees for each gene. Scale bar = 0.4 nucleotide substitutions/site. Coloured branches correspond to the coloured groups in Figures 2.2, A.1.

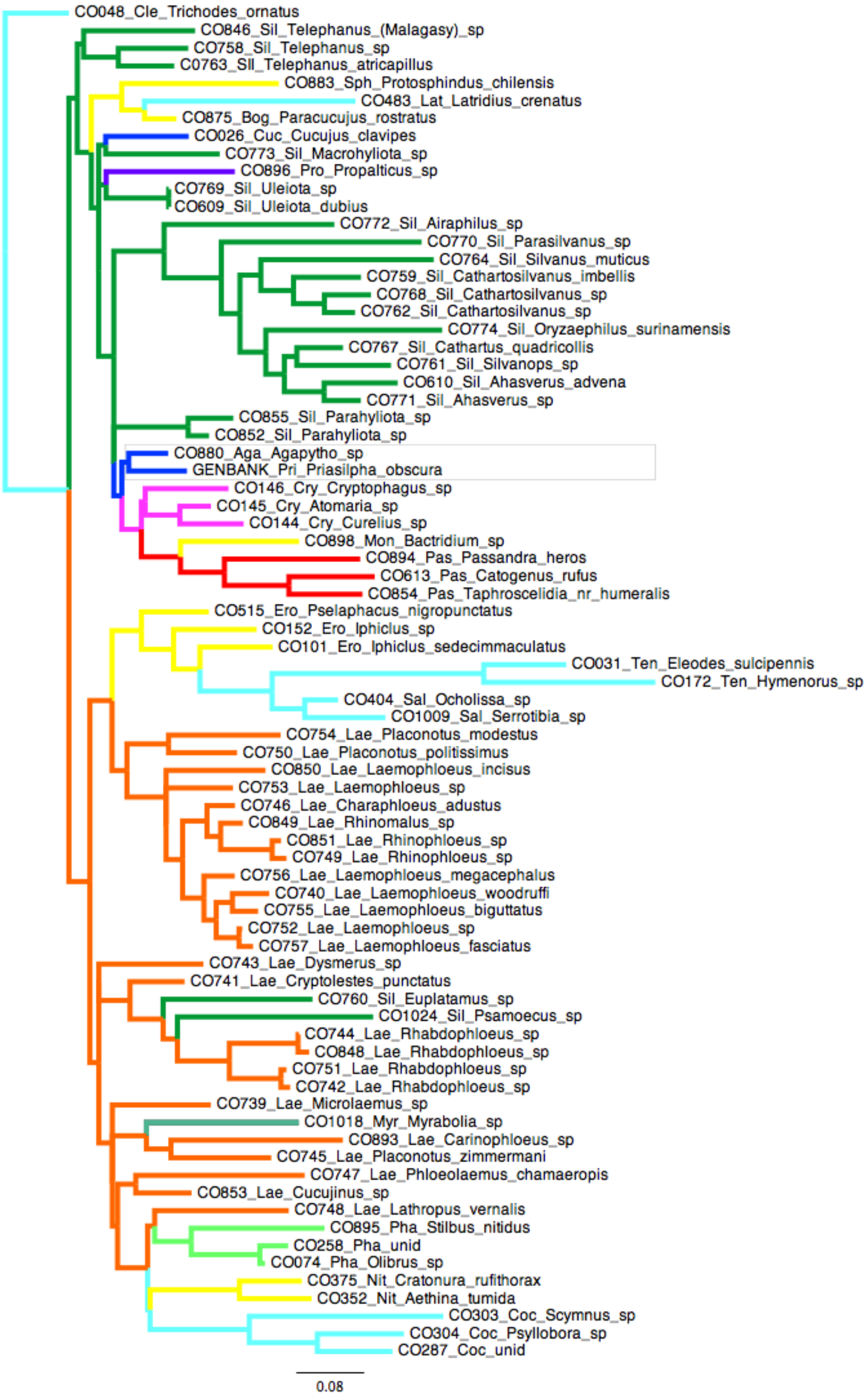

Figure A.3. RaxML most likely gene tree for the 12S gene. Scale bar = nucleotide substitutions/site. Coloured branches correspond to the coloured groups in Figures 2.2, A.1.

