Diversity and Distribution of the Desert Stink Beetles:

Systematics of the Amphidorini LeConte, 1862 (Coleoptera: Tenebrionidae)

by

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ABSTRACT

Understanding the diversity, evolutionary relationships, and geographic distribution of species is foundational knowledge in biology. However, this knowledge is lacking for many diverse lineages of the tree of life. This is the case for the desert stink beetles in the tribe Amphidorini LeConte, 1862 (Coleoptera: Tenebrionidae) – a lineage of arid-adapted flightless beetles found throughout western North America. Four interconnected studies that jointly increase our knowledge of this group are presented. First, the darkling beetle fauna of the Algodones sand dunes in southern California is examined as a case study to explore the scientific practice of checklist creation. An updated list of the species known from this region is presented, with a critical focus on material now made available through digitization and global aggregation. This part concludes with recommendations for future biodiversity checklist authors. Second, the psammophilic genus *Trogloderus* LeConte, 1879 is revised. Six new species are described, and the first, multi-gene phylogeny for the genus is inferred. In addition, historical biogeographic reconstructions along with novel hypotheses of speciation patterns within the Intermountain Region are given. In particular, the Kaibab Plateau and Kaiparowitz Formation are found to have promoted speciation on the Colorado Plateau. The Owens Valley and prehistoric Bouse Embayment are similarly hypothesized to drive species diversification in southern California. Third, a novel phylogenomic analysis for the tribe Amphidorini is presented, based on 29 *de novo* partial transcriptomes. Three putative ortholog sets were discovered and analyzed to infer the relationships between species groups and genera. The existing classification of the tribe is found to be highly inadequate, though the earliest-diverging relationships within the tribe are still in question. Finally, the new phylogenetic framework is used to provide a genus-level revision for the Amphidorini, which previously contained six valid genera and 253 valid species. This updated classification includes more than 100 taxonomic changes and results in the revised tribe consisting of 16 genera, with three being described as new to science.

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Chapter 1. Introduction

Inadequate knowledge of species diversity and distributions, respectively named the Linnean and Wallacean shortfalls, is a major hurdle across the biological sciences (Bini *et al*. 2006, Brito 2010, Hortal *et al*. 2015). With roughly 400,000 species known, beetles in the order Coleoptera represent a quarter of the global described species diversity (Slipinski *et al*. 2011). Perhaps only one half to one quarter of the existing beetle species have yet been described (Stork *et al*. 2015).

The megadiverse darkling beetles, family Tenebrionidae Latrielle, 1802, comprise some 20,000 described species and are especially diverse in arid ecosystems around the world (Matthews *et al*. 2010). Over 2,800 species of darkling beetles are known from North America (Bousquet *et al*. 2018). Amphidorini LeConte, 1862 is the largest tribe in North America. Known as the desert stink beetles, there are over 253 currently valid species-group taxa and over 400 available names (Bousquet *et al*. 2018). Though the nomenclature was recently clarified (Bousquet *et al*. 2018), no comprehensive revision has been done in over a century (Blaisdell 1909).

This dissertation presents four interconnected studies related to the species diversity and distribution of the desert stink beetles. Each study is presented below as an internally cohesive chapter, complete with its own introduction, methods, and results sections. The chapters are arranged in increasing scope, starting with understanding regional species diversity to broadly reclassifying the entire tribe. The chapters presented here are the continuation of several independent and collaborative works already published during my doctoral research (Johnston 2015, Johnston *et al.* 2015, Johnston 2016, Gimmel *et al* 2018, Bousquet *et al.* 2018).

First, a collaborative study on the darkling beetle fauna of the Algodones dunes is presented. This fauna is used as a case study to detail the practical steps involved in documenting species occurrences and to explores the potential of large-scale aggregated biodiversity data for regional treatments. Second, a broader study on sand dunes from western North America is given through the phylogenetic revision of the genus *Trogloderus* LeConte, 1879. *Trogloderus* is a dune-dwelling lineage of Amphidorini whose evolutionary history is used to assess speciation patterns related to geography.

The final two chapters take a broader focus on the tribe as a whole. A phylogenetic study is presented from 29 newly generated partial transcriptomes. These data are used to infer the relationships between Amphidorini species groups in order to assess the current tribal classification. The last chapter, a generic revision of Amphidorini, presents the culmination of the previously published works and the other chapters presented herein. This synthetic treatment includes over 100 formal taxonomic changes, the description of three new genera, and provides identification keys to the constituent groups.

All parts of this dissertation are hereby disclaimed as an available work for zoological nomenclature. Following Article 8.2 of the International Code of Zoological Nomenclature (ICZN 1999), the proposed nomenclatural changes and new names are not considered valid by this publication.

Chapter 2. An updated checklist of the Tenebrionidae sec. Bousquet et al. 2018 of the Algodones Dunes of California, with comments on checklist data practices

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Abstract

Generating regional checklists for insects is frequently based on combining data sources ranging from literature and expert assertions that merely imply the existence of an occurrence to aggregated, standard-compliant data of uniquely identified specimens. The increasing diversity of data sources also means that checklist authors are faced with new responsibilities, effectively acting as filterers to select and utilize an expert-validated subset of all available data. Authors are also faced with the technical obstacle to bring more occurrences into Darwin Core-based data aggregation, even if the corresponding specimens belong to external institutions. We illustrate these issues based on a partial update of the Kimsey *et al.* 2017 checklist of darkling beetles - Tenebrionidae sec. Bousquet *et al.* 2018 - inhabiting the Algodones Dunes of California. Our update entails 54 species-level concepts for this group and region, of which 31 concepts were found to be represented in three specimen-data aggregator portals, based on our interpretations of the aggregators' data. We reassess the distributions and biogeographic affinities of these species, focusing on taxa that are precinctive (highly geographically restricted) to the Lower Colorado River Valley in the context of recent dune formation from the Colorado River. Throughout, we apply taxonomic concept labels (taxonomic name according to source) to contextualize preferred name usages, but also show that the identification data of aggregated occurrences are very rarely well-contextualized or annotated. Doing so is a pre-requisite for publishing open, dynamic checklist versions

that finely accredit incremental expert efforts spent to improve the quality of checklists and aggregated occurrence data.

2.1. Introduction – the branching out of checklist data

Best practices of how to generate species checklists are evolving, because investments into the on-line aggregation of occurrence data (Wieczorek *et al.* 2012, Page *et al.* 2015) are generating new circumstances for creating regional biodiversity checklists (Ferro and Flick 2015, Sikes *et al.* 2016, GBIF 2017). For instance, at the time of preparing this article (March, 2018), the "Symbiota Collections of Arthropods Network" portal (SCAN; Gries *et al.* 2014, Seltmann *et al.* 2017) returned nearly 6.65 million occurrence records for the query "Hexapoda, USA". However, this number may only represent 5-10% of the corresponding material (estimated: >110 million) stored in North American research collections (Cobb *et al.* 2016). Checklist authors who strive to balance taxonomic comprehensiveness with best data science practices therefore face pragmatic choices; in effect acting as filterers of available data sources that range from published literature that merely imply the existence of an occurrence record, to physically vouchered but non-digitized records, to digital records that may lack a uniquely identified physical voucher and finally, to aggregated, fully standard-compliant and, hence, "research-ready" specimens (Seltmann *et al.* 2017). The latter often represent the most desirable minority of the available data.

Standard-formatted occurrence data are still fairly novel elements of published regional checklists, at least in the case of North American hexapod surveys. We might say that the increasing on-line presence of these data complicates the practice of creating checklists, in a good sense: they offer relevant data sources that an expert can access and potentially integrate into their checklist by querying an on-line portal. Opportunities to move such Darwin Core-compliant data from aggregator sites into peer-reviewable checklist manuscripts are becoming more widely available (e.g. Smith *et al.* 2013). However, doing so requires authors to apply their expertise in deciding which records and in what form, to incorporate into the checklist. Furthermore, there is also a novel social responsibility that comes with the ability to digitize occurrence data. For instance, should authors be responsible for bringing on-line any non-digitized vouchered specimens from external institutions that were included in their research? In summary, the scientific and social decision tree for checklist authors is branching out in several new ways. This also means that the term checklist stands for an increasingly variable set of biodiversity data products, when 1-2 decades ago, it tended to refer to publications that could be fully explored off-line.

This paper aims to draw attention to some of the new scientific, technical and social aspects of checklist authorship in a Darwin Core-driven data culture. We illustrate these points based on a partial update of the Kimsey *et al.* 2017 checklist of insects inhabiting the Algodones Dunes of California. We limit our reassessment and discussion to the beetle family Tenebrionidae sec. (according to) Bousquet *et al.* 2018. Although we are critical of certain data sources and practices of Kimsey *et al.* (2017), our update often reflects similar pragmatic choices. It is therefore susceptible to many of the same criticisms and is far from being offered as a definitive solution to all novel checklist data representation challenges. Instead, our intention is simply to broaden the discussion of what it means to author high-quality checklists when aggregated occurrence data are available.

2.2. Taxonomic and regional background

Note. We follow Packer *et al.* (2018), who in turn cite Franz and Peet (2009), in using taxonomic concept labels - i.e. taxonomic name (author, year) according to source - whenever such precision is needed or desired. When only a taxonomic name is provided, this means that we accept the ambiguity that comes with this practice. For further discussion see Berendsohn (1995), Sterner and Franz (2017).

The family Tenebrionidae Latreille, 1802 sec. Bousquet *et al.* 2018 is a highly diverse lineage of beetles - commonly called darkling beetles - with more than 2,800 species currently recognized in North America, whose members are particularly abundant in arid habitats (Matthews *et al.* 2010, Thomas 1983, Bousquet *et al.* 2018). Their distribution includes the Algodones, or Imperial Sand Dunes, the largest active dune field in the United States located in Imperial County, California (Muhs *et al.* 1995, Kimsey *et al.* 2017). The region lies in the Lower Colorado River Valley subdivision of the Sonoran Desert, often referred to as the Colorado Desert (Shreve 1942, Shreve 1951, Brown 1994). Andrews *et al.* (1979) completed a landmark study of the Coleoptera sec. Bouchard *et al.* 2011 inhabiting sand dunes in southern California, reporting on 23 species of Tenebrionidae sec. Bousquet *et al.* 2018 from the Algodones. In constrast, Kimsey *et al.* (2017) list only four "putative endemics" of darkling beetles from these dunes.

2.3. Checklist generation methods

Faunistic studies such as Andrews *et al.* (1979) and Kimsey *et al.* (2017) have historically been generated by experts utilizing published legacy information, as well as accumulating occurrence data both from their own field work and from specimens housed in natural history collections. Frequent products of these studies have been ordered lists of taxonomic (species-level) names, which may or may not include explicit references to the underlying occurrence data (e.g. specimen label data, locally or globally unique identifiers). In addition, specimen identifications are rarely annotated with an identification source or reference to a specific taxonomic concept (Packer *et al.* 2018), generally the only associated information is the year of identification which, when given, may help limit the possible taxonomic concepts utilized.

Advances in biodiversity informatics are making it possible to utilize, publish and directly link taxonomic names appearing in checklists to the underlying occurrence data within a taxonomic treatment (Maddison *et al.* 2012, Beck *et al.* 2013, Smith *et al.* 2013). The new data sources can also introduce new uncertainties and errors, particularly regarding the consistency of taxonomic name usages (Mesibov 2013, Ferro and Flick 2015, Franz *et al.* 2016, Mesibov 2018). Nevertheless, occurrence-based studies should strive to make high-quality, standard-compliant biodiversity data openly available (Sikes *et al.* 2016).

This checklist update consists of four interconnected parts: (1) an updated novel, expert-generated list of species-level names; (2) a list of species-level names generated from aggregated occurrence data; (3) a reassessment of the apparent signals of darkling beetle endemicity in sand dunes of the arid south-western United States, including the

Algodones; and (4) a critical comparison of the two checklists in the context of the expanding universe of checklist-relevant data sources.

Taxonomic and nomenclatural conventions for all checklists uniformly follow Bousquet *et al.* (2018). Taxonomic concept labels of the expert-generated checklist include the most congruent primary systematic reference according to which the specimens were identified.

2.3.1. Expert-generated checklist

The checklist of species-level names, published by Andrews *et al.* (1979), was used as the starting point for this study, with nomenclatural updates enacted to reflect the taxonomic concept labels of Bousquet *et al.* (2018). We then surveyed the appropriate subsequent taxonomic literature to add species-level names authoritatively reported from the Algodones; specifically: Papp (1981), Doyen (1984), Doyen (1987), MacLachlan and Olson (1990), Aalbu (2005). The checklist was completed by surveying darkling beetle specimens from the authors' personal collections, particularly the Rolf L. Aalbu Collection (henceforth: RLAC; located in California, USA), which has extensive holdings of Algodones tenebrionid material. In other words, the expert-generated checklist includes a combination of (1) literature records where no individual occurrences are explicitly recognized and (2) under-mobilized RLAC vouchers.

2.3.2. Aggregated occurrence data-based checklist

Excluded sources. In our assessment, the RLAC and the California State Collection of Arthropods (CSCA; located at the California Department of Food and Agriculture in Sacramento, California) are the two research collections with the most comprehensive holdings of Algodones darkling beetles. Neither of these collections currently serves occurrence data to aggregators. Meanwhile, the R.M. Bohart Museum of Entomology (UCDC; University of California, Davis), which houses the Kimsey *et al.* (2017) material, presently serves up data only through their institutional website: http://museums.ucdavis.edu/bohart.aspx. A total of 308 focal records were available through this website as of January 10, 2018 (available online https://doi.org/10.3897/BDJ.6.e24927.suppl1). These records are not Darwin Core-compliant, however, typically lacking information on the date of collection, collector, identifier and georeference data. Therefore, they were not included in the occurrence data-based checklist. The California Terrestrial Arthropods Database (CalBug; see Hill *et al.* 2012; available at http://calbug.berkeley.edu/index.html) had no focal records as of January 10, 2018. Lastly, after carefully inspecting non-vouchered occurrences (observations) in select citizen science/social networks (e.g.,https://www.inaturalist.org), we were unable to confidently identify many of the photo-vouchers ourselves and judged many more non-expert identifications too doubtful to be included.

Included sources. Three major biodiversity data aggregators were queried for darkling beetle occurrence records from the Algodones: (1) the Symbiota Collections of Arthropod Network portal (SCAN), (2) the Integrated Digitized Biocollections portal (iDigBio) and (3) the Global Biodiversity Information Facility portal (GBIF). Records from each aggregator were downloaded on January 02, 2018. The occurrence records were sorted by the Darwin Core term "dwc:scientificName", yielding a list of unique taxonomic names and a count of the total number of records for each. All original scientific names were manually remapped to the classification of Bousquet *et al.* (2018). Species-level names not included in our expert-generated checklist were evaluated at the individual record level and are discussed below.

2.3.2.1. Symbiota Collections of Arthropods Network

The SCAN portal (Seltmann *et al.* 2017; http://scan-bugs.org) was queried for "Tenebrionidae" specimen records (under taxonomic criteria and including synonyms) using the portal's Spatial Module, i.e. by specifying a geographic polygon that includes the Algodones Dunes and surrounding sandy flats. A total of 693 occurrence records were returned and then downloaded as a Darwin Core Archive (DwC-A) dataset (available online https://doi.org/10.3897/BDJ.6.e24927.suppl2).

2.3.2.2. Integrated Digitized Biocollections portal

The Integrated Digitized Biocollections portal (Page *et al.* 2015; https://www.idigbio.org) was queried for specimen records using the portal's map search function to draw the smallest rectangle possible covering the Algodones and using "Tenebrionidae" (search all fields), while limiting the "Basis of Record" criterion to "PreservedSpecimen". A total of 454 occurrence records were returned and then downloaded as a DwC-A dataset (available online https://doi.org/10.3897/BDJ.6.e24927.suppl3). The default occurrence file (data file: occurrence.csv in the DwC-A package) was analyzed. Most of the records included a flag that the scientific name did not match the GBIF backbone taxonomy (see below), but the original data providers identifications were still returned in the scientific name field.

2.3.2.3. Global Biodiversity Information Facility portal

The Global Biodiversity Information Facility portal (Edwards 2004; https://www.gbif.org) was queried for specimen records by adding "Tenebrionidae" as the "Scientific Name" constraint, then using the map search function under the "Location" search parameter to draw the smallest rectangle possible covering the Algodones and selecting "Preserved Specimen" under the "Basis Of Record" search criterion. A total of 133 records were returned and then downloaded as a DwC-A dataset (available online https://doi.org/10.3897/BDJ.6.e24927.suppl4). The default occurrence data file delivered by GBIF only includes taxonomic names accepted in the GBIF backbone taxonomy (GBIF Secretariat 2017). No occurrence records in that default file were returned with a species-level name, but instead were matched to higher taxonomic ranks (*e.g*. genus level). Therefore, the verbatim records (data file: verbatim.txt in the DwC-A package) were analyzed instead of the GBIF taxonomy-validated records (data file: occurrence.txt in the DwC-A package).

2.4. Checklist results

The presentation of the checklist results follows the order of Section 2.3.

2.4.1. Expert-generated checklist

A total of 54 darkling beetle species-level names are included in the expert-generated Algodones checklist (Table 2.1). Of these, 34 were previously documented in the literature; the remaining 20 are formally published here for the first time. This increase in recognized species relative to the study of Andrews *et al.* (1979) (23 recorded species) is remarkable, as the new total amounts to nearly half of the 113 species-level entities reported for the entire Sonoran Desert region of California by Aalbu and Smith (2014).

Not surprisingly, access to reliable taxonomic identifications of vouchered specimens was the greatest challenge to creating the checklist, given also the scarcity of modern systematic treatments for many of the recognized species. Several groups - *e.g.* *Edrotes* LeConte, 1851 sec. Bousquet *et al.* 2018 and *Ulus* Horn, 1870 sec. Bousquet *et al.* 2018 - have revisions in progress, whereas others such as *Helops* Fabricius, 1775 sec. Bousquet *et al.* 2018 and *Hymenorus* Mulsant, 1852 sec. Bousquet *et al.* 2018 are in great need of revision. Hence, future studies could drastically change the species-level names and concepts employed here. Indeed, the genera *Hylocrinus* Casey, 1907 sec. Bousquet *et al.* 2018 and *Metoponium* Casey, 1907 sec. Bousquet *et al.* 2018 were last revised by Casey (1907) - a treatment that entails so many poorly differentiated species-level concepts that we know of no subsequent specialist who would confidently identify new specimens to these concepts. We similarly refrain from this task in the expert-generated checklist.

Table 2.1. Expert-generated checklist of the Tenebrionidae species (sec. auctorum) known to occur in the Algodones. Records formally documented here for the first time are annotated with a "*". See Section 3 for further detail.

Taxonomic Name (Author, Year)	**According To (Source)**	**Information Sources**
1. *Alaephus macilentus* Casey, 1924 *	Fall 1907	RLAC
2. *Anepsius delicatulus* LeConte, 1851	Doyen 1987	Doyen 1987; RLAC
3. *Araeoschizus andrewsi* Papp, 1981	Papp 1981	Andrews *et al.* 1979, Papp 1981; RLAC
4. *Araeoschizus hardyi* Papp, 1981	Papp 1981	Andrews *et al.* 1979, Papp 1981; RLAC
5. *Araeoschizus wasbauerorum* Papp, 1981 *	Papp 1981	RLAC
6. *Asbolus laevis* LeConte, 1851	Aalbu 2005	Andrews *et al.* 1979, Aalbu 2005; RLAC
7. *Asbolus papillosus* (Triplehorn, 1964)	Aalbu 2005	Aalbu 2005; RLAC
8. *Asbolus verrucosus* LeConte, 1851	Aalbu 2005	Andrews *et al.* 1979, Aalbu 2005; RLAC
9. *Batuliodes obesus* Doyen, 1987	Doyen 1987	Doyen 1987; RLAC
10. *Batuliodes wasbaueri* Doyen, 1987	Doyen 1987	Doyen 1987; RLAC
11. *Batuliomorpha imperialis* Doyen, 1987	Doyen 1987	Doyen 1987; RLAC
12. *Batulius setosus* LeConte, 1851	Doyen 1987	Doyen 1987; RLAC
13. *Blapstinus histricus* Casey, 1890	Davis 1970	Davis 1970; RLAC
14. *Cerenopus concolor* LeConte, 1851	Berry 1973	Andrews *et al.* 1979; RLAC
15. *Cheirodes californicus* (Horn, 1870)	Horn 1870	Andrews et *al.* 1979; RLAC
16. *Chilometopon abnorme* (Horn,1870)	MacLachlan and Olson 1990	MacLachlan and Olson 1990; RLAC
17. *Chilometopon brachystomum* Doyen, 1983	MacLachlan and Olson 1990	MacLachlan and Olson 1990; RLAC
18. *Chilometopon helopioides* Horn, 1974	MacLachlan and Olson 1990	MacLachlan and Olson 1990; RLAC
19. *Chilometopon pallidum* Casey, 1890	MacLachlan and Olson 1990	MacLachlan and Olson 1990; RLAC
20. *Cnemodinus testaceus* (Horn, 1870)	Casey 1907	Andrews *et al.* 1979; RLAC
21. *Conibiosoma elongatum* (Horn, 1870) *	Casey 1890	RLAC
22. *Conibius opacus* (LeConte, 1866) *	Casey 1890	RLAC
23. *Craniotus pubescens* LeConte, 1851 *	Aalbu et al. 2015	RLAC
24. *Cryptoglossa muricata* (LeConte, 1851)	Aalbu 2005	Aalbu 2005; RLAC
25. *Edrotes arens* La Rivers, 1947	Doyen 1968	Andrews *et al.* 1979; RLAC
26. *Edrotes ventricosus* LeConte, 1851	Doyen 1968	Andrews *et al.* 1979; RLAC
27. *Eleodes armata* LeConte, 1851	Johnston et al. 2015	Andrews *et al.* 1979; RLAC
28. *Embaphion depressum* (LeConte, 1851)	Johnston et al. 2015	Andrews *et al.* 1979; RLAC
29. *Eupsophulus castaneus* (Horn, 1870)	Spilman 1959	Andrews *et al.* 1979; RLAC

Taxonomic Name (Author, Year)	**According To (Source)**	**Information Sources**
30. *Eupsophulus horni* (Champion, 1885) *	Spilman 1959	RLAC
31. *Eusattus dilatatus* LeConte, 1851	Doyen 1984	Andrews *et al*. 1979, Doyen 1984; RLAC
32. *Eusattus productus* LeConte, 1858	Doyen 1984	Doyen 1984; RLAC
33. *Helops arizonensis* Horn, 1874 *	Horn 1874	RLAC
34. *Hylocrinus sp.* *	Casey 1907	RLAC
35. *Hymenorus exiguus* Casey, 1891 *	Fall 1931	RLAC
36. *Hymenorus irritus* Fall, 1931 *	Fall 1931	RLAC
37. *Hymenorus thoracicus* Fall, 1931 *	Fall 1931	RLAC
38. *Latheticus prosopis* Chittenden, 1904	Chittenden 1904	Andrews *et al*. 1979; RLAC
39. *Lepidocnemeplatia sp*. (nov.) *	Aalbu *et al.* (in prep.)	RLAC
40. *Lepidocnemeplatia sericia* (Horn, 1870)	Aalbu *et al.* (in prep.)	Andrews *et al*. 1979; RLAC
41. *Mecysmus angustus* (LeConte, 1851)	Thomas 1890	Andrews *et al*. 1979; RLAC
42. *Metoponium sp.* *	Thomas 1907	RLAC
43. *Mycotrogus angustus* Horn, 1870 *	Spilman 1963	RLAC
44. *Nocibiotes crassipes* (Casey, 1890) *	Casey 1895	RLAC
45. *Nocibiotes granulatus* (LeConte, 1851)	Thomas 1895	Andrews *et al*. 1979; RLAC
46. *Notibius puberulus* LeConte, 1851	Horn 1894	Andrews *et al*. 1979; RLAC
47. *Stenomorpha confluens* (LeConte, 1851)	Triplehorn and Brown 1971	Andrews *et al*. 1979; RLAC
48. Stenomorpha hirsuta (LeConte, 1851)	Casey 1912	Andrews *et al*. 1979; RLAC
49. Telabis serrata (LeConte, 1866) *	Casey 1890	RLAC
50. Tonibius sulcatus (LeConte, 1851) *	Casey 1895	RLAC
51. Tribolium castaneum (Herbst, 1797) *	Hinton 1948	RLAC
52. Trichoton sordidum (LeConte, 1851) *	Casey 1890	RLAC
53. Triorophus laevis LeConte, 1851 *	Horn 1870	RLAC
54. Ulus crassus (LeConte, 1851)	Casey 1890	Andrews *et al*. 1979; RLAC

2.4.2. Aggregated occurrence data-based checklists

The results of all three aggregated occurrence data-based checklists for the Algodones darkling beetles are summarized in Table 2.2. The underlying raw portal data and steps taken to process and interpret them in relation to the expert-generated checklist, are provided online (https://doi.org/10.3897/BDJ.6.e24927.suppl6). Accordingly (Section I of Table 2.2), the SCAN portal contains 559 valid occurrences corresponding to 31 species-level concepts as recognized in Table 2.1 (with 108 ~ 19.3% records needing nomenclatural adjustments); the iDigBio portal serves up 386 such occurrences representing 25 species-level concepts (with 175 ~ 45.3% records needing nomenclatural adjustments; and GBIF offers 100 valid occurrences of 15 species-level concepts (with 34 ~ 34.0% needing nomenclatural adjustments).
In addition (Section II), each portal includes occurrences not considered valid for the focal taxonomic entities, mostly due to erroneous or uncertain identification (in our judgment), as follows: SCAN includes 133 occurrences corresponding to 21 taxonomic concepts; iDigBio contains 59 occurrences representing 21 taxonomic concepts; and GBIF serves up 34 records pertaining to 11 taxonomic concepts.

The patterns of occurrence-level overlap amongst the three data portals tell a potentially interesting story about biodiversity data meta-aggregation and signal propagation (or loss), as well as the relationship between regionally and/or taxonomically constrained portals and data quality (Mesibov 2013, Gries *et al.* 2014, Franz and Sterner 2018, Mesibov 2018). However, these topics reside somewhat outside of our current focus. Similarly, with the exception of the select occurrences discussed.

Table 2.2. Summary of the aggregated occurrence (specimen) data for Algodones Tenebrionidae species (sec. auctorum) available through the SCAN, iDigBio and GBIF portals, respectively. Totals include occurrences identified to synonymous or misspelled names in relation to herein accepted source. The table is arranged in two sections for occurrences considered valid and invalid, respectively and for various reasons in the latter case. "syn." = synonym; "lap." = lapsus. See also Table 1 and Section 3

Taxonomic concept label	**SCAN**	**iDigBio**	**GBIF**
I. Occurrences considered *valid* (including identifications to synonymous or misspelled names)			
1. *Alaephus macilentus* Casey, 1924 sec. Fall 1907	–	–	–
2. *Anepsius delicatulus* LeConte, 1851 sec. Doyen 1987	3	3	3
3. *Araeoschizus andrewsi* Papp, 1981 sec. Papp 1981	37	22	1
4. *Araeoschizus hardyi* Papp, 1981 sec. Papp 1981	3	3	–
5. *Araeoschizus wasbauerorum* Papp, 1981 sec. Papp 1981	1	1	–
6. *Asbolus laevis* LeConte, 1851 sec. Aalbu 2005	133 (25 syn.)	44 (9 syn.)	5 (5 syn.)
8. *Asbolus verrucosus* LeConte, 1851 sec. Aalbu 2005	7 (1 syn.)	–	–
9. *Batuliodes obesus* Doyen, 1987 sec. Doyen 1987	–	–	–
10. *Batuliodes wasbaueri* Doyen, 1987 sec. Doyen 1987	–	–	–
11. *Batuliomorpha imperialis* Doyen, 1987 sec. Doyen 1987	6	6	–
12. *Batulius setosus* LeConte, 1851 sec. Doyen 1987	2	–	1
13. *Blapstinus histricus* Casey, 1890 sec. Davis 1970	2	1	–
14. *Cerenopus concolor* LeConte, 1851 sec. Berry 1973	10	10	9
15. *Cheirodes californicus* (Horn, 1870) sec. Horn 1870	–	–	
16. *Chilometopon abnorme* (Horn, 1870) sec. MacLachlan and Olson 1990	7	6	–
17. *Chilometopon brachystomum* Doyen, 1983 sec. MacLachlan and Olson 1990	–	–	–
18. *Chilometopon helopioides* Horn, 1974 sec. MacLachlan and Olson 1990	–	–	–
19. *Chilometopon pallidum* Casey, 1890 sec. MacLachlan and Olson 1990	19	16	–
20. *Cnemodinus testaceus* (Horn, 1870) sec. Casey 1907	43	1	–
21. *Conibiosoma elongatum* (Horn, 1870) sec. Casey 1890	–	–	–

Taxonomic concept label	**SCAN**	**iDigBio**	**GBIF**
22. *Conibius opacus* (LeConte, 1866) sec. Casey 1890	–	–	–
23. *Craniotus pubescens* LeConte, 1851 sec. Aalbu *et al.* 2015	–	–	–
24. *Cryptoglossa muricata* (LeConte, 1851) sec. Aalbu 2005	18 (16 syn.)	17 (16 syn.)	15
25. *Edrotes arens* La Rivers, 1947 sec. Doyen 1968	55 (2 lap.)	23 (2 lap.)	6 (2 lap.)
26. *Edrotes ventricosus* LeConte, 1851 sec. Doyen 1968	51	23	9
27. *Eleodes armata* LeConte, 1851 sec. Johnston *et al.* 2015	44 (39 lap.)	142 (137 lap.)	28 (24 syn.)
28. *Embaphion depressum* (LeConte, 1851) sec. Johnston *et al.* 2015	8	11	4
29. *Eupsophulus castaneus* (Horn, 1870) sec. Spilman 1959	16 (1 lap.)	14 (1 lap.)	1
30. *Eupsophulus horni* (Champion, 1885) sec. Spilman 1959	–	–	–
31. *Eusattus dilatatus* LeConte, 1851 sec. Doyen 1984	22 (3 syn.)	11 (3 syn.)	3
32. *Eusattus productus* LeConte, 1858 sec. Doyen 1984	1	–	–
33. *Helops arizonensis* Horn, 1874 sec. Horn 1874	–	–	–
34. *Hylocrinus* sp. sec. Casey 1907	–	–	–
35. *Hymenorus exiguus* Casey, 1891 sec. Fall 1931	–	–	–
36. *Hymenorus irritus* Fall, 1931 sec. Fall 1931	–	–	–
37. *Hymenorus thoracicus* Fall, 1931 sec. Fall 1931	–	–	–
38. *Latheticus prosopis* Chittenden, 1904 sec. Chittenden 1904	–	–	–
39. *Lepidocnemeplatia* sp. (nov.) sec. Aalbu et al. (in prep.)	3 (3 syn.)	3 (3 syn.)	3 (3 syn.)
40. *Lepidocnemeplatia sericia* (Horn, 1870) sec. Aalbu et al. (in prep.)	7	–	–
41. *Mecysmus angustus* (LeConte, 1851) sec. Casey 1890	1	–	–
42. *Metoponium* sp. sec. Casey 1907	–	–	–
43. *Mycotrogus angustus* Horn, 1870 sec. Spilman 1963	–	–	–
44. *Nocibiotes crassipes* (Casey, 1890) sec. Casey 1895	–	–	–
45. *Nocibiotes granulatus* (LeConte, 1851) sec. Casey 1895	–	–	–
46. *Notibius puberulus* LeConte, 1851 sec. Horn 1894	6 (4 syn.)	8 (4 syn)	–
47. Stenomorpha confluens (LeConte, 1851) sec. Triplehorn and Brown 1971	15 (6 syn.)	6	6
48. *Stenomorpha hirsuta* (LeConte, 1851) sec. Casey 1912	2	1	–
49. *Telabis serrata* (LeConte, 1866) sec. Casey 1890	3	1	–
50. *Tonibius sulcatus* (LeConte, 1851) sec. Casey 1895	–	–	–
51. *Tribolium castaneum* (Herbst, 1797) sec. Hinton 1948	–	–	–

Taxonomic concept label	**SCAN**	**iDigBio**	**GBIF**
52. *Trichoton sordidum* (LeConte, 1851) sec. Casey 1890	–	–	–
53. *Triorophus laevis* LeConte, 1851 sec. Horn 1870	1	1	–
54. *Ulus crassus* (LeConte, 1851) sec. Casey 1890	–	–	–
Totals	569 (108 syn./lap.)	368 (175 syn./lap.)	100 (34 syn./lap.)
II. Occurrences considered invalid (including misidentifications, misspellings and uncertain identifications)			
1. [*Araeoschizus costipennis* sec. Bousquet *et al.* 2018] – misidentified	2	2	–
2. [*Conibius gagates* sec. Bousquet *et al.* 2018] – misidentified	4	4	–
3. [*Leptohoplia* sp.] – *not* a darkling beetle	5	5	–
4. [*Argoporis* sp. sec. Bousquet *et al.* 2018] – not a sand dune dweller	1	1	–
5. [*Chilometopon* sp. sec. Bousquet *et al.* 2018] – misspelled name	2	2	–
6. [*Telabis* sp. sec. Bousquet *et al.* 2018] – misspelled name	4	4	–
7. [Anepsiini sp. sec. Bousquet *et al.* 2018] – uncertain identification	4	–	–
8. [*Cheirodes* sp. sec. Bousquet *et al.* 2018] – uncertain identification	1	1	1
9. [*Batuliodes* sp. sec. Bousquet *et al.* 2018] – uncertain identification	3	3	3
10. [*Batulius* sp. sec. Bousquet *et al.* 2018] – uncertain identification	3	3	3
11. [*Chilometopon* sp. sec. Bousquet *et al.* 2018] – uncertain identification	2	1	2
12. [*Cnemodinus* sp. sec. Bousquet *et al.* 2018] – uncertain identification	3	3	3
13. [*Cryptoglossa* sp. sec. Bousquet *et al.* 2018] – uncertain identification	1	1	–
14. [*Edrotes* sp. sec. Bousquet *et al.* 2018] – uncertain identification	30	6	4
15. [*Eleodes* sp. sec. Bousquet *et al.* 2018] – uncertain identification	1	1	1
16. [*Eusattus* sp. sec. Bousquet *et al.* 2018] – uncertain identification	1	1	–
17. [*Notibius* sp. sec. Bousquet *et al.* 2018] – uncertain identification	1	1	–
18. [Pimeliinae sp. sec. Bousquet *et al.* 2018] – uncertain identification	2	2	2
19. [*Telabis* sp. sec. Bousquet *et al.* 2018] – uncertain identification	5	5	3
20. [Tenebrionidae sp. sec. Bousquet *et al.* 2018] – uncertain identification	58	11	11
21. [*Triorophus* sp.sec. Bousquet *et al.* 2018] – uncertain identification	1	1	1
22. [*Zopherus tristis* LeConte, 1851] – *not* a darkling beetle	–	1	–
Totals	133	59	34

below, we will not dissect in detail the various apparent instances of nomenclatural adjustments and incorrect or uncertain identifications that the portal data represent

2.4.2.1. Symbiota Collections of Arthropods Network portal

Three records require in-depth discussion. First, occurrence BYUC065760 is identified in SCAN to the genus-level name *Argoporis* Horn, 1870 and located in "Vista" County, California, which - unlike the city of Vista (San Diego County) - is not a recognized area. Hence the georeferencing of this record is suspect. Two species of *Argoporis* sec. Berry 1980 are known from the general region (Aalbu and Smith 2014) and their members could potentially occur near the Algodones. However, the occurrence BYUC065760 is here regarded as not being a dune dweller due to the locality uncertainty and lack of other valid records.

Second and third, occurrences {X1016339, X1036349, X1012882, X1012952} are identified to the species-level name *Conibius gagates* (Horn, 1870); whereas occurrences {X1002077, X1001631} are identified to *Araeoschizus costipennis* LeConte, 1851. All six specimen identifications were made by a non-specialist and we consider them to be doubtful. There are no additional records available either via Andrews *et al.* (1979), Papp's (1981) revision or other surveyed collections. Occurrences of *Conibius gagates* sec. Casey 1890 are otherwise known from Phoenix, Arizona and eastward thereof. We therefore cannot consider the aforementioned records as valid at this time.

2.4.2.2. Integrated Digitized Biocollections portal

The portal propagates many of the issues originating with SCAN (see Section 2.4.2.1.). Occurrence BYUC087901, identified to the species-level name *Zopherus tristis* LeConte, 1851, is returned under the "Tenebrionidae" search criterion by matching an identification reference citation. However, the nominal genus has long been recognized in the family Zopheridae sec. Crowson 1955 and is classified accordingly in the iDigBio backbone taxonomy.

2.4.2.3. Global Biodiversity Information Facility portal

The portal internally reclassifies the aggregated occurrence data specimen data according to the GBIF backbone taxonomy (GBIF Secretariat 2017). As none of the species-level names included in the expert-generated checklist is recognized in the GBIF backbone taxonomy, we could only utilize the verbatim occurrence data which pertained to only 15 species-level concepts according to our interpretation (see https://doi.org/10.3897/BDJ.6.e24927.suppl6).

2.5. Precinctive tenebrionid species

Following Frank and McCoy (1990), we prefer the term precinctive in the sense of "confined only to the area specified", to connote a restricted geographic range, over the broader term endemic which can generally be applied to mean indigenous to, though the latter is often used in a synonymous sense. Two levels of precintion are assessed: (1)

entities restricted to the Gran Desierto de Altar and (2) those restricted to the Lower Colorado River Valley.

Table 2.3 summarizes our assessment of patterns of precinction relative to the expert-generated checklist (Table 2.1). The patterns are based on data taken from primary literature sources; including most recently Aalbu and Smith (2014). Pertinent SCAN occurrences were added to this dataset and used to evaluate distributional boundaries. Recognized species were scored in one of three ways: (1) only known from the Algodones and the Gran Desierto de Altar; (2) only known from the Lower Colorado River Valley region of the Sonoran Desert, including at least one locality not within the Algodones or Gran Desierto; and (3) known to extend beyond the boundaries of the Lower Colorado River Valley. For the latter category, distributions were further differentiated as follows: (1) inhabiting the Mohave Desert; (2) inhabiting other parts of Baja California - generally the Vizcaíno region of the Sonoran Desert (see Shreve 1951, Brown 1994); and (3) inhabiting other geographic regions.

2.5.1. Gran Desierto de Altar

The nearly contiguous Algodones Dune formation and the large sand sea of the Gran Desierto de Altar are both derived from sediments from the Colorado River (Lancaster *et al.* 1987, Muhs *et al.* 1995) and are narrowly separated by the river's current course. The Colorado River begain draining into this region around 4 mya (Winker and Kidwell 1986, Derickson *et al.* 2008), depositing sediments that formed the Colorado River Delta, which now marks the northern limit of the Gulf of California (Waters 1983). The presently dry Salton Trough, the low-lying region north of the

Table 2.3. Pattern of precinction of Tenebrionidae species (sec. auctorum) known to occur in the Algodones. Taxonomic concept labels are numbered in accordance with Tables 1, 2 to facilitate comparisons. Abbreviations: Gran Desierto = Gran Desierto de Altar; Lower Col. RV = Lower Colorado River Valley; Baja Calif. = Baja California. See text for further detail.

Taxonomic concept label	**Gran Desierto**	**Lower Col. RV**	**Mohave Desert**	**Baja Calif.**	**Other Areas**
3. *Araeoschizus andrewsi* Papp, 1981 sec. Papp 1981	+				
5. *Araeoschizus wasbauerorum* Papp, 1981 sec. Papp 1981	+				
10. *Batuliodes wasbaueri* Doyen, 1987 sec. Doyen 1987	+				
11. *Batuliomorpha imperialis* Doyen, 1987 sec. Doyen 1987	+				
39. *Lepidocnemeplatia sp*. (nov.) sec. Aalbu *et al.* (in prep.)	+				
4. *Araeoschizus hardyi* Papp, 1981 sec. Papp 1981		+			
12. *Batulius setosus* LeConte, 1851 sec. Doyen 1987		+			
25. *Edrotes arens* La Rivers, 1947 sec. Doyen 1968		+			
28. *Embaphion depressum* (LeConte, 1851) sec. Johnston *et al.* 2015		+			
30. *Eupsophulus horni* (Champion, 1885) sec. Spilman 1959		+ (?)			
31. *Eusattus dilatatus* LeConte, 1851 sec. Doyen 1984		+			
32. *Eusattus productus* LeConte, 1858 sec. Doyen 1984		+			
37. *Hymenorus thoracicus* Fall, 1931 sec. Fall 1931		+			
43. *Mycotrogus angustus* Horn, 1870 sec. Spilman 1963		+ (?)			
1. *Alaephus macilentus* Casey, 1924 sec. Fall 1907			+	+	+
2. Anepsius delicatulus LeConte, 1851 sec. Doyen 1987			+	+	+
6. *Asbolus laevis* LeConte, 1851 sec. Aalbu 2005			+		
7. *Asbolus papillosus* (Triplehorn, 1964) sec. Aalbu 2005			+		
8. *Asbolus verrucosus* LeConte, 1851 sec. Aalbu 2005			+	+	+
9. *Batuliodes obesus* Doyen, 1987 sec. Doyen 1987			+		
13. *Blapstinus histricus* Casey, 1890 sec. Davis 1970			+		+
14. *Cerenopus concolor* LeConte, 1851 sec. Berry 1973			+	+	
15. *Cheirodes californicus* (Horn, 1870) sec. Horn 1870			+		+
16. *Chilometopon abnorme* (Horn, 1870) sec. MacLachlan and Olson 1990			+	+	+

Taxonomic concept label	**Gran Desierto**	**Lower Col. RV**	**Mohave Desert**	**Baja Calif.**	**Other Areas**
17. *Chilometopon brachystomum* Doyen, 1983 sec. MacLachlan and Olson 1990			+	+	+
18. *Chilometopon helopioides* Horn, 1974 sec. MacLachlan and Olson 1990			+	+	+
19. *Chilometopon pallidum* Casey, 1890 sec. MacLachlan and Olson 1990			+	+	+
20. *Cnemodinus testaceus* (Horn, 1870) sec. Casey 1907			+		
21. *Conibiosoma elongatum* (Horn, 1870) sec. Casey 1890			+		+
22. *Conibius opacus* (LeConte, 1866) sec. Casey 1890				+	
23. *Craniotus pubescens* LeConte, 1851 sec. Aalbu et al. 2015			+	+	+
24. *Cryptoglossa muricata* (LeConte, 1851) sec. Aalbu 2005			+	+	
26. *Edrotes ventricosus* LeConte, 1851 sec. Doyen 1968			+		+
27. *Eleodes armata* LeConte, 1851 sec. Johnston *et al.* 2015			+	+	+
29. *Eupsophulus castaneus* (Horn, 1870) sec. Spilman 1959			+		+
33. *Helops arizonensis* Horn, 1874 sec. Horn 1874					+
35. *Hymenorus exiguus* Casey, 1891 sec. Fall 1931					+
36. *Hymenorus irritus* Fall, 1931 sec. Fall 1931					+
38. *Latheticus prosopis* Chittenden, 1904 sec. Chittenden 1904					+
40. *Lepidocnemeplatia sericia* (Horn, 1870) sec. Aalbu *et al.* (in prep.)			+		+
41. *Mecysmus angustus* (LeConte, 1851) sec. Casey 1890					+
44. *Nocibiotes crassipes* (Casey, 1890) sec. Casey 1895				+	
45. *Nocibiotes granulatus* (LeConte, 1851) sec. Casey 1895					+
46. *Notibius puberulus* LeConte, 1851 sec. Horn 1894			+		+
47. *Stenomorpha confluens* (LeConte, 1851) sec. Triplehorn and Brown 1971			+		
48. *Stenomorpha hirsuta* (LeConte, 1851) sec. Casey 1912					+
49. *Telabis serrata* (LeConte, 1866) sec. Casey 1890			+	+	+
50. *Tonibius sulcatus* (LeConte, 1851) sec. Casey 1895			+	+	
51. *Tribolium castaneum* (Herbst, 1797) sec. Hinton 1948			+	+	+
52. *Trichoton sordidum* (LeConte, 1851) sec. Casey 1890			+		+
53. *Triorophus laevis* LeConte, 1851 sec. Horn 1870			+		+
54. *Ulus crassus* (LeConte, 1851) sec. Casey 1890			+	+	+
Totals	5	9 (2?)	29	17	28

Colorado River Delta, has seen periodic flooding during the Holocene - by the Colorado River changing course westward and draining into the prehistoric Lake Cahuilla - at least three times in the past two thousand years (Waters 1983). Sediments from these sequential fillings of Lake Cahuilla are thought to have formed the Algodones Dunes (Norris and Norris 1961, Derickson *et al.* 2008). As a biogeographic factor, the Colorado River could present a barrier to gene flow and dispersal for sand-dune restricted lineages, particularly if these are flightless and thus dispersal-limited. Nevertheless, it is unclear whether any species-level entities of darkling beetles are unique to either the Algodones Dunes or the Gran Desierto de Altar. Moreover, historical shifts in the placement and volume of the Colorado River may have facilitated the homogenization of faunal distributions. Thus we consider the Colorado River-derived dunes - spanning both the Algodones Dunes and the Gran Desierto de Altar - as a single cohesive biogeographic region and we refer to it simply as the Gran Desierto.

