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Taxonomic review of the North American dung beetle genus *Boreocanthon* Halffter, 1958 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini)

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Taxonomic review of the North American dung beetle genus *Boreocanthon* Halffter, 1958 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini)

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Abstract. This paper presents a taxonomic review of the genus *Boreocanthon* Halffter, **restored generic status**, a group of ball-rolling (telocoprid) dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) endemic to North America. The genus, heretofore treated as a subgenus of *Canthon*, comprises 13 species, each keyed, diagnosed, illustrated and presented with information on distribution, relationships, and biology (*signifies **restored generic combination**): **Boreocanthon ateuchiceps* (Bates, 1887); *B. coahuilensis* (Howden, 1966); **B. depressipennis* (LeConte, 1859c); **B. ebenus* (Say, 1823); **B. forreri* (Bates, 1887); **B. integricollis* (Schaeffer, 1915); **B. lecontei* (Harold, 1868); **B. melanus* (Robinson, 1948); **B. praticola* (LeConte, 1868); **B. probus* (Germar, 1823); **B. puncticollis* (LeConte, 1866); **B. simplex* (LeConte, 1857); as well as *Boreocanthon halffteri* Edmonds here described as a **new species**. Other actions taken are a) *Canthon mixtus* Robinson declared junior subjective **new synonym** of *Boreocanthon puncticollis*; b) *Canthon bisignatus* Balthasar, 1939, declared junior subjective **new synonym** of *Boreocanthon simplex*; c) *Boreocanthon coahuilensis* (Howden) **new generic combination**; and d) **neotype** designated for the type species of the genus *Boreocanthon*, *Ateuchus ebenus* Say, 1823, here *Boreocanthon ebenus* (Say).

Key words. *Canthon*, new species, new synonymies, neotype, key to species.

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Introduction

The genus *Canthon* Hoffmannsegg, 1817, is a large (~200 species), very diverse New World group with a long, somewhat complicated taxonomic history (Cupello and Vaz-de-Mello 2018). As defined by Halffter and Martínez (1977) and adopted by most workers since (e.g., Vaz-de-Mello et al. 2011), *Canthon* comprises nine subgenera (including *Boreocanthon*) and several residual species groups that lie outside current subgeneric limits. The species-level taxonomic picture of the deltochiline fauna of North America has remained relatively stable for the last 150 years or so, during which time it has been treated in numerous comprehensive works (LeConte 1859c, 1863; Harold 1868; Blanchard 1885; Bates 1887; Horn 1870; Leng 1920; Schmidt 1922; Balthasar 1939; Robinson 1948; Halffter 1958, 1961; Halffter and Martínez 1977). All of these works include species now assigned to *Boreocanthon*. In the mid-20th century, *Canthon* became the focus of intense taxonomic splitting as various workers sought to separate distinctive groups of species into new genera (Martínez 1948a,b; Pereira and Martínez 1956; Martínez and Pereira 1956; Halffter 1958). The emergent generic level reorganization was summarized by Vulcano and Pereira (1964) and Halffter and Martínez (1977).

Halffter (1958) established *Boreocanthon* to accommodate a distinctive group of North American *Canthon* characterized primarily by their smaller size (4–10 mm), often strongly quadridentate clypeus (sometimes accompanied by dentate paraocular areas so as to produce a sexdentate head margin), and lack of a carinate line along the anterior margin of the metafemora. He initially moved ten species from *Canthon* to *Boreocanthon*: *B. simplex* (LeConte), *B. melanus* (Robinson), *B. lecontei* (Harold), *B. probus* (Germar), *B. puncticollis* (LeConte), *B. praticola* (LeConte), *B. depressipennis* (LeConte), *B. ebenus* (Say), *B. integricollis* (Schaeffer), and *B. mixtus* (Robinson) (here considered a synonym of *B. puncticollis*). *Ateuchus ebenus* Say was designated type species of the new genus, as *Canthon ebenus* (Say). He later (Halffter 1961) added *Canthon ateuchiceps* Bates and *C. forreri* Bates to the genus, considering them distinct enough to perhaps represent a new subgenus of *Boreocanthon*. Howden

(1966) added a new species to the group that he named *Canthon coahuilensis*, and assigned it with doubt to *Boreocanthon*, which he regarded as a subgenus (see comments for *B. coahuilensis*). Halffter and Martínez (1977) later confirmed membership of *C. coahuilensis* in *Boreocanthon*, which, in step with Howden (1966), they reduced in rank to subgenus; they also added to the group *C. bisignatus* Balthasar, here regarded as a synonym of *B. simplex*. With the addition here of *Boreocanthon halffteri* and the deletions resulting from two new synonymies (*B. mixtus* and *B. bisignatus*) the total number of valid species in the genus becomes thirteen.

To the limited extent member species have figured in cladistic studies (Kohlmann and Halffter 1990; Medina et al. 2003; Halffter et al. 2022), there is evidence that the genus is a monophyletic group nested within the loose assemblage of North American representatives of the deltochiline Scarabaeinae. Kohlmann and Halffter (1990) is the most comprehensive of the three studies in the context of *Boreocanthon* (regarded a subgenus by them). In their study, the genus (minus *B. coahuilensis*) is clearly resolved as a monophyletic group closely related to *Melanocanthon*, the two taxa forming the sister group of *B. coahuilensis*. Within *Boreocanthon* there is little resolution: *B. simplex* is an outlier; *B. depressipennis-ebenus-praticola* resolve as a clade within a large polytomy uniting it with the remaining seven species. The cladistic analysis presented by Medina et al. (2003), while it clearly united *Melanocanthon* and *Boreocanthon*, includes too few species of the latter to provide further insight. The phylogenetic analysis by Halffter et al. (2022) placed the *Boreocanthon – Melanocanthon* duo as sister to *Bajacanthon*, a monobasic subgenus for *Canthon obliquus* Horn, endemic to the southern tip of Baja California Sur.

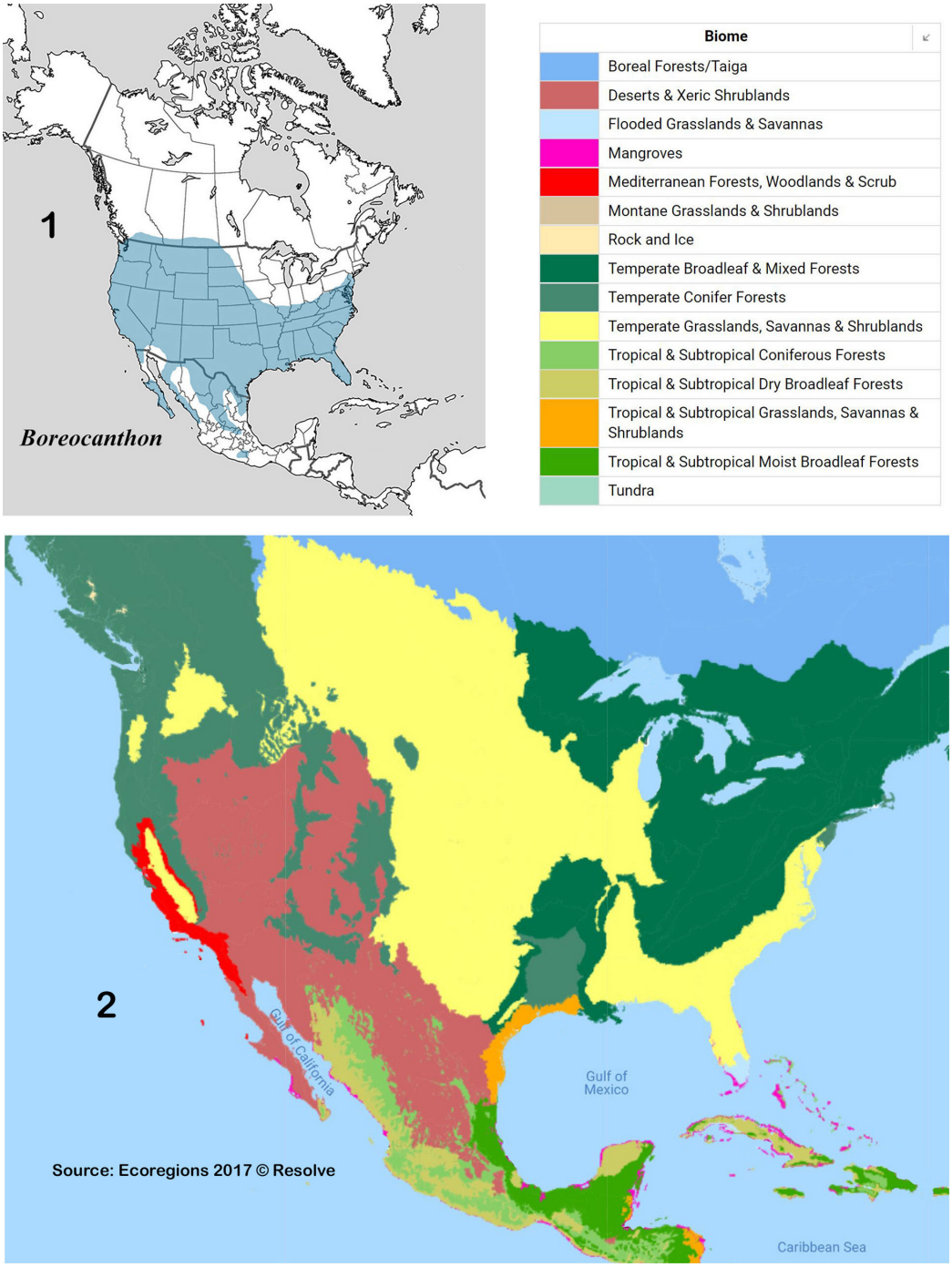
Materials and Methods

This study is based almost exclusively on museum specimens where species limits and definitions are morphology-based concepts whose practical purpose is to sort observable variation. While the basic unit of the resulting classification is the species, I cannot claim that those recognized here are "biological" in the sense that they represent anything other than a hypothesis of the current manifestation (morphological, molecular, behavioral, ecological, geographical and phylogenetic) of several putative historical lineages (in the present case, 13). The classification proposed here is conservative (see Zachos (2014) for context), provisional and subject to future changes as additional information becomes available and existing information is re-analyzed. It is but a snapshot of what one taxonomist now knows about a defined group of beetles named *Boreocanthon*.

This review is based on examination of approximately 9550 specimens, all of which were graciously provided by the caretakers of the institutional and private collections cited in the Acknowledgements. Species and supraspecific diagnoses employ the terminology used by Edmonds (1972 and elsewhere) unless noted otherwise. In addition, presented below is a summary of morphological variation observed in *Boreocanthon* focused primarily on its taxonomic context as well as notations on the use of certain terms. Specified body lengths include the head; these measurements are approximate and intended only for comparing relative size.

Collection localities were gleaned mainly from specimens seen by me. Localities are arranged alphabetically by country followed by first-order political subdivisions (state, department, province or equivalent) and second-order divisions (county, municipality, etc.). Individual collection points follow their second-order division, each preceded by a solid black dot (● or, in the case of certain *B. simplex*, a red diamond ♦) and followed in brackets by month(s) of collection, if specified. The symbols are used to clearly punctuate locality lists, otherwise visually difficult to separate using more conventional marks. If a label cites only a U.S. county location, the name of the county is entered followed by the notation "(no data)." In order to minimize errors, no attempt is made to convert distance and elevation, which are presented as transcribed (miles or kilometers, or, feet or meters). Similarly, I have not standardized the format of geographical coordinate data; these are presented as they appear on labels, but each was checked for consistency with accompanying information (name of town, or distance from point, elevation, etc.) using Google Earth. The geographical distribution maps (base map modified from original source: https://www.gifex.com/fullsize-en/2009-11-08-10949/North_America_Political_Outline_Map.html) represent my current inferences about species geographic distributions based on the collection data presented in the species treatments; they are not intended to be static representations of range. On the contrary, the margins of the shaded areas should be regarded as tenuous, but I do regard them as reliable enough for supporting generalizations and comparisons about geographical distributions. In a very general way, ecogeographic characteristics of

each species are indicated by reference to the vegetational mapping in Figure 2, and in the section "Ecogeographic environment" at the end of each species diagnosis. This section consists of a designated biome followed parenthetically, when appropriate, by ecoregion(s) inhabited by a given species. Figure 2 is modified from *Ecoregions 2017* © Resolve (https://ecoregions.appspot.com/), an interactive website where the limits of specified ecoregions (subunits of biomes) for each species, as well as other biogeographical information can be viewed (Olson et al. 2001; Dinerstein et al 2017).



Figures 1–2. 1) Approximate corporate distribution of the genus *Boreocanthon*. **2)** Generalized depiction of vegetation biomes of the United States (Biome key in box; See Materials and Methods for explanation).

A weakness of this study is the fact that I was unable to examine directly type material. In most cases, however, photographs of putative type material was available, and these have been critical to achieving an acceptable degree of nomenclatorial confidence. For each species treatment, the section "Type Material" will provide information I have about the species-group name(s) in question. Location of type material, where known, is indicated by name of museum/collection and city. In using the term "holotype" I have been mindful of ICZN Recommendation 73F, "Avoidance of assumption of holotype". Consequently, I have reserved reference to "holotype" only to cases I regard as highly reliable and have used "syntype" in other cases. To my knowledge, no lectotypes have been designated for species in the genus, and I hesitate to do so here because I have not been able to examine available type material directly.

Type localities are determined in accordance with ICZN Article 76. In all cases, I rely upon information provided in the original description of the taxon corroborated by label data accompanying specimens and reliable information from published sources.

Morphology of *Boreocanthon*. The following summary is offered as an aid to understanding and assessing the taxonomic features cited in the key and various diagnoses for *Boreocanthon*. It is neither exhaustive nor meant to apply directly to other groups, although none of the morphology described here is unique to the genus.

Color: Viewed from reading distance, almost all *Boreocanthon* appear dull and sombre-colored, usually black or nearly so; *B. forreri* (Fig. 102–103) while dark, presents a subdued, metallic green or coppery green dorsum, and *B. ateuchiceps* (Fig. 38–39) is bright, shiny green or yellow green. Many of the "black" species at least occasionally show dull green or blue highlights on the head and pronotum revealed under magnification (×5) under broad spectrum light. *Boreocanthon depressipennis* (Fig. 11) almost always presents conspicuous green highlights. Such highlights, while usually much subdued on casual inspection, are sometimes much enhanced on specimens submerged in liquid (for example, blue in *B. puncticollis* and usually green in *B. melanus*). Pigmented color (as opposed to the structural colors just mentioned) is found in but one species, *B. simplex*, certain populations of which include individuals with orange/red-orange elytral umbones (Fig. 96–97). Mario Cupello (pers. comm.) reports that individuals with similar orange umbones occur as intraspecies variants in several distantly related South American dung beetles, including *Ateuchus globulus* (Boucomont 1928) and *Canthidium bituberculatus* (Fabricius 1801).

Size: *Boreocanthon* are generally small, robust dung beetles with lengths often below 6 mm. The lengths of all species vary by at least 50%, sometimes by almost 100%. The average length of the smaller species ranges from about 4–6 mm, that of the larger species (*B. ebenus, B. depressipennis, B. praticola* and *B. coahuilensis*) from about 5–8 mm, with exceptional individuals reaching 10 mm.

Sculpturing: Dorsal (head+pronotum+elytra+pygidium) sculpturing is highly variable in *Boreocanthon* and is a primary consideration in diagnosing species. Terminology applied to sculpturing of the integument has a complicated, sometimes inconsistent lexicon (see Harris 1979); that adopted below is for convenience and clarity in the context of this review. Much of the sculpturing is subtle and highly subject to distortion caused by the wear and tear exacted by a fossorial lifestyle. Assessment of sculpturing for taxonomic purposes, therefore, is best based on "fresh" specimens. Sculpturing in the genus consists of a suite of four features best assessed under moderate (>10× magnification).

1) *Shagreen* (primary granulation; microgranulation) (Fig. 13, 48, 71, 75)—The upper surface of all *Boreocanthon* species is more or less evenly covered by very small, densely packed (contiguous), rounded granules giving the magnified (×25) surface an evenly roughened, or "alutaceous" or shagreen texture resembling that of untanned leather, cobblestone or calade ground cover. The shagreen commonly also extends to the ventral surfaces. This sculpture feature is almost always distinct and coexistent as a background to other surface features (punctures, etc.). In *B. ateuchiceps* (Fig. 38) and less so in *B. forreri* (Fig.105), the shagreen is largely effaced to produce a polished, shiny surface; in *B. lecontei* (Fig. 31), it is largely obscured on the pronotum by the very fine, densely compacted secondary granulation characteristic of this species.

