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A Phylogenetic Analysis of Bostrichoidea (Coleoptera) and Revisions of the Southern African Spider Beetle Genera Meziomorphum and Eutaphroptinus (Ptinidae: Coleoptera)

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A PHYLOGENETIC ANALYSIS OF BOSTRICHOIDEA (COLEOPTERA) AND REVISIONS OF THE SOUTHERN AFRICAN SPIDER BEETLE GENERA *MEZIOMORPHUM* AND *EUTAPHROPTINUS* (PTINIDAE: COLEOPTERA)

A Thesis
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The Faculty of the Department of Biology
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Bowling Green, Kentucky

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

By
Olivia M. Gearner

May 2019

A PHYLOGENETIC ANALYSIS OF BOSTRICHOIDEA (COLEOPTERA) AND REVISIONS OF THE SOUTHERN AFRICAN SPIDER BEETLE GENERA *MEZIOMORPHUM* AND *EUTAPHROPTINUS* (PTINIDAE: COLEOPTERA)

Date Recommended 17 Apr. 2019

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Grobbelaar (National Collection of Insects, Pretoria). I would like to thank Peter Koniar (Prague, Czech Republic) for providing us specimens of the newly described *M. boroveci* and *M. nama* as well as a new record for *M. krimpvarkie.* I would also like to thank Y. Marusik (Magadan, Russia) who brought to our attention and mailed us specimens he collected resulting in the new record for *M. speldekussing*. I also appreciate the support of the Center for Biodiversity Studies at Western Kentucky University as well as the following funding sources: an NSF Biological Surveys and Inventories grant (DEB 0430132), a Faculty-Undergraduate Student Engagement (FUSE) grant (17-SP253), and the WKU Graduate School (221533).

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A Revision of the Spider Beetle Genus *Eutaphroptinus* Borowski (Coleoptera: Ptinidae)

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Olivia M. Gearner May 2019 110 Pages

Directed by: T. Keith Philips, Albert J. Meier, and Carl W. Dick

Department of Biology Western Kentucky University

Proposals for the internal relationships and classification of the bostrichoids are currently poorly supported, and almost all are based on morphology alone. This study improves upon on previous phylogenetic analyses of the group by including more taxa using the standard genes for many phylogenetic analyses. Cytochrome C oxidase subunit 1 (CO1), 28S small subunit rRNA, and 16S small subunit rRNA mitochondrial genes were sequenced or obtained from Genbank, then analyzed using parsimony and Bayesian analyses. Topologies differed depending on genes used. A three gene tree and a two gene (28S and CO1) tree both supported relationships in which a basal bostrichid clade was sister to Ptinidae *s. s.* + anobiids, with another bostrichid clade within the ptinids. Current bostrichid and anobiid subfamilies tested were not supported as monophyletic in any of the trees obtained.

Additionally, five new species of spider beetles in the genus *Meziomorphum* Pic from South Africa are described including *M. endrödyi*, *M. boroveci,* and *M. nama* from the Richtersveld, *M. bulla* from south-central Namaqualand, and *M. cederbergensis* from the Cederberg. Genitalia are illustrated for the genus for the first time for six of the 10 species now known. A brief discussion of the evolution of generic morphology and biology as well as the relationships of the genus to other spider beetle groups are also provided.

Finally, a revision of the genus *Eutaphroptinus* is presented. *Eutaphroptinus pseudonatalensis* is considered a synonym of *Eutaphroptinus natalensis*. New species records of *E. natalensis* are also provided, as well as illustrations of the genus.

HYPOTHESIZING RELATIONSHIPS WITHIN BOSTRICHOIDEA (COLEOPTERA) USING MOLECULAR PHYLOGENETICS

Introduction

Insects are the most diverse and speciose group of organisms on the planet. Coleoptera alone comprise 25% of described animal species worldwide (Hammond, 1992). One less commonly known group of beetles that is vastly understudied but highly diverse is the bostrichoids, which include four main groups, the dermestids, bostrichids, anobiids, and the spider beetles. In Ptinidae alone (the anobiids and spider beetles), there are around 230 genera and 2200 species currently known (Philips and Bell 2010; Lawrence 1991; Lawrence and Viedma 1991). Additionally, there are likely numerous taxa worldwide that have yet to be documented due to lack of awareness of these organisms by many entomologists and collectors, high levels of endemicity present in the group, and the obscure nature and small body size of these beetles (Bell and Philips 2012).

The bostrichoids are currently classified into three families, the Dermestidae, Bostrichidae, and the Ptinidae. Within the Ptinidae, there are nine subfamilies of "anobiids" (formerly the family Anobiidae), as well as the two subfamilies that constitute the spider beetles, the Gibbiinae and Ptininae (Borowski and Zahradníc 2007). Henceforth, bostrichids will refer to members of Bostrichidae, anobiids will refer to members of the former family Anobiidae, and ptinids will refer to members of Ptininae and Gibbiinae.

In the early 1800s, the Bostrichidae, Anobiidae, and Ptinidae were classified in the family Ptinidae by coleopterists like LeConte and Horn (Philips and Bell 2010). Fall (1905) later classified the bostrichids as their own family, and Pic (1912a, 1912b) recognized Anobiidae and Ptinidae as separate families. Decades later, Lawrence and Newton (1995) combined anobiids and ptinids into the family Anobiidae, despite the fact the name Ptinidae had priority. Most recently, the anobiids and ptinids were rejoined in the family Ptinidae (Borowski and Zahradníc 2007). However, all of these classifications, as well as most of the subfamilies, tribes, and genera, are largely based on morphological data using the traditional Linnaean system of classification, rather than on phylogenetic analyses.

Anobiid and some ptinid larvae typically bore into wood, bark, seeds, and fungi and can be serious pests to buildings, furniture, and book bindings (White 1962; Lawrence et al. 1999). However, most Ptinidae are not wood, bark, or fungal borers. Many species feed on dried animal and plant material (Howe 1959), while some breed in animal dung such as that of rodents, hyraxes, or bats (Philips and Bell 2010). Some inhabit bird or animal nests (Philips and Bell 2010) likely feeding on detritus, and a few, such as *Ptinus californicus* and *Ptinus sexpunctatus*, can be found in solitary bee nests feeding upon pollen stores and perhaps dead bee larvae (Linsley and MacSwaine 1942). One species of *Pitnus* is a leaf miner (Philips et al. 1998), and a species of *Stereocaulophilus* reportedly grazes on lichen (Bellés 1994). Additionally, there are several myrmecophilous (ant-associated) species in Ptininae (e.g. Lawrence and Reichardt 1969; Philips 1998; Bell and Philips 2008). The biology of these taxa is unknown with the exception of a laboratory observation where a species of *Gnostus* solicited and received food from a host via trophallaxis (Thomas et al. 1992). Ptinidae larvae usually pupate in their feeding chambers, and some form distinctive cocoons from their peritrophic membrane, a membrane that lines and protects the midgut in insects (Tristam 1977).

Ptinidae are distributed throughout the world and are currently known to be most diverse in temperate regions rather than tropical regions (White 1974; Philips 2000a). However, this may be an artifact of poor sampling and lack of knowledge of diversity in the tropics, and not representative of the true distribution of the family. Diversity hotspots for the ptinids appear to be in the southwestern Palaearctic (especially the circum-Mediterranean) region and in southern Africa (Philips and Bell 2010).

The phylogenetic relationships within Bostrichoidea are still both poorly known and supported. The most recent, expansive phylogenetic study was performed by Bell and Philips (2012), in which they used a mitochondrial gene, Cytochrome C oxidase subunit 1 (CO1), and two ribosomal genes, the nuclear large subunit rRNA (28S) and the mitochondrial large subunit rRNA (16S) to build a molecular phylogeny. They found that Bostrichidae may be the most basal group, with the ptinids and anobiids as sister taxa (see Figure 1). However, some of their analyses also suggested that the ptinids could be the basal group, with bostrichids and anobiids as sister taxa. This study aims to improve on the phylogenies proposed by Bell and Philips by including a much denser taxon sampling with more than three times number of the taxa included (from 82 to 251), as well as including CO1 and 28S genes that were missing in some taxa included by Bell and Philips (2012).

Materials and Methods

Sampling

Taxa representing 11 subfamilies and about 75 genera of Ptinidae were included in the study. Subfamilies represented were Anobiinae, Dorcatominae, Dryophilinae, Ernobiinae, Eucradinae, Gibbiinae, Mesocoelopodinae, Ptilininae, Ptininae, and Xyletininae. No species from Alvarenganiellinae (which contains only one genus: *Dasytanobium*) were included. Additionally, 25 genera of bostrichids and 7 genera of dermestids were included.

One hundred and twenty-three sequences from Bell and Philips (2012) were included, as well as an additional 160 sequences accessed from GenBank. Additionally, DNA from recently collected specimens was isolated and sequenced (87 sequences).

DNA Sequencing

DNA was extracted using the Omega Biotek E.Z.N.A. Insect DNA kit. Sequences for three genes—CO1, 28S, 16S—were amplified using the polymerase chain reaction. Typical PCR reactions contained 12.5 µL of GoTaq Hotstart Master Mix, 15 pmol of each primer, 2 mM $Mg(OAc)_2$, and 1-7.5 µL of DNA template (usually ~100 ng DNA), for a total volume of 25 µL. PCR cycles for CO1 included an initial 2 minute denaturation step at 96°C, followed by 35 cycles of 35 seconds at 96°C, 1 minute at 48°C, and 30 seconds at 72°C, and a final extension step for 10 minutes at 72°C. PCR cycles for 28S included an initial 2 minute denaturation step at 95°C, followed by 44 cycles of 35 seconds at 95°C, 45 seconds at 62°C, and 1 minute at 72°C, and a final extension step for 10 minutes at 72°C.

PCR products for CO1 and some 28S samples were sequenced using ABI DYE-TERMINATOR 3.1, following the standard protocol, on an ABI 3130 sequencer. Several 28S samples were outsourced to GENEWIZ for Sanger Sequencing. DNA sequences were edited using Geneious 7.1.9.

Table 1. Primers used in the current study.

Gene	Primer	Sequence
CO1	CO1-Forward Mixed	5’-TAYTAGGRTTTATTGTDTTGRGC-3’
	CO1-Reverse Mixed	5’-GCATCWGGRTARTCWGARTATCG-3’
28S	Olivia-F	5’-GGTAAACTCCATCTAAGG-3’
	Olivia-R	5’-CCTGAAAKYACCCAA-3’

Phylogenetic Analysis

Sequences were aligned using the ClustalW algorithm in Geneious. The default gap opening penalty of 5 was used for CO1 and 28S gene sequences. A gap opening penalty of 0.5 was used for aligning 16S sequences, as this was found by Bell and Philips (2012) to result in the least incongruency between length variable and length invariable regions. The default gap extension penalty of 6.66 was used for all three genes. Parsimony analyses were performed using the NONA program in WINCLADA 1.00.08 (Nixon, 1999). Each analysis was run for 5,000 repetitions with taxon order randomized, time used as the random seed, and 100,00 trees total held in the memory.

Bayesian analyses were performed using MRBAYES 3.2 (Ronquist et al. 2012). Optimal models for sequence evolution for each gene region were determined using JModelTest 2.1 (Darriba et al. 2012), based on Bayesian information criterion (BIC). For CO1 and 16S, general time reversal (GTR) with a gamma distribution (G) was used. For 28S, the Hasegawa, Kishino and Yano (HKY) model was used with invariable sites (I) and a gamma distribution (G). Two simultaneous searches were run, each with four

Markov chain Monte Carlo (MCMC) chains (one cold and three hot), with a sample frequency of 100. These were run for several generations at a time, until the standard deviation of the split frequencies between the two analyses fell below 0.01. A burn-in of 25% was used for the three gene dataset and 35% for the two gene (28S and CO1) dataset.

All trees were rooted using Dermestidae, as this family has been found to be sister to the clade of bostrichids, ptinids, and anobiids (Hunt et al. 2007; Lawrence et al. 2011).

Results

CO1 Gene

A parsimony analysis of 221 taxa using the CO1 gene region resulted in 36 trees (L=12716, CI=10, RI=70). A strict consensus of these trees is quite unresolved, with a few large polytomies (Fig 1). Conserved clades of note include monophyletic clades of some genera such as *Dorcatoma*, *Lyctus*, and *Xyletinus* and one containing most, but not all, species of *Ptinus.* Another clade contains the Australasian genera *Kedirinus* and *Sundaptinus* (but including the dermestid- *Anthrenus*), one containing the genera *Ochina*, *Xestobium*, and *Ernobius,* all of which are classified in the subfamily Ernobiinae, and several other clades of bostrichids, anobiids, and spider beetles.

In the majority rules consensus tree (Fig 2), there is a great deal more resolution although the ptinids, bostrichids, and anobiids are all polyphyletic. Additionally, some taxa from the outgroup (Dermestidae) have been placed in the ingroup.

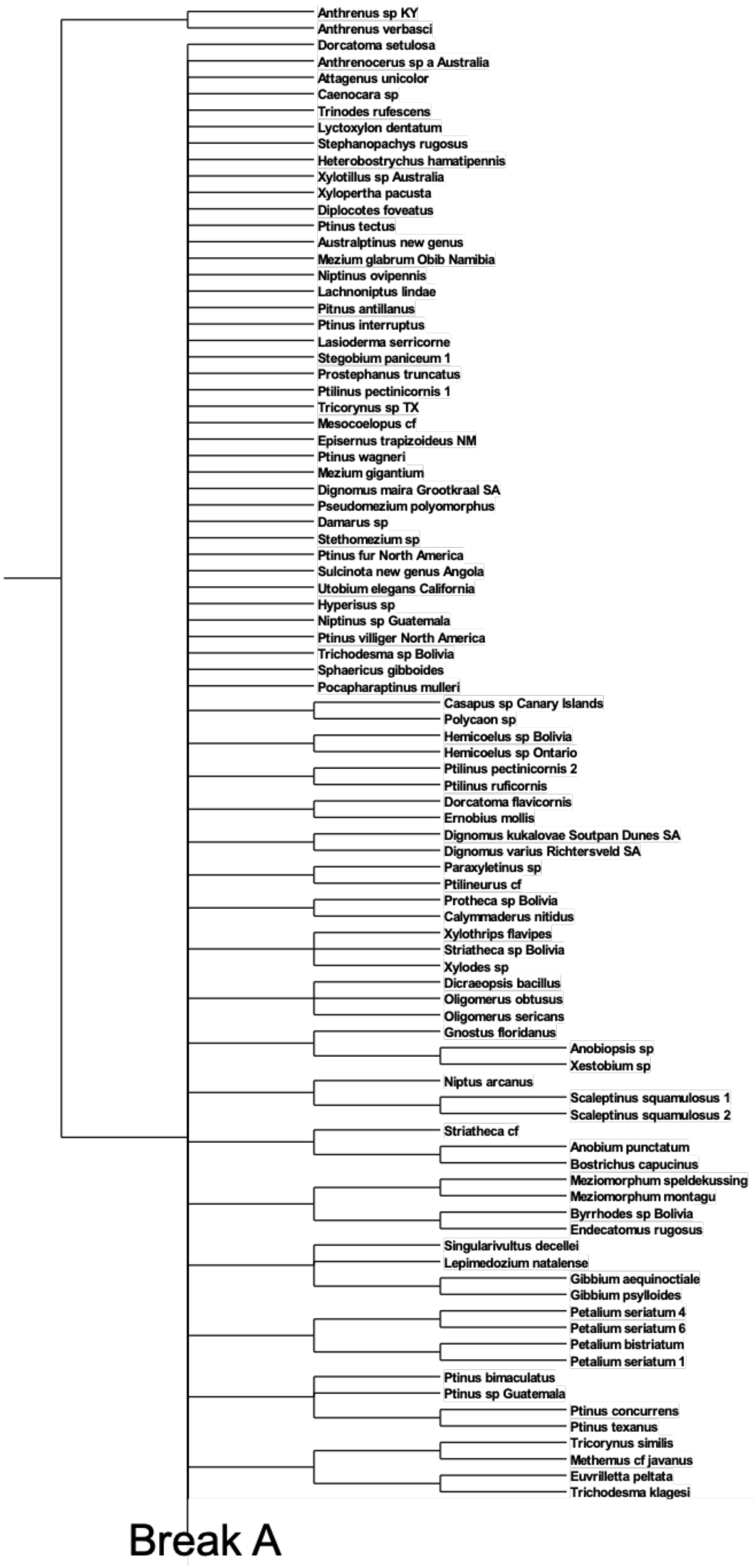


Figure 1

Strict consensus of 36 trees from a parsimony analysis of the CO1 gene region.

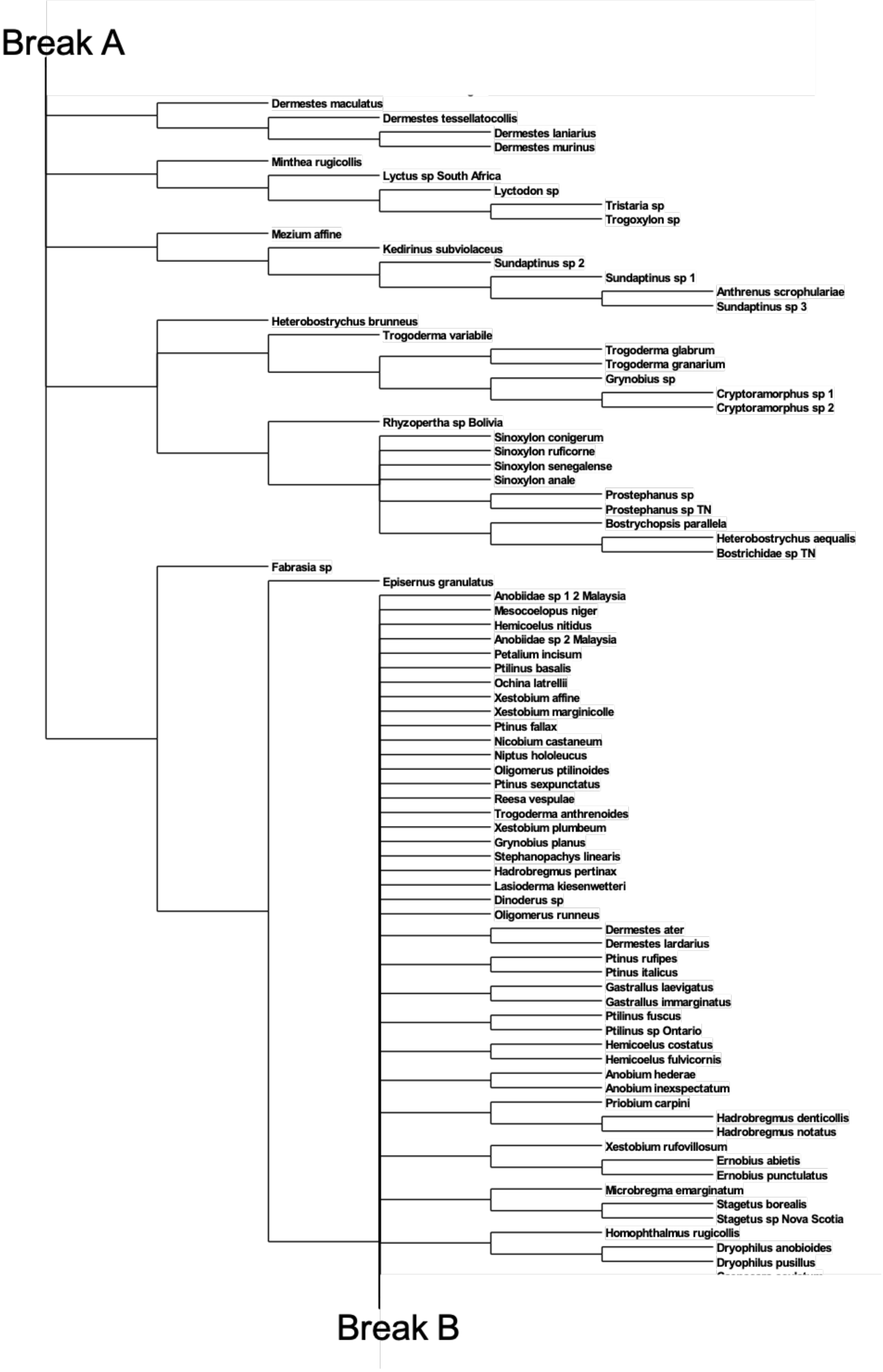


Figure 1. ***Continued***

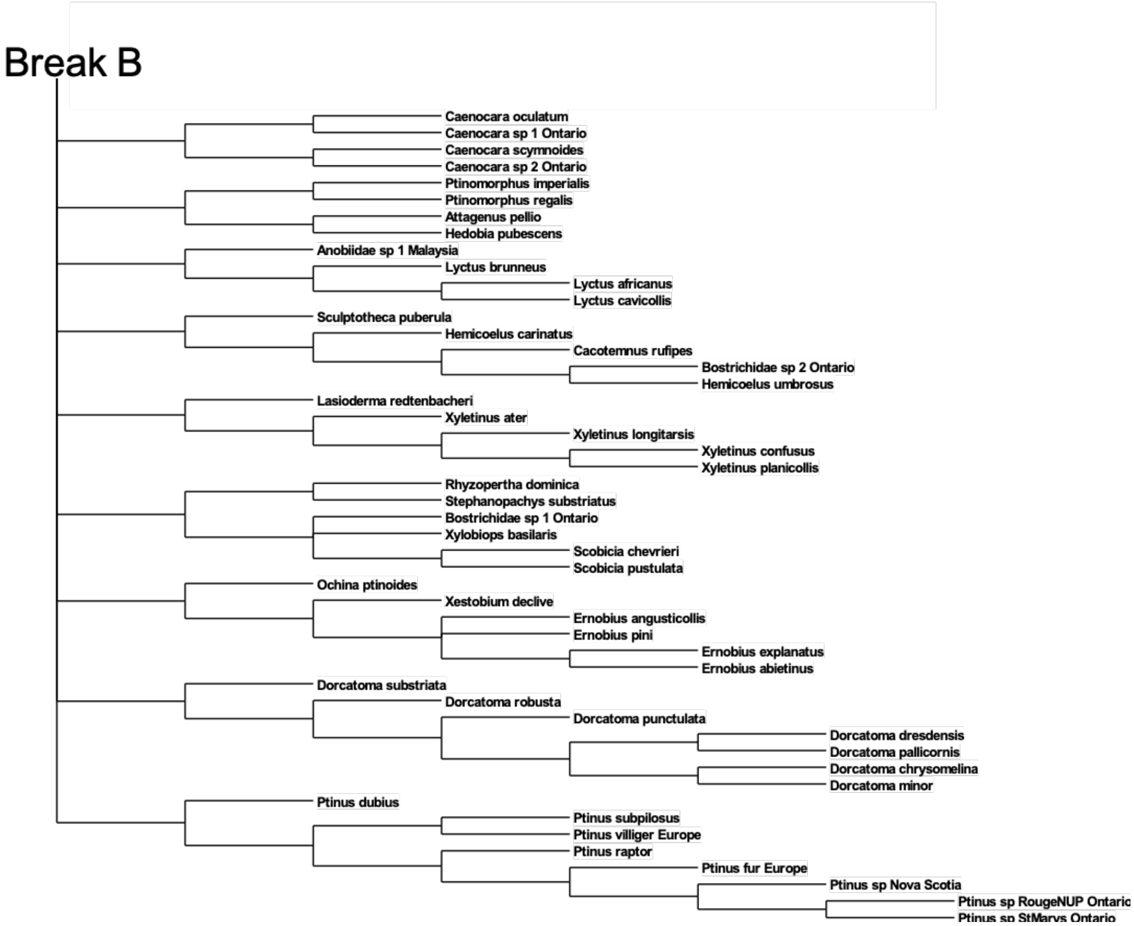


Figure 1. *Continued*

28S Gene

The parsimony analysis of 114 taxa using the 28S gene region resulted in 114 trees (L=5019, CI=31, RI=69). The strict consensus of these trees (Fig 3) was better resolved than in the CO1 trees, but there is a large polytomy consisting of nine clades at the base. One conserved clade to note is one containing the genera *Dignomus, Pseudomezium,* and *Casapus*, suggesting that *Pseudomezium* and *Casapus* are derived *Dignomus.*

In the majority rules consensus (Fig 4), *Kedirinus subviolaceous* is the most basal taxon and sister to all other ingroup taxa, followed by a basal clade of ptinids. This clade is sister to all bostrichids and nearly all anobiids. The next most basal clade is one containing anobiids and a group of bostrichids. This clade in turn is sister to another clade of mainly bostrichids + nearly all included anobiids.

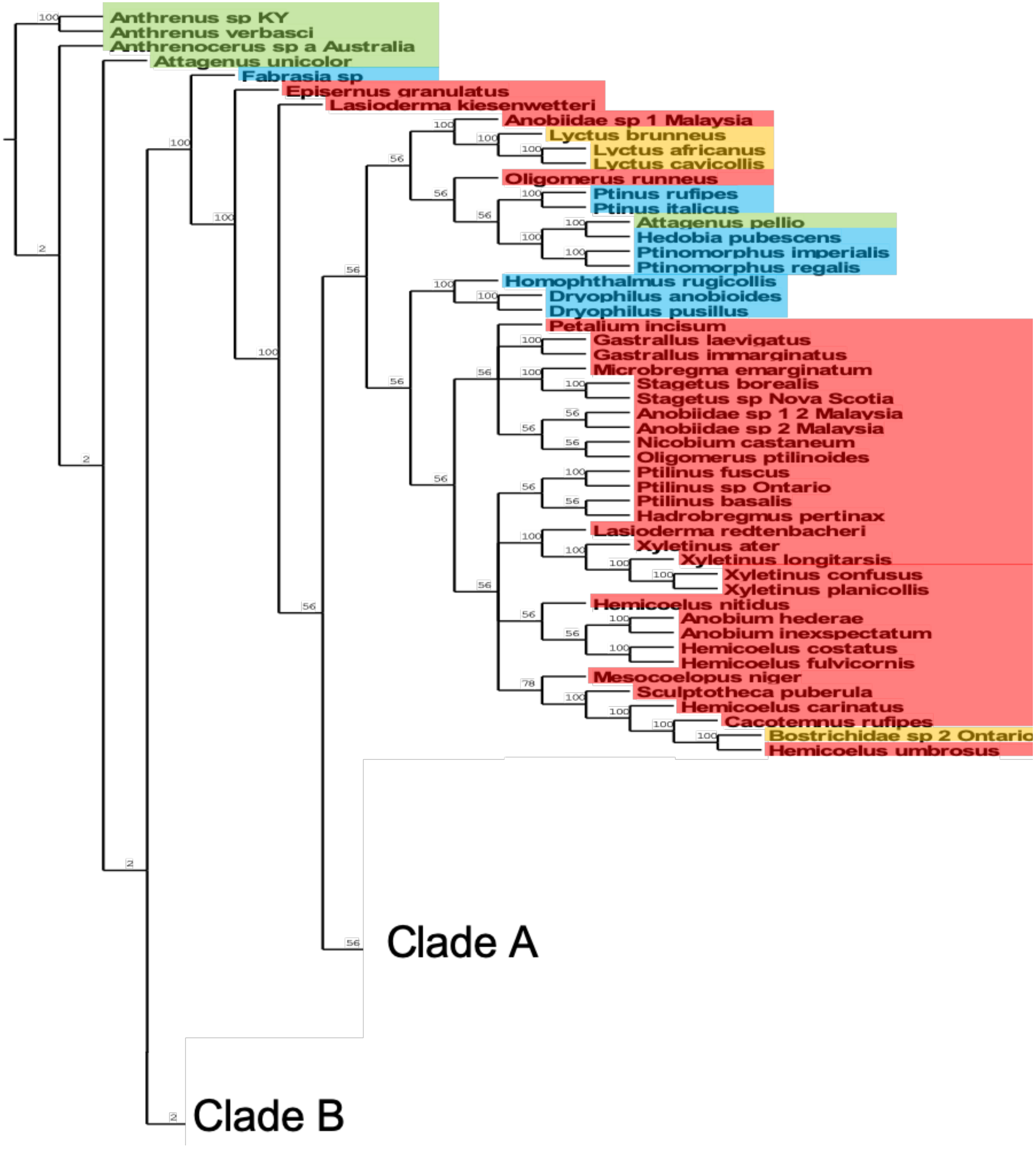


Figure 2
Majority rules consensus of 36 trees from a parsimony analysis of the CO1 gene region. Yellow taxa represent bostrichids, red are anobiids, and blue are ptinids.