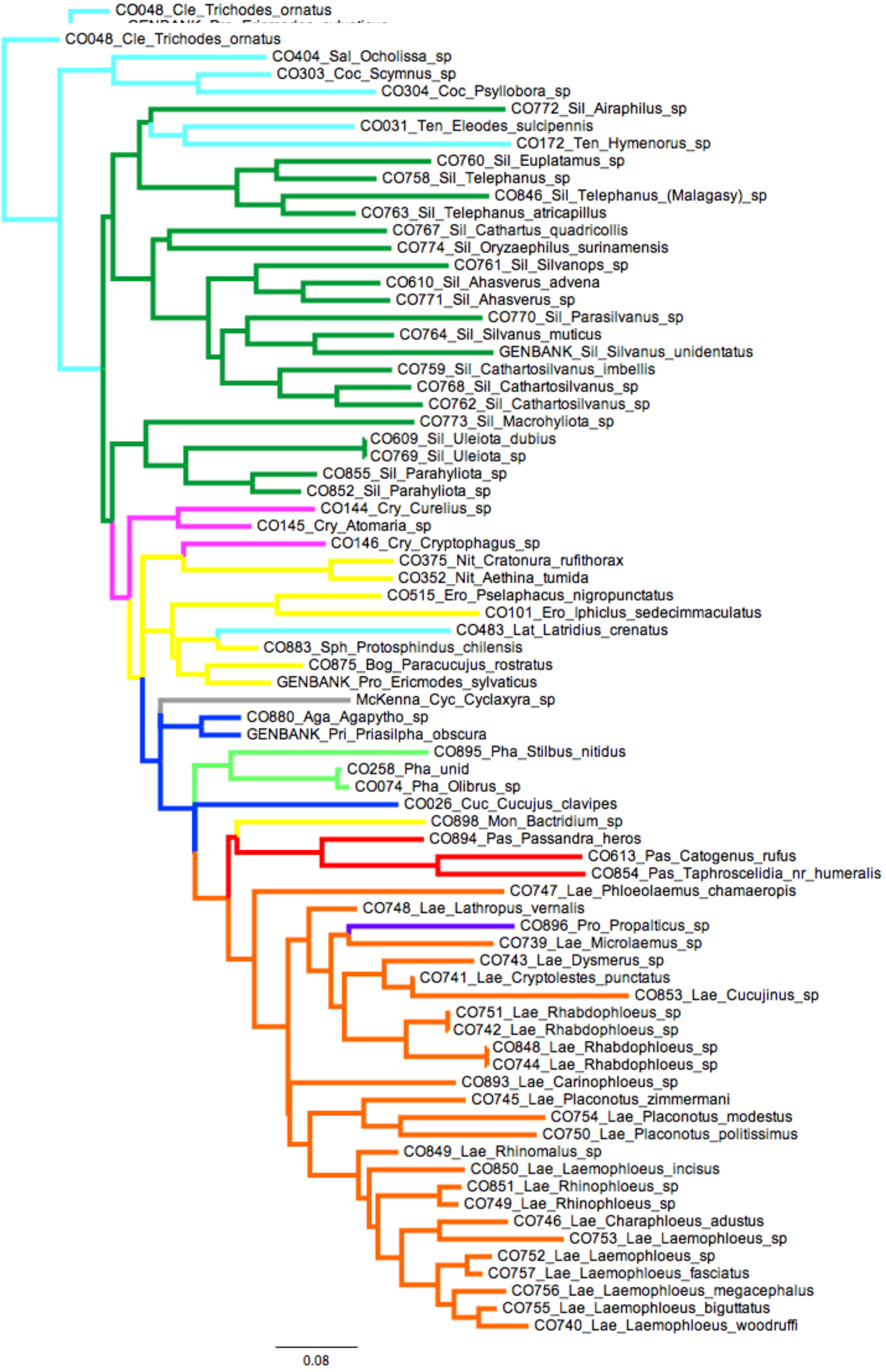

Figure A.4. RaxML most likely gene tree for the 16S gene. Scale bar = nucleotide substitutions/site. Coloured branches correspond to the coloured groups in Figures 2.2, A.1.