2) *Granulation* (secondary granulation; macrogranulation)—In three species, *B. ebenus* (Fig. 27), *B. depressipennis* (Fig. 11, 13), and *B. praticola* (Fig.8), the upper and some ventral surfaces are uniformly covered by a field of coarse, rounded, elevated granules. These are usually discrete (not contiguous) but regularly coalesce on the pronotum of *B. ebenus*. A fourth species, *B. lecontei* (Fig. 31) is unique in that the head and pronotum are covered

by a fine, dense, secondary granulation that largely obscures the shagreen background; unlike the preceding three species, the granulation does not extend to the elytral interstriae. Macrogranulation is only very rarely accompanied by distinct puncturing, and then only in limited areas (such as the pygidium). The other North American groups of deltochilines, *Melanocanthon* and the *Canthon pilularius* species group (sensu Halffter 1961, Halffter and Martínez 1977), share the macrogranulate condition (see Medina et al. 2003).

3) *Microspots* (maculae)—In all species lacking distinct macrogranulation, the dorsum presents a field of small, shiny spots, or maculae, usually accompanied by distinct puncturing (Fig. 61, 88, 115). The size and distribution of microspots strongly suggest that they are vestigial granules, with which they never coexist, and that a granulated surface is the likely plesiomorphic condition of *Boreocanthon*. Circumstantial evidence of plesiomorphy resides in a single, unusual specimen of *B. simplex* observed for this study that conserves limited elytral granulation accompanied by maculae (see Comments for *B. simplex*).

4) *Puncturing*—As for microspots, the upper surface of species lacking secondary granulation almost always presents puncturing. Puncturing is generally weak, very fine and usually sparse and difficult to assess without at least low (5×) magnification (Fig. 59, 75, 109). Puncturing usually extends to ventral surfaces and is usually absent from the elytral interstriae. Punctures on the pygidium as well as elsewhere over the dorsal surface sometimes bear minute setae visible only at higher magnification (50×) from an oblique angle. While never dense and always simple, pronotal puncturing varies mainly in the degree of conspicuousness, or "crispness," especially on the pronotum, from clearly expressed (*B. puncticollis*, Fig. 61) to very weak and nearly effaced (*B. coahuilensis* [Fig. 48] as well as some *B. probus* [Fig. 75] and *B. halffteri*).

Head: A conspicuously dentate outer head margin is a hallmark feature of *Boreocanthon*. The clypeus bears four, usually prominent, upturned teeth, of which the median pair is always larger than the lateral pair. The head margin behind the lateral teeth (at the junction of the fronto-clypeal suture) is almost always interrupted by an indentation of variable size and shape, here called the paraocular notch, that sets off the anterior angle of the paraocular area (gena auct.). The size of the paraocular notch and corresponding shape of the paraocular angle provide important diagnostic characters. If the notch is small and inconspicuous (as in *B. simplex* [Fig. 92] and *B. lecontei* [Fig 32], for example), setting off only a small angular portion of the paraocular area, the head will appear decidedly quadridentate or only weakly sexdentate. If the U- or V-shaped notch is large, setting off a strongly developed, acute angle (as in *B. probus* [Fig. 74] and *B. ebenus* [Fig. 11], for example), the head will appear decidedly sexdentate. Some species (*B. melanus* [Fig. 112] and *B. simplex* [Fig. 92], for example) present intermediate shapes. In *B. coahuilensis* (Fig. 52) certain individuals have very poorly developed lateral clypeal teeth and obsolete paraocular notches such that the head is virtually bidentate, a condition that prompted Howden (1966) to question its placement in *Boreocanthon*. The dentition of the head (as well as protibiae) is highly prone to distortion/obliteration resulting from wear produced by digging in the rocky, sandy soils common to the habitats of these beetles, which, at beetle scale (Fig. 78), present formidable obstacles to digging. Figure 62 compares the clypeal margin in "fresh" and highly abraded individuals of *B. puncticollis*. Reliance on well-worn specimens for taxonomic assessment can, unsurprisingly, lead to avoidable errors (e.g., the case of *Canthon bisignatus* Balthasar; see *B. simplex*.)

Sculpturing of the upper surface of the head, especially in non-granulate species, consists of two zones (Fig. 47, 55, 92): Immediately following the marginal teeth, the surface is usually roughened to some degree for about one-half the length of the clypeus and thereafter that of the remainder of the clypeus, the frons and the paraocular areas approximates the surface of the pronotum. The reflectivity of the head surface is usually uniform but occasionally somewhat brighter anteriorly. In *B. probus* (Fig. 79), the clypeus often presents a conspicuous shiny, transverse band, a condition often also seen in *B. integricollis*.

The labio-gular fimbria marks the putative boundary between the mentum and gular sclerites. It consists of an array of long, recumbent setae of variable shape mixed with median field of coarse punctures. The fimbria may consist of a simple, posteriorly bowed row of setae (Fig. 69), or, more commonly, display a posteriorly directed, narrowed, V-shaped configuration (Fig. 7, 15, 60) extending up to one-half the length of the gula. In either case, it often includes a group of coarse punctures arranged along the gular midline.

Prothorax: Sculpturing of the pronotum is usually evenly expressed over its entire surface. Among *Boreocanthon* species, there are two principal patterns: granules on a shagreen background (Fig. 13), and punctures mixed with microspots on a shagreen background (Fig. 48, 75). As the clarity of puncturing varies from hardly visible to bold, so, too, does the expression of microspots. (See puncturing, above)

The anterolateral angles of the pronotum are usually little, if at all, upturned (explanate). In *B. probus* (Fig. 73) they can be narrowly elevated, especially in western populations, while in the closely related *B. halffteri* (Fig. 87) they are broadly elevated between the lateral and anterior angles of the pronotal margin.

The curving of the dorsal profile of the pronotum (viewed laterally, Fig. 53) usually reaches only slightly above the level of the elytral surface. In *B. coahuilensis,* as well as *B. ebenus*, the curvature is much stronger, producing a humpbacked profile.

At times the underside of the pronotal margin, near the anterior end, bears a small, rounded tubercle or small group of tubercles that has been regarded as diagnostic by Robinson (1948) for certain species (*B. melanus*, *B. lecontei, B. mixtus* [=*puncticollis*]). This feature is variable in these species, to the extent that I have not regarded it as diagnostic. Only in *B. coahuilensis* does the presence of "Robinson's tubercle" appear to be a reliable species character.

The posterior margin of the procoxal cavity is usually thickened only to a point near its lateral limit (Fig. 24). In some *Boreocanthon* (*B. ateuchiceps* [Fig. 40], *B. forreri* [Fig. 108], *B. melanus, B. praticola* and *B. simplex*) it "escapes" the coxal margin as a fine carina making a broad turn laterally to a point approximately one-fifth to one-fourth of the distance to the lateral pronotal margin. I here refer to this line as the hypomeral carina, which, in the case of these species, is incomplete and, as pointed out by Blanchard (1885), sometimes variable in expression within a single species, such as *B. simplex*. In some North American *Canthon* (e.g., *C. humectus* and *C. viridis*), it is complete, continuing uninterrupted to the lateral margin. Similar hypomeral carinae (complete and incomplete) are found in numerous other scarabaeines.

Pterothorax: The mesoventrite (mesosternum of Edmonds (1972)) is very short and broad and usually smooth, or with any puncturing confined to its lateral extremities (Fig. 12). In some *Boreocanthon*, notably *B. integricollis* (Fig.70), it is uniformly punctured. The pleura and metaventrite (metasternum of Edmonds (1972)) usually present sculpturing similar to the elytra (except for microspotting), although the metaventrite is often smooth, shiny and sparsely, but sharply punctate (Fig. 70).

Legs: The outer protibial margin is strongly tridentate in all *Boreocanthon*, and the margin between the teeth and along its basal one-half are conspicuously serrate. The inner margin varies from gently curved from base to apex (Fig. 104) to strongly offset (stepped) near its midpoint (Fig. 16, 51), with some species showing an intermediate shape. In the granulate species (*B. ebenus*, *B. depressipennis*, and *B. praticola*), the anterior end of the inner margin is prolonged as a conical tooth (Fig. 16, arrow; weakest in *B. praticola*). In most *Boreocanthon*, the protibial spurs are sexually dimorphic: strongly curved laterad and tapering to an acute point in the female (Fig. 116a); curved laterad, apically slightly expanded and asymmetrically, acutely bidentate in the male (Fig. 116b); in two species (*B. ebenus* and *B. depressipennis*) this spur is curved inward and tapering to an acute point in both sexes. *Boreocanthon* lack any trace of the fine ridge along the anterior face of the metafemora common in other North American deltochilines. All leg features mentioned above are highly susceptible to abrasive wear distorting or obliterating the pristine condition.

Elytra: Elytral sculpture is always similar to that of the pronotum except for distinct puncturing, which can extend to the humeral angle (Fig. 71). Interstriae 1–6 are generally flat (For convenience, the space between the elytral suture and first stria is here considered the first interstria). The anterior ends of the first (sutural) interstriae are usually depressed to some degree. In a few species (most notably *B. puncticollis*, Fig. 59), the anterior ends of interstriae 2 and 3 are conspicuously raised and tumid. Not uncommonly, the anterior edges of various interstriae (most commonly the 3rd and 5th, Fig. 8) each bear a minute, round, often acute tubercle, sometimes obscured by the posterior margin of the pronotum; but the variability of these tubercles renders them only minimally useful taxonomically.

Boreocanthon possess nine elytral striae. The discal striae (1–6) are superficial, not perceptibly impressed, and usually extend to the elytral apex; the lateral striae (7–9) vary in definition. In a few species (especially *B. puncticollis*, Fig. 59, 61), the strial margins are carinulate and the striae thus sharply marked; in most, the strial margins are not sharply defined and the striae appear somewhat effaced ("fuzzier"). The 7th (humeral) stria is effaced basally where it would cross the umbone, and extends from the umbone to the elytral apex. In several species the 8th (subhumeral) stria can be marked by a fine carina extending from near the base to a point mid-way or beyond the length of the elytron (Fig. 81, 88, arrow). The 9th (epipleural) stria, if not effaced, is expressed only posteriorly in the narrow space between the 8th stria and upper edge of the elytral epipleuron.

Abdomen: The pygidium in *Boreocanthon* is completely margined and always separated from the propygidium by a transverse ridge; its apex is commonly raised and more convex than the rest of the surface (Fig. 6). In two species, *B. ebenus* (Fig. 27) and *B. depressipennis* (Fig. 14), the basal area of the pygidium is strongly impressed (concave) on either side of the midline. Sculpturing of the pygidium mimics that of the pronotum, although it is usually more weakly expressed; punctures, if present, often bear very short, minute setae visible only at a steep angle under higher magnification (25×).

The last (6th) ventrite (visible abdominal sternum of Edmonds (1972)) is usually sculptured like the pronotum; its posterior margin is broadly, weakly emarginate in the male and more-or-less straight in the female, although the difference is often subtle and difficult to assess. Ventrites 1–5 always exhibit weaker sculpturing than the 6th, especially medially.

Male genitalia: I here use the term genital capsule (sensu Edmonds (1972)) to refer to the sclerotized, tubular structure enclosing the penis/endophallus and consisting of a tubular base and pair of apical appendages, the parameres; it is very often referred to (including by me) as the aedeagus (but see Lawrence et al. 2010). In all *Boreocanthon*, the parameres are laterally flattened, obliquely truncated and closely appressed apically; their lateral profile and lower angles of the apical margin (viewed caudally) can assume species-characteristic shapes (cf. Fig. 50, Fig. 56–57 and Fig. 77). The form of the parameres in *Boreocanthon* is shared by *Melanocanthon* (Robinson 1948) and *Bajacanthon* (Halffter et al. 2022); that of the pilularius group of *Canthon* is quite distinctive, the lower apical angle being extended as a finger-like appendage (Fig. 43). The endophallus and its components were not examined for this study.

Female genitalia: The paraprocts (genital plates of Martínez-Morales and Morón (2015); see also Cristóvão and Vaz-de-Mello (2020)) of the female are elongate, apically rounded and slightly twisted appendages arising below the genital opening. Their cupped apical margins (Fig. 80, arrow *a*) appear to form a curved shelf that combines with the semicircular emargination of the marginal flange of the pygidium (Fig. 80, arrow, and Fig. 21, asterisk), presumably forming a guide for engaging the parameres. The paraprocts of *Boreocanthon* were not examined systematically for this study, but they appear to vary in ways that could later prove to be taxonomically useful.

Systematics

Genus *Boreocanthon* Halffter, 1958, restored generic status

Boreocanthon Halffter 1958: 208 (as genus)

Canthon (*Boreocanthon* Halffter) (downgraded to subgenus of *Canthon* Hoffmannsegg per Halffter and Martínez 1977: 81)

Type species. *Ateuchus ebenus* Say, 1823, by original designation (as *Canthon ebenus* [Say]).

Summary diagnosis. North American dung beetles, ball-rolling species attracted to a wide range of animal feces; usually dark or black in color, small-sized (length usually 4–7 mm); head margin conspicuously quadri- or sexdentate; parameres compressed laterally, truncate apically, lacking elongate projection of lower apical angle; hind femora lacking fine carina along anterior edge; metatibia with single apical spur.

Diagnosis. Dorsum (head + pronotum + elytra + pygidium) shagreened (alutaceous), with either punctures (Fig. 38, 48, 75, 105) or raised granules (Fig. 8. 19), punctures often accompanied by field of faintly lustrous microspotting (Fig. 61, 88); pterothoracic and abdominal sclerites shagreened, usually with accompanying flattened granules or punctures. *Head*: Clypeus quadridentate (Fig. 20, 66, 79, 112) (sometimes virtually bidentate in *B. coahuilensis*, Fig. 47); paraocular areas often also angulate such that head appears sexdentate (Fig. 66, 79). Clypeal teeth reflexed, surface behind concave, finely rugose and often somewhat shinier than rest of head surface, which is usually punctate on shagreened background. Clypeal process a low, transverse ridge. Labiogular fimbria always setose, often V-shaped, usually with associated field of coarse punctures at midline (Fig. 60, 69). *Prothorax*: Subapical tubercle beneath anterior angle of pronotum usually absent. Hypomeral carina usually absent (Fig. 24), sometimes partially developed but never long, extending at most only one-fifth to one-quarter of distance to edge of prothorax (Fig. 40, 108, arrow). *Legs:* Protibia strongly tridentate, usually serrate along

lateral margin and between large teeth, inner margin smoothly curved (Fig. 104) or offset at level of basal tooth (Fig. 51). Anterior tibial spurs sexually dimorphic in most species: acute apically in female (Fig. 116a), unequally bifurcate apically in male (Fig. 116b); apex acute in both sexes in *B. ebenus* and *B. depressipennis* (Fig. 16). Posterior femora not margined anteriorly. Posterior tibiae with single apical spur. *Elytra*: Nine elytral striae; striae superficial, not impressed, lateral margins sometimes sharpened by fine carinulae (Fig. 61, 71); 9th (epipleural) stria, if distinct, effaced anteriorly; 8th (subhumeral) sometimes carinulate (Fig. 88, arrow); 7th and 8th sometimes almost effaced anteriorly (Fig. 99). Interstriae always shagreened, either microspotted or granulate, sometimes presenting distinct humeral puncturing; anterior ends of first elytral interstriae depressed below level of second interstriae; anterior ends of 2nd and 3rd interstriae sometimes swollen (Fig. 67, 111), otherwise discal interstriae flattened. *Genital capsule*: Distal portion of parameres laterally compressed, truncate, posterior edges straight, appressed, profile varies from abbreviated (Fig. 113) to elongate triangle (Fig. 85), lacking any curved elongation of the lower apical angle (as in Fig. 43a). *General*: Small, length rarely over 7.5 mm, usually 4.5–6 mm. North America from Trans-Mexican Volcanic Belt in southern Mexico, through the United States into far south-central Canada (Fig. 1).

Comments. *Boreocanthon* is here restored to its original status of genus because, like its close relative, *Melanocanthon*, it exhibits a distinguishing suite of morphological features (see Diagnosis) and a plainly North American distribution. I have not discovered any unique feature (synapomorphy) that both unites its 13 species and separates them from other "*Canthon*," sensu lato, and, therefore, I cannot argue with a high degree of confidence that the group is monophyletic. *Boreocanthon* and *Melanocanthon*, along with the *pilularius* species-group of *Canthon* (sensu Halffter 1961) constitute the endemic United States contingent of the North American fauna of deltochiline Scarabaeinae. All other deltochilines occurring in temperate North America, north of the Rio Grande, are recently arrived representatives of southern groups; these include *Deltochilum gibbosum* (Fabricius), *Pseudocanthon perplexus* (LeConte), *Canthon* (*Glyphrocanthon*) *viridis* (Palisot de Beauvois), *C.* (*Canthon*) *humectus* (Say), *C.* (*C.*) *indigaceus* LeConte and *C.* (*C.*) *cyanellus* LeConte.