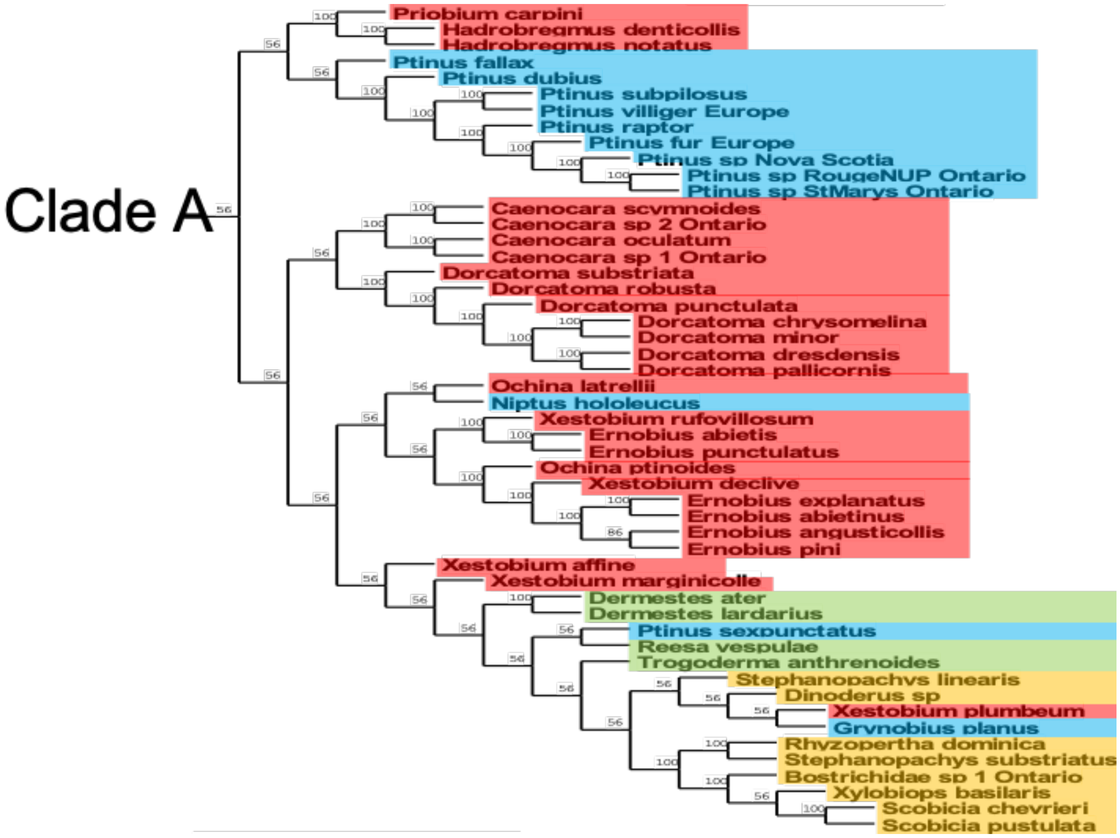
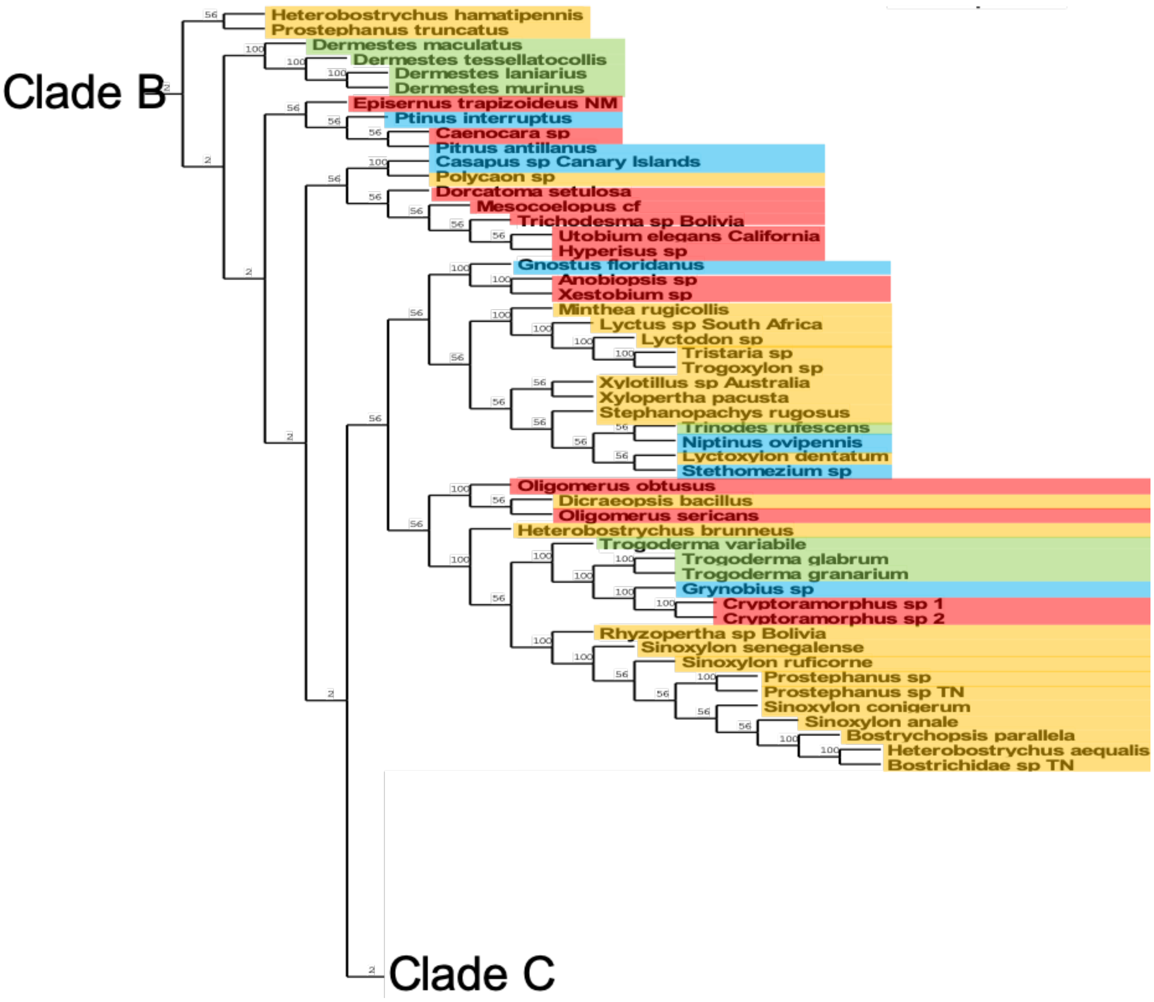


Figure 2. *Continued*



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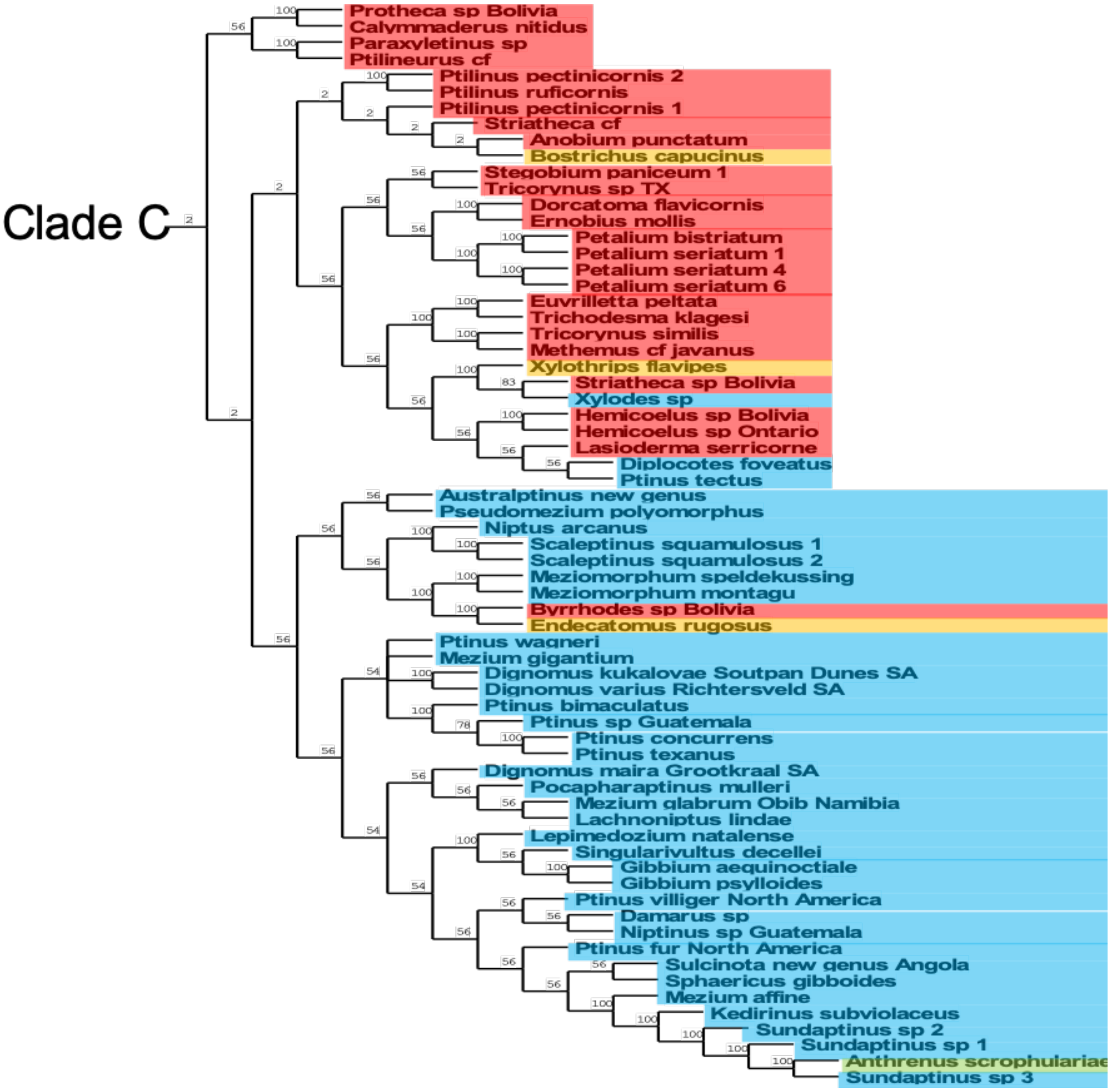


Figure 2. ***Continued***

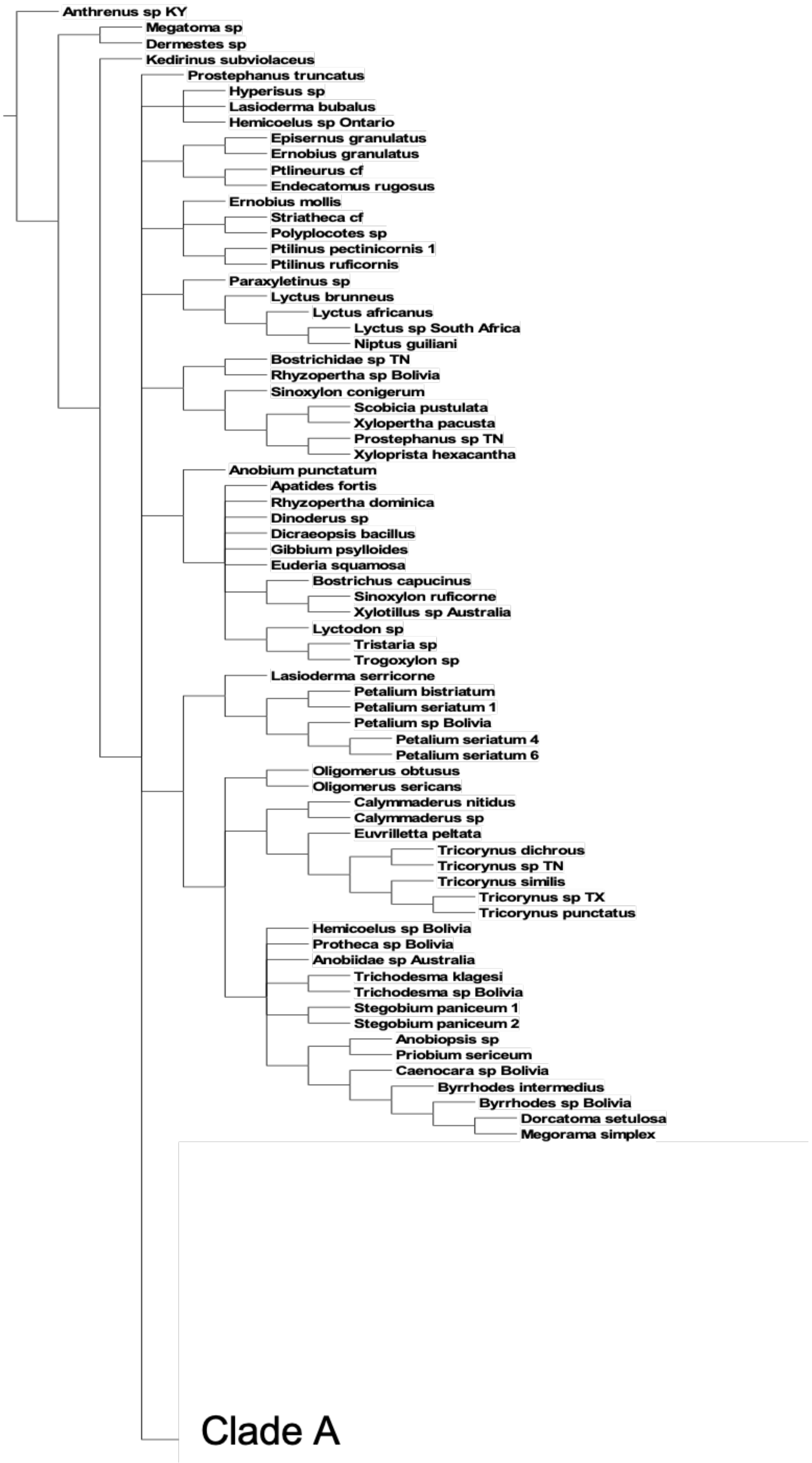


Figure 3

Strict consensus of 114 trees from a parsimony analysis of the 28S gene region.

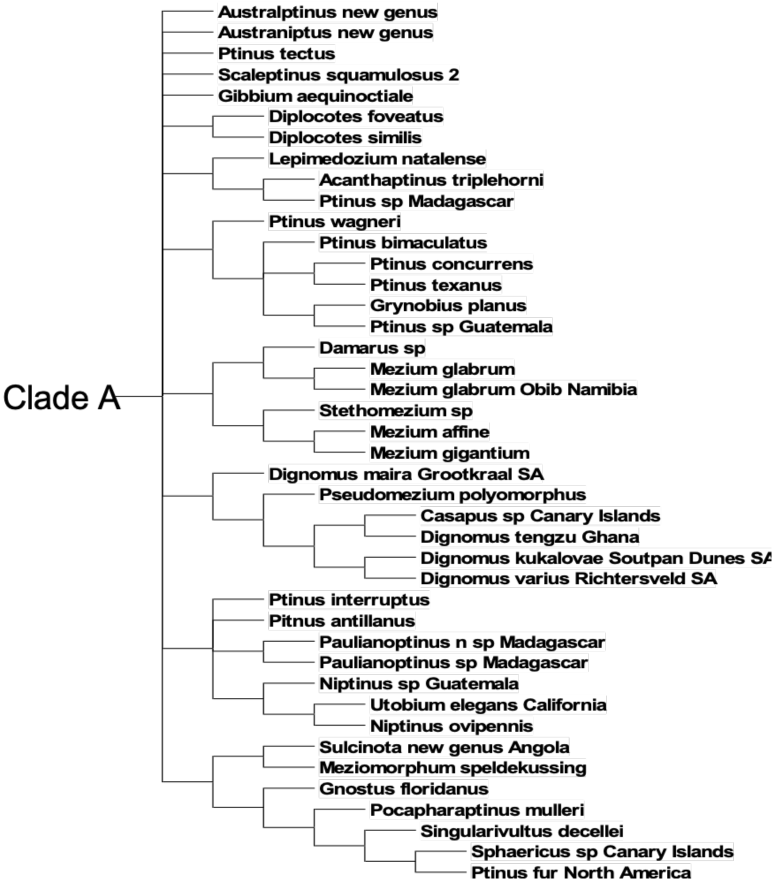


Figure 3. ***Continued***

<u>CO1 plus 28S Genes</u>

A parsimony analysis of the combined dataset using CO1 and 28S, and only including taxa with both gene regions, resulted in 4 trees (L=10751, CI=26, RI=49). Similar to the tree derived from only the 28S data, a strict consensus of these trees (Fig 5) places the Australian ptinid species *Kedirinus subviolaceous* as basal to all other clades. The next most basal clade is a group of bostrichids with a few anobiid species included in the clade. This is followed by two clades of anobiids. Finally, at the apical most part of the tree is a clade of all the ptinids that includes one derived anobiid, *Utobium elegans*, and a derived clade of bostrichids.

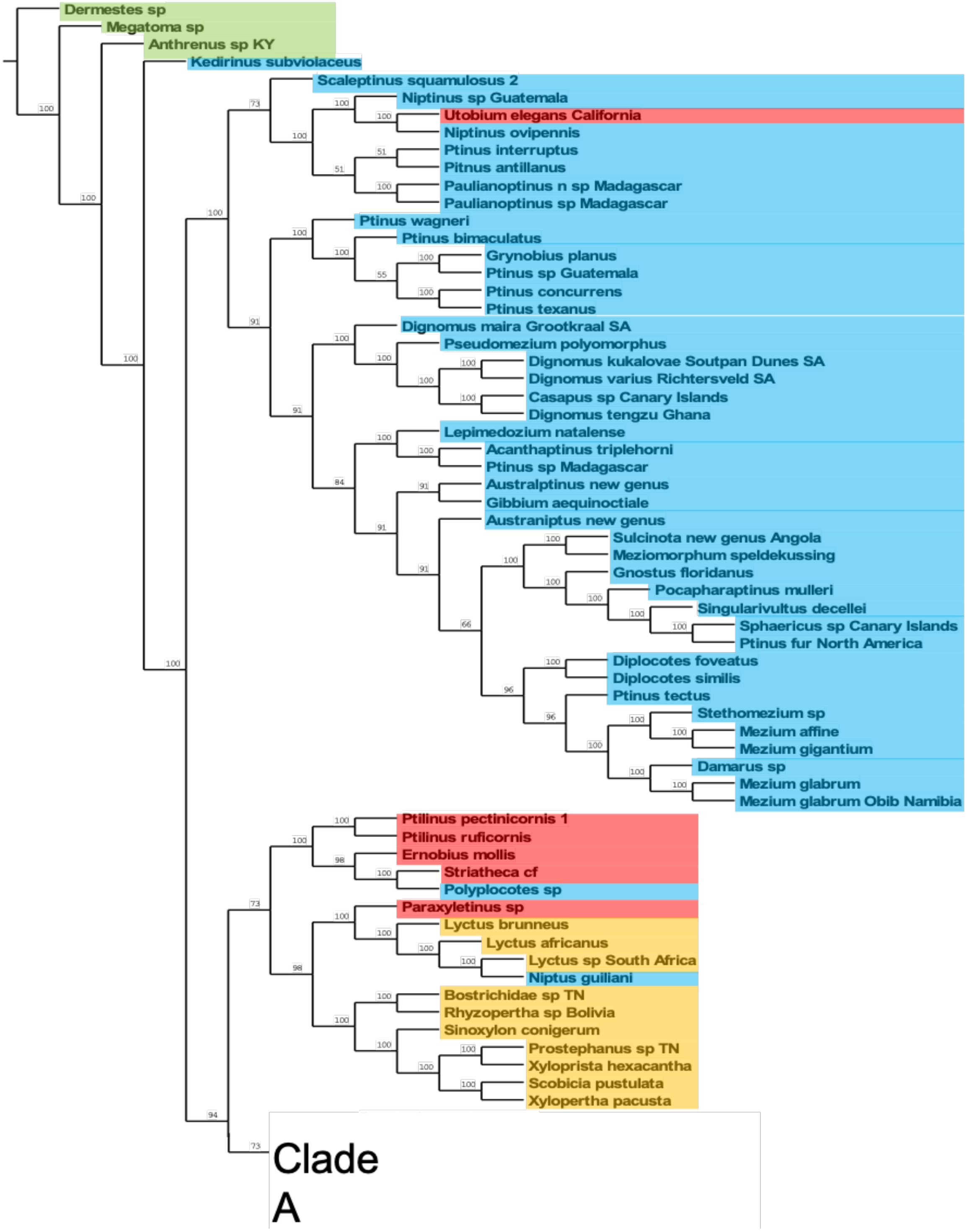
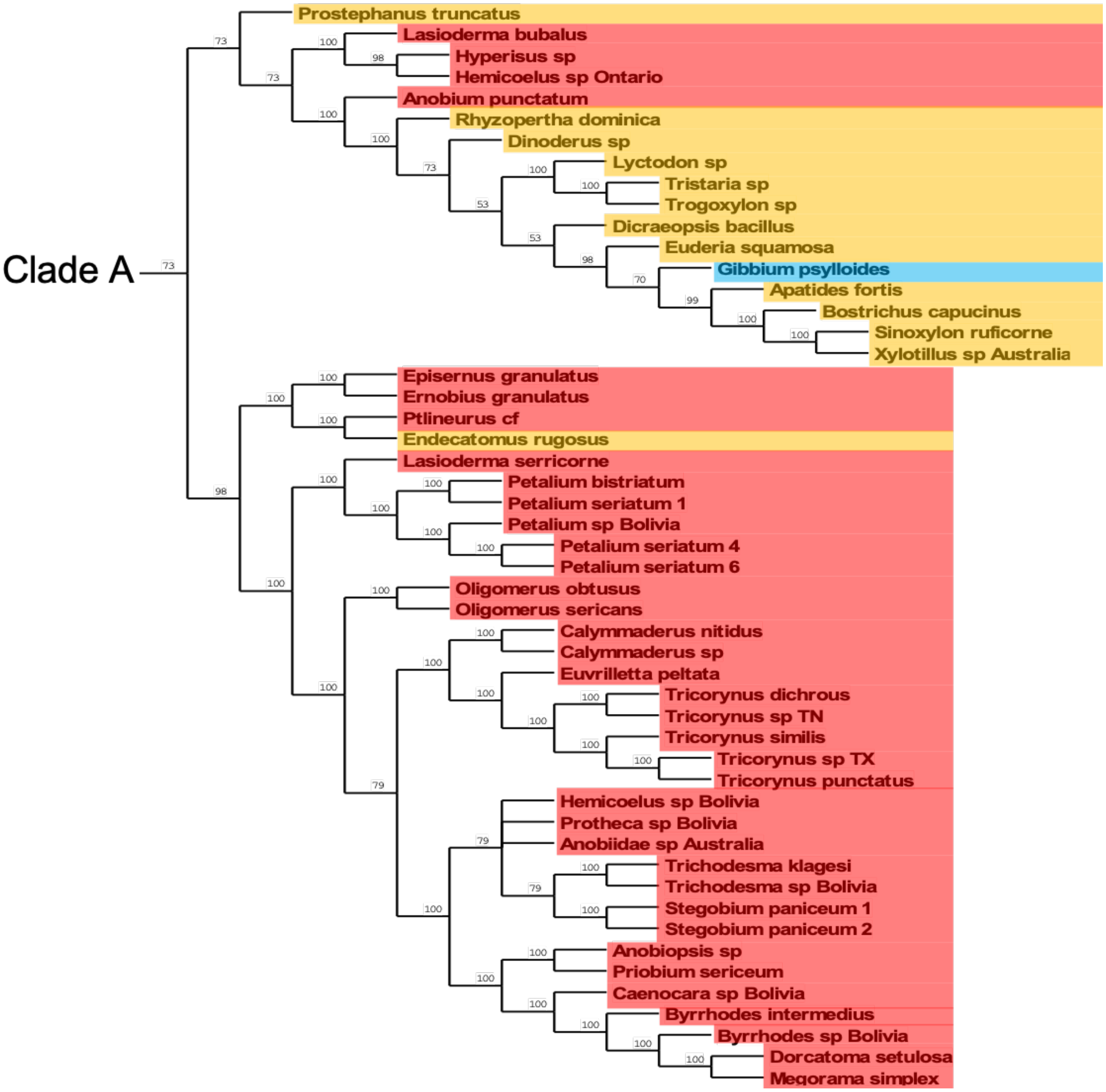


Figure 4

Majority rules consensus of 114 trees from a parsimony analysis of the 28S gene region. Yellow taxa represent bostrichids, red are anobiids, and blue are ptinids.



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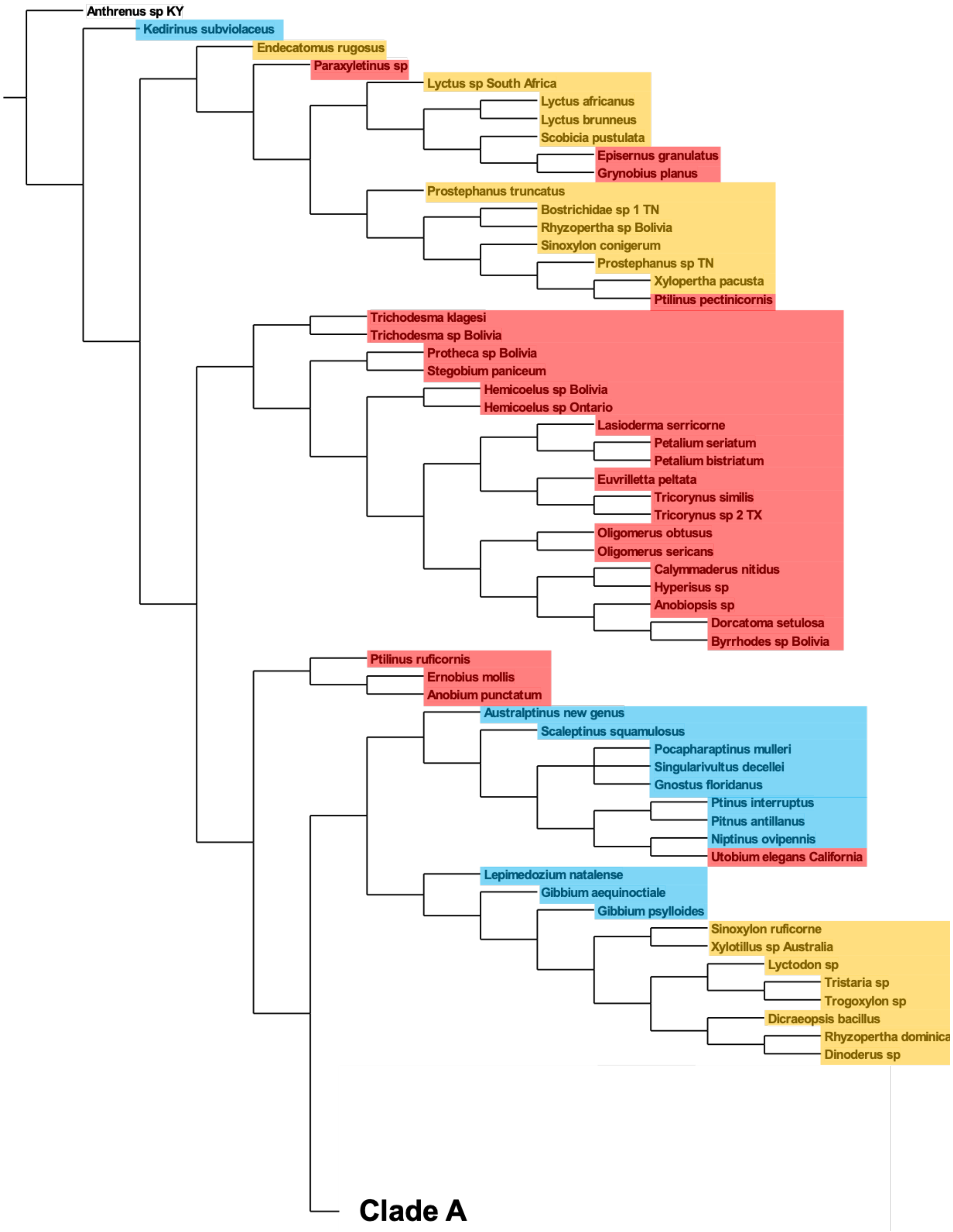


Figure 5

Strict consensus of four trees generated from a parsimony analysis of 28S and CO1 gene regions. Only includes taxa where both gene regions were available. Yellow taxa represent bostrichids, red are anobiids, and blue are ptinids.

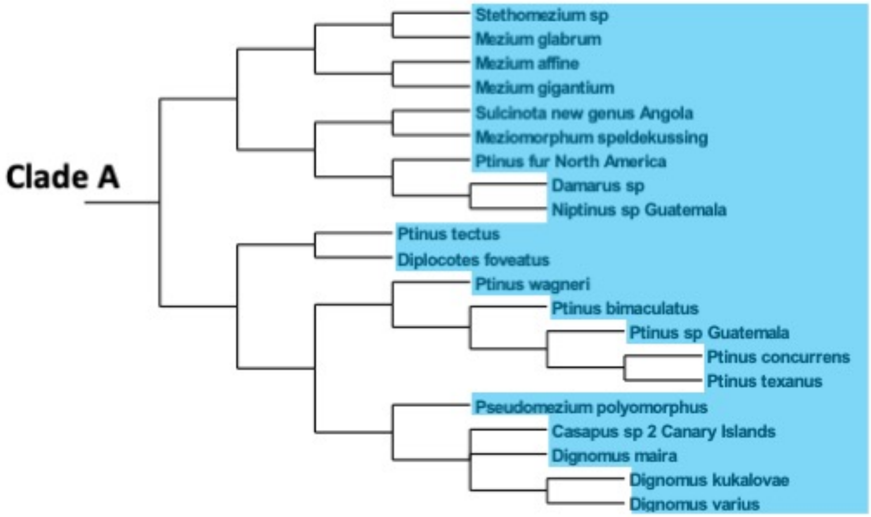


Figure 5. ***Continued***

A parsimony analysis of the expanded dataset using CO1 and 28S, which also includes taxa for which only one gene region was available, resulted in 20 trees (L=18612, CI=16, RI=68). A strict consensus of these trees (Fig 6) contains several conserved clades and shows basal similarities with the contracted data set, including a basal southeast Asian ptinid clade (Australasian ptinid genera *Kedirinus* and *Sundaptinus*) and then a clade of bostrichids sister to the remaining taxa. This tree reveals ptinids, bostrichids, and anobiids as polyphyletic, and places some members of Dermestidae within the ingroup. After the southeast Asian ptinid clade, there is a clade of bostrichids sister to all remaining taxa. This is followed by a large clade of mainly anobiids with a few bostrichids and ptinids at the base. This is sister to a clade consisting of a large clade of ptinids and anobiids. While the ptinid clade has only a few non-ptinid taxa, the anobiids, in contrast, have a large set of both bostrichids and dermestids and a single ptinid. Examination of a majority rules consensus topology (Fig 7), resolves the two polytomies of the basal dermestids and the anobiid genus *Dorcatoma*.

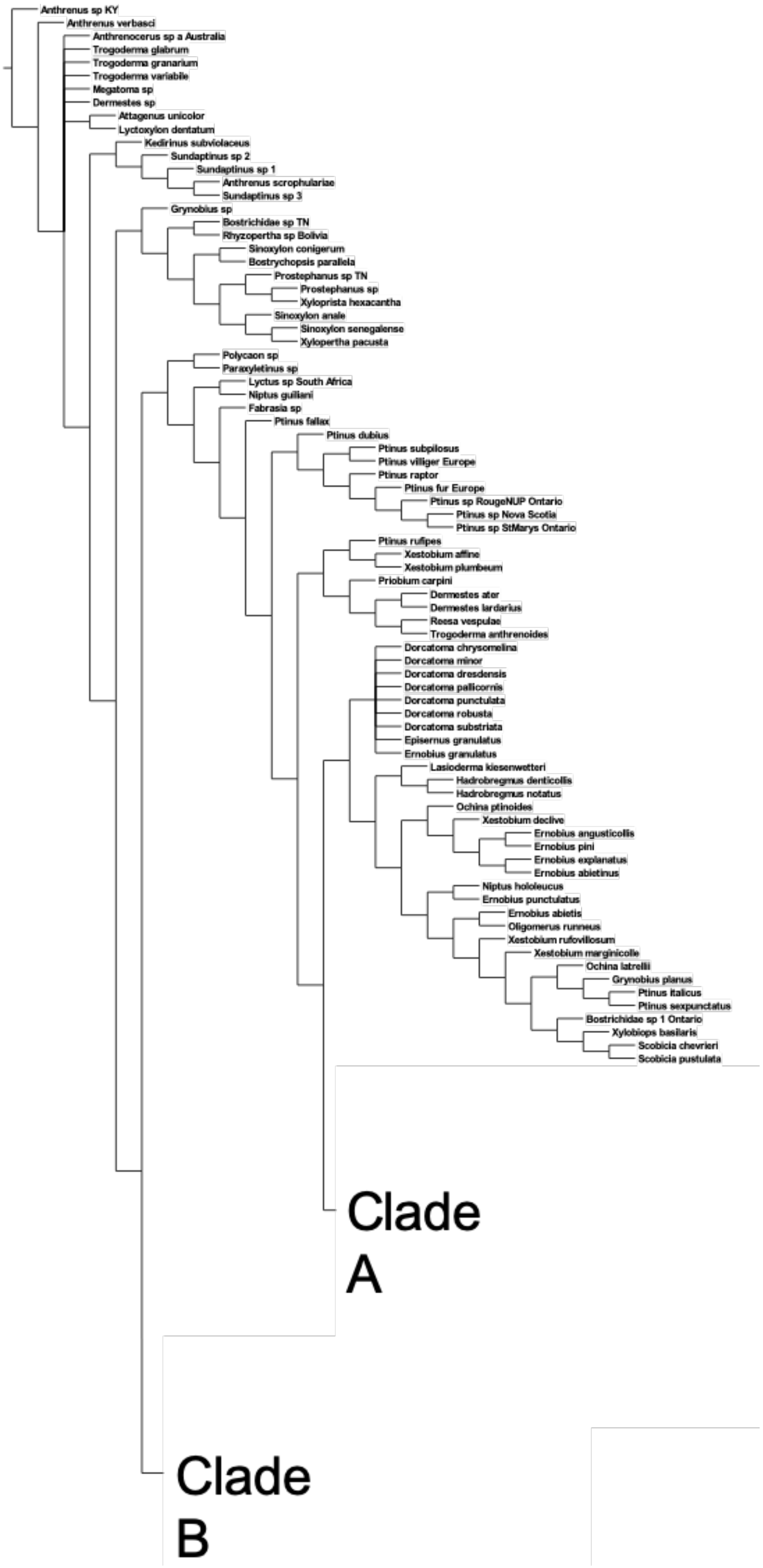


Figure 6

Strict consensus of 20 trees generated from a parsimony analysis of 28S and CO1 gene regions. Taxa with one or both gene regions were included.