As shown in Table 2.3, the following five entities are seemingly restricted to the Gran Desierto. *Araeoschizus andrewsi* sec. Papp 1981 and *Araeoschizus wasbauerorum* sec. Papp 1981 are both known from the Algodones and the Gran Desierto de Altar. *Batuliodes wasbaueri* sec. Doyen 1987 is known from the Algdones as well as from a small remnant sand dune area, located approximately 20 miles southeast of Mexicali, Mexico, near the Colorado River. The congruent distributions of these three flightless species reinforce the notion of a single biogeographic subregion. *Batuliomorpha imperialis* sec. Doyen 1987 and *Lepidocnemeplatia* sp. (nov.) sec. Aalbu *et al.* (in prep.) are both small species (~ 3 mm in length) collected mainly by sifting sand. They are currently only recorded from the Algodones, though we may expect them to be more widespread but uncollected throughout the Gran Desierto.

Kimsey *et al.* (2017) considered the following four species as "only recorded from the [Algodones] dunes": *Edrotes arens* sec. Doyen 1968, *Eusattus dilatatus* sec. Doyen 1984, *Nocibiotes crassipes* sec. Casey 1895 and *Tonibius sulcatus* sec. Casey 1895. We hereby refute all of these assessments of Algodones-constrained precinction. *Edrotes arens* sec. La Rivers 1947 was originally described based on three specimens from the Yuma Dunes in Arizona, with subsequent literature reports from many sand dune localities throughout California (Andrews *et al.* 1979). SCAN and iDigBio hold multiple occurrences of *Edrotes arens* sec. Doyen 1968 from Arizona and California localities. Specimens of *Eusattus dilatatus* sec. Doyen 1984 have been reported in literature from deep sands throughout the Lower Colorado River Valley, ranging from Puerto Peñasco, Mexico, to Blythe, California (Doyen 1984). Again, SCAN and iDigBio serve up the corresponding non-Algodones occurrences. *Nocibiotes* Casey, 1895 sec. Bousquet *et al.* 2018 is in need of revision, with many specimens in research collections currently not identified to the species level. However, specimens of *Nocibiotes crassipes* sec. Casey 1895 are known to occur in Baja California and throughout southern California (RLA, unpublished data). *Tonibius* Casey, 1895 sec. Bousquet *et al.* 2018 is presently monotypic, containing only *Tonibius sulcatus* (LeConte, 1851) sec. Casey 1895, which is the entity presumably referred to in Kimsey *et al.* 2017, with misattributed name authorship ("Casey"). The type locality for *Tonibius sulcatus* sec. Casey 1895 is "San Diego" (LeConte 1851) and additional occurrences are recorded in literature from Baja California (Blaisdell 1943) and Nevada (Thomas 1983). Again, SCAN and iDigBio contain respective occurrences from non-Algodones localities.

2.5.2. Lower Colorado River Valley

Nine entities present in the Algodones appear to have distributions wider than the Gran Desierto yet are still restricted to the Lower Colorado River Valley (Table 2.3). Two of these, *Eupsophulus horni* sec. Spilman 1959 and *Mycotrogus angustus* sec. Spilman 1963, are poorly known both in terms of their natural history and distributions. The remaining seven recognized species are typically found in areas with sandy soils. Some are only found in deeper sand dune habitats - *e.g. Edrotes arens* sec. Doyen 1968 and *Eusattus dilatatus* sec. Doyen 1984 - whereas others inhabit sandy washes and alluvial flats (e.g. *Hymenorus thoracicus* sec. Fall 1931). A total of 259 occurrences are available for these nine species in SCAN, of which 234 are considered valid in our assessment (see https://doi.org/10.3897/BDJ.6.e24927.suppl5). These occurrences are also mapped in Fig. 2.1 and suggest the presence of a shared distributional pattern: both towards the north, along the Colorado River and east, throughout the low desert regions of the Yuma Desert in south-western Arizona and north-western Sonora. The pattern is tentative, though plausible given similarities in habitat temperatures, rainfall and soil type. More than half of the specimens (125 occurrences) are from the well-sampled Algodones, thus offering little data regarding broader distributions of the respective species. We predict that further sampling and taxonomic identification efforts will reveal more extensive distributions for many of these.

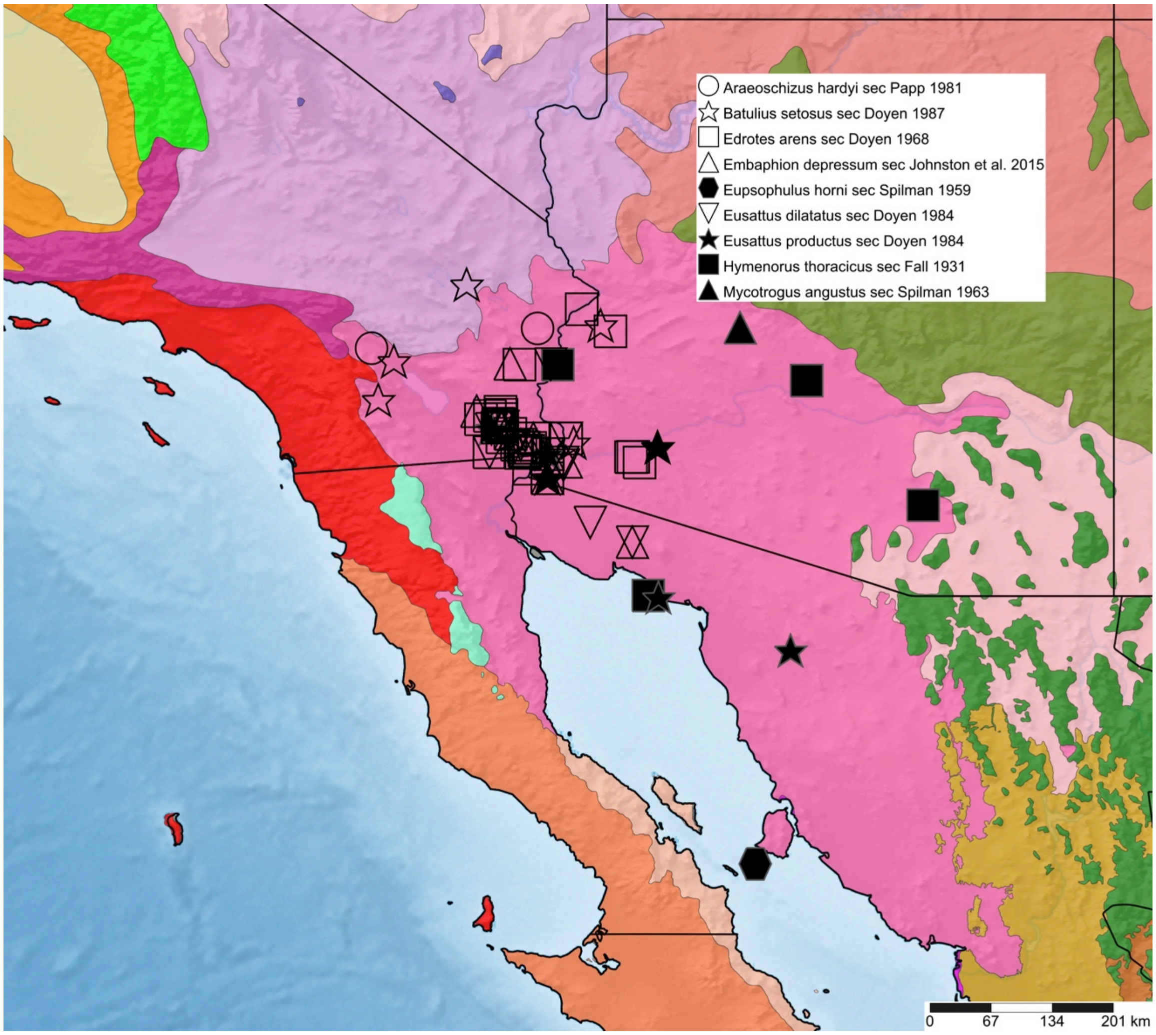

Figure 2.1. Lower Colorado River Valley Restricted Species Distributions. 239 digitized records from SCAN for 9 species. Map generated using www.simplemappr.net with background colors indicating ecoregions. The bright pink region encompassing the occurrence records roughly corresponds to the Lower Colorado River Valley subregion of the Sonoran Desert.

2.5.3. Broader biogeographic relationships

The Algodones and surrounding desert environs of southern California, though usually classified as part of the Sonoran Desert (Brown 1994), have strong floristic ties to both the Mohave Desert to the north and the Vizcaíno Region in the center of the Baja California peninsula (Shreve 1942). The tenebrionid fauna of the Algodones also has strong biogeographic ties to these regions (Table 2.3). The strongest faunal overlap is with the Mohave Desert, which shares 29 herein recognized species with the Algodones. In contrast, only 17 species extend their distributions into non-Lower Colorado River Valley regions in Baja California. Only 28 out of the 52 examined species have ranges that extend into other biogeographic areas, which typically included either coastal California or other subregions of the Sonoran desert. This rich tenebrionid fauna of the Algodones may owe its diversity in part to the blending of psammophilic faunas from the surrounding regions.

2.6. Discussion – new opportunities for authoring checklists

2.6.1. Review of the checklist update

Regional checklists are published to be used, corrected, expanded and inevitably become outdated - the sooner the better. In that sense and only for the subcomponent of the Tenebrionidae sec. Bousquet *et al.* 2018, the checklist of Kimsey *et al.* (2017) has already served its purpose. At the same time, we have shown that these authors (and the reviewers, presumably) could have worked more thoroughly on their checklist product (see also https://doi.org/10.3897/BDJ.6.e24927.suppl7). In addition to significant literature record omissions (e.g. Andrews *et al.* 1979) and nomenclatural errors, we may consider the institutional-only, non-Darwin Core database to be inadequate in the context of global biodiversity data aggregation (Maddison *et al.* 2012, Page *et al.* 2015). Moreover, occurrences of as many as 31 focal recognized species of Tenebrionidae sec. Bousquet *et al.* 2018 in the Algodones could have been discovered and included just by querying the SCAN portal. Indeed, every species recognized in Table 2.1 has at least one occurrence record in SCAN, though not necessarily from the Algodones. Thirteen species reported on SCAN from the Algodones were not listed in Andrews *et al.* (1979), including five which have never been reported from the region in published literature until now. In our view and considering the presence of nearly 7 million North American occurrences in SCAN currently (see Introduction), this suggests that any author, aspiring to generate a comprehensive and reliable checklist of North American insects, is well advised to explore and selectively include aggregated, occurrence data to their product. At a minimum, we would expect an explanation why such data were discarded, following their exploration (see also Ferro and Flick 2015, Sikes *et al.* 2016).

Of course, the flipside of the above message is this: a very considerable subsection of the Table 2.1 checklist depends solely on our access to and reliance on, specimen material from the Rolf L. Aalbu Collection. This collection has no on-line presence at the moment, nor foreseeable support to digitize these data moving forward. The RLAC data are both invaluable in their content and unsuited in their current form for a strictly Darwin Core-based checklist approach.

2.6.2. Evolving checklist data practices

Aggregated occurrence data typically come with a combination of data formatting and quality insufficiencies that are justly attributed to the digitizing source collection, plus other shortcomings newly generated in the process of aggregation (Mesibov 2013, Mesibov 2018, Franz and Sterner 2018). Rather than reviewing these issues (once more) in the context of our particular checklist update, we limit our discussion to a few pragmatic as well as more future-oriented solutions to enhancing occurrence data-based checklists.

We believe that the emergence of aggregated occurrence data should not only enrich the types of information sources and data formats that contribute to checklists, but should increasingly obviate altogether the notion of static, closed, print or digital checklist publications. Indeed, from a technical and perhaps also scientific point of view, the interaction between the Kimsey *et al.* (2017) checklist and our update need not take the form of two structurally unconnected information packages, each wholly attributed to either one or the other author team. Instead, we can envision the two respective contributions, or checklist versions, to develop as finely attributed bundles of annotations (Morris *et al.* 2013), managed on top of an underlying, unified Darwin Core-based occurrence data network. Similarities and differences between each version could then be expressed - almost entirely via automated services - as a differential ("delta" - Δ) between two Darwin Core-compatible sets of occurrence records. Subsequent authors would receive credit mainly for occurrences added, or reviewed and newly annotated, in relation to previously published records sets.

For such incremental, wholly Darwin Core-based published checklist versions to become reality, however, several aspects of authoring checklists need to receive careful attention. In particular, authors should express clearly which data sources of the current checklist version are also traceable to aggregated occurrences, or are solely reliant on expert assessment of non-mobilized records (compare Table 2.1 and Table 2.2). Our update shows that the latter category remains essential. At the same time, moving most or all occurrence records into the former category is highly desirable and a pre-requisite for fully Darwin Core standard-based checklists.

Likely, this also means that the biodiversity data community should strive to lower or remove technical and social barriers to mobilizing occurrences from private or institutional collections that currently lack the resources to accomplish aggregation. In other words, we believe that data mobilization by outsiders should become more frequent.

From a technical point of view, it is possible to set up a portal collection where any checklist author can mobilize and annotate any occurrence they are able to process as part of their research and data filtering effort - even and especially if the specimens in question belong to other individuals or institutions. We have done so, on an exploratory scale, with the "ARTSYS" collection (Externally Processed Specimens - Arthropod Systematics Research) in SCAN: http://scan-bugs.org/portal/collections/misc/collprofiles.php?collid=114. However, the prevalent culture for North American insect collections is that decisions regarding formal specimen digitization are strongly tied to the constraints of specimen ownership. This position is not well aligned with checklist author motivations to produce open, reusable data packages. An increased decoupling between the physical specimen repository and the ability to mobilize the associated occurrence data is needed.

Lastly, the notion of open, dynamic data checklists requires additional efforts to contextualize each version's - and indeed each occurrence record's - taxonomic concept usages and concept-referencing identification assertions. Too often the tradition of publishing static biodiversity data products is tied to an underlying assumption that readers will reliably understand the authors' name usages in context (though see Franz *et al.* 2016, Remsen 2016, Franz and Sterner 2018, Packer *et al.* 2018, Senderov *et al.* 2018).

Our use of taxonomic concept labels is one component of making checklists version-ready, by connecting the name usages in the above table to particular systematic treatments in which the corresponding evolutionary entities are circumscribed. Yet we should also note that, at the level of occurrences, our data are not fully there yet. Of the 693 occurrences taken from SCAN, maximally 229 records (33.0%) entail some information regarding the terms dwc:identifiedBy and/or dwc:dateIdentified. Only five occurrences (0.7%) have the term dwc:identificationReference filled with data. These ratios are unsatisfactory; and yet this low degree of concept/identification reference annotation is still better in relation to the data served up by the other two aggregators. iDigBio offers 454 occurrences, which detail no identification data at all. Meanwhile GBIF has 133 records, of which 92 (69.2%) show identification data. However, these data are very frequently altered - *i.e.*,"elevated" to the higher-ranked taxonomic name that the GBIF taxonomy recognizes - while (falsely) retaining the original identifier attribution (see also Franz and Sterner 2018). We note in passing that only the Symbiota portal allows us to directly (via username/password log in) contribute occurrence-level identifications and taxonomic concept information.

For regional, occurrence data-based checklists to become fully open and versioning-ready, the first version should set a high bar of decoupling both taxonomic name usages and the identifications of occurrences from under-contextualized taxonomic names. We have attempted this for our tabular Tenebrionidae sec. Bousquet *et al.* 2018 of the Algodones checklist update, but are falling short regarding the underlying occurrence-level data. Moving forward, we need to treat every occurrence like a prospective micropublication that can stand on its own (see also Packer *et al.* 2018), by carrying sufficient taxonomic and identification-related information to be re-aggregated and re-published in updated checklist versions while retaining the provenance of its taxonomic identity and expert work effort. Only then can we assign proper credit to these experts and their work of enhancing the quality of regional checklists.

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Chapter 3. Phylogenetic revision of the psammophilic *Trogloderus* LeConte (Coleoptera: Tenebrionidae), with biogeographic implications for the Intermountain Region

3.1. Introduction

The psammophilic genus *Trogloderus* LeConte, 1879, was originally erected for a unique species and specimen of the family Tenebrionidae (sensu Bouchard *et al.* 2011, Bousquet *et al.* 2018). Described as *Trogloderus costatus* LeConte, 1879, from Rock Creek, Idaho, this heavily sculptured species was thought to be similar to the old-world Scaurini Billberg, 1820, but has long since been associated with the desert stink beetles in the genus *Eleodes* Eschscholtz, 1829 in what is now considered the tribe Amphidorini LeConte, 1862 (LeConte 1879, Blaisdell 1909, Doyen & Lawrence 1979, Bousquet *et al.* 2018). Blaisdell (1909) described a second congeneric species, *Trogloderus tuberculatus* Blaisdell, 1909 from Los Angeles County, California during his revision of the tribe. A third species, *Trogloderus nevadus* La Rivers, 1943, was described from the dunes around Pyramid Lake, Nevada (La Rivers 1943). The genus was then revised by La Rivers (1946), where the three previously recognized species were sunk to subspecies of an again monotypic genus and a fourth subspecies, *Trogloderus costatus vandykei* La Rivers, 1946, was described from outside Twentynine Palms, California.

The recognition of subspecies (La Rivers 1946) was supported by invoking the theory of orthogenesis, a teleological view of evolution where species have an internal mutational force which drives them not only to a point of adaptation but then continues to push the species onward towards extinction (Eimer 1898, Mayr 1982; see also Grehan and Ainsworth 1985). Following this reasoning, it was hypothesized that *Trogloderus* has “embarked on that phase of evolutionary growth which seems to characterize any ancient group in the last stages of its existence – they are developing fluidly and rapidly into grotesque caricatures of their plain and drab ancestors” (La Rivers 1946: 35).

Following the 1946 revision, very little systematic research has been dedicated to this genus; except for two additional subspecies described as *Trogloderus costatus pappi* Kulzer, 1960, and *Trogloderus costatus mayhewi* Papp, 1961. All species and subspecies were described from a small number of specimens, with *T. nevadus* having the largest type series of 14 individuals. Subsequent to the above works, specimens in natural history collections have variously been determined as simply *Trogloderus costatus* or somewhat haphazardly assigned to subspecies. The last taxonomic changes to the genus were made by this author (MAJ) in the recent catalog of North American Tenebrionidae to stabilize the nomenclature in anticipation of this revision; namely, the subspecific names were all eliminated while restoring *T. costatus*, *T. tuberculatus*, *T. nevadus*, and *T. vandykei* to specific standing, and *T. costatus mayhewi* (= *T. vandykei*) and *T. costatus pappi* (= *T. tuberculatus*) were synonymized (Bousquet *et al.* 2018).

Over the last half century, a large number of *Trogloderus* specimens have been accumulated in North American natural history collections. These, along with targeted fieldwork for molecular vouchers, have made a thorough taxonomic and biogeographic study of *Trogloderus* possible for the first time.

Trogloderus is distributed throughout the Intermountain Region, which encompasses the generally arid lands of western North America between the Rocky and Sierra Nevada mountains. This region spans the Great Basin and Mojave deserts to the west along with the Colorado Plateau to the east. The most comprehensive biogeographic work on the region was completed by Reveal (1979), based largely on his extensive botanical fieldwork. The vast landscape with limited access, particularly in the state of Nevada, has resulted in a paucity of distributional knowledge and available specimens of beetles in natural history collections (Will *et al.* 2017).

The molecular phylogenies inferred for the herein revised species-level entities are used in diversification analyses and biogeographic reconstructions. The biogeographic hypotheses generated from these investigations are discussed in relation to other regional treatments. It is hoped that these insights will spur additional studies within the region and provide a framework to understand sand dune relationships.

3.2. Materials and Methods

3.2.1. Morphological methods

A total of 3,734 specimens were studied. Remarkably, over half (1957) came from non-institutionalized collections, which is a testament to the importance of individual collections and collectors for documenting North American darkling beetle diversity. The following collections were used for this study:

ADSC	– Aaron D. Smith Collection, Flagstaff, AZ
AMNH	– American Museum of Natural History, New York, NY
ASUHIC	– Hasbrouck Insect Collection, Arizona State University, Tempe, AZ
CASC	– California Academy of Sciences, San Francisco, CA

CSCA – California State Collection of Arthropods, Sacramento, CA
CIDA – Orma J. Smith Museum of Natural History, College of Idaho, Caldwell, ID
EMEC – Essig Museum of Entomology, University of California, Berkeley, CA
FSCA – Florida State Collection of Arthropods, Gainesville, FL
FWSC – Frederick W. Skillman Collection, Pearce, AZ
KKIC – Kojun Kanda Insect Collection, Flagstaff, AZ
LACM – Natural History Museum of Los Angeles County, Los Angeles, CA
MAJC – M. Andrew Johnston Collection, Tempe, AZ
OSUC – Triplehorn Insect Collection, The Ohio State University, Columbus, OH
RLAC – Rolf L. Aalbu Collection, Sacramento, CA
SWC – Samuel Wells Collection, Cedar City, UT
UCDC – Bohart Museum of Entomology,University of California, Davis, Davis, CA
USNM – National Museum of Natural History, Washington, DC
WBWC – William B. Warner Collection, Chandler, AZ

Specimens were examined using a Leica MZ16 stereomicroscope fitted with an ocular graticule for measurements. Internal anatomy was studied via 16 whole-body disarticulations where specimens were cleared in warm 10% KOH, neutralized in acetic acid, and then separated into constituent sclerotized sections in glycerin. Beetle terminalia were further studied from many more specimens by dry dissection. This technique involved prying abdominal ventrites 4-5 and associated internal structures from the pinned specimens, soaking them in distilled water, and separating out the sclerotized reproductive structures. These structures (ovipositor or aedeagus) were then pointed along with the dismembered ventrites and surviving tergites underneath the original pinned specimen.

Morphological terminology generally follows Doyen (1966). Female terminalia morphology follows Iwan and Kaminski (2016), whereas male terminalia follow Iwan (2001) except for the usage of the term clavae (following Blaisdell 1909) over laciniae for the ventral articulated structures of the fused parameres that flank the penis. A detailed internal and external description is provided for the genus and each species is then accompanied by a smaller differential description for the limited variable characters between species.

The evolutionary species concept of Wiley and Mayden (2000) is employed in this study. Unique combinations of morphological characters, diagnosable monophyletic clades, and coherent geographic distributions were evaluated together to diagnose putative lineages with a shared evolutionary past and unique evolutionary trajectory.

3.2.2. Molecular and biogeographic methods

A total of 36 specimens of *Trogloderus* and an additional eight outgroup species from Amphidorini are included in the final matrix. For *Trogloderus*, all type localities were visited and specimens representing each described species and subspecies were collected. Specimens were collected from as many known localities as possible, with sampling covering all broadly recognized goegraphic subregions. The collecting locality of each voucher is shown in Fig. 3.1, and the voucher numbers are included in all presented phylogenetic trees. An additional eight outgroups were included which span the known generic and subgeneric diversity of Amphidorini (Bousquet *et al.* 2018).

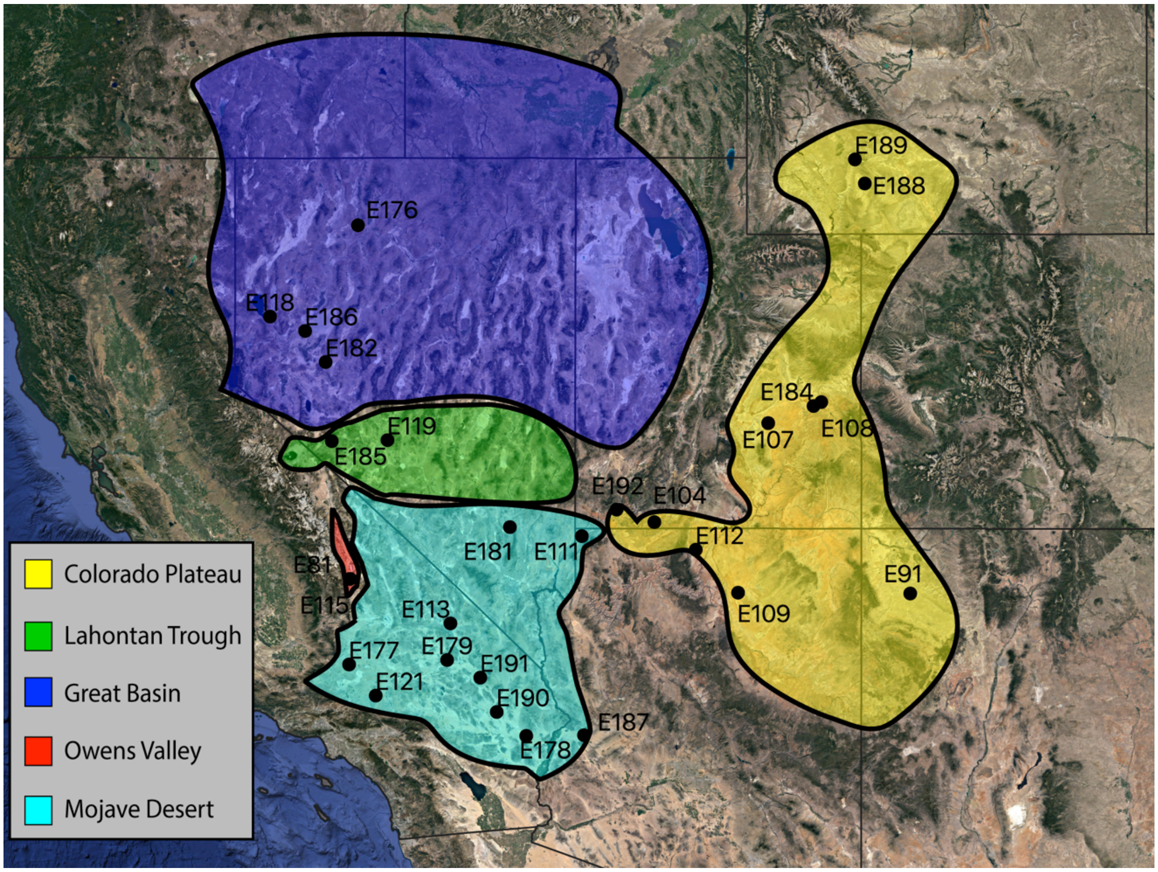


Figure 3.1. Collection localities of *Trogloderus* molecular vouchers and biogeographic regions.

Fresh specimens were collected and preserved in 95% ethanol at -20°C. DNA extractions were made from either the head capsule or a leg and associated thoracic musculature using the DNEasy Blood & Tissue Kit (QIAGEN, www.qiagen.com). Six loci amplified via PCR for this study are given in Table 3.1, generally following Kanda (2017). Forward and reverse sequences were obtained for each PCR product using an Applied Biosystems 3730 DNA Analyzer. The resultant chromatograms were edited for final base calls using Geneious version 7 and aligned using MAFFT version 7 (Katoh and Standley 2013) as implemented through Mesquite (Maddison and Maddison 2018). The final aligned dataset contained 3707 base pairs.

All loci were separated into codon position, except for the ribosomal 12s and 28s, and analyzed by PartitionFinder 2 (Lanfear et al. 2016) using unlinked branch lengths and the greedy search algorithm (Lanfear et al. 2012). The resultant two-partition scheme was used in downstream phylogenetic and diversification analyses. Phylogenetic reconstruction was performed both by RAxML version 8 (Stamatakis 2014) with support values calculated by rapid bootstrap analysis with 500 replicates, and by MrBayes version 3.2 (Ronquist and Huelsenbeck 2003) which was run using four chains for 10 million generations sampled every 1000 with the first 25% being discarded as burnin. Trees were rooted by using the clade containing the three *Eleodes* subgenera *Eleodes*, *Metablapylis* Blaisdell, 1909, and *Steneleodes* Blaisdell 1909 based on phylogenomic analyses for the whole tribe (see Chapter 4).

Diversification analyses were performed using two methods. First, RelTime (Tamura et al. 2012) as implemented in MEGA7 (Kumar et al. 2016) was used to infer a timetree given the maximum-likelihood (ML) tree from RAxML and the aligned

Table 3.1. Loci and associated primers used.

Locus	Alignment length (bp)	Primers used	Primer source
Cytochrome c oxidase subunit 1 (COI)	792	Jerry (F) Pat (R)	Simon et al. 1994
Cytochrome c oxidase subunit 2 (COII)	700	F-lue (F) 9b (R)	Whiting 2002
12S mitochondrial ribosomal RNA (12S)	350	SR-J-14233 (F) SR-N-14588 (R)	Simon et al. 1994
28S ribosomal RNA (28S)	1030	NLF184 (F)	Van der Auwera et al. 1994
		D3ar (R)	Maddison 2008
Histone 3 (H3)	361	Haf (F) Har (R)	Colgan et al. 1998
Wingless (wnt)	474	wg550f (F) wfAbrZ (R)	Wild and Maddison 2008

nucleotide data. Second, the BEAST2 package (Bouckaert et al. 2014) was used to infer a dated phylogeny under both a Yule and Birth-Death model. The latter two analyses had unlinked exponential relaxed clocks for each partition and were run for 500 million generations and sampled every 20000 with parameter convergence being assessed via Tracer 1.7 (Rambaut et al. 2018) and a maximum clade credibility tree being computed by TreeAnnotator from the BEAST2 package with the first 25% of trees being discarded as burnin.

Two geological calibration points were used for all diversification analyses, due to the lack of any fossils for the tribe. The first calibration is the uplift of the Inyo and White Mountains, which form the eastern bounds of the Owens Valley and separate it from the Great Basin and Mojave Desert. The uplift of these mountains started between 2.8 and 2.3 mya (Backman 1978, Lee *et al.* 2009), and the calibration prior for the common ancestor of the three *Trogloderus* species distributed across these mountains was set as a normal distribution with a mean of 2.5 mya and standard deviation of 1 my. The second calibration is the deeply incised eastern margin of the Grand Canyon in northern Arizona. Two populations of a new species were sampled, one from sand dunes north of the Colorado river just below the Vermillion Cliffs, and one south of the Colorado river near Moenkopi. These two populations are separated by the gorge just downstream from Marble Canyon, which was been dated as 0.83 my old (Polyak *et al.* 2008). The calibration prior for the common ancestor of these two populations was set as a normal distribution with a mean of 0.83 mya and a standard deviation of 0.35 my.

Historical biogeographic reconstructions were performed in the BioGeoBEARS package (Matzke 2013) in R (R Core Team 2018) using the calibrated tree from the

RelTime analysis. Six geographic areas of endemism were defined (Fig. 3.1) based primarily on previous biogeographic work of the intermountain (Reveal 1979) and southwestern desert (Van Dam and Matzke 2016, Wilson and Pitts 2010) regions. The six areas are as follows: (1) Great Basin – centered around northern Nevada, northwestern Utah and southern Idaho in the regions shaped by the prehistoric lakes Lahontan and Bonneville and including the Snake River plain (Reveal 1979, Britten and Rust 1996, Wilson and Pitts 2010); (2) Mojave Desert – the southwestern-most region of *Trogloderus* distribution which includes much of southeastern California, southern Nevada as well as far western Arizona and southwestern Utah (Shreve 1942, Reveal 1979, Wilson and Pitts 2010, Van Dam and Matzke 2016); (3) Lahontan Trough – a transverse transition zone between the Mojave and Great Basin deserts which shares floristic components with both regions and was never part of the prehistoric Lake Lahontan (Reveal 1979, Pavlik 1989, Britten and Rust 1996, Hafner *et al.* 2006); (4) Colorado Plateau – the desert areas surrounding the four-corners region west of the Rocky Mountains and generally east of the Wasatch mountains of Utah (Reveal 1979, Wilson and Pitts 2010); (5) Owens Valley – a narrow region bounded by the eastern Sierra Nevada mountains to the west and the Inyo and White mountains to the east, this transition region also has strong floral and faunal similarities with both the Mojave and Great Basin deserts (Reveal 1979, Andrews *et al.* 1979, Macey 1986, Pavlik 1989, Van Dam and Matzke 2016); and (6) Widespread – this was used for outgroup taxa whose ranges extend into other areas of western North America.

3.2.3. Data management and availability

All specimens examined were digitized and are available online through the Symbiota Collections of Arthropods Network (SCAN; Gries *et al.* 2014, http://scan-bugs.org). Collecting events lacking GPS data on the label were georeferenced using Google Earth Pro version 7.3 and GEOLocate (www.geo-locate.org) as implemented in SCAN. Specimens from external institutions, which constituted the majority of those examined, were digitized using the SCAN Collection of Externally Processed Specimens (ARTSYS, see Johnston *et al.* 2018). All molecular and disarticulation vouchers are deposited in the MAJC and have images available with the pertinent specimen records on SCAN. Due to the fully digitized and available specimen data, verbatim label data are not included in the main text except for holotypes.

3.3. Systematics

3.3.1. Amphidorini LeConte, 1862

The complex nomenclatural and taxonomic history of Amphidorini has been summarized by Doyen and Lawrence (1979) and Johnston *et al.* (2015), and is only outlined here. The tribe has frequently and historically been treated within the subfamily Tenebrioninae Latreille, 1802 (Bouchard *et al.* 2005, 2011; Bousquet *et al.* 2018), but recent phylogenetic studies place the Amphidorini in a clade with several other tribes in what has been referred to as the subfamily Opatrinae Brullé, 1832 (Aalbu *et al.* 2002, Kanda 2017, Kaminski *et al.* 2018).

The North American genera of this tribe can be separated from other members of Tenebrionidae by the following combination of characters: abdominal ventrites III-IV with visible membrane along hind margin; antennae lacking compound stellate sensoria; tarsal claws simple, not pectinate; penultimate tarsomeres not lobed beneath; elytra fused medially, hind wings reeuced to small folds; paired defensive glands present between abdominal sternites VII and VIII, glands separate lacking a common volume, glands smooth, not annulated; mentum trilobed with mesal face more or less produced anterad, often concealing insertion of ligula; female paraproct and coxite short, coxite 1-segmented, with short subapical gonostyle; female with single, bursa-derived spermatheca.

The tribe is currently comprised of seven genera, six of which are known only from North America. Published keys to genera (Aalbu *et al*. 2002, Johnston *et al*. 2015) are sufficient to separate *Trogloderus* from other Amphidorini, though a generic revision of the tribe is in progress (see Chapter 5).

3.3.2. *Trogloderus* LeConte, 1879

Type species *Trogloderus costatus* LeConte, 1879, by monotypy

Diagnosis. *Trogloderus* (Fig. 3.2) can be distinguished from other members of Amphidorini by the following characters: body roughly sculptured, pronotum either tuberculate or roughly punctured. Elytron with four sharply carinate longitudinal costae, elytral suture costate or not. Tarsi lined beneath with yellow to castaneus spicules, never with tomentose pads, probasitarsus thickened ventrally near distal margin.

Male: Body elongate, roughly sculptured, ferruginous to black. Length 9–16 mm. Width 4–6 mm.

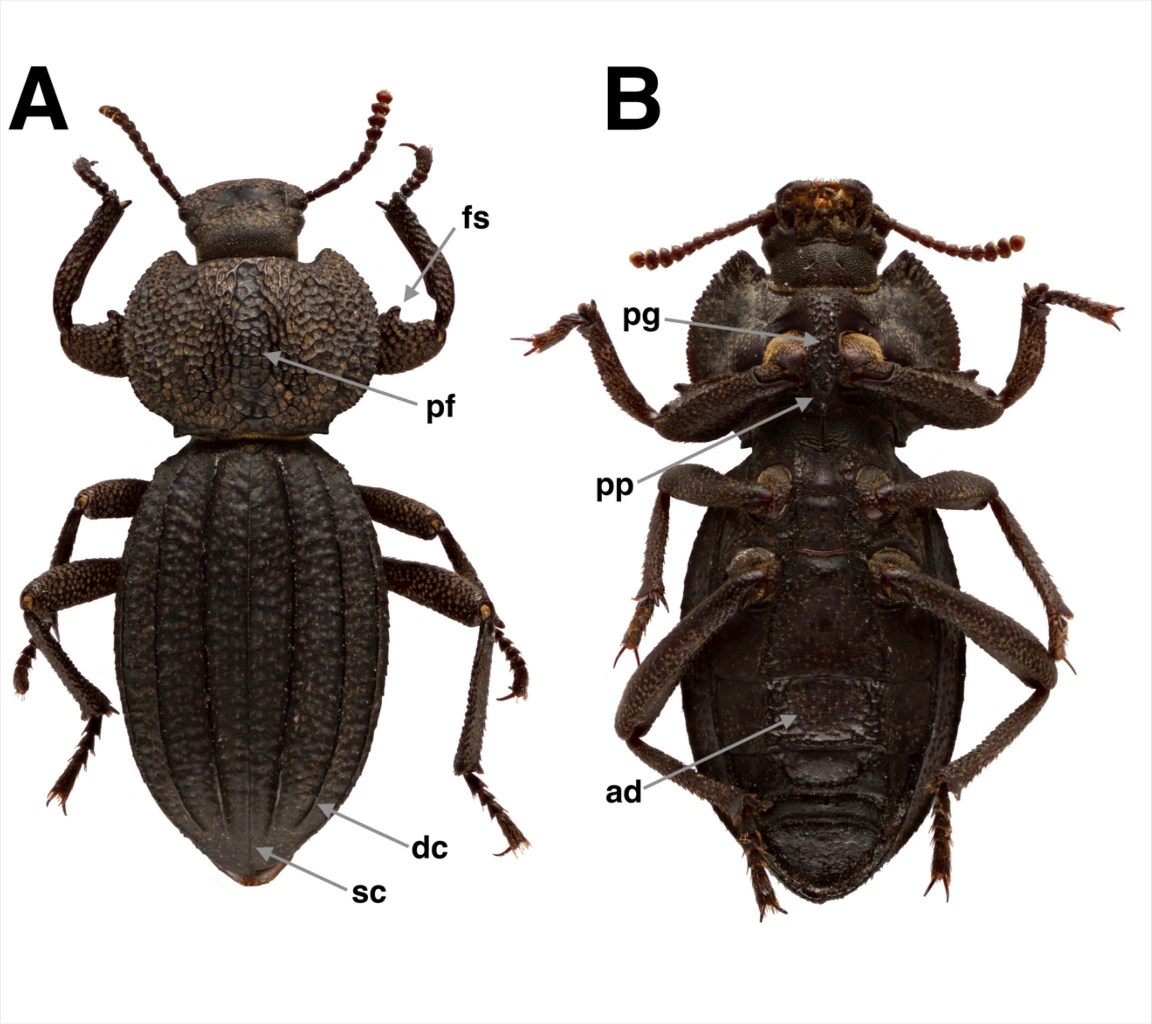


Figure 3.2. *Trogloderus* external morphology. A. Dorsal habitus, *Trogloderus vandykei* La Rivers. B. Ventral habitus, *Trogloderus vandykei* La Rivers. *ad* – abdominal depression, *dc* – elytral discal costa, *fs* – femoral spine, *pf* – pronotal foveae, *pg* – prosternal groove, *pp* – prosternal process, *sc* – elytral sutural costa.

Head. As broad as long. Antenna 11-segmented, extending to posterior 2/3 of pronotum; antennomere III 1.5× as long as IV, IV–VII obconical, roughly as long as wide, VIII–XI wider than long, VIII with sensory patch of yellow setae along outer margin of apical face, IX–XI with sensory patch forming continuous ring around apical face. Labrum free, partially exposed, broader than long; anterior margin rounded laterally, deeply sinuate mesally; each lobe bearing tuft of short yellowish setae; dorsal surface punctate, each puncture bearing a long yellow seta, punctures becoming denser anteriorly; hypopharynx originating just posteriorly of anterior ventral margin, anterior hypopharyngeal sclerite ovoid, transverse, 1.5× wide as long. Mandibles (Fig. 3.3A–B) roughly symmetrical, bidentate, the left slightly larger than and overlapping the right at rest; dorsal face striate, more strongly so anterolaterally; lateral face with longitudinally elongate punctures, each bearing a single seta; ventral surface concave, smooth; mola present, strongly sclerotized, finely granulate; prostheca large, membranous, extends laterally around mola to form a large submola. Maxillae (Fig. 3.3C–D) ferruginous, symmetrical; cardo subtriangular, narrowing proximaly, lightly punctate; basistipes bearing thickened setae, subtriangular, narrowing distally, articulated with cardo basally and basigaleaanterolaterally, mediostipes anteromesolly, and palpifer anterolaterally; mediostipes subtransverse, glabrous, articulated with lacinia distally; lacinia well developed, mesal surface bearing a terminal digitus followed proximally by robust lacinial teeth which become setae in basal 1/3; basigalea thin, articulated with distigalea apically, bearing fine, long setae; distigalea 1.5x longer than wide, anterior and mesal surface densely clothed with thick yellowish setae, dorsal surface bearing moderately separated, long yellowish setae; palpifer digitate ventrally, bearing stout setae; palpi with 4 palpomeres, palpomere I small, subtriangular, II elongate, obconical, III slightly shorter than II, clavate, IV securiform, apical surface bearing yellowish membranous

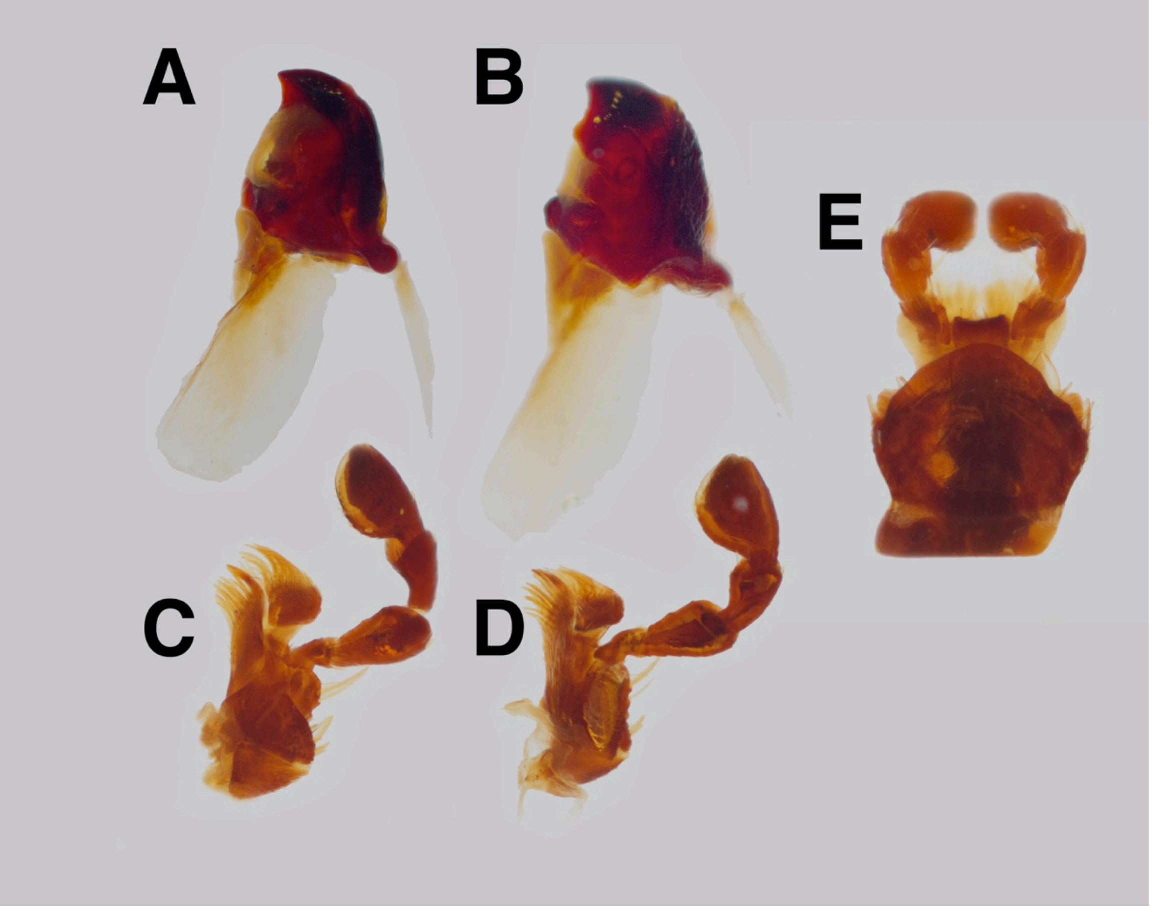


Figure 3.3. *Trogloderus* mouthparts. Dissected from MAJC0004230, *T. major* Johnston n.sp. A. Right mandible, ventral view. B. Left mandible, dorsal view. C. Right maxilla, ventral view. D. Left maxilla, dorsal view. E. Labium, ventral view.

sensorium. Mentum (Fig. 3.3E) trilobed, with mesal region of dorsal face produced anteriorly into arcuate lobe, covering insertion of ligula; ligula transverse, bearing two apical tufts of stout setae along dorsal face; labial palp with 3 palpomeres, palpomere I obconical, as long as wide, II clavate, 1.5× long as wide, III fusiform and evenly setose; hypopharyx moderately sclerotized along anterior margin, hypopharyngeal brush forming thickened longitudinal band from anterior margin of hypopharynx to posterior margin of mentum. Clypeus fused to frons, roughly sculptured, broadly sinute at middle, frontoclypeal suture indistinct to faintly traceable in teneral individuals. Frons usually slightly sunken, less roughly sculptured than clypeus, with slightly elevated bilobed tubercle centrally; epistomal lobes produced, distinctly offset from clypeus. Eyes entire, reniform, dorsal lobe 5–6 facets wide, ventral lobe 3 facets wide. Vertex at same level and contiguous with central tubercle of frons; becoming strongly granulate towards occiput. Submentum short, arcuate posteriorly, faintly evident; gular sutures diverging posteriorly, well rounded, gula less coarsely sculptured than surrounding head capsule.