Boreocanthon is closely related to *Melanocanthon*, and the two are sometimes confused in collections. The latter group, however, is distinguished by having two apical spurs on the hind tibia (rather than one) as well as, among other features, subtle differences in dorsal sculpturing and the shape of the head and sides of the prothorax and elytra, and a distribution largely confined to the southeastern quadrant of the United States, including the eastern one-half of Texas. There are presently four recognized species of *Melanocanthon*, but my informal impression is that there may be but three. A future, more rigorous look at *Melanocanthon* is very much in order. Halffter et al. (2022) recently created the subgenus *Bajacanthon* to accommodate the unique Baja California endemic species, *Canthon obliquus* Horn. In their phylogenetic analysis (*Melanocanthon* was not included) the new genus emerged as sister group to *Boreocanthon*, with which it shares several features, especially the form of the parameres (Fig. 44a,b).

Boreocanthon is a Nearctic taxon with deep Neotropical roots. The center of diversity of the genus is clearly the United States and adjacent northern Mexico, where it undoubtedly originated. It, as well as *Melanocanthon* and the *pilularius* species group of *Canthon*, are the only representatives of the Neotropical tribe Deltochilini that originated and diversified in the Nearctic. The historical biogeographic perspective proposed by Kohlmann and Halffter (1990) seems reasonable in the context of the results of this study: "The ancestor of *Melanocanthon-Boreocanthon* would have been distributed in northern Mexico and south-central USA, while the area was covered by tropical deciduous forest. By the end of Miocene the forest started to be replaced by grasslands and piñon-oak woodland, a process that was advanced in the Pliocene by the spread of pine forest and very recently the appearance of deserts. Most *Boreocanthon* species … live in this area, which leads us to think that this was the main evolutionary arena for this group. Nowadays, many of the species live in grasslands of the Great Plains … or in arid zones …" (p. 13). In the context of Gonzalo Halffter's theory of the Mexican Transition Zone (Morrone 2015; Halffter 2017; Halffter and Morrone 2017 and numerous references therein), the modern Nearctic taxa, including *Boreocanthon*, are the descendants of deltochilines among a wave of Neotropical immigrants that arrived in North America during early Cenozoic, where they originated and began to radiate during Miocene-Pliocene times. This early wave of taxa from the south produced the founding cenocron of Halffter's Mexican Plateau Dispersal Pattern, one of five distribution patterns comprising the biogeographical panorama of the

Mexican Transition Zone (Halffter and Morrone 2017). This cenocron included many other scarabaeines and other insects, including *Phanaeus*, whose biogeographical history in part parallels that of the *Boreocanthon* and other Nearctic deltochilines (Kohlmann and Halffter 1990; Halffter and Morrone 2017) as well as other groups (Edmonds 1994).

The distribution of the genus covers much of North America (Fig. 1). Of interest is the fact that the distributions of the member species of putative species pairs (*B. ebenus-B. depressipennis*, Fig. 28; *B. melanus-B. forreri*, Fig. 45; *B. puncticollis-B. integricollis*, Fig. 63; *B. probus-B. halffteri*, Fig. 82; and *B. simplex-B. coahuilensis*, Fig. 100) are allopatric or nearly so, which suggests a long history of vicariant/dispersal events punctuating the history of the group (see, for example, Gámez et al. 2016). The ecogeographic distributions of *Boreocanthon* species conform rather closely to the vegetation biomes depicted in Figure 2: *B. depressipennis* and most *B. probus*, to eastern coniferous open-canopy forests; *B. praticola* and *B. ebenus*, to mid-latitude steppe and prairie; *B. lecontei* and *B. integricollis* to arid south Texas shrubland; and *B. simplex* to the complex highly variable mosaic of biomes present west of the Rocky Mountains. Western populations of *B. probus*, as well as *B. halffteri*, have colonized west Texas/New Mexico steppe and desert shrub habitats. All the Mexican species (*B. melanus*, *B. forreri*, *B. ateuchiceps*, *B. coahuilensis*, and *B. puncticollis*) are associated with desert and desert shrub areas.

That the diversity hotspot for *Boreocanthon* lies in the southwestern portion of the United States is unsurprising in that it is the focus of diversity for numerous vertebrate and invertebrate groups (see Parmenter et al. 1995). In this complex assemblage of arid and semi-arid range and basin habitats characteristic of western Texas, and southern New Mexico and Arizona, seven species come together: *B. puncticollis*, *B. melanus*, *B. ebenus*, *B. halffteri*, *B. simplex*, *B. praticola* and *B. probus*. Only two, however, are endemics: *B. halffteri* and *B. melanus*. For comparison, in the United States west of the Rocky Mountains north of about 34° latitude, an area much larger than the U.S. Southwest, is home to a single, albeit highly variable species, *B. simplex*. All other species, *B. lecontei*, *B. integricollis*, *B. depressipennis*, *B. coahuilensis*, *B. ateuchiceps* and *B. forreri* can be considered peripheral, relatively localized relatives of these seven. What this says about the biogeographical history of the genus is ripe for analysis.

Available data bespeak a group that is fundamentally coprophagous, with but very few records of attraction to carrion and none to fungi or other decomposing organic matter. Available information suggests the group to be almost exclusively coprophagous but highly generalist in food choice. Reported dung sources include a wide variety of wild and domestic animals: humans, hog, cattle, bison, horses, burros, deer, elk, rabbit, prairie dog, fox, bear, coyote, dog, domestic cat, javelina (collared peccary), opossum, chicken. In only one known instance does a species exhibit a preference for a particular food source: *B. praticola* (q.v.) for dung pellets of prairie dogs (*Cynomys* spp.). Zunino and Halffter (2007) report several casual associations between species of *Boreocanthon* and various vertebrate nests: *B. simplex* with ground squirrel (*Citellus*) burrows; *B. puncticollis* with packrat (*Neotoma*) and kangaroo rat (*Dipodomys*) nests. Presumably, all *Boreocanthon* conserve the ball-making/rolling (telocoprid) strategy characteristic of deltochilines (see Tonelli 2021). While there are some anecdotal observations that they do, I know of no formal corroborative studies on the feeding and nesting behaviors of any species of *Boreocanthon*.

Pollock and Lavigne (2019) reported that *B. praticola*, along with *Digitonthophagus gazella* (Fabricius 1787) and *Canthon floridanus* Brown, 1946 (until recently known as *C. imitator* Brown; see Génier 2019) are regular prey items for various species of robber flies (Diptera: Asilidae) in eastern New Mexico.

Robinson (1948) presented the first modern key to the species of this genus. He included the ten then-known species of *Boreocanthon* in the United States and his study heretofore has been the standard taxonomic reference for the group. *Boreocanthon* species group in his key to *Canthon* (couplets [0] through 2) on the basis of the following combination of characters: a) no [complete] hypomeral carina; b) anterior edge of hind femora not bearing a carina; and c) hind tibia with a single apical spur. As defined here, *Boreocanthon* embraces the thirteen valid species listed below. A total of 22 available and one unavailable species-group names, and their status as valid or otherwise, are assigned to the genus and listed below (original generic placement in parentheses; brackets enclose reference to designator; valid names and new nomenclatural actions are in bold type):

abrasus LeConte 1859c: 11 (*Canthon*)—jr. subj. syn. *probus* Germar [Horn 1870: 45]
antiguus Pierce 1946: 120 (*Canthon*)—jr. subj. syn. *simplex* LeConte [Miller et al. 1981:626]

***ateuchiceps* Bates** 1887: 35 (*Canthon*)—valid name
bisignatus Balthasar 1939: 229 (*Canthon*)—jr. subj. syn. *militaris* Horn, **new synonymy**
***coahuilensis* Howden** 1966: 732 (*Canthon*)—valid name
corvinus Harold 1868: 129 (*Canthon*)—jr. subj. syn. *simplex* LeConte [Horn 1870: 46]
***depressipennis* LeConte** 1859c: 11 (*Canthon*)—valid name
***ebenus* Say** 1823: 208 (*Ateuchus*)—valid name
ebeneus Say 1823: 208 (*Ateuchus*)—suppressed (see Comments for *ebenus*)
***forreri* Bates** 1887: 31 (*Canthon*)—valid name
***halffteri* Edmonds** (*Boreocanthon*)—**new species**
humeralis Horn 1870: 46 (*Canthon*)—jr. subj. syn. *simplex* LeConte [Robinson 1948: 87]
***integricollis* Schaeffer** 1915: 50 (*Canthon*)—valid name
***lecontei* Harold** 1868: 68 (*Canthon*)—valid name
***melanus* Robinson** 1948: 88 (*Canthon*)—valid name
militaris Horn 1870: 46 (*Canthon*)—jr. subj. syn. *simplex* LeConte [Robinson 1948: 87]
mixtus Robinson 1948: 91 (*Canthon*)—jr. subj. syn. *puncticollis* LeConte, **new synonymy**
nyctelius Bates 1887: 31 (*Canthon*)—jr. subj. syn. *puncticollis* LeConte [Schaeffer 1915: 50]
***praticola* LeConte** 1859c: 10 (*Canthon*)—valid name
***probus* Germar** 1823: 98 (*Ateuchus*)—valid name
***puncticollis* LeConte** 1866: 381 (*Canthon*)—valid name
***simplex* LeConte** 1857: 41 (*Canthon*)—valid name
vetustus Pierce 1946: 122 (*Canthon*)—jr. subj. syn. *praticola* LeConte [Robinson 1981: 626]

Key to the Species of *Boreocanthon* Halffter

Note. *Boreocanthon* comprises species that are often widely distributed and patently variable. The following key relies mostly upon generalizations about structure and, therefore, cannot be expected to accommodate inevitable exceptions. Reliability of identifications will be enhanced if target specimens are free or largely so of significant wear, especially to the head margin and to the dorsal surface. Since closely related *Boreocanthon* species are commonly allopatric, accurate locality information is an important corroborator of diagnostic structural features in this genus. The text page position for each species treatment is indicated in brackets following the species name.

1. Dorsal sculpturing (including the pygidium) consisting of coarse granulation on shagreen (alutaceous) background (Fig. 8, 13, 27); granules discrete, round, raised above surface, distinct punctures and shiny microspots lacking. Notch separating clypeus from paraocular area large, setting off tooth-like anterior angle of paraocular area such that head appears strongly sexdentate (Fig. 4, 11, 20) **2**

— Dorsal sculpture variable but not including discrete, raised, rounded granules; pronotum either punctate on shagreen background, or (*B. lecontei*, Fig. 31) covered by dense, fine granulation largely supplanting shagreen background. Dorsum (Fig. 48, 75) usually presenting shiny microspots, especially on pronotum (except *B. lecontei*), elytra and often also on head and pygidium. Paraocular areas and dentition variable **4**

2. Form of protibial spur same in both sexes, viz, strongly curved laterad and tapering to acute point (Fig. 20). Posterior portion of lateral pronotal margin asperate (serrate). Hypomeral carina absent (Fig. 24). Protibia (viewed along inner margin) abruptly widened (offset) at level of third (basal) tooth; inner apical angle produced as small, conical, apically-directed tooth (Fig. 16, arrow). Pygidium distinctly impressed basally, resulting transverse concavity often divided by median, longitudinal swelling (Fig. 14, 27). Compressed tip of parameres (viewed laterally) in form of elongate triangle (Fig. 18) **3**

— Protibial spur sexually dimorphic: strongly curved laterad and tapering to acute point in female; nearly straight to curved laterad, apically slightly expanded and obliquely truncated or asymmetrically notched in male (as in Fig. 116a,b). Posterior portion of lateral pronotal margin smooth. Hypomeral carina present, sometimes only slightly developed. Protibia usually only gently sinuous at level of basal tooth. Pygidium evenly convex, not impressed basally (Fig. 6). Compressed tip of parameres short, truncated.

Length 5–10.5 mm. Very widely ranging from south central Canada to northern Mexican Plateau, extending westward into eastern Arizona (Fig. 10) ..... ***Boreocanthon praticola* (LeConte) [p. 13]**

3. Pronotal granules uniform in size and shape, evenly and densely distributed and seldom coalescent (Fig. 11, 13b). Surface granulation extending to pteropleura but much weaker on median area of metaventrite and absent or only weakly evident on abdominal ventrites. Circumnotal ridge becoming very fine posteriorly, extending around posterior pronotal angle mesally to point adjacent to 7th or 8th elytral stria (Fig. 13b, arrows). Dorsum dark but almost always presenting metallic green coloration (viewed under bright light). Length 6–10 mm. Southeastern United States from Louisiana to North Carolina (Fig. 28) .... ***Boreocanthon depressipennis* (LeConte) [p. 18]**

— Pronotal granules larger, variable sized and frequently coalescent, especially on disk (Fig. 13a, 19). Surface granulation extending to pteropleura, at least anterior portion of median area of metaventrite, and at least sides of all abdominal ventrites. Circumnotal ridge ending at posterior pronotal angle, not extending onto posterior pronotal margin (Fig. 13a). Black, only very rarely with any hint of color. Length 6–11 mm. United States west of Mississippi River to Rocky Mountains with southwestern extension through Texas to southeast Arizona (Fig. 28) ..... ***Boreocanthon ebenus* (Say) [p. 20]**

4. Pronotum very finely, densely granulate, granulation highly coalescent largely supplanting shagreen background; punctures absent (Fig. 29–31). Paraocular notch very small, sometimes almost obsolete, scarcely if at all breaching raised lateral margin of head (Fig. 29, 32). Smaller beetles, overall length not exceeding 5 mm. Southern Texas and northern Tamaulipas (Fig. 100) ... ***Boreocanthon lecontei* (Harold) [p. 26]**

— Pronotum distinctly punctate, usually on distinctly shagreen background, punctures can be bold or very fine and widely dispersed such that pronotal surface appears almost smooth; pronotum never granulate. Paraocular notch variable **5**

5. Dorsum bright metallic green, often with yellow or coppery highlights (Fig. 36–39). Pronotum strongly but not densely punctate, shiny, shagreen background mostly effaced, sometimes detectable in isolated patches near anterior angles (Fig. 38). Upper surface of head strongly roughened by large, closely packed, coalesced punctures. Length 4.5–6.0 mm. Sierra Madre del Sur, Mexico (Fig. 45) .... ***Boreocanthon ateuchiceps* (Bates) [p. 28]**

— Dorsum dark, usually black, sometimes with blue or green highlights (producing dark, metallic green color in *B. forreri*). Pronotum punctate, often finely and sparsely so; shagreen background and shiny spots distinct, only rarely obscured. Upper surface of head smooth, with subtle punctures except anterior portion of clypeus, which is usually distinctly roughened. Length variable. Distribution north of Transverse Volcanic Range in Mexico northward to southern Canada **6**

6. Paraocular notch obsolete, anterior angle of paraocular area never accentuated (Fig. 47, 52). Clypeal margin usually bearing four perceptible teeth, median pair short, broadly rounded, wider at base than long, lateral two always small and inconspicuous and sometimes virtually absent such that clypeus appears bidentate (Fig. 46–47). Pronotum (viewed in profile) strongly raised above level of elytra ("humpbacked," Fig. 53b). Protibia abruptly widened, inner margin offset at level of basal lateral tooth (Fig. 51). Larger sized, length 7–11 mm. Distribution restricted to northwestern flank of Sierra Madre Oriental in southwest Nuevo Leon/southeast Coahuila, Mexico (Fig. 101) .... ***B oreocanthon coahuilensis* (Howden) [p. 31]**

— Paraocular notch (in *unworn* specimens) evident, sometimes very small, more often excising head margin and setting off angular prominence of paraocular area; shape of head margin variable but always distinctly quadridentate or sexdentate. Pronotum (viewed in profile) most often evenly rounded and at most only slightly raised above level of elytra. Protibia only gradually widened toward apex, any offset only weakly indicated. Smaller, length generally less than 7 mm. Widely distributed in Mexico and the United States **7**

7. Lower apical angles of parameres expanded laterally as thin rounded or elongate flanges (Fig. 56–57, 68a). Margins of elytral striae 1–4 and sometimes also 5–6 sharply defined by carinulae extending from base

at least one-third total length (Fig. 71). Paraocular notch deep, setting off strong, angulate portion of paraocular area, head appearing clearly sexdentate (Fig. 62, 66) **8**

— Lower apical angles of parameres in form of elongate, distally rounded swellings (Fig. 77, 86, 93), not flanged. Margins of elytral striae either not carinulate, or only briefly so anteriorly and then in occasional specimens showing metallic highlights. Paraocular notch variable **9**

8. Ventral apical angle of parameres, viewed caudally, with ear-shaped, rounded or slightly angulate flanges (Fig. 56–57). Second and third elytral interstriae conspicuously swollen anteriorly, these raised areas flanking deeply impressed first interstriae (Fig. 59). Pronotum distinctly impressed posteromedially, resulting concavity almost smooth and contiguous with depression formed by first interstriae of elytra (Fig. 55). Epipleural (9th) stria usually visible posteriorly. Mesoventrite at most with few central punctures. Dorsum, viewed in bright light under magnification, with strong, royal blue (very rarely green) undertone (intensified when surface is wet). Length 4.0–6.5 mm. Baja California del Sur, the Mexican Plateau and adjacent areas of Arizona, New Mexico and western Texas (Fig. 63) . . . . . ***Boreocanthon puncticollis* (LeConte) [p. 33]**

— Ventral apical angle of parameres, viewed caudally, in form of elongate flanges (Fig. 68). Second and third elytral interstriae usually not conspicuously swollen; pronotum lacking distinct posteromedian concavity. Epipleural (9th) stria effaced. Mesoventrite completely coarsely punctured (Fig. 70). Dorsum black, lacking strong blue undertone. Length 4.0–5.5 mm. Southern Texas and far northeast Mexico (Fig. 63) . . . . . ***Boreocanthon integricollis* (Schaeffer) [p. 38]**

9. Paraocular notch large, lateral margin of paraocular area strongly salient (Fig. 72, 74). Clypeal teeth large, acute. United States east of the Rocky Mountains and central New Mexico **10**

— Paraocular notch obscure, anterior angle of paraocular area interrupting curve of head margin as small, angulate corner (Fig. 92, 106, 112). Clypeal teeth obtuse, broadly rounded apically. Southeastern Arizona southward along coast of mainland Mexico to Nayarit **11**

Note. Couplet 10 separates taxa for which intermediate populations exist in west Texas and eastern New Mexico. Some specimens from Ward and Winkler Counties in Texas, and Eddy and Lea Counties in New Mexico can be difficult to sort morphologically; they are here regarded as *B. probus* on the basis of distribution. See Comments for *B. probus*.