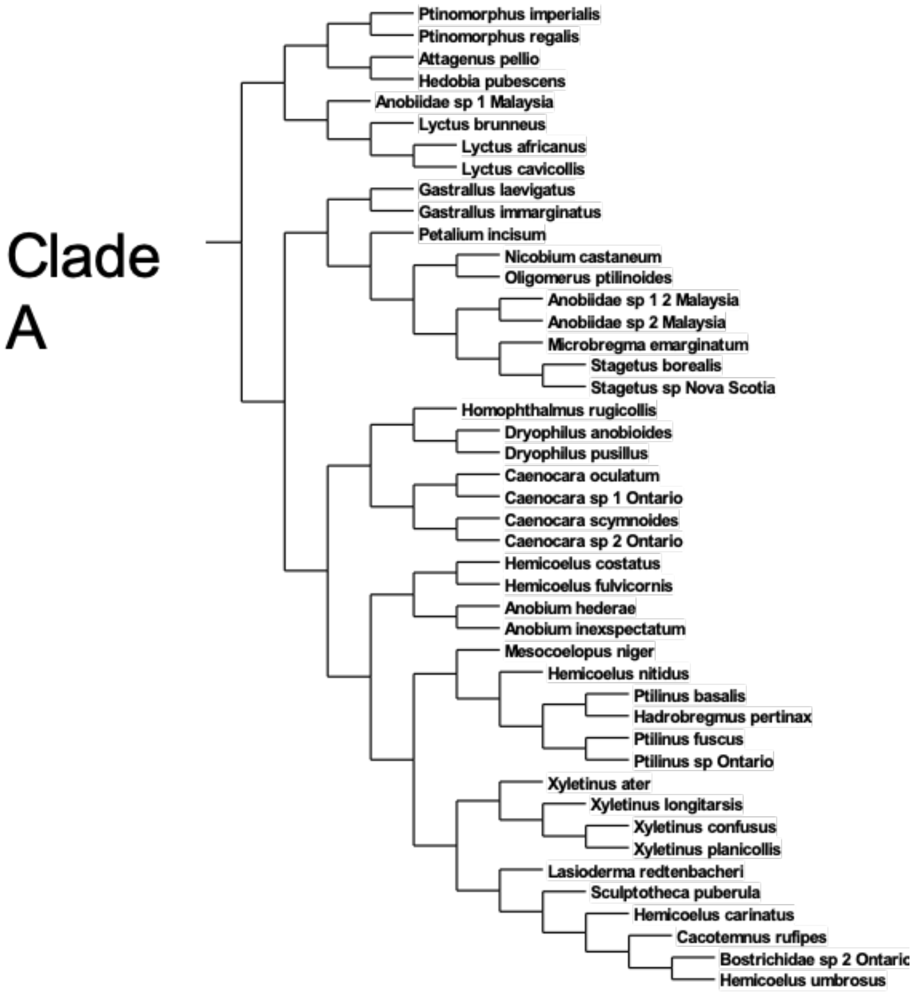


Figure 6. ***Continued***

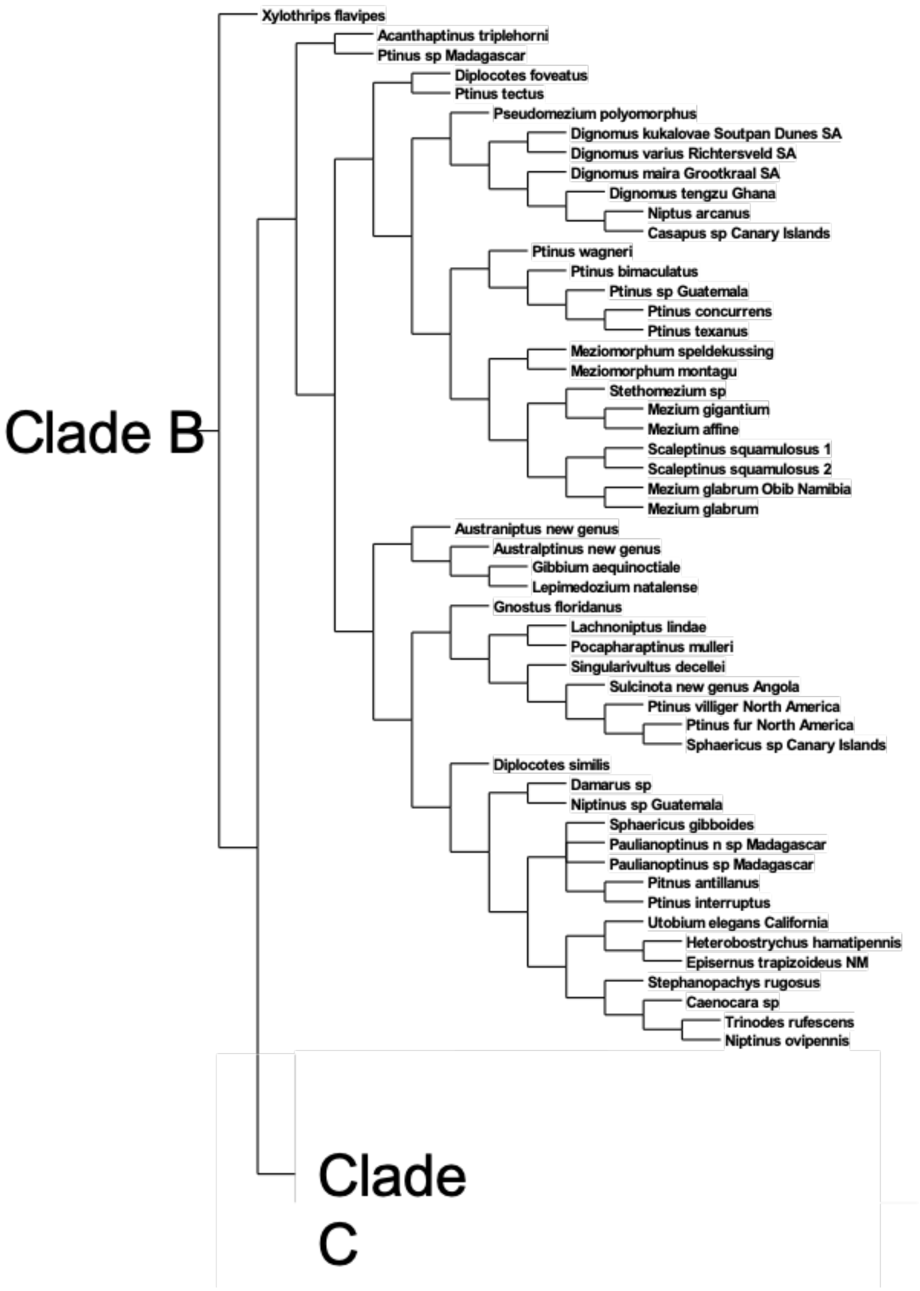


Figure 6. ***Continued***

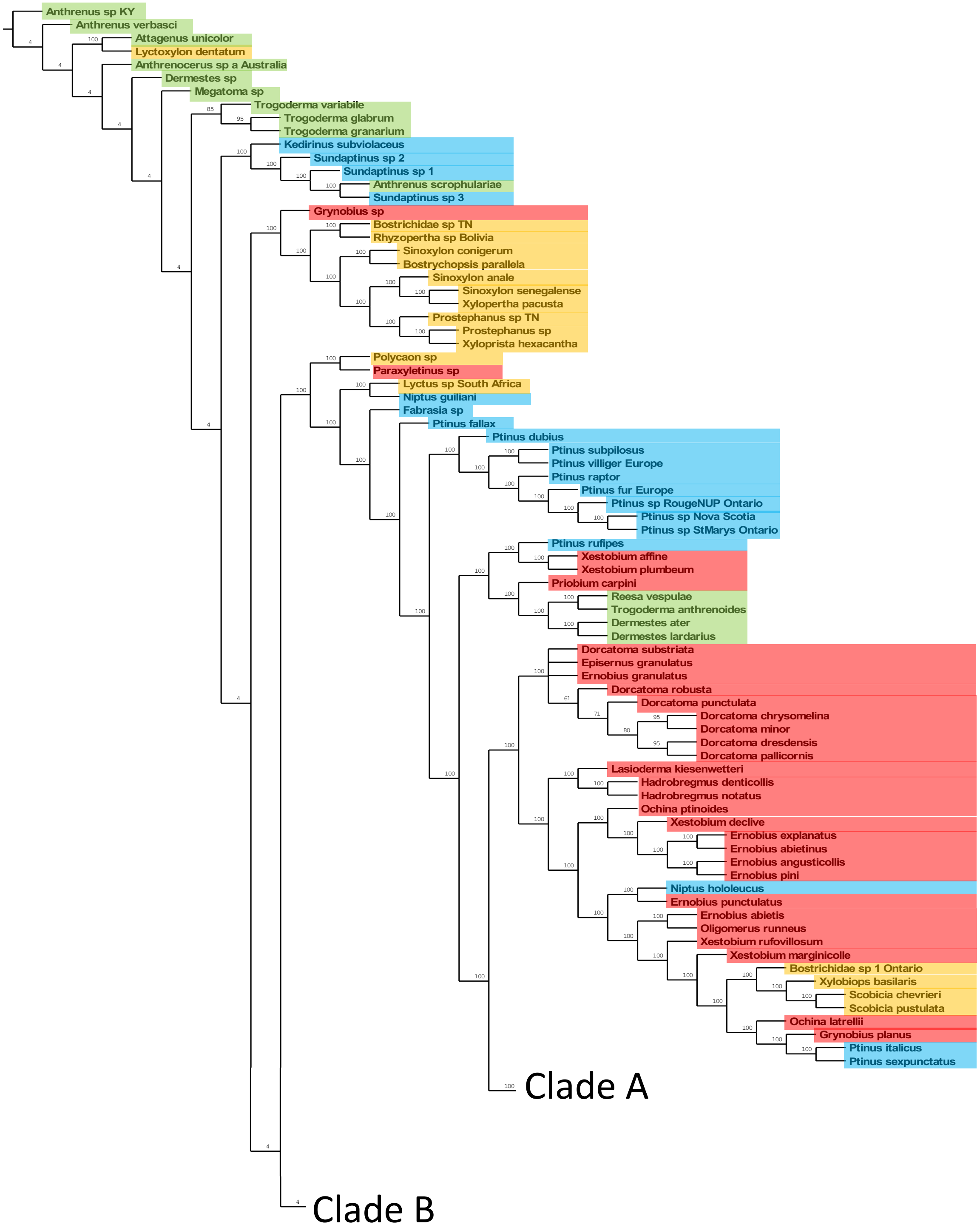
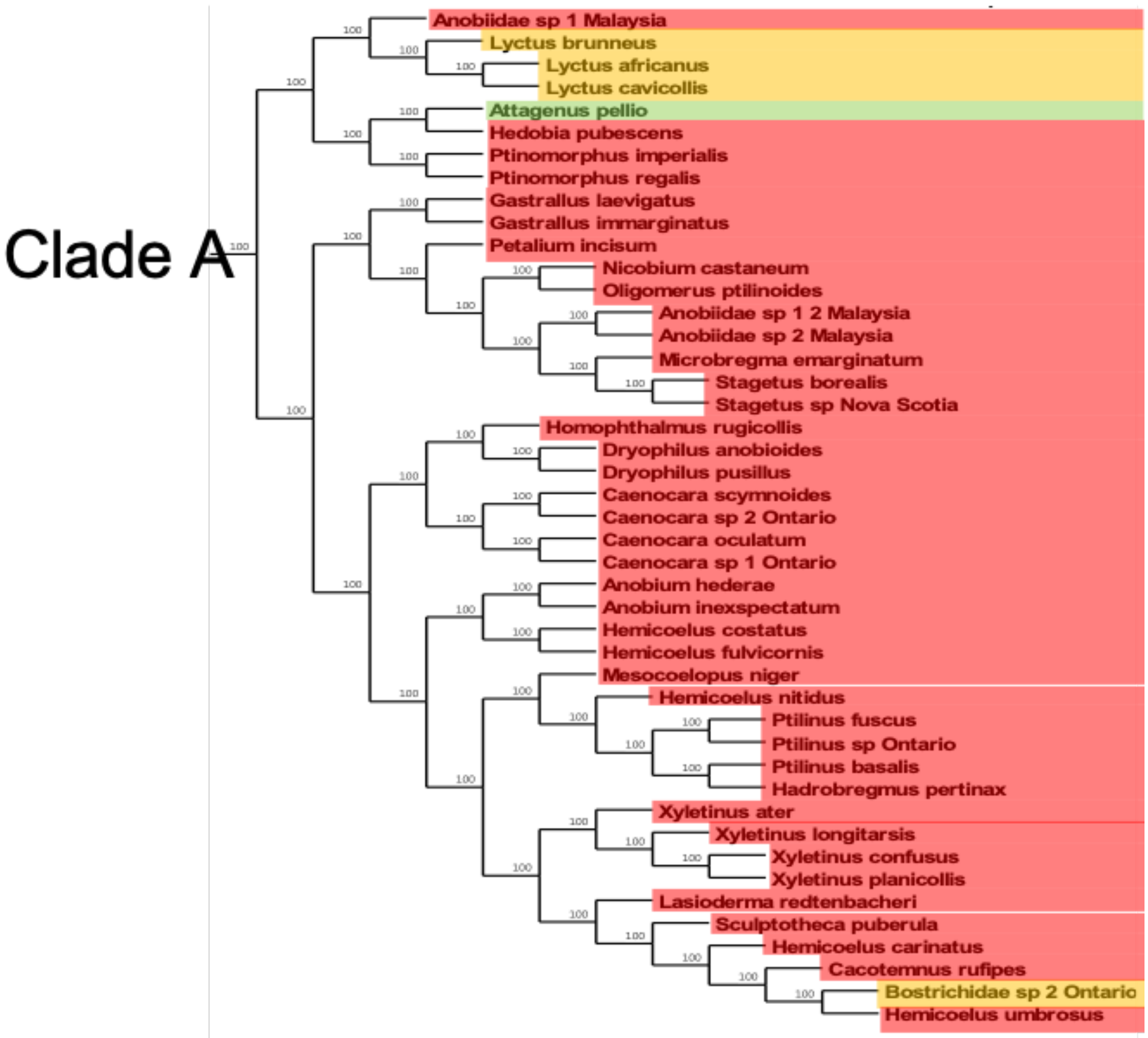


Figure 7

Majority rules consensus of 20 trees generated from a parsimony analysis of 28S and CO1 gene regions. Taxa with one or both gene regions were included. Yellow taxa represent bostrichids, red are anobiids, and blue are ptinids.



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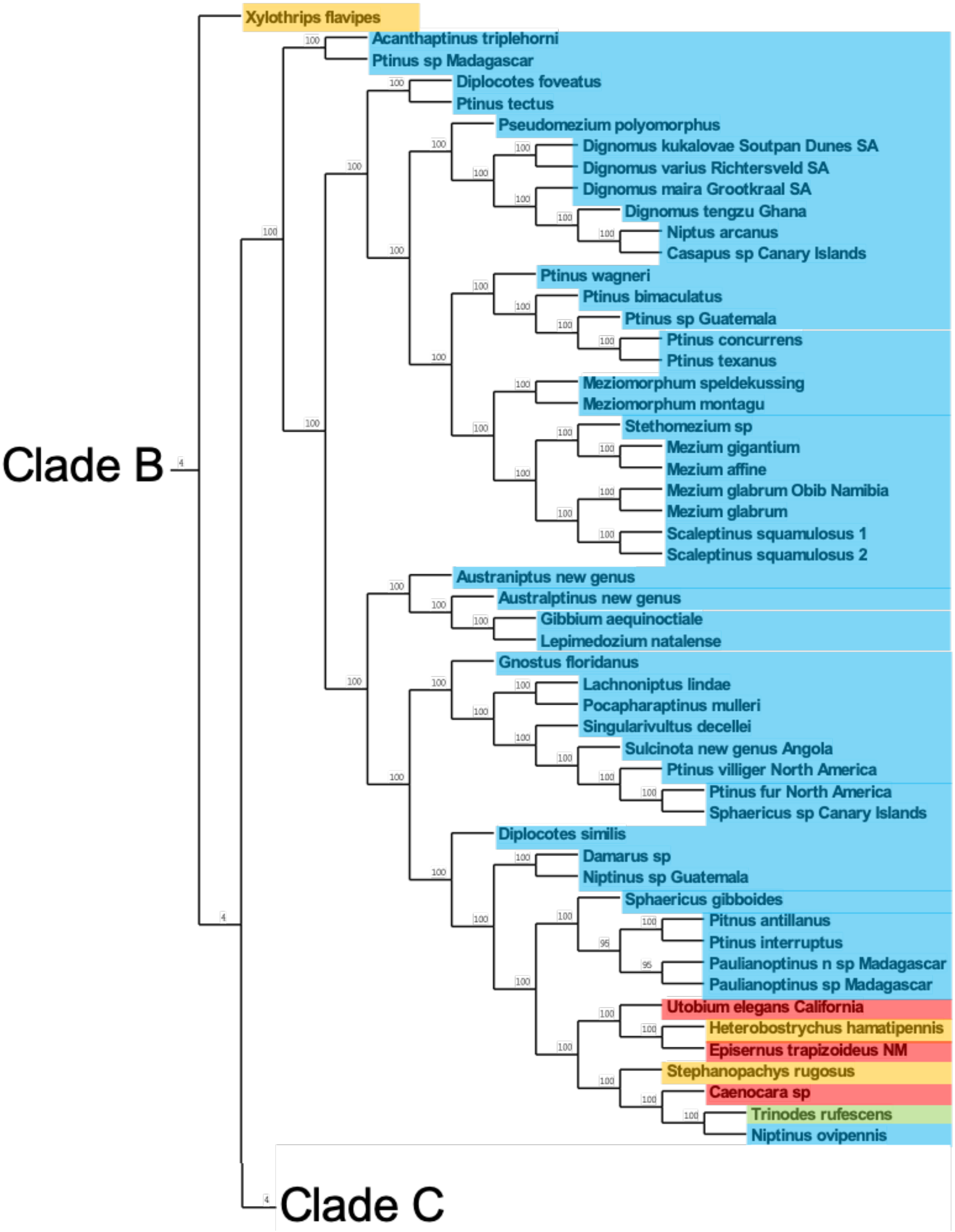

Figure 7. *Continued*

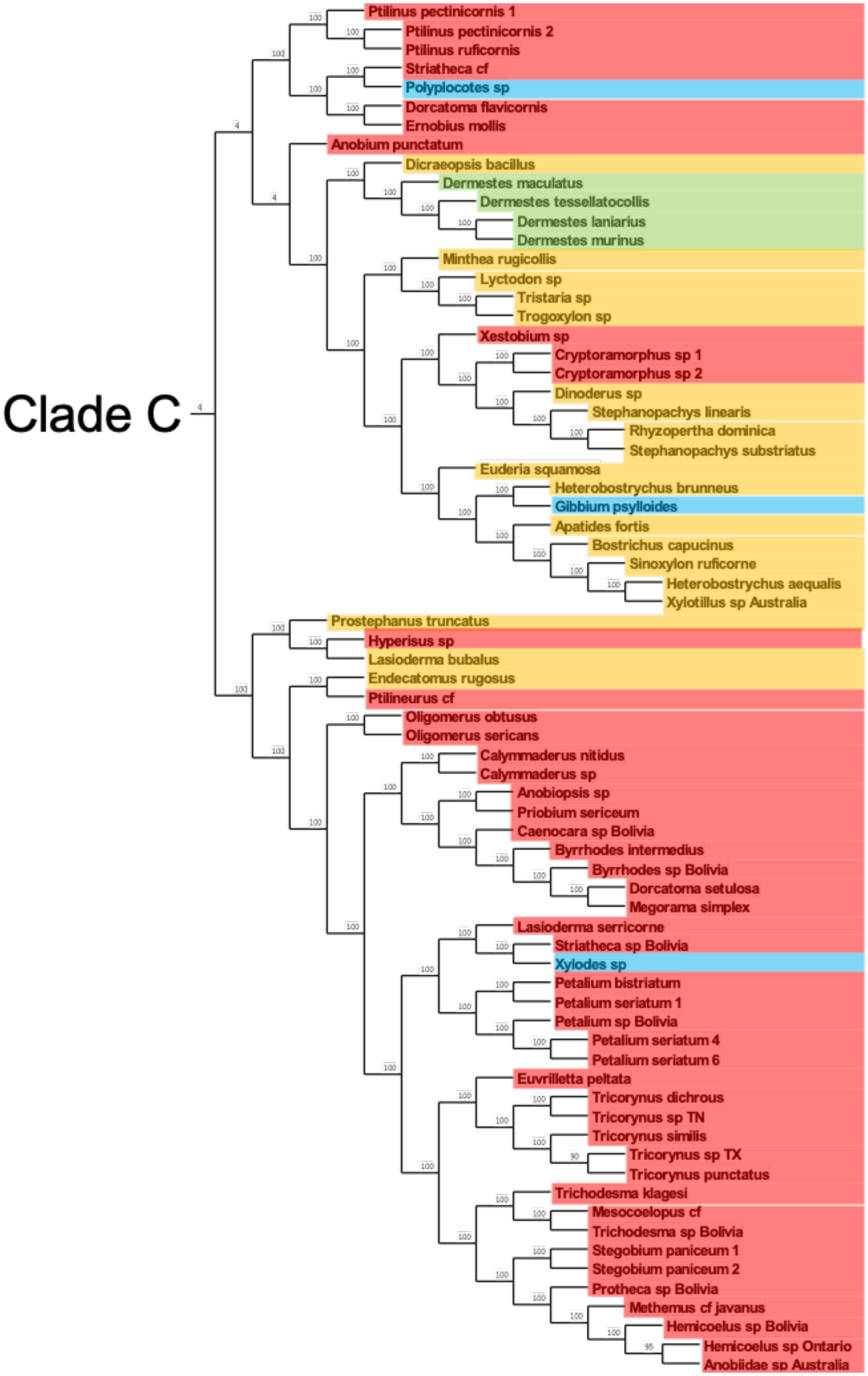

Figure 7. ***Continued***

A Bayesian analysis was also run on this dataset, but after 5,000,000 generations the split frequencies were still above 0.2, well above the desired level of 0.01. Due to this and the fact that the resulting tree was highly unresolved, the results are not included in this study. However, an unrooted phylogram demonstrating genetic distance was obtained (Fig 8). This tree contained two large clusters, both containing a mix of all four families, and *Fabrasia* on one long branch apart from the two clusters.

CO1, 28S, and 16S Genes

The parsimony analysis of a combined dataset using three gene regions (CO1, 28S, and 16S) for taxa in which all three sequences were available resulted in 2 most parsimonious trees (MPTs) with length of 8086 steps (CI=45, RI=53). In a strict consensus of the two trees (Fig 9), a clade of bostrichids was found to be basal. The anobiids came out in a monophyletic clade, sister to a clade containing all the ptinids and a derived clade of bostrichids, that render the former paraphyletic.

In a Bayesian analysis of the same dataset, a convergence of the two simultaneous runs occurred after 3,000,000 generations (Fig 10). This tree displayed similar results to the parsimony analysis but placed the anobiid *Ptilinus pectinicornis* in the basal clade of bostrichids. When including evolutionary distance in the tree (Fig 10B), we find that there are several long branches in the derived clade of bostrichids. This suggests that the placement of this clade may be an artefact of long branch attraction.

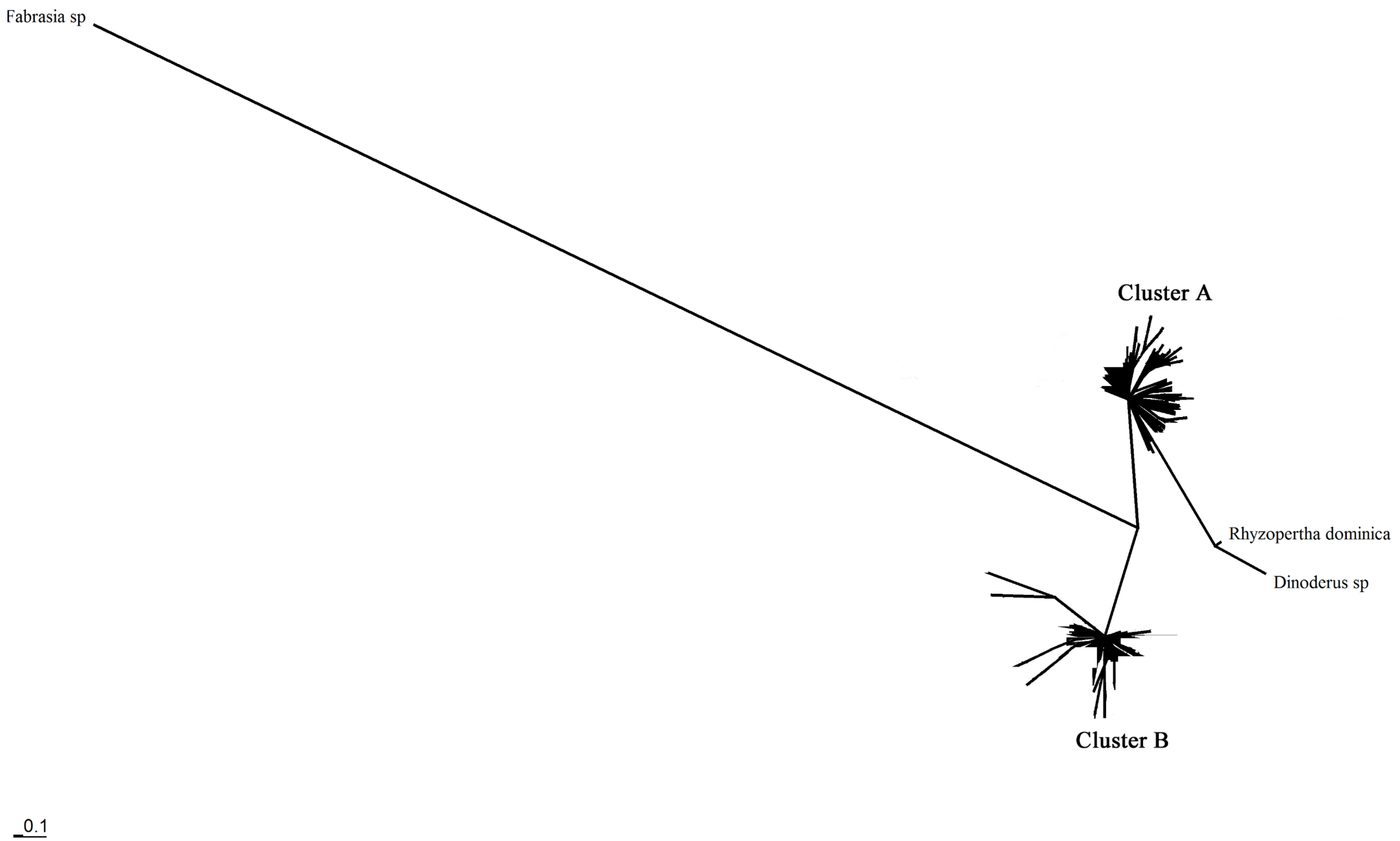

Figure 8
Unrooted phylogram depicting genetic distance obtained from a Bayesian analysis of 28S and CO1 gene regions. Taxa with one or both gene regions were included. Due to the large number of taxa included, taxon names in taxon clusters A and B were removed from the image. Both of these clusters contain a mix of all four families (Dermestidae, Bostrichidae, Anobiidae, and Ptinidae).

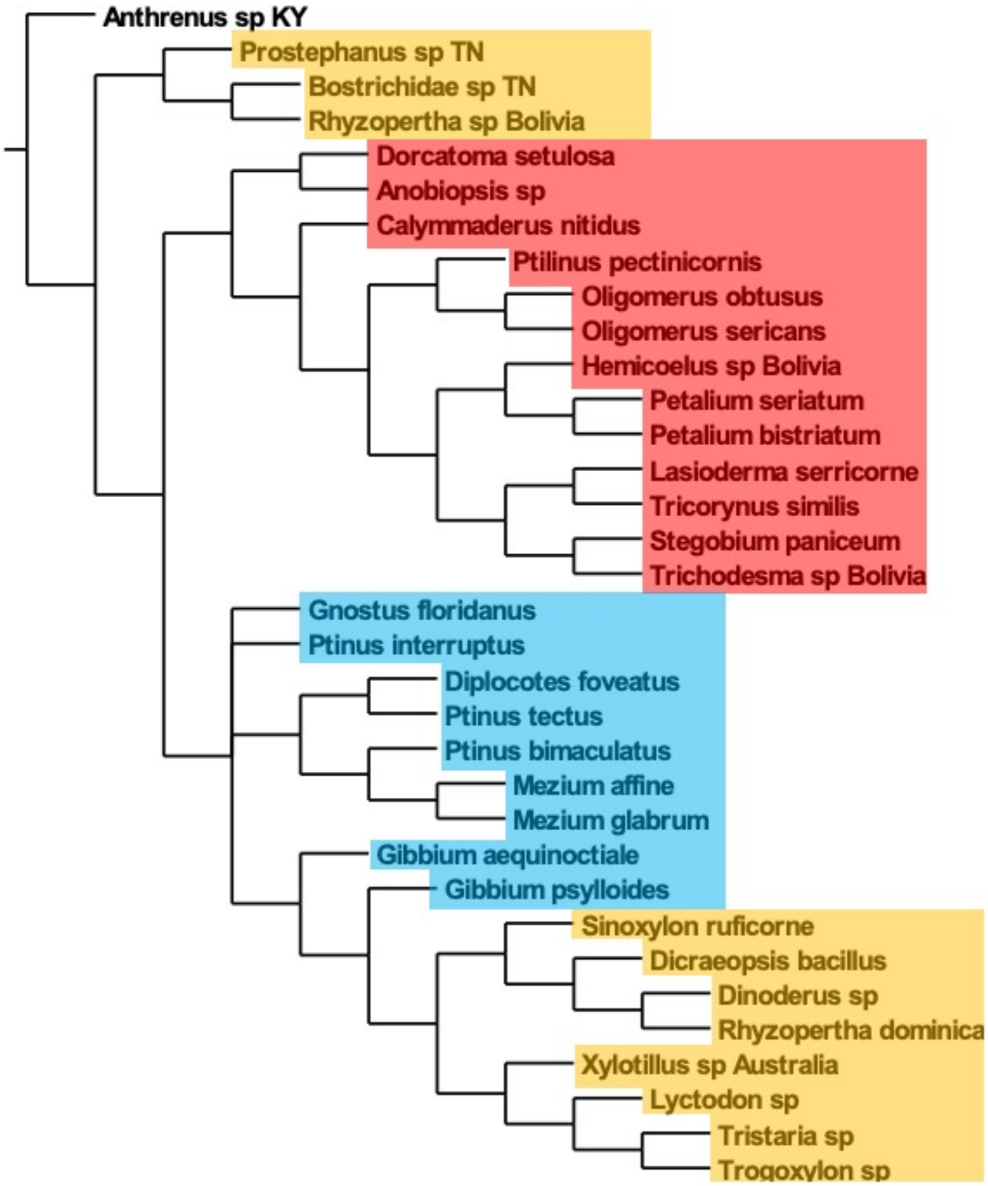

Figure 9

Strict consensus of two trees generated from a parsimony analysis of three genes, 16S, 28S, and CO1. Only includes taxa where all three gene regions were available. Yellow taxa represent bostrichids, red are anobiids, and blue are ptinids.