Thorax. Pronotum roughly sculptured; lateral margins strongly curved, crenulate along entire length, sinuate at posterior angle, anterior angles acute, projected, with longitudinal depression along midline, often separated into anterior and posterior foveae (Fig. 3.2A, pf); prosternal length from anterior margin to procoxae subequal to procoxal diameter; procoxae separated by approximately ½ procoxal diameter; prosternal process (Fig. 3.2B, pp) projected posteriorly; procoxal cavities closed posteriorly by postcoxal bridge of pronotum which meets the prosternal process mesally; pleural apophysis (Fig. 3.4A) directed anterodorsally, becoming laminar and longitudinally expanded near ventral surface of pronotum, with short dorsal coxal articulation extended mesally around basal 1/3; prosternal apophysis straight, extending dorsolaterally, terminating

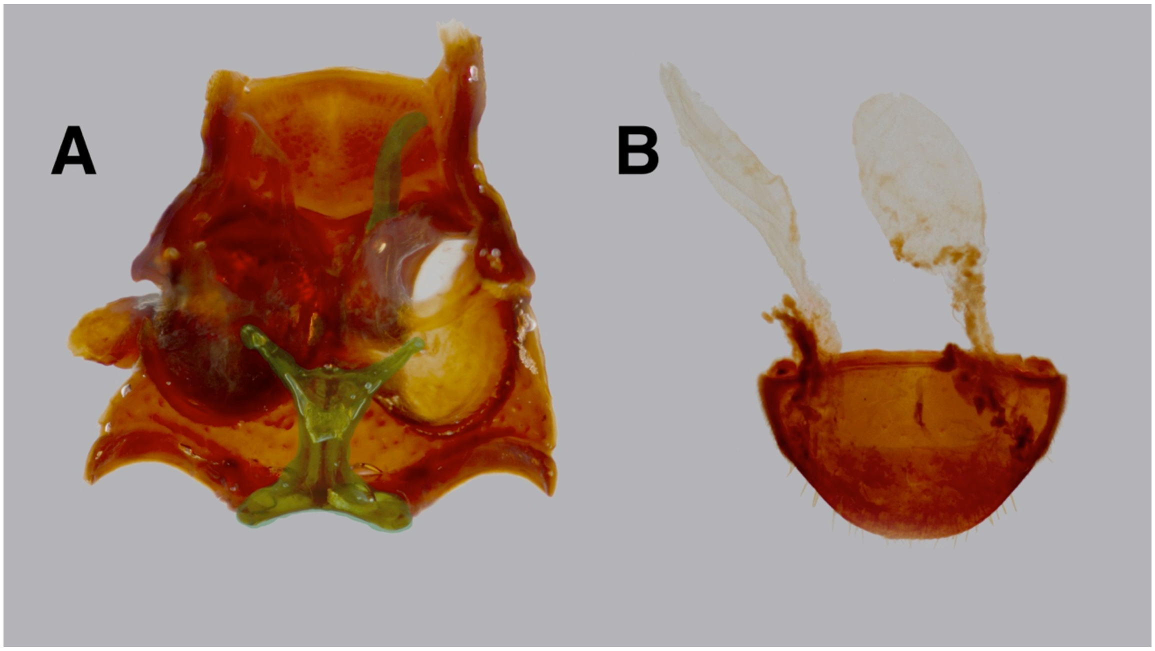


Figure 3.4. *Trogloderus* internal morphology. A. Pterothorax venter, dorsal internal view; Metendosternite and right mesosternal apophysis highlighted; Dissected from MAJC0004244, *T. warneri* Johnston n.sp. B. Defensive glands and abdominal ventrite V, dorsal internal view; Dissected from MAJC0004231, *T. arcanus* Johnston n.sp.

near dorsal margin of coxa. Mesonotum strongly transverse, triangular, densely papillose; scutellar shield wide and short, lacks papillae, strongly microsculptured; mesanepisternum subtriangular, narrowing posteroventrally, anterior 1/3 with integument thickened, papillose, offset from posterior 2/3 by posteriorly concave ridge demarking a section of thinner integument, punctate in posterior 1/3; mesepimeron short, fairly evenly punctate; mesoventrite with anterior 1/2 covered by prothorax at rest, posterior 1/2 projected ventrally between coxae, with longitudinal groove to receive prosternal process; mesocoxal cavities closed externally by mesoventrite, mesepimeron, and metaventrite; mesosternal apophyses extend anteriorly from apex of mesocoxal cavity, recurved dorsally and then posteriorly around anterior 1/4 of mesoventrite. Metanotum greatly reduced, prescutum forming narrow arch, strongly connected to the mesonotum, remainder of metanotum forming short, somewhat heavily sclerotized membrane, without discernable subregions; metepimeron forming narrow rod-like longitudinal sclerite along length of metathorax, concealed beneath elytron, posteriorly with short ventrally projected metepimeral process which is fused with metepisternum above metacoxal cavity; metepisternum elongate, subrectangular; metaventrite short, length less than mesocoxal diameter, antecoxal ridge deeply impressed above anterior coxal margin, discrimen not apparent; metacoxal cavities closed externally by metaventrite, metepisternum, metepimeral process, and first abdominal ventrite; metendosternite (Fig. 3.4A) stout, stalk broad, ventral longitudinal flange very well sclerotized, furcae as wide as stalk, relatively immovable, furcal apicies reflexed posterolaterally, forming horizontal pad for furca-trochanteralis muscle attachment, anterior tendons inserted at apical 1/4 of furcae. Elytra fused, suture elevated or not; elytron disc (Fig. 3.2A, dc) with 4 longitudinal carinate costae; epipleuron narrow throughout length, not or slightly widened anteriorly, attaining elytral apex posteriorly.

Hind wings greatly reduced, forming veinless tubular sac, approximately the size of first abdominal spiracle.

Legs. Fore leg slightly enlarged, weakly fossorial; femur clavate, heavily punctate, dorsal anterior margin carinate from base to apical 1/5, ending in short recurved spine (Fig. 3.2A, fs); tibia with inner face excavated in basal 1/5, outer face carinate from base to near tarsal insertion, apex bearing row of ferruginous spicules dorsally, tibial spurs subequal, extending to apex of tarsomere II; tarsus bearing furriginous spicules, tarsomere I ventrally thickened at apex, maximum height equal to length, II–IV subequal, relatively short, about as tall as long, V slightly clavate, as long as II–IV combined; empodium minute, hidden within tarsal apex, bearing 2 yellowish setae; tarsal calws simple, evenly arcuate, 2/3 length of tarsomere V. Middle and hind legs similar to fore leg, tibia subcylindrical, not expanded; all tarsomeres simple, not thickened beneath.

Abdomen. 5 visible ventrites, ventrite I intercoxal process truncate, rectangular, twice as broad as long, I–III connate, fused to elytra laterally, III–IV with visible membrane posteriorly, I–II bearing variously developed longitudinal ridges demarking flattened abdominal depression (Fig 2B, ad) in line with thoracic intercoxal region; tergites membranous, weakly sclerotized; paired defensive glands (Fig 4B) present posterior to ventrite V (between sternites VII–VIII), glands lacking a common volume, each gland elongate, subfusiforme, extending anterior of ventrite II, membrane finely strigose, lacking annular pleats, gland openings centered around lateral 1/5.

Terminalia. Tergite VIII weakly sclerotized, posterior margin evenly arcuate, bearing row of fine golden setae; sternite VIII weakly sclerotized, bilobed, deeply emarginate posteriorly, each lobe subtriangular, clothed ventrally and posteriorly with long yellowish setae, anterior deeply margin bisinuate, thickened into apodemes. Spicules V-shaped, fused anteriorly, 1.5× length of tergite VIII, spicule plates moderately small, 4x width of spicules, twice as long as wide. Adeagus (Fig. 3.5C) elongate, cylindrical; basal piece 4x as long as wide, lateral margins (alae) reflexed inwardly, leaving ventral face open, apicodorsal margin concave; parameres fused, ½ length of basal piece, widest basally, 1.5x long as wide, apical half curved ventrally; clavae (Fig. 3.5C) narrow, about as long as parameres, 1/6 maximum width of parameres; penis narrow, lightly sclerotized, fully hidden dorsally by parameres at rest.

Female. As male but generally more stout, fore femoral spines variable, typically less developed than males, base of tibia generally not constricted, central abdominal groove less developed.

Terminalia. Tergite VIII moderately sclerotized, posterior margin evenly arcuate, bearing golden setae; sternite VIII moderately sclerotized, evenly arcuate podsteriorly, bearing golden setae, fused medially to spiculum ventrale along anterior margin, spiculum ventrale 1.5× medial length of tergite VIII. Proctiger (Fig. 3.5A) slightly longer than wide, posterior margin weakly emarginate, bearing single row of short yellow setae. Paraproct subrectangular dorsally (Fig. 3.5A), subtriangular ventrally (Fig. 3.5B), bacculus obliquely pointed psoteromesally, thickened mesally. Coxite 1-segmented, subrectangular in dorsal view, narrowing posteriorly, subtriangular in ventral view, bacculus obliquely pointed anteromesally. Gonostyle short, inserted ventrally, at most

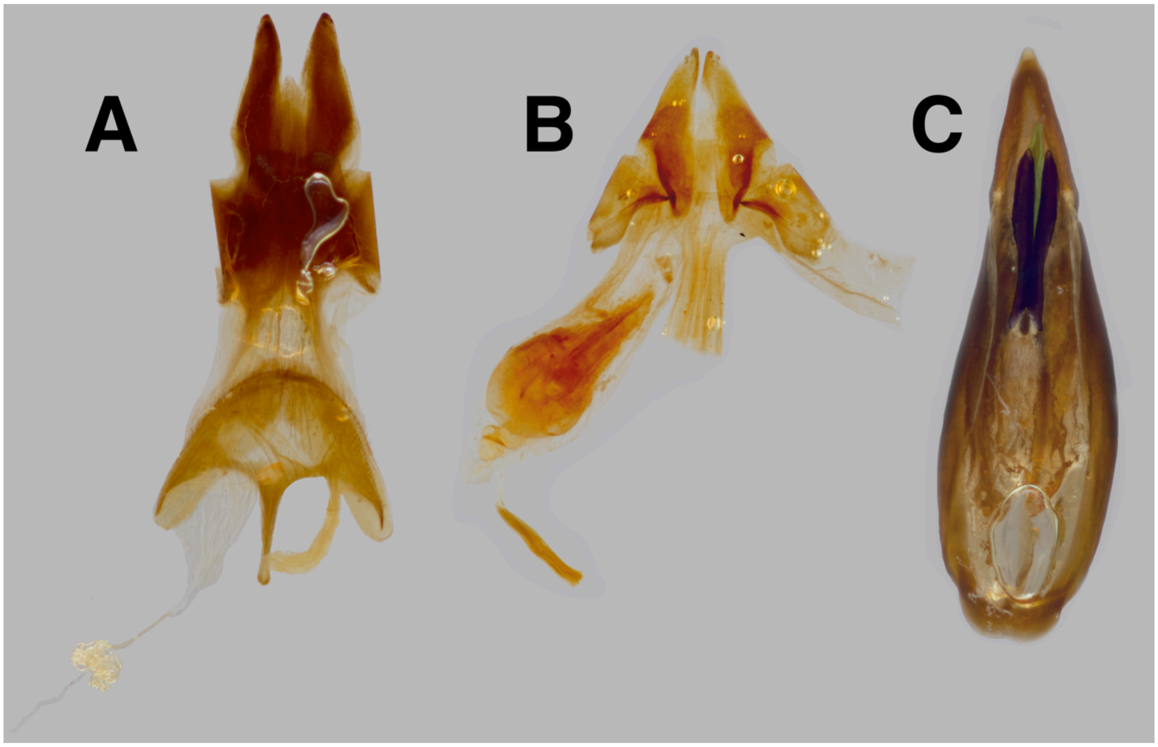


Figure 3.5. *Trogloderus* terminalia. A. Female terminalia, dorsal view, showing bursa-derived spermatheca; *T. vandykei* La Rivers. B. Female terminalia, ventral view, showing bursa copulatrix and oviduct; Dissected from MAJC0004243, *T. major* Johnston n.sp. C. Male adeagus, ventral view; clavae and penis highlighted; *T. vandykei* La Rivers.

weakly visible from above. Bursa copulatrix (Fig. 3.5B) about 2× length of coxite, bearing single spermatheca (Fig. 3.5A) off of duct from anterior margin with single long spermathecal gland.

3.3.3. *Trogloderus* variation and natural history.

Sexual dimorphism is primarily observed in the fore tibiae and abdominal ventrites. The fore tibiae of males are generally more explanate along the outer edge and are more strongly constricted proximally. The femoral spines are often slightly stronger in the males as well, where they pair with the constricted tibiae to form a grasping mechanism – presumably used to hold the females legs or antennae during copulation. The abdominal depression also tends to be stronger in males, with the marginal ridge more produced and the central region more depressed. This is also assumed to help the male in positioning during copulation.

Relatively little is known of *Trogloderus* biology. Adults have not been successfully cultured in the lab and larvae and pupae remain unknown and undescribed from the wild. Adult beetles are able to burrow into loose sand, where the immature stages presumably live. More commonly, adults are observed emerging from mammal burrows after dark where they seem to take shelter underground during the day. Like other Amphidorini, adults can also be found, though not particularly abundantly, under rocks or loose boards. *Trogloderus* are very active at night, and seem to travel good distances across open ground likely in search of food, mates, or new sites to shelter during the day.

Collection records and field observations indicate that this genus is restricted to habitats with loose sand. While the largest populations seem to be from deep aeolian sand formations, they can also be found in areas of fine loose sand along rivers and across desert flats, e.g. in small sand hummocks around the base of desert shrubs.

3.4. Key to the species of *Trogloderus*

3.4.1. Diagnostic utility of characters

The extreme sculpturing of *Trogloderus* makes the genus readily recognizable among Amphidorini, but also seems to magnify the relatively broad individual and geographic intraspecific variation found throughout the tribe (*e.g.* see Triplehorn and Thomas 2012; Johnston 2015, 2016). The female ovipositor has been heavily relied upon to classify species into genera and subgenera (Blaisdell 1909; Triplehorn and Thomas 2012; Johnston 2015, 2016), yet it is fairly constant throughout *Trogloderus* and was found unreliable for species identification. Male terminalia can be diagnostic for some species, but not for all (Somerby 1972, Aalbu *et al.* 2012). Within *Trogloderus*, the basic shape of the parameres can sometimes aid in distinguishing some species from each other by examining the curvature of the lateral margins, but do not alone reliably distinguish one species from all others.

General facies, elytral sculpturing, and body size were found to be largely unreliable for species recognition as they can vary within populations and especially between populations. It is not uncommon to find locally homogenous populations to have strong differences between them. Whether this is due to some environmental variable such as food or water availability or simply stochastic due to limited gene flow is unclear. The sculpturing of the pronotum and head seems to be more stable within species and are heavily relied upon in the following identification key.

Though coloration was previously used as a secondary diagnostic character (La Rivers 1946, Papp 1961), it is here found to be unusable for species determinations. Rather, it seems that the cuticle of adult *Trogloderus* takes a fairly long time to fully harden and that more teneral specimens exhibit a red coloration, which then matures to a darker black in the longest-lived individuals. This is based on the observation that in almost every large series known there is a spectrum of red to castaneus to black individuals. Specimens with a brighter red coloration seem to have thinner cuticle (personal observation while pinning specimens) and even less strongly sclerotized terminalia. This is perhaps a strategy for these desert-dwelling beetles to limit the duration of the potentially more susceptible immature stages in preference of a longer hardening period as an adult. It is not clear whether the teneral adults are reproductively viable as no eggs have been observed in such individuals when dissected, and this could be an example of Reifungsfraß, the need for a maturation feeding period (see McNee *et al.* 2000).

3.4.2 Dichotomous key to the species of adult *Trogloderus*

1 Pronotal surface distinctly tuberculate... 2
1’ Pronotal surface not tuberculate, heavily punctate to cribrate..............................5

2 (1) Each elytron with large subapical tubercle at outer carinal terminus; pronotal foveae delimited laterally by raised longitudinal ridges (Mojave Desert) .... *Trogloderus tuberculatus* Blaisdell (Fig. 3.6A)

2’ Elytra without posterior tubercles; pronotum lacking elevated ridges, foveae lined by tubercles originating from same surface as those of the disc (widespread) 3

3 (2’) Posterior pronotal angles more or less inflated; lateral margins of pronotal disc slightly depressed, lacking tubercles (western Colorado Plateau)... *Trogloderus warneri* n. sp. (Fig. 3.6C)

3’ Posterior pronotal angles not at all inflated; lateral regions of pronotal disc not depressed, tubercles relatively evenly dispersed from foveae to lateral margins .. 4

4 (3’) Male parameres triangular, evenly tapering from base to apex; elytral carinae often granulately tuberculate on sides (west of Kaibab Plateau).. *Trogloderus skillmani* n. sp. (Fig. 3.6D)

4’ Male parameres distinctly constricted near base, then evenly tapering to apex; elytral carinae usually lacking tubercles on sides (east of Kaibab Plateau) ....*Trogloderus verpus* n. sp. (Fig. 3.6B)

5 (1’) Pronotal dorsum bilobed in anterior view; pronotum strongly explanate laterally; pronotal foveae joined into single longitudinal groove (Mojave Desert) .... *Trogloderus vandykei* La Rivers (Fig. 3.1)

5’ Pronotum evenly convex in anterior view; pronotum weakly to moderately explanate laterally; pronotal foveae variable, often distinctly separated (widespread) 6

6 (5') Pronotum cribrately punctured, margins of punctures strongly elevated; intervals between elytral carinae bearing short, transverse secondary ridges ....*Trogloderus costatus* LeConte (Fig. 3.6F)

6' Pronotum heavily punctate, margins of punctures not strongly elevated; intervals between elytral carinae usually smooth, lacking well-defined secondary ridges 7

7 (6') Propleurae lacking tubercles on dorsal half, never with tubercles anteriorly just underneath pronotal margin; pronotal foveae joined into single well-demarked longitudinal groove .... *Trogloderus major* n. sp. (Fig. 3.6H)

7' Propleurae wth tubercles in dorsal half, at least anteriorly underneath pronotal margin; pronotal foveae variable, usually not forming single longitudinal groove 8

8 (7') Epistoma roughly punctured, individual punctures evident above antennal insertion; pronotal punctures fairly evenly circular, discrete; elytral costae moderately to strongly produced; male parameres broadly triangular in dorsal view, sides straight and evenly tapered (southern Owens Valley).. *Trogloderus kandai* n. sp. (Fig. 3.6I)

8' Epistoma finely to roughly tuberculate, individual punctures not evident above antennal insertions; pronotal punctures often longitudinally oval, sometimes coalescent anteriorly; elytral costae weakly to moderately produced; male parameres narrowly triangular in dorsal view, sides gently to moderately arcuately concave (widespread).. 9

9 (8’) Frontoclypeal suture forming a complete transverse ridge, frons apex below the plane of clypeus base; male parameres broadly triangular, evenly converging; prosternal process horizontal, on the same plane as the prosternum between the procoxae; punctures larger (northern Great Basin)... .... *Trogloderus nevadus* La Rivers (Fig. 3.6G)

9’ Frontoclypeal suture usually not forming complete transverse ridge, mesal region of frons apex on the same plane as clypeus; male parameres usually noticeably constricted near base, with sides slightly convexly arcuate; prosternal process often narrowed at posterior procoxal margin, sometimes dorsally offset from plane of prosternum; pronotal punctures usually smaller (Lahontan Trough including Mono Lake region of Owens Valley) ....*Trogloderus arcanus* n. sp. (Fig. 3.6E)

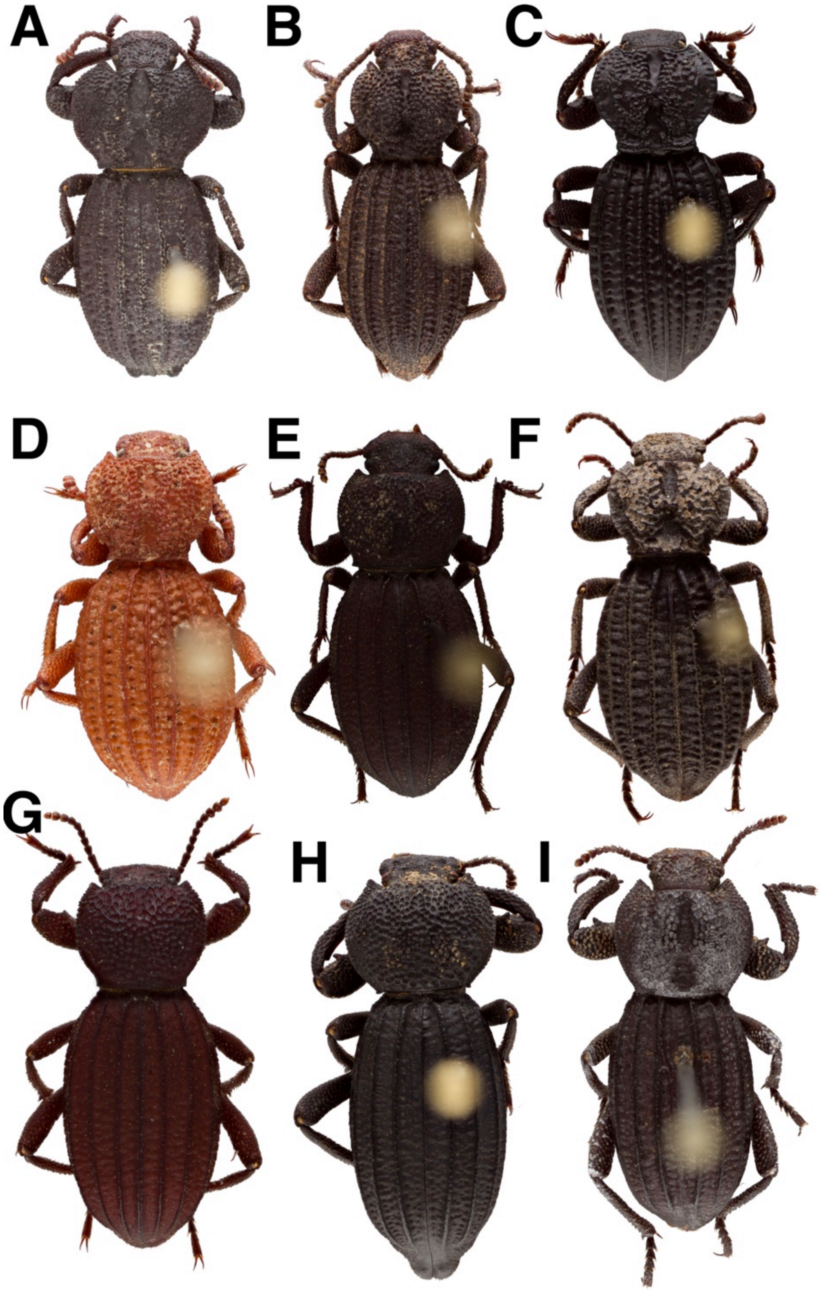


Figure 3.6. *Trogloderus* species, dorsal habitus. A. *T. tuberculatus* Blaisdell (non-type). B. *T. verpus* Johnston n.sp. (holotype). C. *T. warneri* Johnston n.sp. (holotype). D. *T. skillmani* Johnston n.sp. (holotype). E. *T. arcanus* Johnston n.sp. (holotype). F. *T. costatus* LeConte (non-type). G. *T. nevadus* La Rivers (non-type). H. *T. major* Johnston n.sp. (holotype). I. *T. kandai* Johnston n.sp. (holotype).

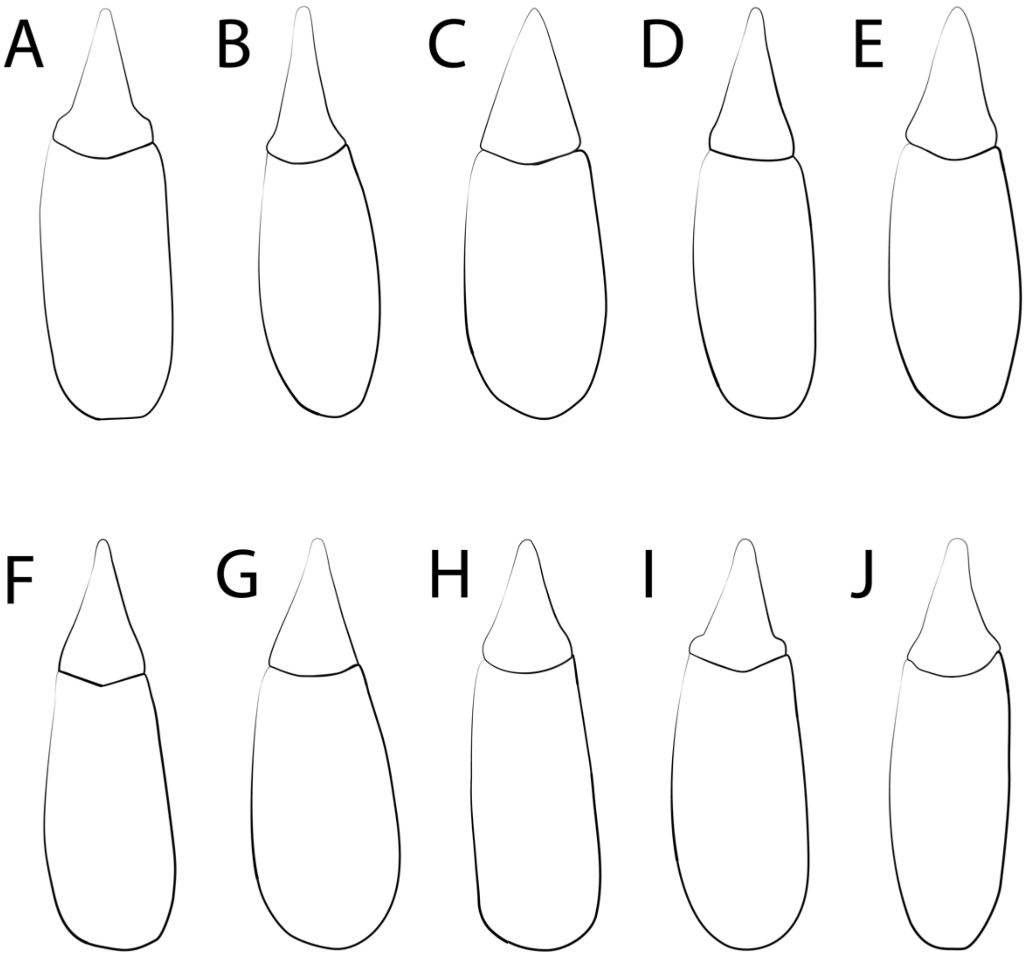


Figure 3.7. *Trogloderus* species, adeagus dorsal view. A. *T. arcanus* Johnston n.sp. B. *T. costatus* LeConte. C. *T. kandai* Johnston n.sp. D. *T. major* Johnston n.sp. E. *T. nevadus* La Rivers. F. *T. skillmani* Johnston n.sp. G. *T. tuberculatus* Blaisdell. H. *T. vandykei* La Rivers. I. *T. verpus* Johnston n.sp. J. *T. warneri* Johnston n.sp.

3.5. *Trogloderus arcanus* Johnston, New Species

Figures 3.6E, 3.7A, 3.8

Diagnosis. *Trogloderus arcanus* can be distinguished from all congeners, except *T. nevadus*, by the combination of tuberculate propleurae, frons, and clypeus. To separate it from the latter, the characters given in the key will usually separate the two species, but see the variation and remarks below.

Description. As genus with the following: Length 7.0–10.5 mm, width 3.5–4.5 mm. Head. Epistoma and frons tuberculate, lacking distinct punctures; mesal region of frons elevated, usually on same plane as clypeus, rendering transverse ridge along frontoclypeal suture incomplete, lateral regions of frons usually evenly tuberculate. Thorax. Pronotum evenly convex dorsally; heavily punctate, punctures longitudinally elongate, tending to coalesce anteriorly; lateral margins moderately arcuate, sinuate along basal fifth; posterior pronotal angles obliquely acute, relatively small; anterior fovea usually obsolete to moderately impressed, posterior fovea always distinct, round, deeper than anterior. Propleurae usually tuberculate throughout, tubercles always present anteriorly underneath pronotal margin. Prosternal process usually narrowed along posterior procoxal margin, often narrowed and on slightly dorsal plane than prosternum between procoxae. Elytral costae weakly to moderately developed, intervals usually smooth, occasionally with slight transverse ridges; elytral suture elevated along poster half, nearly as prominent as discal costae. Abdomen. Abdominal depression relatively weak, usually not discernable on ventrite II. Male terminalia. Parameres (Fig. 3.7A) usually appearing narrow, arcuately constricted near base, sides usually slightly concave, occasionally appearing roughly evenly triangular.

Variation. The diagnostic characters of this species are quite variable both within and between populations. Specimens from Crescent Dunes south to Sarcobatus Flats tend to have a distinctly narrowed prosternal process, while specimens from Teel's Marsh and Silver Peak west to Mono Lake tend to have a horizontal, evenly narrowing prosternal process. Specimens from lower elevation regions (typically Nevada) are fairly weakly sculptured, having rather small pronotal punctures, sometimes becoming separated by as much as half of their diameter, and fairly weakly developed elytral costae. Specimens from higher elevation (e.g. Mono County, CA) tend to be more roughly sculptured on the pronotum and elytra. The latter populations tend to also have the frontoclypeal ridge more or less complete throughout. The northern and eastern populations (e.g. Crescent Dunes and Coal Valley) have more distinctly narrowed parameres, while the southern populations (e.g. Silver Peak) tend to have slightly broader and more evenly tapered parameres.

Distribution. Fig. 3.8. This species is distributed throughout the region known as the Lahontan Trough (Reveal 1979), a region which was never part of the prehistoric Lake Lahontan to the north.

Type material. Holotype. "USA: NEV: Nye Co., 12 mi / NW Tonopah, Crescent / Dunes; 38°13'47"N, 117° / 20'06"W; JUN 30-JUL 9 / 2011; barrier pitfalls w. / fish bait; W.B. Warner", "ARTSYS0007057" bearing red holotype label. Deposited in USNM. Paratypes. 765 specimens from throughout the range bearing blue paratype labels (see SCAN for full data).

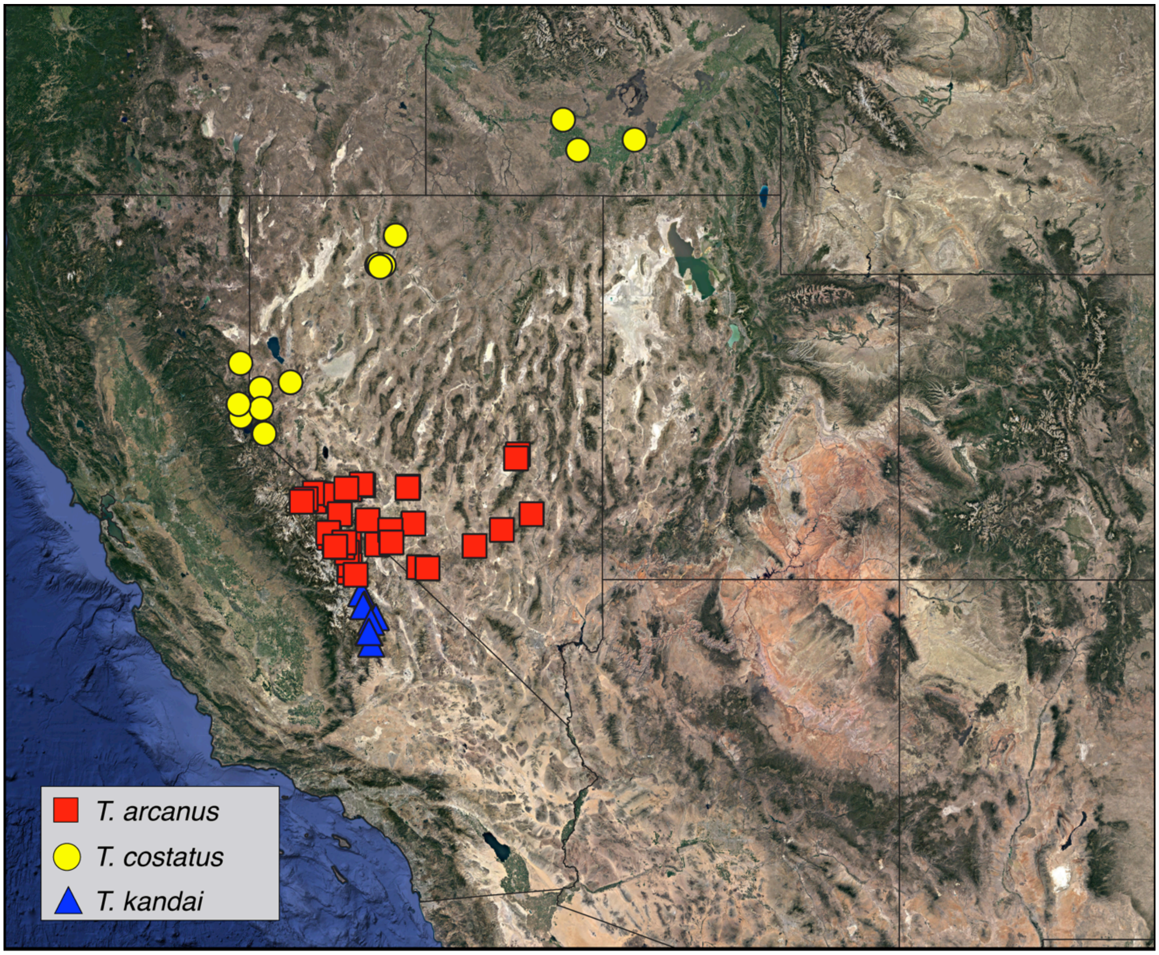


Figure 3.8. Distribution map, *Trogloderus arcanus* Johnston n.sp., *T. costatus* LeConte, *T. kandai* Johnston n.sp.

Etymology. The specific epithet, meaning secret, or mysterious, is given for this cryptic species that was very difficult to separate from *T. nevadus* and was first revealed as a distinct species through the phylogeny presented below.

Remarks. The geographically linked morphological variation in this species warrants further study, which will rely on increased collecting efforts in an under-collected region and likely more molecular data. The slightly heterotypic species as circumscribed here may represent a cryptic species complex. Strong differences between populations may be the result of reproductive isolation and diverging evolutionary lineages, or could be linked to environmental conditions. The roughly sculptured populations from California are from cooler and more mesic habitats, whereas the central Nevada populations face much drier and warmer conditions. There also may be some competitive exclusion or prezygotic isolation pressures, which shape the Nevada populations which border along the range of *T. nevadus*.

3.6. *Trogloderus costatus* LeConte, 1879

Figures 3.6F, 3.7B, 3.8

Diagnosis. *Trogloderus costatus* can be easily separated from all congeners by the cribrately punctate pronotum, where the margins of the punctures are strongly elevated. The presence of transverse ridges in the intervals of the elytral costae can also separate this species from any others with punctate pronota.

Redescription. Length 10.5–12mm, width 4–4.75mm. Head. Epistoma and frons roughly punctured to tuberculate; frontal tubercle usually roughly punctured, punctures usually becoming discrete tubercles towards clypeus; frontoclypeal suture forming gentle, complete transverse ridge. Thorax. Pronotum relatively evenly convex dorsally; cribrately punctured, punctured region elevated above less punctate lateral margins; anterior and posterior foveae very distinct, deep, impunctate; lateral margins evenly arcuate, recurved just before posterior angles; posterior angles obliquely acute, small. Propleurae distinctly and evenly tuberculate throughout. Prosternal process horizontal, forming short, evenly tapered triangle behind posterior procoxal margin. Elytral costae strongly developed, intervals always with distinct transverse ridges; elytral suture strongly elevated, nearly as prominent as discal coxae along posterior 5/6. Abdominal depression weak, not evident in females, occasionally evident on anterior 1/2 of ventrite I in males. Male terminalia. Parameres (Fig. 3.7B) narrow, arcuately constricted near base, sides concave, weakly arcuately converging to apex.

Variation. As with most other species, the intensity of the body sculpturing is variable both between and within populations. Specimens from near Winnemucca tend to have the weakest sculpturing, though the strongly elevated punctate regions of the pronotum are still diagnostic. *Trogloderus costatus* has the most variable cephalic sculpturing within the genus, with specimens ranging from having the entire dorsal aspect of the head distinctly punctate (Truckee river near Reno) to specimens which are nearly entirely tuberculate heads (Winnemucca). Specimens from other regions have a mixture of both, generally with the frontal tubercle punctate and the punctures becoming distinct tubercles towards the clypeus.

Types**.** Holotype male from Rock Creek Owyhee County, Idaho at the Museum of Comparative Zoology, type number 4624, pictures available on-line from MCZ type specimen database. LeConte (1879: 3) specifically references “one specimen kindly given me by Mr. Reinecke; others are in the collections of Dr. Horn and Mr. Bolter.” This statement is here interpreted to comply with the International Code of Zoological Nomenclature (1999) Article 73.1.1 and the above single specimen is considered the holotype upon which the nominal species was founded, with the secondarily mentioned specimens considered as paratypes.

Material examined. 63 specimens (see SCAN for full data).

Distribution. Fig. 3.8. This species is known from the Northern Great Basin, from regions once dominated by the prehistoric Lake Lahontan through the Snake River Plain.

Remarks. This is the second least abundant species found in natural history collections, yet was the first species described in the genus. While true *T. costatus*, as recircumscribed here, is uncommon in collections, most existing specimens are determined to this species likely following the treatment of La Rivers (1946). *Trogloderus costatus* overlaps most of the range of *T. nevadus*, though the latter is much more frequently collected. Specimens of *T. costatus* seem to retain the most substrate on their cuticle of its congeners, and perhaps this cryptic lifestyle makes it less commonly collected, or perhaps this morphological sculpturing is adapted to more specific substrates. With relatively few specimens known, and many of them lacking very precise locality data, increased collecting efforts may help elucidate drivers of this species’ distribution and intense morphological sculpturing.

3.7. *Trogloderus kandai* Johnston, New Species

Figures 3.6I, 3.7C, 3.8

Diagnosis. *Trogloderus kandai* can be separated from its congeners by having the pronotum punctate, propleurae tuberculate, and the epistoma distinctly punctured, at least above the antennal insertions. Most similar to *T. arcanus*, particularly specimens from the Mono Lake region, *T. kandai* can be further separated from the latter by the pronotal punctures being nearly evenly round and not tending to coalesce (longitudinally oval and tending to coalesce anteriorly in *T. arcanus*).

Description. Length 9–11mm, width 3.5–4.5mm. Head. Epistoma aspirately punctate, distinctly so above antennal insertions, often becoming somewhat tuberculate mesally; frontoclypeal suture forming complete transverse ridge; frons irregularly tuberculate, frontal tubercle fairly distinctly punctate, lobes connected by anterior transverse ridge. Thorax. Evenly convex dorsally; heavily and evenly punctate throughout, punctures round, not becoming coalescent, occasionally slightly elongate near anterior margin; lateral margins evenly arcuate, recurved just before posterior angles; posterior angles obliquely acute, small; anterior fovea usually forming moderately and evenly impressed longitudinal channel connected to posterior fovea, posterior fovea round, deeper than anterior fovea. Propleurae tuberculate, tubercles often obscure posteriorly, always with tubercles anteriorly underneath pronotal margin. Prosternal process horizontal, forming evenly tapered triangle behind posterior procoxal margin. Elytral costae moderately produced, intervals punctate but lacking well developed transverse ridges; elytral suture usually not elevated basally, somewhat elevated in posterior 1/2 but less produced than discal costae. Abdomen. Abdominal depression moderately developed in both sexes, distinctly present on ventrites I–II, smoother than lateral region of ventrite in males, entire ventrite fairly similarly sculptured in females. Male Terminalia. Parameres (Fig. 3.7C) somewhat broad, evenly tapering from base to apex.

Variation. This species exhibits relatively constant morphology, perhaps due to the extremely limited known distribution. The sculpturing of the epistoma can be fairly variable within the population, but individual punctures can be observed along the outer edge above the antennal insertion. The elytral suture is also somewhat variable, usually being elevated in the posterior half, it is occasionally elevated along most of its length.

Distribution. Fig. 3.8. This is the most geographically restricted species of *Trogloderus* and is known only from the southern Owens Valley in California, in the region around Owens Lake between independence and Olancha.

Type material. Holotype. "USA:CA:Inyo Co. / Olancha Dunes OHV area / N36°17.665' W117°59.191' / 3600 ft. KK07_028 / K. Kanda, 22.vii.2007", "ARTSYS0007058" bearing red holotype label. Deposited in the USNM Paratypes. 82 specimens bearing blue paratype labels (see SCAN for full data).

Etymology. I am pleased to name this species after the tenebrionid specialist Kojun Kanda, who both collected the holotype and provided direction on the molecular analyses.

Remarks. The restricted distribution of this species is very interesting, being bounded by the Coso Range to the south and a series of old lava flows to the north which are part of the southern boundary for the Tinemaha Reservoir. South of the Coso Range is traditional Mojave Desert habitat and is dominated by creosote bush (*Larrea tridentata* (DC.) Coville) which is only sporadically present to the north, largely replaced by the Great basin indicative big sagebrush (*Artemisia tridentate* Nutt.). Thus, *T. kandai* is only known from a transition region between the Mojave and Great Basin deserts.

3.8. *Trogloderus major* Johnston, New Species

Figures 3.6H, 3.7D, 3.9

Diagnosis. This species can be recognized by having a punctate and evenly convex pronotum, and the propleurae lacking tubercles on the dorsal half (if propleural tubercles present, they are located on the bulging region covering the procoxae). This species can be further separated from most other species with punctate pronota by the smooth elytral suture, located in a depressed interval between the inner elytral costae. This form of the elytral suture and propleurae lacking tubercles is shared with the sympatric species *T. vandykei*, which has a bilobed dorsum of the pronotum in anterior view.

Description. As genus with the following: Length 9.5–13.5mm, width 4–5.5mm. Head. Epistoma usually distinctly punctured, sometimes becoming irregularly tuberculate mesally; frontoclypeal suture forming complete transverse ridge; frontal tubercle punctate, lateral regions of frons smooth. Thorax. Pronotum evenly convex dorsally; heavily and evenly punctate throughout; lateral margins fairly evenly arcuate, recurved just before posterior angles; posterior angles obliquely acute, very small; anterior fovea forming weakly to moderately impressed longitudinal channel, connecting to posterior fovea; posterior fovea round, moderately impressed, slightly deeper than anterior fovea. Propleurae lacking punctures on dorsal half, always lacking punctures anteriorly underneath pronotal margin, usually with indistinct tubercles on inflated region covering procoxal cavity. Prosternal process robust, horizontal, forming evenly tapered triangle behind procoxal posterior margin. Elytral costae weakly to moderately elevated, intervals relatively smooth, bearing faint traces of transverse ridges; elytral usually suture not elevated, or if elevated posteriorly then significantly shorter than the discal costae. Abdomen. Ventrites relatively smooth laterally; abdominal depression strong, distinct in both sexes, stronger in males, margins of depression roughly punctured, depression distinctly margined throughout ventrites I–II; ventrite III flattened anteriorly in males, lacking a distinct margin. Male Terminalia. Parameres (Fig. 3.7D) subparallel in basal 1/5, then concave and arcuately tapering to apex.