10. Pronotum not at all or only weakly (narrowly) explanate anterolaterally. Paraocular notch narrow, setting off strong, anteriorly directed tooth, head strongly sexdentate (Fig. 72, 74). Anterior portion of head behind clypeal teeth often abruptly shinier and rougher than posterior portion, which is smooth and punctate over shagreen background (Fig. 79). Subhumeral (8th) stria simple or only weakly, if at all carinulate. Profile of compressed distal portion of parameres in form of equilateral triangular (Fig. 76). Length 4.0–5.5 mm. Eastern United States from Atlantic coast to Rocky Mountains roughly south of 41st parallel, Texas and New Mexico east of the Pecos River (Fig. 82) . . . . . ***Boreocanthon probus* (Germar) [p. 40]**

— Pronotum widely explanate, upturned narrowly at lateral angle and progressively more widely so toward anterior angle (Fig. 84, 87). Paraocular notch setting off transverse anterior margin of paraocular area, head strongly quadridentate (Fig. 83, 89). Anterior portion of clypeus dull, only rarely weakly shinier than rest of head surface (Fig. 89). Subhumeral (8th) elytral stria carinulate, usually sharply so from umbone to midpoint of elytral margin or slightly beyond (Fig. 88, arrow). Compressed distal portion of parameres, viewed laterally, in shape of elongate triangle (Fig. 85). Length 4.5–6.5 mm. Rio Grande drainage of New Mexico and Texas from Albuquerque southward to El Paso and Chihuahua (Fig. 82, inset) . . . . . ***Boreocanthon halffteri*, new species [p. 45]**

11. Median clypeal teeth broadly rounded, lateral clypeal teeth small, length less than half that of median teeth; margin of head appearing quadridentate (Fig. 92). Pronotal puncturing usually only weakly indicated, only occasionally conspicuous (×10). Subhumeral (8th) elytral stria never carinulate (Fig. 99); striae 7 and 8, sometimes also 6, often noticeably weaker than discal striae, anterior one-half or more of 7th and 8th sometimes nearly effaced. Compressed distal portion of parameres (viewed laterally) triangular (Fig. 94). Widely distributed in the western United States and Canada from the Rocky Mountains westward

to Pacific coast, extending northward to southern British Columbia and southward to northwestern Baja California (Fig. 100–101) ..... ***Boreocanthon simplex* (LeConte) [p. 48]**

— Median clypeal teeth rounded or acute, lateral teeth prominent, length at least one-half that of median teeth, margin of head hardly sexdentate (Fig. 106, 112). Pronotal puncturing always conspicuous (×10; Fig. 105). Subhumeral (8th) elytral stria always at least finely carinulate (Fig. 107, 115); elytral striae usually uniform, although base of 7th usually effaced at elytral umbone. Compressed distal portion of parameres (viewed laterally, Fig. 113) very short, truncate ("snub nosed"). Southern Arizona and west coast of mainland Mexico **12**

12. Dorsum dark metallic green or yellow-green, rarely black; venter with green reflections on legs and pleura (Fig. 102–103, 107). Anterior ends of 2nd and 3rd elytral interstriae not swollen or only very weakly so (Fig. 102–103). Western coast of mainland Mexico from far southern Sonora to Nayarit (Fig. 45) ..... ***Boreocanthon forreri* (Bates) [p. 56]**

— Dorsum and venter black, often with green or blue sheen (intensified when surface is wet). Anterior ends of 2nd and 3rd elytral interstriae distinctly swollen (Fig. 110–111). South-central Arizona southward into northwestern Sonora (Fig. 45) ..... ***Boreocanthon melanus* (Robinson) [p. 58]**

Species Treatments

Boreocanthon praticola (LeConte, 1859), restored generic combination

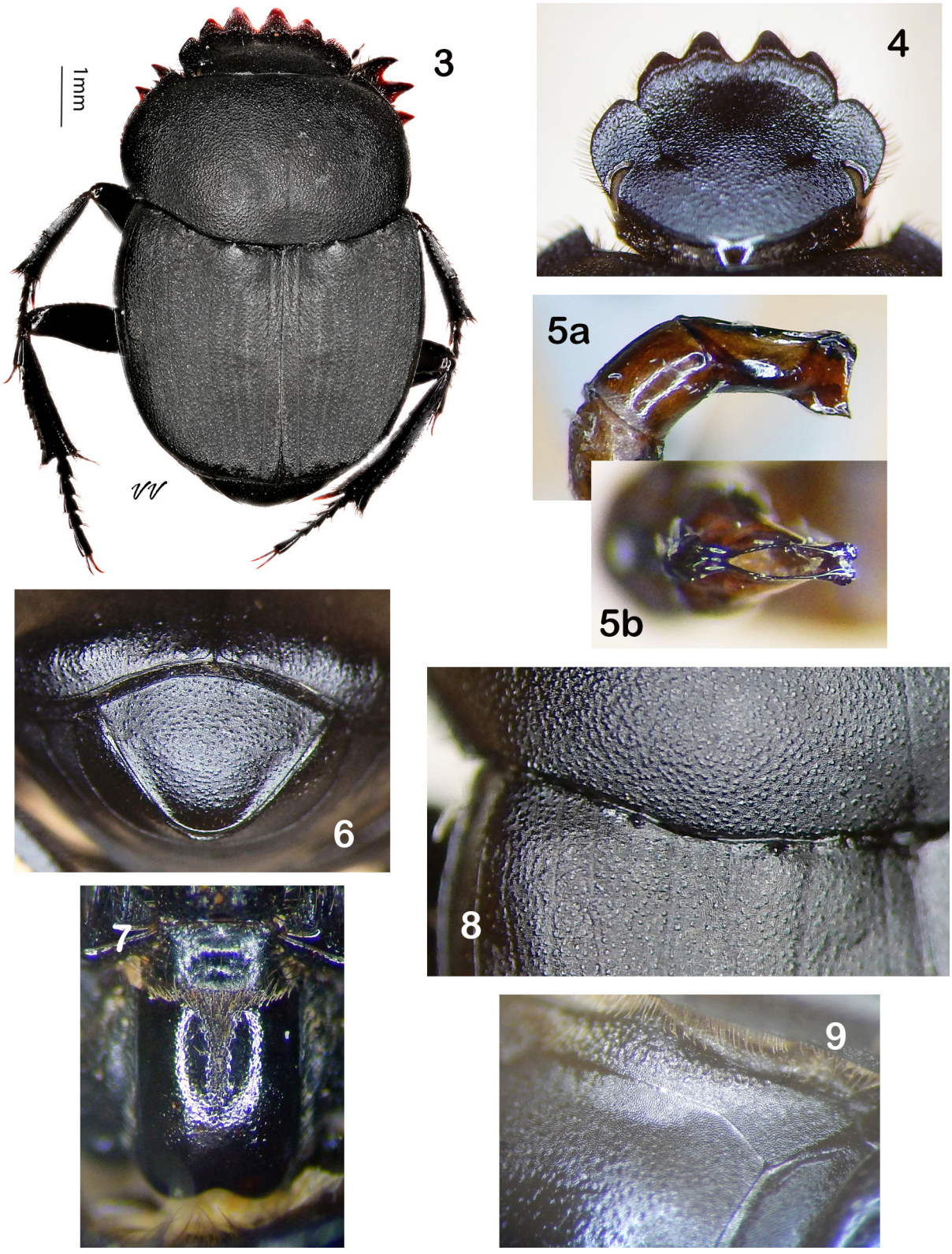
Fig. 3–10

Canthon praticola LeConte 1859c: 11.
Canthon praticola vetustus Pierce 1946: 122 (new synonym per Miller et al. 1981: 626).
Boreocanthon praticola (LeConte) (new combination per Halffter 1958: 210).
Canthon (*Boreocanthon*) *praticola* LeConte (new combination per Howden 1966: 727).
Boreocanthon praticola (LeConte), **restored generic combination**.

Type material. 1) *Canthon praticola* LeConte: syntype (female). Museum of Comparative Zoology, Cambridge (MCZ-ENT00003697). Examined by photograph (https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:3697); **2)** *Canthon praticola vetustus* Pierce (sex undetermined): holotype (sex undetermined). Los Angeles County Museum of Natural History, LACMIP 2592. Not examined.

Type localities. 1) *Canthon praticola* LeConte: Kansas and New Mexico; **2)** *Canthon praticola vetustus* Pierce: Rancho La Brea, Tar Pit 81, Hancock Park, Los Angeles, California.

Diagnosis. *Head*: Granulorugose anteriorly, becoming distinctly granulate on vertex; granules small, surface evenly reflective (Fig. 4). Median pair clypeal teeth rounded, lateral teeth subangulate (Fig. 4). Paraocular notch conspicuous, acute, setting off angular projection of paraocular area, head appearing sexdentate (Fig. 4). Labio-gular fimbria (Fig. 7) gently curved posteriorly, interrupted medially by narrow, elongate field of coarse, setigerous punctures extending one-half length of gula. *Prothorax*: Pronotum (Fig. 3, 8) completely, evenly granulate on weakened shagreen background, granules irregularly shaped on disk, becoming rounded laterally. Anterior pronotal angles at most only weakly upturned, posterior portion of circumnotal ridge entire, not serrate. Hypomeral carina present, extending about one-fifth distance to lateral margin. *Pterothorax*: Mesoventrite (Fig. 9) rugose medially, smooth laterally. Metaventrite (Fig. 9) rather densely, sharply punctured. *Elytra*: Interstriae flat, shagreened, evenly granulate, granules uniformly rounded (Fig. 8). Striae superficial, lateral margins ill-defined; subhumeral (8th) stria often very finely carinulate along lower margin, epipleural (9th) stria rarely visible. *Legs*: Protibia evenly dilated, inner margin not offset. Protibial spurs sexually dimorphic (as in Fig. 116a, b). Metafemora lacking row of conspicuous setae along anterior margin. *Abdomen*: Pygidium (Fig. 6) weakly granulate, apex sometimes more conspicuously convex than base. Last (6th) ventrite weakly granulate; other ventrites smooth medially. *Genital capsule*: Distal portion of parameres attenuated, truncate (Fig. 5a); lower apical angle in form of elongate, rounded knob (Fig. 5b). *General*: Dull black, no hint colorful undertones anywhere. Length: 4.5–8.5 mm. *Geographic distribution* (Fig. 10): Great Plains from Canada to Texas, extending westward into southern New Mexico and Arizona into northern Mexico. *Ecogeographic environment* (Fig. 2): Temperate Grasslands, Savannas and Shrublands, and Deserts and Xeric Shrublands biomes. *Specimens examined*: 1750.



Figures 3–9. *Boreocanthon praticola* (LeConte). **3)** Dorsal habitus. **4)** Dorsal view of head. **5)** Genital capsule, a: lateral view, b: apical view. **6)** Posterior view of pygidium. **7)** Ventral view of mentum and gula. **8)** Dorsal view of union of pronotum and elytra. **9)** Oblique ventral view of meso- and metaventrites.

Collection localities.

CANADA—ALBERTA: *Cypress County* (*Mpal. Dist*.) ●Medicine Hat [Apr, Aug] ●Cypress Hills [Jun]; *Wheatland County* (*Mpal. Dist.)* ●Cluny [Jun]; *Ranchland Mpal. Dist.* ●36 km SW Longview, 50.264° -114.264°, 1400 m [May]. **MANITOBA**: *Mpal. Two Borders* ●Lyleton.

MEXICO—CHIHUAHUA: *Mpio. Cuauhtémoc* ●11 mi W Cuauhtémoc [Oct]; *Mpio. Huejotitán* ●Valle de Olivos, 5500 ft [Jul]; *Mpio. Janos* ●20 km W Janos, 30°50′33.8″ N 108°23′25.1″ W [Oct] ●80 mi NNW Casas Grandes [Aug]; ●45 mi NW Casas Grandes [Aug]; *Mpio. Juarez* ●Samalayuca [Jun] ●Samalayuca, Laguna de Riataso [Aug]; *Mpio. López* ●Salaices [Jul]; *Mpio. Matamoros* ●Mariano Matamoros, 6000 ft [Aug]; *Mpio. Metachí* ●Metachí [Aug]. **DURANGO**: *Mpio. Diez de Octubre* ●San Lucas, 6700 ft [Aug]; *Mpio. Lerdo* ●Cd. Lerdo; *Mpio. Ocampo* ●173 mi N Durango [Aug]. **SONORA**: *Mpio. Alamos* ●Alamos [Jul] ●San Bernardo [Jul]; *Mpio. Cananea* ●Cananea, 1525 m [Aug]; *Mpio. Hermosillo* ●Hermosillo [Jul]; *Mpio. Naco* ●Naco, 5000 ft [Aug].