A

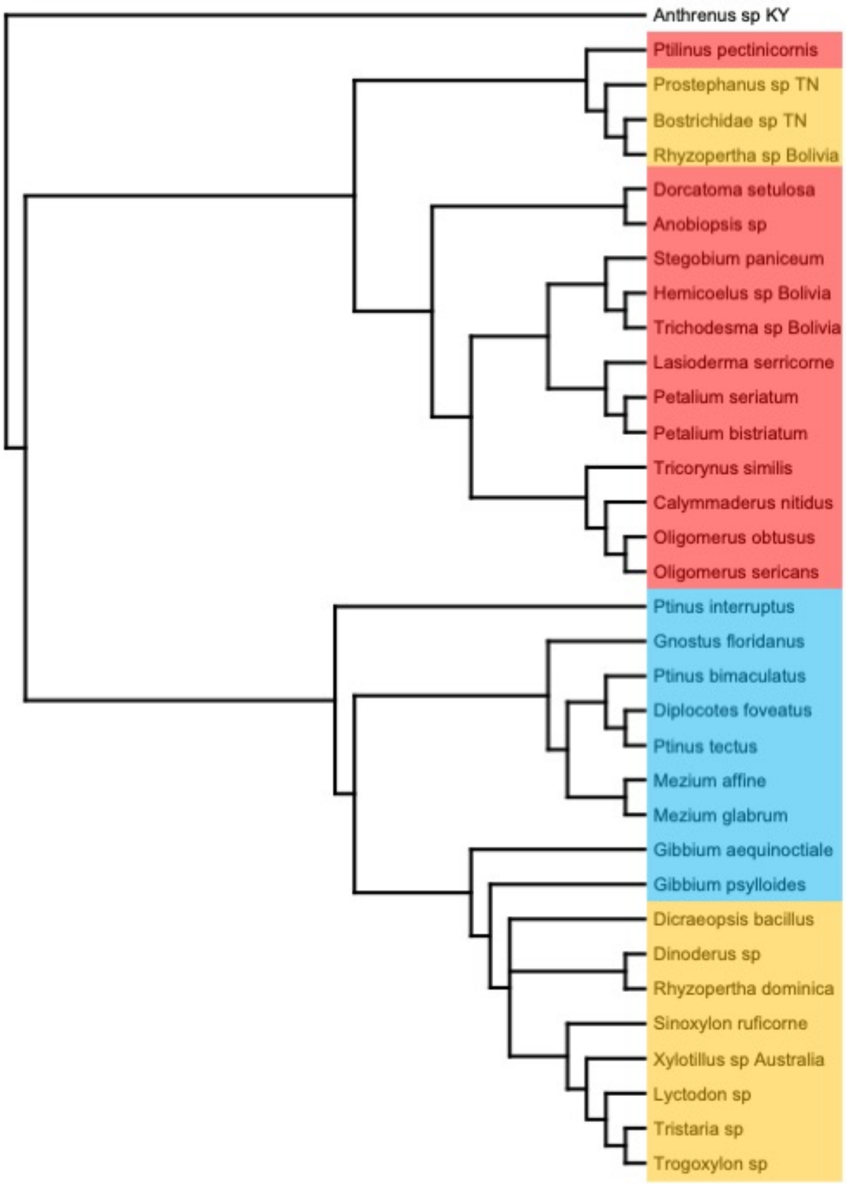

Figure 10

Bayesian analysis of three genes, 16S, 28S, and CO1. Only includes taxa where all three gene regions were available. **A:** Tree not including genetic distance. Yellow taxa represent bostrichids, red are anobiids, and blue are ptinids. **B:** Tree where branch length represents genetic distance.

Figure 10. ***Continued***

Discussion

When examining the three gene trees (16S, 28S, and CO1), the parsimony analysis includes anobiids as a monophyletic group. However, Ptinidae is paraphyletic, due to a derived group of bostrichids within the clade of ptinids. Given that there is a disproportionate number of long branches among the apical bostrichids (Fig 10B) it is possible that the placement of this clade is due to long branch attraction and may not represent true relationships. It is also possible that rapid evolution among a group of ptinids resulted in a convergence of phenotypes causing them to look like and be misclassified as bostrichids. However, this is unlikely given the large number of hypothesized synapomorphies supporting bostrichid monophyly. A third possible explanation for the placement of the two bostrichid clades is that the bostrichids are paraphyletic with ptinids and anobiids derived from within the bostrichids, having evolved from bostrichid-like ancestors. This explanation would provide further evidence that wood boring is an ancestral trait in the group, as the majority of bostrichids are wood-borers. However, there are alternative life histories documented in the bostrichids, including, for example, some species that are stored food pests.

The Bayesian tree has a similar topology to the parsimony, but places *Ptilinus pectinicornis* sister to the basal bostrichid clade, rendering the anobiids paraphyletic. This is most likely not indicative of a true relationship, as nearly all other topologies show *Ptilinus* species well within the anobiids.

The restricted two-gene tree (CO1 and 28S) had similar results to the three-gene topology, with basal bostrichids and apical ptinids and a derived group of bostrichids within the ptinids. Notable differences are the appearance of a couple ptinids and anobiids in the basal bostrichids, and *Kedirinus subviolaceous* (absent from the three gene trees) as the most basal taxon. The expanded two gene dataset resulted in substantial polyphyly among all of the families. However, there are numerous taxa in this dataset for which only one gene region was available, and so many of these taxa are likely misplaced. This is especially apparent given the many members of Dermestidae (for which only one gene region was available) placed within the ingroup. Members of this family are fairly morphologically homogeneous and the dermestids are fairly well established as sister to the clade containing bostrichids, anobiids, and ptinids. Therefore, it is highly unlikely that the placement of these dermestid species represent true relationships.

If the placement of *Kedirinus subviolaceous* at the base of this tree represents true relationships, this could suggest that this taxon is misclassified as a ptinid and instead is a basal bostrichoid. This could also suggest that the larger clade of bostrichids, anobiids, and ptinids originated in Southeast Asia or Australia.

When comparing the strict consensus trees of the single gene 28S and CO1 trees, we find that the 28S gene tree is much better resolved with fewer polytomies and a larger number of conserved clades. This suggests that 28S may provide more phylogenetic signal and is therefore potentially more useful for resolving relationships in this group. Additionally, the presence of members of Dermestidae in the outgroup suggests that there are likely several misplaced taxa in the CO1 tree. This could be due to the fact that CO1 is too quickly evolving to accurately resolve relationships. Additionally, many of these sequences (including all of the ingroup dermestids) were obtained from Genbank. Because the identifications cannot be confirmed, it is possible that some of the taxa are misidentified, although this is less likely at the family level. Finally, as the quality of the sequences obtained from Genbank cannot be assessed, it is possible that some of these sequences are inaccurate due to noise from spurious amplicons during sequencing.

Bell and Philips (2012) hypothesized two alternative relationships among the three families, one with the bostrichids as sister to the anobiids + ptinids and the other placed ptinids as sister to bostrichids + anobiids. While our trees did have bostrichids as sister to ptinids + anobiids, the presence of a second bostrichid clade within the ptinid clade renders the trees in this study very different than those of Bell and Philips (2012).

Notes on Taxonomic Classifications

The close relationship of the anobiids and ptinids requires further investigation. Interestingly, a recently collected specimen from New Zealand supports the recognition of both of these groups as a single family. This beetle has the classic anobiid characteristic of three connate abdominal ventrites but also the ptinid characters of close antennal insertions and lack of a lateral pronotal margin.

Among all of the trees obtained, none of the anobiid subfamilies for which more than one genus was available were monophyletic. In the CO1 tree and two gene expanded dataset, the genera *Hedobia* and *Ptinomorphus* (Eucradinae), are nearly monophyletic except for the presence of *Attagenus pellio* in the clade. However, not all eucradine genera were included in the study. The lack of monophyly in the families and subfamilies included in the study suggests the need for serious internal reclassification within the Bostrichoids.

There is little support for the bostrichid subfamilies as well. While Lyctinae is monophyletic in the three gene tree, in the restricted two gene tree this subfamily is split into two clades, one in the basal bostrichid clade and the other in the apical clade. None of the other bostrichid subfamilies were supported by any of the phylogenies obtained. In the restricted two gene tree (Fig 5), *Endecatomus rugosus* is placed basal to the bostrichids. This genus, though sometimes considered a bostrichid, is classified in its own family, Endecatomidae (LeConte 1861) and its location at the base of the bostrichids in the phylogeny could justify this placement, but more research into genetic distance would need to be performed.

Within the past few decades, many species of the speciose genus *Ptinus* have been reclassified as new genera (e.g. Belles 1991). There are likely several more species in the genus that should be elevated to new genera. For example, *Ptinus tectus,* currently a member of its own sub-genus, is a good candidate for reclassification. This Australian species was placed as sister to *Diplocotes foveatus*, another Australian ptinid, outside a major *Ptinus* clade in the restricted two gene phylogeny (Fig 5). Other *Ptinus* species placed outside this clade include *Ptinus fur* from North America and *Ptinus interruptus,* which came out sister to *Pitnus*.

Dignomus Clade

Both two gene trees (limited and expanded dataset), as well as the 28S gene tree, support the hypothesis proposed by Smiley and Philips (2011) that the genus *Pseudomezium* is a derived *Dignomus,* or is at least closely related. The presence of *Casapus* in this clade, a genus known only from the Canary Islands, suggests that this too many be derived from *Dignomus.* All of these taxa possess a similar modified pronotum with a basal cleft.

Myrmecophily

When examining the myrmecophilous taxa included in this study, including *Fabrasia*, *Diplocotes, Polyplocotes*, and *Gnostus*, we find evidence that this lifestyle likely evolved multiple times within Ptinidae. This is consistent with findings by Mynhardt (2012). It is also unsurprising, considering mymecophily has evolved independently numerous times among and within other beetle families (see Parker 2016, for a comprehensive review of myrmecophily in Coleoptera). Additionally, the CO1 tree suggests that *Fabrasia* could be a basal anobiid. If so, this would be the first documentation of a myrmecophilous anobiid. The phylogram obtained from the Bayesian analysis of the expanded CO1 and 28S dataset suggests that *Fabrasia* is extremely genetically different from any other bostrichoid taxa. *Fabrasia* is also very morphologically distinct from other ptinids due to its unique body shape including well developed humeral callosities, greatly modified femora with trichomes, large elytral punctures (glandular pores) at middle arranged transversely, and a unique pronotal shape with lateral spines. Based on these morphological and genetic differences, it could be argued that this genus belongs in its own family.

Biogeography

Examination of the distributions of spider beetle taxa present in the restricted two-gene dataset reveals two New World ptinid clades nested within Old World clades (Fig 11). The New World species *Gnostus floridanus* is also placed within an Old World clade. Overall, the relationships hypothesized by this phylogeny suggest an Old World origin of the spider beetles (possibly in Australia or southern Africa). A formal biogeographic analysis would still need to be performed on this data, and inclusion of more representative species from all regions where spider beetles are known to exist is needed to really understand where this group originated and how it has dispersed across the globe.

Flightlessness

Philips (2000b) hypothesized at least three independent origins of complete flightlessness in the spider beetles, with winged species capable of flight being the ancestral trait. The relationships within the spider beetles hypothesized by our restricted two-gene dataset suggests two alternative hypotheses for winglessness in the spider beetles. One hypothesis is that possessing wings is the ancestral trait, and that wing-loss has evolved at least 13 times within this group (Fig 12). The other is that winglessness is the ancestral trait in the group, and that wings have been regained at least 6 times within the group. The latter hypothesis is the most parsimonious and would be more likely if the gain and loss of wings are equally likely and caused by random mutations. It is also possible and more likely, however, that environmental pressures on the group have selected for the evolution of wing loss, leading to numerous evolutionary origins of this trait within the ptinids. Selective advantages of wing loss in insects include increased ova production in females (Roff 1990; Roff and Fairbairn 1991), which is likely the case for many members of the genus *Ptinus* where only females are flightless (Philips 2000b). Further, the loss of wings in xeric habitats helps to reduce water loss via elytral fusion (Philips 2000b). Additional investigations including a denser taxon sampling of represented species in this group would further support the multiple origins of wing loss within the spider beetles.

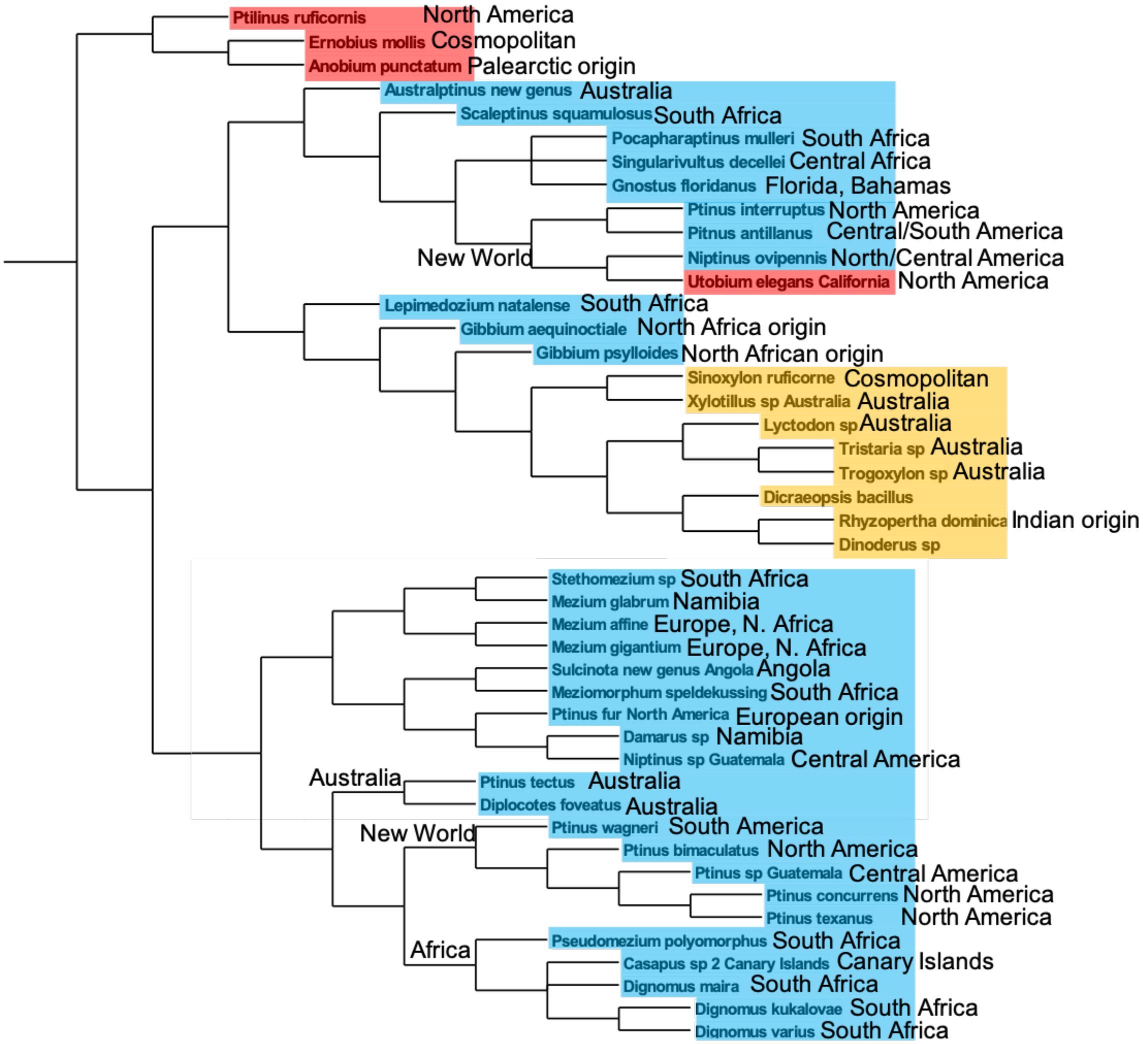

Figure 11
Distributions of spider beetle taxa from the restricted two gene analysis. For cosmopolitan pest species, known or hypothesized origins of the species are identified.

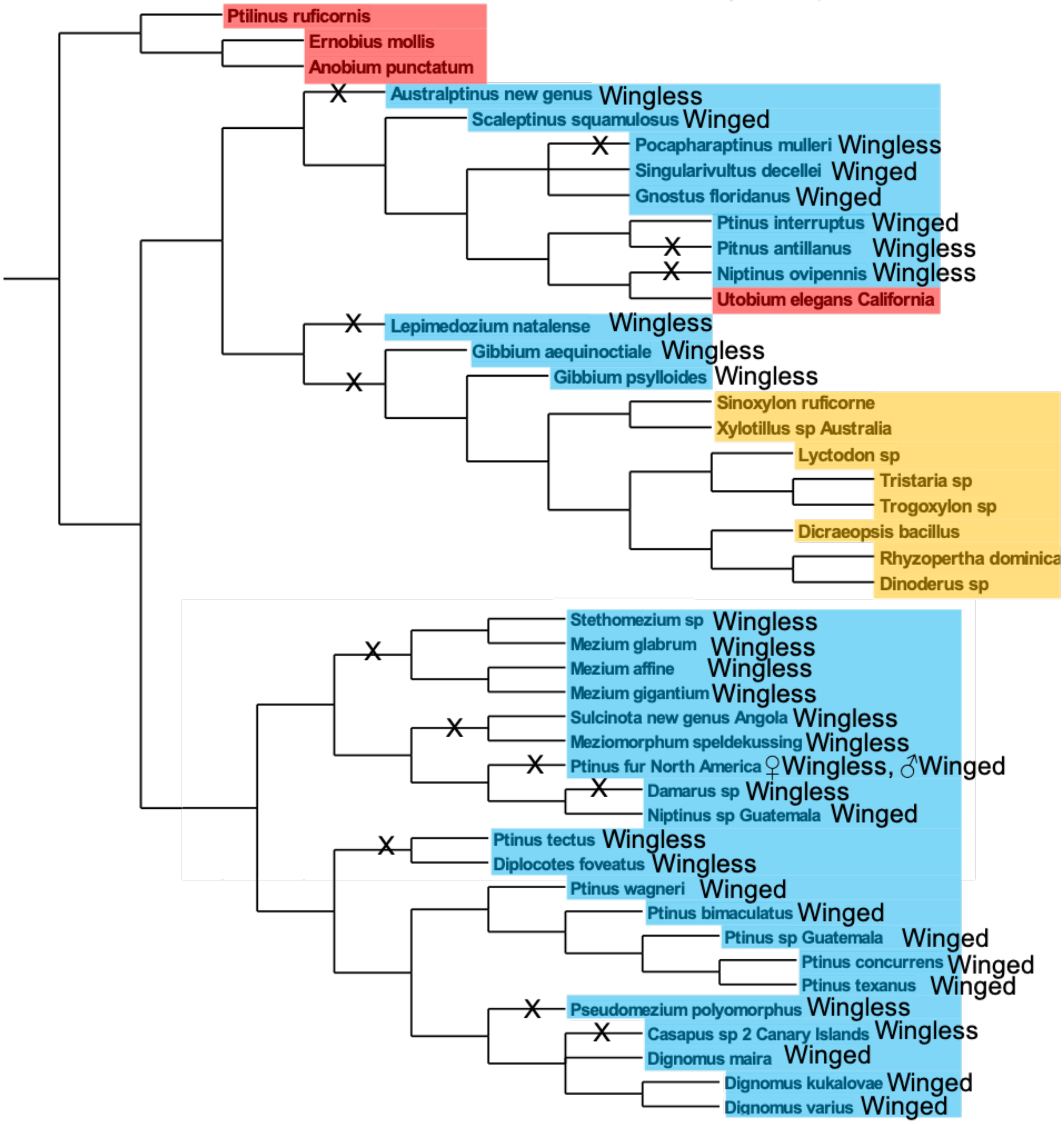

Figure 12

Evolution of winglessness among spider beetle taxa from the restricted two gene analysis. X's represent hypothesized evolutionary origins on wing loss. The two *Gibbium* species are treated as a monophyletic clade, as the bostrichid taxa are assumed to be misplaced due to long branch attraction.

Conclusions and Future Directions:

Our data suggests that there is likely major taxonomic revision needed within Bostrichoidea, particularly at the subfamily level but even potentially at the family level. However, more genetic data is likely needed before many of these revisions can occur.

More gene sequences are needed for taxa for which only one or two sequences are available. A more extensive three gene phylogeny would likely yield a useful, well resolved tree on which new taxonomic classifications could be based. Ultimately, future studies using next generation sequencing will be needed to verify the results obtained in this study, and further clarify relationships in this group. Additionally, once the relationships within the spider beetles are clarified, many of the mysteries surrounding this fascinating group of beetles (where this group originated, how certain morphological adaptations, such as winglessness, and alternative lifestyles have evolved, and when and where radiations occurred) can begin to be solved.

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NEW SPECIES OF THE BIZARRE SOUTH AFRICAN ENDEMIC GENUS *MEZIOMORPHUM* PIC (COLEOPTERA: PTINIDAE)

Olivia M. Gearner, T. Keith Philips, and Peter Koniar

Introduction

At present, there are 48 species of South African spider beetles described, of which there are 14 endemic and four widespread genera (for the most recent works, see Irish 1996a, 1996b; Philips and Foster 2004; Borowski 2006a, 2006b, 2009; Bell and Philips 2008; Akotsen-Mensah and Philips 2009; Smiley and Philips 2011; Trimboli and Philips 2011; Wood and Philips 2013). Thus, South Africa is home to some of the highest spider beetle diversity currently known in the world. Undoubtedly many species still remain undocumented due to their small size, potentially small populations, and for some, limited distributions.

When describing three new species of *Meziomorphum*, Irish (1996a) also noted four additional undescribed taxa as species A, B, C and D. One of these (species D) was formally described by Trimboli and Philips (2011) after additional specimens were collected. The other three are described herein, along with two more species relatively recently discovered.

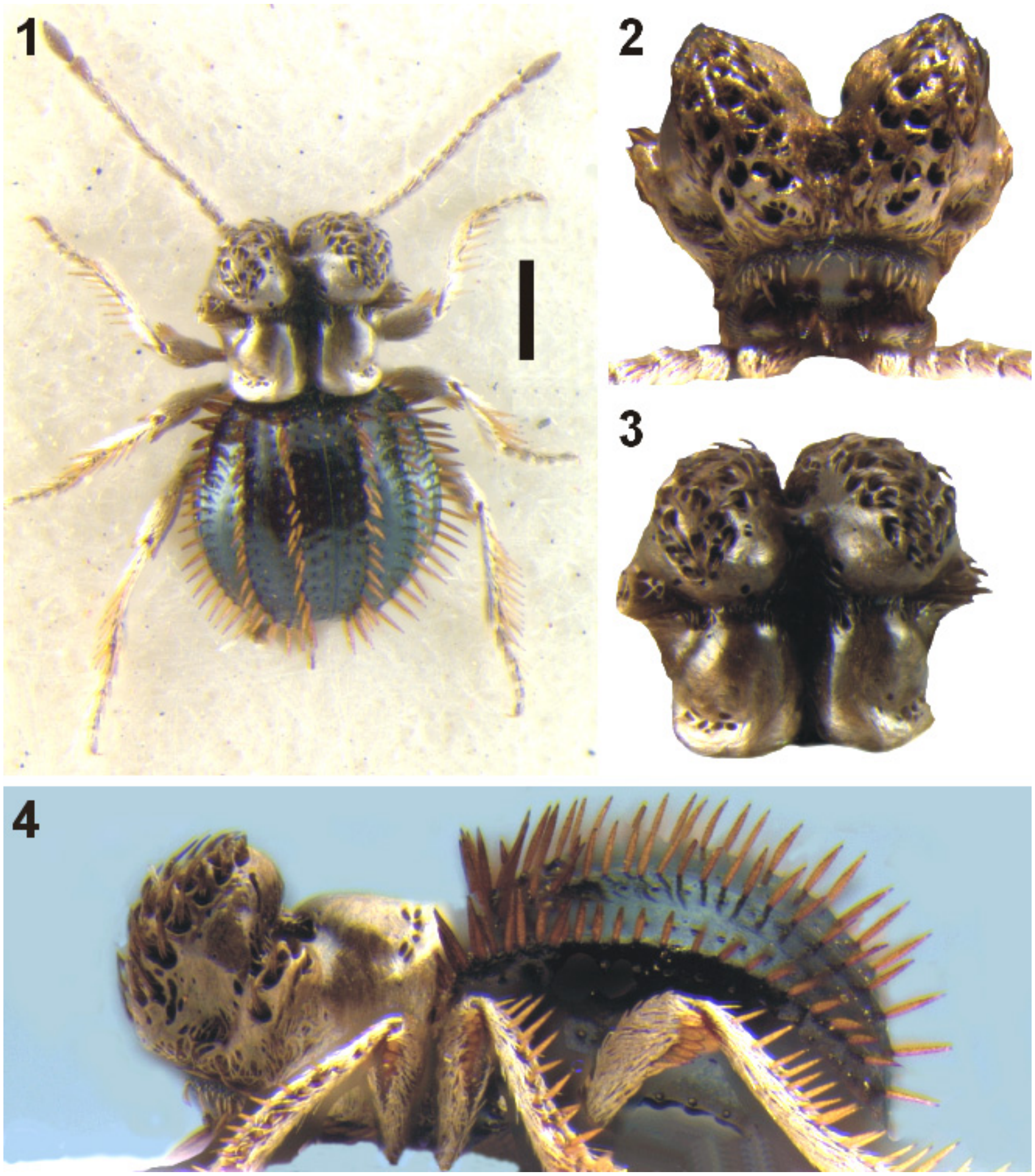
Materials and Methods

This study was based on the examination of about 150 specimens from the following collections: Iziko South African Museum, Cape Town (SAM), Ditsong National Museum of Natural History (formerly the Transvaal Museum), Pretoria (TMSA), National Collection of Insects, Pretoria (SANC), the South African Museum (SAMC) and the collection of one author (TKPC), Western Kentucky University, Bowling Green.

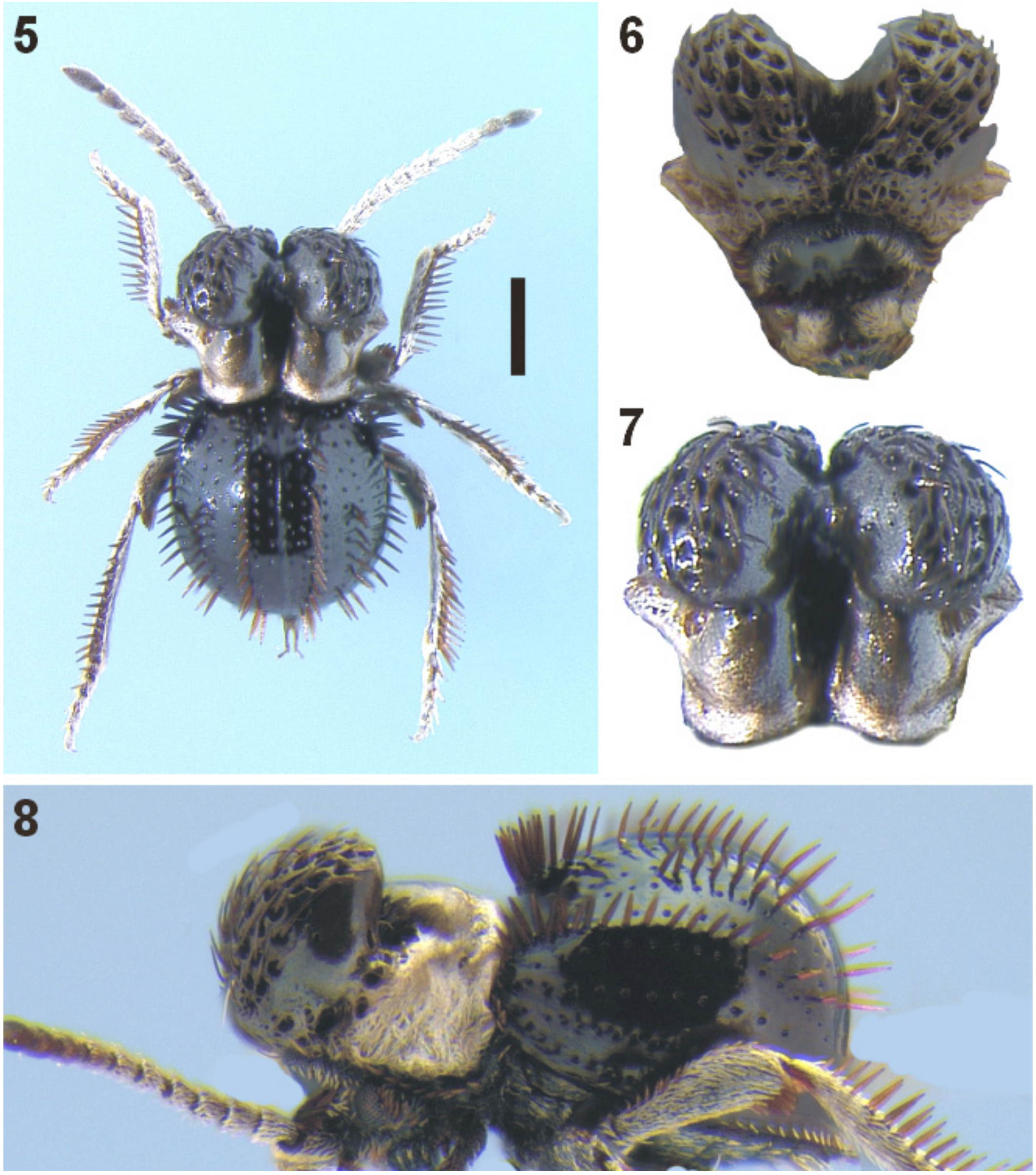
Label data for the new species and new distribution records are recorded verbatim with labels on the same pin separated by a "/" and a comma inserted at the end of each line. QGIS was used to create distribution maps with Google Satellite Image WMS imported using the OpenLayers plugin for the base map layer.

All holotypes are deposited in the Ditsong National Museum of Natural History, Pretoria, South Africa (TMSA). Paratypes are deposited in the same collection as well as two of the authors for some of the species (T. K. Philips (TKPC) and P. Koniar (PKCI)).

Previously described species are also illustrated to enable easy comparison with our new taxa as follows: *M. ystervarkie* Irish (Figs 1–4), *M. speldekussing* Irish (Figs 5–8), *M. echinatum* Péringuey (Figs 9–12), *M. krimpvarkie* Irish (Figs 13–15), *M. montagu* Trimboli and Philips (Figs 17–20). Genitalia from species that were available to us are also illustrated (Figs 21–26).