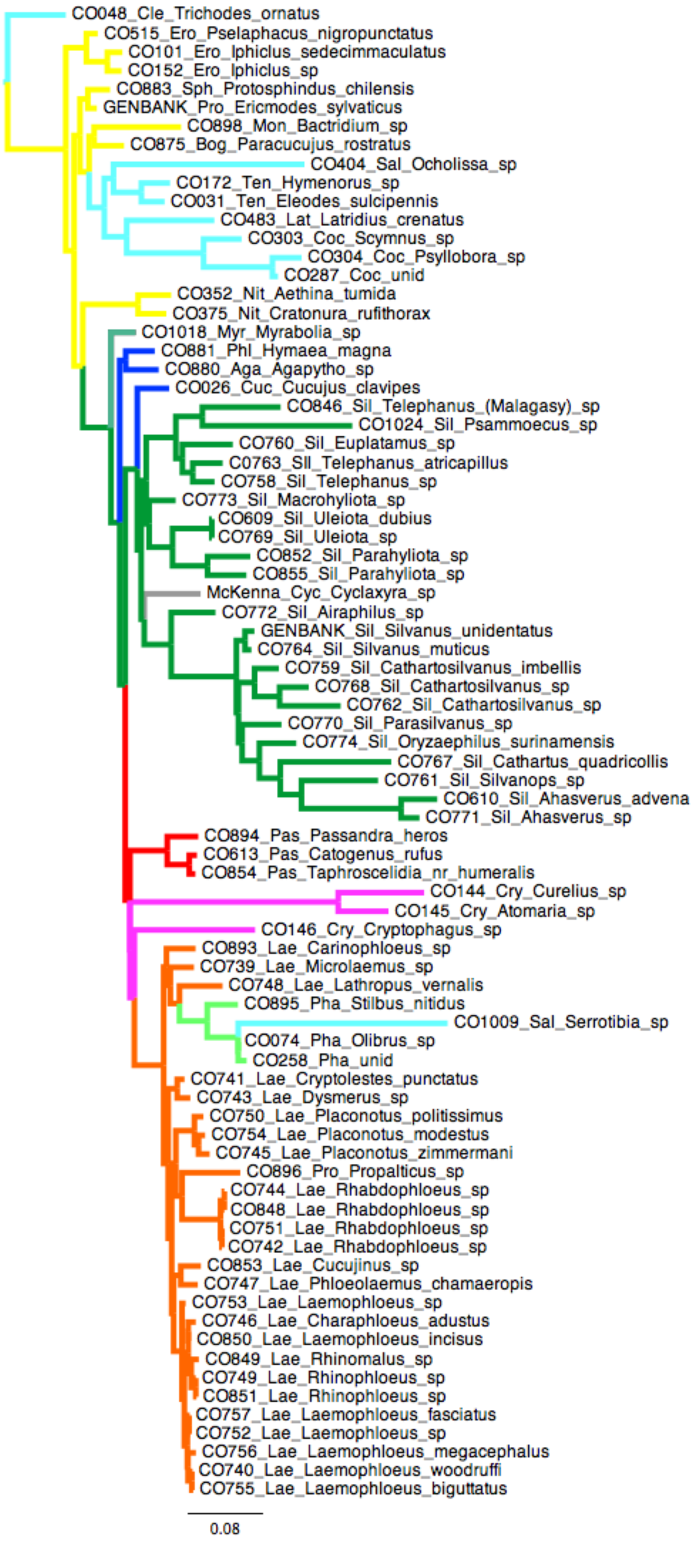

Figure A.6. RaxML most likely gene tree for the 28S gene. Scale bar = nucleotide substitutions/site. Coloured branches correspond to the coloured groups in Figures 2.2, A.1.