UNITED STATES—ARIZONA: *Apache Co*. ●16–19 mi N St. Johns [Sep] ●Lyman Lake [Aug] ●6 mi N St. Johns, 34.5858° N 109.3288° W, 1720 m [Aug]; *Cochise Co*. ●2 mi SE Apache, 4400 ft [Aug] ●8.5 mi S Apache [Aug] ●Douglas [Jun-Sep] ●12 mi NE Douglas [Aug] ●1 mi E Douglas [Aug] ●McNeal [Sep] ●Sycamore Canyon, Peloncillo Mountains [Jul] ●8 mi E Portal [Jul, Sep] ●1 mi NE Portal [Sep] ●5 mi SW Portal, Southwest Research Station [Aug] ●Guadalupe Canyon [Jul] ●2.3 mi WNW Chiricahua [Jul]; ●22.5 and 36 mi SE Willcox [Jul]; ●5.8 km SE Willcox, 32°13′10″ N 109°46′51″ W [Aug] ●Willcox Playa [Jul-Aug] ●Chiricahua Mountains, mouth of Pinery Canyon, 5300 ft [Jun-Aug] ●Palominas [Aug] ●Texas Canyon [Aug] ●Dos Cabezas [Aug] ●Kansas Settlement [Jul]; ●Hereford [Jul] ●Huachuca ●Skeleton Canyon [Aug] ●10 mi NW Bisbee [Jul] ●Rustler Park [Aug]; *Coconino Co*. ●4.5 mi E Moenkopi [Jun] ●Tuba City [Aug] ●5 mi NE Cow Springs [Jul] ●Williams [Aug]; *Gila Co*. ●Pine ●Globe [Aug]; *Graham Co*. ●65 mi N Willcox, Deer Creek Ranch, Galiuro Mts. [Jul]; *Greenlee Co*. ●16 mi S Clifton [Aug] ●Franklin [Aug]; *Maricopa Co*. ●Webb [Jul] ●El Dorado [Jun]; *Pima Co*. ●Tucson [May, Aug] ●Boboquivari Mt. [Jul]; *Santa Cruz Co*. ●Patagonia [Aug-Sep] ●Sonoita [Jul] ●4 mi S Sonoita [Jul]; ●12 mi NE Sonoita [Jul, Sep]; ●10 mi SE Patagonia; ●3 and10 mi E Patagonia [Aug]; ●Santa Cruz River, 2.5 mi E Lochiel, 4500 ft [Sep]; ●Madera Canyon ●Coronado National Forest, Parker Canyon at FM 61, 4800 ft [Sep] ●Elgin [Sep]; *Yavapai Co*. ●17 mi W Jerome [Aug]; ●Seligman [Aug] ●Prescott Valley [Jul-Sep]; ●2 mi W Dewey [Oct] ●5 mi N Dewey [May] ● Hwy I-40, exit 103, Jolly Rd., 35°15.412′ N 113°10.090′ W, 5300 ft [May] ●Mayer [Aug]. **COLORADO**: *Conejos Co*. ●Antonito [Jun]; *Denver Co*. ●Denver [Jul]; *El Paso Co*. ●Colorado Springs [Jun, Oct]; *Huerfano Co*. ●Gardner [Jun]; *Jefferson Co*. ●Leyden [Aug]; *La Plata Co*. ●Durango [Jul]; *Larimer Co*. ●Ft. Collins [May]; *Mesa Co*. ●Mesa [Jul] ●10 mi NW Mack [Apr]; *Moffat Co*. ●Craig, 6200 ft [Jun]; *Morgan Co*. ●Hwy 52, 6.3 mi N Fort Morgan [May]; *Prowers Co*. ●Lamar [Aug]; *Weld Co*. ●Greeley. **KANSAS**: *Barber Co*. ●10.5 km W Hardtner, 37.02047 -98.76700 [Sep] ●2mi W Hardtner [Nov]; *Clark Co*. ●(no data), 1962 ft [Jun]; *Gove Co*. (no data); *Gray Co*. (no Data); *Hamilton Co*. ●Syracuse [Jun]; *Kiowa Co*. ●10 mi NW Mullinville [Jun] ●13 mi S Greensburg [Jan-Feb, Apr, Jul]; *Logan Co*. (no data); *Meade Co*. ●Meade [Jul]; *Morton Co*. (no data); *Norton Co*. ●Prairie Dog State Park [May]; *Reno Co*. ●Medora [May]; *Republic Co*. ●Kakley [Jul]; *Sheridan Co*. (no data) *Thomas Co*. Colby [May]; *Wallace Co*. (no data) [Jul]. **MONTANA**: *Beaverhead Co*. ●Dillon [Apr-May] ●Bond [Aug] ●P&O Ranch [Aug] ●Blacktail Creek [Aug]; *Big Horn Co*. ●Lodge Grass [Jun]; *Blaine Co*. ●Chinook [Jul]; *Cascade Co*. ●Great Falls [May]; *Chouteau* Co. ●15 mi S Loma [Jun]; *Custer Co*. ●4 mi S Miles City [Aug]; *Fergus Co*. ●Suffolk [Jun]; *Gallatin Co*. ●Bozeman [May-Jul] ●20 mi N Bozeman [Jun] ●Three Forks [Jul]; *Glacier Co*. ●Glacier National Park [Jul]; *Jefferson Co*. (no data) [Mar]; *Judith Basin Co*. ●Hobson [Aug]; *Madison Co*. (no data) [Jun]; *Petroleum Co*. 3 mi NW Winnett [Sep]; *Teton Co*. ●Bynum [Jul]; *Yellowstone Co*. ●Broadview [Jul]. **NEBRASKA**: *Buffalo Co*. ●10 mi W Amherst, 40.859° N 99.380° W, 715 m *Chase Co*. ●Imperial [Jul]; *Cheyenne Co*. ●3mi SE Lodgepole [Aug]; *Dundy Co*. ●Sanborn, 5 mi W Haigler, 40.06°W 102.02° W, 1010 m ●4 mi E Haigler, 40°01′25″ N 101°51′36″ W, 285 m [Aug]; *Frontier Co*. ●Red Willow Reservoir State Wildlife Management Area, 40.40° N 100.68° W, 800 m [May]; *Greeley Co*. ●7.3 mi S Greeley [Apr]; *Keith Co*. ●Lake McConaughy [May, Jul, Sep] ●5mi S, 2 mi W Paxton [Jul]; *Morrill Co*. ●8 mi W Bridgeport, 41.68° N 103.25° W, 1130 m [Jul]; 2.7 mi W Bridgeport [May]; *Red Willow Co*. ●McCook [May]; *Sioux Co*. ●42°54′59.88″ N 103°45′35.82″ W, 1125 m *Thomas Co*. ●Nebraska National Forest, Whitetail Campground, 41.79413 -100.27381 [Sep]. **NEW MEXICO**: *Bernalillo Co*. ●Albuquerque [Aug]; *Catron Co*. ●Luna; *Chaves Co*. ●Bottomless Lakes State Park [Jun]; *Colfax Co*. ●Maxwell [Jul] ●Koehler [Jul]; *Doña Ana Co*. ●Jornada Range [Jul] ●Isaack Lake [Jul]; *Hidalgo Co*. ●Lordsburg [Jul] ●40 mi S Lordsburg [Jul] ●1.5 mi NE Rodeo [Jul]; ●39 mi SW Animas [Sep] ●Rodeo, 4000 ft [Jul-Aug]

●34 mi S, 3 mi W Animas [Sep] ●8 mi S Animas [Jul] ●32 mi S Animas, Double Adobe Ranch, 5500 ft [Jul-Aug]; *Luna Co*. ●7.5 mi W Akela Flats [Jul] ●Deming [Aug]; *Roosevelt Co*. ●8 mi NE Portales, ENMU Natural History Preserve [Apr, Jul]; *Sandoval Co*. ●La Ventana, Jemez Mountains, 7200 ft [Jul]; *San Juan Co*. ●Aztec; *Santa Fe Co*. ●Santa Fe [May, Jul]; *Socorro Co*. ●20 mi E Bernardo, 34°02.4′ N 106° 36.49′ W, 1607 m [Sep] ●Sevilleta National Wildlife Reserve [Aug]; *Union Co*. ●8 mi N, 2.5 mi W Sofia (Kimble Ranch) [Sep]●10 mi S, 0.5 mi E Sofia (Britt Ranch) [Sep]. **NORTH DAKOTA**: *Billings Co*. ●South Unit, Theodore Roosevelt National Park [Apr]; *Morton Co*. (no data); *Richland Co*. (no data). **OKLAHOMA**: *Comanche Co*. ●Wichita Refuge [Aug]; *Noble Co*. ●(no data); *Payne Co*. ●(no data) [Aug]. **SOUTH DAKOTA**: *Custer Co*. ●Custer State Park [Jun]; *Jackson Co*. ●vicinity

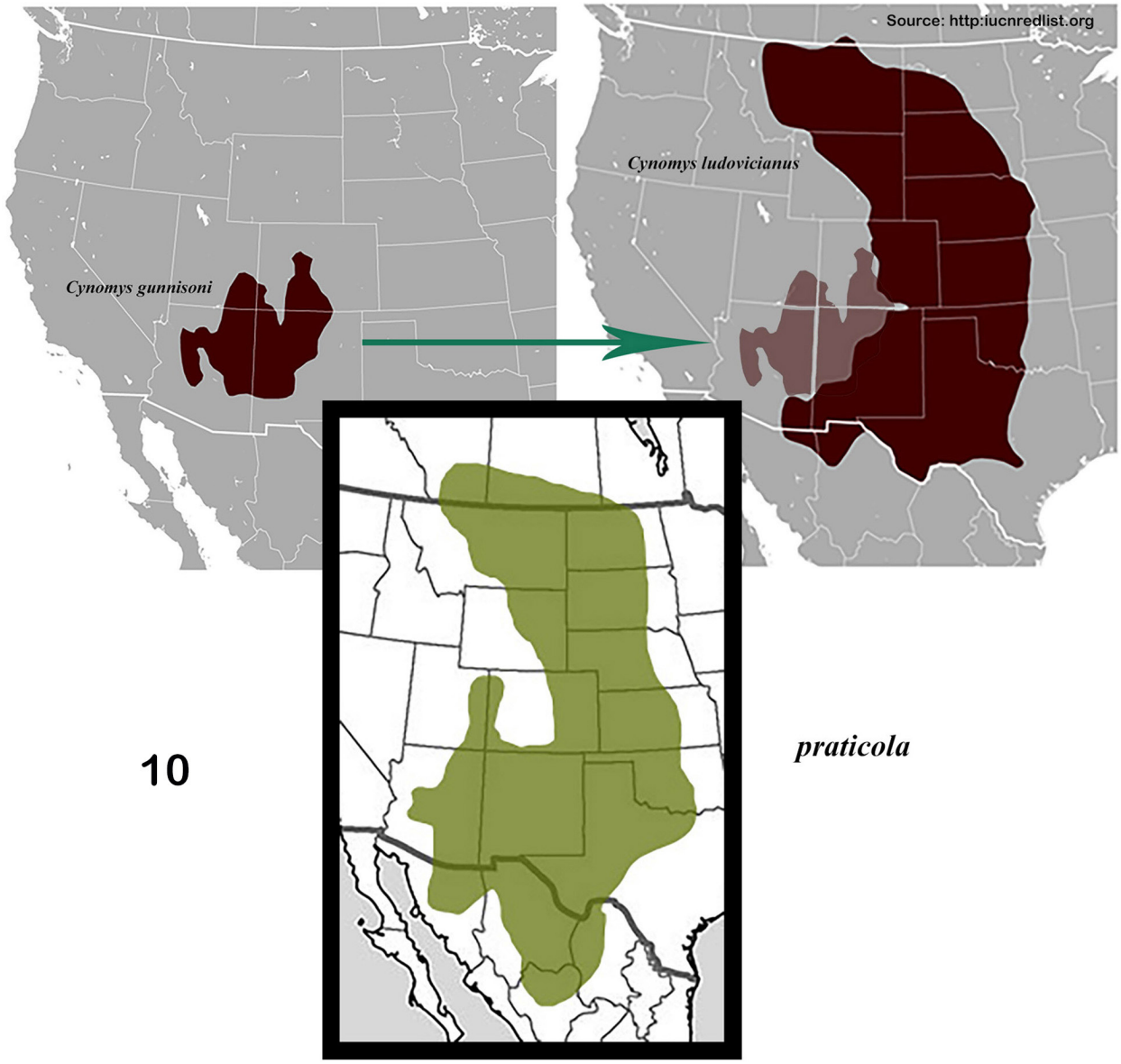


Figure 10. *Boreocanthon praticola* (LeConte). Upper diagrams depict consolidation of ranges of the prairie dog species, *Cynomys gunnisoni* and *C. ludovicianus*. Inset depicts approximate distribution of *B. praticola*.

Badlands National Park [Jun]; *Pennington Co*. ●Hill City [Sep]; *Perkins Co*. ●Grand River National Grasslands [Aug]. **TEXAS**: *Brewster Co*. ●Alpine [Jun] ●7 mi NW Alpine [Jun] ●Marathon [Jun]; *Callahan Co*. ●Baird [Jun]; *Culberson Co*. (no data); *Dallam Co*. ●Perico [Aug]; *Dallas Co*. ●Dallas; *Dawson Co*. ●Lamesa [May]; *Jeff Davis Co*. ●Ft. Davis [Jul-Aug] ●Valentine [Jun]; ●8 mi SE Valentine [Jul] ●16 km S Fort Davis (along TX 17), 30°27′48″N 103°58′59″W, 1600 m (Aug); ● ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs), 30°40′50″N 104°20′22″W, 1555 m (Jul); ● ~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs, near headquarters), 30°40′28″N 104°24′07″W, 1475 m (Jul); *Lubbock Co*. ●Lubbock [Aug] ●Ransom Canyon [Sep]; *Presidio Co*. ●Marfa [Jun] ●37 km SSW Marfa (along FM 2810, Petan Ranch – Cherry Hills sector), 30°07′35″N 104°19′24″W, 1630 m (Jun); ●20–26 km SSE Marfa (along FM 169), 1355–1415 m (Jun); ●8 km W La Viuda Peak, 29°42′30″N 103°54′30″, 1200 m (Sep) ● ~16 km W Valentine (Miller Ranch, near headquarters), 30°33°30″N 104°38′44″W, 1350 m (Jul–Aug); ● ~6.5 km W Marfa (Hip-O Ranch), 30°21′54″N 104°07′12″W, 1530 m (Aug–Sep) ●4 mi SE Presidio [Jul]; *Reeves Co*. ●Toyah [Jun]; *Wichita Co*. ●Foster Ranch [Aug]; *Wilbarger Co*. ●Vernon [Aug]. **UTAH**: *Duchesne Co*. ●Monument Butte, near Myton [Jul]; *San Juan Co*. ●Blanding [Jul] ●9.7 mi ENE Monticello, 2063 m [May]. **WYOMING**: *Albany Co*. ●Laramie [Jun]; *Crook Co*. ●4 mi N Sundance [Jun] ●Devil's Tower National Monument [Jun]; *Laramie Co*. ●Cheyenne [Jul]; *Sheridan Co*. ●25mi E Sheridan [Jun].

Comments. *Boreocanthon praticola* is a very common, widespread species often confused with *B. ebenus*, from which it is easily distinguished by its convex (not impressed basally) pygidium and sexually dimorphic protibial spurs. The two are widely sympatric where cool (elevations >1200 m south, >800 m north) grasslands are punctuated by enclaves of vegetated sand habitat. Because it conserves a macrogranulated sculpture as well as dimorphic protibial spurs, I regard it a taxonomic isolate and annectant between *B. ebenus-B. depressipennis* (granulate dorsum) and rest of genus (sexually dimorphic protibial spurs). *Boreocanthon praticola* is subject to a considerable amount of variation, especially in size and surface texture — smaller individuals are routinely more finely granulose and require close inspection (10×). Populations from northern portions of its range (Nebraska north and northwestward) tend to be smaller and with finer dorsal granulation. I have examined specimens labeled Brazoria Co., Texas, and Benton Co, Arkansas; I consider them records that require corroboration.

Pierce's (1946) fossil taxon, *Canthon praticola vetustus* (along with *B. simplex*, q.v.) was collected from substrate drawn from Pit 81 of the Rancho La Brea Tar Pits in Los Angeles, California, excavated in 1915 (Miller et al. 1981; Miller 1986); co-occurring *Equus* remains were later dated ca. 11,000 years BP (Miller 1986). Pierce's decision to place it near *B. praticola* is clearly reasonable inasmuch as the holotype (an elytron) is of the proper size (4.5 mm) and exhibits the dual granulation one would expect of this species. Moreover, while it does not presently occur west of Arizona, the presence of *B. praticola* at La Brea from the Pleistocene/Holocene boundary (ca. 11,000 years BP) is a reasonable assumption. The scarabaeine fauna at that time included at least *Canthon*, *Copris*, *Onthophagus* and *Phanaeus* (Pierce 1946, Miller 1983, Edmonds 1994). At the time, when the biotic landscape was quite different than now, the scarabaeine fauna of southern California was evidently very similar to the modern fauna of southern Arizona.

Ample evidence suggests that *B. praticola* maintains a strongly preferential association with prairie dogs. Indeed, its US distribution corresponds rather closely to the combined ranges of Gunnison's Prairie Dog, *Cynomys gunnisoni* (Baird, 1855) and the more widespread Black-Tailed Prairie Dog, *C. ludovicianus* (Ord, 1815) (Fig. 10). Field studies by Gordon and Cartwright (1974) in North Dakota and Colorado revealed that these beetles are commonly found in mounds surrounding burrow entrances where dung pellets were plentiful; they observed no activity in nearby bison droppings. James Saulnier (pers. comm.) has collected specimens in large numbers from active prairie dog colonies in northern Yavapai Co., Arizona. Floate and Gill (1998) found *B. praticola* to be a rare member of the cattle dung beetle community in southern Alberta, Canada, a coprofauna overwhelmingly dominated by aphodiines. Other than prairie dog droppings, *B. praticola* has been recorded from cattle feces as well as that of pig, bison, humans and rabbits. Edmonds (2018) reported *B. praticola* from open grasslands of the Big Bend region of west Texas, where it is commonly collected on cattle and human feces. McNamara (2013) recorded *B. praticola* from four Canadian provinces: Alberta, Saskatchewan, Manitoba and British Columbia; the latter, while not out of the question, needs confirmation.