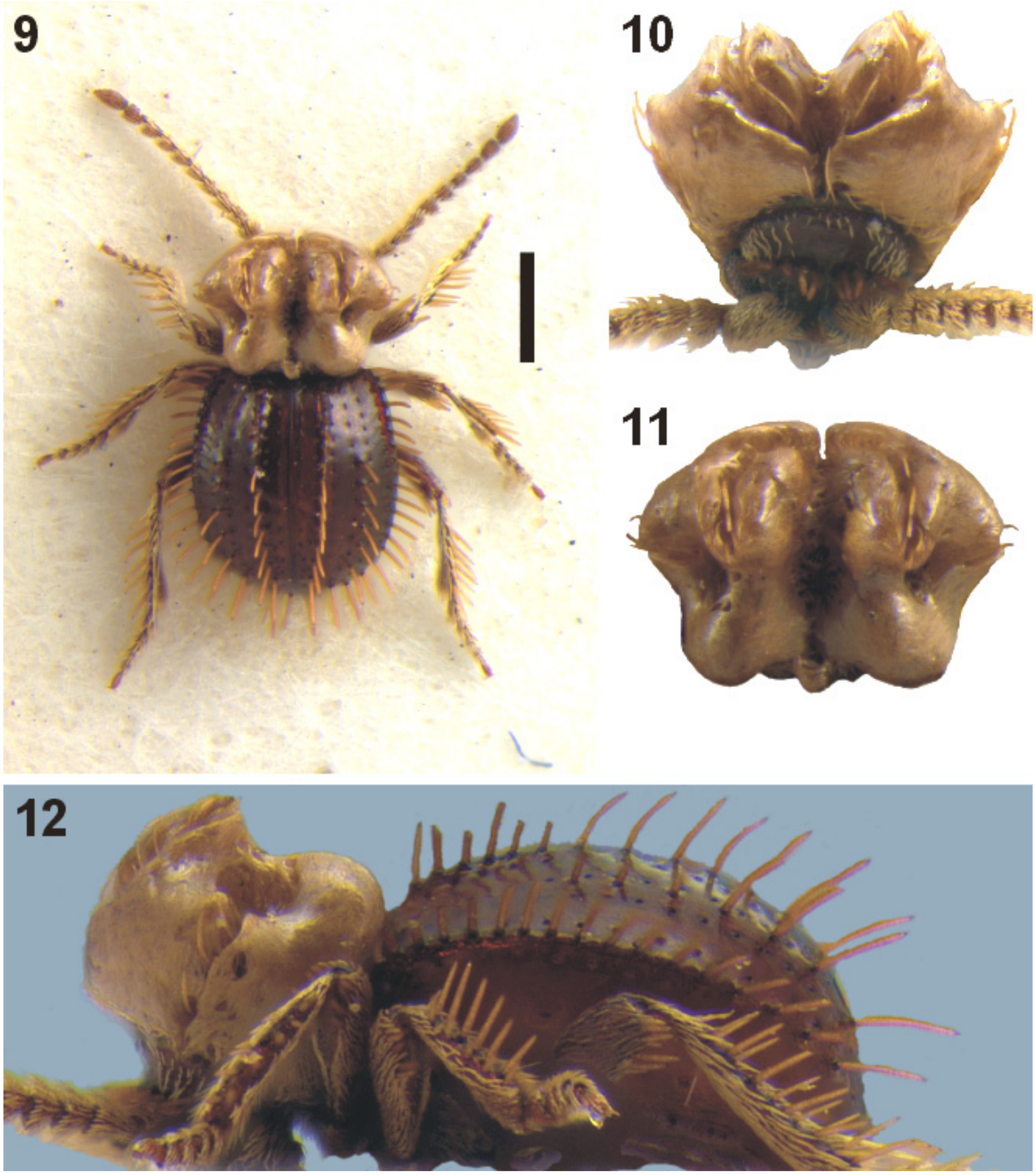


Figures 1–4
M. ystervarkie Irish. **1:** Dorsal habitus; **2:** frontal view of head; **3**: dorsal pronotum; **4:** lateral habitus. Scale bar: 0.5 mm



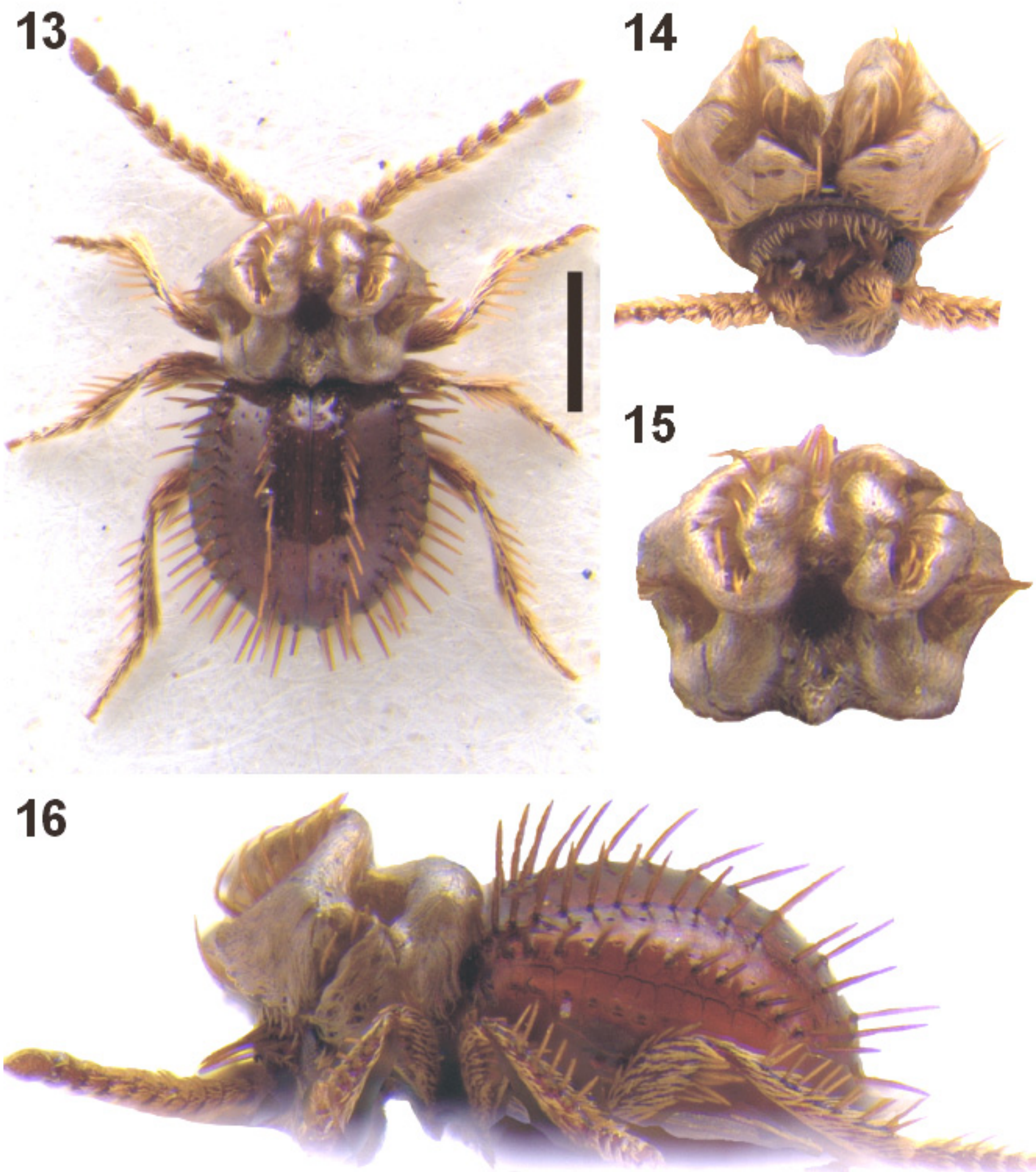
Figures 5–8

M. speldekussing Irish. **5:** Dorsal habitus; **6:** frontal view of head; **7**: dorsal pronotum; **8:** lateral habitus. Scale bar: 0.5 mm



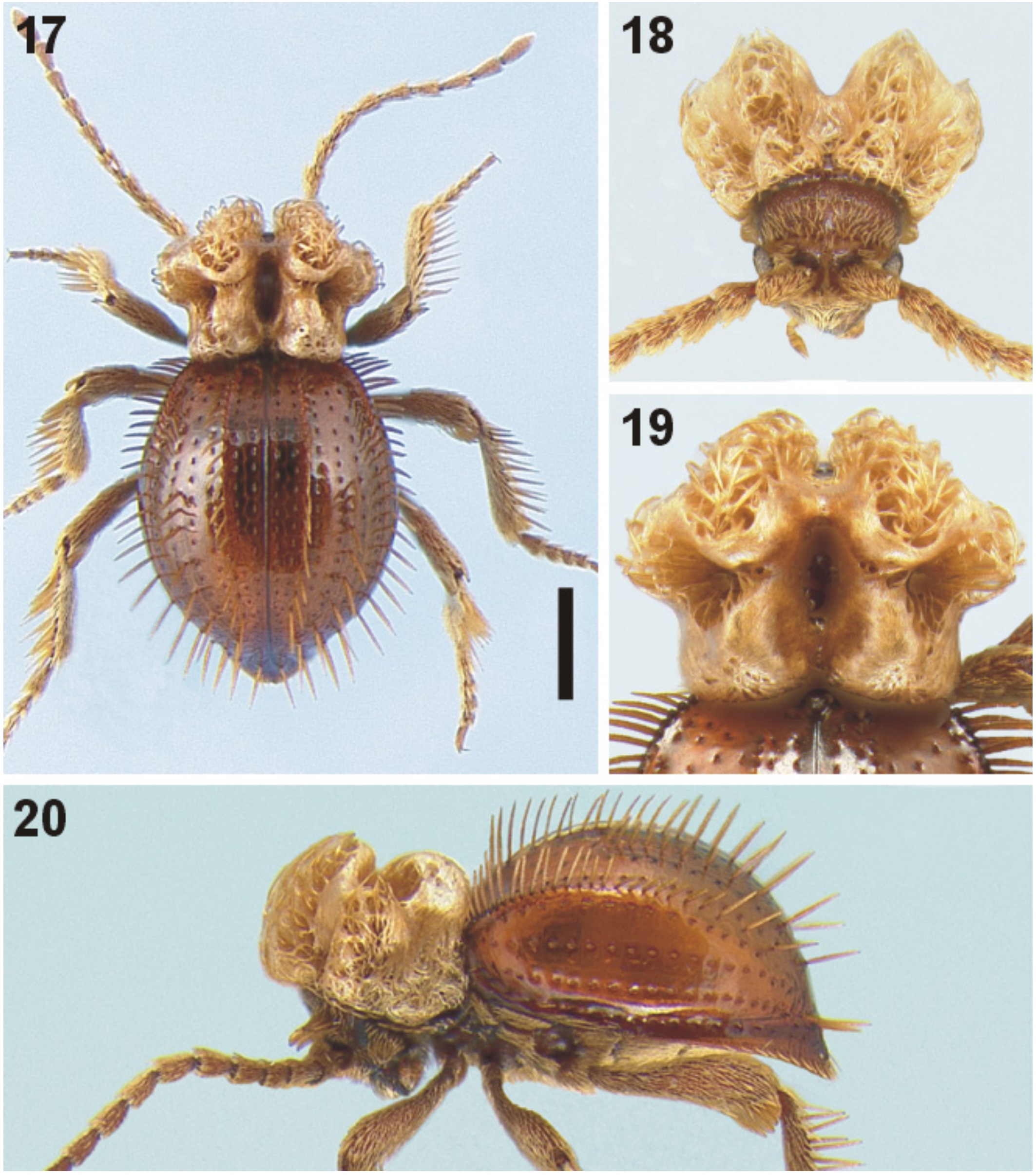
Figures 9–12

M. echinatum Péringuey. **9:** Dorsal habitus; **10:** frontal view of head; **11**: dorsal pronotum; **12:** lateral habitus. Scale bar: 0.5 mm

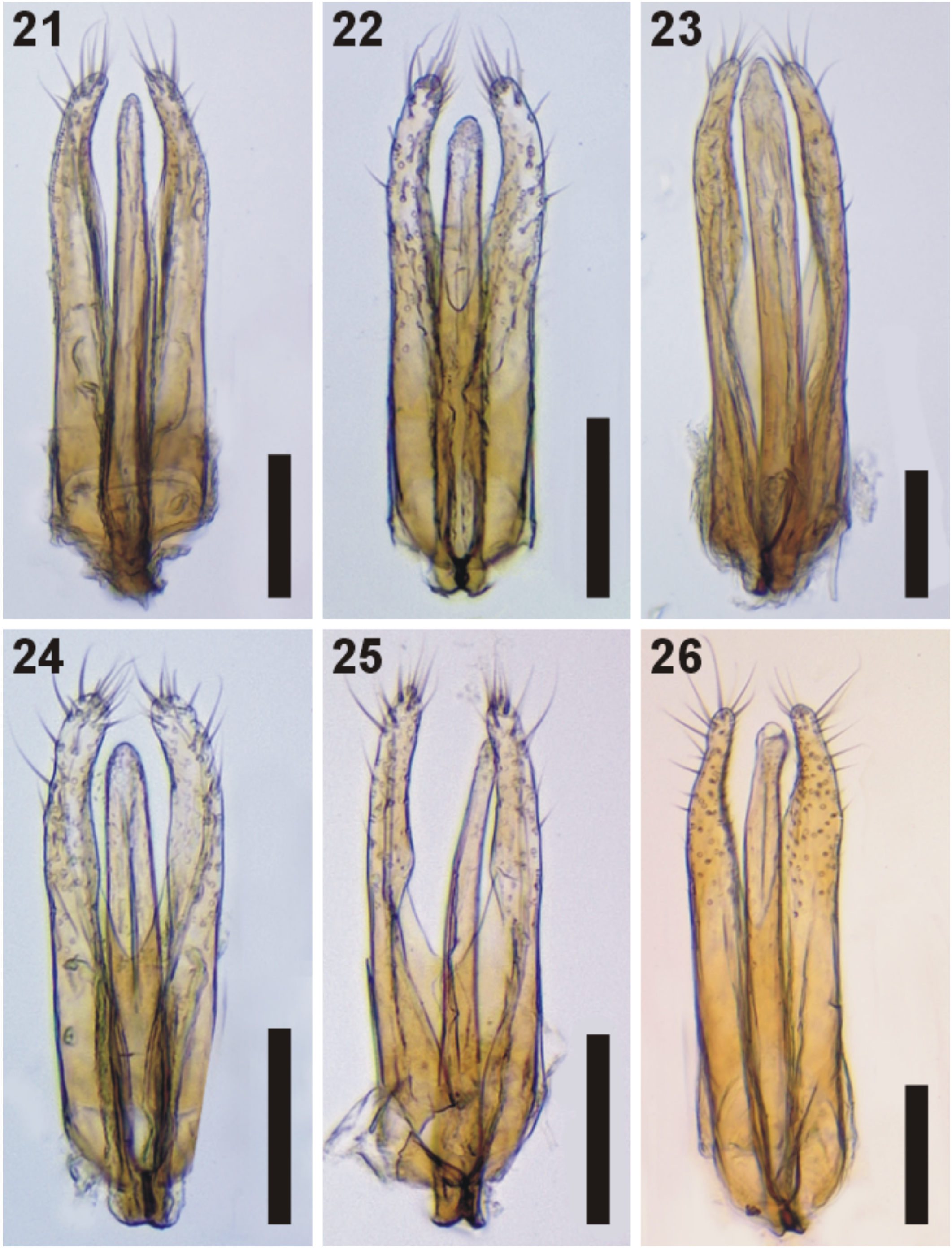


Figures 13–16

M. krimpvarkie Irish. **13:** Dorsal habitus; **14:** frontal view of head; **15**: dorsal pronotum; **16:** lateral habitus. Scale bar: 0.5 mm



Figures 17–20
M. montagu Trimboli and Philips. **17:** Dorsal habitus; **18:** frontal view of head; **19**: dorsal pronotum; **20:** lateral habitus. Scale bar: 0.5 mm



Figures 21–26
Genitalia. **21:** *M. cederbergensis*; **22:** *M. boroveci*; **23:** *M. speldekussing*; **24:** *M. echinatum*; **25:** *M. krimpvarkie*; **26:** *M. montagu*. Scale bar: 100 µm.

Descriptions

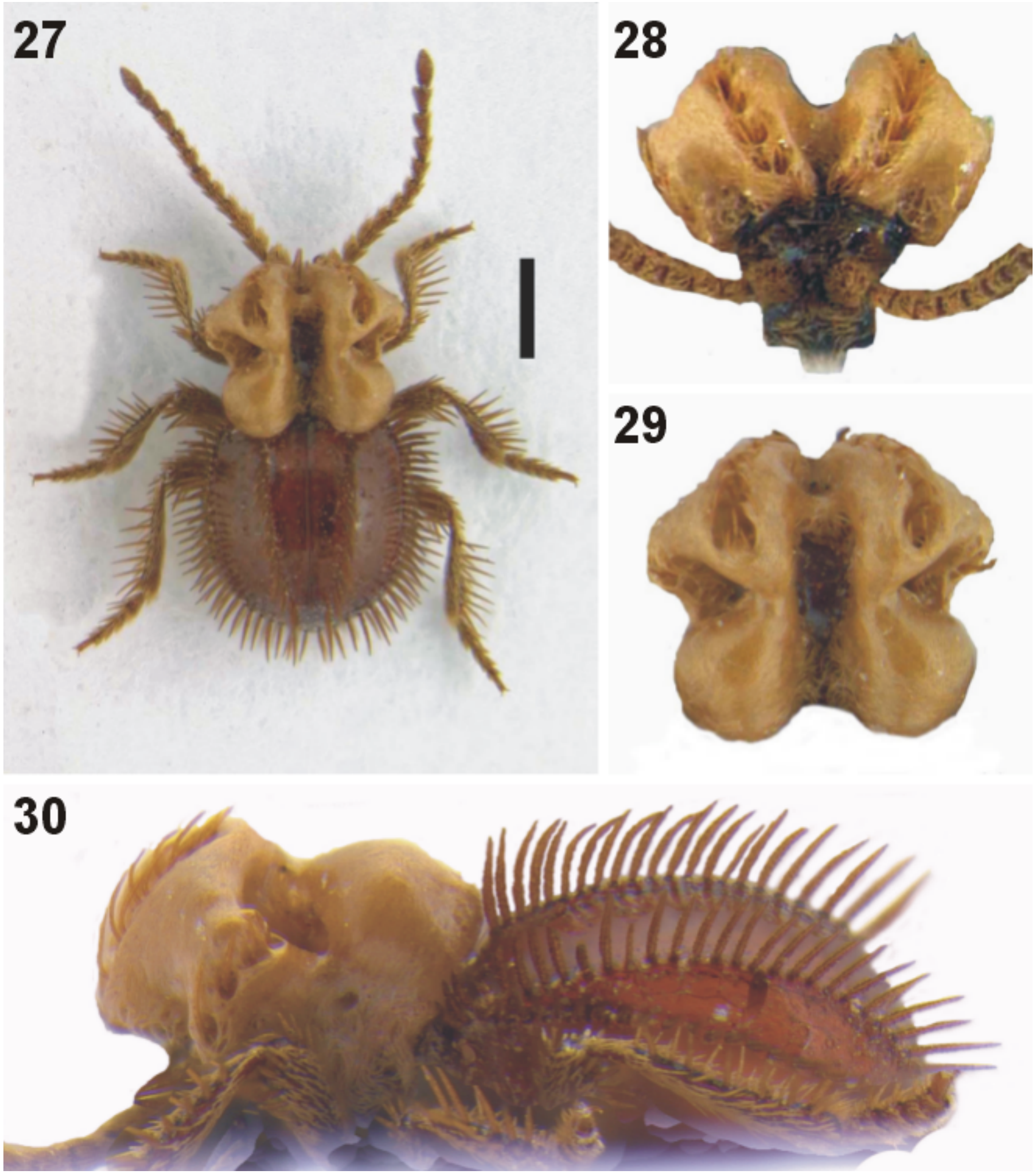
Meziomorphum boroveci **spec. nov. (Figs 27–30, 31)**

Diagnosis: This species with reddish brown elytra possesses three full rows of elytral spines. It can be separated from the similar *M. bulla* and *M. krimpvarkie* by the lack of a medial dorsal projection at the basal margin of the pronotum.

Description: Length: 1.84 mm ± 0.01 (*n*=2); elytra integument reddish brown; pronotum pale yellowish tan; pubescence tan to brown. **Head:** Antennae about half the length of body; antennomeres slightly longer than wide; appressed setae on clypeus obscuring most of surface; frons-vertex with elongate robust brown setae including one small clump below and a second above antennal insertions at middle, an interrupted transverse row of setae near pronotal margin forming four distinct clumps with three to four setae per clump. **Pronotum:** In dorsal view, setal covering divided into symmetric right and left portions by medial longitudinally oriented ovoid cavity at posterior ⅔, exposing cuticular surface, completely separating portions except near anterior margin by a narrow transverse connection; projecting laterally at anterior ⅓; posterior to this a small, deep cavity in middle ¼; in frontal view inflation on either side of middle with narrow cavity oriented dorsoventrally, but interrupted by several narrow transverse connections close to anterior margin, with some projecting setae; laterally just below and behind lateral projection with a series of four cavities oriented dorsoventrally, each with a single seta; posterior half on either side of middle in dorsal view with larger, lower, smoothly rounded dorsal projection than anterior; lacking medial projection near posterior margin; a single long brown seta on anteriolateral margin similar to those on head above eye. **Elytra:** On each elytron, nine aligned full puncture rows, punctures elongated, at middle separated longitudinally by 2x length, separated transversely by 4x width; three interpuncture spine-like setal rows running from base to apex, first row slightly shorter than the others and interrupted near apex, setal length equal to 1.5x–2x the width of the transverse space between puncture rows at middle of elytron; first setal row between 2nd and 3rd puncture rows, second setal row between 6th and 7th puncture rows, and third setal row between 8th and 9th puncture rows; a scattered group of setae near apex.

Etymology. This species is named in honour of one of the collectors of this distinctive species, R. Borovec, to whom we are grateful for his efforts in the field.

Type Material. Holotype (sex unknown). South Africa: RSA Northern Cape, Richtersveld area 580 m, Ploeberg 18.ix.2013, 28°37’818 S, 17°00’462 E, R. Borovec (TMSA). Two paratypes (one male and one female) with the same data except with R. Borovec, M. Meregalli lgt. And a second label: Sifting of detritus, died [dead] leaves and branches, below shrubby *Euphorbia* (TKPC and PKIC).



Figures 27–30

M. boroveci spec. nov. **27:** Dorsal habitus; **28:** frontal view of head; **29**: dorsal pronotum; **30:** lateral habitus. Scale bar: 0.5 mm

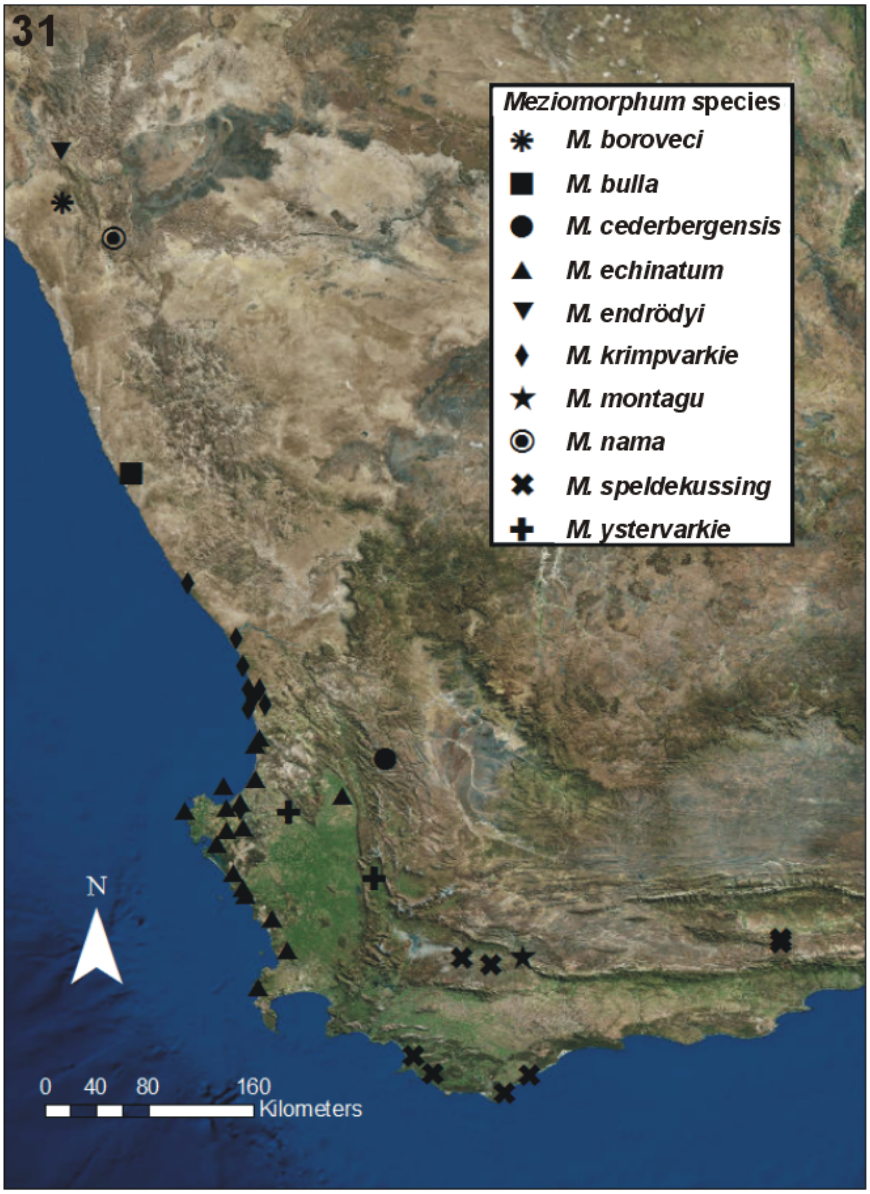


Figure 31
Distribution map of *Meziomorphum* species in South Africa: *M. boroveci*, *M. bulla*, *M. cederbergensis*, *M. echinatum*, *M. endrödyi*, *M. krimpvarkie*, *M. montagu*, *M. nama*, *M. speldekussing*, and *M. ystervarkie*.

Meziomorphum bulla **spec. nov. (Figs 32–35, 31)**

Diagnosis: This species, with dark brown elytra and a yellowish pronotum, possesses three full rows of elytral spines. Two other species can be confused with this taxon; *M. boroveci* lacks a median projection at the basal margin of the pronotum, and *M.*

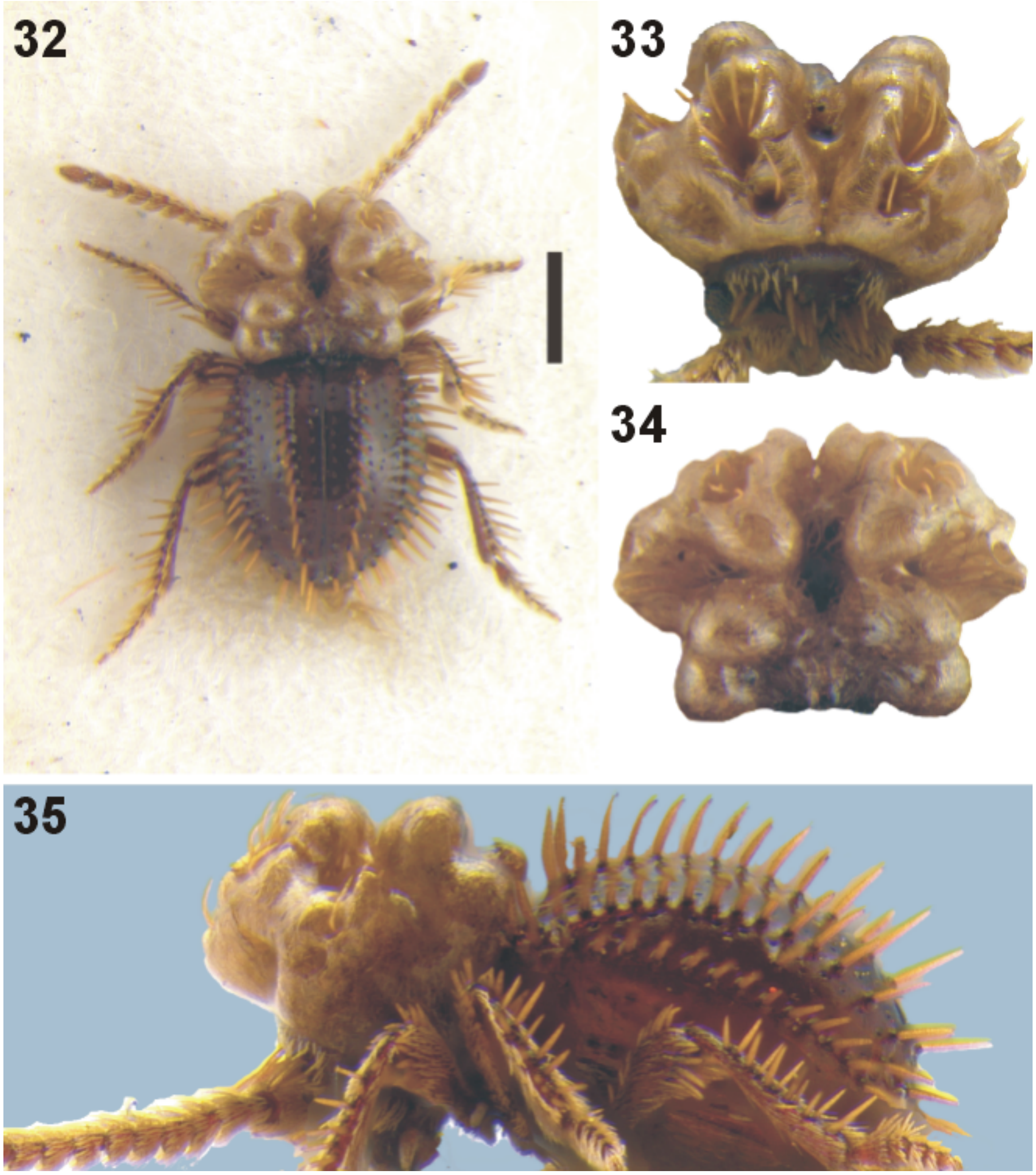
krimpvarkie has a pronotum with two processes on each side while this new species has three, although the third and lower one near the posterior margin is less conspicuous.

Description: Length: 1.73 mm (*n*=1); elytra integument dark reddish-brown; pronotum light bronze-tan; pubescence brown to yellow. **Head:** Antennae about ⅓ length of body, antennomeres slightly wider than long except those near apex; appressed setae on clypeus and genae obscuring most of the surface, frons-vertex also with a single transverse interrupted row of large and a few small erect, robust setae above antennal fossae forming three or four distinct clumps, much smaller recumbent white setae above those, surface medially glabrous. **Pronotum:** In dorsal view, setal covering divided into symmetric right and left portions by medial longitudinally oriented ovoid cavity at middle ⅓, exposing cuticular surface; each symmetric half with a large, deep cavity at middle ⅓ exposing cuticle below and a shallow, more elongate to rounded pair of smaller cavities in anterior declivous portion with setae curved posteriorly extending beyond surrounding surface; paired dorsal projections on either side of middle, with posterior lobe higher, one shorter projection on posterior margin; projection on middle of each half pointed laterally, with two small cavities; pronotal covering also with very small projection pointed posteriorly in middle of posterior margin. **Elytra:** On each elytron, seven aligned full puncture rows and one or two partial rows (three or four punctures) between 3rd and 4th full puncture row, punctures elongate, at middle separated longitudinally by about 2x their length, separated transversely by 4x–5x their width; three inter-puncture rows of erect, spine-like setae, all of roughly the same length, and equal to 1.5x–2x the width of the transverse space between puncture rows at middle of elytron; first inter-puncture setal row between 2nd and 3rd puncture rows and running from elytral base to apex; second setal row between the 4th and 5th puncture rows from base to apex; third setal row between 6th and 7th puncture row from base to apex; apex with row of small recumbent setae.

Etymology. From Latin *bulla* (-*ae*), a bubble, after the many distinct rounded bubble shapes on the pronotum of this taxon.

Type Material. Holotype (sex unknown). South Africa: S. Afr., Namaq. Coast, Gemsbok vlakte farm, 30.30 S-17.29 E/ 1.9.1977; E-Y: 1365, groundtraps, 58 days, leg. Endrödy-Younga/ groundtrap, with millipede bait (TMSA).

Discussion. This is species “A” in Irish (1996a).