Variation. This species is fairly constant in its robust form. The main variation observed was in the elytral suture, which is usually entirely not elevated, but is occasionally produced in the posterior half, though is still very much shorter than the discal costae.

Distribution. Fig. 3.9. Mojave Desert, from Edwards and Ridgecrest California, east through Mercury and Alamo, Nevada. This species is particularly abundant from sand dunes in the eastern Mojave and Death Valley (e.g. Kelso, Eureka, and Big Dune).

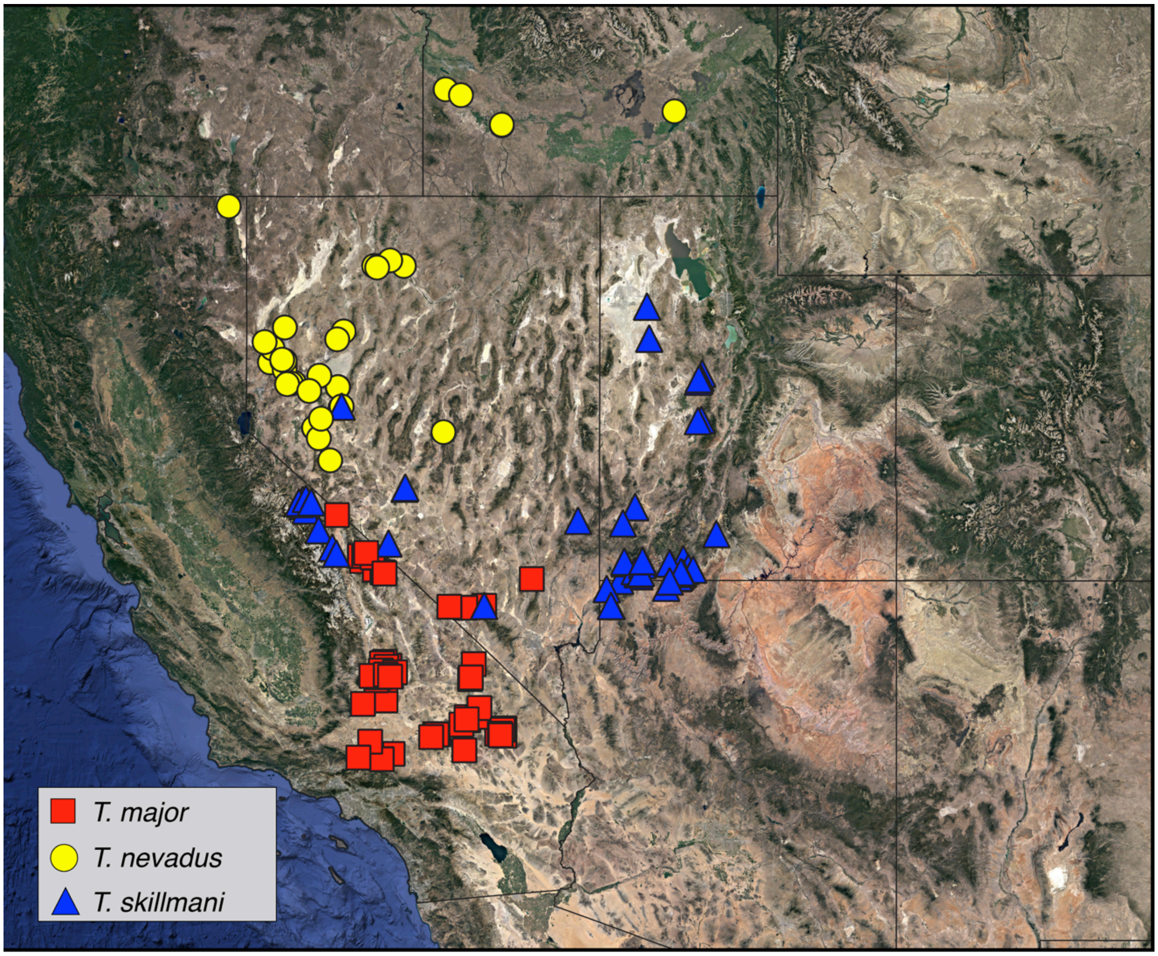


Figure 3.9. Distribution map, *Trogloderus major* Johnston n.sp., *T. nevadus* La Rivers, *T. skillmani* Johnston n.sp.

Type material. Holotype. “USA:CA: San Brndno / Co., Kelso Dunes; 34° / 53’23”N, 115°43’04”W / April 16-17. 2011; at / night gleaning & UV / lights; W.B. Warner”, “ARTSYS0007056”, bearing red holotype label. Deposited in the USNM. Paratypes. 724 specimens from across its range, bearing blue paratype labels. (see SCAN for full data).

Etymology. This species is named for its robust stature among *Trogloderus*.

Remarks. This species can often be recognized by gestalt, owing to its generally robust outline with a fusiform abdomen. One of the most abundant species in natural history collections, specimens were often previously been determined as *T. nevadus*. *Trogloderus major* is sympatric with *T. tuberculatus* and *T. vandykei*, where they are often taken in mixed series. This is the species from the Nevada Test Site referred to as *T. costatus nevadus* in Tanner and Packham (1965), who reported this species active from March through October, with a distinct peak in abundance in August.

3.9. *Trogloderus nevadus* La Rivers, 1943

Figures 3.6G, 3.7E, 3.9

Diagnosis. The combination of a punctate, evenly convex pronotum, tuberculate propleurae and epistoma, and the frontoclypeal suture forming a complete transverse ridge will separate this species from all congeners but some specimens of *T. arcanus*. See the key characters and diagnosis of the latter species to further separate the two.

Redescription. As genus with the following: Length 8.5–10mm, width 3.5–4mm. Head. Epistoma and frons tuberculate throughout, lacking distinct punctures; frontoclypeal suture forming complete transverse ridge. Thorax. Pronotum evenly convex dorsally; heavily punctate throughout, punctures longitudinally oval, tending to coalesce anteriorly; lateral margins moderately arcuate, sinuate in basal 1/5; posterior angles obliquely acute, small; anterior fovea weakly impressed, connected to posterior fovea; posterior fovea similarly weakly impressed, sometimes slightly deeper. Propleurae granulately tuberculate throughout, always with tubercles present anteriorly underneath pronotal margin. Prosternal process horizontal, usually distinctly margined along entire outline, forming evenly tapering triangle behind posterior procoxal margin. Elytral costae moderately produced, intervals punctate, lacking transverse ridges; elytral suture weakly elevated in posterior ½. Abdomen. Abdominal depression indistinct to weak in females, discernable only on ventrite I, relatively weak in males, discernable on ventrites I–II, but lateral margin forming ridge only on ventrite I. Male terminalia. Parameres (Fig. 3.7E) triangular, evenly tapering from base to apex.

Variation. This species is fairly constant throughout its range. The pronotal foveae are sometimes moderately pronounced, generally in larger and more roughly sculptured individuals, whereas the typical form has the foveae very weakly depressed.

Distribution. Fig. 3.9. This species is distributed throughout the northern Great Basin, throughout the Lake Lahontan drainage and into the Snake River Plain.

Type material. Holotype male from Pyramid Lake Dunes, Washoe County, Nevada, not seen. Deposited in Ira La Rivers' collection (La Rivers 1943: 439), which was later deposited at the state collection of Nevada in Reno, the type was not located there (K. Tonkel, personal communication), nor found at the CASC where a sizable amount of La Rivers material is located. The description, examined paratypes, and abundant subsequent collecting from the type locality leave no doubt as to this species identity.

Material examined. 332 specimens including 4 paratypes (see SCAN for full data).

Remarks. This species is broadly sympatric with *T. costatus*, but seemingly has a slightly broader range, extending south to the dunes around Walker Lake and north to Pyramid Lake. It is surprising that no specimens were found from southeastern Oregon, which seems to have appropriate habitat without any significant barriers to dispersal. Increased collecting efforts may produce specimens from the periphery of the currently known range. Many specimens referred to the present species in natural history collections belong to the herein described species with punctate pronota.

3.10. *Trogloderus skillmani* Johnston, New Species

Figures 3.6D, 3.7F, 3.9

Diagnosis. This species can be recognized by the relatively evenly tuberculate pronotum, lack of subapical elytral tubercles, and relatively evenly tapering male parameres. This species is most similar to *T. verpus*, which can be separated by the male terminalia (parameres strongly constricted near base in *T. verpus*, parameres not strongly constricted, evenly tapering to apex in *T. skimmnani*). The present species is also fairly similar to *T. warneri* which can be separated by the pronotal characters given under the diagnosis for that species.

Description. As genus with the following: Length 9.5–12.5mm, width 3.5–4mm. Head. Epistoma and frons tuberculate throughout; mesal region of frons on same plane as clypeus; frontoclypeal suture not or weakly forming transverse ridge. Thorax. Pronotum relatively evenly convex forsally; evenly tuberculate throughout, lateral regions of pronotum more or less depressed, but similarly tuberculate as remainder of disc; lateral margins fairly evenly arcuate, recurved just before posterior angles; posterior angles small, acute; posterior margin straight, mesal region forming continuous line laterally to terminus of posterior angle. Propleurae evenly and densely tuberculate throughout. Prosternal process short, usually offset dorsad from plane of prosternum between procoxae. Elytral costae moderately to strongly produced; intervals usually tuberculate, tubercles originating from center of interval as well as lateral faces of costae; elytral suture elevated in poster ¾, nearly as produced as discal costae. Abdomen. Abdominal depression lacking in both sexes. Male parameres (Fig. 3.7F) narrowly triangular, evenly to slightly arcuately converging to apex.

Variation. This species as circumscribed here is the most widespread of any *Trogloderus* and has some significant variation accordingly. Specimens near the type locality,from northern Arizona and southern Utah, tend to have extremely tuberculate elytra intervals, strongly produced elytral costae, and small prosternal processes. Specimens from more typical great basin regions of Utah and Nevada (e.g. Little Sahara dunes, Crescent Dunes) tend to be less strongly sculptured on the elytra and have slightly enlarged prosternal processes. Specimens from the far western end of the distribution near Mono Lake have stronger elytral sculpturing and large, nearly horizontal prosternal processes. The posterior pronotal angles are always acute and usually form a continuous posterior margin to the pronotum, but occasionally the angles are obliquely oriented. This seems to be individual variation and not tied to geography.

Distribution. Fig. 3.9. This species has the widest distribution of any *Trogloderus*, extending from the Coral Pink sand dunes and surrounding regions north to the Little Sahara Dunes and west to Mono Lake.

Type material. Holotype. "USA: AZ: Mohave Co. / 6m E Colorado City / Rosy Canyon Road / 1.5m S UT state line / 12-VII-2016 / F.W. & S.A. Skillman", "ARTSYS0007053", bearing red holotype label. Deposited in the USNM. Paratypes**.** 920 specimens from the western regions of the Colorado Plateau around the Coral Pink Sand Dunes, Hurricane, and Toquerville Utah, bearing blue paratype labels (See SCAN for full data)

Other material. 182 specimens from the Northern and Western reaches of this species range.

Etymology. This species is named after Frederick W. Skillman, who both collected the holotype and has been a constant help throughout this study. His generous sharing of specimens, knowledge of natural history, and long drives to remote sand dunes are greatly appreciated.

Remarks. A broader molecular sampling and increased collections from Nevada localities may eventually find this taxon to be a cryptic species complex. Apparently able to cross boundaries that limit other species of *Trogloderus*, *T. skillmani* may be more adept at dispersing than its congeners.

3.11. *Trogloderus tuberculatus* Blaisdell, 1909

=*Trogloderus costatus pappi* Kulzer, 1960

Figures 3.6A, 3.7G, 3.10

Diagnosis. This species can be readily identified by the presence of tubercles on the pronotum and the large, subapical tubercle at the terminus of the outer costa on each elytron. The present species can be further separated from the others with tuberculate pronota by the thick, raised ridges demarking the lateral margins and boundary between the pronotal foveae.

Redescription. As genus with the following: Length 10.5–12mm, width 4–4.5mm. Head. Epistoma and frons tuberculate throughout, lacking distinct punctures above antennal insertion; frontoclypeal suture forming complete, though gentle, transverse ridge; frontal tubercle covered with smaller tubercles. Thorax. Pronotum with dorsal silhouette appearing somewhat bilobed in anterior view; distinctly tuberculate throughout; lateral margins strongly arcuate, recurved just before posterior angles; posterior angles obliquely acute, small; foveae well demarked laterally by continuous strongly elevated longitudinal ridges; anterior fovea distinct, smooth, separated from posterior fovea by strongly elevated ridge; posterior fovea circular, usually smooth mesally. Propleurae fairly smooth, with dorsal longitudinal row of irregular tubercles running just beneath pronotal margin; often tuberculate on bulge covering procoxae. Prosternal process small, subtriangular, not margined laterally, slightly offset dorsad of prosternum between procoxae. Elytral costae strongly produced, crenulate; intervals with deep punctures, lacking transverse ridges; each elytron with subapical tubercle, formed by terminus of outer elytral carina, often formed by confluence of outer 1–3 costae; elytral suture very weakly produced, much shorter than discal carinae. Abdomen. Ventrites tuberculate throughout; abdominal depression weak, present on ventrites I–II in both sexes, without marginal ridge, usually somewhat smooth in males. Male terminalia. Parameres (Fig. 3.7G) narrowly triangle, more or less evenly tapering to apex.

Variation. The subapical elytral tubercles, unique to this species of *Trogloderus*, are somewhat variable. It is always made up of the thickened terminus of the outter elytral costa, and is variably formed by the confluence of any combination of the outer three costae. This seems to be individual variation and not correlated with geography. Specimens from Kelso Dunes (the only confirmed locality where *T. tuberculatus* is sympatric with another species, *T. major*) are distinctly smaller than all other examined localities, and possess less developed subterminal elytral tubercles.

Distribution. Fig. 3.10. This species is found in the Mojave Desert, and is generally found around the periphery from the western high desert reaches and in the northern Death Valley region.

Types. The holotype of *T. tuberculatus* Blaisdell, collected from “L.A. County, California,” was examined at the USNM. The holotype of *T. costatus pappi* Kulzer, from Lancaster, Mojave Desert, Southern California, was not examined.

Material examined. 41 specimens (see SCAN for full data)

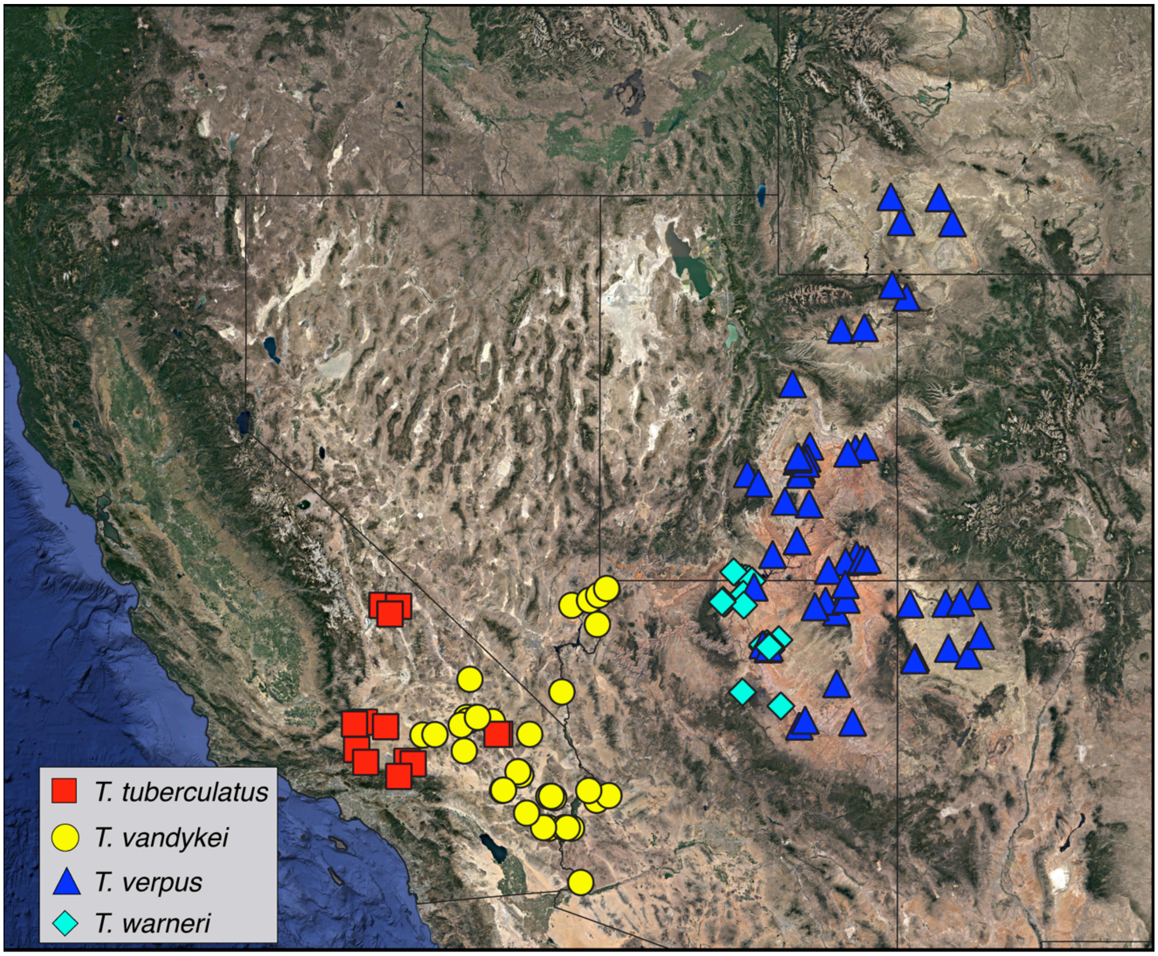


Figure 3.10. Distribution map, *Trogloderus tuberculatus* Blaisdell, *T. vandykei* La Rivers, *T. verpus* Johnston n.sp., *T. warneri* Johnston n.sp.

Remarks. Similar to *T. costatus*, it is remarkable that this species, the least common in natural history collections, was the second species described in the genus. Papp and Pierce (1960) reported this species feeding on stored chicken feed in Lancaster, California. Specimens from this collecting event (the largest known for this species, at least ten individuals) were sent to the Frey museum in Germany (Papp 1961: 35), which became the type series for *Trogloderus costatus pappi* Kulzer (Kulzer 1960: 331). Though the type itself was not examined, seven specimens from Papp's (1961) original series were studied and were all certainly conspecific with *T. tuberculatus* as herein circumscribed. This species was very difficult to recollect, particularly due to lack of suitable habitat. The western Mojave Desert has been largely developed, and after multiple targeted trips to the region only a single, ca. 0.25 acre, dune near California City was found to support a population of this species. Most specimens in natural history collections determined to this species (or subspecies as *T. costatus tuberculatus*) actually belong to other tuberculate species described herein.

3.12 *Trogloderus vandykei* La Rivers, 1946

=*Trogloderus costatus mayhewi* Papp, 1961

Figures 3.1, 3.7H, 3.10

Diagnosis. This species can be readily separated from all other *Trogloderus* by the pronotal dorsum being bilobed when viewed from the front. Its pronotum is also punctate and more broadly explanate than any of its congeners. Most similar to and sympatric with *T. major*, the two can be readily separated by the given characters.

Description. As genus with the following: Length 9–11.5mm, width 3.5–4.5mm. Head. Epistoma punctato-tuberculate; frons smooth, mesal region on same plane as clypeus; frontoclypeal suture not forming complete ridge, obsolete at least mesally; frontal tubercle punctate, not very prominent. Thorax. Pronotal dorsum bilobed in anterior view; pronotum strongly explanate, punctate, punctured becoming irregular tubercles laterally; lateral margins strongly and evenly arcuate, recurved just before posterior angles; posterior angles obliquely acute, small; foveae bounded by raised lobed on either side, anterior fovea moderately impressed, forming continuous channel with posterior fovea, posterior fovea usually slightly deeper. Propleurae smooth, lacking tubercles throughout, occasionally with granulate tubercles ventrally around procoxae. Prosternal process horizontal, prominent, strongly margined, especially in males, forming evenly tapering triangle behind posterior procoxal margin. Elytral costae moderately produced, intervals relatively smooth, bering two rows of punctures, lacking any transverse ridges; elytral suture not at all elevated, situated in concavity formed by inner discal costae. Abdomen. Abdominal depression very strong in both sexes, exceedingly so in males, visible on ventrites I–III, demarked by strongly punctate lateral ridges which curve mesad and form distinct posterior margin on ventrite III. Male terminalia. Parameres (Fig. 3.7H) more or less arcuately converging from base to apex, apical 1/2 subparallel.

Variation. This species exhibits consistent morphology throughout its range. Occasionally smaller specimens are observed in which the pronotum appears less explanate, but this form seems sporadic, not tied to geography, and is likely a result of water or nutrient availability for the larva.

Distribution. Fig. 3.10. Eastern and central Mojave Desert, especially abundant in dunes along the Colorado River.

Types. The holotype of *T. costatus vandykei* La Rivers, from Baker, San Bernardino County, California, was examined at the CASC. The holotype of *T. costatus mayhewi* Papp, from Dale Dry Lake, San Bernardino County, California, was examined at the LACM.

Material examined. 327 specimens (see SCAN for full data)

Remarks. This species ranges the furthest south of any *Trogloderus* members, having been collected just north of Yuma, Arizona. *Trogloderus vandykei* has never been collected from the Algodones or other sand dunes in the Colorado Desert (Johnston *et al.* 2018). This is perhaps simply because they have not yet dispersed to these dunes. While there may be some other competitive or environmental factors at play, both *T. vandykei* and other congeners persists very well in regions of seemingly similar intense annual heat and dry conditions (e.g. Death Valley, Wiley's Well, Bouse Dunes, etc.).

3.13. *Trogloderus verpus* Johnston, New Species

Figures 3.6B, 3.7I, 3.10

Diagnosis. This species can be recognized by the evenly tuberculate pronotum, lack of subapical elytral tubercles, and the male parameres being strongly constricted basally. It is most similar to *T. skillmani* which can be separated by the male terminalia (parameres not constricted in *T. skillmani*).

Description. As genus with the following: Length 9.5–11.5mm, width 3.5–4.5mm. Head. Epistoma and frons evenly tuberculate, tubercles often irregularly shaped; frontoclypeal suture not forming complete transverse ridge, mesal region of frons more or less on same plane as clypeus. Thorax. Pronotum evenly convex dorsally, occasionally with lateral regions slightly flattened posteriorly; lateral marginsfairly evenly arcuate, recurved just before posterior angles; posterior angles small, acute; posterior margin usually straight, mesal region forming continuous line to terminus of posterior angle. Propleurae densely and evenly tuberculate throughout. Prosternal process acute, usually small, offset dorsad from plane of prosternum between procoxae. Elytral costae moderately to strongly developed, intervals variable from smooth to moderately tuberculate; elytral suture moderately to strongly elevated in posterior ½, usually distinctly shorter than discal costae. Abdomen. Abdominal depression absent in both sexes. Male Terminalia. Parameres (Fig. 3.7I) strongly constricted near basal 1/6, then narrowly and evenly tapered to apex.

Variation. This species is fairly consistent across its range, but presents some variation in the elytral sculpturing. In some specimens the intervals between discal costae are noticeably tuberculate, while most are smooth. The elytral suture is usually less strongly elevated than the discal costae, but in some New Mexico populations (e.g. near Farmington), it is nearly the same height as the discal costae. Specimens from the sand dunes near Moenkopi, where they are sympatric with *T. warneri*, are distinctly smaller and less roughly sculptured than anywhere else in its range.

Distribution. Fig. 3.10. This species is broadly distributed throughout the Colorado Plateau, from Moenkopi, Arizona east to central new Mexico and north to the Killpecker Dunes in Wyoming.

Type material. Holotype. “USA: UT: Grand Co. / 22m NW Moab, Dubinky / Well Rd. @ Dubinky Well / 25-VI-2016 / Skillman & Johnston”, “ARTSYS0007055”, bearing red holotype label. Deposited in the USNM. Paratypes. 185 specimens from throughout the species range (see SCAN for full data).

Etymology. This species name is given for the strongly constricted male parameres, which look as though a portion has been cut away from the fairly regularly triangular shape found in the rest of the genus.

Remarks. The remarkably small specimens from near Moenkopi may be an example of competition forcing allometry. Indeed, the specimens of *T. warneri* from Moenkopi are a very similar size to specimens of *T. verpus* from the rest of its range.

3.14. *Trogloderus warneri* Johnston, New Species

Figures 3.6C, 3.7J, 3.10

Diagnosis. This species can be recognized by the combination of a tuberculate pronotum and large, inflated posterior pronotal angles. The species can be further recognized by the depressed lateral regions of the pronotum lacking tubercles, the lack of an abdominal impression, and the lack of subapical elytral tubercles.

Description. As genus with the following: Length 9–11mm, width 3.5–5mm. Head. Epistoma and frons tuberculate throughout, frontoclypeal suture not developed as transverse ridge, mesal region of frons on same plane as clypeus. Thorax. Pronotum relatively evenly conxex dorsally; heavily tuberculate; disc laterally depressed, usually lacking tubercles, especially posteriorly; lateral margins arcuate, more strongly narrowed posteriorly, recurved just before posterior angles; posterior angles large, obliquely angles, usually well inflated, sometimes broadly acute. Propleurae evenly tuberculate, tubercles fairly large and rounded. Prosternal process short, triangular, offset dorsad from plane of prosternum between procoxae. Elytral costae well developed, intervals with deep punctures, sometimes giving appearance of short transverse ridges; elytral suture weakly to moderately produced in posterior half, always shorter than discal costae. Abdomen. Ventrites tuberculate; without abdominal depression, ventrite I sometimes smooth mesally in males. Male terminalia. Parameres (Fig. 3.7J) subparallel in basal 1/5, then arcuately converging to apex.

Variation. The pronotum, while diagnostic for this species, is somewhat variable in the specimens examined. The typical form has very strongly inflated posterior angles and the disc distinctly depressed and lacking tubercles laterally. In some specimens the posterior angles are less inflated and the depressed lateral region is much smaller, tending to be restricted to the posterior third. However, these reduced characters were distinctly discernable in all specimens studied, reliably separating them from other *Trogloderus* species.

Distribution. Fig. 3.10. Distributed in the western Colorado Plateau, the species seems bounded on the west by the Kaibab Plateau, and are distributed as far east as Moenkopi, Arizona.

Type material. Holotype. "USA:AZ:Coconino Co. / Hwy. 264 2.2mi SE jct / US160; 36°05'57"N, / 111°12'03"W; dunes at / night; April 20, 2012; W.B. Warner, J.P. Gruber". "ARTSYS0007054", bearing red holotype label. Deposited in the USNM. Paratypes. 237 specimens from across the species range (see SCAN for full data).

Etymology. I am honored and thankful to name this species for William B. Warner, an ardent collector, coleopterist, and natural historian. His assistance and encouragement throughout this project in both the field and the lab is greatly appreciated.

Remarks. This species has a relatively small geographic range, yet extends across the eastern reaches of the Grand Canyon. This is perhaps the reason for the observed moderate genetic diversity within the species. Most specimens in natural history collections have been determined as *T. tuberculatus*.

3.15. Phylogenetic reconstruction

Both maximum likelihood and Bayesian analyses converged on a single topology with moderately strong support throughout (Fig. 3.11). Within the outgroups, the genus *Eleodes* Eschscholtz was notably recovered as paraphyletic with respect to the genera *Neobaphion* Blaisdell, *Embaphion* Say, *Lariversius* Blaisdell, and *Trogloderus*. This

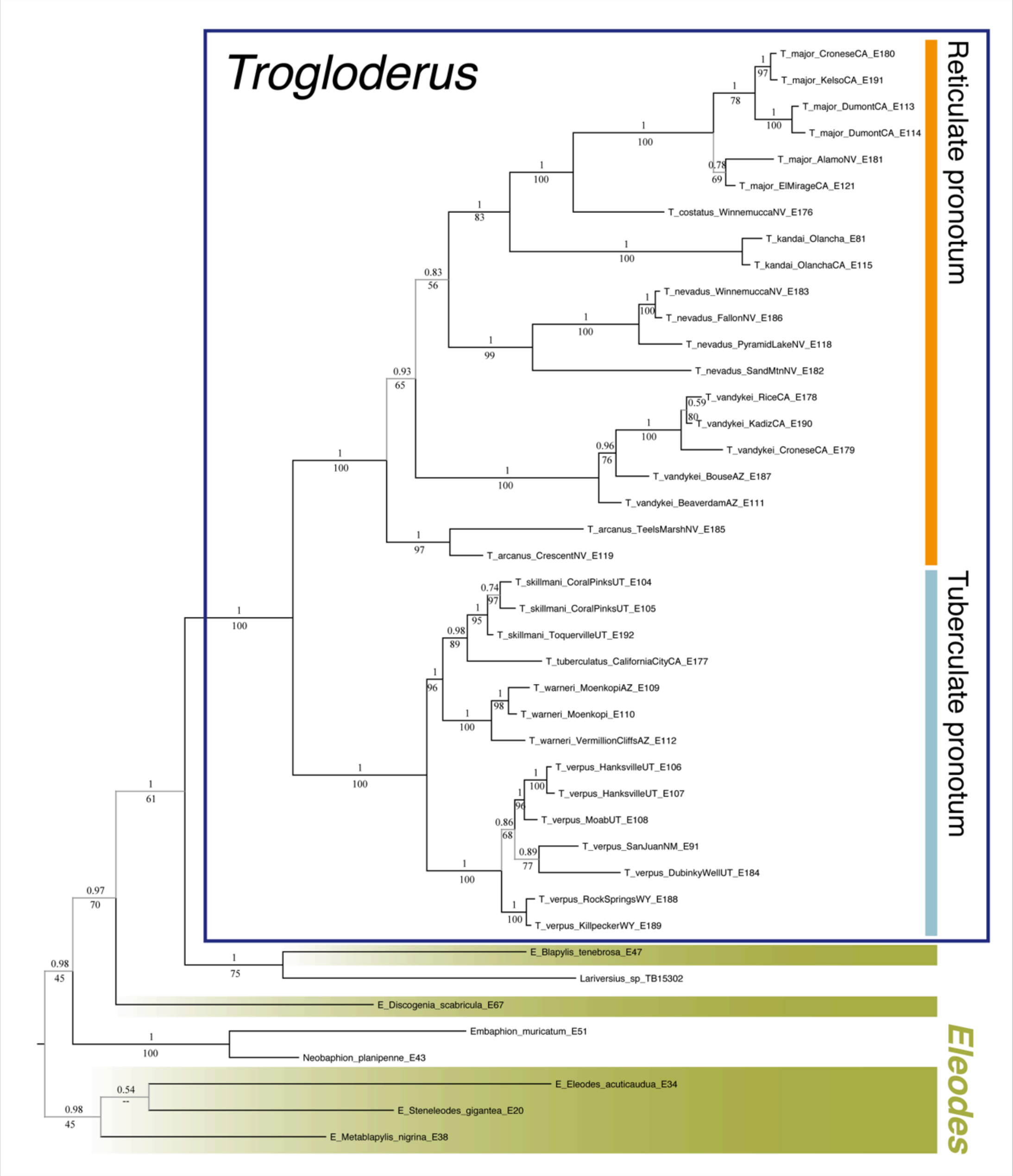


Figure 3.11. Phylogenetic reconstruction of *Trogloderus*. Tree shown is from the MrBayes analysis, numbers above branches are posterior probabilities, numbers below the branches arethe corresponding RAxML bootstrap support values. Outgroup specimens belonging to the genus *Eleodes* are highlighted. The monophyletic *Trogloderus* is indicated by a box, and the reciprocally monophyletic reticulate-pronotum and Tuberculate-pronotum clades are indicated by vertical bars.

poses larger taxonomic questions for the tribe as a whole as currently recognized (Bousquet *et al.* 2018), but the sampling for this study is not sufficient to make any changes at this time. *Trogloderus* was recovered as monophyletic, and is further subdivided into two strongly supported clades – the tuberculate-pronotum clade containing all species that bear distinct tubercles on the pronotal disc, and the reticulate-pronotum clade containing all species whose pronotal discs have deep punctures that make the intervals appear to be elevated into reticulate sculpturing. All *Trogloderus* species as circumscribed above were similarly found to be monophyletic with posterior probabilities of 1 and bootstrap support of 95 or higher.

The tuberculate-pronotum clade contains four species and is well resolved (Fig. 3.11), with internal nodes between species all having posterior probabilities greater than .95 and bootstrap values above 85. The relationships between these species imply an east-to-west diversification pattern. The easternmost species, *T. verpus* (Fig. 3.10) known from the Colorado Plateau, is recovered as sister to a clade containing the remaining three species. The latter clade shows the same trend with its easternmost species, *T. warneri* (Fig. 3.10) distributed east of the Kaibab Plateau, sister to the species *T. skillmani* (Fig. 3.9) and *T. tuberculatus* (Fig. 3.10), which are distributed west of the Kaibab Plateau.

The reticulate-pronotum clade contains six species (Fig. 3.11) with notably western distributions, ranging from the Mojave Desert to the Great Basin. The relationships between these species are less well resolved than for those of the tuberculate-pronotum clade, though each species is supported as monophyletic with posterior probabilities of 1 and bootstrap support values of 95 or higher. While analyses converged on a single topology, the underlying data do not give unequivocal support to the relationships of the early-diverging species. *Trogloderus arcanus*, *T. vandykei*, and *T. nevadus* are inferred to have diverged before a clade containing the other three reticulate-pronotum species. However, these branches all have posterior probabilities lower than .95 and bootstrap support values below 75. The clade consisting of *T. kandai*, *T. costatus*, and *T. major* is strongly supported with a posterior probability of 1 and a bootstrap support value of 83. The reticulate-pronotum clade seems to indicate a latitudinal pattern to diversification. Neither of the two sympatric pairs of species in this clade, the southern *T. vandykei* with *T. major* and the northern *T. costatus* with *T. nevadus*, form monophyletic groups. This supports the notion that multiple vicariant or dispersal events between these regions were involved in the diversification of this lineage.

Trogloderus arcanus and *T. nevadus* exhibit longer branch lengths between sampled populations within the species than any others sampled for this study (Fig. 3.11). This may simply be due to limited sampling, but further molecular and morphological investigations from the under-sampled regions of Nevada may provide evidence for the two herein circumscribed species to represent more complex taxonomic groups.

3.16. Diversification analyses

Trogloderus is here inferred to be relatively young, with the most recent common ancestor (MRCA) for the genus occurring during the late Miocene or earliest Piocene (Fig. 3.12). Furthermore, most speciation events are inferred to have taken place during the Pleistocene. Based on these inferrences, it seems evident that La River's (1946) hypothesis of an ancient lineage approaching extinction can be refuted for *Trogloderus*. Instead, *Trogloderus* seems to postdate the Neogene Uplift, having originated and diversified in conjunction with the recent desert formations of western North America (Wilson and Pitts 2010).

Diversification analyses for *Trogloderus* using BEAST (Fig. 3.12A–B) inferred comparatively older dates than RelTime (Fig. 3.12C–D) but are not particularly reliable, having failed to converge after 500 million generations. The MRCA of *Trogloderus* was dated to 10.27 mya, and ages for both calibrated nodes were older than expected, namely 4.03 mya for the Inyo-White mountains calibration, with the prior mean set at 2.5mya, and 1 mya for the Grand Canyon calibration, with a prior mean set at .83mya. The estimated sample sizes for mutation rates did not exceed 10 and those for calibration times and tree height were well under 100. Additional analyses under different locus partition and model schemes and modified taxon inclusion similarly failed to converge. This may be due either to limitations with the underlying molecular dataset, or because the coalescent-based priors may be inappropriate for this class of data. The results using the Yule model are shown in Fig. 3.12A–B, displaying the median node age and 95% highest posterior density respecively. Due to this lack of convergence, the timetree from RelTime was used for subsequent historical biogeographic inference.

RelTime analyses infer *Trogloderus* to have begun diversifying in the earliest Pliocene with most current species arising during the mid-Pleistocene. Divergence estimates from RelTime were consistently later than those inferred from BEAST, with

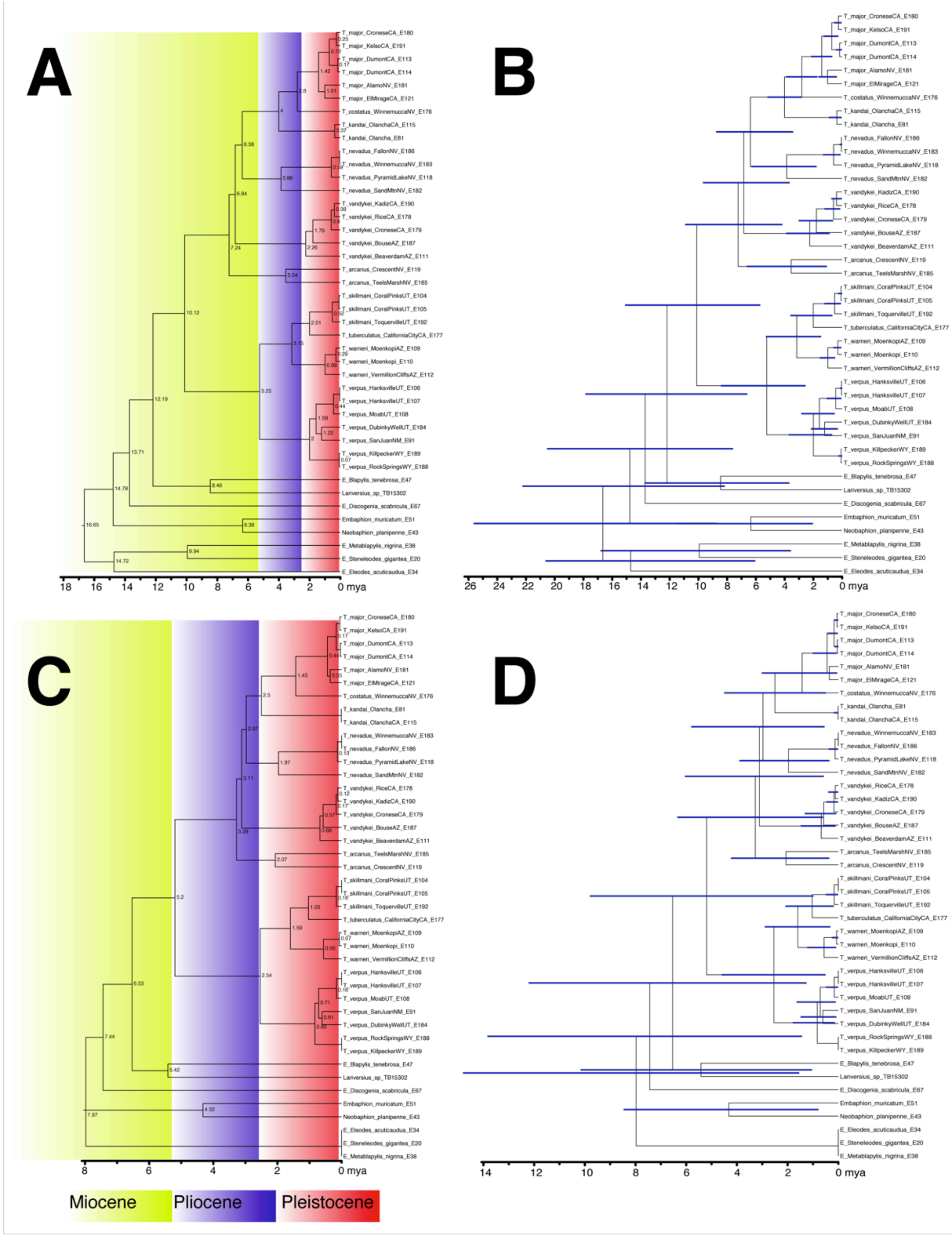


Figure 3.12. Diversification estimates for *Trogloderus*. A. Timetree generated from BEAST showing inferred median node ages. B. Same showing 95% highest posterior density for node ages. C. Timetree generated from RelTime showing inferred median node ages. D. Same showing 95% confidence intervals for node ages.

the MRCA of *Trogloderus* dated to 5.2 mya, and the dates of 2.5 mya and 0.56 mya for the calibration clades split by the Inyo-White mountains and the Grand Canyon respectively. Median node ages and 95% confidence intervals inferred from RelTime are shown in Fig. 12C-D respecitvely.

The Sierra Nevada mountains offer one line of geological evidence for the age of *Trogloderus* to be closer to 5 my as the RelTime analysis infers. The timing of the uplift of the Sierra Nevadas remains contested in the geological literature (Wilson and Pitts 2010), but significant evidence suggests that the majority of the uplift occurred between 5-8 mya and was a primary force in creating the Great Basin and Mojave deserts (Jones *et al.* 2004, Wilson and Pitts 2010). Were *Trogloderus* older than this uplift event, we might expect them to be present outside of the intermountain region. Indeed, members of the genus are able to endure cold winters from central Wyoming as well as the extreme heat from Death Valley and surrounding environs. Beyond living in sandy substrates, there are no other clear environmental limits to their distribution.

The MRCA of all included Amphidorini taxa with was dated to 7.97mya with a 95% confidence interval of 1.5–14.5 mya using RelTime. This date range, though the first inferred for this fossil-lacking tribe, is younger than expected based on phylogenetic work at the family level. The new-world Amphidorini appear to be sister the old-world tribe Blaptini Leach, 1815 (Kanda 2017). The latter was estimated by Kergoat *et al.* (2014) to have an origin closer to 55mya, but no members of Amphidorini were included in that study. The young age inferred here for the tribe may again be a symptom of low species-level taxon sampling. Hypotheses about the origin and diversification of Amphidorini will have to wait for future studies with a broader scope.

3.17. Historical biogeographic estimation

The MRCA of *Trogloderus* was inferred to inhabit the Colorado Plateau (Fig. 3.13), where the majority of the tuberculate-pronotum clade still resides. The ancestors of the reticulate-pronotum clade are inferred to have dispersed into the Lahonton Trough, and from there radiated into the Mojave Desert, Great Basin, and Owens Valley. Three separate radiations into the Mojave Desert are inferred for the three species sympatric there. The insights given by this biogeographic estimation for specific subregions are discussed in detail below.

Historical biogeographic estimation in BioGeoBEARS supports the use of a model incorporating founder-event jump dispersal (Matzke 2014). This process is not only important for taxa distributed across islands (Matzke 2014, Zhang *et al.* 2017), but also for taxa living on sand dunes or other isolated habitats which can functionally act the same as islands (Van Dam and Matzke 2016). The DEC model resulted in a most likely estimation with a log likelihood score of -46.5. The DEC+J model, which employs a single extra parameter for jump dispersal, produced an estimation with a log likelihood of -35.77. By performing a likelihood ratio test (Huelsenbeck and Crandall 1997), the DEC+J model provides a significantly better fit to the data than the DEC model at a P-value of 1e-5.