In addition to the syntype cited above, there is another probable syntype also present in the LeConte Collection at the Museum of Comparative Zoology, Harvard University (Crystal Maier, pers. comm).

Boreocanthon depressipennis (LeConte, 1859), restored generic combination

Fig. 11–18, 28

Canthon depressipennis LeConte 1859c: 11.
Boreocanthon depressipennis (LeConte) (new combination per Halffter 1958: 209).
Canthon (*Boreocanthon*) *depressipennis* LeConte (new combination per Howden 1966: 727).
Boreocanthon depressipennis LeConte, **restored generic combination**.

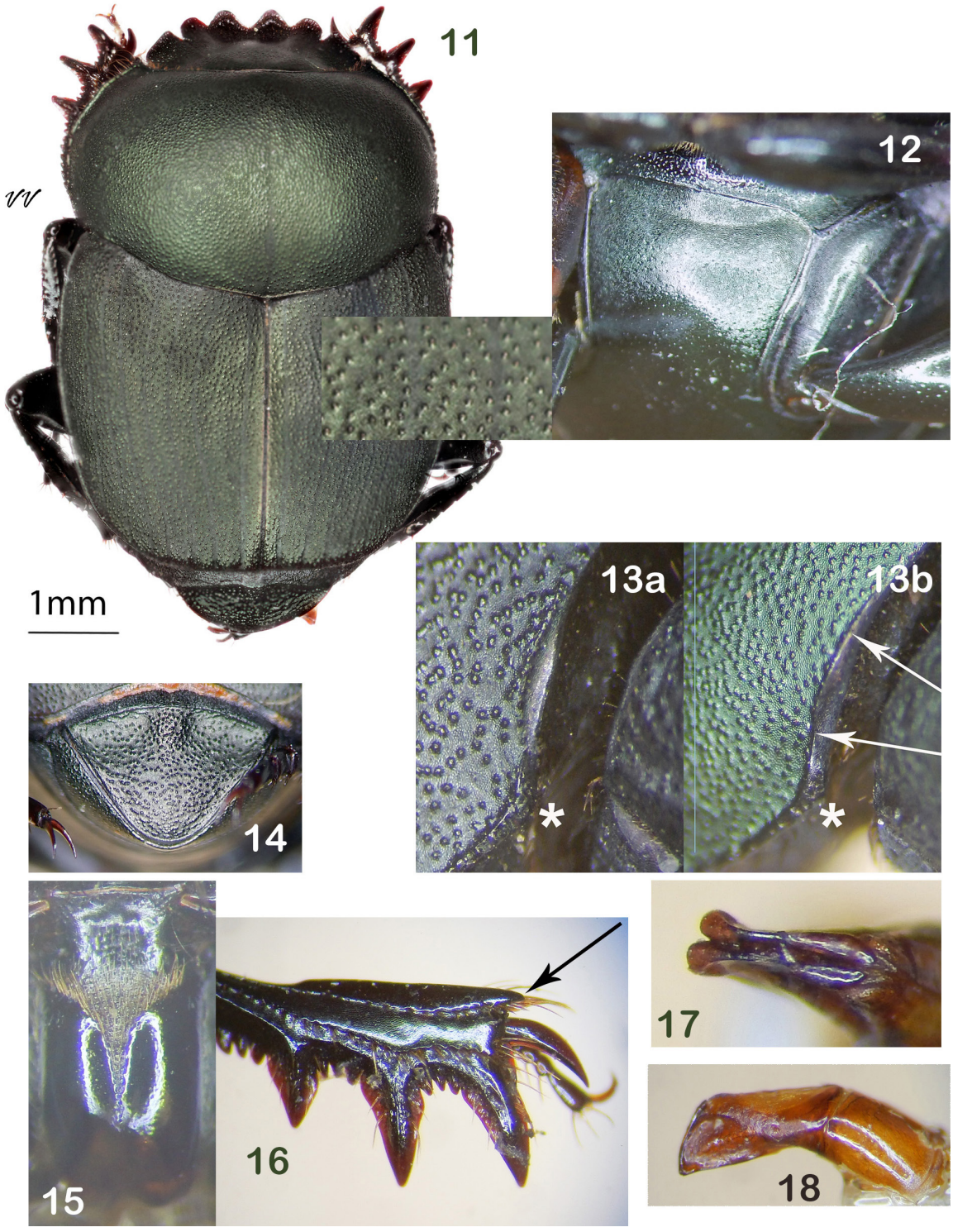
Type material. Syntype (sex undetermined), Museum of Comparative Zoology, Cambridge (MCZ-ENT00003696). Examined by photograph (https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:3696).

Type locality. Georgia.

Diagnosis. *Head*: Anterior portion of clypeus finely roughened, only slightly shinier than rest of head; posterior portion evenly granulate on shagreen background. Sexdentate (Fig. 11); clypeus with four strong teeth, paraocular notch deep, setting off dentate anterior angle of paraocular area. Labio-gular fimbria (Fig. 15) widely V-shaped, strongly narrowed medially, length exceeding one-half that of gula. *Prothorax*: Evenly, rather densely covered by smaller, rounded granules, granules isolated, only rarely coalescent (Fig. 11, 13b). Anterior pronotal angles not upturned; circumnotal ridge serrate posterolaterally, ridge extending beyond posterior angle to point even with elytral umbone (Fig. 13b, arrows). Hypomeral carina obsolete or only feebly indicated. *Pterothorax*: Mesoventrite densely, finely punctate medially, smooth laterally. Metaventrite (Fig. 12) with obsolete granules and scattered, minute punctures on shagreen background. *Elytra*: Interstriae (Fig. 11) evenly, rather densely granulate on shagreen background; 2nd and 3rd weakly raised. Striae superficial, edges ill-defined, course determined by lack of granulation (tracks through field of granules). Suhumeral (8th) stria not carinulate; epipleural (9th) clearly indicated. *Legs*: Inner margin of protibia (Fig. 16) clearly offset at level of basal (3rd) tooth, prolonged apically as conical tooth (Fig. 16 arrow). Protibial spur (Fig. 16) acute, curved mesally in both sexes. Hind femur lacking row of conspicuous setae along anterior margin. *Abdomen*: Pygidium (Fig. 14) depressed basally on each side of median swelling; evenly granulate. Sixth ventrite completely granulate; granules on remaining ventrites confined to lateral (upper) areas adjacent to elytral epipleuron. *Genital capsule*: Compressed, distal portion of parameres elongate, triangular (Fig.18), lower apical angles in form of elongate knobs (Fig. 17). *General*: Dorsum dark, often appearing black to unaided eye, almost always displaying dull green or yellow-green highlights under magnification. Length: 4.5 – 9.0 mm. *Geographic distribution* (Fig. 28): Southeastern United States, from eastern Louisiana to southern North Carolina, southward into the Florida peninsula. *Ecogeographic environment* (Fig. 2): Temperate Grasslands, Savannas and Shrublands biome (Southeast U.S. conifer savannas ecoregion). *Specimens examined*: 567.

Collection localities.

UNITED STATES—ALABAMA: *Dale Co.* ●Fort Rucker Military Reservation [May]. **FLORIDA**: *Alachua Co.* ●0.75 mi W Archer [Jun] ●4 mi N High Springs [Mar] ●10 mi SW Gainesville [Aug]; *Baker Co.* ●Glen St. Mary [Sep]; *Calhoun Co.* ●Clarksville [Mar]; *Citrus Co.* ●Inverness [May]; *Clay Co.* ●Camp Crystal (Mar-Apr]; *DeSoto Co.* ●27°19.356′ N 81°48.640′ W, 8 mi N Arcadia; *Dixie Co.* ●29°34.6′ N 82°58.3′ W, near Old Town ●3.7 and 5 mi N Old Town [May]; *Duval Co.* ●Jacksonville [Apr]; *Escambia Co.* ●Pensacola; *Flagler Co.* ●Hwy 1, 2 mi S Hwy I-95 [Oct]; *Gilchrist Co.* ●5 mi W Newberry (Alachua Co.) [Jun]; *Hernando Co.* ●Powell [Jul]; *Highlands Co.* ●Archbold Biological Station [Mar, Jun] ●Dover; *Hillsborough Co.* ●Tampa, University South Florida campus [May-Jun]; *Lafayette Co.* ●Picket Lake [Mar]; *Lee Co.* ●Hwy 41, 3.4 mi NW Koreshan State Park [Apr]; *Lake Co.* (no data); *Levy Co.* ●3.8 mi SW Archer [Mar]; ●2 mi W Archer [Jun]; ●Route 24, 0.2 mi S Alachua county line [Mar] ●Hwy 241, 1 km N Santa Fe River ●11 mi W Otter Creek [Nov]; *Liberty Co.* ●Apalachicola Bluffs & Ravines Preserve, Alum Bluff [Jul]; *Madison Co.* ●Pinetta [Aug]; *Okaloosa Co.* ●Valparaiso [Jul]; *Orange Co.* ●Walt Disney World [Aug]; *Putnam Co.* ●Red Water Lake [Jul]; *Saint Johns* ●St. Augustine; *Sarasota Co.* ●Myakka River State Park, 27°17.541′ N 82°17.420′ W [Sep]; *Seminole Co.* ●Econ River Wilderness Area [Jul]; *Suwanee Co.* ●7 mi N Live Oak [Mar]; *Taylor Co.* ●County Road 150, 5 mi W Hwy 19 [May]. (See also Woodruff for additional Florida records.) **GEORGIA**: *Baker Co.* ●Newton [Jun] ●Ichauway Ecological Reserve [Mar]; *Burke Co.* ●10.2 km NW Girard, Yuchi Wildlife Management Area, 33°05′36″ N 81°48′04″ W [Apr]; *Charlton Co.* ●Billys Island, Okefenokee Swamp [Oct] ●Camp Cornelia [May]; *Chatham Co.* ●12 km NNW Richmond Hill, 32°02′41″ N 81°20′13″ W [May]; *Cook Co.* ●Reed Bingham State Park [Jul]; *Decatur Co.* ●Spring Creek [Jul-Aug]; *Dodge Co.*



Figures 11–18. *Boreocanthon depressipennis* (LeConte). **11)** Dorsal habitus (inset magnifies elytral sculpturing). **12)** Oblique ventral view of meso- and metaventrites. **13)** Comparison of posterolateral margin of pronotum; asterisks mark posterolateral angle of pronotum; arrows mark posterior extension of circumnotal ridge in *B. depressipennis*. **a)** *Boreocanthon ebenus*. **b)** *Boreocanthon depressipennis*. **14)** Posterior view of pygidium. **15)** Ventral view of mentum and gula. **16)** Anterior view of protibia (arrow indicates apical tooth). **17**) Apical view of parameres. **18)** Lateral view of genital capsule.

●1.2 mi NE Gresston [Mar]; *Dougherty Co*. ●(no data) [Sep]; *Emanuel Co*. ●Swainsboro [Jul]; *Glynn Co*. ●Brunswick [Jul]; *Jenkins Co*. ●Millen [Jul]; *Johnson Co*. ●0.5 mi E Kite [Oct]; *Lowndes Co*. ●Vidalia [Jul-Aug]; *McIntosh Co*. ●Sapelo Island, Nanny Goat Beach, 31.39065° -81.26533° [May]; *Telfair Co*. ● McRae (McRae-Helena) [Jul]; *Thomas Co*. ●Thomasville; *Tift Co*. ●Tifton [May, Jul]; *Toombs Co*. ●Vidalia [Aug]; *Ware Co*. ●Waycross [Sep]; *Wheeler Co*. ●Bells Ferry Road, along Ocmulgee River [Apr, Sep]. **LOUISIANA**: *West Feliciana Par*. ●Feliciana Natural Area, 30°47.7′ N 91°15.2′ W [Sep]. **MISSISSIPPI**: *Jones Co*. ●Laurel [Aug]. **NORTH CAROLINA**: Moore Co., ●Eastwood [Jul]. **SOUTH CAROLINA**: *Aiken Co*. ●Aiken Gopher Tortoise Preserve, 10.7 km NE White Pond, 33°30′15″ N 81°24′22″ W, 259 ft [Apr]; *Beaufort Co*. ●Beaufort [Apr]; *Colleton Co*. ●Islandton [Jun]; *Florence Co*. ●Florence [Sep]; *Georgetown Co*. ●10 km E Georgetown [May]; *Horry Co*. ●Myrtle Beach [Apr, Jul].

Comments. I regard this species as the sister of *B. ebenus*, the two having arisen from Pleistocene glaciation splitting the founding ancestral population into two enclaves, one on the Florida Peninsula and the other in a south-central refuge, probably in present day Texas. Holocene expansion may have brought the two into closer proximity than suggested by their presumed distributions (Fig. 28). I have seen two specimens (Louisiana State Arthropod Museum database 0243611 and 0305000) here regarded as *B. depressipennis* from eastern Louisiana (West Feliciana Parish) very near the Mississippi River. These specimens have the expected weak greenish cast and prolonged pronotal ridge but exhibit the coarser, more coalesced pronotal granulation of *B. ebenus*. On the other hand, I have also recorded *B. ebenus* adjacent to the Mississippi River in Bolivar Co., Mississippi (see Comments for that species). This area, along the southern portion of the Mississippi River, would be a good venue to test the notion that it is a zone of hybridization, whether by secondary contact or nascent divergence.

On the type locality of *B. depressipennis* Woodruff (1973) stated, "Originally described from Kansas, although Robinson [1948] … erroneously listed the type locality as Georgia." Woodruff in fact erroneously corrected Robinson as LeConte explicitly states that it is "… a species found in Georgia …" The distribution of *B. depressipennis* follows the coastal lowlands of the southeastern United States, including the Florida peninsula. Woodruff's (1973) distribution map extends it also to the west and northward into a large portion of the Great Plains, which I assume is based upon erroneous records attributable to *B. ebenus* and *B. praticola*, which are very common in the region. This species very often presents a dark green color, but it can be black like its close relative, *B. ebenus*, within a single population.

Fincher et al. (1970) reported that this species was commonly collected on chicken droppings, as well as opossum, rabbit, swine, fox and rat feces, but not those of human, sheep or dog, in Tift County, southern Georgia. Woodruff (1973) found it common in cow dung in open, sandy Florida pastures.

In addition to the syntype cited above, there is another probable syntype also present in the LeConte Collection at the Museum of Comparative Zoology, Harvard University (Crystal Maier, pers. comm).