Figures 32–35
M. bulla spec. nov. **32:** Dorsal habitus; **33:** frontal view of head; **34**: dorsal pronotum; **35:** lateral habitus. Scale bar: 0.5 mm

Meziomorphum cederbergensis **spec. nov. (Figs 36–39, 31)**

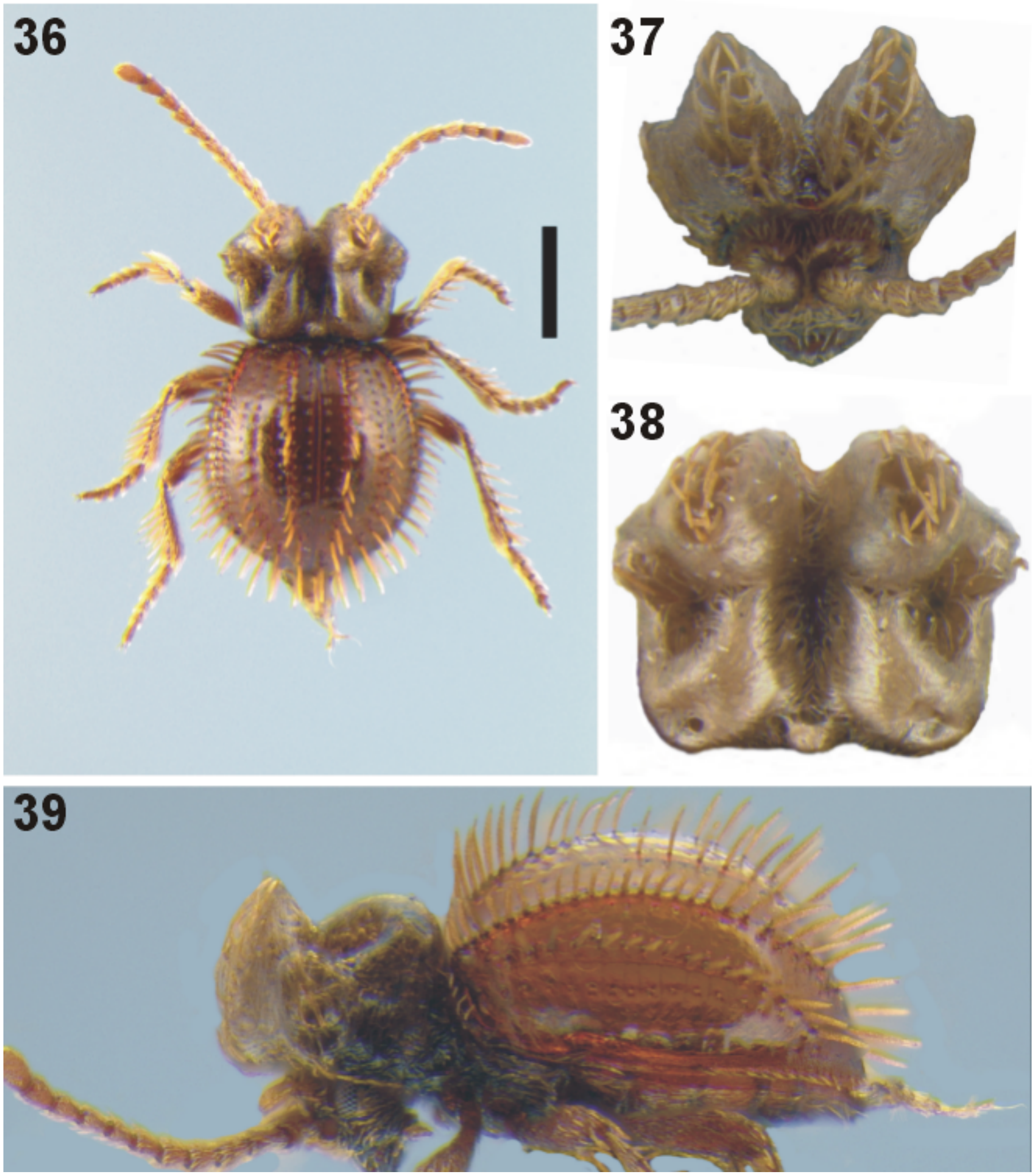
Diagnosis: This species has brown elytra and is one of two that possesses four rows of elytral spines on each elytron. It is most similar to *M. endrödyi* but the new species has a small rounded dorsal projection centrally located adjacent to the posterior margin of the pronotum that is lacking in the former species.

Description: Length: 1.60 ± 0.22 mm (*n* =3); elytra integument reddish-brown, pronotum pale tan to bronze, pubescence pale yellowish orange. **Head**: Antennae approximately half the length of body, antennomeres slightly longer than wide; appressed setae on clypeus, genae, and frons-vertex moderately obscuring surface, frons-vertex also with a single transverse row of erect, robust setae above antennal fossae decreasing in length laterally and a single clump directly below interantennal space at middle. **Pronotum**: Setal covering divided into symmetric right and left portions by a medial longitudinally oriented ovoid cavity at posterior half, exposing cuticular surface at about middle ⅓; one very small pointed projection at middle at posterior margin; each symmetric half with an acutely pointed dorsal projection on anterior half directed slightly posteriorly, a rounded low projection on posterior half, and a lateral projection at middle; each half with a large, deep ovoid cavity at middle extending to ⅓ of total length; in frontal view an elongate narrower cavity oriented dorsoventrally in anterior declivous portion from peak to anterior margin with several long setae projecting out, and a small series of cavities on laterally-facing projection oriented dorsoventrally with a few setae projecting out. **Elytra**: On each elytron, nine aligned puncture rows, punctures elongate, at middle separated longitudinally by 2x–3x their length, separated transversely by 4x–5x their width; four inter-puncture rows of erect, spine-like setae present, greatest setal length at middle equal to 1.5x the width of the transverse space between puncture rows at middle of elytron; first inter-puncture setal row between 2nd and 3rd puncture rows and running from near elytral base to about apical ⅓, then with two distinct interruptions, one posterior of middle and the other near the apex, second short setal row between the 4th and 5th puncture rows running from middle to about apical ¼, third setal row between 6th and 7th puncture rows from base to near apex; fourth setal row between 8th and 9th puncture rows from near base to apex; a similar very short transverse row of setae at apex.

Etymology. This species is named after the location where it was discovered; the beautiful Cederberg in the southwest region of South Africa.

Type Material. Holotype (sex unknown). South Africa: S. Afr., Cape-Cederbg, jeep track, 1130 m, 32.28 S-19.14 E/ 7.11.1983; E-Y: 2055, sifted, marsh shore, leg. Endrödy-Younga (TMSA). Two paratypes (one male, one unsexed) with the same data except "Cedarbg" (TKPC)

Discussion. This is species "C" in Irish (1996a).



Figures 36–39
M. cederbergensis spec. nov. **36:** Dorsal habitus; **37:** frontal view of head; **38**: dorsal pronotum; **39:** lateral habitus. Scale bar: 0.5 mm

Meziomorphum endrödyi **spec. nov. (Figs 40–43, 31)**

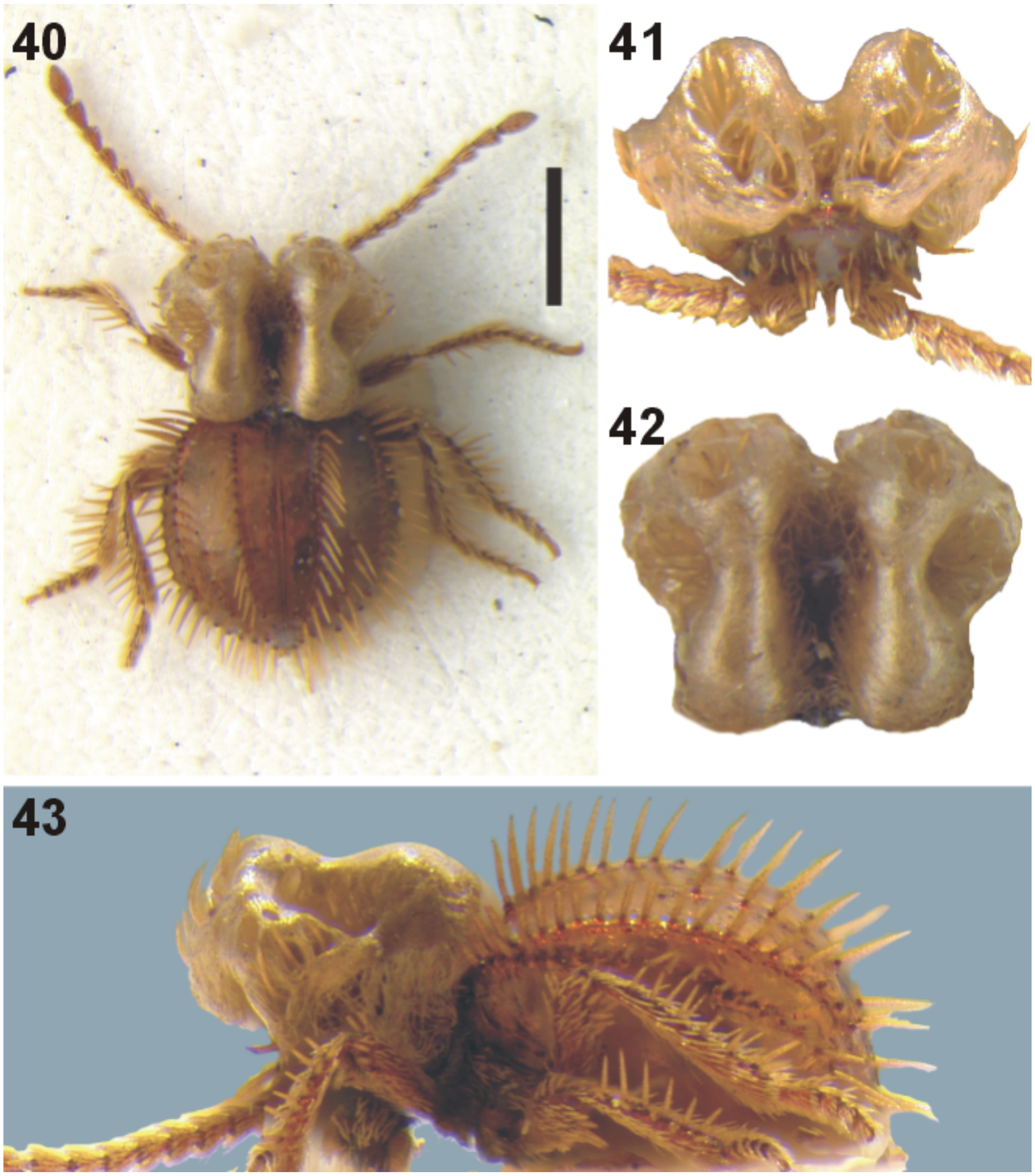
Diagnosis: This species with brown elytra is one of two that possesses four rows of elytral spines on each elytron. This species is most similar to *M. cederbergensis* but the latter has a small rounded dorsal projection centrally located adjacent to the posterior margin of the pronotum, which is completely lacking in this new species.

Description: Length 1.51 mm (*n*=1); elytra integument light orange-brown; pronotum pale yellow-tan; pubescence light brown. **Head:** Antennae approximately ⅔ the length of the body; antennomeres slightly longer than wide; appressed setae mostly obscuring surface on genae and clypeus, a few scattered on vertex; frons-vertex also with a single transverse row of erect, robust setae above antennal fossae with some in distinct pairs. **Pronotum:** Setal covering divided into symmetric right and left portions by medial longitudinally oriented ovoid cavity at posterior ⅔, exposing cuticular surface; each symmetric half with a large, deep dorsolateral cavity at middle ⅓ and narrowly exposing cuticular surface and a smaller cavity extending along majority of anterior declivous portion with extending setae; each anterior half with a projection pointed dorsally, a slightly lower, rounded dorsal and slightly lateral projection on posterior half, and a large, rounded lateral projection on anterior ⅖; no medial projection at posterior margin. **Elytra:** On each elytron, nine aligned full puncture rows, punctures elongated, at middle separated longitudinally by 1x–2x their length, separated transversely by 5x–6x their width; four inter-puncture rows of erect, spine-like setae, all of roughly the same length, and equal to 1.5x the width of the transverse space between puncture rows at middle of elytron; first inter-puncture setal row between 2nd and 3rd puncture rows and running from elytral base to a little over halfway down elytron length; second row between the 4th and 5th puncture rows short, from about middle of elytron to near apex, third row between 6th and 7th puncture row from base to apex, fourth row between 8th and 9th puncture row from base to apex, apex with row of small recumbent setae.

Etymology. This species is named after the late Sebastian Endrödy-Younga in recognition of his amazing efforts in sampling the obscure beetle fauna of South Africa including this and many other spider beetle taxa.

Type Material. Holotype (sex unknown). South Africa: S. Afr.; Richtersveld, Noemeesberg, 28.17 S-16.59E/ 4.9.1976; E-Y:1215, groundtraps, 30 day, leg. Endrödy-Younga/ ground traps, with meat bait (TMSA).

Discussion. Based on the coordinates, the type locality is in the Noemeesberg, the southern end of which is approximately 3 km west of De Koei (28.2869, 17.0027). This is species “B” in Irish (1996a).



Figures 40–43
M. endrödyi spec. nov. **40:** Dorsal habitus; **41:** frontal view of head; **42**: dorsal pronotum; **43:** lateral habitus. Scale bar: 0.5 mm

Meziomorphum nama **spec. nov. (Figs 44–47, 31)**

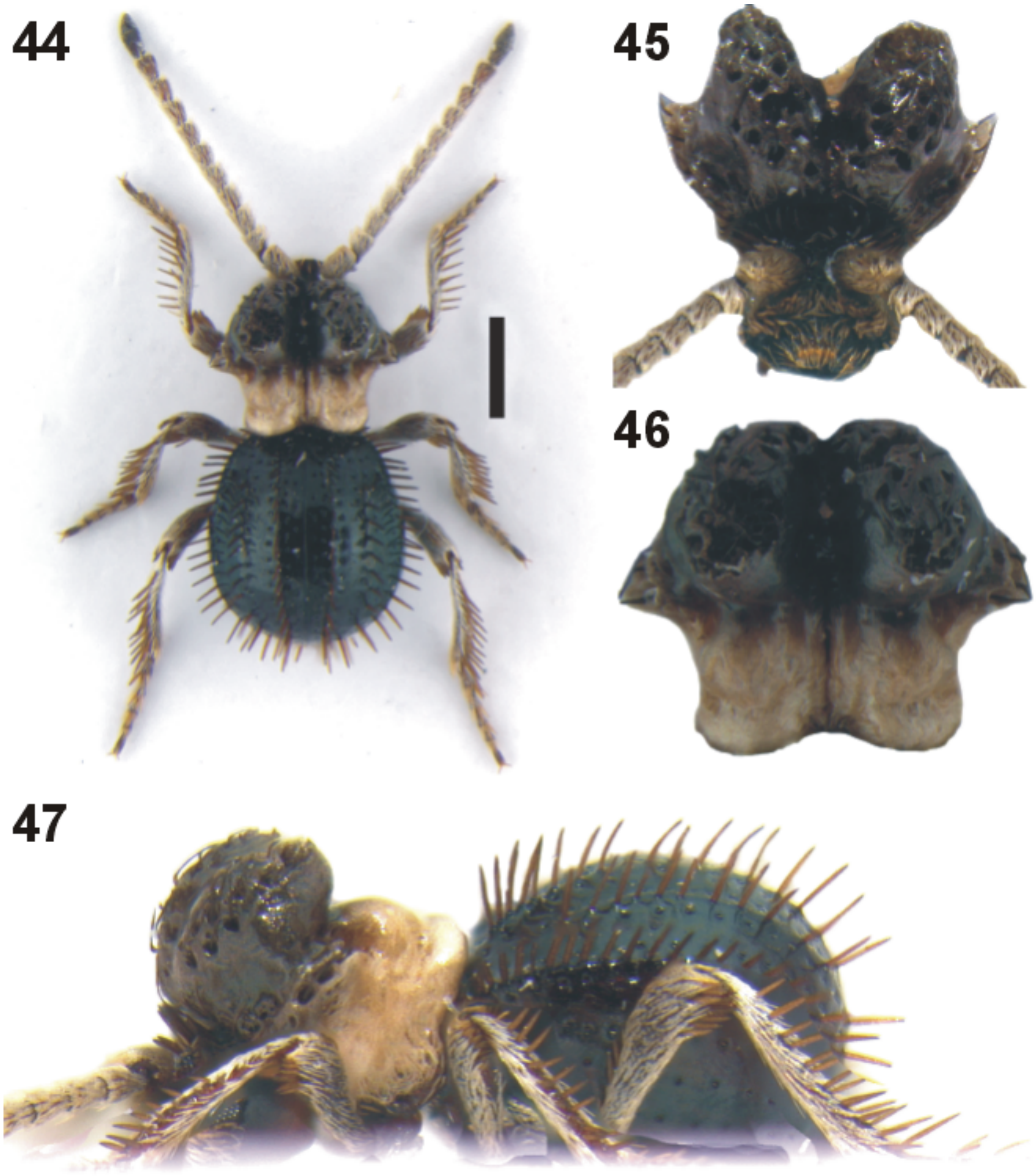
Diagnosis: This species is one of three with black elytra. *Meziomorphum ystervarkie* possesses three full rows of spines on each elytron, in *M. speldekussing* this row is absent from the basal ½, while in *M. nama* the middle row is absent from the basal ⅓.

This species is closest to *M. speldekussing* but can also be distinguished by a cavity at the middle of the pronotum that does not extend to the cuticle surface as in the latter species. Additionally, *M. nama* is slightly more elongate overall compared to *M. speldekussing*.

Description: Length: 2.03 mm (*n*=1); elytra integument black; anterior half of pronotum dark brownish black, at posterior half with a short gradient to tan at middle to light tan at posterior margin; pubescence brown to dark brown. **Head:** Antennae as long or slightly longer than body, antennomeres slightly longer than wide; recumbent setae on clypeus and genae obscuring most of the surface, also a cluster of robust setae between antennal fossae and a transverse row of robust setae above antennae near anterior margin of pronotum. **Pronotum:** Setal covering divided into symmetric right and left portions by linear crevice; each symmetric half with tall lobe projecting dorsally and slightly posteriorly on anterior half, a small pointed lateral projection on anterior half, a short rounded projection on posterior half, and a distinct wide transverse ridge on posterior margin; each half also with a small laterally-facing cavity slightly above and posterior to lateral projection and halfway between black and tan portions of pronotum. **Elytra:** On each elytron, nine full puncture rows, punctures nearly round; three inter-puncture rows of erect, spine-like setae all of roughly the same length and equal to 1.5x–2x the width between puncture row at middle of elytron; first setal row between 2nd and 3rd puncture rows from base to about apical ¼; second setal row between 4th and 5th puncture row from about basal ¼ to before apical ¼; third setal row between 6th and 7th puncture row from base to near apex, extra setae near apex of elytra.

Etymology. This species is named in honor of the Nama people of South Africa who inhabit the area where this taxon is found.

Type Material. Holotype (sex unknown). South Africa: RSA, Northern Cape, S. Eksteeinfontein [sic] 612 m, dir. Vioolsdrift 23.ix.2012, 28°51’957 S, 17°21’503E, R. Borovec lgt (TMSA).



Figures 44–47
M. nama spec. nov. **44:** Dorsal habitus; **45:** frontal view of head; **46**: dorsal pronotum; **47:** lateral habitus. Scale bar: 0.5 mm

Discussion

Morphology

All known species in the genus *Meziomorphum* possess a bizarre and unique morphological synapomorphy within the ptinids: distinctive rows of long robust setal spines on the elytra and legs. Most if not all spider beetles typically use a defense of retracting their legs and antennae and playing dead when disturbed, a behavior known as thanatosis. This trait, together with the large spines, may be adequate protection against predators. The small size of these beetles (1.5 – 2.0 mm in length) suggests that their predators might also be relatively small-bodied and may include invertebrates such as ants. Vertebrate predators, including perhaps lizards, may also have provided selective pressure for the evolution of spines.

Pronotal morphology is also very distinctive in this genus and appears similar to a dessert food composed largely of whipped egg whites known as a meringue that has a fluffy interior and a thin solid outer surface layer. In specimens with large openings on their pronotum or damage to the surface layer, the interior appears as an irregular skeletal scaffold and is mostly an air-filled hollow space (Fig 48). This morphology may help in crypsis by appearing like a small lizard, or other vertebrate, dropping. The different and odd shapes seen among species may also be evolving via genetic drift; some populations appear to be very small

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Figure 48
Broken pronotum of *M. krimpvarkie* showing the internal honeycomb structure of setae beneath the surface.

and random genetic changes are more likely to become fixed and affect morphological traits.

Biology

Although there are no rearing records for any species, like so many of the other spider beetles, they are almost certainly detritus feeders, particularly using older dried dung of various vertebrates, including that from various mammals such as bats (Trimboli and Philips 2011) as well as lizards, snakes, tortoises, and birds. Accumulations of plant detritus might also be used by some taxa, but this food source will need confirmation.

Relationships

Both parsimony and Bayesian analyses of CO1 data show *Meziomorphum* as sister to *Mezium* Curtis. Additionally, parsimony topologies show this clade as sister to *Gibbium* Scopoli + *Lepimedozium* Bellés. In contrast, morphological data place *Meziomorphum* as sister to the Gibbiinae, and has *Mezium* in a more derived position within this subfamily (Mynhardt, unpublished). The morphological study of Bellés (1985) also supports *Meziomorphum* as a sister clade to most of the Gibbiinae, and this larger clade as sister to *Gibbium* + *Sulcatogibbium* Bellés.

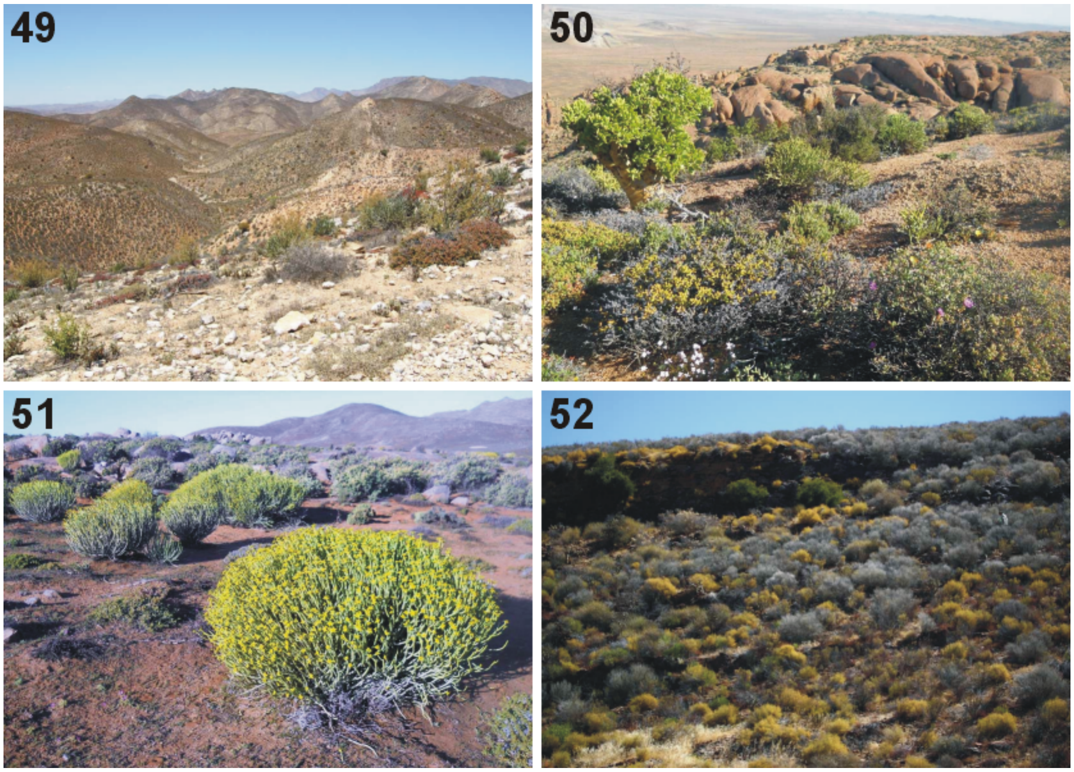
Distribution

All ten species are found from northwest South Africa down to the Cape Town and as far east as north of Port Elizabeth in the Eastern Cape (Fig 31). No records of any species are more than 100 km from the coast. Some species distributions on the west coast are similar to those found in other species of spider beetles, such as *Cryptopeniculus nigrosetus* Philips and *Carinomezium namaquaensis* Wood and Philips, perhaps indicating the same vicariant events resulted in cladogenesis in different lineages.

Four of the five new species are from Namaqualand and the other is from the Cederberg. Based on gaps in the distribution, we expect that additional populations representing new species will most likely be found from the Cederberg north up into northwest South Africa when more sampling is done. Species are typically found in dry environments, from the Richtersveld south through Namaqualand to the Cape Peninsula and east into the Karoo and near-coastal habitats in the Western Cape Province (Figs 49–52).

Revised Species Status

Borowski (2000) synonymized three species that Irish (1996a) described. After examination of these taxa we have concluded that they are all valid species. Therefore, *M. krimpvarkie* Irish, *M. ystervarkie* Irish, and *M. speldekussing* Irish are removed from synonymy with *M. echinatum* Péringuey, 1888 and re-established as valid species (**stat. rev.**).



Figures 49–52
49: Habitat of *M. endrödyi* in the Richtersveld (Photo by John Andersland); **50:** Habitat of *M. boroveci* in the Ploeberg Mountains, Richtersveld; **51:** *Euphorbia mauritanica*, where *Meziomorphum* may be found. **52:** Potential habitat for *M. cederbergensis* in the Cederberg near Keurbosfontein (S 32° 27'58" E 19° 18'51").

New Records

Meziomorphum krimpvarkie Irish: South Africa, Western Cape, 33 m, Doring Bay, sifting, cliff, 32°48'591 S18°14'102 E, 29.x.2011, R. Borovec lgt./sifting of detritus bellow [*sic*] different low plants and shrubs, cliff.

Meziomorphum speldekussing Irish: South Africa, Western Cape, nr Worcester, Karoo Botanical Gardens, 33°36'50.0" S19°27'01.2" E, 25.01.2017. coll. Y. M. Marusik

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Wood, M. V. and T. K. Philips. 2013. *Carinomezium* (Coleoptera: Ptinidae): A new genus from the Namaqualand region of South Africa. *Tijdschrift voor Entomologie* **156**: 11–19.

A REVISION OF THE SPIDER BEETLE GENUS *EUTAPHROPTINUS* BOROWSKI (COLEOPTERA: PTINIDAE)

Introduction

A new genus of spider beetle, *Eutaphroptinus* Borowski, was described in 2009 with two new species, *E. natalensis* and *E. pseudonatalensis*. While examining material currently in our possession, it became difficult to identify some of our specimens at species level. Hence, we became suspicious that this genus is represented by two species as first hypothesized. Examination of the holotypes of the two species of *Eutaphroptinus* supported our hypothesis of a single species and therefore and *E. pseudonatalensis* is in fact a junior synonym of *E. natalensis*. We take this opportunity to clarify the taxonomy, more thoroughly illustrate features of the genus, and report several new records for this species.

Materials and Methods

Examination of the type specimens took place during a visit to the Natural History Museum, London (BMNH). Photographs were used after to confirm some of the morphological variation of the type specimens and for comparison with material in our possession. Specimens from the following collections were also examined: Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria (TMSA), National Collection of Insects, Pretoria (SANC), and the collection of T. Keith Philips, Western Kentucky University, Bowling Green (TKPC).

Label data for type specimens was recorded new records was recorded verbatim. Label data for all other materials was recorded as follows: COUNTRY; geographic locality; coordinates; altitude; date; collector; additional collecting data; specimen code.

Taxonomy

Eutaphroptinus natalensis Borowski, 2009: 13

Eutaphroptinus pseudonatalensis Borowski, 2009: 14. **Syn. Nov.**

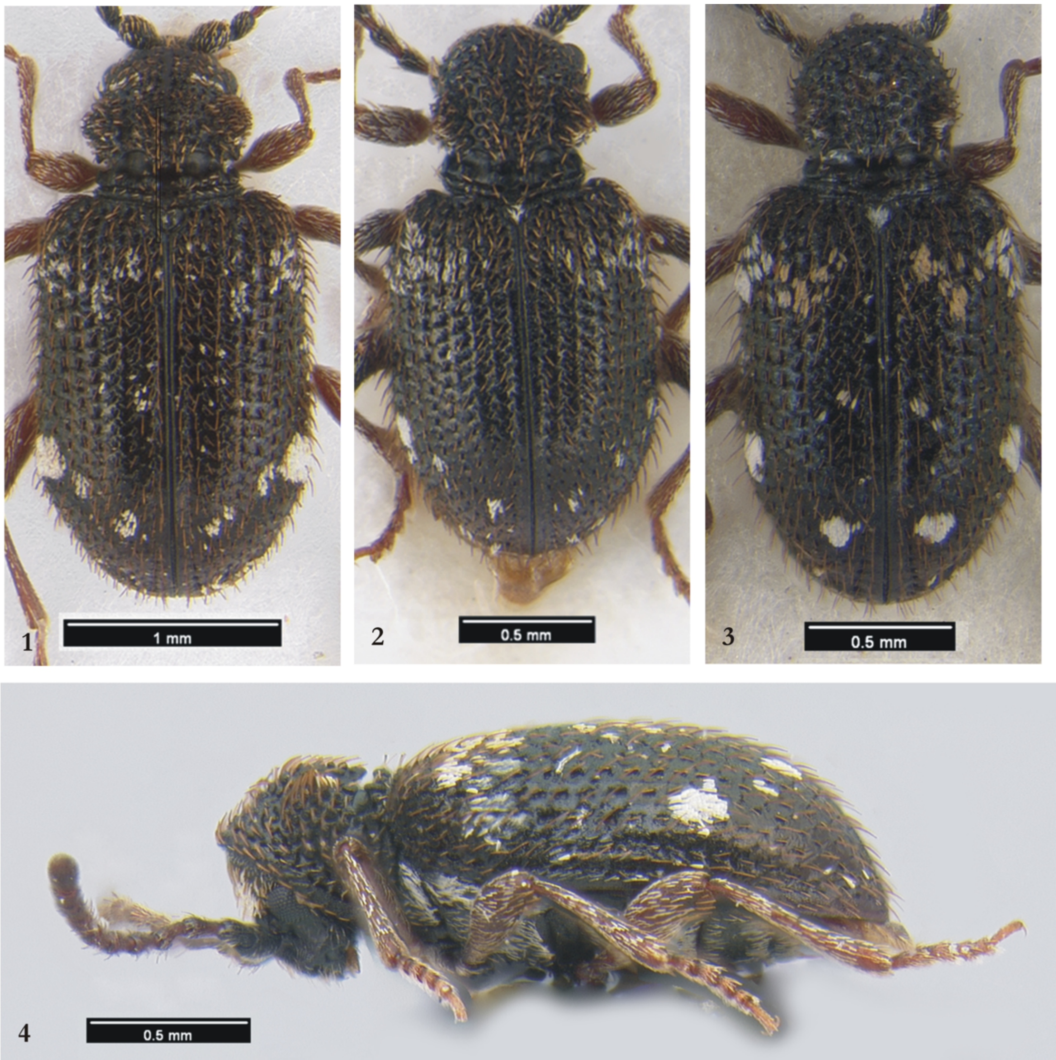
Discussion

E. natalensis and *E. pseudonatalensis*, were described from 14 and three specimens respectively (Borowski 2009). The characters used to differentiate the two species are based on a number of features, including some that are known to be highly variable within spider beetles.

For example, antennomere color is described in *E. natalensis* as “first two black, others bicolorous: basal halves red, apical (*sic*) black,” while the antennomeres of *E. pseudonatalensis* are “first two black, others reddish-brown.” However, among the specimens of *Eutaphroptinus* examined, the amount of red and black in the antennomeres is variable and not consistent with other differentiating characters. Excluding the basal antennomeres which are typically dark colored, the remaining antennomeres are typically a combination of colors or can be nearly entirely red or reddish- brown. Additionally, the holotype of *E. pseudonatalensis* does have some black coloration in the more distal antennomere apices similar to that seen in *E. natalensis*.

Elytral scales in *E. natalensis* are described only as “narrowly elliptical”, while the elytral scales of *E. pseudonatalensis* are “short, wide, silvery-white or greyish-blue.” Indeed, the holotypes do possess different scale color and morphology: dorsally *E. natalensis* has more elliptical “yellowish” (or pale tan colored) scales while *E. pseudonatalensis* has teardrop-shaped whitish colored scales. However, examination of other specimens of *Eutaphroptinus* reveal that some individuals possess both scale shapes or have intermediates of those shapes. Moreover, both scale morphologies can be either “yellowish”, white, or tan colored, even within the same specimen (see Figs 1–3 for examples of scale variation).

The pattern on the elytra formed by the scales was also used to differentiate the species. *E. natalensis* was described as possessing “two transverse bands” of elytral scales in the anterior and posterior portions of the elytra, while *E. pseudonatalensis* has scales “dispersed all-over elytral surface sometimes with tendency to gather into transverse bands.” In fact, although less distinct, the scales on the *E. pseudonatalensis* holotype tend toward transverse bands in the same location as the bands in *E. natalensis.* The only noticeable difference in the scale patterns seen in the holotypes is that *E. pseudonatalensis* has more scattered scales present between the two bands. Other specimens examined possess varying numbers of scales, all tending toward the transverse band pattern and sometimes with additional scales located between the bands. Further, the transverse band near the elytral apex typically consists of two more patches with occasionally a smaller one between these on each elytron. One should note that scale patterns in spider beetles can be quite variable within a species (e.g. see Philips, 1998 for variability in *Niptinus niveus* (Gorham)) and can sometimes simply be due to the loss of scales from abrasion that in some cases can cause some difficulty in species differentiation.