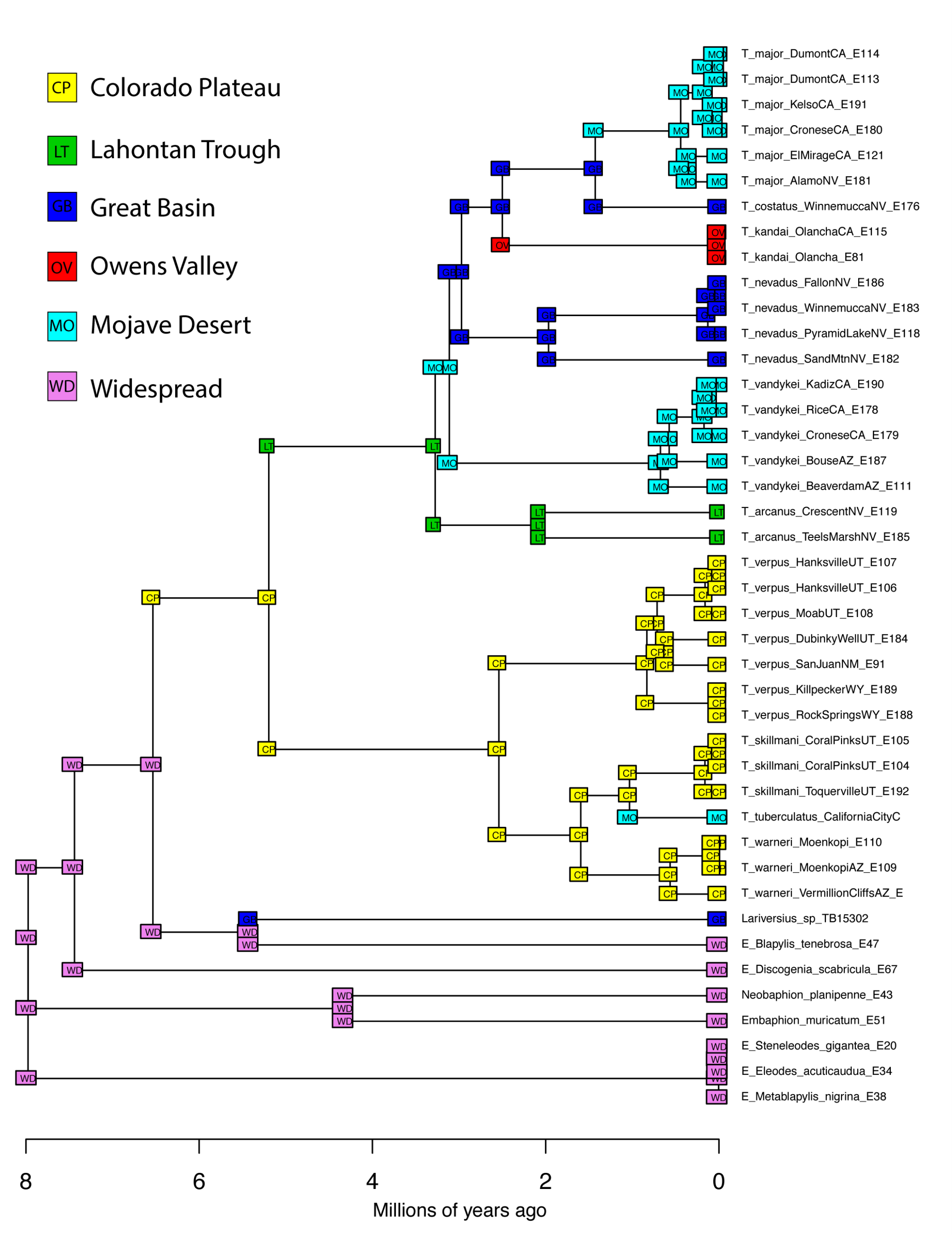


Figure 3.13. Historical biogeographic estimation of *Trogloderus*. Generated from BioGeoBEARS using the DEC+J model. Nodes colored by inferred most likely biogeographic region.

3.18. Biogeographic relationships of the Intermountain Region

The historical biogeography of *Trogloderus* supports the distinction of the Lahontan Trough as a unique element of the intermountain region, and is the first to provide molecular and historical biogeographic support for the area to play a part in the migration of clades throughout the intermountain region. The appraisal of the biogeography of the Intermountain Region by Reveal (1979) was a landmark study based largely on floristic distributions and extensive field observations. A comprehensive biogeographic review of the region has not been published since. One major hypothesis put forth in this work is that the Lahontan Trough acts as a migration route into and out of the region. Following the establishment of the Lahontan Trough as a biogeographic entity by Reveal (1979), multiple studies have found populations from this area to be distinct from populations of the same species from the Mojave and Great Basin deserts (Britten and Rust 1996, Hafner *et al.* 2006), and at least one psammophilic plant is unique to the area (Pavlik 1989). Together, these studies suggest that the Lahontan Trough is likely to play an important role in the evolutionary history of any sand-dune restricted or dispersal-limited taxa in the region.

The newly described *Trogloderus kandai* is the first sand-dune species known to be restricted to the southern Owens Valley. The region has been relatively well studied for changes in plant communities (Koehler and Anderson 1995, Elmore *et al.* 2003) and fish conservation (Galicia *et al.* 2015). However, the sand dunes, which are comprised of particles originating from the surrounding Sierra Nevada and Coso mountains (Lancaster *et al.* 2015), have not had any beetle species reported only from them

(Andrews *et al.* 1979). Whether *T. kandai* is truly the only species restricted to this habitat or if there are others waiting to be described, additional faunal surveys of the sand dunes around the dry Owens Lake should be completed to understand what further importance this area may have for Intermountain biodiversity.

The three sympatric species of *Trogloderus* with independent dispersal events into the Mojave Desert are consistent with the inference of an eastern origin for the genus with a continual movement westward. The relatively recent timing for incursions into the Mojave Desert is also consistent with the fact that *Trogloderus* does not range south into the dunes of the Colorado and Sonoran deserts (Aalbu and Smith 2014, Johnston *et al.* 2018). The relationships of the dune systems within the Mojave Desert were subdivided and well-tested by Van Dam and Matzke (2016), but are here treated as a single unit. The barriers between these sand systems within this area seem to not be a major limiting factor for *Trogloderus* as *T. tuberculatus* and *T. major* are fairly evenly spread throughout.

The predicted footprint of the prehistoric lakes making up the Bouse Embayement is almost identical to the distribution of *T. vandykei*. This region, spanning along the lower Colorado River between Arizona and California (Wilson and Pitts 2010), was covered by three large prehistoric lakes that ran from just north of present-day Bullhead City, Arizona south past Blythe, Arizona. The drainage was bounded along the south by the Chocolate Mountains, and extended west into the Bristol basin (Spencer *et al.* 2013). These lakes likely appeared around 4.9 mya and ended relatively shortly thereafter when the Colorado River eventually connected to the Gulf of California (Spencer *et al.* 2013). It is very likely that the sand derived from these lakes and the geological boundaries that formed their drainage basins have shaped the diversification and distribution of *T. vandykei*. The lakes are also implicated in genetically structuring the populations of a desert scorpion (Graham *et al.* 2017). The Bouse Embayment is further supported as a separate biogeographic entity based on the distribution of other psammophilic Tenebrionidae. Though the Algodones dunes are in extremely close proximity to the southern edge of the Bouse Formation, not only does *Trogloderus* not cross over the Chocolate Mountains and occur there, but multiple species restricted to the Algodones and Gran Desierto de Altar similarly do not extend north into the Bouse Embayment (Johnston *et al.* 2018).

Within the Colorado Plateau, three subregions are suggested by *Trogloderus* distributions. The distribution of the eastern *T. verpus* is somewhat surprising in that no previous biogeographic hypotheses were found to explain why it does not range as far west as the Vermillion Cliffs. One explanation is competitive exclusion within the genus, and this is somewhat supported by the populations near Moenkopi, Arizona. Both *T. verpus* and *T. warneri* occur on these dunes, and all studied specimens of *T. verpus* were significantly smaller than those of *T. warneri*. However, throughout the rest of its range, *T. verpus* has roughly the same body size as *T. warneri*. Another possible explanation is that the Kaiparowitz Formation around Grand Staircase-Escalante national Monument acts as a barrier between sand systems from the Kaibito and Moenkopi plateaus of north-central Arizona and those from the northern reaches of the greater Colorado Plateau. This formation along with the Wasatch Mountains formed the western boundary of the western interior seaway during the Cretaceous (Hettinger *et al.* 1996, Roberts 2007) and are implicated in the speciation of large dinosaurs at the time (Sampson *et al.* 2010). No studies of modern taxa that study this boundary were found.

Even though the Colorado River and its tributaries have carved large canyons through this formation, it may still be a significant barrier between sand-dune restricted taxa. The third subregion is separated by the Kaibab Plateau. This tall formation separates *T. warneri* from its eastern *T. skillmani* and *T. tuberculatus*. The effect of the Kaibab Plateau on dune-dwelling taxa is apparently similarly unstudied.

The revision and historical biogeography of *Trogloderus* help to bring the biogeographic trends of the intermountain region into focus. The cohesive distributional patterns of *Trogloderus* species build upon the foundational work of Reveal (1979) and highlight regions that should be critically evaluated during future phylogenetic, taxonomic, and biogeographic studies. It is hoped that continued research on the under-studied biodiversity of the Intermountain Region will continue to bring clarity to the relationships between sand-dune systems of western North America.

Chapter 4. Phylotranscriptomic Reconstruction of Higher-Level Relationships in the Darkling Beetle Tribe Amphidorini LeConte, 1862 (Coleoptera: Tenebrionidae)

4.1. Introduction

The desert stink beetles of the tribe Amphidorini LeConte, 1862 (Coleoptera: Tenebrionidae sensu Bousquet *et al.* 2018) were last revised by Blaisdell (1909). In this groundbreaking monographic treatment, possibly the first phylogenetic trees for beetles were drawn based on the author's hypotheses of species relationships (e.g. Blaisdell 1909: 39). The tribe is presently comprised of 253 valid species-level taxa with an additional 158 species-level synonyms (Bousquet *et al.* 2018). This diverse lineage is in need of a comprehensive revision, which is in part hindered by a lack of phylogenetic knowledge of the deeper amphidorine relationships (Johnston 2015, Johnston *et al.* 2015, Johnston 2016).

The constituent species groups proposed by Blaisdell (1909) are supported primarily by morphological characters of the female terminalia. Though these groups have remained constant through subsequent taxonomic work, no broader study has critically examined their monophyly or proposed hypotheses of inter-relationships. To address this shortfall, a molecular phylogeny was developed using eight loci and 165 terminals representing over 100 species-level taxa from across Amphidorini (Smith, Johnston, *et al.* in prep). This phylogeny provides strong support for the monophyly of many species groups, but lacks consensus on the relationships *between* those groups (Fig. 4.1).

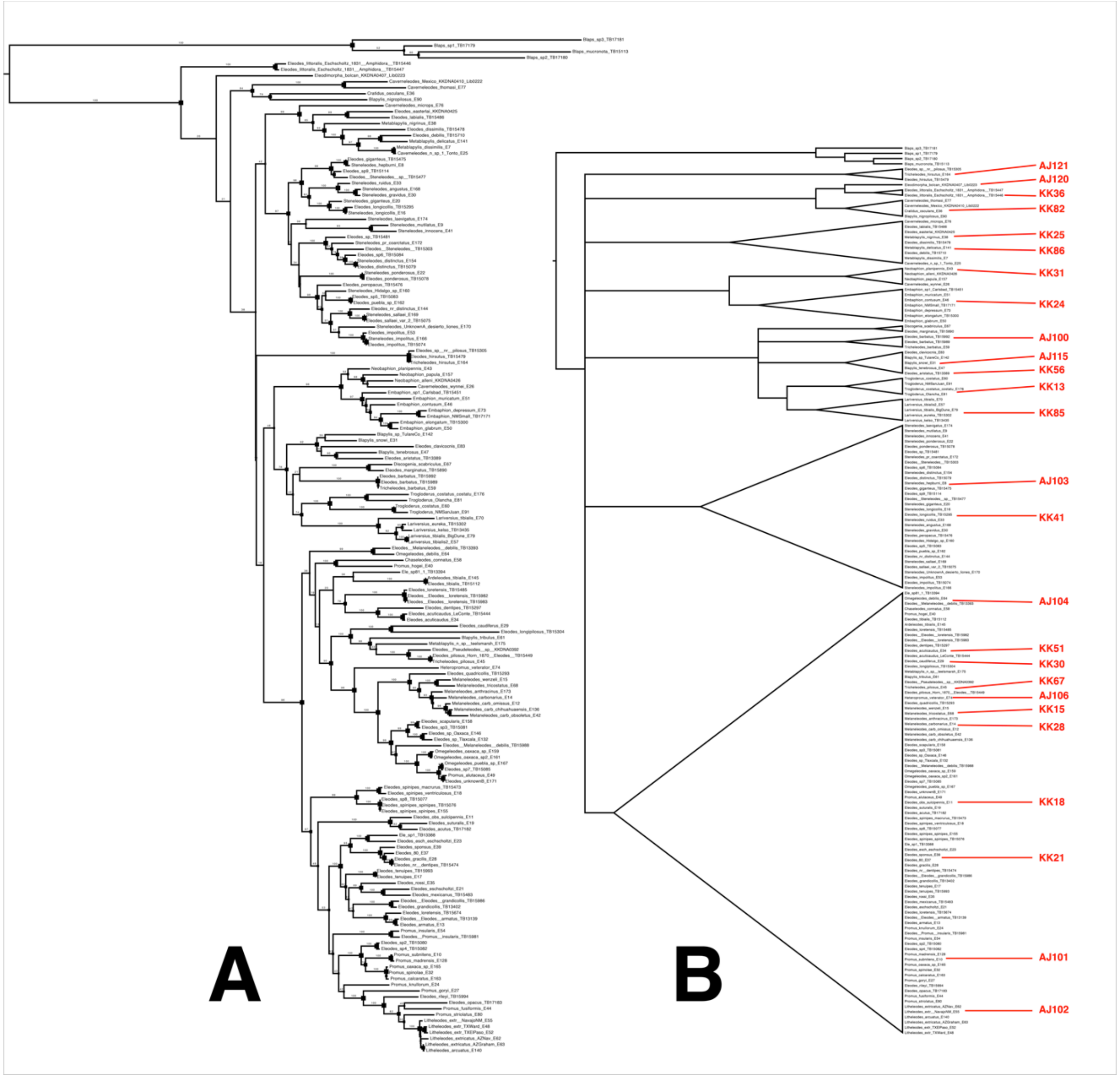


Figure 4.1. Amphidorini 8-locus phylogeny (from Smith, Johnston *et al*. in prep) used to design taxon sampling for the present study. **A.** Maximum Likelihood tree showing bootstrap support values; larger boxes on nodes indicate strong support, small boxes on nodes indicate weak support. **B.** Majority rule consensus tree of 1000 bootstrap replicates showing species groups with moderate support and a poorly resolved backbone; annotations are specimen identifiers which are resolved to taxonomic names in Table 4.1.

Recent advances in sequencing technology and bioinformatics analysis now make it possible to assemble and analyze hundreds to thousands of loci even for groups of organisms which are not widely studied (Oakley *et al.* 2012, Lemmon *et al.* 2012, Dunn *et al.* 2013, Misof *et al.* 2014, Schwartz *et al.* 2015, Faircloth 2017). In order to better evaluate the relationships of the species groups of Amphidorini, a phylotranscriptomic approach is here employed to reconstruct the higher-level evolutionary relationships within the tribe. There are no prior genomic resources available for the Amphidorini, with the closest available genome belonging to *Tribolium castaneum* (Herbst, 1797) (*Tribolium* Genome Sequencing Consortium 2008) whose most recent common ancestor with Amphidorini diverged approximately 120 million years ago (Kergoat *et al.* 2014).

4.2. Materials and methods

4.2.1. Taxon sampling and transcriptome sequencing

Transcriptomes were assembled from a total of 29 specimens, two outgroup and 27 ingroup, which were selected to maximize coverage from the tribe. Sampling was conducted to maximize both the phyloegenetic diversity identified in the 8-locus phylogeny (Fig. 4.1) and the currently recognized taxonomic diversity. Table 4.1 summarizes the current species diversity of Amphidorini in relation to the taxon sampling of this study. The specimens were collected alive into RNA*later* (Ambion, Inc.) or were brought live from the field into the lab for extraction. All specimens were identified to species after examination in the lab. The identification resources used for species determinations are shown in Table 4.1.

Table 4.1. Amphidoroni diversity and taxon sampling. For each genus and subgenus within the tribe, the currently valid species and subspecies are given. Species sampled in this study are shown and the appropriate identification resource used for each taxon is listed.

Genus	**Subgenus**	**Current Valid sp/ssp**	**Sampled Species**	**Author**	**ID Resource Used**	**Specimen ID**
Eleodes	*Amphidora*	3	*littoralis*	(Eschscholtz, 1829)	Bousquet *et al.* 2018	KK36
Eleodes	*Blapylis*	51	*snowii*	Blaisdell, 1909	Somerby 1972	AJ115
Eleodes			*sp.*		Somerby 1972	KK56
Eleodes	*Caverneleodes*	12	[not sampled, polyphyletic, distributed throughout sampled clades]			
Eleodes	*Cratidus*	2	*osculans*	(LeConte, 1851)	Triplehorn 1996	KK82
Eleodes	*Discogenia*	4	[not sampled, closely related to *Blapylis*]			
Eleodes	*Eleodes*	37	*acuticauda*	LeConte, 1851	Triplehorn *et al.* 2015	KK51
Eleodes			*armata*	LeConte, 1851	Triplehorn *et al.* 2015	KK17
Eleodes			*hispilabris*	(Say, 1824)	Triplehorn *et al.* 2015	KK21
Eleodes			*obscura*	(Say, 1824)	Triplehorn *et al.* 2015	KK18
Eleodes	*Heteropromus*	1	*veterator*	Horn, 1874	Triplehorn *et al.* 2009	AJ106
Eleodes	*Litheleodes*	9	*arcuata*	Casey, 1884	Johnston *et al.* 2015	AJ104
Eleodes			*extricata*	(Say, 1824)	Triplehorn and Thomas 2015	AJ102
Eleodes	*Melaneleodes*	24	*carbonaria*	(Say, 1824)	Triplehorn and Thomas 2015	KK28
Eleodes			*tricostata*	(Say, 1824)	Triplehorn and Thomas 2015	KK15
Eleodes	*Metablapylis*	9	*delicata*	Blaisdell, 1929	Johnston *et al.* 2015	KK86
Eleodes			*nigrina*	LeConte, 1858	Johnston *et al.* 2015	KK25
Eleodes	*Omegeleodes*	1	[not sampled, closely related to *Melaneleodes*]			
Eleodes	*Promus*	21	*subnitens*	LeConte, 1851	Johnston 2015	AJ101
Eleodes	*Pseudeleodes*	8	*caudifera*	LeConte, 1858	Johnston 2016	KK30
Eleodes			*pilosa*	Horn, 1870	Johnston 2016	KK67
Eleodes	*Steneleodes*	29	*hepburni*	Champion, 1884	Johnston *et al.* 2015	AJ103
Eleodes			*longicollis*	LeConte, 1851	Johnston *et al.* 2015	KK41
Eleodes	*Tricheleodes*	1	*hirsuta*	LeConte, 1861	Johnston 2016	AJ121
Eleodes	*(incertae sedis)*	18	*barbata*	Whickham, 1918	Johnston 2016	AJ100
Eleodimorpha		1	*bolcan*	Blaisdell, 1909	Blaisdell 1909	AJ120
Embaphion		11	*contusum*	LeConte, 1858	Johnston *et al.* 2015	KK24
Lariversius		1	*n.sp.*		Aalbu *et al.* 2002	KK85
Neobaphion		4	*planipenne*	(LeConte, 1866)	Johnston *et al.* 2015	KK31
Trogloderus		10	*kandai*	Johnston, n.sp.	Johnston (chapter 2)	KK13

Specimens were dissected live or straight out of RNA*later* to sample internal tissues for RNA extraction. A variety of tissues, generally including a mixture of hindgut, reproductive tract, thoracic musculature, and defensive glands, were homogenized and total RNA was extracted using RNeasy kits (Qiagen, Inc.). Libraries were then prepared by using NEBNext® Poly(A) mRNA magnetic isolation kits (New England BioLabs, Inc.) to isolate mRNA from the more abundant ribosomal RNA. Libraries with an insert size of 400-550 bp were then indexed by unique dual adapters using the NEBNext® Multiplex Oligos kit (New England BioLabs, Inc.). Libraries were then pooled into groups of either 12 or 16 samples which were then run on a single lane of an Illumina® HiSeq2500 high-throughput sequencer (sequenced at the University of Arizona Genetics Core facility, Tucson, Arizona), which resulted in a range of 4 to 18 million paired-end reads per sample (Table 4.2).

4.2.2. Transcriptome assembly

Transcriptomes were assembled following the Agalma (Dunn *et al.* 2013) pipeline for preassembly and assembly, which further filters out ribosomal RNA reads and employs Trinity (Grabherr *et al.* 2011) to assemble the reads into contigs. Transdecoder (Haas and Papanicolaou N.D.) was then used to identify unique contigs that contained an open reading frame of at least 100 amino acids and to provide this filtered assembly in both nucleotide and amino acid form. The number of contigs, total base pairs, and N50 of each transcriptome assembly are given in Table 4.2. Assembled transcriptomes are available on-line (https://github.com/mandrewj/Amphidorini-transcriptomics - archived at archived at https://doi.org/10.5281/zenodo.1482785).

Table 4.2. Amphidorini transcriptome assembly summary. The number of raw paired end reads for each taxon is provided. Summary statistics are given for each transcriptome assembly using Trinity and Transdecoder following the Agalma pipeline.

	Sample Identification				**Trinity + Transdecoder Assembly**		
	Species	**Subgenus**	**Specimen ID**	**Raw paired end reads**	**Number of contigs**	**Total base pairs**	**N50**
Outgroup	*Blapstinus sp.*		KK60	13,586,016	26,264	27,856,290	1,533
	Notibius sp		KK53	12,858,013	29,203	31,727,223	1,569
Ingroup	*Eleodes littoralis*	*Amphidora*	KK36	5,712,013	26,292	26,411,703	1,470
	Eleodes snowii	*Blapylis*	AJ115	6,512,020	28,603	27,153,528	1,344
	Eleodes (Blapylis) sp.	*Blapylis*	KK56	18,129,962	40,797	40,355,298	1,473
	Eleodes osculans	*Cratidus*	KK82	13,516,652	40,232	39,523,290	1,455
	Eleodes acuticauda	*Eleodes*	KK51	15,920,789	28,710	27,048,054	1,347
	Eleodes armata	*Eleodes*	KK17	18,377,925	29,798	30,652,242	1,536
	Eleodes hispilabris	*Eleodes*	KK21	15,221,319	34,694	34,820,490	1,458
	Eleodes obscura	*Eleodes*	KK18	15,427,039	31,197	31,935,843	1,497
	Eleodes veterator	*Heteropromus*	AJ106	9,527,531	23,371	19,083,303	1,083
	Eleodes arcuata	*Litheleodes*	AJ104	9,168,825	27,425	27,673,341	1,464
	Eleodes extricata	*Litheleodes*	AJ102	11,265,708	27,230	24,962,061	1,284
	Eleodes carbonaria	*Melaneleodes*	KK28	13,393,302	29,266	29,282,034	1,467
	Eleodes tricostata	*Melaneleodes*	KK15	10,308,757	27,501	27,623,331	1,470
	Eleodes delicata	*Metablapylis*	KK86	12,729,035	30,599	31,538,523	1,506
	Eleodes nigrina	*Metablapylis*	KK25	15,345,441	31,711	33,201,267	1,551
	Eleodes subnitens	*Promus*	AJ101	11,118,159	27,826	28,684,821	1,509
	Eleodes caudifera	*Pseudeleodes*	KK30	4,312,831	22,496	21,995,427	1,404
	Eleodes pilosa	*Pseudeleodes*	KK67	13355267	34,468	35,486,649	1,530
	Eleodes hepburni	*Steneleodes*	AJ103	11,417,547	27,254	28,176,684	1,515
	Eleodes longicollis	*Steneleodes*	KK41	4,421,031	29,246	25,273,692	1,218
	Eleodes hirsuta	*Tricheleodes*	AJ121	4,734,186	18,417	13,329,072	858
	Eleodes barbata	*(incertae sedis)*	AJ100	11,460,120	34,912	34,812,786	1,455
	Eleodimorpha bolcan		AJ120	5,554,652	26,402	24,295,191	1,275
	Embaphion contusum		KK24	13,658,152	29,410	29,727,144	1,494
	Lariversius n.sp.		KK85	9,977,350	32,601	32,507,268	1,470
	Neobaphion planipenne		KK31	5,084,505	24,981	24,567,351	1,425
	Trogloderus kandai		KK13	16,259,456	36,132	35,723,937	1,452
			Mean:	11,322,538	29,553	29,152,684	1,418

4.2.3. Ortholog identification

Three different methods were employed to identify orthologs from the 29 sampled taxa. The pipelines, scripts, and results from all three methods are documented and available online (https://github.com/mandrewj/Amphidorini-transcriptomics). First, a set of orthologs was developed *de novo* generally following the methods of Kanda (2017). In this approach, the amino-acid fasta files were analyzed by FastOrtho (Wattam *et al.* 2014), which conducts an all-by-all blast search for the given contigs and then utilizes OrthoMCL (Li *et al.* 2003) to cluster similar sequences into putative ortholog groups. The putative ortholog groups were then stringently filtered down to only those containing putative 1:1 orthologs, i.e. groups with exactly one sequence from each and every included taxon, to eliminate as much paralogy as possible. For each of these 1:1 ortholog groups, the sequences were aligned with MAFFT (Katoh and Standley 2013). From these alignments, if any single sequence contained more than 40% gaps, the group was discarded in a further attempt to remove potential paralogs or abberant ortholog assessments. This process resulted in 232 groups with high confidence of being 1:1 orthologs because they contain a single gene expressed from each taxon with 300 or more nucleotides that coherently align to each other.

Second, the program SISRS (Schwartz *et al.* 2015) was used to generate putative orthologous loci from the unassembled paired end reads. The loci function of SISRS was employed with an estimated genome size of 50,000 to generate a composite assembly using subsampled reads from each taxon, which was then used as a reference in order to map all reads from each individual taxon back onto (Schwartz *et al.* 2015). Putative orthologous loci were extracted from these contig mappings by selecting only those that were 400 base pairs or longer and that had sequences from all 29 taxa were selected. These loci were then aligned in MAFFT and any groups that contained more than 40% gaps were removed. This filtering resulted in a total of 372 remaining ortholog groups.

The third and final ortholog set was generated by using SISRS in combination with the highly conserved ortholog set from the 1KITE initiative of Misof *et al.* (2014). The orthologs developed by 1KITE were generated for use across the insect tree of life, and are putatively single or low copy genes conserved throughout all insects. The darkling beetle *Tribolium castaneum* was included in the 1KITE study, and its ortholog sequences were used as a reference set of loci for SISRS to align the present Amphidorini samples to. The loci alignments generated were then screened for those groups that contained sequences from all 29 taxa, were aligned in MAFFT, and then were screened for any sequences containing 40% or more gaps with the offending groups removed. The final set included 291 loci.

4.2.4. Ortholog sets analyzed

Five datasets of orthologs were used in the following analyses (Table 4.3). Two datasets were generated from the 232 FastOrtho orthologs in both the nucleotide alignments per locus (*FO-nt*) and amino-acid alignments per locus (*FO-aa*). Two more ortholog datasets were made from the SISRS pipeline, one containing the 372 loci generated from the loci command (*SISRS-loci*) and one containing the 291 loci generated from mapping to the 1KITE orthologs (*SISRS-1k*). All orthologs included in these sets are available online (https://github.com/mandrewj/Amphidorini-transcriptomics).

Table 4.3. Summary of ortholog sets. The number of individual loci, the total length of those loci concatenated together in either nucleotides (nt) or amino acids (aa), and the total percent of gaps or nucleotide ambiquities (e.g. ‘N’) for the final alignments are shown for each ortholog set.

Data set	Number of Loci	Concatenated Length	% missing data (gaps and nt ambiquities)
FO-nt	232	199567 nt's	6.60%
FO-aa	232	66364 aa's	6.60%
SISRS-loci	372	196587 nt's	4.70%
SISRS-1K	291	408419 nt's	13.20%
Combined-nt	844	728670 nt's	9.00%

The final ortholog dataset was created by combining the previous three nucleotide sets together. This first required identifying any potential duplicate loci generated through separate discovery pipelines. Sequences from *Eleodes littoralis* (Eschscholtz, 1829) were compiled from all orthologs and compared to each other using BLAST (Altschul *et al.* 1990). Surprisingly, only 54 pairs of orthologs were found to be shared between multiple ortholog sets (see https://github.com/mandrewj/Amphidorini-transcriptomics for comparison scripts and results). After removing one of each of the duplicate ortholog pairs, a total of 844 loci were included in the final dataset (*Combined-nt*).

4.2.5. Concatenation analyses

Concatenated phylogenetic analyses were performed on all five datasets. For each dataset, the constituent aligned loci were combined into a single sequence and then analyzed under maximum likelihood using RAxML version 8 (Stamatakis 2014). Analyses were performed using a single partition and the GTRGAMMA substitution model (PROTGAMMA for the*FO-aa* dataset) for ten independent runs and 1000 bootstrap replicates.

4.2.6. ASTRAL-II species-tree analyses

Concatenation of genes may not infer the relationships between species if there is discordance between gene trees, e.g. due to incomplete lineage sorting (Carstens and Knowles 2007, Degnan and Rosenberg 2009, Mirarab *et al.* 2016). Therefore, the coalescent-based ASTRAL-II (Mirarab and Warnow 2015) was used to infer species trees from the underlying gene trees. For each dataset, a gene tree was inferred for each individual locus alignment under maximum likelihood using RAxML version 8 (Stamatakis 2014). For each RAxML analysis, ten independent tree searches and 100 bootstrap replicates were conducted under the GTRGAMMA substitution model with the best tree retained and bootstrap supports written onto it. ASTRAL-II was then used to compute a species tree with 100 bootstrap replicates from the inferred gene trees. A majority rule consensus tree was then created for the 100 bootstrap trees in Mesquite 3.5 (Maddison and Maddison 2018) in order to evaluate underlying coalescent-informed clade support.

4.3. Results

4.3.1. Concatenation analyses

All datasets produce highly congruent phylogenies, with only two alternate topologies represented (Fig. 4.2). Each topology strongly supports the monophyly of Amphidorini but differ in the deepest branching patterns of the tribe. For both the *SISRS-loci* and *SISRS-1k* datasets, *Eleodes (Amphidora) littoralis* and *Eleodimorpha bolcan* are found sister to each other and together sister to the rest of the tribe (Fig 2A), whereas *FO-nt*, *FO-aa*, and *Combined-nt* recover *Eleodes (Amphidora) littoralis* alone as sister to the rest of the tribe (Fig. 4.2B).

Three clades were consistently recovered and are worth noting First, the *Embaphion*-clade is here defined to include the four currently valid genera *Embaphion* Say, 1824, *Lariversius* Blaisdell, 1947, *Neobaphion* Blaisdell, 1925, and *Trogloderus*

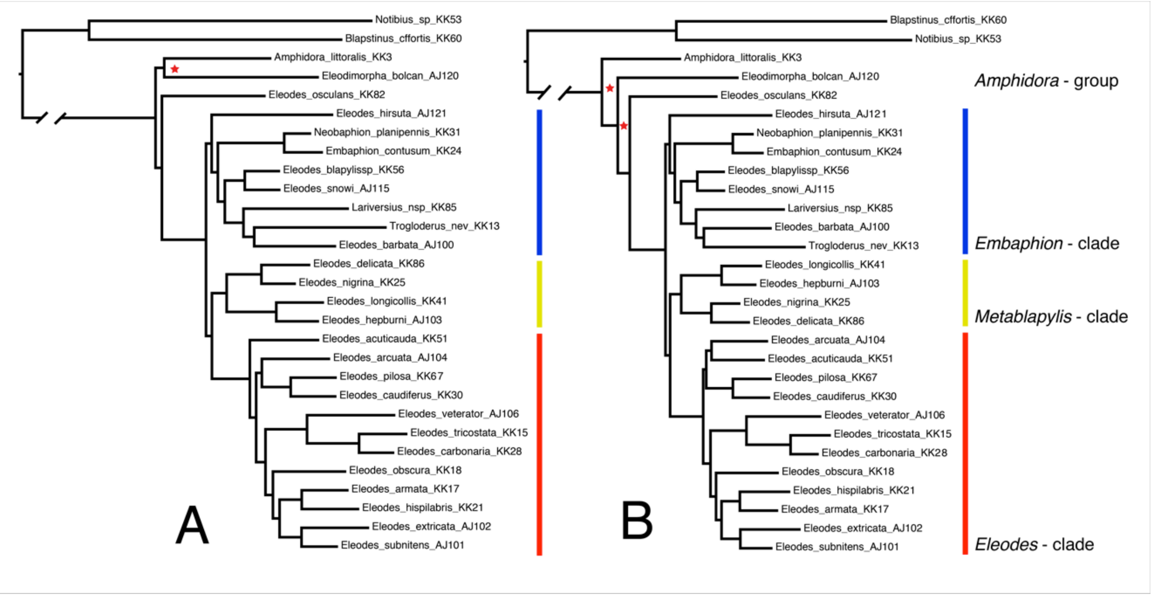


Figure 4.2. Phylogenetic inference from concatenation with maximum likelihood. A. Phylogeny produced from the *SISRS-1k* dataset, identical to *SISRS-loci* analysis. B. Phylogeny produced from the *Combined-nt* dataset, identical to *FO-nt* and *FO-aa* analyses.

LeConte, 1879, along with the *Eleodes* Eschscholtz, 1829 subgenera *Blapylis* Horn, 1870 and *Tricheleodes* Blaisdell, 1909. This clade was recovered in four of the analyses, but was rendered paraphyletic in the *SISRS-loci* analysis (Fig. 2A) with *Tricheleodes* placing outside of the group. However, only the *FO*-nt, *SISRS*-1k, and *Combined*-nt analyses had support (bootstrap higher than 70) for the placement of *Tricheleodes*, where it was included within the *Embaphion*-clade. Second, the monophyletic *Metablapylis*-clade is newly defined to include the *Eleodes* subgenera *Metablapylis* Blaisdell, 1909 and *Steneleodes* Blaisdell, 1909. Third, the monophyletic *Eleodes*-clade is defined here to comprise the *Eleodes* subgenera *Eleodes*, *Litheleodes* Blaisdell, 1909, *Melaneleodes* Blaisdell, 1909 *Promus* LeConte, 1862, *Pseudeleodes* Blaisdell, 1909. Lastly, a non-monophyletic assemblage, the *Amphidora*-group, is pragmatically named to include the earliest diverging taxa in these analyses, which belong to the genus *Eleodimorpha* Blaisdell, 1909 and *Eleodes* subgenera *Cratidus* LeConte, 1862 and *Amphidora* Eschscholtz, 1829.

Despite some ambiguity near the root of the tribe, these analyses strongly support a paraphyletic *Eleodes* with respect to all of the other North American Amphidorini genera.

4.3.2. ASTRAL-II analyses

ASTRAL-II analysis of all datasets produced the same three clades defined above in addition to the monophyletic *Amphidora*-clade. The latter is identical in composition to the non-monophyletic *Amphidora*-group of the concatenated analyses. Two general topologies were recovered. The first supports a sister relationship between the *Eleodes*-clade and all other Amphidorini (Fig. 4.3). It is found in the *FO-nt*, *SISRS-loci* and *Combined-nt* analyses. The second topology supports a sister relationship between the *Amphidora*-clade and all other Amphidorini (Fig. 4.4) – recovered in the *GO-aa* and *SISRS-1K* analyses. The bootstrap support for these deep relationships is variable, yet each topology is moderately strongly supported in at least one dataset analysis. The bootstrap consensus analyses provide mounting support for the *Eleodes*-clade being sister to the remainder of Amphidorini with all but *FO-aa* in agreement (Fig. 4.5).

4.4. Discussion

4.4.1. Ortholog discovery

The assembled transcriptomes and identification of over 800 orthologs for 27 species of Amphidorini are incredible steps forward for an understudied group that has merely 25 partial gene sequences, mostly mitochondrial barcodes, available on GenBank (Benson *et al.* 2013, access 17 October 2018). However, the limited overlap between the three groups of orthologs is somewhat surprising. This is likely due to the stringent 1:1 filtering employed during ortholog selection. For instance, the FastOrtho approach generated 5,400 groups that contained sequences for all 29 taxa. However, most of these contained extra sequences for some or all taxa, with the largest group consisting of 1,249 sequences. This large volume of newly available data opens Amphidorini up to a wide range of additional phylogenetic, molecular, and evolutionary studies in the future.

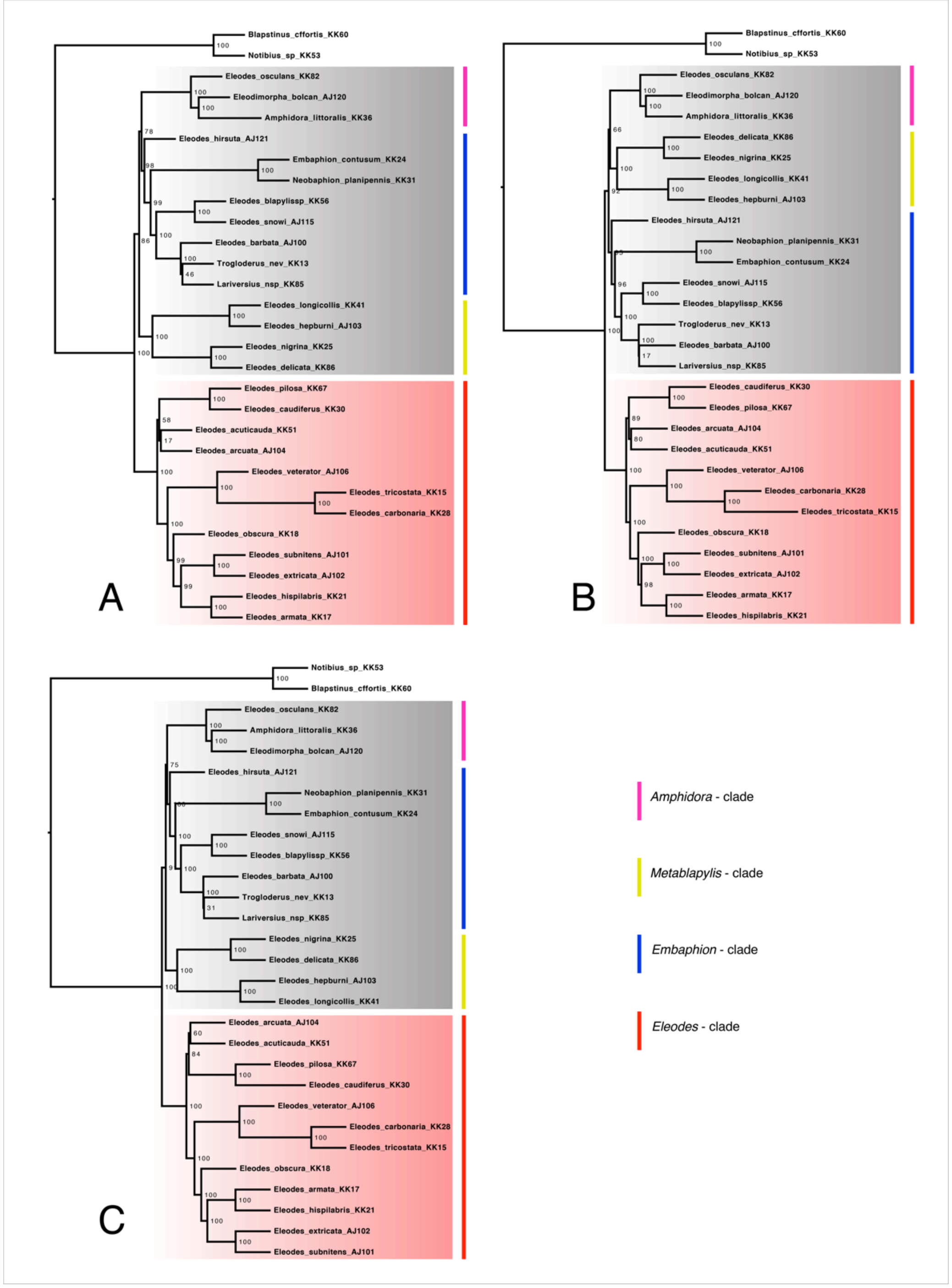


Figure 4.3. ASTRAL-II analyses with earliest-diverging clades highlighted, *Eleodes*-clade sister to remaining Amphidorini. A. *FO-nt* analysis. B. *SISRS-loci* analysis. C. *Combined-nt* analysis.

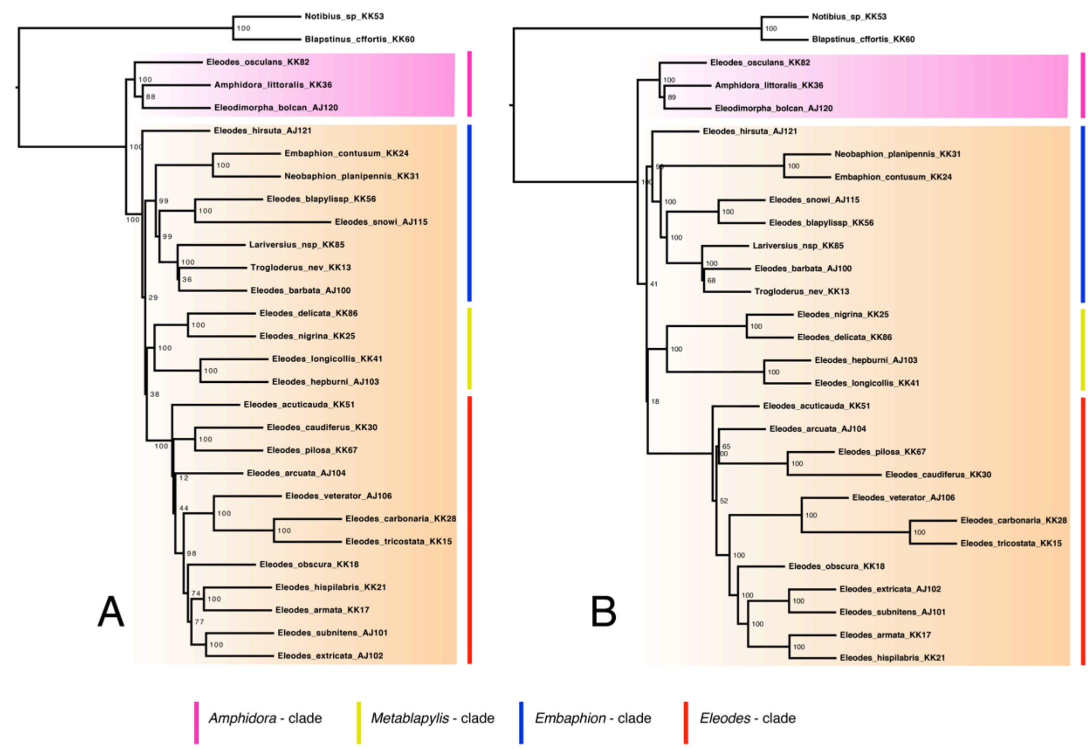


Figure 4.4. ASTRAL-II analyses with earliest-diverging clades highlighted, *Amphidora*-clade sister to remaining Amphidorini. A. *FO-aa* analysis. B. *SISRS-1k* analysis.

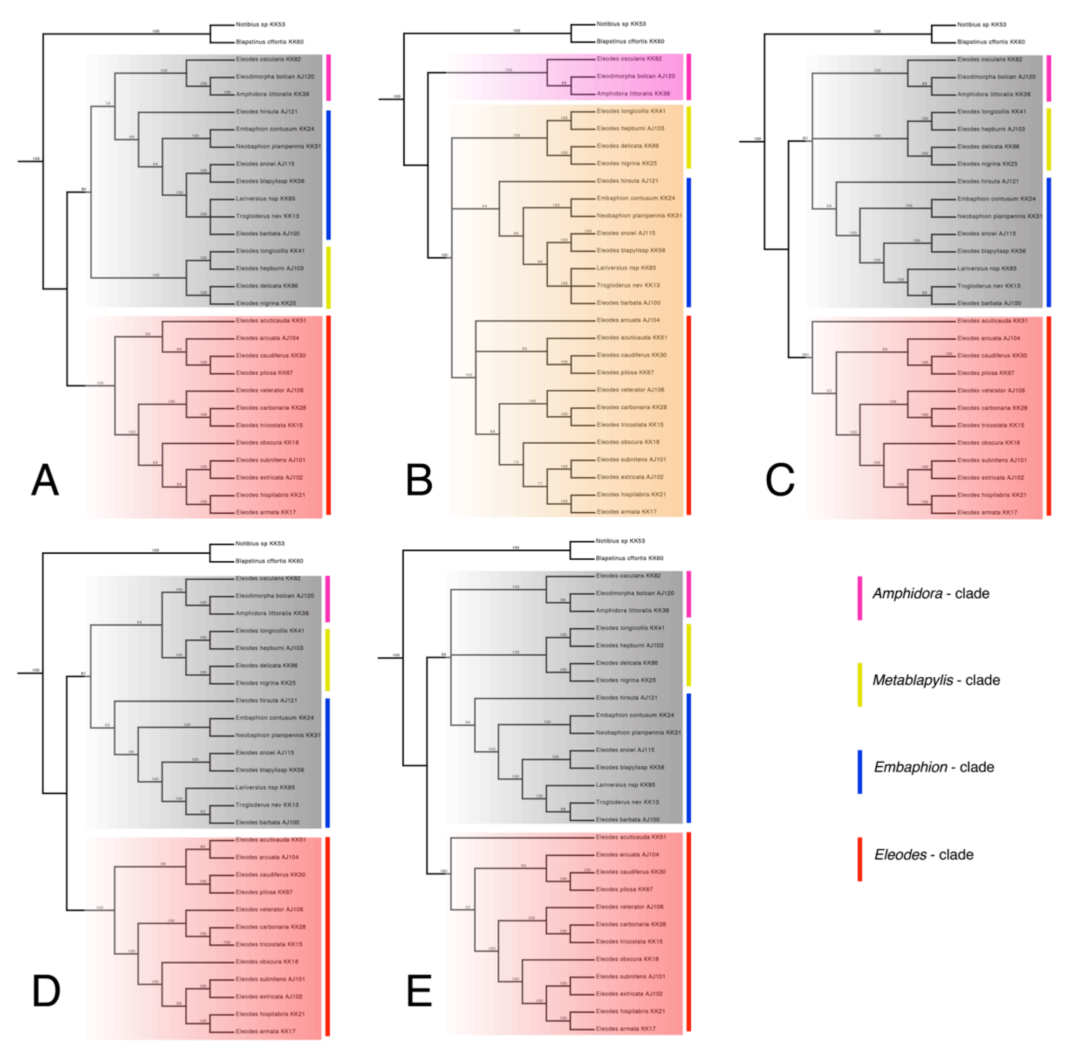


Figure 4.5. ASTRAL-II Bootstrap consensus analyses with earliest-diverging clades highlighted. A. *FO-nt* analysis. B. *FO-aa* analysis. C. *SISRS-1k* analysis. D. *SISRS-loci* analysis. E. *Combined-nt* analysis.