Boreocanthon ebenus (Say, 1823). restored generic combination

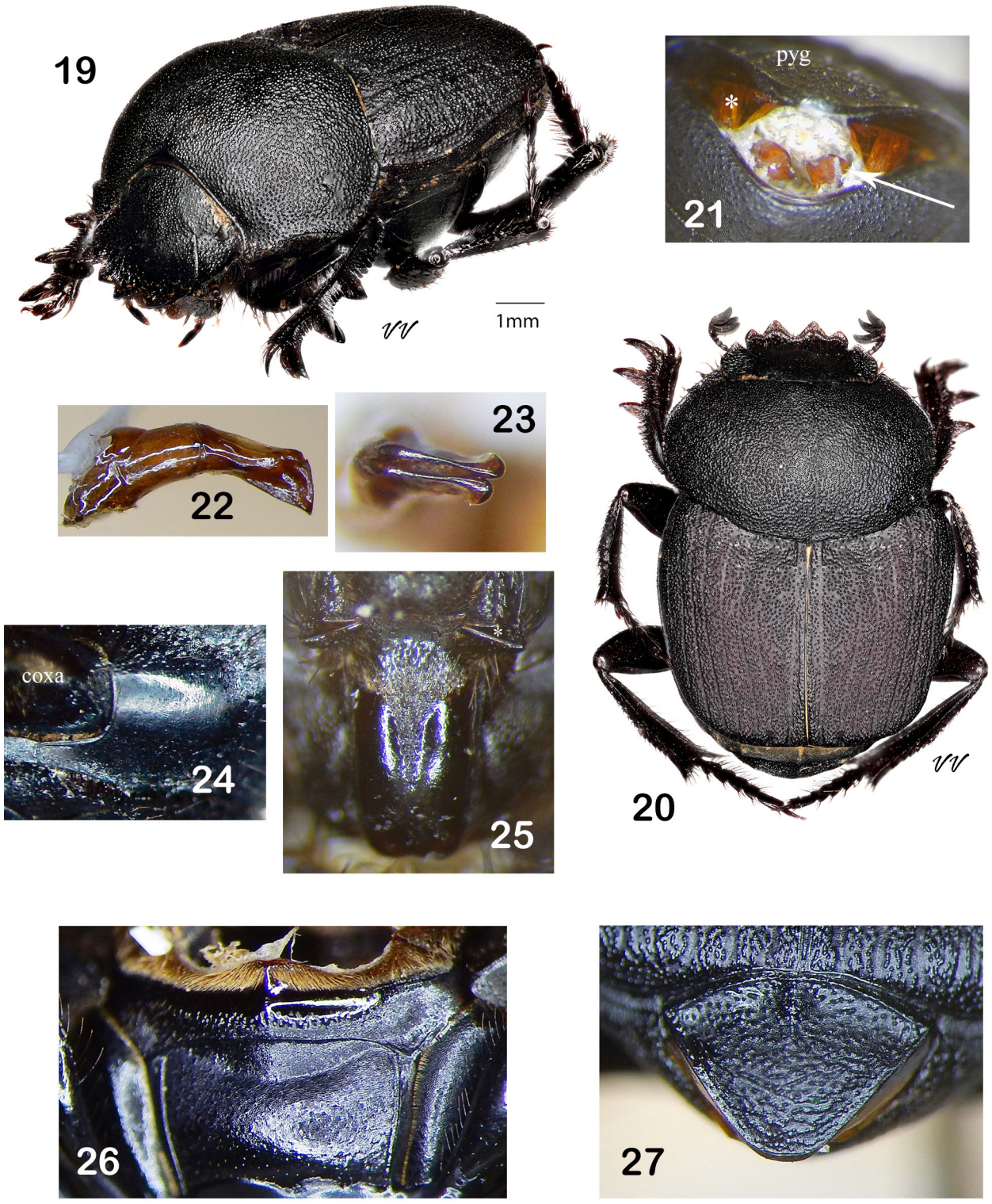
Fig. 13, 19–28

Ateuchus ebenus Say 1823: 208
Canthon ebenus (Say) (new combination per Melsheimer 1853: 53)
Boreocanthon ebenus (Say) (new combination per Halffter 1958: 209)
Canthon (*Boreocanthon*) *ebenus* (Say) (new combination per Howden 1966: 727)
Boreocanthon ebenus (Say) **restored generic combination**

Type. Neotype, **here designated.** Snow Entomological Collections, Biodiversity Institute, University of Kansas (*see Comments below*).

Type locality. Kansas, 10 mi NW Mullinville, **here restricted** (*see Comments below*).

Diagnosis. *Head*: Anterior portion of clypeus very finely roughened, weakly shiny, remainder of head densely covered by coarse granules on shagreen background. Strongly sexdentate, median clypeal teeth acute, separated by V-shaped emargination (Fig. 20); lateral teeth acute. Paraocular notch deep, setting off strong, dentate anterior angle of paraocular area. Labio-gular fimbria broadly V-shaped, reaching mid-length of gula (Fig. 25). *Prothorax*: Pronotum densely, coarsely granulate (Fig. 13a, 19–20); granules on disk frequently joined into short, irregular chains, those on sides usually isolated. Lateral margin not at all explanate anteriorly; circumnotal ridge serrate posteriorly, not extending beyond posterior angle (Fig. 13a). Hypomeral carina absent (Fig. 24) or rudimentary,



Figures 19–27. *Boreocanthon ebenus* (Say). **19)** Habitus, anterolateral view; **20)** same, dorsal view. **21)** Apical view of female abdomen (pyg = pygidium; arrow indicates apices of paraprocts; asterisk indicates extended marginal flange of pygidial margin). **22)** Lateral view of genital capsule. **23)** Apical view of parameres. **24)** Ventral view left hypomeron. **25)** Ventral view of gula and submentum. **26)** Oblique ventral view of meso- and metaventrites. **27)** Posterior view of pygidium.

indicated only by angular projection of procoxal margin. *Pterothorax*: Pleurites granulate, granulation extending to sides of metaventrite (Fig. 26); mesoventrite shagreened, weakly punctate laterally; middle of metaventrite with weakened granulation and scattered punctures on shagreen background. *Elytra*: Interstriae bearing strong field of isolated granules, anterior ends of 2nd and 3rd interstriae weakly raised, that of 1st interstria depressed. Striae superficial, lacking discrete margins other than bordering granules; subhumeral (8th) stria never carinulate, epipleural (9th) stria sometimes indicated. *Legs*: Protibia (as in Fig. 16) abruptly widened, inner margin stepped at level of third (basal) tooth; inner apical angle prolonged as conical tooth. Protibial spur strongly curved and acute in both sexes. Hind femora with conspicuous row of long setae along anterior margin. *Abdomen*: Pygidium (Fig. 27) sculptured as elytra, impressed basally on each side of raised midline, or as continuous transverse concavity. Ventrites usually more or less evenly granulate, granules becoming weaker medially on ventrites 1–5, uniform across ventrite 6. *Genital capsule*: Compressed apical portion of genital capsule triangular (Fig. 22), lower apical angles in form of elongate, rounded lobes (Fig. 23). *General*: Black, very rarely showing strong green or weak blue undertones. Length: 6.0–11.0 mm. *Geographic distribution* (Fig. 28): Central United States generally west of the Mississippi River to the Rocky Mountains south of the 44th parallel, with southern extension through Texas and New Mexico west to southern Arizona. *Ecogeographic environment* (Fig. 2): Temperate Grasslands, Savannas and Shrublands, and Deserts and Xeric Shrubland biomes. *Specimens examined*: 1278.

Notes on the neotype. The male neotype conforms with the diagnosis above annotated as follows: Specimen exhibits moderate wear, especially notably rounded marginal teeth of head and protibiae. Left protarsus missing. Hypomeral carina suggested by angular projection of raised procoxal margin. First ventrite with scant, weak granulation, almost smooth; ventrites 2–5 with weak lateral granulation; 6th ventrite completely granulate, posterior margin strongly emarginate medially. Genital capsule not extracted. Completely black at low magnification (< ×5), very weak green undertones emerge under strong light and moderate magnification (×15). Length 10 mm. Neotype was chosen because of its appropriate collection locality (see discussion below). Label information is given below.

Collection localities.

MEXICO — CHIHUAHUA: *Mpio. Juarez* ●Samalayuca [Jun] ●Samalayuca, Laguna de Riataso [Aug].

UNITED STATES — ARIZONA: *Cochise Co*. ●Chiricahua Mountains, Horseshoe Canyon, 1.6 mi W Hwy 80 [Sep]●5.8 km SE Willcox, 32°13′10″ N 109°46′51 W″ [Aug]. **COLORADO**: *Denver Co*. ●Denver [May-Aug]; *El Paso Co*. ●Peyton, 5675 ft [Jul] ●Cheyenne Mt., 6300 ft [Sep]; *Logan Co*. ●Meringo [Aug]; *Morgan Co*. ●3mi N Orchard [Jun]; *Prowers Co*. ●Lamar [Jun]; *Weld Co*. ●Nunn [Sep] ●Roggen [Aug] ●9 mi NE Roggen [May]. **KANSAS**: *Barber Co*. (no data); *Cheyenne Co*. ●9 mi NNE Wheeler [May]; *Clark Co*. ●5 mi N Englewood [Jun]; *Clay Co*. ●(no data) [Jun]; *Comanche Co*. ●4 mi NW Coldwater [Sep]; *Cowley Co*. ●10 mi SW Winfield; *Douglas Co*. ●Lawrence, 900 ft; *Hamilton Co*. ●Syracuse, 3500 ft [May]; *Jefferson Co*. ●Medina; *Kiowa Co*. ●10 mi NW Mullinville [Jun] ●Belvidere [Jul] 5 mi N Greensburg [Apr, Jun]; *Meade Co*. ●13 mi S Meade [Jul]; *Morton Co*. (no data); *Reno Co*. ●Medora [May-Jun]; *Sedgwick Co*. ●(no data); *Trego Co*. (no data); *Wallace Co*. ●(no data). **MISSISSIPPI**: *Bolivar Co*. ●2 mi W Rosedale [May-Jun]. MISSOURI: *Jasper Co*. (no data) [Aug.]. **NEBRASKA**: *Arthur Co*. ●4.5 mi N Arthur [May]●Arapaho Prairie [Jun-Jul]; *Blaine Co*. ●10 mi SW Brewster [Jul] ●3 mi N Brewster, 41.9721 N 99.8515 W; *Brown Co*. ●Koshopah [Jun]; *Chase Co*. ●Imperial; *Cherry Co*. ●Merritt Dam [Aug] ●Ft. Niobrara [Aug] ●2 mi W, 1 mi S Sparks [Jul] ●42.1643 N 100.5299 W [Jun]; *Dakota Co*. ●Sioux City [Jun]; *Dundy Co*. ●Benkleman [May] ●Sanborn, 5 mi W Haigler, 40.06° N 102.02° W, 1010 m [Jun]; *Garfield Co*. ●21 km E Taylor, 41.8179° N 99.1075° W; *Hooker Co*. ●41.9815° N 101.1139° W [Jun]; *Keith Co*. ●Cedar Point Biological Station [Jun]; *Loup Co*. ●41.8658 N 99.3773 W [Jul]; *McPherson Co*. ●Tryon [Jun] ●Gudmundsen Sandhills Laboratory [Jul]; *Sheridan Co*. ●10-13 mi E Alliance [Jun]; *Thomas Co*. ●Halsey [Aug] ●Nebraska National Forest, 1.3 km SSW Bessey Campground, 41.88937° N 100.30676° W [Sep] ●Nebraska National Forest, Whitetail Campground, 41.79413° N 100.27381° W [Sep]. **NEW MEXICO**: *Bernalillo Co*. ●Albuquerque [Apr, Jun]; *Catron Co*. ●Luna; *Chaves Co*. ●5.5 km SW Elkins [Jul] ●38 mi E Roswell, Mescalero Sand Dunes [Jul]; *Cibola Co*. ●Laguna [Jul]; *Colfax Co*. ●6.3 mi E Springer, Canadian River [Jun]; *Doña Ana Co*. ●Jornada Experimental Range, 15 mi N Las Cruces [Jul, Sep] ●Las Cruces [Jul] ●Rincon ●8 mi W Las Cruces [Jul]; *Eddy Co*. ●16 mi E Loving, Los Medanos [Aug] ●near Waste Isolation Pilot Plant, 32°23.6′N 103°46.1°′W [Jun]; *Harding Co*. ●33.5 km SE Gallegos, 1200 m [Apr]; *Lea Co*. ●3 mi E Jal [Jun] ●32°22.8′N 103°43.3′W [Jul]; *Otero Co*. Newman,

4000 ft [May]; *Quay Co*. ●Tucumcari [Sep] ●7 mi SW Logan [Jun] ●Glenrio [Jul] ●3 mi N San Jon; *Roosevelt Co*. ●Oasis State Park [Jul] ●Portales, 34.12371° -103.58029° [Jul] ●8 mi E Portales, ENMU Natural History Preserve [May-Jul, Oct] ●14 mi SW Portales; *Sandoval Co*. ●Jemez Pueblo [Jul] ●San Ysidro [Jun]; *San Miguel Co*. ●Las Vegas [Jul]; *Sierra Co*. ●Elephant Butte Lake State Park [Jul]; *Socorro Co*. ●19km W Bernardo, 34.401° N 107.028° W ●18 km SE Bernardo ●Sevilleta National Wildlife Refuge, Saltbush [Jun] ●Sevilleta National Wildlife Refuge, San Lorenzo [Jun] ●Sevilleta National Wildlife Refuge, Black Butte [Jun] ●Sevilleta National Wildlife Refuge, 34.311° N 106.678° W [Jun, Aug]; *Union Co*. ●18 mi W and 4 mi S Clayton (Snyder Ranch) [Aug]. **OKLAHOMA**: *Cimarron Co*. ●Boise City [Jul]; *Cleveland Co*. ●Norman [Apr] ●Hwy 62 at South Canadian River [Apr]; *Cotton Co*. ●Hwy 281 at Red River [Apr]; *Jefferson Co*. ●Hwy 79 at Red River [Apr] ●Ryan [Jul]; *Kingfisher Co*. ●Dover [Jul]; *Love Co*. Hwy I-35 at Red River [Apr]; *Marshall Co*. ●5 mi N Willis [Jun]; *McCurtain Co*. ●Red River sand bars [Jul]; *Payne Co*. ●(no data) [May]; *Woods Co*. ●Little Sahara State Park, 2 mi S Waynoka [May-Jun]; *Woodward Co*. ●Woodward [Jul]. **SOUTH DAKOTA**: *Bennett Co*. ●10 mi E Martin. Lacreek National Wildlife Refuge [May]; *Perkins Co*. ●Grand River National Grassland [Jul]. **TEXAS**: *Anderson Co*. ●Engeling Wildlife Management Area [Jul-Aug] ●25 mi NW Palestine [Apr]; *Angelina Co*. ●10 mi N Zavalla [May]; *Atascosa Co*. ●8 mi NW Poteet [Apr-May] ●5 mi SW Somerset (Bexar Co.) [Mar]; *Bastrop Co*. ●8.6 km N Bastrop, Camp Swift ●10 mi N Bastrop [Sep]; *Bexar Co*. ●San Antonio [Oct] ●10 mi W San Antonio [Oct] ●Hwy 281, 6 mi S Loop 1604 [Oct] ●Applewhite Rd. at Loop 1604 [Nov]; *Brazos Co*. ●College Station [Apr, Sep]; *Bosque Co*. ●2 mi SE Clifton; *Briscoe Co*. ●Quitaque [Jun]; *Brooks Co*. ●9 mi S Falfurrias [Jul]; *Burleson Co*. ●2 mi N junction Hwy 21 and FM 908 [Feb-Mar];●4 mi W Cooks Point [Mar]; *Callahan Co*. ●Baird [Apr]; *Cameron Co*. ●San Benito [Jul] ●14 mi E Rio Hondo [Oct]; *Colorado Co*. ●Columbus; *Comal Co*. ●Bulverde [Apr]; *Comanche Co*. ●Comanche [Jun-Jul]; *Crane Co*. ●Junction routes 1053 and 1233, 31°29′N 102°39′W [Jul]; *Crosby Co*. ●White River Lake [May]; *Dallas Co*. ●Dallas [May]; *Dickens Co*. ●2 mi SW Dickens [Oct] ●10 mi NE Dickens [Aug-Sep]; *Dimmit Co*. ●4 mi W Carrizo Springs [Sep] ●8 mi W Artesia Wells (LaSalle Co.), Chaparral State Wildlife Management Area [Mar]; *El Paso Co*. ●El Paso [Jun]; *Freestone Co*. ●Old Spring Seat Church, near Donie [May]; *Gaines Co*. ●10 mi SW Seagraves; *Gillespie Co*. ●1 mi S Fredricksburg [Oct]; *Grimes Co*. ●Lamb Spring [Mar]; *Hall Co*. ●6 mi SE Turkey [May-Jul]; Hardin Co. ●3 mi W Silsbee, Sandylands Preserve, 30°20′57″ N 94°14′16″ W [Jun]; *Hardeman Co*. ●20 mi N Goodlett, Farm Road 680 at Red River [Aug]; *Henderson Co*. ●Athens, Sand Flats Cemetery [Apr]; *Hidalgo Co*. ●Santa Ana Wildlife Refuge [Apr] ●7-10 mi N Linn [Apr]; *Karnes Co*. Ecleto Metz Ranch [Mar]; *Kenedy Co*. ●Turcotte Ranch, 2 mi S Sarita [May] ●Armstrong [Mar-Apr] ●3 and 5 mi S Sarita [Jun, Sep-Oct]; ●20 mi N Raymondville [Apr] ●Kenedy Ranch, San Pedro Camp, 26°57′03.9″N 97°39′22.2″W [Apr]; ●20 mi SW Riviera [Nov] ●Norias [Oct]; *Leon Co*. ●1.5 mi N Centerville [Jun]; *Lipscomb Co*. ●Higgins [Jun]; *Live Oak Co*. ●Mestena Ranch, 12 mi S George West [May] ●10 mi S George West [Aug]; *Lubbock Co*. ●Lubbock [Apr]; *Mason Co*. ●Double Helix Ranch, 30.87053 -99.05167; *McColloch Co*. ●2 mi SE Brady [Sep]; *Mills Co*. (no data); *Montague Co*. ●3 mi N Forestburg [Apr] ●Hwy 81 at Red River [Apr] *Parker Co*. ● Dennis [Jul]; *Randall Co*. ●Canyon [Jul]; *Refugio Co*. ●Austwell [May]; *Robertson Co*. ●Hearne [Apr]; *Starr Co*. ●2 mi NE La Gloria [May]; *Terry Co*. ●Brownfield [Jul]; *Travis Co*. ●Austin [Oct]; *Val Verde Co*. ●Del Rio, 955 ft [Jun]; *Ward Co*. ●Wickett [Jun] ●9.4 km ENE Monahans, 31°37′11″ N 102°47′52″ W [May] ●Monahans [May, Jul] ●Monahans Sandhills State Park, 31.639357° -102.829678° , 825 m [Apr -Jul]; *Washington Co*. ●Hwy 105, 8 mi SW Brazos River [Apr]; *Wichita Co*. ●2 mi ENE Burkburnett, US Hwy 281/I-44 at Red River [Jun]; *Webb Co*. ●Laredo [Jul]; *Willacy Co*. Lyford [Jul] ●Point Mansfield (May); *Wilson Co*. ●Floresville [Jul]; *Winkler Co*. ●Co. Rd. 404, 17 mi E Hwy 18, 31.792° N 102.791° W●11 mi NE Kermit, 3200 ft [Sep]. **WYOMING**: *Goshen Co*. ●Lingle [Jul]; *Laramie* Co. ●Cheyenne; *Platte Co*. ●Uva [Jul].