Figures 1–4
1–3: Dorsal habitus of three different specimens of *Eutaphroptinus natalensis* from **1:** Mbotje Forest, Eastern Cape, **2:** Lajuma Nature Reserve, Limpopo Province, and **3:** Kosibay, Manguzi Forest, Kwazulu-Natal; **4:** lateral habitus of *E. natalensis* from DeHoop, Western Cape.

Elytral setae orientation in each species is reported as slightly different. In *E. natalensis*, setae “on first 4 intervals, hairs point in part obliquely towards sides and apex.” In *E. pseudonatalensis*, they are described as “directed somewhat obliquely lateroposteral on first two intervals, towards elytral apex otherwise.” Although the elytral setae were not carefully examined during the visit to the NHM, they are visible in photographs taken of the type specimens. We conclude that these are minor differences and importantly are variable depending upon which specimen is studied.

Notably, there are up to four types of elytral setae in many spider beetles. One minute type is found within the punctures, a second is located between the puncture rows, while a third is along the puncture row. The fourth are composed of fine recumbent setae or scales that are distributed in patterns that are species specific.

In all of the other specimens examined, the hairs on the intervals were directed posteriorly as in a typical ptinid spider beetle pattern. The puncture row setae in this species that are angled obliquely posteriorly appear to be another variable characteristic due to individual differences or even in some cases movement of individual hairs during the processing of the specimens.

Leg coloration for *E. pseudonatalensis* was described as yellowish-red*,* while *E. natalensis* was described as possessing reddish brown tarsi and tibia, with the "femora darkened apically or blackish brown." However, additional specimens examined reveal a continuum of leg coloration from yellowish-red to dark reddish-brown. Additionally, none of the characters used to differentiate the two species (leg and antennal coloration, elytral scales and setae, etc.) correlate with each other in the specimens that were examined. Instead, specimens possessed characteristics of both species or characteristics intermediate of the two species described.

Although the genitalia, as illustrated, show slight differences between the two species; these differences are similar to what has been documented elsewhere within various species (e.g., see Bellés 1985; Philips and Smith 2016; Philips and Dickmann 2018) and are hypothesized to represent only intraspecific variation.

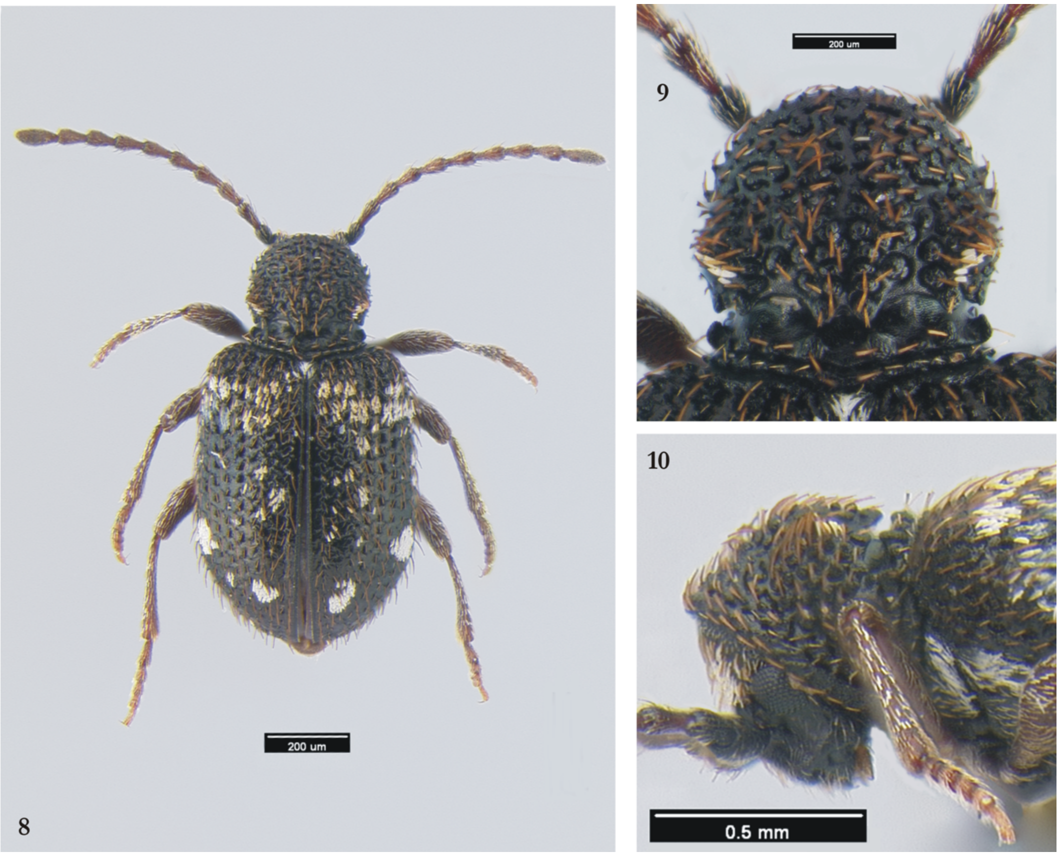
Finally, in Figure 2 of Borowski (2009), the punctures are illustrated in a northeast to southwest direction. However, among specimens examined, the punctures are actually oriented on the opposite diagonal (refer to Fig 7).

Figures 5–7
Eutaphroptinus natalensis. **5:** ventral; **6:** frontal; **7:** close up of elytral punctures

Notes on the Genus

This genus is distinct from all others known in particular by a deep and transverse pronotal groove near the base of the pronotum (see Figs 8–10), a feature found in other spider beetle taxa. Other genera known to possess a similar groove include *Eutaphrimorphus* Pic (1898), *Dignomus* Wollaston (1862), *Silisoptinus* Pic (1917), and *Trymolophus* Bellés (1990). *Eutaphroptinus* can be distinguished from *Eutaphrimorphus* (another similar South African taxa) by the structure of the pronotum and the groove. *Eutaphroptinus* possesses three dorsally projecting knobs on the disc of the pronotum (one larger one medially and two slightly smaller ones laterally (Fig 6)), compared to four shorter knobs in *Eutaphrimorphus* (all on either side of the midline). Additionally, the medial portion of the pronotal groove is much larger in *Eutaphrimorphus* than in *Eutaphroptinus*. *Dignomus,* another genus which can be found in southern Africa, possesses only two projections on the pronotum which are often more setose than in *Eutaphroptinus. Dignomus* also possesses lateral cavities on the pronotum, which are lacking in *Eutaphroptinus.*

Silisoptinus, known from Zanzibar (Tanzania) and the Socotra Island (Yemen), also has a much larger medial depression in the transverse pronotal groove than in *Eutaphroptinus. Silisoptinus* can be further differentiated from *Eutaphroptinus* by a very characteristic anteriorly widened prosternum in the latter genus. *Trymolophus* can be differentiated from *Eutaphroptinus* by a lack of a medial depression in the transverse groove which is present in *Eutaphroptinus.* A transverse pronotal groove can also be found in *Ptinus espanyoli* Bellés (1997), *Ptinus augustithorax* Bellés (1986), and in the genus *Tropicoptinus* Bellés (1998). However, these taxa are all neotropical and are easily distinguishable from *Eutaphroptinus.*



Figures 8–10.
Eutaphroptinus natalensis. **8:** dorsal habitus; **9:** dorsal pronotum; **10:** lateral pronotum and head.

Type Material Examined

Eutaphroptinus natalensis. Holotype. "Natal: Kloof. 1500 ft. Aug. 1926, S. Africa, R. E. Turner, Brit. Mus. 1926-350" (BMNH).

Eutaphroptinus pseudonatalensis. Holotype. "Port St. John, Pondoland, July 10-31.1923, S. Africa, R.E. Turner, Brit. Museum. 1923-398" (BMNH).

Additional Material Examined/New Records:

SOUTH AFRICA; Eastern Cape, Mbotjie forest; 31.27 S – 29.43 E; 30 Nov. 2003; leg. M. Burger, R. Müller; forest litter & bark; E-Y:3580 (TMSA)

SOUTH AFRICA; Limpopo Province, Lajuma National Reserve, 23.02 S-29.26 E; 12 Dec. 2017; leg. Ruth Müller; sifting canopy forest; E-Y:4012 (2 spec.) (TMSA)

SOUTH AFRICA; KwaZulu-Natal, KosiBay, Manguzi Forest; 26.59 S-32.44 E; 15 Nov 2002; leg. Burger, Harrison, Müller; sifting; E-Y:3537 (TMSA)

SOUTH AFRICA; KwaZulu-Natal, KosiBay, Manguzi Forest; 26.59 S-32.44 E; 15 Nov. 2002; leg. Burger, Harrison, Müller; general collecting; E-Y:3538 (TMSA)

SOUTH AFRICA; Cape Province, The Claims' Farm, nr. Komga Kubusi R. Valley; 32.29S 27.53E; 01 Dec. 1992; leg. R. Oberprieler (SANC)

SOUTH AFRICA; Western Cape, De Hoop; S34°27'15'E20°23'49"; 17m; 10 Jan. 2008; leg. T. K. Philips (2 spec.) (TKPC)

References

Bellés, X. 1998. El género *Tropicoptinus* nov. (Coleoptera: Ptinidae) de la región neotropical. *Elytron* **12**: 85–96.

Borowski, J. 2009. The spider beetles of the continental Africa (Coleoptera: Ptinidae). Part III. *Eutaphroptinus* gen. n. from South Africa with description of two new species belonging to the new genus. *Studies and Reports of District Prague-East*, **Taxonomic Series 5**: 11–16.

Pic, M. 1898. Diagnoses de deux *Ptinus* de l'Afrique austral et sous-genre *Eutaphrimorphus*. *Miscellanea Entomologica* **6**: 54–55.

Pic, M. 1917. Descriptions abrégées diverses. *Mélanges Exotico-Entomologiques* **24**: 2–24.

Philips, T. K., and R.L. Dickmann. 2018. A new species of *Mezium* Curtis (Coleoptera: Ptinidae) from South Africa, with notes on the genus and species limits. *The Coleopterists Bulletin* **72**: 317–330.

Philips, T. K., M. A. Ivie, and L. L. Ivie. 1998. Leaf-mining and grazing in spider beetles (Coleoptera: Anobiidae: Ptininae): an unreported mode of larval and adult feeding in the Bostrichidae. *Proceedings of the Entomological Society of Washington* **100**: 147–153.

Philips, T. K., and A. L. Smith. 2016. New records for *Ptinus peringueyi* Pic (Coleoptera: Ptinidae) and a discussion of morphological variation in this species. *The Coleopterists Bulletin* **70**: 403–406.

Appendix A

List of taxa used in this study, their localities, and Genbank accession numbers for DNA sequences.

Taxon	Location Sampled	CO1	28S	16S
Ptinidae *s. l.*				
Ptinidae *s. s.*				
Ptininae				
Gibbiini				
Gibbium aequinoctiale	Kentucky, USA	JN097703	JN097666	JN097763
Gibbium psylloides		DQ221970		DQ202568
Meziini				
Damarus sp		*Current study*	*Current study*	
Lepimedozium natalense		*Current study*	*Current study*	
Meziomorphum montagu		*Current study*		
Meziomorphum speldekussing		*Current study*	*Current study*	
Mezium affine	Laboratory culture	JN097707	JN097663	JN097759
Mezium gigantium		*Current study*	*Current study*	
Mezium glabrum	Obib, Namibia	JN097707	JN097662	JN097758
Pseudomezium polyomorphus		*Current study*	*Current study*	
Stethomezium sp		*Current study*	*Current study*	
Ptinini				
Acanthaptinus triplehorni	Madagascar		JN097680	
"Australptinus" new genus	Australia	JN097715	JN097678	
"Australniptus" new genus	Australia		JN097682	
Casapus sp	Canary Islands	*Current study*	*Current study*	
Dignomus kukalovae	Soutpan Dunes, South Africa	*Current study*	*Current study*	
Dignomus maira	Grootkraal, South Africa	*Current study*	*Current study*	
Dignomus tengzu	Ghana		*Current study*	
Dignomus varius	Richtersveld, South Africa	*Current study*	*Current study*	
Diplocotes foveatus	Queensland, Australia	JN097714	JN097659	JN097762
Diplocotes similis	South Australia		JN097681	
Fabrasia sp		*Current study*		
Gnostus floridanus	Florida, USA	JN097702	JN097658	JN097760
Kedirinus subviolaceus	Australia	JN097701	JN097696	
Lachnoniptus lindae	Virgin Islands	JN097706		
Nicobium castaneum	Germany	KU494146		
Niptinus ovipennis	Texas	JN097712	JN097690	

Niptinus sp	Guatemala	*Current study*	*Current study*	
Niptus arcanus		*Current study*		
Niptus guliani			*Current study*	
Niptus hololeucus		KX087321		
Paulianoptinus n sp	Madagascar		JN097688	
Paulianoptinus sp	Madagascar		JN097689	
Pitnus antillanus		JN097716	JN097698	
Pocapharaptinus mulleri		*Current study*	*Current study*	
Polyplocotes sp			*Current study*	
Ptinus bimaculatus	Texas, USA	JN097708	JN097664	JN097764
Ptinus concurrens	Georgia, USA	*Current study*	JN097675	
Ptinus dubius	Germany	KM444597		
Ptinus fallax	British Columbia, CA	MG058738		
Ptinus fur	Europe: Germany	KM451550		
Ptinus fur	North America	*Current study*	*Current study*	
Ptinus interruptus	Texas, USA	JN097717	JN097665	JN097765
Ptinus italicus	France	KM285868		
Ptinus raptor	Manitoba, CA	MG053947		
Ptinus rufipes	Germany	KM451624		
Ptinus sexpunctatus	France	KM285914		
Ptinus sp	Guatemala	*Current study*	*Current study*	
Ptinus sp	Madagascar		JN097679	
Ptinus sp	Nova Scotia, CA	MG055377		
Ptinus sp	Ontario, CA	KR131178		
Ptinus sp	Ontario, CA	KR482683		
Ptinus subpilosus	Germany	KM449099		
Ptinus tectus	New Zealand	JN097713	JN097660	JN097761
Ptinus texanus	Texas, USA	JN097709	JN097674	
Ptinus villiger	Europe	KR487437		
Ptinus villiger	North America	*Current study*		
Ptinus wagneri		*Current study*	*Current study*	
Scaleptinus squamulosus 1		*Current study*		
Scaleptinus squamulosus 2		*Current study*	*Current study*	
Singularivultus decellei		*Current study*	*Current study*	
Sphaericus sp	Canary Islands		*Current study*	
Sulcinota new genus	Angola	*Current study*	*Current study*	
Sundaptinus sp 1		EF213939		
Sundaptinus sp 2		EF213944		
Sundaptinus sp 3		EF213949		
Xylodes sp		*Current study*		
Sphaericini				

Sphaericus gibboides		*Current study*		
Anobiidae *s.s*				
Unplaced				
Anobiidae sp 1a	Malaysia	KF946234		
Anobiidae sp 1b	Malaysia	KF946216		
Anobiidae sp 2	Malaysia	KF946322		
Anobiidae sp	Australia		JN097700	
Anobiinae				
Anobiopsis sp	Bolivia	JN097735	JN097649	JN097753
Anobium hederae	France	KM285941		
Anobium inexspectatum	France	KM286383		
Anobium punctatum		*Current study*	*Current study*	
Cacotemnus rufipes (=*Hemicoelus*?)	Finland	KJ961900		
Gastrallus immarginatus	Germany	KM452193		
Gastrallus laevigatus	France	KM286251		
Hadrobregmus denticollis	France	KM286298		
Hadrobregmus notatus	Ontario, CA	MG054940		
Hadrobregmus pertinax	France	KM286260		
Hemicoelus carinatus	Ontario, CA	KR485810		
Hemicoelus costatus	Germany	KM448655		
Hemicoelus fluvicornis	France	KM285854		
Hemicoelus nitidus	France	KM286179		
Hemicoelus sp	Bolivia	JN097734	JN097651	JN097745
Hemicoelus sp	Ontario, CA		*Current study*	
Hemicoelus umbrosus	Ontario, CA	MG057455		
Microbregma emarginatum	Yukon, CA	MG062271		
Nicobium castaneum	Germany	KU494146		
Oligomerus obtusus	Tennesee, USA	JN097724	JN197644	JN097747
Oligomerus ptilinoides	France	KU494191		
Oligomerus brunneus	France	KM285893		
Oligomerus sericans	Tennesee, USA	JN097725	JN097643	JN097748
Priobium carpini	France	KU494210		
Priobium sericeum	Tennesee, USA		JN097683	
Stegobium paniceum 1	Laboratory culture	JN097737	JN097646	JN097752
Stegobium paniceum 2	Laboratory culture		JN097668	JN097769
Trichodesma klagesi	Tennesee, USA	JN097720	JN097677	
Trichodesma sp	Bolivia	JN097705	JN097652	JN097756
Dorcatominae				
Byrrhodes sp	Bolivia	JN097719	JN097695	
Byrrhodes intermedius		*Current study*	*Current study*	
Caenocara scymnoides	Yukon, CA	MG062126		

Caenocara sp	Bolivia	JN097718	JN097650	
Caenocara sp 1	Ontario, CA	MG058671		
Caenocara sp 2	Ontario, CA	MG061158		
Caenocara oculatum	Ontario, CA	MG061776		
Calymmaderus nitidus	Tennessee, USA	JN097739	JN097645	JN097744
Calymmaderus sp	Texas, USA		JN097669	
Cryptoramorphus sp 1		*Current study*		
Cryptoramorphus sp 2		*Current study*		
Dorcatoma chrysomelina	Germany	KM452163		
Dorcatoma dresdensis	Germany	KM450153		
Dorcatoma flavicornis		HQ164974		
Dorcatoma minor	Germany	KM447525		
Dorcatoma pallicornis	Prince Edward Island, CA	KR128050		
Dorcatoma punctulata	Germany	KM442894		
Dorcatoma robusta	Germany	KM452348		
Dorcatoma setulosa	Tennessee, USA	*Current study*	JN097694	JN097776
Dorcatoma substriata	Germany	KM443200		
Methemus cf *javanus*		EF213937		
Petalium bistriatum	Tennessee, USA	JN097726	JN097655	JN097751
Petalium incisum	Ontario, CA	MG054493		
Petalium seriatum 1	Tennessee, USA	JN097727	JN097672	
Petalium seriatum 4	Tennessee, USA	JN097729	JN097654	JN097750
Petalium seriatum 6	Tennessee, USA	JN097728	JN097653	JN097749
Petalium sp	Bolivia		JN097676	
Protheca sp	Bolivia	JN097738	JN097691	
Sculptotheca puberula	Ontario, CA	MG054316		
Stagetus borealis	Finland	KJ962117		
Stagetus sp	Nova Scotia, CA	KR490600		
Striatheca cf	South Africa	*Current study*	*Current study*	
Striatheca sp	Bolivia	JN097731		
Dryophilinae				
Dryophilus anobioides	Germany	KM451570		
Dryophilus pusillus	Germany	KM448413		
Grynobius planus		KM286036	*Current study*	
Grynobius sp		*Current study*		
Homophthalmus rugicollis	Germany	KM446864		
Ptilineurus cf		*Current study*	*Current study*	
Ernobiinae				

Episernus granulatus		KM451410	JN121118	
Episernus trapizoideus	New Mexico?	*Current study*		
Ernobius abietinus	Germany	KM452233		
Ernobius abietis	Germany	KM441562		
Ernobius angusticollis	Germany	KM441156		
Ernobius explanatus	Finland	KJ967342		
Ernobius mollis		*Current study*	*Current study*	
Ernobius pini	Germany	KM451756		
Ernobius punctulatus	British Columbia, CA	MG054129		
Hyperisus sp (=*Xestobium*?)		*Current study*	*Current study*	
Ochina latrelli	France	KM286326		
Ochina ptinoides	France	KM286161		
Utobium elegans	California, USA	*Current study*	*Current study*	
Xestobium affine	British Columbia, CA	MG058143		
Xestobium declive	France	KM286164		
Xestobium marginicolle	British Columbia, CA	KM842291		
Xestobium plumbeum	France	KM286116		
Xestobium rufovillosum	France	KM286197		
Xestobium sp		*Current study*		
Eucradinae				
Hedobia pubescens	France	KM285833		
Ptinomorphus imperialis	France	KM285895		
Ptinomorphus regalis	France	KM286002		
Mesocoelopodinae				
Mesocoelopus cf		EF213955		
Mesocoelopus niger	Germany	KM452504		
Tricorynus dichrous	Tennesee, USA		JN097684	
Tricorynus punctatus	Tennesee, USA		JN097687	
Tricorynus similis	Tennesee, USA	JN097733	JN097755	JN097755
Tricorynus sp	Tennesee, USA		JN097686	
Tricorynus sp	Texas, USA	JN097736	JN097685	
Ptilininae				
Ptilinus basalis	British Columbia, CA	KM850880		
Ptilinus pectinicornis 1		*Current study*	*Current study*	
Ptilinus pectinicornis 2		*Current study*		
Ptilinus fuscus	France	KM285986		EF213870
Ptilinus ruficornis	Tennessee, USA	*Current study*	*Current study*	
Ptilinus sp	Ontario, CA	MG061663		
Xyletininae				
Euvrilletta peltata	Tennessee, USA	JN097732	JN097746	JN097648

Lasioderma bubalus			*Current study*	
Lasioderma kiesenwetteri	Slovenia	KM442426		
Lasioderma redtenbacheri	Germany	KM440778		
Lasioderma serricorne	Laboratory culture	JN097730	JN097656	JN097754
Megorama simplex	Tennessee, USA		JN097693	
Paraxyletinus sp		*Current study*	*Current study*	
Xyletinus ater	Germany	KM447403		
Xyletinus confusus	Alberta, CA	KM847860		
Xyletinus longitarsis	Germany	KM451626		
Xyletinus planicollis	Finland	KJ963076		
Dermestidae				
Anthrenocerus sp a	Australia	HQ419106		
Anthrenus scrophulariae		EF213950		
Anthrenus sp	Kentucky, USA	JN097704	JN097657	JN097742
Anthrenus verbasci	Australia	HQ419076		
Attagenus pello	Germany	KM452310		
Attagenus unicolor		KJ001639		
Dermestes ater		KP331472		
Dermestes laniarius		EF213947		
Dermestes lardarius		AY165734		
Dermestes maculatus		KJ001640		
Dermestes sp	Kentucky, USA		JN097697	
Dermestes tessellatocollis		KJ001641		
Megatoma sp	Tennesee, USA		JN097692	
Reesa vespulae	South Korea	KJ909793		
Trinodes rufescens		EF213946		
Trogoderma anthrenoides		KP331485		
Trogoderma glabrum		FJ589737		
Trogoderma granarium	Australia	HQ419105		
Trogoderma variabile	Australia	HQ419111		
Bostrichidae				
Unplaced				
Bostrichidae sp 1	Ontario, CA	KM845859		
Bostrichidae sp 2	Ontario, CA	KJ092549		
Bostrichidae sp	Tennesee, USA	JN097740	JN097641	JN097767
Dicraeopsis bacillus		EF213936	EF213906	EF213836
Bostrichinae				
Apatides fortis			KP419358	
Bostrichus capucinus		*Current study*	EF213916	
Bostrychopsis parallela		HM002623		
Heterobostrychus aequalis		HM002620		
Heterobostrychus brunneus		HM002625		

Heterobostrychus hamatipennis		HM002631		
Scobicia chevrieri	Slovenia	KM440069		
Scobicia pustulata		KM286368	*Current study*	
Sinoxylon anale		HM002618		
Sinoxylon conigerum		HM002628	LC072658	
Sinoxylon ruficorne		HM002624	DQ202653	
Sinoxylon senegalenese		HM002622		
Xylobiops basilaris	Ontario, CA	MG058307	MG058307	DQ202589
Xylopertha pacusta		*Current study*	*Current study*	
Xyloprista hexacantha			FJ000411	
Xylothrips flavipes		HM002630	HM002630	
Xylotillus sp	Australia	KF801915	KF802081	
Dinoderinae				KF801752
Dinoderus sp		EF213938	EF213911	
Prostephanus sp		*Current study*		
Prostephanus sp	Tennesee, USA	JN097722	JN097667	EF213842
Prostephanus truncatus	Tennesee, USA	JN097721	JN097699	
Rhyzopertha dominica		KY440163	KP419625	JN097768
Rhyzopertha sp	Bolivia	JN097741	JN097642	
Stephanopachys linearis	Finland	KJ964646		HG810040
Stephanopachys substriatus	Finland	KJ963477		JN097766
Stephanopachys rugosus		KJ909900		
Endecatomidae				
Endecatomus rugosus		*Current study*	*Current study*	
Euderiinae				
Euderia squamosa			KP419455	
Lyctinae				
Lyctodon sp	Australia	KF801958	KF802122	
Lyctoxylon dentatum		JX424279		
Lyctus africanus	Japan	LC072651	LC072657	KF801794
Lyctus brunneus	Japan	LC072650	LC072656	
Lyctus cavicollis	Germany	KM439664		
Lyctus sp	South Africa	*Current study*	*Current study*	
Minthea rugicollis		KM652634		
Tristaria sp	Australia	KF801929	KF802095	
Trogoxylon sp	Australia	KF801957	KF802121	
Polycaoninae				KF801793
Polycaon sp		DQ222009		

Appendix B

List of studies from which Genbank sequences were obtained.

Accession code	Study
AY	Yang et al. 2016
DQ	Hunt, Papadopoulou and Vogler; Unpublished
EF	Hunt et al. 2007
FJ	Ma; Unpublished
HG	Hsieh, Huang, Wang, and Wu; Unpublished
HM	Wang and Yu; Unpublished
HQ	Barton and Vogler; Unpublished
JN	Bell and Philips 2012
JX	An, Chang, Hao, Liu, Qian, and Yang; Unpublished
KF	Crampton-Platt, Timmermans, Gimmel, Kutty, Cockerill, Chey and Vogler; Unpublished
KJ	Pentinsaari et al. 2014
KM	Hendrich et al. 2015
KP	Li, Zheng, Zhan, Gao, and Fan; Unpublished
KR	Hebert et al. 2016
KU	Fohrer and Meusnier; Unpublished
KX	Hunter, Moriniere, Tang, Linard, Crampton-Platt, and Vogler; Unpublished
KY	Chandel, Dwivedi, Srivastava, Khurana, and Subramanian; Unpublished
LC	Ide et al. 2016
MG	Dewaard; Unpublished

Appendix C

List of currently known spider beetle genera not included in this study.

Africogenius
Bellesus= *Arachnomimus*
Carinomezium
Cayoptinus
Chilenogenius
Costatomezium
Cryptopeniculus
Cylindroptinus
Cyphoniptus
Diegous
Dignomorphus
Ectrephes
Enasiba
Epauloecus
Eurostodes
Eurostoptinus
Eutaphrimorphus
Eutaphroptinus
Hanumanus
Hiekeptinus
Lapidoniptus
Luzonoptinus
Maheoptinus
Mezioniptus
Myrmecoptinus
Niptodes
Piarus
Prosternoptinus
Pseudeurostus
Silisoptinus
Stereocaulophilus
Sulcatogibbium
Sulcoptinus
Trigonogenioptinus
Trigonogenius
Tropicoptinus
Trymolophus

Appendix D

Log file for the Bayesian analysis of the 3 gene dataset

```
MrBayes >
  Defining charset called '16S'
  Expecting  command

MrBayes >
  Defining charset called '28S'
  Expecting  command

MrBayes >
  Defining charset called 'CO1'
  Expecting  command

MrBayes >
  Defining partition called 'favored'
  Expecting  command

MrBayes >
  Setting favored as the partition, dividing characters into 3 parts.
  Setting model defaults
  Seed (for generating default start values) = 118943888
  Expecting  command

MrBayes >
  Setting Nst to 6 for partition 3
  Setting Rates to Gamma for partition 3
  Successfully set likelihood model parameters to
  partition 3 (if applicable)

MrBayes >
  Setting Nst to 2 for partition 2
  Setting Rates to Invgamma for partition 2
  Successfully set likelihood model parameters to
  partition 2 (if applicable)

MrBayes >
  Setting Nst to 6 for partition 1
  Setting Rates to Gamma for partition 1
  Successfully set likelihood model parameters to
  partition 1 (if applicable)

Setting number of generations to 100000
  Running Markov chain
  MCMC stamp = 2577801277
```

```
Seed = 730034476
Swapseed = 1550179765
Model settings:

   Settings for partition 1 --
      Datatype  = DNA
      Nucmodel  = 4by4
      Nst       = 6
                  Substitution rates, expressed as proportions
                  of the rate sum, have a Dirichlet prior
                  (1.00,1.00,1.00,1.00,1.00,1.00)
      Covarion  = No
      # States  = 4
                  State frequencies have a Dirichlet prior
                  (1.00,1.00,1.00,1.00)
      Rates     = Gamma
                  The distribution is approximated using 4 categories.
                  Likelihood summarized over all rate categories in each generation.
                  Shape parameter is exponentially
                  distributed with parameter (1.00).

   Settings for partition 2 --
      Datatype  = DNA
      Nucmodel  = 4by4
      Nst       = 2
                  Transition and transversion  rates, expressed
                  as proportions of the rate sum, have a
                  Beta(1.00,1.00) prior
      Covarion  = No
      # States  = 4
                  State frequencies have a Dirichlet prior
                  (1.00,1.00,1.00,1.00)
      Rates     = Invgamma
                  The distribution is approximated using 4 categories.
                  Likelihood summarized over all rate categories in each generation.
                  Shape parameter is exponentially
                  distributed with parameter (1.00).
                  Proportion of invariable sites is uniformly dist-
                  ributed on the interval (0.00,1.00).

   Settings for partition 3 --
      Datatype  = DNA
      Nucmodel  = 4by4
      Nst       = 6
                  Substitution rates, expressed as proportions
                  of the rate sum, have a Dirichlet prior
```

```
            (1.00,1.00,1.00,1.00,1.00,1.00)
   Covarion  = No
   # States  = 4
            State frequencies have a Dirichlet prior
            (1.00,1.00,1.00,1.00)
   Rates    = Gamma
            The distribution is approximated using 4 categories.
            Likelihood summarized over all rate categories in each generation.
            Shape parameter is exponentially
            distributed with parameter (1.00).

Active parameters:

                  Partition(s)
  Parameters        1  2  3
  ---------------------------
  Tratio            .  1  .
  Revmat            2  .  2
  Statefreq         3  3  3
  Shape             4  4  4
  Pinvar            .  5  .
  Ratemultiplier    6  6  6
  Topology          7  7  7
  Brlens            8  8  8
  ---------------------------

  Parameters can be linked or unlinked across partitions using 'link' and 'unlink'

  1 --  Parameter  = Tratio{2}
      Type       = Transition and transversion rates
      Prior      = Beta(1.00,1.00)
      Partition  = 2

  2 --  Parameter  = Revmat{1,3}
      Type       = Rates of reversible rate matrix
      Prior      = Dirichlet(1.00,1.00,1.00,1.00,1.00,1.00)
      Partitions = 1 and 3

  3 --  Parameter  = Pi{all}
      Type       = Stationary state frequencies
      Prior      = Dirichlet
      Partitions = All

  4 --  Parameter  = Alpha{all}
      Type       = Shape of scaled gamma distribution of site rates
      Prior      = Exponential(1.00)
```

```
         Partitions = All

   5 --  Parameter  = Pinvar{2}
         Type       = Proportion of invariable sites
         Prior      = Uniform(0.00,1.00)
         Partition  = 2

   6 --  Parameter  = Ratemultiplier{all}
         Type       = Partition-specific rate multiplier
         Prior      = Fixed(1.0)
         Partitions = All

   7 --  Parameter  = Tau{all}
         Type       = Topology
         Prior      = All topologies equally probable a priori
         Partitions = All
         Subparam.  = V{all}

   8 --  Parameter  = V{all}
         Type       = Branch lengths
         Prior      = Unconstrained:GammaDir(1.0,0.1000,1.0,1.0)
         Partitions = All



The MCMC sampler will use the following moves:
   With prob.  Chain will use move
      1.82 %   Dirichlet(Tratio{2})
      0.91 %   Dirichlet(Revmat{1,3})
      0.91 %   Slider(Revmat{1,3})
      0.91 %   Dirichlet(Pi{all})
      0.91 %   Slider(Pi{all})
      1.82 %   Multiplier(Alpha{all})
      1.82 %   Slider(Pinvar{2})
      9.09 %   ExtSPR(Tau{all},V{all})
      9.09 %   ExtTBR(Tau{all},V{all})
      9.09 %   NNI(Tau{all},V{all})
      9.09 %   ParsSPR(Tau{all},V{all})
     36.36 %   Multiplier(V{all})
     12.73 %   Nodeslider(V{all})
      5.45 %   TLMultiplier(V{all})

Division 1 has 844 unique site patterns
Division 2 has 615 unique site patterns
Division 3 has 607 unique site patterns
Initializing conditional likelihoods
```

```
  Using standard SSE likelihood calculator for division 1 (single-precision)
  Using standard SSE likelihood calculator for division 2 (single-precision)
  Using standard SSE likelihood calculator for division 3 (single-precision)
  Initializing invariable-site conditional likelihoods

  Initial log likelihoods and log prior probs for run 1:
    Chain 1 -- -57236.709262 -- 90.094022
    Chain 2 -- -58737.696397 -- 90.094022
    Chain 3 -- -59382.554150 -- 90.094022
    Chain 4 -- -59336.670095 -- 90.094022

  Initial log likelihoods and log prior probs for run 2:
    Chain 1 -- -58856.899639 -- 90.094022
    Chain 2 -- -57166.455499 -- 90.094022
    Chain 3 -- -58429.323817 -- 90.094022
    Chain 4 -- -59162.405895 -- 90.094022


  Using a relative burnin of 25.0 % for diagnostics
```