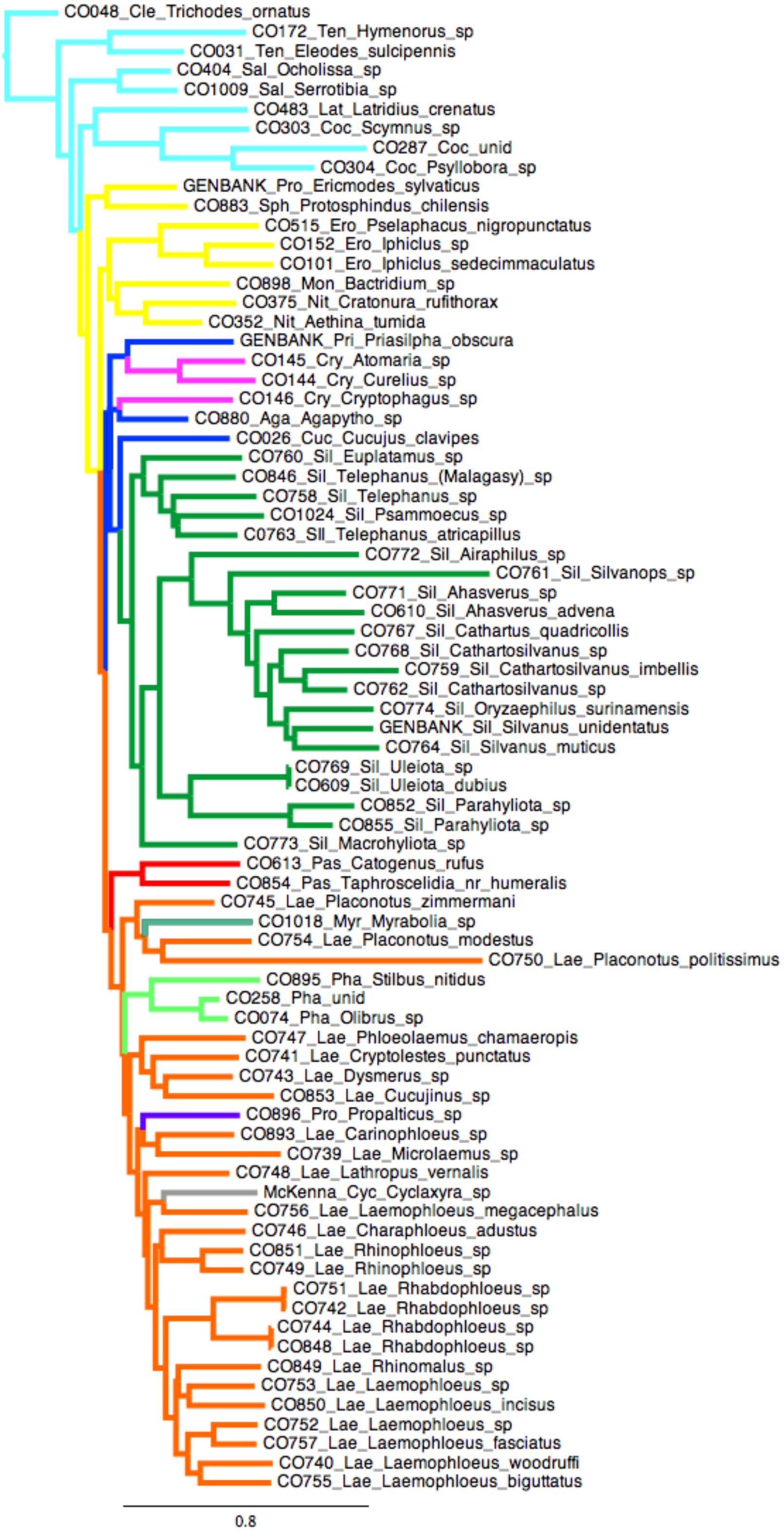

Figure A.7. RaxML most likely gene tree for the COI gene. Scale bar = nucleotide substitutions/site. Coloured branches correspond to the coloured groups in Figures 2.2, A.1.