The FastOrtho, and underlying OrthoMCL, approach to ortholog discovery has been widely and reliable used (Chen *et al.* 2006, Misof *et al.* 2014, see http://orthomcl.org), and therefore provides some confidence in the robustness of the method. In addition, this method produces a single transcriptome assembly for each taxon, which can be leveraged for further studies, such as investigating the underlying sequence evolution of chemical defenses or other physiological processes. The main drawback to using this method is the required computational resources. The modest 29 taxon dataset used here required roughly two weeks straight of processing using eight cores, with somewhat limited scalability due to the all-by-all blast component.

The two SISRS methods applied here are relatively new, with few empirical applications (but see Harkins *et al.* 2016, Yesson *et al.* 2018). Nevertheless, the results herein are largely consistent with the FastOrtho method. SISRS provides a clear advantage in terms of computational scalability, where the 29 taxon dataset here required roughly 30 hours to complete on the same eight-core machine. The composite assembly process should also scale fairly linearly with additional taxa (Schwartz *et al.* 2015).

The coupling of SISRS with a pre-defined set of loci provides a powerful tool for future phylogenomic analysis. Here, the extraction of the 1KITE orthologs from the 29 Amphidorini taxa was not only the fastest method, requiring less than 12 hours with eight cores, but also produced the largest number of 1:1 orthologs. SISRS makes it simple to extract conserved orthologs or develop target capture probe sets for under-studied lineages without prior genomic resources.

4.4.2. Early-diverging incongruence

While there is strong overall support for the four clades defined above, no unambiguous consensus was found for relationships between them. Although the concatenation analyses did not unambiguously support the *Amphidora*-clade and the *Embaphion*-clade, they also do not support a clear alternative. Rather, a set of trees including these groups as monophyletic are preferred due to the consistent recovery of both clades in all ASTRAL-II analyses.

The incongruence across all analyses for the deepest branches of Amphidorini is problematic, requiring further resolution beyond the present scope. The more conservative ASTRAL-II analyses, *FO-aa* - which is the only amino acid analysis and may reduce saturation issues of the third codon position - and *SISRS-1k* - a subset of putative single copy genes present in all insects - both generally align with concatenation analyses in support of the *Amphidorini*-clade as sister to the rest of the tribe. Conversely, the bulk of the ASTRALL-II analyses support the *Eleodes*-clade as sister to the rest of the tribe.

All analyses concur that the *Amphidora*-clade and the *Eleodes*-clade do not form a single monophyletic group. However, there is further conflict with the placement of the *Metablapylis*-clade and the *Embaphion*-clade. There is no consensus that these latter two clades form a monophyletic group, or that they definitively belong with either of the first two clades.

In sum, the monophyletic Amphidorini are here considered to have a 4-way polytomy at their root. Genomic scale phylogenies are still subject to methodological limitations, and increased gene sampling or especially taxon sampling may clarify relationships in the future (Johnson *et al.* 2013, Fiarcloth *et al.* 2015, Branstetter *et al.* 2017). Nevertheless, the taxon sampling of this study is highly representative of the known phylogenetic diversity of the tribe, and therefore this may be another example of a phylogenetically irreducible polytomy in the tree of life (Whitfield and Kjer 2008, Stanley *et al.* 2011, Suh 2016).

4.4.3. Taxonomic and biological implications

The lack of congruent relationships between larger clades notwithstanding, the phylogenetic relationships supported in this study strongly conflict with the existing Amphidorini classification. The genus *Eleodes* is here found to be paraphyletic with respect to all other presently recognized genera. Additionally, to make *Eleodes* monophyletic using any of the topologies described above, the genus *Embaphion* would necessarily be included. Because *Embaphion* has nomenclatural priority to *Eleodes*, this synonymy would require over 200 species-level nomenclatural changes.

The inadequacy of the existing classification is due, in large part, to the high degree of morphological similarity at the species, subgeneric, and generic levels (Johnston *et al.* 2015, Johnston 2016). This seemingly conserved morphotype, which is putatively aposematic and reinforced by inter-species mimicry (Doyen and Somerby 1974, Smith *et al.* 2015), is found in all four identified clades as well as in the majority of the tribe's species. However, the groups diagnosed as subgenera by Blaisdell (1909) were done so based on morphology, and those species groups have largely stood the test of time (Smith, Johnston *et al.* in prep). The lack of morphological characters previously found to support the clades reported here seem to reinforce the notion that Amphidorini underwent an early rapid radiation, which has left little evidence for phylogenetic inference.

All known members of the *Amphidora*-clade are geographically restricted to the pacific coast and coastal mountain ranges of California and Baja California. If further evidence emerges to support this clade as sister to the rest of the tribe, that might help explain the sister relationship between Amphidorini and the Palearctic Blaptini Leach, 1815 (Kanda 2017, Smith, Johnston *et al.* in prep). The combined Holarctic distribution could indicate a Laurasian origin with continental vicariance, but this would require the lineage to be at least 175 million years old, which is the estimated age of the entire family (Kergoat *et al.* 2014). However, the inferred age of Blaptini is closer to 55 million years old (Kergoat *et al.* 2014). If the Amphidorini stem-group inhabited this pacific region, then it is very plausible that the North American Amphidorini, like many mammals, have diversified through dispersal across a land-bridge at the beginning of the Eocene, approximately 55.5 mya (Smith *et al.* 2006).

The present study significantly advances our understanding of desert stink beetle relationships and hints at new evolutionary hypotheses for the origin of the Amphidorini. It is also clear that genus-level rearrangements are necessary. It is hoped that future studies with larger taxon sampling will bring further clarity to the deepest relationships within the tribe and provide evidence for the geographic and temporal origin of the tribe.

Chapter 5. Revision of the genera of Amphidorini LeConte, 1862 (Coleoptera: Tenebrionidae)

5.1 Introduction

The desert stink beetles in the tribe Amphidorini LeConte, 1862 in the sense of Bouchard *et al.* (2011) represent a large arid-adapted lineage, and the largest North American tribe within the family Tenebrionidae Latrielle, 1802 (Bousquet *et al.* 2018). Despite an increasing body of work at the species and regional levels (Triplehorn *et al.* 2009, 2015; Triplehorn and Thomas 2012; Aalbu *et al.* 2012; Johnston *et al.* 2015; Johnston 2015, 2016), a comprehensive review of the genera and subgenera has not been completed since that of Blaisdell (1909) from over a century ago.

The few available regional treatments for Baja California (Triplehorn 1996), Colorado (Bernett 2008), Texas (Triplehorn *et al.* 2009), and Arizona (Johnston *et al.* 2015) are very useful and manageable tools for species identifications, and are largely complementary to the present work. However, recent systematic reviews of species groups have come with the caveat that there are no adequate resources to separate the groups from each other (Triplehorn and Thomas 2009, Triplehorn *et al.* 2015, Johnston 2016). Nevertheless, these revisionary studies, paired with intensive nomenclatural works (Thomas 2005, Bousquet *et al.* 2018), have clarified the species-level entities well enough to allow for the revision presented here.

The primary goal of this study is to clarify the generic boundaries within Amphidorini, which is currently comprised of seven genera, the largest of which, *Eleodes*

Eschscholz, 1829, is further subdivided into 16 subgenera (Gebien 1938, Bousquet *et al.* 2018). A diagnosis, differential description, and summary of constituent species are given for each genus herein recognized. The secondary goal of this study is to provide species-level reviews, where practical, for genera that lack a recent revision. With the exception of several large groups lacking modern taxonomic studies, this revision provides treatments and links together those cited above such that identification keys exist to separate all 253 valid species-group taxa within the tribe.

5.2. Rationale for recognizing generic groupings

The complex taxonomic and nomenclatural history of Amphidorini is mainly due to a large number of species with relatively few discrete, external morphological characters available to separate them (Triplehorn and Thomas 2012, Johnston *et al.* 2015, Johnston 2016). The taxonomic result of this has been the description of strongly (aut-/)apomorphic genera, e.g. *Trogloderus* LeConte, 1879 and *Lariversius* Blaisdell, 1947, while the remainder of the less well-differentiated species-level diversity has remained allocated in the large genus *Eleodes* (Bousquet *et al.* 2018). Phylogenetic analyses (Chapters 3,4, Smith, Johnston *et al.* in prep), however, strongly support a paraphyletic *Eleodes* with respect to the other presently recognized genera in the tribe.

Modern systematics by and far advocates for the diagnosis and naming of monophyletic groups (Vences *et al.* 2013, Ward *et al.* 2016, though see Seifert *et al.* 2016), which leaves two general options for a revision of Amphidorini: splitting previously delimited genus-level concepts apart or lumping them together. To determine how to treat the constituent species groups within Amphidorini, the application of priority Taxon Naming Criteria (TNC) proposed by Vences *et al.* (2013) were applied.

The first TNC considered was that of monophyly. In general, there were many clades well supported by the molecular analyses (see 5.3 below), which correspond to historically identified species groups, primarily subgenera of *Eleodes* in the sense of Bouchard *et al.* (2018). Monophyly has therefore been readily adopted in the following classification. The second TNC considered was clade stability. This TNC suggests that only clades that are strongly and/or consistently supported should be classified as genera, thereby using the best available evidence to reduce the risk of future studies recovering discordant phylogenies that require new nomenclatural changes. The lack of concordance for the interrelationships of species groups in Amphidorini thus supports the notion of increased splitting since broader groupings remain tenuous. Therefore, by naming each constituent strongly supported group, the present classification is maximally robust to any changes among deeper phylogenetic nodes.

The third and most difficult TNC considered was phenotypic diagnosability. Unfortunately, the best characters for diagnosis are typically located on the female ovipositor, which is not conducive for identifying live specimens, males, or the majority of museum specimens, without dissection. Nevertheless, these characters exist and coincide with molecular hypotheses of monophyly. (see also 5.3 below).

On the whole, these three priority TNCs, proposed to promote an economy of nomenclatural change (Vences *et al.* 2013), support the decision to split Amphidorini into narrower genus-level concepts than have been used in past classifications. Indeed, and under the presumption of monophyly, the more granular generic composition presented below is actually the least disruptive approach possible, leaving 103 valid species circumscribed within *Eleodes*. The alternative of lumping groups together to retain the current composition of the genus would require the priority-carrying name *Embaphion* Say, 1824 to be brought into synonymy, and thereby necessitating more than 200 new binominal combinations.

5.3. Materials and methods

The seven current genera of Amphidorini, along with the 17 current subgenera of the largest genus *Eleodes* Eschscholtz (Bousquet *et al.* 2018), are herein reevaluated. A comprehensive molecular phylogeny of Amphidorini (Smith, Johnston, *et al.* in prep, see chapter 4) was used as a scaffold for morphological investigations. The phylogeny is shown in Fig. 1 and is annotated with the generic names used below.

Primary type specimens for over 200 species of Amphidorini were examined and imaged from their housing institutions. Tens of thousands of specimens were broadly surveyed from the following entomological collections:

ADSC – Aaron D. Smith Collection, Flagstaff, AZ
AMNH – American Museum of Natural History, New York, NY
ASUHIC – Hasbrouck Insect Collection, Arizona State University, Tempe, AZ
AUIC – University of Arizona Insect Collection, Tucson, AZ
BMEC – Bohart Museum of Entomology, Davis, CA
BMNH – The Natural History Museum, London, United Kingdom

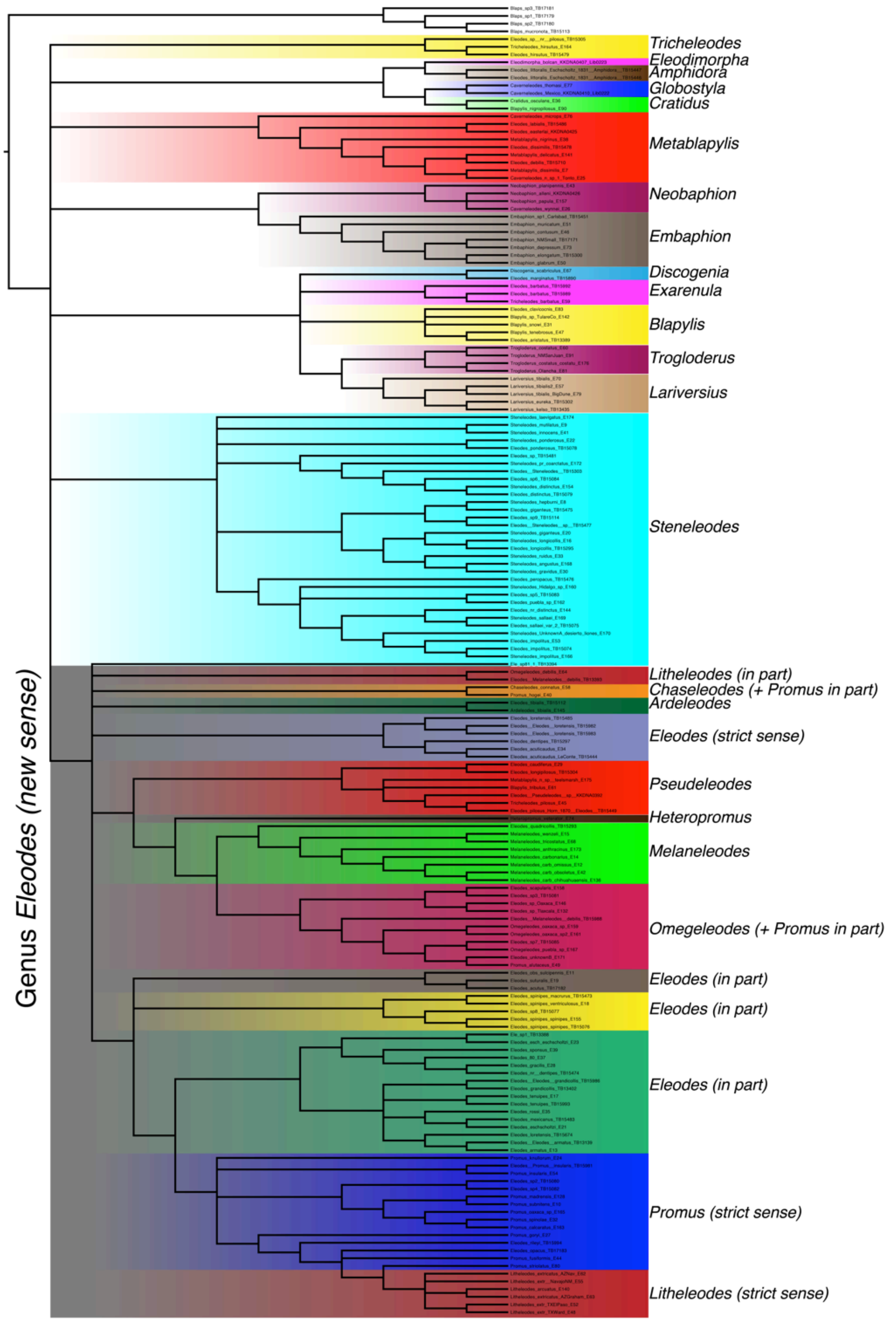


Figure 5.1. Annotated phylogeny of Amphidorini genera. Tree is a majority-rule consensus from 500 bootstrap replicates based on an 8-locus maximum-likelihood analysis for the tribe. Each highlighted clade corresponds to a genus (or *Eleodes* subgenus) circumscribed in this revision.

CASC – California Academy of Sciences, San Francisco, CA
CSCA – California State Collection of Arthropods, Sacramento, CA
CMN – Canadian Museum of Nature, Ottawa, ON, Canada
CNC – Canadian National Collection of Insects, Ottawa, ON, Canada
CSUC – C.P. Gillete Museum of Arthropod Diversity, Fort Collins, CO
EMEC – Essig Museum of Entomology, Berkeley, CA
FSCA – Florida State Collection of Arthropods, Gainseville, FL
LACM – Los Angeles County Museum of Natural history, Los Angeles, CA
MAJC – M. Andrew Johnston Collection, Tempe, AZ
MNHN – Muséum National d'Histoire Natural, Paris, France
MTEC – Montana State University, Bozeman, MT
NAUF – Northern Arizona State University, Flagstaff, AZ
OSUC – Triplehorn Insect Collection, Ohio State University, Columbus, OH
RLAC – Rolf L. Aalbu Collection, Sacramento, CA
RMBC – Royal British Columbia Museum, Victoria, BC, Canada
SBMNH – Santa Barbara Museum of Natural History, Santa Barbara, CA
TAMU – Texas A&M University Insect Collection, College Station, TX
UDCC – University of Delaware, Newark, DE
UNAM – Universidad Nacional Autonoma de Mexico, Mexico City, Mexico
USNM – U.S. National Museum, Smithsonian Institution, Washington D.C.
WBWC – William B. Warner Collection, Chandler, AZ

From these, approximately 10,000 specimens were studied in detail using a Leica MZ16 stereomicroscope. Male and female terminalia (aedeagus and ovipositor respectively) were examined from approximately 3,000 specimens, either from specimens mounted with terminalia extruded or via dry dissection (see Chapter 3 for details). Full-body disarticulations were performed on 50 individuals from across the tribe (see Chapter 3 for details) but no internal, non-terminalia, characters were found to be useful for genus-level delimitation.

Female ovipositor characters are predominantly what have been used to group species in genera and subgenera (Blaisdell 1909, Triplehorn and Thomas 2009, Johnston 2016). While they are also the most heavily relied upon morphological characters here, a very deliberate attempt was made to use external characters for genus recognition so that specimens of both sexes can hopefully be determined without dissection.

5.4 Systematics

Amphidorini is hereby recircumscribed and diagnosed from the rest of the family Tenebrionidae and a key to all herein included genera is provided. Each genus is then treated, in alphabetical order, accompanied by a diagnosis, differential redescription, and remarks on its species-level composition. Bousquet *et al.* (2018) provide a comprehensive and up-to-date treatment of nomenclature and synonymy for Amphidorini, so it is not repeated here and only new taxonomic acts are detailed at the species level. Newly described genera are recognized as such with the phrase ‘New Genus.’ Genera which were formerly treated as subgenera but never valid at the genus-level are identified with the phrase ‘New Status.’ Similarly, genera herein reinstated as valid that were last treated as subgenera (i.e. in Bousquet *et al.* 2018), yet at one point were treated as valid genera, are denoted as such by the phrase ‘Revised Status.’ Species-level binomens are treated likewise as New or Revised Combinations.

5.4.1. Removal of *Nycterinus* Eschscholtz, 1829

The South American genus *Nycterinus* Eschscholtz, 1829 (Fig. 5.2) has long been classified near *Eleodes* Eschscholtz, 1829 (Lacordaire 1859, Blaisdell 1909, Gebien 1938, Peña 1971). However, the two genera have never been included in the same phylogenetic study to confirm this association. *Eleodes* and related genera were studied by Tschinkel and Doyen (1980), where they were found to have characteristics very similar to groups within the Opatrinae Brullé, 1832; namely paired abdominal defensive glands lacking a common volume and lacking sclerotized annulations, and a shortened paraproct with oblique baculi that partially covers a short coxite. *Nycterinus* was later included in the phylogenetic study of Doyen and Tschinkel (1982) where it was found closely related to several genera from the tribe Tenebrionini Latreille, 1802; namely short paired abdominal defensive glands with shared volume and cuticular annulations, a four-lobed coxite, and an elongated paraproct (Fig. 5.2B). In addition to these characters, *Nycterinus* possesses an elongate head similar to those of *Cerenopini* Horn, 1870 and lacks the distinct yellow setal sensory patches on the terminal 3-4 antennomeres present in *Eleodes*.

These morphological differences in conjunction with molecular phylogenetic studies within the tribe and family (Kanda 2017, Smith *et al.* in prep) clearly exclude *Nycterinus* from the Amphidorini in the present sense. Without a further comparative study across the family, *Nycterinus* is hereby placed as *Incertae sedis* within the subfamily Tenebrioninae Latreille, 1802 **New Placement**.

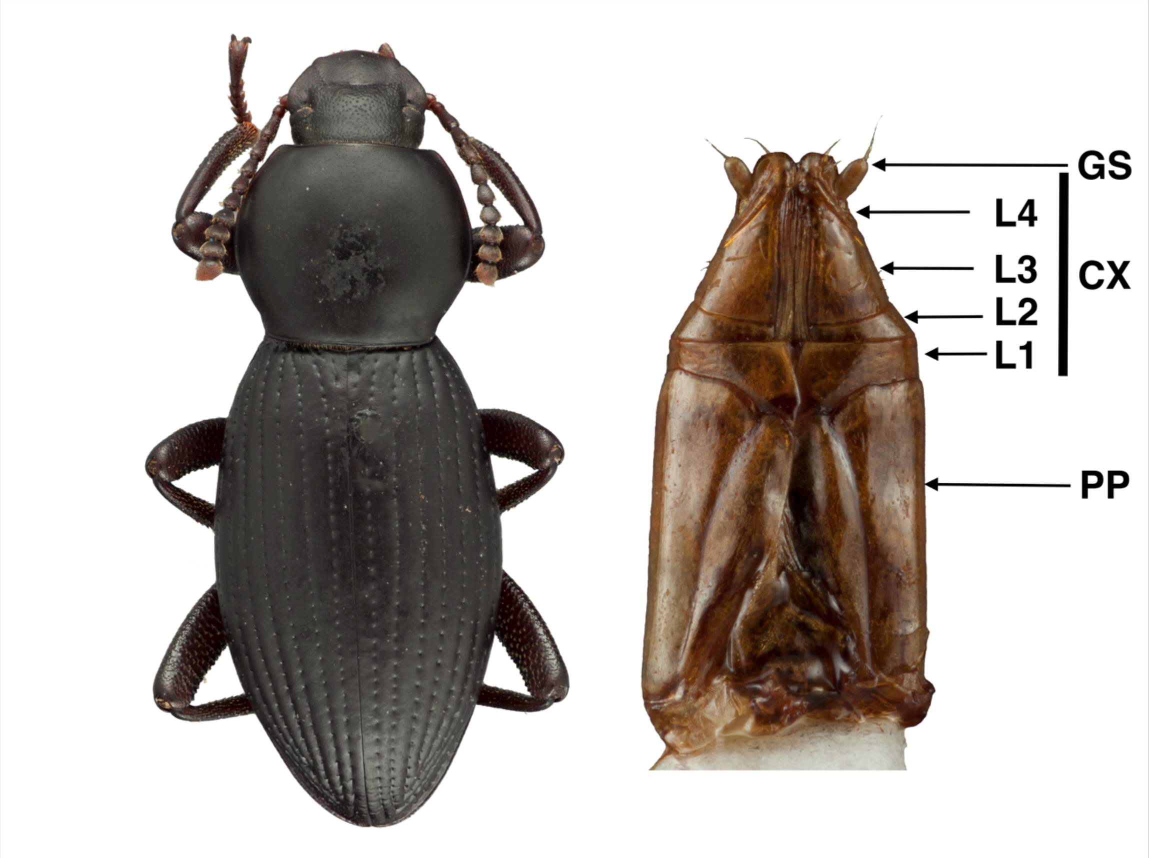


Figure 5.2. *Nycterinus rugiceps* Curtis, 1845. A. Dorsal habitus. B. Female terminalia, ventral view. *CX* – coxite, *GS* – gonostyle, *L1-4* – lobes of coxite, *PP* – paraproct.

5.4.2. Amphidorini LeConte, 1862:239

Type genus: *Amphidora* Eschscholtz, 1829

Diagnosis. Amphidorini can be separated from other members of Tenebrionidae by the following combination of characters: abdominal ventrites III-IV with visible membrane along hind margin; antennae lacking compound stellate sensoria; tarsal claws simple, not pectinate; penultimate tarsomeres not lobed beneath; paired defensive glands present between abdominal sternites VII and VIII, glands separate lacking a common volume, glands smooth, not annulated; female paraproct and coxite short, coxite 1-segmented, with short subapical gonostyle; elytra fused medially, hind wings reduced to small folds; mentum trilobed with mesal face more or less produced anterad, often concealing insertion of ligula; female with single, bursa-derived spermatheca.

The simple tarsi, visible abdominal membranes, presence of paired defensive glands, and lack of antennal sensoria place Amphorini within the Tenebrioninae (sensu Bouchard *et al.* 2011 and Bousquet *et al.* 2018). The reduced ovipositor and defensive glands lacking common volume further implicate a close relationship with the tribes formerly placed in the Opatrinae Brullé, 1832 (sensu Aalbu *et al.* 2002). The flightless bodyform, female ovipositor, defensive glands and mentum distinguish this tribe from any other tenebrionines. Externally, they are most similar to the old world Blaptini Leach, 1815, but can be separated by the mentum and 1-segmented ovipositor coxite. The tribe is here circumscribed to contain 16 genera, detailed below.

5.4.3. Key to the genera of Amphidorini.

1. Epistoma deeply incised medially, antennal length subequal to head width .... *Lariversius* Blaisdell

1'. Epistoma truncate or broadly arcuate; antenna much longer than head width 2

2. Elytron with 4 longitudinal carinae; pronotum roughly sculptured (tuberculate or reticulately punctate)... *Trogloderus* LeConte

2'. Elytron lacking longitudinal carinae, or if carinate pronotum not roughly sculptured 3

3. Buccal process of subgena strongly projected; all tibiae strongly arcuate .... *Eleodimorpha* Blaisdell

3'. Buccal process not projected, or if weakly projected tibiae not strongly arcuate 4

4. Antennomere 3 subequal to 4, body clothed in golden setae .... *Amphidora* Eschscholtz

4'. Antennomere 3 subequal to 4 and 5 combined, body hirsute or not 5

5. Genae swollen into large protuberances over antennal insertions; body densely punctate throughout..*Torugena* **New Genus**

5'. Genae not swollen above antennal insertions; surface sculpturing variable, almost never thoroughly covered in large punctures 6

6. Epipleuron very wide, epipleural fold strongly carinate; mesal lobe of mentum bearing short finger-like process; ovipositor gonostyle very large, sub-spherical.........

………………………………………………………………………… *Globostyla* **New Genus**

6'. Epipleuron narrow to moderately wide, epipleural fold usually weakly rounded; mentum variable, usually without finger-like process; gonostyle minute to moderately elongate, never large and spherical ……………………………………………7

7. Mesanepisternum evenly sculptured, lacking dorso-ventral ridge; relatively small, hirsute beetles……………………………………………………………………………… 8

7'. Mesanepisternum bearing arcuate dorso-ventral ridge near posterior margin of prothorax; body setae and size variable………………………………………………… 9

8. Body clothed with golden setae; antennomere 8 bearing setose sensory patch on outer apical margin……………………………………………………*Exarenula* **New Genus**

8'. Body clothed with dark black setae; antennomere 8 lacking setose sensory patch on outer apical margin…………………………………………………………*Tricheleodes* Blaisdell

9. Submentum thickened, bilobed, bearing central longitudinal channel; body densely hirsute (coastal California and Baja California) ………………………… *Cratidus* LeConte

9'. Submentum not thickened or bilobed, lacking central channel; body hirsute or not (widespread) ……………………………………………………………………………………10

10. Pronotum and elytra with lateral carinae moderately to strongly produced and elevated; fore femora lacking spines; inner apical lobe of ovipositor coxite strongly produced ……………………………………………………………………… *Embaphion* Say

10’. Pronotum and elytra lacking lateral elevated carinae, or if bearing produced carinae then fore femora with spines; fore femora spined or not; ovipositor coxite variable, usually lacking strongly produced inner apical angle... 11

11. Epipleuron relatively narrow, evenly tapering from base to apex, not attaining humeral angle; inner apical lobe of ovipositor coxite strongly produced 12

11’. Epipleuron more or less arcuately expanded basally, often reaching humeral angle; ovipositor coxite roughly triangular or rectangular, inner apical angle acute or not, usually not strongly produced 13

12. Male probasitarsus thickened beneath; middle lobe of mentum concealing insertion of ligula; inner apical angles of ovipositor coxites elongate, oblique, directed posterolaterally.. *Neobaphion* Blaisdell

12’. Male probasitarsus not thickened, lacking apical pencil brush; middle lobe of mentum short, base of ligula mostly or entirely visible; inner apical angles of ovipositor coxites elongate, subparallel, directed posteriorly ....
....*Metablapylis* Blaisdell

13. Pronotum more or less cordate, strongly arcuate laterally and constricted basally; pronotum and elytra moderately strongly punctate to scabrous; ovipositor coxite with apicolateral submarginal groove 14

13’. Pronotum variable, if strongly arcuate laterally and constricted basally pronotum usually weakly to moderately punctate; pronotal and elytral sculpturing variable; ovipositor coxite with or without apicolateral submarginal groove 15

14. Mentum large, transversely oval, outer lobes visible only by dissection; fore femora bearing blunt tooth in males; inner apical angles of ovipositor coxite strongly produced .... *Discogenia* LeConte

14’. Mentum smaller, narrowing anteriorly, outer lobes visible in ventral view; fore femora lacking tooth in both sexes, usually sinuate; inner apical angles of ovipositor coxite not strongly produced .... *Blapylis* Horn

15. Mentum transverse, anterior edge arcuate; femora always lacking spines; all tarsi bearing yellow spicules and/or yellow setae; inner apical lobe of ovipositor coxite produced, oblique, directed posterolaterally .... *Steneleodes* Blaisdell

15’. Mentum generally acute anteriorly; fore, and rarely all, femora bearing spines or not; tarsi variable, often bearing only black spicules, sometimes bearing pads or rows of golden setae; inner apical angle of ovipositor coxite acute or reduced, not strongly projected, if acute, directed posteriorly ....*Eleodes* Eschscholtz

5.4.4. *Amphidora* Eschscholtz, 1829:9 **Revised Status**

Type species: *Amphidora littoralis* Eschscholtz, 1829

Diagnosis. This genus (Fig. 5.3) can be readily identified by the short third antennomere. The body being clothed in golden setae and tarsi bearing long golden setae underneath are not unique to this genus but aid recognition by gestalt. Externally most similar to the genus *Cratidus*, the antennal character clearly distinguishes the two.

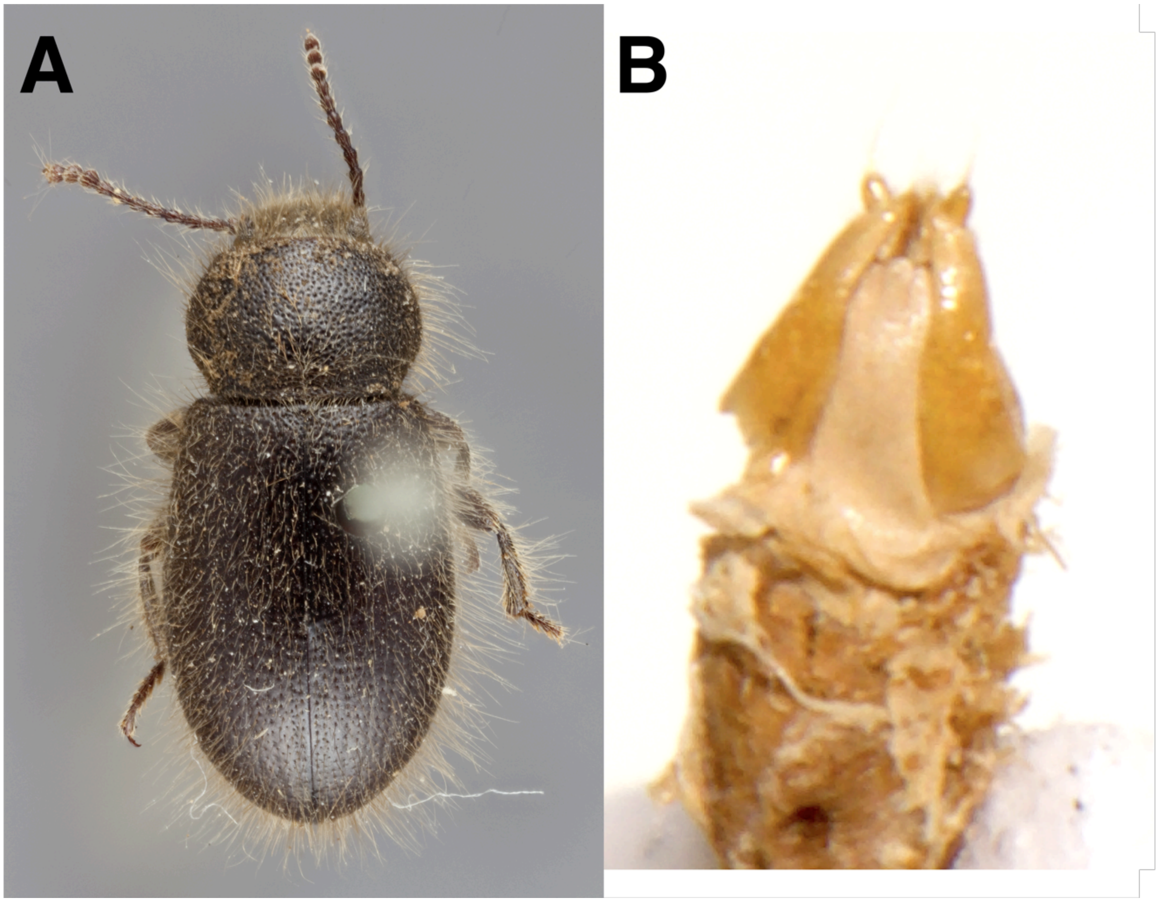


Figure 5.3. *Amphidora littoralis* Eschscholtz, 1829. A. Dorsal habitus, holotype. B. Female ovipositor, dorsal view.

Differential redescription. Body relatively small, ferruginous to black, all surfaces bearing both long, suberect golden setae and shorter recumbent setae. Mentum trilobed, mesal lobe small, acute, not concealing insertion of ligula. Pronotum moderately convex, lateral margins arcuate. Antennomere 3 subequal in length to 4, antennae much longer than head width. All femora lacking spines; outer margin of tibiae bearing row of short yellow spicules, inner apical margin of protibiae bearing setal brush; all tarsi bearing long golden setae beneath in both sexes, brobasitarsus with dense setal pad in males. Ovipositor coxite elongate trapezoidal, inner apical angle acute, subequal in length to well-developed gonostyle.

Remarks. *Amphidora* is here circumscribed as monotypic, containing only *Amphidora littoralis* Eschscholtz, 1829 **Revised Status** from California and western Nevada. The species formerly placed within *Amphidora*, according to Bousquet *et al.* (2018) are herein transferred to the genus *Cratidus*, based on antennal, ovipositor, and molecular characters.

5.4.5. *Blapylis* Horn, 1870:315 **New Status**

Type species: *Eleodes cordata* Eschscholtz, 1829

= *Eleodopsis* Blaisdell, 1939, type species *Eleodipsis subvestita* Blaisdell, 1939

Diagnosis. *Blapylis* (Fig. 5.4) can be recognized by the combination of a more or less cordate pronotum which is at least somewhat constricted basally, fore femora lacking spines, males with setal pads on at least probasitarsus, sometimes on protarsomeres 2-4, female ovipositor with well-developed submarginal groove, and moderately strongly punctate to scabrous pronotum.

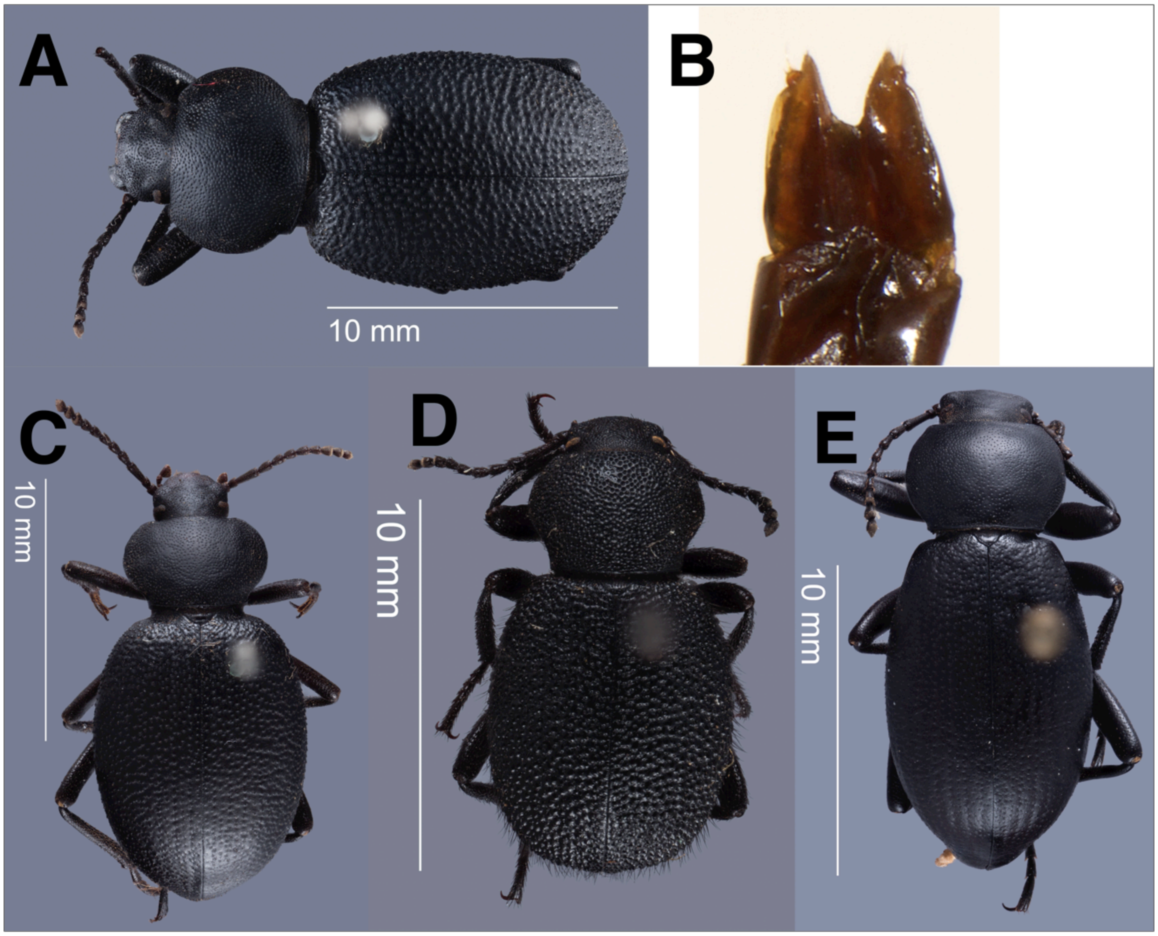


Figure 5.4. *Blapylis* Horn, 1870. A. *B. blanchardii* (Blaisdell, 1909) holotype, dorsal habitus. B. *B. blanchardii* female ovipositor, dorsal view. C. *B. fuchsii* (Blaisdell, 1909) holotype, dorsal habitus. D. *B. propinqua* (Blaisdell, 1918) holotype, dorsal habitus. E. *B. triplehorni* (Somerby and Doyen, 1967) holotype, dorsal habitus.

Differential redescription. Body small to large, generally roughly sculptured, often covered in short, bristling setae. Mentum trilobed, msal lobe elongate, acute or truncate apically, concealing insertion of ligula. Antennomere 3 subequal to length of 4 and 5 combined, antennae much longer than head width. Pronotum strongly arcuate laterally, typically cordate, roughly punctate to scabrous. Femora always lacking spines; protarsi of males bearing pads of yellow setae beneath at least first if not first 3-4 tarsomeres, legs rufous to black. Ovipositor coxite elongate trapezoidal, inner apical angle acute, produced slightly further than gonostyle, gonostyle fully visible from above; submarginal groove well-developed and evident in ventral view.

Remarks. This genus was partially revised in the unpublished dissertation by Somerby (1972), the new species from which were published subsequently (Somerby and Doyen, 1976, Somerby 1977). All currently valid species following the rearrangements by Bousquet *et al.* (2018) are retained, though the genus is still in need of a comprehensive species-level revision. Species identification keys were provided by the previous revisers Horn (1870), Blaisdell (1909), and Somerby (1972).

Checklist of currently valid species names for *Blapylis*
(see Bousquet et al. 2018 for synonymies).

Blapylis alticola (Blaisdell, 1925)[*Eleodes*] **New Combination**
Blapylis aristata (Somerby, 1977) [*Eleodes*] **New Combination**
Blapylis bishopensis (Somerby and Doyen, 1976) [*Eleodes*] **New Combination**
Blapylis blanchardii (Blaisdell, 1909) [*Eleodes*] **New Combination**
Blapylis brunnipes (Casey, 1890) [*Eleodes*] **New Combination**

Blapylis caseyi (Blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis clavicornis (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Blapylis consobrina (LeConte, 1851) [*Eleodes*] **New Combination**

Blapylis constricta (LeConte, 1858) [*Eleodes*] **New Combination**

Blapylis cooperi (Somerby and Doyen, 1976) [*Eleodes*] **New Combination**

Blapylis cordata (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Blapylis fuchsii (blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis hoppingii (Blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis hornii (Blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis hybrida (Blaisdell, 1917) [*Eleodes*] **New Combination**

Blapylis inculta (LeConte, 1861) [*Eleodes*] **New Combination**

Blapylis kaweana (Blaisdell, 1933) [*Eleodes*] **New Combination**

Blapylis lariversi (Somerby and Doyen, 1976) [*Eleodes*] **New Combination**

Blapylis lecontei (Horn, 1870) [*Eleodes*] **New Combination**

Blapylis manni (Blaisdell, 1917) [*Eleodes*] **New Combination**

Blapylis nana (Blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis neotomae (Blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis novoverrucula (Boddy, 1957) [*Eleodes*] **New Combination**

Blapylis nunenmacheri (Blaisdell, 1918) [*Eleodes*] **New Combination**

Blapylis oregona (Blaisdell, 1941) [*Eleodes*] **New Combination**

Blapylis orophila (Somerby, 1977) [*Eleodes*] **New Combination**

Blapylis panamintensis (Somerby, 1977) [*Eleodes*] **New Combination**

Blapylis parvicollis (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Blapylis patulicollis (Blaisdell, 1925) [*Eleodes*] **New Combination**

Blapylis pimelioides (Mannerheim, 1843) [*Eleodes*] **New Combination**

Blapylis planata (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Blapylis producta (Mannerheim, 1843) [*Eleodes*] **New Combination**

Blapylis propinqua (Blaisdell, 1918) [*Eleodes*] **New Combination**

Blapylis robinetti (Boddy, 1957) [*Eleodes*] **New Combination**

Blapylis rotundipennis (LeConte, 1857) [*Eleodes*] **New Combination**

Blapylis scabripennis (LeConte, 1859) [*Eleodes*] **New Combination**

Blapylis scabriventris (Blaisdell, 1933) [*Eleodes*] **New Combination**

Blapylis scabrosa (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Blapylis schlingeri (Somerby and Doyen, 1976) [*Eleodes*] **New Combination**

Blapylis schwarzii (Blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis snowii (Blaisdell, 1909) [*Eleodes*] **New Combination**

Blapylis spilmani (Somerby and Doyen, 1976) [*Eleodes*] **New Combination**

Blapylis strumosa (Blaisdell, 1932) [*Eleodes*] **New Combination**

Blapylis subvestita (Blaisdell, 1939)[*Eleodopsis*] **New Combination**

Blapylis tenebrosa (Horn, 1870) [*Eleodes*] **New Combination**

Blapylis triplehorni (Somerby and Doyen, 1976) [*Eleodes*] **New Combination**

Blapylis trita (Blaisdell, 1917) [*Eleodes*] **New Combination**

Blapylis tuberculata (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Blapylis versatilis (Blaisdell, 1921) [*Eleodes*] **New Combination**

Blapylis volcanensis (Somerby, 1977) [*Eleodes*] **New Combination**

Blapylis wakelandi (Somerby, 1977) [*Eleodes*] **New Combination**

5.4.6. *Cratidus* LeConte, 1862:239 **Revised Status**

Type species: *Amphidora osculans* LeConte, 1851

Diagnosis. *Cratidus* (Fig. 5.5) can be separated from other Amphidorini based on the densely hirsute body, tarsi bearing yellow setae underneath, elongate third antennomere, and the enlarged submentum with medial longitudinal channel. The submentum is unique within the tribe and is particularly striking in the larger species.