NOTE: Chain results removed for space

```
Average standard deviation of split frequencies: 0.003916

  Continue with analysis? (yes/no):    Enter yes or no:
  Analysis completed in 15 hours 18 mins 6 seconds
  Analysis used 55085.99 seconds of CPU time
  Likelihood of best state for "cold" chain of run 1 was -36706.96
  Likelihood of best state for "cold" chain of run 2 was -36707.81

  Acceptance rates for the moves in the "cold" chain of run 1:
    With prob.   (last 100)   chain accepted proposals by move
       25.2 %     ( 20 %)     Dirichlet(Tratio{2})
       20.1 %     ( 30 %)     Dirichlet(Revmat{1,3})
       26.5 %     ( 28 %)     Slider(Revmat{1,3})
       12.6 %     ( 20 %)     Dirichlet(Pi{all})
       22.6 %     ( 31 %)     Slider(Pi{all})
       24.5 %     ( 27 %)     Multiplier(Alpha{all})
       25.0 %     ( 25 %)     Slider(Pinvar{2})
        4.7 %     (  2 %)    ExtSPR(Tau{all},V{all})
        4.1 %     (  7 %)    ExtTBR(Tau{all},V{all})
        7.0 %     (  6 %)    NNI(Tau{all},V{all})
        1.6 %     (  1 %)    ParsSPR(Tau{all},V{all})
       25.7 %     ( 21 %)     Multiplier(V{all})
       18.3 %     ( 20 %)     Nodeslider(V{all})
       24.4 %     ( 30 %)     TLMultiplier(V{all})
```

```
Acceptance rates for the moves in the "cold" chain of run 2:
   With prob.   (last 100)   chain accepted proposals by move
      24.8 %     ( 23 %)     Dirichlet(Tratio{2})
      20.3 %     ( 19 %)     Dirichlet(Revmat{1,3})
      26.4 %     ( 18 %)     Slider(Revmat{1,3})
      12.3 %     ( 22 %)     Dirichlet(Pi{all})
      22.4 %     ( 23 %)     Slider(Pi{all})
      24.5 %     ( 27 %)     Multiplier(Alpha{all})
      25.0 %     ( 19 %)     Slider(Pinvar{2})
       4.7 %     (  8 %)     ExtSPR(Tau{all},V{all})
       4.1 %     (  1 %)     ExtTBR(Tau{all},V{all})
       7.0 %     (  5 %)     NNI(Tau{all},V{all})
       1.6 %     (  3 %)     ParsSPR(Tau{all},V{all})
      25.6 %     ( 23 %)     Multiplier(V{all})
      18.1 %     ( 19 %)     Nodeslider(V{all})
      24.6 %     ( 30 %)     TLMultiplier(V{all})

Chain swap information for run 1:

            1       2       3       4
     ----------------------------------
   1 |            0.65    0.38    0.21
   2 |  499563            0.67    0.42
   3 |  499768  501868            0.69
   4 |  500111  499325  499565

Chain swap information for run 2:

            1       2       3       4
     ----------------------------------
   1 |            0.65    0.39    0.21
   2 |  500983            0.67    0.42
   3 |  500135  500388            0.70
   4 |  499573  499953  499168

Upper diagonal: Proportion of successful state exchanges between chains
Lower diagonal: Number of attempted state exchanges between chains

Chain information:

  ID -- Heat
 -----------
   1 -- 1.00  (cold chain)
   2 -- 0.91
   3 -- 0.83
```

```
     4 -- 0.77

   Heat = 1 / (1 + T * (ID - 1))
     (where T = 0.10 is the temperature and ID is the chain number)

MrBayes >
   Summarizing trees in files "bost3gene.nex.txt.run1.t" and "bost3gene.nex.txt.run2.t"
   Using relative burnin ('relburnin=yes'), discarding the first 25 % of sampled trees
   Writing statistics to files bost3gene.nex.txt.<parts|tstat|vstat|trprobs|con>
   Examining first file ...
   Found one tree block in file "bost3gene.nex.txt.run1.t" with 6007 trees in last block
   Expecting the same number of trees in the last tree block of all files

   Tree reading status:

   0      10      20      30      40      50      60      70      80      90     100
   v-------v-------v-------v-------v-------v-------v-------v-------v-------v-------v
*****************************************************************************
*********

   Read a total of 12014 trees in 2 files (sampling 9012 of them)
     (Each file contained 6007 trees of which 4506 were sampled)

   General explanation:

   In an unrooted tree, a taxon bipartition (split) is specified by removing a
   branch, thereby dividing the species into those to the left and those to the
   right of the branch. Here, taxa to one side of the removed branch are denoted
   '.' and those to the other side are denoted '*'. Specifically, the '.' symbol
   is used for the taxa on the same side as the outgroup.

   In a rooted or clock tree, the tree is rooted using the model and not by
   reference to an outgroup. Each bipartition therefore corresponds to a clade,
   that is, a group that includes all the descendants of a particular branch in
   the tree.  Taxa that are included in each clade are denoted using '*', and
   taxa that are not included are denoted using the '.' symbol.

   The output first includes a key to all the bipartitions with frequency larger
   or equual to (Minpartfreq) in at least one run. Minpartfreq is a parameter to
   sumt command and currently it is set to 0.10.  This is followed by a table
   with statistics for the informative bipartitions (those including at least
   two taxa), sorted from highest to lowest probability. For each bipartition,
   the table gives the number of times the partition or split was observed in all
   runs (#obs) and the posterior probability of the bipartition (Probab.), which
   is the same as the split frequency. If several runs are summarized, this is
```

```
followed by the minimum split frequency (Min(s)), the maximum frequency
(Max(s)), and the standard deviation of frequencies (Stddev(s)) across runs.
The latter value should approach 0 for all bipartitions as MCMC runs converge.

This is followed by a table summarizing branch lengths, node heights (if a
clock model was used) and relaxed clock parameters (if a relaxed clock model
was used). The mean, variance, and 95 % credible interval are given for each
of these parameters. If several runs are summarized, the potential scale
reduction factor (PSRF) is also given; it should approach 1 as runs converge.
Node heights will take calibration points into account, if such points were
used in the analysis.

Note that Stddev may be unreliable if the partition is not present in all
runs (the last column indicates the number of runs that sampled the partition
if more than one run is summarized). The PSRF is not calculated at all if
the partition is not present in all runs.The PSRF is also sensitive to small
sample sizes and it should only be considered a rough guide to convergence
since some of the assumptions allowing one to interpret it as a true potential
scale reduction factor are violated in MrBayes.

List of taxa in bipartitions:

   1 -- Lyctodon_sp
   2 -- Tristaria_sp
   3 -- Trogoxylon_sp
   4 -- Xylotillus_sp_Australia
   5 -- Dicraeopsis_bacillus
   6 -- Dinoderus_sp
   7 -- Ptilinus_pectinicornis
   8 -- Bostrichidae_sp_TN
   9 -- Prostephanus_sp_TN
  10 -- Sinoxylon_ruficorne
  11 -- Dorcatoma_setulosa
  12 -- Gibbium_psylloides
  13 -- Diplocotes_foveatus
  14 -- Ptinus_bimaculatus
  15 -- Mezium_affine
  16 -- Mezium_glabrum
  17 -- Ptinus_tectus
  18 -- Gnostus_floridanus
  19 -- Gibbium_aequinoctiale
  20 -- Anthrenus_sp_KY
  21 -- Stegobium_paniceum
  22 -- Anobiopsis_sp
  23 -- Lasioderma_serricorne
  24 -- Oligomerus_obtusus
```

```
   25 -- Oligomerus_sericans
   26 -- Calymmaderus_nitidus
   27 -- Petalium_seriatum
   28 -- Petalium_bistriatum
   29 -- Hemicoelus_sp_Bolivia
   30 -- Ptinus_interruptus
   31 -- Trichodesma_sp_Bolivia
   32 -- Tricorynus_similis
   33 -- Rhyzopertha_sp_Bolivia
   34 -- Rhyzopertha_dominica

Summary statistics for informative taxon bipartitions
   (saved to file "bost3gene.nex.txt.tstat"):

  ID   #obs    Probab.     Sd(s)+      Min(s)      Max(s)   Nruns
  ----------------------------------------------------------------
  35   9012    1.000000    0.000000    1.000000    1.000000    2
  36   9012    1.000000    0.000000    1.000000    1.000000    2
  37   9012    1.000000    0.000000    1.000000    1.000000    2
  38   9012    1.000000    0.000000    1.000000    1.000000    2
  39   9012    1.000000    0.000000    1.000000    1.000000    2
  40   9012    1.000000    0.000000    1.000000    1.000000    2
  41   9012    1.000000    0.000000    1.000000    1.000000    2
  42   9012    1.000000    0.000000    1.000000    1.000000    2
  43   9012    1.000000    0.000000    1.000000    1.000000    2
  44   9012    1.000000    0.000000    1.000000    1.000000    2
  45   9012    1.000000    0.000000    1.000000    1.000000    2
  46   9012    1.000000    0.000000    1.000000    1.000000    2
  47   9012    1.000000    0.000000    1.000000    1.000000    2
  48   9011    0.999889    0.000157    0.999778    1.000000    2
  49   9011    0.999889    0.000157    0.999778    1.000000    2
  50   9010    0.999778    0.000000    0.999778    0.999778    2
  51   9010    0.999778    0.000314    0.999556    1.000000    2
  52   9009    0.999667    0.000157    0.999556    0.999778    2
  53   9006    0.999334    0.000000    0.999334    0.999334    2
  54   8954    0.993564    0.000314    0.993342    0.993786    2
  55   8950    0.993120    0.001569    0.992011    0.994230    2
  56   8576    0.951620    0.007846    0.946072    0.957168    2
  57   8434    0.935863    0.005649    0.931869    0.939858    2
  58   8337    0.925100    0.008317    0.919219    0.930981    2
  59   7577    0.840768    0.007689    0.835331    0.846205    2
  60   6573    0.729361    0.005492    0.725477    0.733245    2
  61   6191    0.686973    0.012397    0.678207    0.695739    2
  62   5522    0.612739    0.000942    0.612073    0.613404    2
  63   5405    0.599756    0.026834    0.580781    0.618731    2
  64   4838    0.536840    0.000942    0.536174    0.537506    2
```

```
65  3651    0.405126    0.006434    0.400577    0.409676    2
66  3363    0.373169    0.023696    0.356414    0.389925    2
67  3087    0.342543    0.007689    0.337106    0.347980    2
68  3021    0.335220    0.002040    0.333777    0.336662    2
69  2798    0.310475    0.013809    0.300710    0.320240    2
70  2434    0.270084    0.005649    0.266090    0.274079    2
71  1898    0.210608    0.007532    0.205282    0.215934    2
72  1548    0.171771    0.000942    0.171105    0.172437    2
73  1429    0.158566    0.008003    0.152907    0.164225    2
74  1184    0.131380    0.002511    0.129605    0.133156    2
------------------------------------------------------------
+ Convergence diagnostic (standard deviation of split frequencies)
  should approach 0.0 as runs converge.


Summary statistics for branch and node parameters
   (saved to file "bost3gene.nex.txt.vstat"):

                                          95% HPD Interval
                                        --------------------
Parameter          Mean       Variance     Lower       Upper       Median     PSRF+  Nruns
-----------------------------------------------------------------------------------------
length{all}[1]     0.046561    0.000038    0.034947    0.058928    0.046280    1.000    2
length{all}[2]     0.045052    0.000029    0.034673    0.055308    0.044888    1.000    2
length{all}[3]     0.056637    0.000034    0.045266    0.067980    0.056415    1.000    2
length{all}[4]     0.145942    0.000206    0.117807    0.174126    0.145922    1.001    2
length{all}[5]     0.115903    0.000222    0.085499    0.143941    0.115970    1.000    2
length{all}[6]     0.080376    0.000276    0.049494    0.114126    0.079652    1.000    2
length{all}[7]     0.340361    0.000844    0.285314    0.399153    0.339226    1.000    2
length{all}[8]     0.122132    0.000145    0.098935    0.145540    0.121892    1.000    2
length{all}[9]     0.213951    0.000310    0.178505    0.247561    0.213224    1.001    2
length{all}[10]    0.143182    0.000327    0.107880    0.177679    0.142792    1.000    2
length{all}[11]    0.172114    0.000276    0.141418    0.206364    0.171402    1.000    2
length{all}[12]    0.022815    0.000093    0.004461    0.041269    0.021918    1.000    2
length{all}[13]    0.133630    0.000146    0.109690    0.156256    0.133117    1.001    2
length{all}[14]    0.116126    0.000125    0.094738    0.138820    0.115720    1.000    2
length{all}[15]    0.086699    0.000109    0.066506    0.107093    0.086359    1.000    2
length{all}[16]    0.077958    0.000123    0.057546    0.100355    0.077377    1.000    2
length{all}[17]    0.073026    0.000081    0.056605    0.091613    0.072606    1.000    2
length{all}[18]    0.156721    0.000170    0.131222    0.181841    0.156555    1.000    2
length{all}[19]    0.027683    0.000101    0.009139    0.047693    0.027152    1.000    2
length{all}[20]    0.249225    0.000354    0.212862    0.285584    0.248837    1.000    2
length{all}[21]    0.167729    0.000207    0.140332    0.197078    0.167216    1.000    2
length{all}[22]    0.134990    0.000181    0.108151    0.160838    0.134607    1.000    2
length{all}[23]    0.165322    0.000185    0.138693    0.192202    0.164820    1.000    2
length{all}[24]    0.129112    0.000137    0.106485    0.152440    0.128842    1.000    2
```

length{all}[25]	0.083754	0.000094	0.065042	0.102466	0.083455	1.000	2
length{all}[26]	0.156381	0.000176	0.131051	0.182715	0.156202	1.000	2
length{all}[27]	0.044412	0.000043	0.031913	0.057188	0.044091	1.000	2
length{all}[28]	0.041917	0.000042	0.029550	0.054785	0.041633	1.000	2
length{all}[29]	0.136832	0.000159	0.112463	0.161716	0.136657	1.001	2
length{all}[30]	0.197642	0.000256	0.167399	0.229481	0.197004	1.000	2
length{all}[31]	0.182190	0.000225	0.153668	0.211795	0.181756	1.000	2
length{all}[32]	0.164262	0.000206	0.137469	0.192898	0.163627	1.000	2
length{all}[33]	0.114587	0.000144	0.093143	0.139904	0.114181	1.000	2
length{all}[34]	0.325707	0.001255	0.254211	0.391901	0.324207	1.000	2
length{all}[35]	0.269111	0.000589	0.221812	0.315609	0.268402	1.000	2
length{all}[36]	0.121255	0.000330	0.085457	0.156178	0.120842	1.000	2
length{all}[37]	0.034724	0.000060	0.020543	0.050636	0.034438	1.000	2
length{all}[38]	0.104055	0.000281	0.072552	0.137329	0.103522	1.000	2
length{all}[39]	0.056932	0.000137	0.035043	0.080422	0.056489	1.000	2
length{all}[40]	0.094530	0.000210	0.067507	0.123710	0.094437	1.000	2
length{all}[41]	0.045724	0.000140	0.022946	0.068527	0.044812	1.000	2
length{all}[42]	0.047426	0.000101	0.027676	0.067008	0.046899	1.000	2
length{all}[43]	0.066070	0.000105	0.046639	0.086581	0.065665	1.000	2
length{all}[44]	0.405941	0.000941	0.348115	0.466662	0.405299	1.000	2
length{all}[45]	0.026813	0.000028	0.016386	0.037088	0.026608	1.000	2
length{all}[46]	0.445316	0.001462	0.371457	0.520351	0.443905	1.000	2
length{all}[47]	0.071975	0.000085	0.054173	0.089969	0.071742	1.000	2
length{all}[48]	0.037979	0.000057	0.023575	0.052659	0.037621	1.000	2
length{all}[49]	0.026704	0.000058	0.012576	0.041615	0.026392	1.000	2
length{all}[50]	0.045176	0.000168	0.020389	0.070643	0.044444	1.000	2
length{all}[51]	0.037611	0.000095	0.020358	0.058298	0.037052	1.000	2
length{all}[52]	0.018543	0.000038	0.007270	0.030993	0.018094	1.000	2
length{all}[53]	0.019894	0.000039	0.008540	0.032744	0.019525	1.000	2
length{all}[54]	0.030316	0.000094	0.012142	0.049661	0.029864	1.000	2
length{all}[55]	0.030294	0.000065	0.014797	0.046028	0.029803	1.000	2
length{all}[56]	0.029278	0.000072	0.012656	0.045859	0.028804	1.000	2
length{all}[57]	0.014700	0.000036	0.003680	0.026617	0.014183	1.000	2
length{all}[58]	0.018780	0.000038	0.006946	0.030854	0.018354	1.000	2
length{all}[59]	0.015508	0.000033	0.005266	0.027077	0.015089	1.000	2
length{all}[60]	0.021713	0.000055	0.006874	0.035497	0.021404	1.000	2
length{all}[61]	0.027640	0.000197	0.001183	0.053394	0.026659	1.001	2
length{all}[62]	0.017122	0.000053	0.003102	0.031278	0.016646	1.001	2
length{all}[63]	0.013633	0.000040	0.001517	0.025431	0.013070	1.000	2
length{all}[64]	0.011965	0.000034	0.001124	0.022915	0.011594	1.000	2
length{all}[65]	0.009891	0.000024	0.001047	0.019175	0.009455	1.000	2
length{all}[66]	0.016545	0.000063	0.001736	0.031462	0.015928	1.000	2
length{all}[67]	0.014568	0.000089	0.000022	0.031577	0.013170	1.000	2
length{all}[68]	0.013090	0.000036	0.001648	0.024347	0.012637	1.000	2
length{all}[69]	0.016639	0.000137	0.000006	0.038314	0.014529	1.000	2
length{all}[70]	0.022733	0.000063	0.008270	0.039129	0.022310	1.000	2

```
length{all}[71]   0.016416   0.000060   0.003001   0.032390   0.015730   1.001   2
length{all}[72]   0.007313   0.000044   0.000003   0.021041   0.005515   0.999   2
length{all}[73]   0.020135   0.000047   0.006942   0.033115   0.019558   1.001   2
length{all}[74]   0.009526   0.000055   0.000004   0.023919   0.007853   1.000   2
------------------------------------------------------------------------------------------
+ Convergence diagnostic (PSRF = Potential Scale Reduction Factor; Gelman
  and Rubin, 1992) should approach 1.0 as runs converge. NA is reported when
  deviation of parameter values within all runs is 0 or when a parameter
  value (a branch length, for instance) is not sampled in all runs.


Summary statistics for partitions with frequency >= 0.10 in at least one run:
    Average standard deviation of split frequencies = 0.003927
    Maximum standard deviation of split frequencies = 0.026834
    Average PSRF for parameter values (excluding NA and >10.0) = 1.000
    Maximum PSRF for parameter values = 1.001


Clade credibility values:

Subtree rooted at node 59:

                          /---------------- Ptilinus_pectin~ (7)
                          |
                          |          /----- Bostrichidae_sp~ (8)
          /------100------+    /--99-+
          |               |    |     \----- Rhyzopertha_sp~ (33)
          |               \-100+
          |                    \----------- Prostephanus_sp~ (9)
          |
          |                          /----- Dorcatoma_setu~ (11)
          |     /---------100--------+
     /-95-+     |                    \----- Anobiopsis_sp (22)
     |    |     |
     |    |     |              /----------- Stegobium_pani~ (21)
     |    |     |              |
     |    |     |         /-100+     /----- Hemicoelus_sp_~ (29)
     |    |     |         |    \--60-+
     |    \-100-+         |          \----- Trichodesma_sp~ (31)
     |          |    /-93-+
     |          |    |    |    /----------- Lasioderma_ser~ (23)
     |          |    |    |    |
     |          |    |    \-100+     /----- Petalium_seria~ (27)
/-100+          |    |         \-100-+
|    |          |    |               \----- Petalium_bistr~ (28)
|    |          \-99-+
```

```
             |  |           |           /----- Oligomerus_obt~ (24)
             |  |           |      /-100-+
             |  |           |      |    \----- Oligomerus_ser~ (25)
             |  |           |  /-61-+
        /-73-+  |              |   |   \----------- Calymmaderus_n~ (26)
        |   |   |           \-94-+
        |   |   |              \---------------- Tricorynus_sim~ (32)
        |   |   |
        |   |   \------------------------------------ Anthrenus_sp_KY (20)
        |   |
        |   \---------------------------------------- Ptinus_interru~ (30)
        |
    /-100-+                                  /----- Diplocotes_fov~ (13)
    |   |                          /-100-+
    |   |                          |    \----- Ptinus_tectus (17)
    |   |                      /-54-+
    |   |                      |   \----------- Ptinus_bimacul~ (14)
    |   |                   /-100+
--100+    |                    |   |       /----- Mezium_affine (15)
    |   |                   |   \----100---+
    |   \------------84-----------+            \----- Mezium_glabrum (16)
    |                       |
    |                       \--------------------- Gnostus_florid~ (18)
    |
    \---------------------------------------------------- Gibbium_aequin~ (19)
```

Root part of tree:

```
/-------------------------------------------------------- Lyctodon_sp (1)
|
|                                  /------------ Tristaria_sp (2)
|--------------------100---------------------+
|                                  \------------ Trogoxylon_sp (3)
|
+         /------------------------------------------- Xylotillus_sp_A~ (4)
|         |
|         |                /---------------------- Dicraeopsis_bac~ (5)
|         |                |
|         |                |       /------------ Dinoderus_sp (6)
\----100----+                   |----100---+
          |       /-----69----+        \------------ Rhyzopertha_do~ (34)
          |       |        |
          |       |        |       /------------ (59)
          \----100---+          \----100---+
                  |                 \------------ Gibbium_psyllo~ (12)
                  |
```

```
                        \---------------------------------- Sinoxylon_rufi~ (10)

   Phylogram (based on average branch lengths):


/-- Lyctodon_sp (1)
   |
   |/-- Tristaria_sp (2)
   |+
   |\-- Trogoxylon_sp (3)
   |
   | /------ Xylotillus_sp_A~ (4)
   | |
   | |          /----- Dicraeopsis_bac~ (5)
   | |          |
   | |          |                /--- Dinoderus_sp (6)
   | |          |-----------------+
   | |          |                \------------- Rhyzopertha_do~ (34)
   | |          |
   + |           |                            /-------------- Ptilinus_pectin~ (7)
   | |          |                           |
   | |          |                           |     /----- Bostrichidae_sp~ (8)
   | |          |                          /+    /+
   | |          |                          ||    |\---- Rhyzopertha_sp~ (33)
   | |          |                          |\----+
   | |          |                          |     \-------- Prostephanus_sp~ (9)
   | |          |                          |
   | |          |                          |  /------- Dorcatoma_setu~ (11)
   | |          |                          | /+
   | |          |                         /+ |\----- Anobiopsis_sp (22)
   | |          |                         || |
   | |          |                         || | /------- Stegobium_pani~ (21)
   | |          |                         || | |
   \-+           |                          || |/+/----- Hemicoelus_sp_~ (29)
     |          |                         || ||\+
     |          |                         |\-+| \------- Trichodesma_sp~ (31)
     |          |                         |  ||
     |          |                         |  || /------ Lasioderma_ser~ (23)
     |          |                         |  || |
     |         /+                          |  ||-+  /- Petalium_seria~ (27)
     |         ||                        /-+  || \--+
     |         ||                        | |  ||    \- Petalium_bistr~ (28)
     |         ||                        | |  \+
     |         ||                        | |   |  /----- Oligomerus_obt~ (24)
     |         ||                        | |   |/--+
```

```
   |         ||                    | |   ||  \--- Oligomerus_ser~ (25)
   |         ||                    | |   |+
   |         ||                   /+ |   |\------ Calymmaderus_n~ (26)
   |         ||                   || |   |
   |         ||                   || |   \------- Tricorynus_sim~ (32)
   |         ||                   || |
   |         ||                   || \--------- Anthrenus_sp_KY (20)
   |         ||                   ||
   |         ||                   |\-------- Ptinus_interru~ (30)
   |         ||                   |
   \----------+|                   /---+  /----- Diplocotes_fov~ (13)
             ||                |   | /+
             ||                |   | |\--- Ptinus_tectus (17)
             ||                |   |/+
             ||                |   ||\---- Ptinus_bimacul~ (14)
             ||                |   |+
             ||   /------------+   ||/---- Mezium_affine (15)
             ||   |            |   |\+
             ||   |            |   | \--- Mezium_glabrum (16)
             ||   |            |   |
             |\----+            |   \------- Gnostus_florid~ (18)
             |    |            |
             |    |            \- Gibbium_aequin~ (19)
             |    |
             |    \- Gibbium_psyllo~ (12)
             |
             \------ Sinoxylon_rufi~ (10)

   |------------------| 0.500 expected changes per site

   Calculating tree probabilities...

   Credible sets of trees (1332 trees sampled):
      50 % credible set contains 53 trees
      90 % credible set contains 540 trees
      95 % credible set contains 882 trees
      99 % credible set contains 1242 trees


MrBayes >
   Summarizing parameters in files bost3gene.nex.txt.run1.p and bost3gene.nex.txt.run2.p
   Writing summary statistics to file bost3gene.nex.txt.pstat
   Using relative burnin ('relburnin=yes'), discarding the first 25 % of samples

   Below are rough plots of the generation (x-axis) versus the log
   probability of observing the data (y-axis). You can use these
```

```
graphs to determine what the burn in for your analysis should be.
When the log probability starts to plateau you may be at station-
arity. Sample trees and parameters after the log probability
plateaus. Of course, this is not a guarantee that you are at sta-
tionarity. Also examine the convergence diagnostics provided by
the 'sump' and 'sumt' commands for all the parameters in your
model. Remember that the burn in is the number of samples to dis-
card. There are a total of ngen / samplefreq samples taken during
a MCMC analysis.

Overlay plot for both runs:
(1 = Run number 1; 2 = Run number 2; * = Both runs)

+--------------------------------------------------------+ -36726.33
|   *                                           |
|                                              |
|1                    1                           |
|  1   2  2          2  1                           |
|2         2      2   1      1  1  * 1     1          2  1 |
|       1   2    11 1             1     2 1             |
| 2       1   1         2 2     2      *     2    1 1       1|
| 1        21   1     121  12  1  2       2   2    *21   2   |
|      22      222       12 *     1  2       1   2       11  |
|    1 1       1    *2        22        *11    **1    121    |
|  2  2 1    1                 2 2     1        2      |
|    2       2  1      2      12            2       222|
|     1    1   2              1      2           1     |
|                                              |
|                                 2        2      |
+------+-----+-----+-----+-----+-----+-----+-----+-----+-----+ -36731.25
^                                              ^
748000                                             3000200


Estimated marginal likelihoods for runs sampled in files
   "bost3gene.nex.txt.run1.p" and "bost3gene.nex.txt.run2.p":
   (Use the harmonic mean for Bayes factor comparisons of models)

   (Values are saved to the file bost3gene.nex.txt.lstat)

Run   Arithmetic mean   Harmonic mean
--------------------------------------
  1    -36717.11       -36748.17
  2    -36716.82       -36746.11
--------------------------------------
TOTAL   -36716.95       -36747.60
```

```
  ------------------------------------


  Model parameter summaries over the runs sampled in files
    "bost3gene.nex.txt.run1.p" and "bost3gene.nex.txt.run2.p":
    Summaries are based on a total of 9012 samples from 2 runs.
    Each run produced 6007 samples of which 4506 samples were included.
    Parameter summaries saved to file "bost3gene.nex.txt.pstat".

                                  95% HPD Interval
                                 --------------------
  Parameter      Mean     Variance     Lower      Upper      Median    min ESS*  avg
ESS    PSRF+
  ------------------------------------------------------------------------------------------------
   TL{all}       6.685164    0.031663    6.325343    7.022255    6.683405   3446.37
3701.49    1.000
   kappa{2}       2.271882    0.013257    2.036423    2.490640    2.269723   4185.60
4219.86    1.000
   r(A<->C){1,3}   0.069945    0.000036    0.058567    0.082049    0.069864   1962.44
2331.33    1.000
   r(A<->G){1,3}   0.256124    0.000113    0.236055    0.276845    0.256025   1679.65
1785.27    1.000
   r(A<->T){1,3}   0.218055    0.000057    0.202733    0.232023    0.217964   2064.99
2255.29    1.000
   r(C<->G){1,3}   0.052042    0.000038    0.040369    0.064395    0.051922   2580.12
2675.41    1.000
   r(C<->T){1,3}   0.345942    0.000142    0.323572    0.369978    0.345827   1646.63
1709.90    1.000
   r(G<->T){1,3}   0.057892    0.000023    0.048726    0.067267    0.057800   2168.36
2200.01    1.000
   pi(A){all}     0.284613    0.000027    0.274514    0.294870    0.284569   2190.75
2514.42    1.000
   pi(C){all}     0.177229    0.000023    0.167664    0.186431    0.177192   1832.59
1958.38    1.000
   pi(G){all}     0.189059    0.000026    0.179080    0.198962    0.189049   1972.52
2021.20    1.000
   pi(T){all}     0.349099    0.000030    0.338223    0.359506    0.349114   2387.76
2505.45    1.000
   alpha{all}     0.796580    0.000716    0.744003    0.847921    0.796099   3585.15
4022.62    1.000
   pinvar{2}      0.004139    0.000015    0.000000    0.012120    0.002985   3820.15
4069.52    1.000
  ------------------------------------------------------------------------------------------------
  * Convergence diagnostic (ESS = Estimated Sample Size); min and avg values
    correspond to minimal and average ESS among runs.
    ESS value below 100 may indicate that the parameter is undersampled.
```

+ Convergence diagnostic (PSRF = Potential Scale Reduction Factor; Gelman and Rubin, 1992) should approach 1.0 as runs converge.