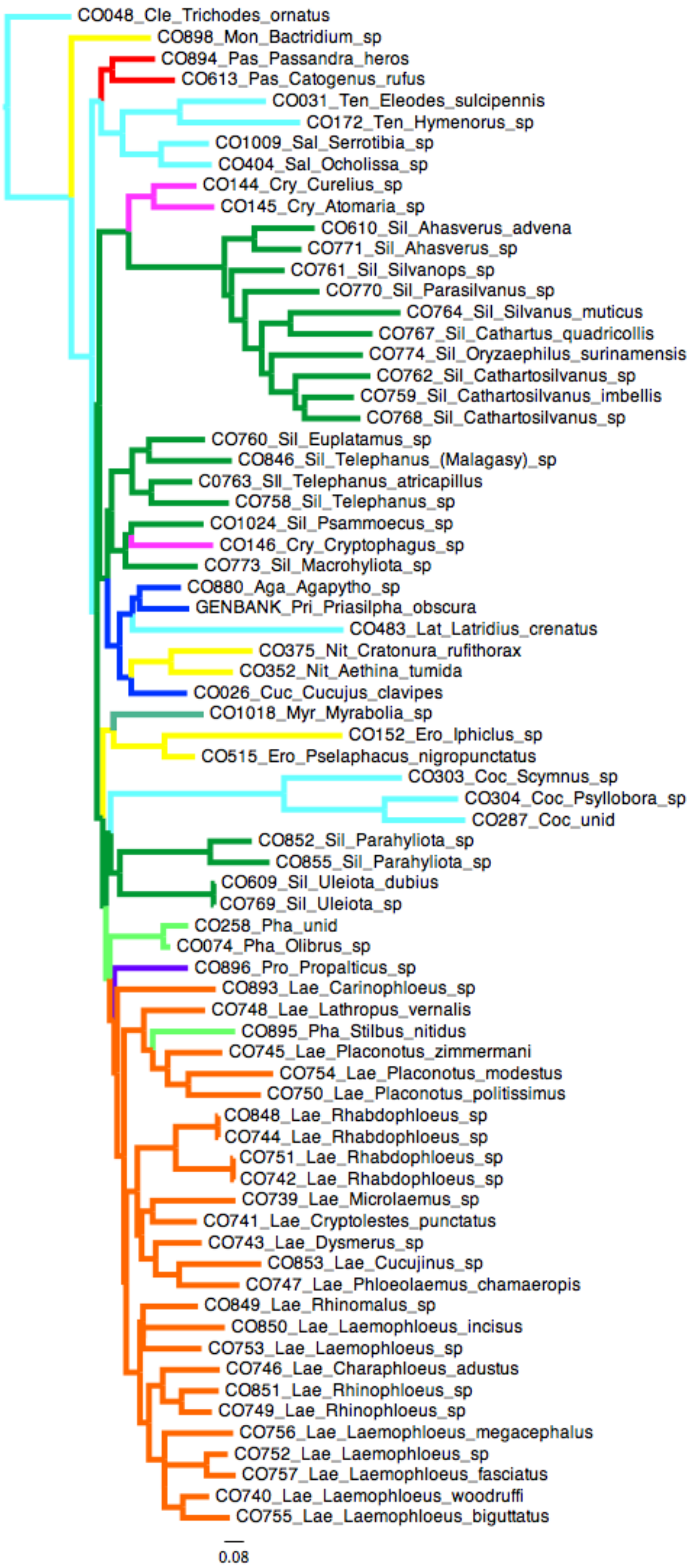

Figure A.8. RaxML most likely gene tree for the COII gene. Scale bar = nucleotide substitutions/site. Coloured branches correspond to the coloured groups in Figures 2.2, A.1.