Differential redescription. Body small to moderately large, rotund, all surfaces bearing conspicuous setae. Mentum trilobed, mesal lobe small, acute, not concealing insertion of ligula. Antennomere 3 subequal to length of4 and 5 combined, antennae much longer than head. Pronotum moderately convex, moderately strongly arcuate laterally, base constricted or not. All femora lacking spines; tarsi clothed with golden setae beneath; inner apical margin of fore tibiae bearing setal brush. Ovipositor coxite strongly sclerotized, inner apical lobe strongly produced, often curved laterad, distinctly longer than gonostyle; gonostyle relatively short, round, partially hidden from above.

Remarks. This genus is here circumscribed to include four species. This includes the type species *Cratidus osculans* (LeConte, 1851) **Revised Status** as well as *Cratidus rotundicollis* Horn, 1870 **Revised Status.** The latter has been known recently as *Eleodes ursus* Triplehorn, 1996, which was a replacement name for the preoccupied specific epithet *rotundicollis* within *Eleodes*. Two species formerly associated with *Amphidora* are herein included, *Cratidus nigropilosus* (LeConte, 1851)[*Amphidora*] **New Combination** and *Cratidus subdeplanatus* (Blaisdell, 1943) [*Amphidora*] **New Combination.**

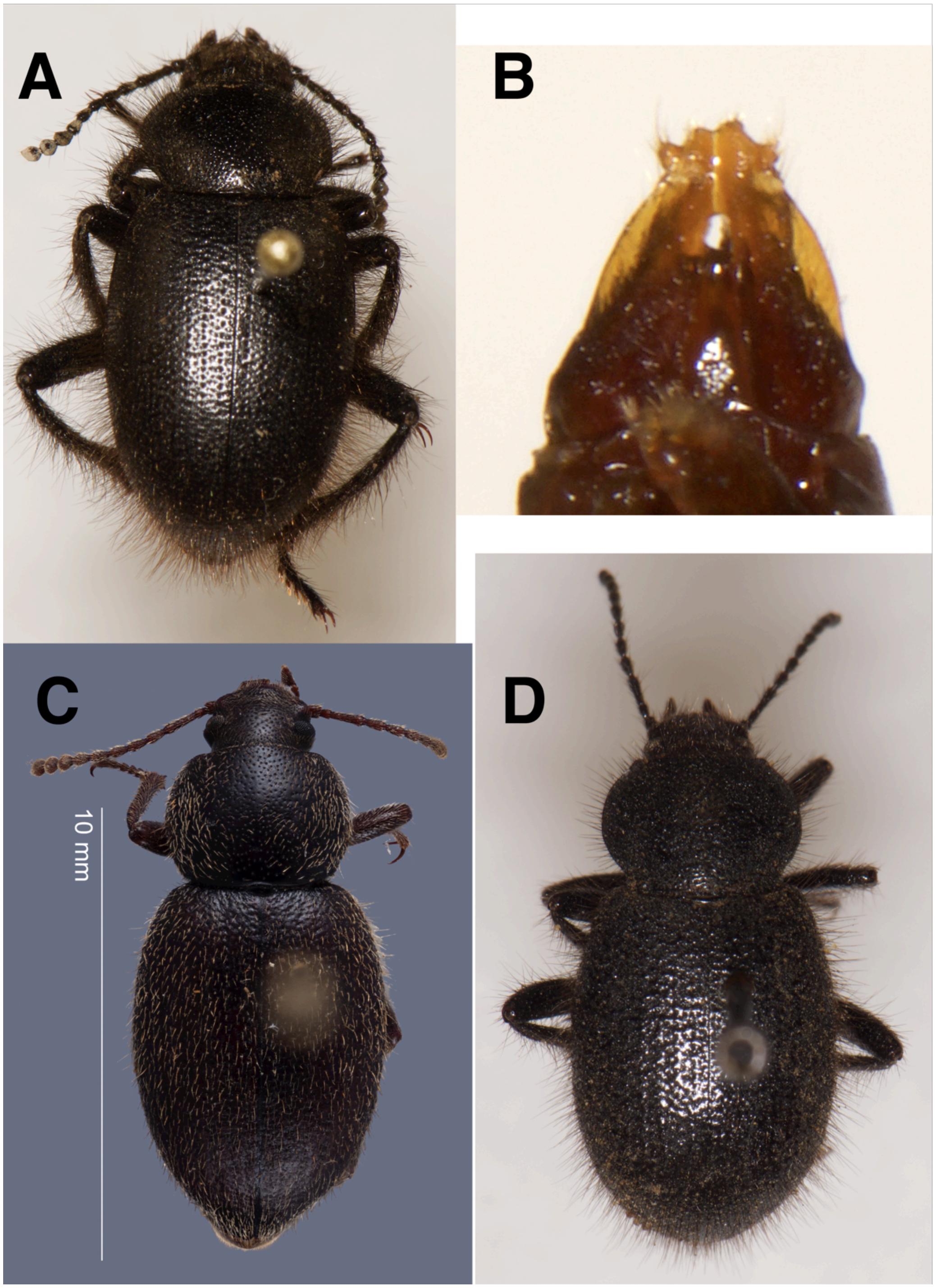


Figure 5.5. *Cratidus* LeConte, 1862. A. *C. osculans* (LeConte, 1851) dorsal habitus. B. *C. osculans* female ovipositor, dorsal view. C. *C. subdeplanata* (Blaisdell, 1943) holotype, dorsal habitus. D. *C. nigropilosa* (LeConte, 1851) dorsal habitus.

Key to the species of *Cratidus* (modified from Triplehorn 1996).

1. Males with subapical spine on inner margin of hind tibia; body 13mm or longer.... 2
1'. Males lacking spine on inner margin of hind tibia; body 12mm or less 3

2. Pronotum constricted basally; basal angles rectilinear .... *C. osculans* (LeConte) (Fig. 5.5A)
2'. Pronotum evenly arcuate from base to apex, not constricted at base; basal angles obtuse ....*C. rotundicollis* Horn

3. Pronotum constricted at base, densely to confluently punctured; clothed in black setae..*C. nigropilosus* (LeConte) (Fig. 5.5D)
3'. Pronotum evenly arcuate laterally, pronotal punctures moderate, well separated; clothed in yellow setae .... *C. subdeplanatus* (Blaisdell) (Fig 5.5C)

5.4.7. *Discogenia* LeConte, 1866:117 **Revised Status**

Type species: *Eleodes scabricula* LeConte, 1858

Diagnosis. *Discogenia* (Fig. 5.6) can be recognized by the large mentum, which, though trilobed, appears to be broadly oval in ventral view, having the outer angles hidden unless dissected. It can similarly be recognized by the combination of a wide, strongly laterally arcuate pronotum which is moderately roughly sculptured and spined femora in the males or by the female ovipositor coxite with a very strongly produced inner apical lobe. In gestalt, they look like large *Blapylis* species but can be separated by the sex-specific characters given above.

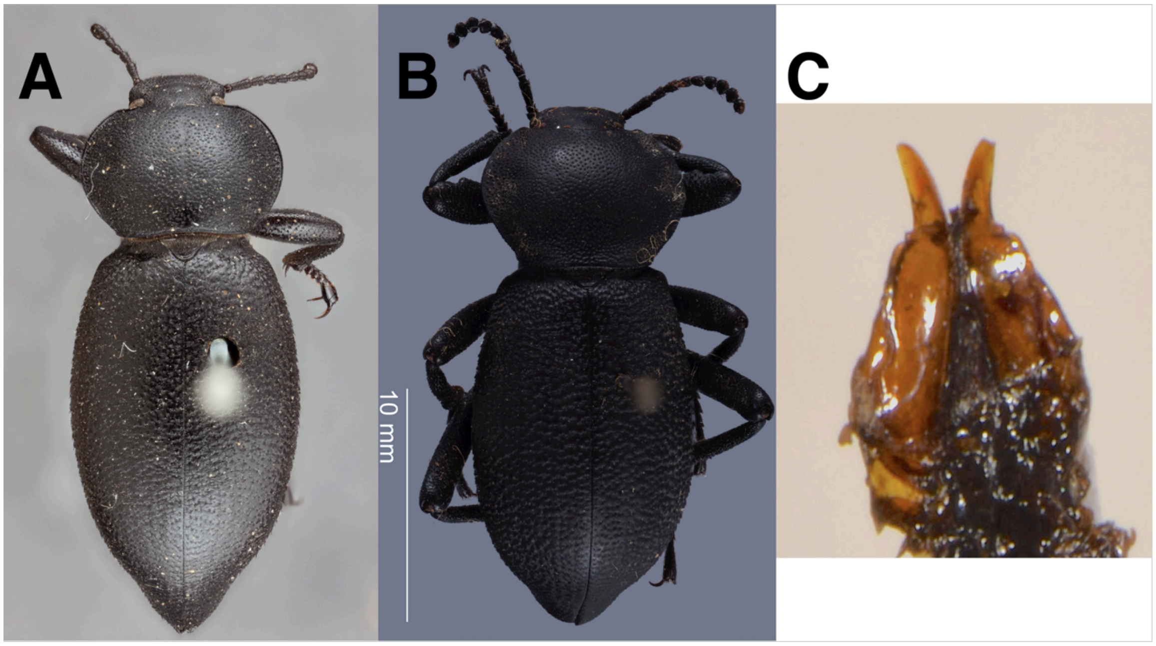


Figure 5.6. *Discogenia* LeConte, 1866. A. *D. marginata* (Eschscholtz, 1829) holotype, dorsal habitus. B. *D. scabricula* (LeConte, 1858) [holotype of *Eleodes acutangula* Blaisdell, 1921] dorsal habitus. C. *D. scabricula* female ovipositor, dorsal view.

Differential redescription. Body moderate to large, glabrous. Mentum large, transversely oval, outer lobes hidden in ventral view. Antennomere 3 subequal to length of 4 and 5 combined, antennae much longer than head width. Pronotum wider than long, strongly arcuate laterally, moderately punctate centrally, becoming granulate laterally. Fore femora always bearing spines in males, occasionally in females; all tarsi bearing thick, dark-golden spicules in both sexes. Ovipositor coxite elongate, inner apical lobe very long, recurved; gonostyle small, often obscured by inner apical lobe of coxite; submarginal groove moderately developed in ventral view.

Remarks. The genus is circumscribed to include the same two species as in the original description by LeConte (1866), namely *Discogenia scabricula* (LeConte, 1858) [*Eleodes*] **Revised Status** and *Discogenia marginata* (Eschscholtz, 1829) [*Eleodes*] **Revised Status**. After studying the types and specimens from throughout the Sierra Nevada Mountains of California, several synonymies seem justified. The species *Eleodes acutangula* Blaisdell, 1921 **New Synonymy** and *Eleodes scabricula* forma *deplanata* Blaisdell, 1909 **New Synonymy** represent intraspecific variation of *Discogenia scabricula* LeConte. Specimens from further south (e.g. Tulare and Kern counties, CA) tend to have more acute anterior angles of the pronotum, yet this character varies across the range with intermediate forms found between them and specimens with rounder anterior angles from the regions around San Francisco.

Key to the species of *Discogenia* (modified from Blaisdell 1909):

1. Males with spine on fore femora, females without; elytral apex acute; body smaller, generally shining .... *D. marginata* (Eschscholtz)

1'. Males and females with spine on fore femora; elytral apex narrowed but generally obtuse; body larger, generally opaque .... *D. scabricula* (LeConte)

5.4.8. *Eleodes* Eschscholtz, 1829:8

Type species: *Eleodes dentipes* Eschscholtz, 1829

Diagnosis. *Eleodes* (Fig. 5.7)remains the most speciose and heterotypic genus in the tribe by far, and as such is very difficult to succinctly diagnose. It can generally be recognized by the strongly trilobed mentum, with the mesal lobe concealing the insertion of the ligula, epileuron generally narrow throughout, arcuately broadening basally, fore femora variable but often spined, and female ovipositor only moderately sclerotized, inner apical angle acute or absent, not strongly projected. Several characters, though not shared for the whole genus, are only found in *Eleodes*: elytra greatly extended posteriorly into parallel sided cauda; both fore femora with spines and fore tarsi with ventral pads; basal 3-4 tarsomeres bearing long, black setae extending nearly to apex of following tarsomere; all femora spined; both distinctly sulcate elytra and fore femora spined; inner for tibial spur greatly enlarged, spatulate.

Differential redescription. Body small to large, almost always black, occasionally with reddish longitudinal stripe on elytral suture, glabrous to hirsute. Mentum trilobed, mesal lobe acute or truncate, projected anteriorly, concealing insertion of ligula. Antennomere 3 subequal to length of 4 and 5 combined, antennae much longer than head. Elytra variable, smooth to striate to scabrous, rarely caudate; epipleuron

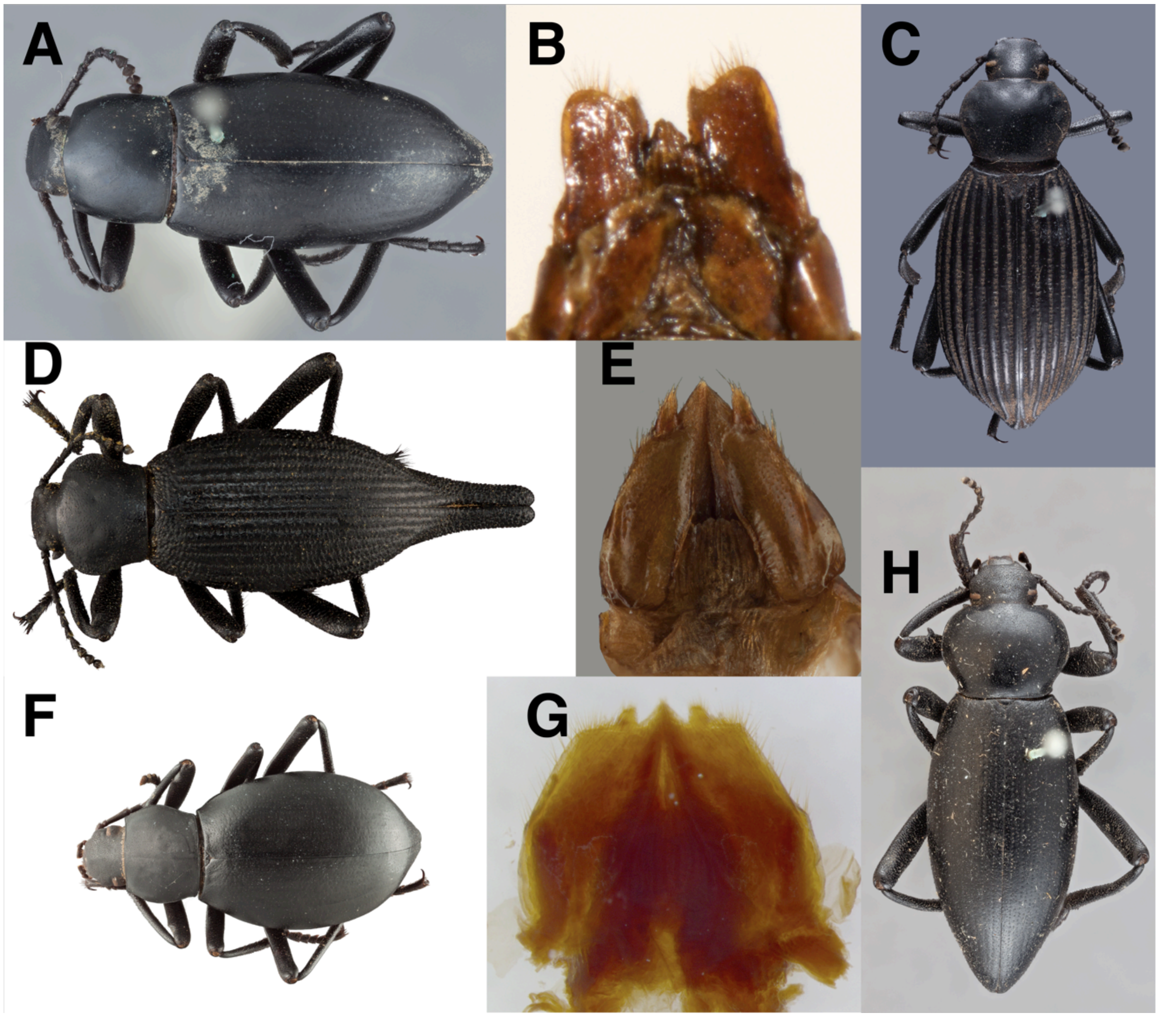


Figure 5.7. *Eleodes* Eschscholtz, 1829. A. *E. (Melaneleodes) carbonaria nitida* Casey, 1890 holotype, dorsal habitus. B. *E. carbonaria nitida* female ovipositor, dorsal habitus. C. *E. (Eleodes) hispilabris* (Say, 1824) [holotype of *Eleodes hispilabris* forma *sculptilis* Blaisdell 1909] dorsal habitus. D. *E. (Pseudeleodes) caudifera* LeConte, 1858. E. *E. caudifera* female ovipositor, dorsal view. F. *E. (Promus) madrensis* Johnston, 2015 dorsal habitus. G. *E. madrensis* female ovipositor, dorsal view. H. *Eleodes (Eleodes) dentipes* Eschscholtz, 1829 holotype, dorsal habitus.

moderately narrow throughout, arcuately broadening basally. Femora spined or not, fore tibiae simple, hind tibiae occasionally sigmoid;tarsal vestiture variable, usually bearing dark spicules, occasionally with yellow setal pads. Ovipositor coxite not strongly sclerotized, lacking submarginal groove, inner apical lobe variable, either reduced or acutely triangular, never much longer than gonostyle; gonostyle occasionally absent (when inner lobe reduced), usually conspicuous from above, cylindrical or flattened.

Remarks. Despite multiple genera being separated out from the group, the genus still contains nine subgenera as currently recognized. A subgeneric revision is beyond the scope of the present study, though phylogenetic analyses (Fig. 5.1) clearly suggests many rearrangements need to be made. Despite the fact that the currently circumscribed subgenera do not all appear to be natural groups, every non-monotypic subgenus has a recent treatment available. In an attempt to facilitate species identification, a temporary key is provided to the subgenera as given in Bousquet *et al.* (2018). The annotated checklist of subgenera provides references to species-level keys for each entity.

Updated annotated checklist of *Eleodes* subgenera.

Eleodes (Ardeleodes) Blaisdell, 1937:128

Monotypic, *E. (Ardeleodes) tibialis* Blaisdell, 1937

Eleodes (Chaseleodes) Thomas, 2015E122

Two species. Key in Thomas, 2015.

Eleodes (Eleodes) Eschscholtz, 1929:8

30 species. Key in Triplehorn *et al.* 2015.

Eleodes (Heteropromus) Blaisdell, 1909:179

Monotypic, *E. (Heteropromus) veterator* Horn, 1874

Litheleodes Blaisdell, 1909:114

Nine species, key in Triplehorn and Thomas 2015

Melaneleodes Blasidell, 1909:36

12 species, key in Triplehorn and Thomas 2012

Omegeleodes Triplehorn and Thomas, 2012:253

Monotypic, *E. (Omegeleodes) debilis* LeConte, 1858

Promus LeConte, 1862:226

21 species, key to U.S. species in Johnston 2015

Pseudeleodes Blaisdell, 1909:146

=*Trichoderulus* Blaisdell, 1923

Eight species, key in Johnston 2016

Incertae sedis

18 species, no key available

Several species-level changes seem appropriate at this time due to generic rearrangements. First, *Eleodes reddelli* Triplehorn, 2007, which was described in the subgenus *Caverneleodes* Triplehorn, 1975, is hereby transferred to the subgenus *Promus* LeConte **New Placement** based on having males with spined fore femora and probasitarsi with yellow setal pads beneath. Second, the subspecies *Eleodes carbonaria nitida* Casey, 1890 **Revised Status** (Fig. 5.7A) is hereby reinstated. Previously synonymized with *Eleodes chihuahuaensis* Champion, 1884 and four other species-group names, the holotype of *E. chihuahuaensis* is not conspecific with the other entities and is dealt with later (see *Metablapylis*). The remaining species-level names are left in synonymy as a subspecies of *Eleodes carbonaria* (Say, 1824), with *E. carbonaria nitida* reestablished due to nomenclatural priority.

Key to currently circumscribed subgenera of *Eleodes* (modified in part from Aalbu *et al.* 2002).

1. Basal 3-4 tarsomeres bearing dorsal and lateral long black setae, extending about to apex of following tarsomere ....*Pseudeleodes* Blaisdell

1'. Tarsomeres glabrous dorsally or with short setae.. 2

2. Pronotum and elytra forming contiguous, broad oval 3

2'. Pronotum and elytra not forming contiguous oval 4

3. Posterior pronotal margin not interrupted by elytral humeri .... *Heteropromus* Blaisdell

3'. Elytral humeral angles projected forward, interrupting posterior pronotal margin ... . *Promus* LeConte (in part)

4. Males with spine on profemora and yellow setal pad on at least bropasitarsus, probasitarsus not thickened; females lacking spines on profemur, gonostyle large and flattened .... *Promus* LeConte (in part)

4'. Profemora variable, males without yellow setal pads on probasitarsus, or if so then probasitarsus thickened ventrally; females variable, gonostyle almost never flattened 5

5. Inner apical angle of ovipositor coxite reduced, shorter than outer angle; femora lacking spines, protibial spurs different between the sexes, females with inner spine enlarged, often spatulate..*Melaneleodes* Blaisdell

5’. Inner apical angle of ovipositor coxite acute, slightly projected, longer than outer angle; femora spined or not; tibial spurs variable, never greatly elongate or spatulate 6

6. Pronotum and elytra flattened dorsally, abdomen and elytra trapezoidal in cross section, femora lacking spines .... *Chaseleodes* Thomas

6’. Pronotum usually convex, elytra and abdomen not trapezoidal in cross section 7

7. Smaller species; femora not spined; femora spined or not; ovipositor coxite with outer apical lobe truncate ....*Omegeleodes* Triplehorn and Thomas

7’. Size variable; femora spined or not; ovipositor coxite with oblique outer apical angle 8

8. Smaller species; ovipositor with large, flattened gonostyle; male sometimes with spine on fore femora ....*Litheleodes* Blaisdell

8’. Larger species; ovipositor with cylindrical mammiliform gonostyle; fore femora almost always spined in males, usually spined in females....................................... 9

9. Femora not spined in males (Sierra La Laguna, Baja Sur, Mexico) ....*Ardeleodes* Blaisdell

9’. Femora spined in males (widespread) ....*Eleodes* Eschscholtz

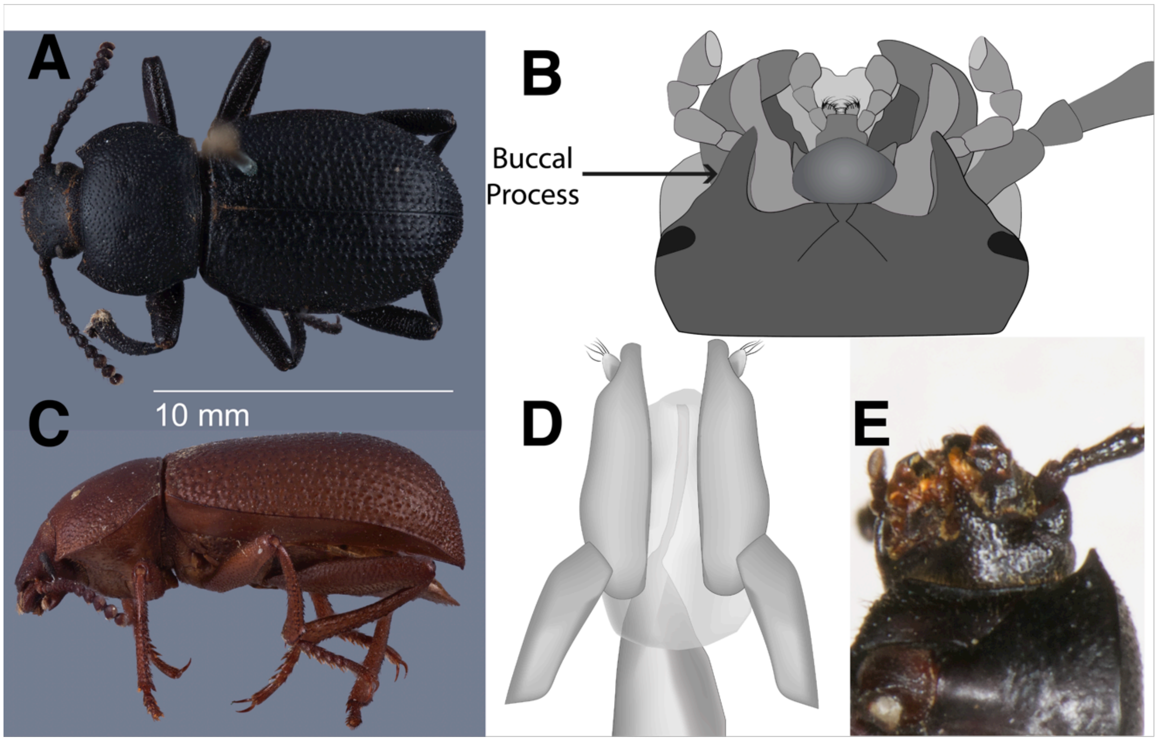
5.4.9. *Eleodimorpha* Blaisdell, 1909:477

Type species: *Eleodimorpha bolcan* Blaisdell, 1909

Diagnosis. This monotypic genus (Fig. 5.8) can be readily recognized by the protruding buccal process of the subgena. The strongly clavate femora and matching arcuate tibia additionally serve to separate this genus from other Amphidorini.

Differential redescription. Body small to moderate, glabrous, matte black. Antennomere 3 subequal to length of 4 and 5 combined; antennae much longer than head width. Mentum extremely large, broadly oval; buccal process of subgena projected anteriorly, reaching beyond insertion of maxillary palpus. Pronotum moderately arcuate laterally, strongly constricted basally, anterior angles acute, strongly projected, disc with large well-separated punctures. Femora clavate, lacking spines; tibiae arcuate; tarsi lined beneath with thick castaneus spicules.

Remarks. The genus has remained unchanged since its original description, containing the sole species *Eleodimorpha bolcan* Blaisdell, 1909. Extremely rare in collections, several large series have recently been taken from Palomar Mountain in San Diego County, California, which were found at night in areas of thick oak leaf litter amassed around rocks.



Figre 5.8. *Eleodimorpha bolcan* Blaisdell, 1909. A. allotype male, dorsal habitus. B. mouthparts, ventral view showing buccal process. C. female holotype, lateral habitus. D. female terminalia dorsal view. E. head, oblique lateral view, showing buccal process.

5.4.10. *Embaphion* Say, 1824:254

Type species: *Akis muricata* Say, 1824

Diagnosis. *Embaphion* (Fig. 5.9) can generally be diagnosed by the distinct carinae on the lateral margins of the pronotum and elytra. The carinae are usually strongly laminar and curled upward (Fig. 5.9A), though occasionally are planar with the dorsal surface of the body. For species with a laterally explanate pronotum and distinct lateral elytral carinae that are not curled upward (Fig 5.9C), they can be distinguished from the few similar species of *Eleodes* by the following: lack of spines on the femora in both sexes (femora with spines at least in males for similarly carinate *Eleodes*). *Embaphion* can be further separated from *Eleodes* by the ovipositor coxite being strongly sclerotized and the inner apical angle strongly produced and recurved (Fig. 5.9B)(moderately sclerotized in similarly carinate *Eleodes* and with inner apical angle not strongly produced or recurved).

Differential redescription. Body moderately small to moderately large, appearing more or less glabrous, sometimes with minute recumbent puntigerous setae. Mentum trilobed, mesal lobe produced anteriorly, broadly arcuate to subtruncate, antennomere 3 subequal to length of 4 and 5 combined, antennae much longer than head width. Pronotum broad, lateral margins carinate, more or less laminar, generally curled upward. Elytral margins carinate, usually laminar and produced upward. Femora always lacking spines; all tarsi bearing stout yellow to castaneus spicules underneath. Ovipositor coxite strongly sclerotized, elongate, inner apical lobe strongly produced, recurved

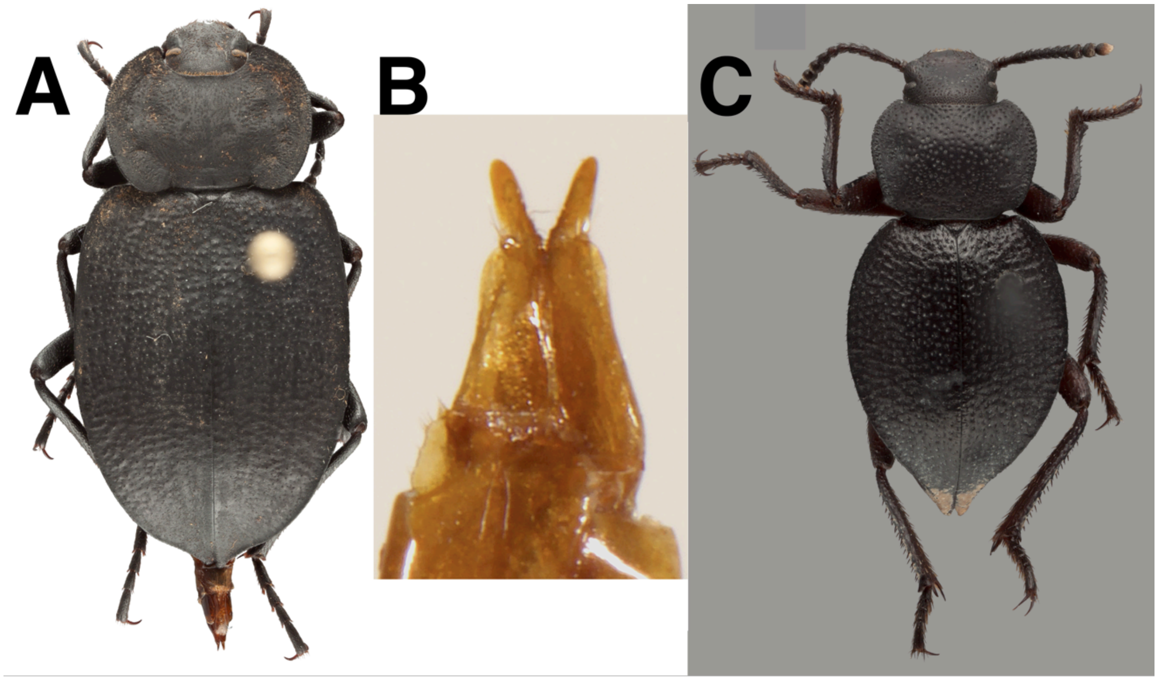


Figure 5.9. *Embaphion* Say, 1824. A. *E. contusum* LeConte, 1858 dorsal habitus. B. *E. glabrum* Blaisdell, 1909 female ovipositor, dorsal viw. C. *E. depressum* (LeConte, 1851) dorsal habitus.

laterally, moderately large subapical groove visible in ventral view; gonostyle moderately small, partially hidden in dorsal view.

Remarks. This genus has not been revised since Blaisdell (1909), and is here left with the same species composition as presented in Bousquet *et al.* (2018). Though only a limited sampling of specimens were examined, initial observations suggest that several rearrangements will be required upon a full review of the genus. The key given by Blaisdell (1909:453) is the most recent and works fairly well to delimit the included species. *Embaphion depressum* (LeConte, 1851) (Fig 5.9C) is the least characteristic species of the genus where the lateral carinae are not laminar and curled upward, but the diagnosis and key should still separate this species from other members of the tribe.

5.4.11. *Exarenula* **New Genus**

Type species: *Eleodes barbata* Wickham, 1918; by present designation

Diagnosis. This monotypic genus (Fig. 5.10) can be recognized by its distinct dorsal habitus: subglobular pronotum and elytra, body ferruginous to castaneus, clothed with both erect golden setae and paler yellow recumbent setae.

Differential description. Body small, globular, ferruginous to castaneus, strongly hirsute throughout bearing long erect golden setae and paler yellow recumbent setae. Mentum trilobed, mesal lobe triangular, acute, extending beyond insertion of ligula. Antennomere 3 subequal to length of 4 and 5 combined, antennae much longer than head width. Pronotum strongly convex, round, densely punctate. Femora lacking spines; tarsi bearing thick dark golden spicules beneath. Ovipositor coxite strongly sclerotized,

Figure 5.10. *Exarenula* New Genus. A. *E. barbata* (Wickham, 1918) dorsal habitus. B. *E. barbata* female ovipositor, dorsal view.

elongate, inner apical lobe strongly produced, recurved laterally; gonostyle minute, largely concealed in dorsal view.

Etymology. *Exarenula* is an arbitrary combination of letters considered feminine. The name is given in reference to sandy habitats the genus is known from, and the behavior where these beetles come out of the sand to walk around at night.

Remarks. This monotypic genus is erected for *Exarenula barbata* (Wickham, 1918) **New Combination**, which is known from the Four-Corners region of the Colorado Plateau. The species was recently excluded from *Tricheleodes* (Johnston 2016), showing no strong affinities to any other circumcised group. Similar to its closely related genera *Trogloderus* and *Lariversius*, *Exarenula* seems well adapted for life in sandy habitats.

5.4.12. *Globostyla* **New Genus**

Type species: *Eleodes thomasi* Aalbu, Smith and Triplehorn, 2012; by present designation

Diagnosis. *Globostyla* (Fig. 5.11) can be recognized by the well-demarked and extremely wide epipleuron and tarsi with long setose patches underneath. The very large, rounded gonostyle of the female ovipositor (Fig. 5.11C,E) is also unique among Amphidorini genera. The mesal lobe of the mentum is produced into a keel, which apically extends into a narrow finger-like process, which is only known from several species of *Metablapylis*.

Figure 5.11. *Globostyla* New Genus. A. *G. thomasi* (Aalbu, Smith, and Triplehorn, 2012) dorsal habitus. B. *G. sprousi* (Tripplehorn and Reddell, 1991) dorsal habitus. C. *B. sprousi* female ovipositor, dorsal view. D. *G. gruta* (Aalbu, Smith, and Triplehorn, 2012) dorsal habitus. E. *G. gruta* female ovipositor, dorsal view.

Differential description. Body moderately large, elongate, black, glabrous dorsally. Mentum trilobed, transverse, subrectangular, mesal lobe forming keel terminating in finger-like projected anteriorly. Antennomere 3 subequal to length of 4 and 5 together, antennae much longer than head. Pronotum finely punctate. subquadrate to slightly wider than long, lateral margins fairly evernly arcuate, anterior angles not strongly projected. Elytra relatively smooth, bearing small punctures in striae; epipleurae very wide, well-demarked dorsally strongly developed ridge. Femora lacking spines; tibiae generally bearing long golden setae; all tibiae sometimes with yellow setal brush on inner apical margin; all tarsi clothed with golden setae beneath, interrupting plantar groove at least apically. Ovipositor coxite well-sclerotized, subtriangular; gonostyle large, round, larger than inner apical angle of coxite, very conspicuous in dorsal view.

Etymology. *Globostyla* is an arbitrary combination of letters and considered as feminine. The name is given in reference to the enlarged and rounded gonostyle of the ovipositor.

Remarks. This genus is erected for three species formerly placed in the *Eleodes* subgenus *Caverneleodes* Triplehorn, 1975, namely *Globostyla gruta* (Aalbu, Smith and Triplehorn, 2012) [*Eleodes*] **New Combination**, *Globostyla sprousi* (Triplehorn and Reddell, 1991) [*Eleodes*] **New Combination**, and *Globostyla thomasi* (Aalbu, Smith and Triplehorn, 2012) [*Eleodes*] **New Combination** whose ovipositors are unique among the Amphidorini by virtue of the enlarged gonostyle. All three species are known only from caves in Coahuila, Nuevo León, and Tamaulipas, Mexico (Aalbu *et al*. 2012).

In addition to the characters given in the diagnosis, an interesting character in *G. sprousi* and *G. gruta* is the presence of a coarse patch of golden setae on the inner apical margin of the tibiae; though not observed in *G. thomasi*, there is a chance that the few specimens examined could have been abraded. This character is only similarly pronounced in the closely related genera *Amphidora* and *Cratidus* whose entire bodies are hirsute. It is very possible that this early-diverging clade was ancestrally hirsute and that *Globostyla* and *Eleodimorpha* subsequently lost the long vestiture. This may be further supported by the observation that the legs and venters of most *Globostyla* individuals studied bore very scattered long setae.

Key to the species of *Globostyla*.

1. Tibiae with scattered flying golden setae, ventral apex of at least fore and middle tibiae with coarse pad of yellow setae 2

1'. Tibiae bearing only short setae, tibial apicies lacking setal pad ....
.... *G. thomasi* (Aalbu *et al.*)

2. Ventral surface of fore and middle tarsi fully covered by setal pads; pronotum evenly and noticeably narrowing posteriorly from about middle..................................
....*G. sprousi* (Triplehorn and Reddell)

2'. Plantar groove visible on ventral surface of fore and middle tarsi, interrupted on at apex by setae; pronotum evenly arcuate laterally, posterior margin subequal to anterior margin .... *G. gruta* (Aalbu *et al.*)

5.4.13. *Lariversius* Blaisdell, 1947:59

Type species: *Lariversius tibialis* Blaisdell, 1947

Diagnosis. *Lariversius* (Fig 5.12) is easily recognized by the deeply notched epistoma and the antennal length subequal to head width. The fossorial fore tibiae and finbriate fringe of yellow setae underneath the pronotal lateral bead are also diagnostic.

Differential redescription. Body small, globular, glabrous dorsally, shining. Mentum triolobed, mesal lobe moderately large, subrectangular, concealing insertion of ligula. Antennae short, subequal to width of head; antennomere 3 subequal to length of 4; antennomeres 9-11 forming moderately distinct club. Pronotum moderately flattened, wider than long, bearing fimbriate fringe of yellow setae underneath lateral marginal bead. All femora flattened, lacking spines; fore and middle tibiae fossorial. Ovipositor coxite moderately strongly sclerotized, elongate, inner apical lobe greatly projected, slightly recurved laterally; gonostyle minute, inconspicuous in dorsal view.

Remarks. *Lariversius* remains monotypic, containing only the type species *L. tibialis* Blaisdell, 1947, which has been recorded from aeolian sand formations in Nevada and California. Though presently treated as a single species, the genus is the subject of an ongoing revision (A.D. Smith, unpublished data).

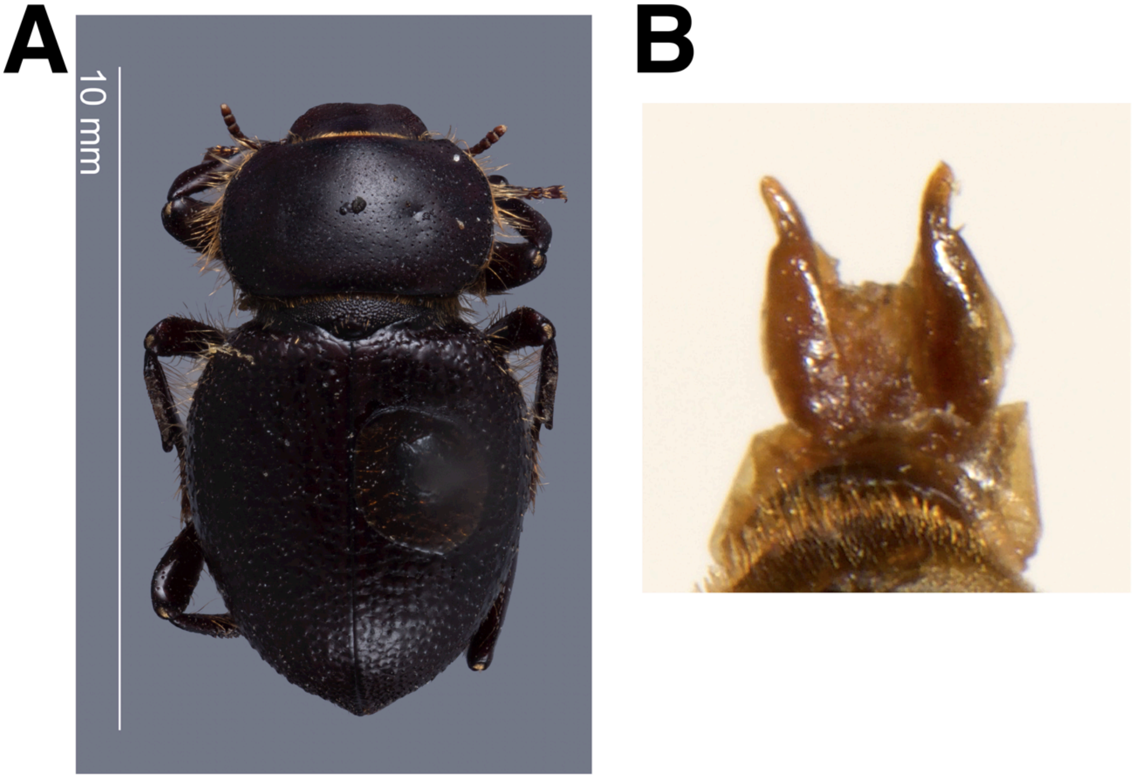


Figure 5.12. *Lariversius* Blaisdell, 1947. A. *L. tibialis* Blaisdell, 1947 holotype, dorsal habitus. B. *Lariversius sp*. female ovipositor, dorsal view.

5.4.14. *Metablapylis* Blaisdell, 1909:391 **New Status**

Type species: *Eleodes nigrina* LeConte, 1858

= *Caverneleodes* Triplehorn, 1975:39; type species *Eleodes easterlai* Triplehorn, 1975 **New Synonymy**

Diagnosis. This genus (Fig. 5.13) of elongate, apparently glabrous, black beetles can be diagnosed by a combination of the following characters: mesal lobe of mentum not concealing insertion of ligula; elytra with punctures in distinct, unimpressed striae; tarsi not thickened, bearing spicules along plantar groove; anterior pronotal angles never sharply acute; epipleuron generally evenly tapered from base to apex, base not suddenly expanded; appendages typically quite long; ovipositor coxite with inner apical lobe strongly produced, directed posteriorly. This genus has a distinct gestalt that is difficult to characterize, particularly in comparison to *Eleodes* and some *Steneleodes*.

Differential redescription. Body moderately large, black, apparently glabrous from above, distinctly elongate. Mentum trilobed, mesal lobe acute, not concealing insertion of ligula. Clypeus comparatively relatively short, not strongly projectedbeyond genae. Antennomere 3 subequal to length of 4 and 5 combined; antennae long, much longer than head width, often with 4 antennomeres extending beyond base of pronotum. Pronotum weakly to moderately convex, lateral marginal bead typically weak, discal punctures small, anterior angles rounded, never acute, ocassionally produced forward. Elytra bearing punctures in distinct, unimpressed striae. Fore femora almost always sinuate, rarely with bluntly angulate tooth; tarsi never thickened ventrally, lined with spicules along plantar groove. Ovipositor coxite well sclerotized, elongate, outer apical lobe distinctly truncate at level of gonostyle, inner apical lobe elongate, strongly projected, directed posteriorly; gonostyle well developed, cylindrical, visible in dorsal view.

Remarks. The circumscription of *Metablapylis* is herein expanded to include most species of the former *Eleodes* subgenus *Caverneleodes* Triplehorn, 1975 **New Synonymy**. The original description of the latter indicated a close relationship with *Metablapylis* and largely differed in the length of the legs and antennae (Triplehorn 1975). The recent revision of the subgenus (Aalbu *et al.* 2012) made very detailed descriptions of the species but did not thoroughly diagnose the group in relation to the rest of Amphidorini. Studies of the female ovipositors, external morphology, and molecular analyses strongly support a polyphyletic *Caverneleodes* with the bulk belonging to the present genus.

Most species of *Metablapylis*, as herein defined, appear to live in close proximity to rock shelters, either in cave systems or near rocky outcroppings and talus slopes. The elongate smooth form that is typical of this genus is perhaps strongly adaptive to life in such habitats As a result of this conserved morphotype, species boundaries within this group are not entirely clear. Most species are fairly rare in collections and are often known from a single or several distinct localities. A thorough revision of this group is very much warranted, especially in regards to the complex of species that inhabit the Mojave and Sonoran deserts which are particularly difficult to diagnose. The key presented below synthesizes the characters given by Aalbu *et al.* (2012) with new morphological observations of this group, but whether some cave-dwelling species are simply local populational variations of more widely distributed species or indeed distinct entities is uncertain.

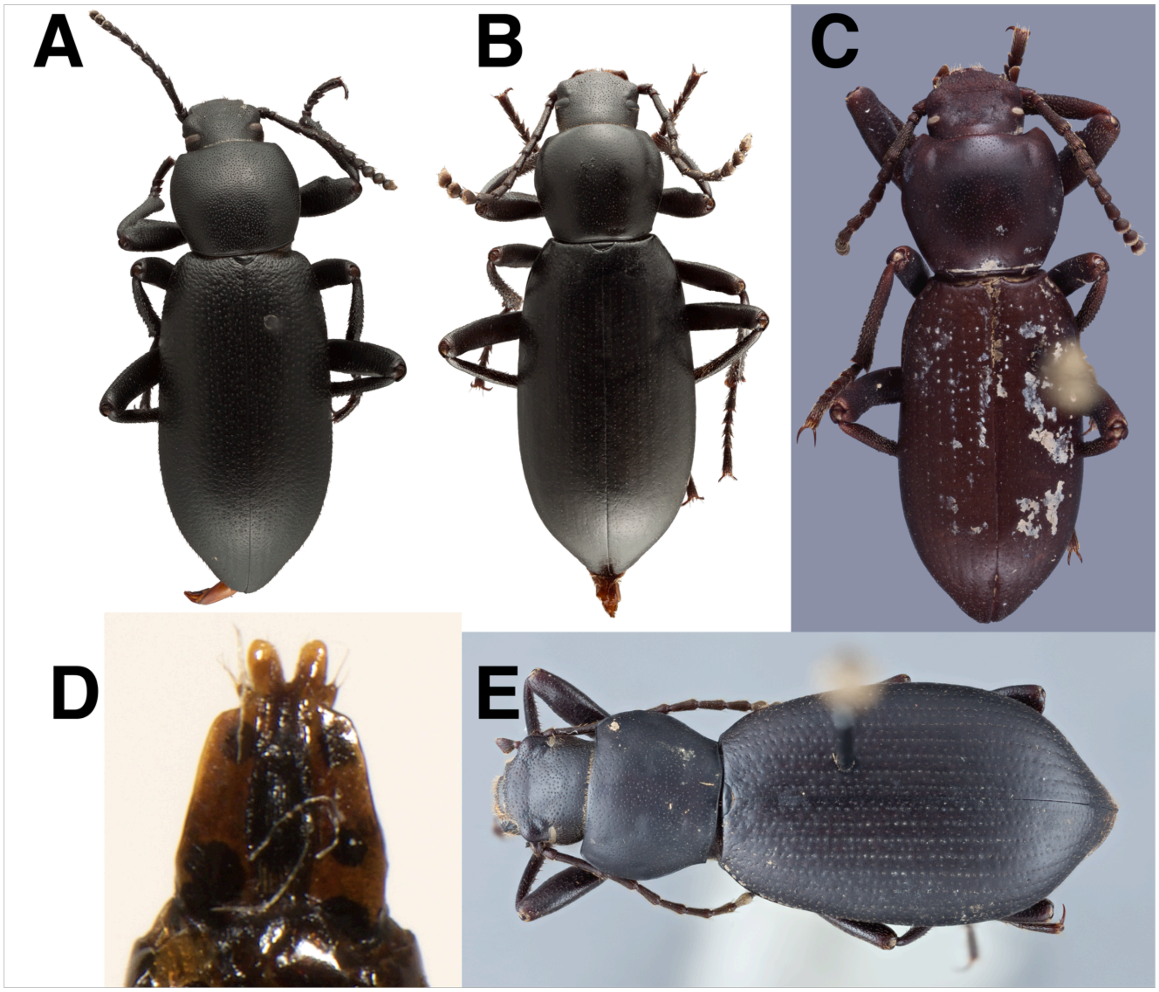


Figure 5.13. *Metablapylis* Blaisdell, 1909. A. *M. nigrina* (LeConte, 1858) dorsal habitus. B. *M. delicata* (Blaisdell, 1929) dorsal habitus. C. *M. aalbui* (Triplehorn, 2007) holotype, dorsal habitus. D. *M. nigrina* female ovipositor, dorsal view. E. *M. easterlai* (Triplehorn, 1975) holotype, dorsal habitus.

Checklist of the species of *Metablapylis*

(see Bousquet *et al.* 2018 for further synonymies).

Metablapylis aalbui (Triplehorn, 2007) [*Eleodes*] **New Combination**

Metablapylis californica (Blaisdell, 1929) [*Eleodes*] **New Combination**

Metablapylis chihuahuaensis (Champion, 1884) [*Eleodes*] **New Combination**

= *Eleodes dissimilis* Blasidell, 1909 **New Synonymy**

Metablapylis easterlai (Triplehorn, 1975) [*Eleodes*] **New Combination**

Metablapylis guadalupensis (Aalbu, Smith and Triplehorn, 2012) [*Eleodes*] **New Combination**

Metablapylis labialis (Triplehorn, 1975) [*Eleodes*] **New Combination**

Metablapylis leptoscelis (Triplehorn, 1975) [*Eleodes*] **New Combination**

Metablapylis microps (Aalbu, Smith and Triplehorn, 2012) [*Eleodes*] **New Combination**

Metablapylis nevadensis (Blaisdell, 1909) [*Eleodes*] **New Combination**

= *Eleodes delicata* Blaisdell, 1929 **New Synonymy**

Metablapylis nigrina (LeConte, 1858) [*Eleodes*] **New Combination**

= *Eleodes nigrina difformis* Blaisdell, **1925 New Synonymy**

= *Eleodes nigrina maclayi* Boddy, 1957 **New Synonymy**

= *Eleodes nigrina* var. *perlonga* Blaisdell, 1909 **New Synonymy**

Metablapylis wheeleri (Aalbu, smith and Triplehorn, 2012) [*Eleodes*] **New Combination**

The species delimitations presented by Aalbu *et al.* (2012) are retained here pending further revisionary work. The four previous subspecies of *M. nigrina* (LeConte) are hereby synonymized, following examination of the types and specimens from across the species range. While there is some geographic variation, namely the southern populations typically having smoother elytral sculpturing than the northern populations and the western populations tending to have a more parallel sided pronotum than the eastern ones, these variations seem to be gradual and assigning many specimens to one or the other subspecies was not possible. This variation is similar to that seen in *Eleodes hispilabris* (Say, 1824) and *Eleodes obscura* (Say, 1824) (Triplehorn *et al.* 2015). Similarly, the two species *M. nevadensis* (Blaisdell) and *M. delicata* (Blaisdell) were presumably separated by ventral punctures bearing short red setae. However, as presented in a regional treatment (Johnston *et al.* 2015), that character seems linked to specimen age and abrasion, and is not species specific. After studying the unique holotype of *Eleodes chihuahuaensis* Champion, 1884, it was immediately clear that the species did not belong to the *Eleodes* subgenus *Melaneleodes* Blaisdell, 1909 where it was currently placed as a subspecies of the widespread *E. carbonaria* (Say, 1824) (Triplehorn and Thomas 2012). Its proper placement is within *Metablapylis* and it is further synonymized with *E. dissimilis* Blaisdell, which is known from mid-elevation regions of the Sierra Madre Occidental Mountains in Mexico and the associated Madrean Sky Islands of the southern United States.

Key to the species of *Metablapylis* (largely modified from Aalbu *et al.* 2012).

1. Fore femur bearing blunt tooth; anterior angles of pronotum strongly projected .... *M. aalbui* (Triplehorn)

1'. Fore femur sinuate, never bearing tooth; anterior angles not strongly projected 2

2. Elytral punctures distinctly muricate to scabrous at least on lateral and apical declivities... *M. nigrina* (LeConte)

2'. Elytral punctures simple, never muricate 3

3. Mentum with mesal lobe projected as blunt finger-like process (Big Bend region) ....*M. labialis* (Triplehorn)

3'. Mentum with mesal lobe smaller, more or less keel-like (widespread) 4

4. Probasitarsus with apical pencilbrush of moderately long yellow setae (Guadalupe Mountains, New Mexico)..*M. guadalupensis* (Aalbu et al.)

4'. Probasitarsus without pencil brush, bearing only spicules..5

5. Elytral strial punctures very small, subequal in size to punctures of intervals; pronotum subquadrate to elongate, typically longer than wide 6

5'. Elytral strial punctures moderate in size, larger than punctures of intervals; pronotum variable, usually wider than long 7

6. Smaller species, inhabiting lower elevation Sonoran Desert; male parameres evenly tapering from base, parallel in apical 1/7, more or less truncate apically ....*M. nevadensis* (Blaisdell)

6'. Larger species, inhabiting northern Arizona and southern Utah; male parameres evenly tapering from base, constricted around apical 1/3, acutely tapered to apex ....*M. wheeleri* (Aalbu et al.)

7. Pronotum typically subquadrate, occasionally longer than broad; posterior margin only slightly narrower than anterior margin (Mojave Desert and Grand Canyon region) 8

7'. Pronotum almost always wider than long, posterior margin usually significantly narrower than anterior margin (widespread) 9

8. Pronotum truncate anteriorly, anterior angles subquadrate (caves in Grand Canyon region) ....*M. leptoscelis* (Triplehorn)

8'. Pronotum broadly arcuate anteriorly, anterior angles slightly projected (Mojave desert)... *M. californica* (Blaisdell)

9. Pronotum sub-cordate (Big Bend region) .... *M. easterlai* (Triplehorn)

9'. Pronotum more evenly arcuate (widespread) 10

10. Elytral strial punctures forming broad depressed dents, elytra almost appearing wrinkled (southern California) ....*M. microps* (Aalbu et al.)

10'. Elytral strial punctures not forming such dents, longitudinal striae distinct (northern Sierra Madre Occidentals and associated sky islands)................................ ....*M. chihuahuaensis* (Champion)

5.4.15. *Neobaphion* Blasidell, 1925:390

Type species: *Eleodes planipennis* LeConte, 1866

Diagnosis. Neobaphion (Fig. 5.14) can be recognized by the combination of a comparatively narrow and evenly tapering epipleuron, lack of lateral carinae on the elytra, prominent acute anterior angles of the pronotum, and either the thickened probasitarsus in males or the female ovipositor with oblique and strongly produced apical lobes. This genus is externally most similar to *Metablapylis* and has extremely similar ovipositor morphology to *Embaphion*. From the latter, *Neobaphion* can be separated by the lack of carinate pronotal and elytral margins. From *Metablapylis*, the present genus can be separated by the mentum concealing the insertion of the ligula or by the sex-specific characters. The pronotum of all known species of *Neobaphion* is broadest before the middle, with the posterior margin narrower than the anterior margin, this character can aide many identifications but is widespread throughout Amphidorini.

Differential redescription. Body moderate to large, elongate, typically matte black, glabrous or with inconspicuous setae. Mentum trilobed, mesal lobe projected anteriorly, concealing insertion of ligula. Antennomere 3 subequal to length of 4 and 5 combined; antennae much longer than head width. Pronotum broadest before middle, anterior margin wider than posterior margin, disc moderately densly punctate to papillose. Fore femora usually strongly sinuate in both sexes, always lacking true spine; probasitarsus thickened in males; all tarsi in both sexes bearing thick dark golden spicules beneath. Ovipositor coxite well sclerotized, elongate, inner apical angoe strongly produced,

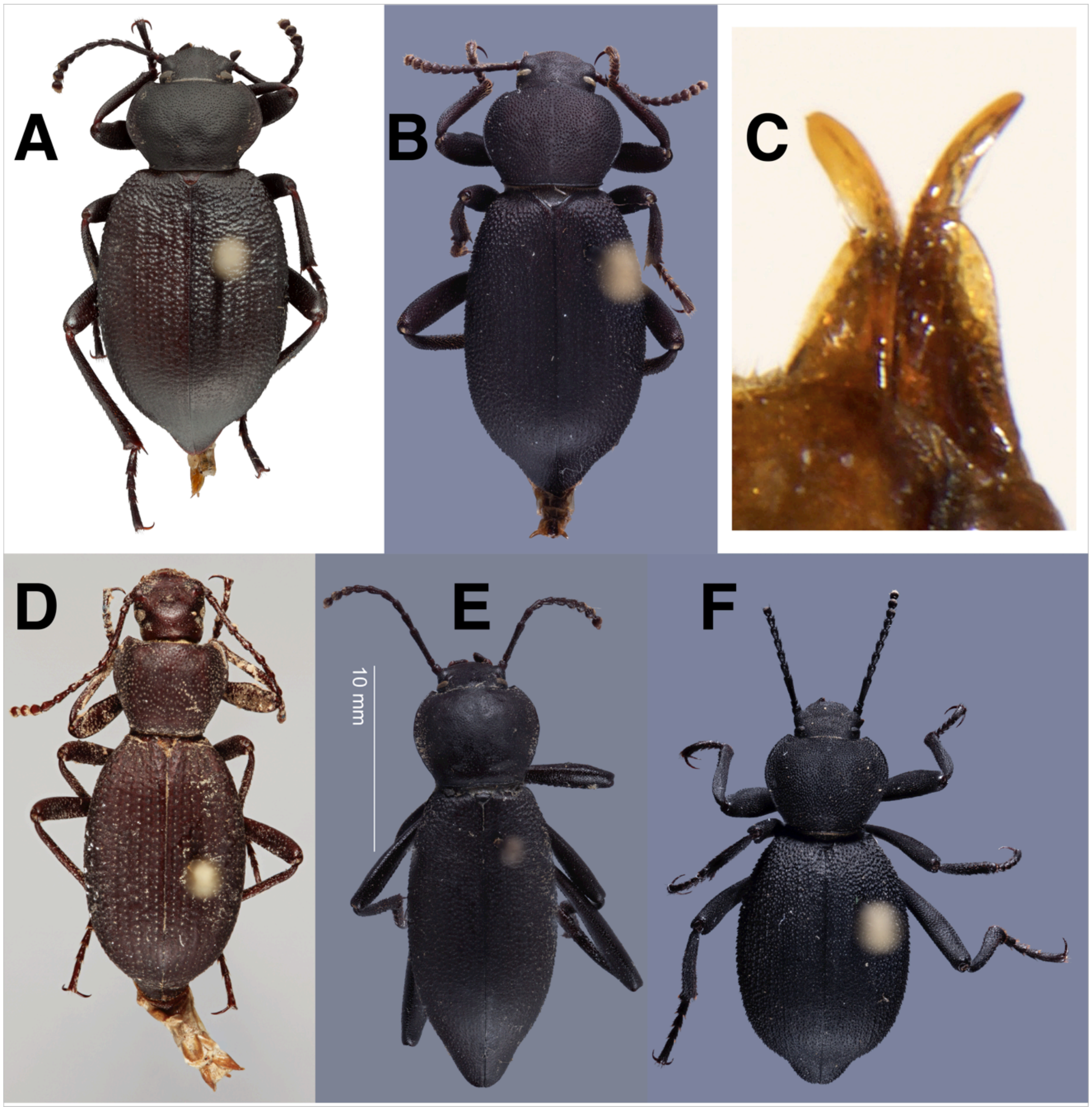


Figure 5.14. *Neobaphion* Blaisdell, 1925. A. *N. planipenne* (LeConte, 1879) dorsal habitus. B. *N. papula* Triplehorn and Aalbu, 1985 holotype, dorsal habitus. C. *N. papula* female ovipositor, dorsal view. D. *N. wynnei* (Aalbu, Smith, an Triplehorn, 2012) holotype, dorsal habitus. E. *N. elongatum* Blaisdell, 1933 holotype, dorsal habitus. F. *E. alleni* Triplehorn, 1989 holotype, dorsal habitus.

oblique, directed posterolaterally, with well developed subapical groove in ventral view; gonostyle small, inconspicuous in dorsal view.

Remarks. This genus, historically characterized as beetles resembling *Eleodes* but bearing the female genitalia of *Embaphion* (Tiplehorn and Aalbu 1985), has been comprised of four species. A fifth species, *Neobaphion wynnei* (Aalbu, Smith and Triplehorn, 2012) [*Eleodes*] **New Combination** is hereby added to the genus. Originally described in the *Eleodes* subgenus *Caverneleodes* Triplehorn, the female genitalia, external morphology, and molecular characters place the species here and the small eyes and long legs are considered convergent with the other species formerly in that subgenus. This genus is more or less restricted to the Intermountain Region of western North America. A key to the included species is given below.

Key to the species of *Neobaphion*.

1. Pronotal disc finely papillose 2
1'. Pronotal disc with simple punctures 3

2. Pronotum strongly explanate laterally; elytral suture not elevated or keel-like .... *N. alleni* Triplehorn, 1989 (Fig. 5.14F)
2'. Pronotum not explanate laterally; elytral suture weakly produced dorsally as a keel. .... *N. papula* Triplehorn and Aalbu, 1985 (Fig. 5.14B)

3. Pronotal and elytral strial punctures moderately large; legs and antennae very long, at least 4 antennomeres extending posteriorly of pronotal base ....

.... *N. wynnei* (Aalbu, Smith and Triplehorn, 2012) (Fig 5.14D)

3'. Pronotal and elytral strial punctures smaller; legs and antennae not particularly long, no more than 3 antennomeres extending posteriorly of pronotal base............ 4

4. Pronotum strongly arcuate laterally, strongly constricted basally; elytra broad ....*N. planipenne* (LeConte, 1866) (Fig. 5.14A)

4'. Pronotum more gently arcuate laterally, evenly sinuate to base; elytra relateively slender... *N. elongatum* Blaisdell, 1933 (Fig. 5.14E)

5.4.16. *Steneleodes* Blaisdell, 1909:409 **New Status**

Type species: *Eleodes longicollis* LeConte, 1851

= *Xysta* Eschscholtz, 1829:9; type species *Eleodes gravida* Eschscholtz, 1829; Junior homonym of *Xysta* Meigen, 1824 [Diptera: Tachinidae] (here established)

= *Holeleodes* Blaisdell, 1937:132; type species *Eleodes beameri* Blaisdell, 1937

Diagnosis. *Steneleodes* (Fig 5.15) can be recognized by the broadly arcuate mesal lobe of the mentum which conceals the insertion of the ligula, epipleuron expanded basally, the profemora always lacking spines, and all tarsi with yellow to dark golden setae or spicules beneath. This genus is very similar to *Eleodes* and *Metablapylis*. From *Eleodes*, it can be separated by the shape of the mentum (acute or truncate in *Eleodes*), the lack of femoral spines (present or not in *Eleodes*) and the tarsal vestiture (variable but often black spicules in *Eleodes*). From *Metablapylis*, it can be recognized by the concealed insertion of the ligula (visible in ventral view in *Metablapylis*) and by the typically broader and more robust body form (elongate and generally parallel sides in *Metablapylis*).

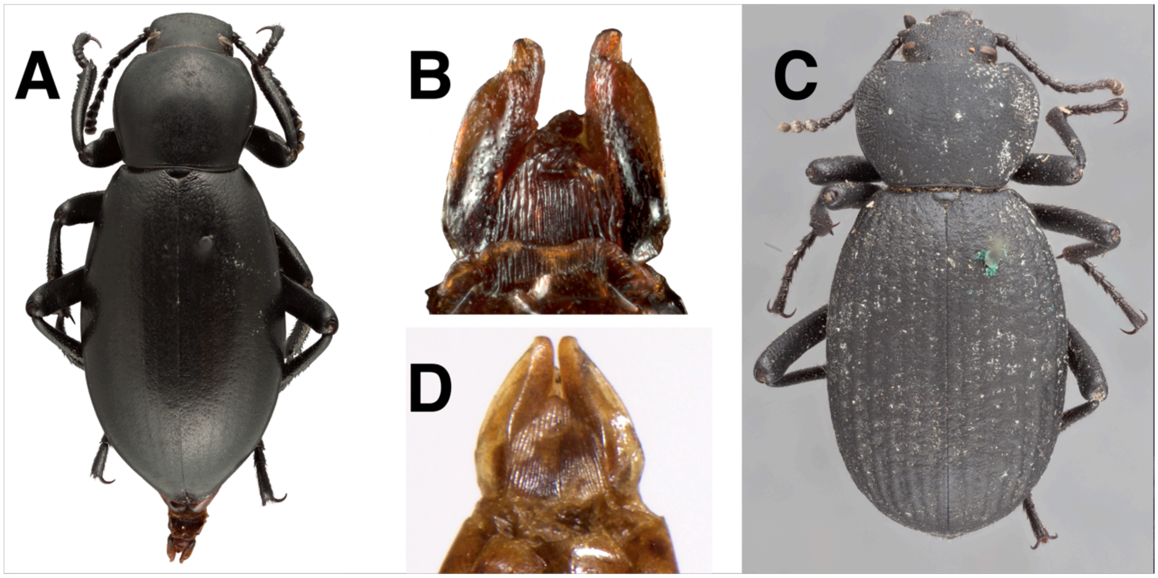


Figure 5.15. *Steneleodes* Blaisdell, 1909. A. *S. hepburni* (Champion, 1884) dorsal habitus. B. *S. hepburni* female ovipositor, dorsal view. C. *S. peropaca* (Champion, 1892) holotype, dorsal habitus. D. *S. longicollis* (LeConte, 1851) female ovipositor.

Differential redescription. Body moderate to large, generally relatively rotund, always glabrous. Mentum trilobed, mesal lobe broadly arcuate, concealing insertion of ligula. Antennomere 3 subequal to length of 4 and 5 combined, antennae much longer than head width. Pronotum often broad, anterior margin usually broadly concave, punctation generally fine. Fore femora almost always sinuate, never bearing spines; tarsi bearing dense golden setae or stout golden spicules. Ovipositor coxite well sclerotized, elongate, inner apical lobe moderately to strongly produced, oblique; gonostyle small, visible in dorsal view.

Remarks. *Steneleodes* was recently synonymzed with the older name *Xysta* Eschscholtz, 1829 (Bousquet *et al.* 2018), which was subsequently discovered as a junior homonym to a genus of tachinid flies. Therefore, the name *Steneleodes* is reinstated for this group of species, which is hereby elevated to genus level. The constituent species, many of which are poorly known from central Mexico, require a thorough revision, which is beyond the scope of the present study. The species composition as given in Bousquet *et al.* (2018) is maintained in the following checklist, though rearrangements within the genus as well as the addition of several species currently *Incertae sedis* within *Eleodes* may be expected from a future revision. Other than the new binomen combinations listed below, the replacement name *Eleodes tenebricosa* Gemminger, 1870 is no longer required for *E. obscura* Solier, 1848.

Checklist of the species of *Steneleodes* (see Bousquet *et al.* 2018 for synonymies).

Steneleodes angulata (Eschscholtz, 1829) [*Xysta*] **New Combination**

Steneleodes angusta (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Steneleodes blapoides (Eschscholtz, 1829) [*Eleodes*] **New Combination**

Steneleodes coarctata (Champion, 1885) [*Eleodes*] **New Combination**

Steneleodes corrugans (Triplehorn, 2007) [*Eleodes*] **New Combination**

Steneleodes distincta (Solier, 1846) [*Eleodes*] **New Combination**

Steneleodes forreri (Champion, 1884) [*Eleodes*] **New Combination**

Steneleodes gigantea (Mannerheim, 1843) [*Eleodes*] **New Combination**

Steneleodes glabricollis (Champion, 1884) [*Eleodes*] **New Combination**

Steneleodes gravida (Eschscholtz, 1829) [*Xysta*] **New Combination**

Steneleodes hepburni (Champion, 1884) [*Eleodes*] **New Combination**

Steneleodes innocens (LeConte, 1866) [*Eleodes*] **New Combination**

Steneleodes laevigata blapsoides (Solier, 1848) [*Eleodes*] **New Combination**

Steneleodes laevigata laevigata (Solier, 1848) [*Eleodes*] **New Combination**

Steneleodes longicollis (LeConte, 1851) [*Eleodes*] **New Combination**

Steneleodes mutilata (Blaisdell, 1921) [*Eleodes*] **New Combination**

Steneleodes olida (Champion, 1892) [*Eleodes*] **New Combination**

Steneleodes ornatipennis (Blaisdell, 1937) [*Eleodes*] **New Combination**

Steneleodes peropaca (Champion, 1892) [*Eleodes*] **New Combination**

Steneleodes platypennis (Triplehorn, 2007) [*Eleodes*] **New Combination**

Steneleodes ponderosa (Champion, 1884) [*Eleodes*] **New Combination**

Steneleodes punctigera (Blaisdell, 1935) [*Eleodes*] **New Combination**

Steneleodes ruida (Say, 1835) [*Blaps*] **New Combination**

Steneleodes sallaei (Champion, 1885) [*Eleodes*] **New Combination**

Steneleodes solieri (Champion, 1885) [*Eleodes*] **New Combination**

Steneleodes stolida (Champion, 1885) [*Eleodes*] **New Combination**

Steneleodes sulcatula (Champion, 1884) [*Eleodes*] **New Combination**

Steneleodes obscura (Solier, 1848) [*Eleodes*] **New Combination**

Steneleodestessellata (Champion, 1892) [*Eleodes*] **New Combination**

5.4.17. *Torugena* **New Genus**

Type species: *Eleodes rugosifrons* Triplehorn and Reddell, 1991 Present Designation

Diagnosis. This monotypic genus (Fig. 5.16) can be easily identified by the swollen genae covering the antennal insertions, densely punctate body, and sulcate-striate elytra. The only other genus approaching this form of sculpturing is *Trogloderus*. The present genus can be separated from the latter by the simple fore tibiae (flattened in *Trogloderus*), males with apically flattened hind tibiae (unmodified in *Trogloderus*), and the sulcate-striate elytra (bearing four elevated costae in *Trogloderus*).

Differential description. Body moderately large, elongate, densely punctured throughout, appearing glabrous. Mentum weakly trilobed, proudly rectangular, mesal lobe taking form of weakly projected keel, lateral lobes projected forward; insertion of ligula visible in ventral view. Antennomere 3 subequal to length of 4 and 5 together, antennae much longer than head width. Head roughly punctate; genae inflated over antennal insertions; epistoma swollen, raised above level of frons. Pronotum strongly punctate, arcuate laterally, posterior margin narrower than anterior margin, anterior angles not projected forward. Femora lacking spines; fore tibiae simple in both sexes, hind tibiae of male flattened and expanded ventrally in apical 1/3; all tarsi bearing stout

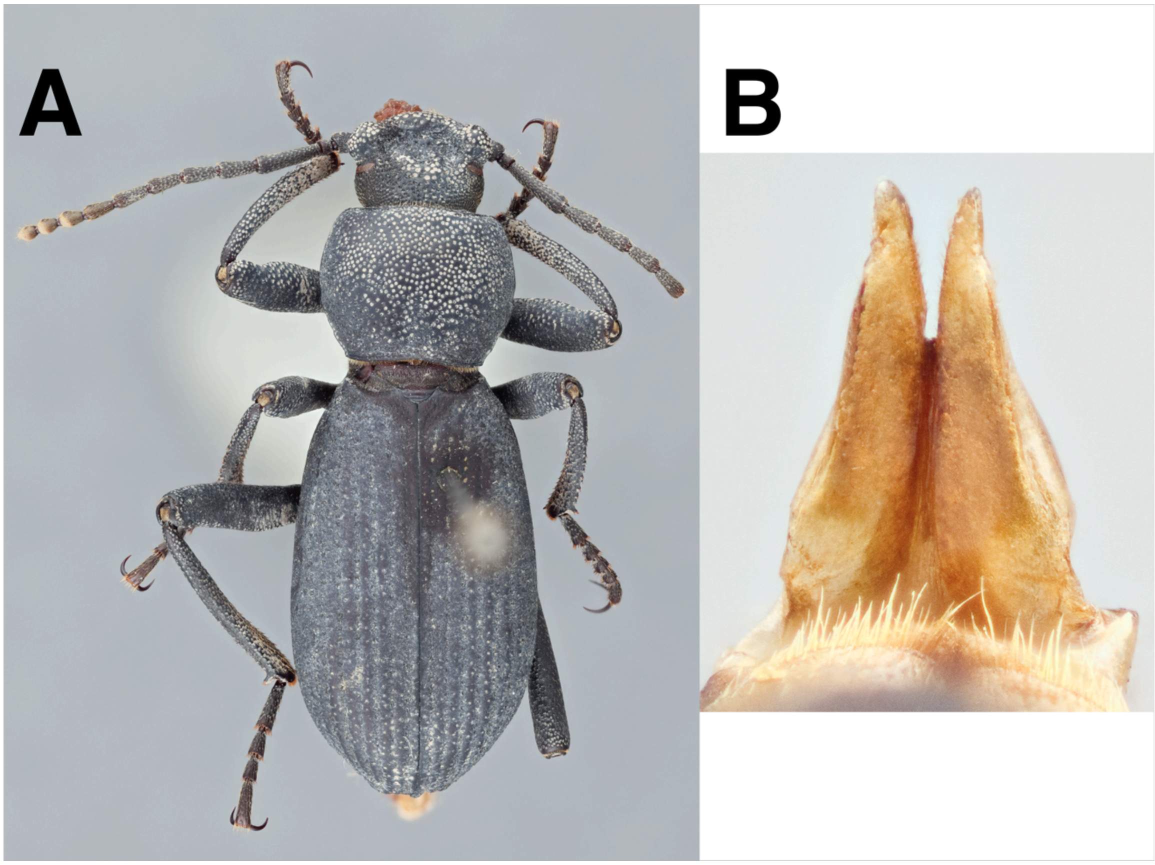


Figure 5.16. *Torugena* New Genus. A. *T. rugosifrons* (Triplehorn and Reddel, 1991) holotype, dorsal habitus. B. *T. rugosifrons* female ovipositor, dorsal view.

ferruginous to castaneus spicules. Female ovipositor with coxite well sclerotized, subtriangular, laterally concave; gonostyle minute, inconspicuous in dorsal view.

Etymology. *Torugena* is an arbitrary combination of letters considered feminine. The name is given in reference to the swollen genae, which cover the insertion of the antennae.

Remarks. The genus is hereby erected for the single species *Torugena rugosifrons* (Triplehorn and Reddell, 1991) [*Eleodes*] **New Combination**. Known only from caves in Nuevo León and Coahuila, Mexico (Aalbu *et al.* 2012), this is the only herein circumscribed genus not included in molecular analyses (Smith, Johnston *et al.* in prep). The body sculpturing is unlike that of any other genus but *Trogloderus*, and the female ovipositor is very similar to those of *Trogloderus*, *Lariversius*, and *Exarenula*. Whether *Torugena* represents a southern extension of that clade of genera from the Intermountain Region, or is merely morphologically convergent with them, *Torugena rugosifrons* does not fit within the bounds of any other known Amphidorini genera.

5.4.18. *Tricheleodes* Blaisdell, 1909:138 **New Status**

Type species: *Eleodes hirsuta* LeConte, 1861

Diagnosis. This monotypic genus (Fig. 5.17) can be readily identified by the combination of the metanepisternum lacking a dorsoventral ridge and antennomere 8 lacking a setose sensory patch. The body is also clothed in moderately long erect black setae and the tarsi are lined with black spicules beneath. The antennae are quite robust

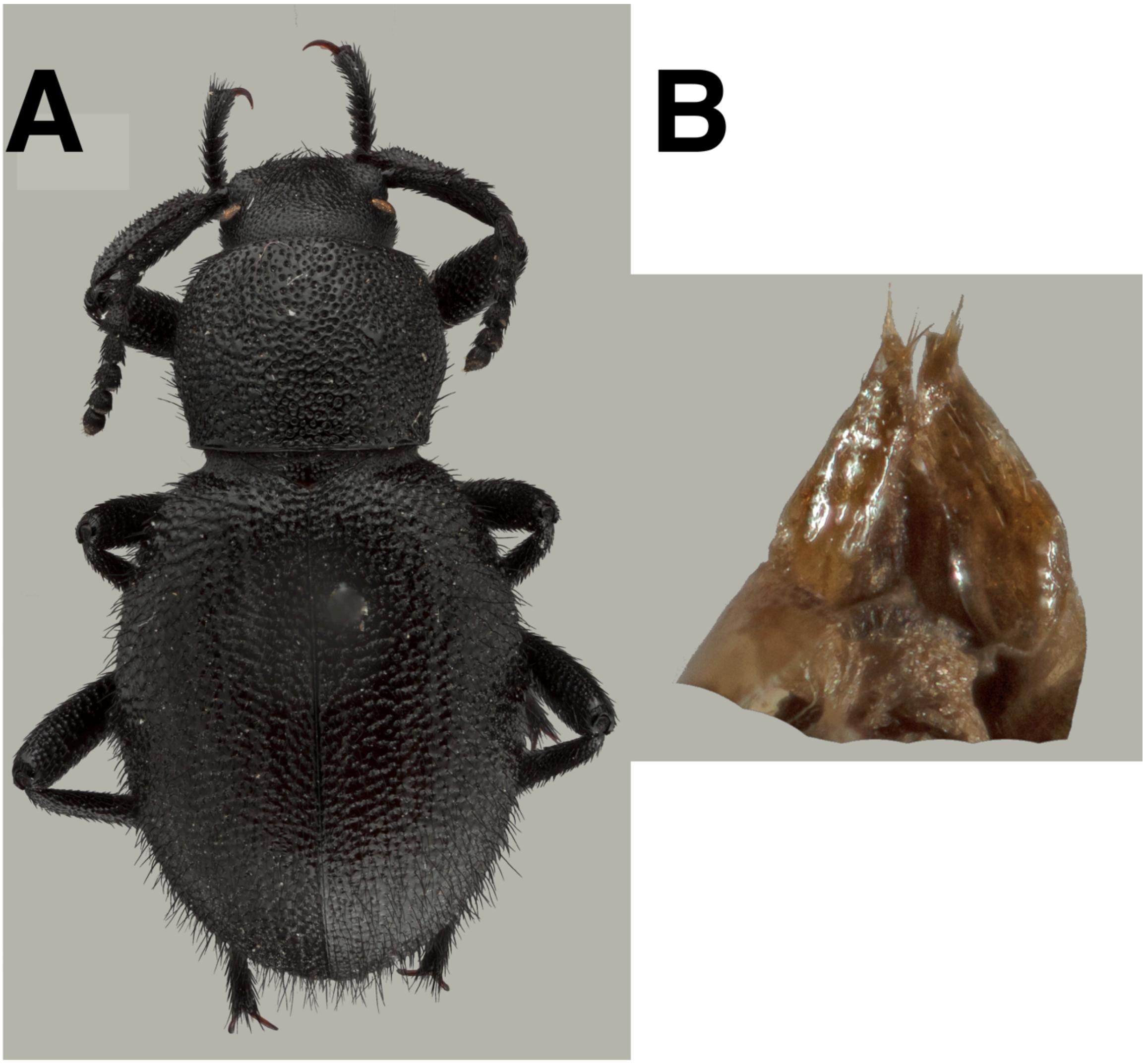


Figure 5.17. *Tricheleodes* Blaisdell, 1909. A. *T. hirsuta* (LeConte, 1861) dorsal habitus. B. *T. hirsuta* female ovipositor, dorsal view.

for the tribe, with most segments appearing rectangular instead of elongate oval or obconical.

Differential redescription. Body moderately small, black, hirsute, bearing black setae throughout. Mentum trilobed, mesal lobe weakly projected, not concealing insertion of ligula. Antennomere 3 subequal to length of 4 and 5 combined, antennae longer than head width, antennomere 8 lacking setose sensory patch, antennomeres more or less rectangular. Pronotum subquadrate, often longer than broad, gently arcuate laterally, not constricted basally, heavily punctate. All femora lacking spines; tarsi bearing black spicules beneath. Ovipositor coxite narrow, elongate, well scleritized, inner apical angle weakly projected, acute, slightly longer than gonostyle; gonostyle visible in dorsal view.

Remarks. *Tricheleodes* was recircumscribed by Johnston (2016) and is here left with the same composition, containing the single species *Tricheleodes hirsuta* (LeConte, 1861) [*Eleodes*] **New Combination**, which is more or less restricted to the Great Basin in the western United States.

5.4.19. *Trogloderus* LeConte, 1879:2

Type species: *Trogloderus costatus* LeConte, 1879

Diagnosis. *Trogloderus* (Fig. 5.18) can be easily recognized by the roughly sculptured pronotum, either reticulately punctate or strongly tuberculate, in combination with each elytron bearing 4 longitudinal carinae. The expanded fossorial protibiae also separate *Trogloderus* from all other genera except *Lariversius*, which lacks the sculpturing characters given above.

Differential redescription. Body size small to moderate, ferrugineus to black, glabrous, roughly sculptured. Mentum trilobed, mesal lobe projected anteriorly, acute or truncate, often partially concealing insertion of ligula. Antennomere 3 subequal to length of 4 and 5 combined, antennae longer than head width. Pronotum arcuate laterally, anterior angles acute, projected, disc roughly sculptured, reticulately punctate or tuberculate. Elytra each with 4 longitudinal carinae. Legs roughly sculptured, fore femora bearing spine in males, spined or not in females, fore tibiae flattened, fossorial, tarsi bearing stout castaneus spicules. Ovipositor coxite elongate, subtriangular, inner apical angle short, rounded; gonostyle hidden from dorsal view, visible in ventral view.

Remarks. The genus is here considered to include 10 species, following the thorough revision presented earlier. For a key to species, see Chapter 3.

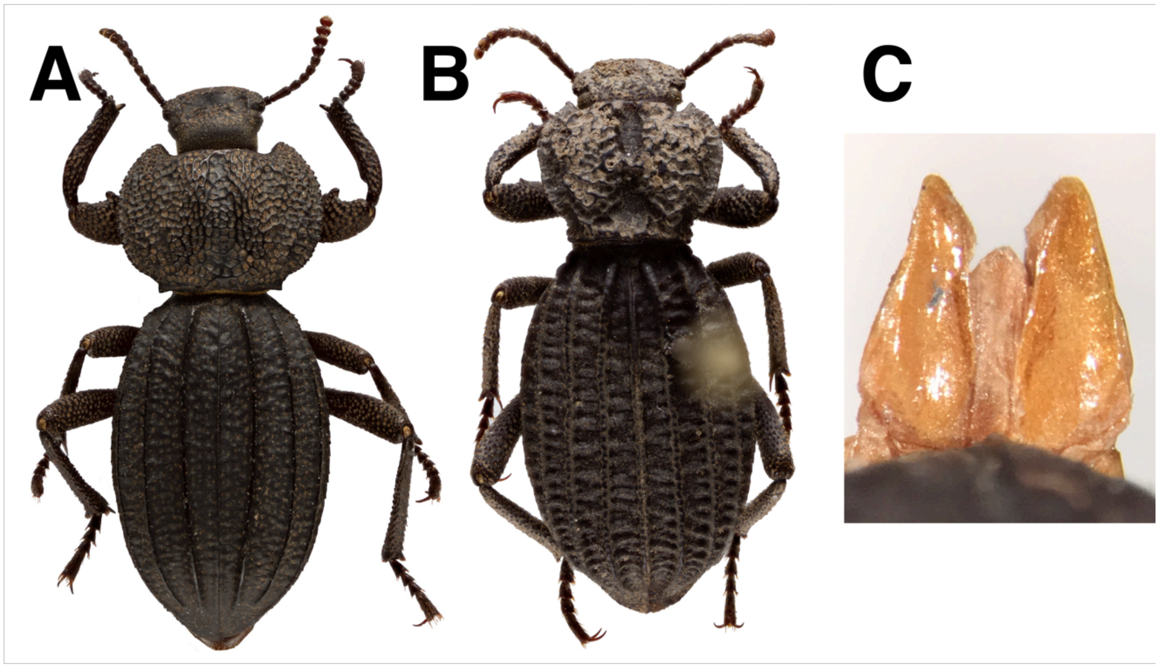


Figure 5.18. *Trogloderus* LeConte, 1879. A. *T. vandykei* La Rivers, 1946 dorsal habitus. B. *T. costatus* LeConte, 1879 dorsal habitus. C. *T. vandykei* female ovipositor, dorsal view.

5.5. Discussion

5.5.1. Morphological variation

Diagnostic morphological characters were found for all 16 circumscribed Amphidorini genera. Nevertheless, many of these characters are subtle and only become clear in the context of the overall tribal diversity. The shape of the epipleuron, mentum, and ovipositor coxite seem to be the most reliable characters across all genera. Secondary characters, such as tarsal pads, femoral spines, and long setae covering the body, are equally important for generic and species recognition, yet have a much higher degree of homoplasy.

Internal morphology proved to be uninformative for both genera and species. The internal thoracic anatomy, *e.g.* metendosternite, mesosternal apophyses, and metanotum, were incredibly similar across 20 species representing ten genera. This could be due to the complete lack of flight wings, which has reduced the demand on thoracic musculature. Both the ventral and lateral thoracic and abdominal sclerites of all species are remarkable consistent, except for the prosternal process which is variable between closely related species. This might be explained by the conserved epigean lifestyle of all species, whereby the ancestral amphidorini converged on a body plan well-adapted for roaming the ground in arid habitats, and have had no pressure to change.

The strongly autapomorphic *Lariversius* and *Trogloderus* indicate that large morphological change is possible within Amphidorini, even on relatively a short timescale. *Lariversius* exhibits a strongly modified body plan (*i.e.* rounded body, fossorial legs, short antennae, incised epistoma, and fimbriate pronotal margins), resembling a larger version of other dune-obligate tenebrionid taxa in the tribe Anepsiini LeConte, 1862 (Doyen 1987). *Trogloderus* exhibits less marked changes to the overall body plan, yet does have extreme diversity in body sculpturing, which is presumably adaptive for crypsis in its psammophilic environment (see Chapter 3). Together, these genera show that there is phenotypic plasticity at least under certain conditions. This further supports the hypothesis that morphological similarity across Amphidorini is evolutionarily conserved and strongly adaptive to their life history.

5.5.2. Summary of taxonomic changes

This revision provides a necessary framework for identifying and studying the evolution and natural history of the desert stink beetles. Moreover, it serves as a unifying link to the numerous regional and narrowly focused taxonomic treatments. The recent catalog of North American Tenebrionidae completed by Bousquet *et al.* (2018) is an important and thorough milestone for darkling beetle systematics. The taxonomic changes made in this study are summarized and aligned to the treatment of Bousquet *et al.* (2018) in Table 5.1.

This is the most comprehensive set of species-level identification keys since those published in the monograph of Blaisdell (1909). There have been roughly 50 taxonomic works published on the tribe in the century since, which simultaneously necessitated and paved the way for the current revision. Despite several large revisionary works still pending, *e.g. Blapylis* and *Steneleodes*, this diverse and abundant lineage is now accessable for evolutionary, biogeographic, and ecological study.

Table 5.1. Summary of taxonomic changes for Amphidorini. The current name and number of species are given for each Amphidorini genus included in this study along with its status and number of species from the recent catalog of Bousquet *et al.* 2018. The total number of genus-group and species-group taxonomic changes presented above are tallied for each genus.

Current Circumscription		Bousquet *et al.* 2018		Taxonomic Changes	
Genus	Total Species	Rank	Total Species	Genus-group	Species-group
Amphidora	1	Subgenus	3	1	1
Blapylis	51	Subgenus	51	1	51
Cratidus	4	Subgenus	2	1	4
Discogenia	2	Subgenus	4	1	4
Eleodes	103	Genus	232	-	2
Eleodimorpha	1	Genus	1	-	-
Embaphion	11	Genus	11	-	-
Exarenula	1	[new]	-	1	1
Globostyla	1	[new]	-	1	3
Lariversius	1	Genus	1	-	-
Metablapylis	11	Subgenus	8	2	15
Neobaphion	5	Genus	4	-	1
Steneleodes	29	Subgenus	29	1	-
Torugena	1	[new]	-	1	1
Tricheleodes	1	Subgenus	1	1	1
Trogloderus	10	Genus	10	-	-
			Total:	**11**	**84**

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APPENDIX A

COAUTHOR APPROVAL FOR CHAPTER 2

Coauthor Approval for Chapter 2

The chapter titled ‘An updated checklist of the Tenebrionidae sec. Bousquet et al. 2018 of the Algodones Dunes of California, with comments on checklist data practices’ was published earlier in 2018 in the Biodiversity Data Journal. This paper had three contributing authors. M. Andrew Johnston was the first and corresponding author. The original publication can be found at: https://doi.org/10.3897/BDJ.6.e24927

Both Rolf L. Aalbu and Nico M. Franz have given consent for the publication to be included in this dissertation by M. Andrew Johnston.