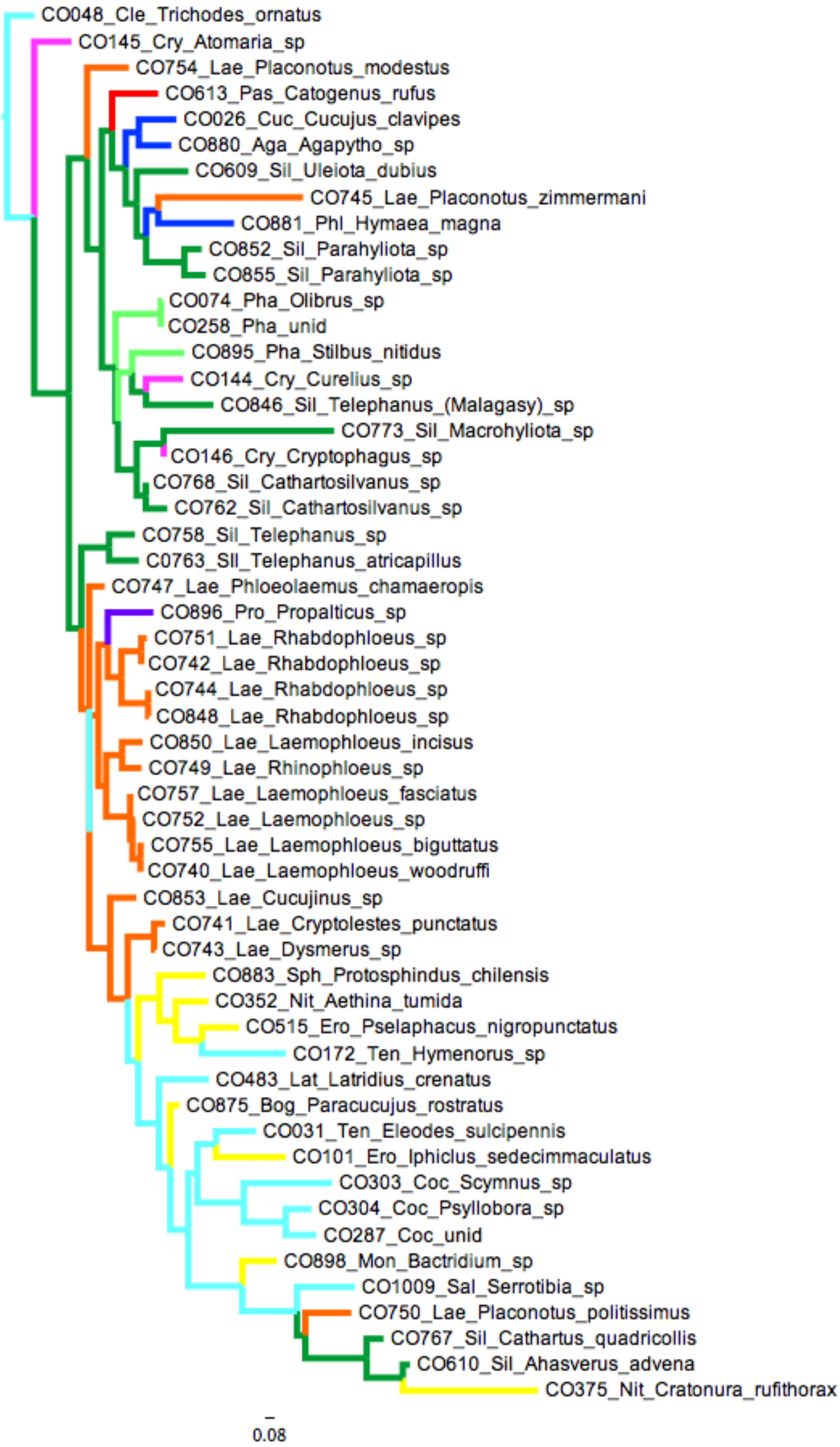

Figure A.9. RaxML most likely gene tree for the H3 gene. Scale bar = nucleotide substitutions/site. Coloured branches correspond to the coloured groups in Figures 2.2, A.1.

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