Comments. *Boreocanthon ebenus* is regarded here as sister to *B. depressipennis* (q.v.). It is a common, large species easily confused with *B. praticola*, from which it differs in a number of ways, most obviously by its basally impressed pygidium. The two species are broadly sympatric and sometimes collected together, in prairie dog colonies, for example. However, *B. ebenus* is clearly closely associated with sand dunes and other habitats with exposed, very sandy substrate (Brown 1927; Nealis 1977; Fincher et al. 1986). Collection locations are very often places where vegetated sand dune habitat is common; indeed, casual searching using Google Earth with precise GPS data often pinpoints places clearly having sand dune or similar habitat. Schoenly (1983) collected *B. ebenus*

Figure 28. Approximate distributions of *Boreocanthon ebenus* (Say) and *B. depressipennis* (LeConte)

from horse/cattle dung-baited pitfalls in the red sandy hills just east of the city of El Paso, where *B. halffteri* also occurs.

Blatchley (1910) included *B. ebenus* in his key to Indiana *Canthon* but cited no state localities, stating only that it "… is known from Maine and Pennsylvania to Kansas and Texas". I have not seen Indiana specimens. The Leng (1920) citation of *B. ebenus* from Maine is a misidentification and should have read *Canthon vigilans* LeConte (Majka et al. 2011.) While I have seen Mexican specimens only from near Ciudad Juárez, Chihuahua, there can be little doubt that *B. ebenus* reaches localities in the far north of Tamaulipas, Nuevo Leon and Coahuila along the Rio Grande as some collection localities literally lie on the northern bank of the river within flight distance to Mexican soil along the southern bank and beyond. Townsend (1902) reported it from Hidalgo Co., Texas, and I have seen specimens from several other Texas counties along the Rio Grande from the Gulf coast to

Del Rio. *Boreocanthon ebenus* was unsuccessfully introduced into Puerto Rico in early 1920s to control the horn fly, *Haematobia irritans* (L.) (Halffter and Matthews 1966; see also Wolcott 1922).

My conjecture is that the dispersal of *B. ebenus* has been facilitated by sandy habitats along riverways, which provide corridors for expansion through otherwise less hospitable terrain. Material I have seen often associates with major river drainages: lower Rio Grande, Pecos River, Arkansas River, Red River, the Platte River and its major tributaries in the Great Plains. Such may explain the occurrence of this species as far east as the Mississippi River. I have seen five specimens from the Paul Lago collection from Bolivar County, Mississippi (2 mi W Rosedale), a site literally on the sand flats of east bank of the Mississippi River at its confluence with the Arkansas River. Curiously, *B. depressipennis* has apparently also reaches the Mississippi River, about 200 air miles south of Rosedale near Baton Rouge, Louisiana (See Comments for that species.)

On the spelling of ebenus. There has been confusion regarding the spelling of the specific name (epithet) of this species name. Say (1823) christened his species *Ateuchus ebeneus*, using a Latin adjective meaning made of ebony wood, in obvious reference to this beetle's deep black color. Melsheimer's (1853) catalogue, which was edited by J. L. LeConte and S. S. Haldeman, listed it by the name *Canthon ebenus* (Say), replacing the adjective form (ebeneus) with the noun (ebenus), with no explanation for the change in spelling. Melsheimer's action must be regarded as an incorrect subsequent spelling (ICZN 1999, Article 33.3), whether made in simple error or as a deliberate change. That the change was, indeed, an editorial decision by LeConte is strongly suggested by the fact that, six years later, in his magnificent compilation of Say's writings, he modified Say's original text of the description of *ebenus* (1859b, p. 134) to read "3. *A. ebeneus* [*ebenus*]." LeConte utilized brackets to correct what he regarded (or perhaps knew to be) typographical errors: "Typographical errors in the original memoirs have been corrected … the corrections have been placed in brackets" (1859a, p. vi of his Preface). LeConte's action only perpetuated the error in the Melsheimer catalogue, to which he continued to refer in later writings (LeConte 1858, 1859c). However, in the case of *ebenus*, the Melsheimer/LeConte spelling has arguably been, since its inception, in prevailing usage and always attributed to the publication of the original spelling and, therefore, in accordance with ICZN Article 33.3.1, it can be deemed to be the correct original spelling. That it has been the prevailing spelling for over 150 years is evidenced by the following comparison (not to be regarded as exhaustive, but, rather, illustrative of usage over time in papers of varying length and scope): spelling as *ebenus* (LeConte 1858, 1859a,1859b; Horn 1870; Ulke 1874; Blanchard 1885; Wickham 1902; Townsend 1902; Blatchley 1910; Gillett 1911; Leng 1920; Dawson 1922; Brown 1927; Robinson 1948; Halffter 1958; Vulcano and Pereira 1964; Halffter and Martínez 1977; Nealis 1977; Schoenly 1983; Howden and Scholtz 1986; Fincher et al. 1986; Kohlmann and Halffter 1990; Lobo 2000; Medina et al. 2003; Riley and Wolfe 2003; Krajcik 2006; Ratcliffe and Paulsen 2008; Edmonds 2018); spelling as *ebeneus* (Dejean 1833; Harold 1868; Harold 1869; Schmidt 1922 (attributed to LeConte); Balthasar 1939; Blackwelder 1944 (as *ebeneum*); Krell 2010). In accordance with Article 33.3.1 of the ICZN (1999), I here regard *ebenus* as the correct original spelling of *Ateuchus ebeneus* Say, 1823, and so use the name *Boreocanthon ebenus* (Say) as the valid name of this species.

On designation of neotype. In explicit regard to designating a neotype for *Ateuchus ebenus* Say, 1823, the following particulars apply to the provisions set forth in Article 75.3 of the ICZN (1999):

1) 75.3.1—This designation of a neotype is made for the express purpose of clarifying the identity and type locality of *Ateuchus ebenus* Say, 1823, here *Boreocanthon ebenus* (Say, 1823), the originally designated type species of the genus *Boreocanthon* Halffter, 1958. In my opinion, lack of a name-bearing specimen for a type species of a genus constitutes an exceptional need for designation of a neotype in the context of Article 75.3. Additionally, the subject species is a close relative of, and often confused with the sympatric species *Boreocanthon praticola* (LeConte, 1859c). A neotype, as name-bearing type specimen, will, therefore, clarify and stabilize the meaning of the species-name as well as the genus-name *Boreocanthon*.

2) 75.3.2—Characters that differentiate *Ateuchus ebenus* (now *Boreocanthon ebenus*) from its congeners are set forth in the key and species treatments presented in this paper.

3) 75.3.3—The pinned specimen **here designated** as neotype bears the following five labels attached on the same pin: (1) USA Kansas: Kiowa Co., 10 mi NW Mullinville, 8 Jun 1996, G. Salsbury, ex: prairie dog dung; (2) *Canthon ebeneus*(Say) det. G. Salsbury 2000; (3) {barcode} SM0349138, KUNHM-ENT; (4) *Boreocanthon ebenus*

(Say, 1823), Det WDEdmonds '22; (5) NEOTYPE, *Ateuchus ebenus* Say 1823 (= *Boreocanthon ebenus* [Say]) Designated by W.D. Edmonds 2022. (The neotype label is printed in black ink on white with "NEOTYPE" in red.)

4) 75.3.4—It is general knowledge (Weiss and Ziegler 1931; Mawdsley 1993) that most of the original collections by Thomas Say were lost or destroyed. No specimens attributable to *A. ebenus* are present in the surviving collection of Say material at the Museum of Comparative Zoology at Harvard University, nor in the Melsheimer, Harris or LeConte collections there (Crystal Maier, pers. comm.). Moreover, no specimens attributable to Say in the collections of his foreign correspondents have been discovered in European museums in recent years (Mario Cupello, Fernando Vaz-de-Mello, Stéphane Boucher, pers. comm.). I harbor little doubt that Say's original type specimen(s) no longer exists.

5) 75.3.5—The specimen here designated as neotype is fully consistent with the original and subsequent descriptions of *Ateuchus ebenus* and subsequent names: *Canthon ebenus* and *Boreocanthon ebenus*.

6) 75.3.6—Say's original description (1823) is based on specimen(s) collected during his 1819–1820 trip from St. Louis to the Rocky Mountains as zoologist to the US Army scientific exploration party led by Major S. H. Long. The stated type locality is "Missouri," but at the time of Say's western travels in June 1819 – October 1820 (Barber 1928), his location must have referred to the Missouri Territory, not the future state of Missouri, which was not organized until 1821. Indeed, in some of his letters to colleagues during the journey, Say explicitly gives his location as "Missouri Terr^{y}" in the dateline (Weiss and Ziegler 1931). So, the precise collection site for his species could well have been anywhere along the roughly 2000-mile route he took from St. Louis along the Missouri River to Council Bluffs, thence along the Platte and South Platte Rivers to the foot of the Rocky Mountains, thence along the Arkansas River to Fort Smith and Cape Girardeau, and thence up the Mississippi to St. Louis — that is, entirely through the present states of Missouri, Nebraska, Colorado, Kansas and northwestern Arkansas. But given the distribution of *B. ebenus* as now understood (Fig. 28) it is reasonable to assume that the original type locality was somewhere on those sections of the party's route along the Platte and South Platte Rivers, in the present region of Denver and Colorado Springs, and along the Arkansas River from, in modern terms, Colorado through Kansas into Oklahoma and Arkansas. All these sections pass through regions where *B. ebenus* is common and where Say presumably collected. It is unlikely that Say collected this species in the present day state of Missouri, where it is unknown to me save for the far southwest corner of the state (Jasper Co.) Accordingly, from available material I have selected a specimen collected from the following location, hereby determined, per ICZN Article 76.3, to be the type locality of *Ateuchus ebenus* Say: Kansas, Kiowa County, 10 mi NW Mullinville. This location places the type locality in grassland habitat adjacent to the Arkansas River (per Google Earth, Image Landsat/Copernicus, accessed February 1, 2022), and is very near the location where Say's exploration detachment, led by Captain John Bell, made camp on August 8, 1820 (Fuller and Hafen 1973: 218, map).

7) 75.3.7—The here designated neotype of *Ateuchus ebenus* Say has been deposited in the collection of the Snow Entomological Collections, Biodiversity Institute, University of Kansas, Lawrence, Kansas USA.

Boreocanthon lecontei (Harold, 1868), restored generic combination

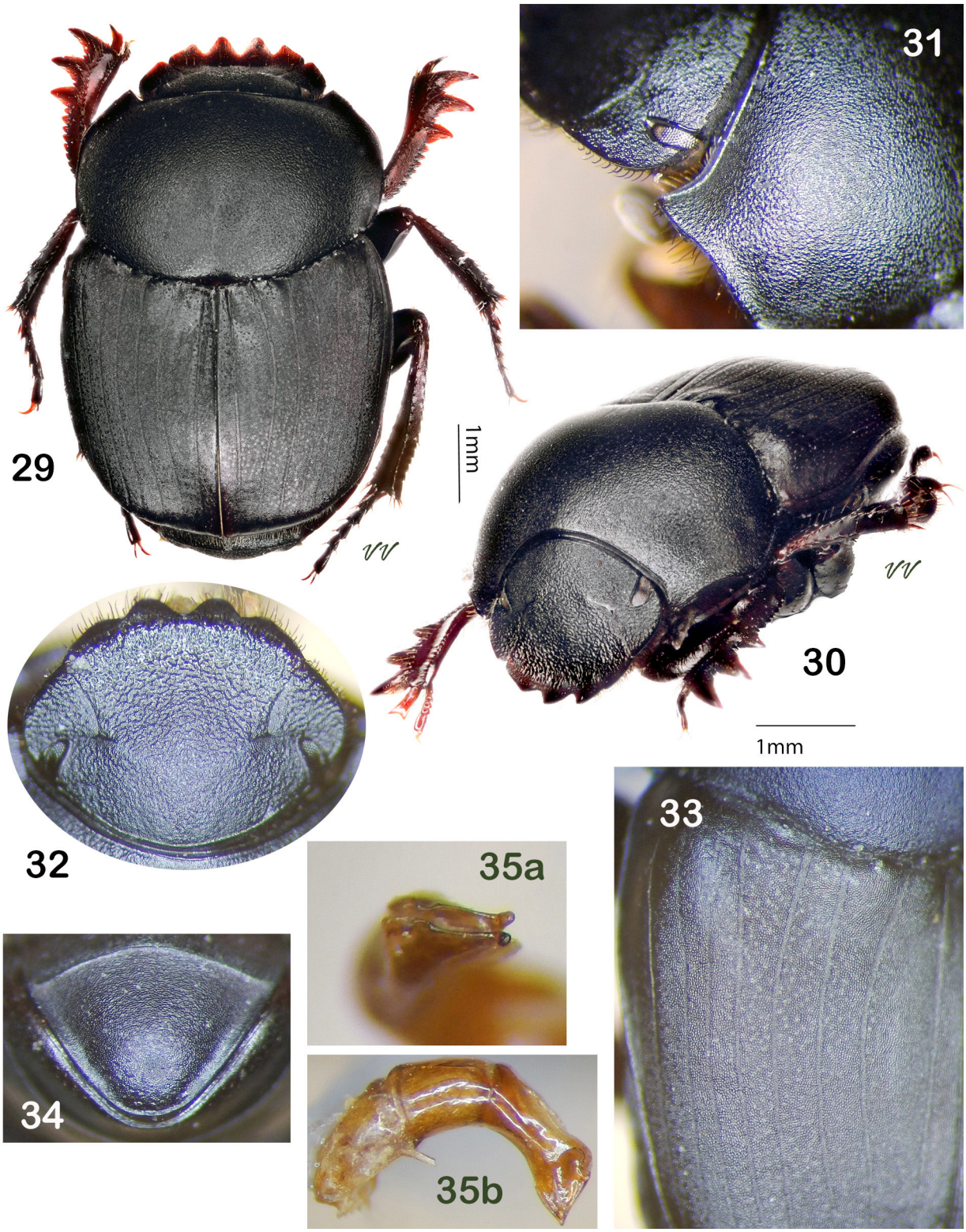
Fig. 29–35, 100

Canthon lecontei Harold 1868: 68.
Boreocanthon lecontei (Harold) (new combination per Halffter 1958: 209).
Canthon (*Boreocanthon*) *lecontei* Harold (new combination per Howden 1966: 727).
Boreocanthon lecontei (Harold), **restored generic combination**.

Type material. Syntype (sex undetermined). Museum für Naturkunde, Berlin. Examined by photograph courtesy of Fernando Vaz-de-Mello.

Type locality. Texas.

Diagnosis. *Head*: Anterior portion roughened, punctatorugose, posterior portion granulorugose, shagreen reduced to isolated patches (Fig. 32). Clypeus quadridentate, teeth subacute, separated by narrow, V-shaped emargination (Fig. 29, 32). Paraocular notch reduced, setting off small, rounded angle of paraocular area. Labiogular fimbria broadly V-shaped medially, apex extending almost half length of gula. *Prothorax*: Pronotum (Fig. 31) evenly, densely, finely granulate; granules irregular, confluent, obliterating most of shagreen background, which survives in small, isolated patches. Anterior pronotal angles only very weakly upturned, posteromedian



Figures 29–35. *Boreocanthon lecontei* (Harold). **29)** Habitus, dorsal view. **30)** Habitus, anterolateral view. **31)** Partial dorsal view of head and pronotum. **32)** Dorsal view of head. **33)** Dorsal view of left elytron. **34)** Posterior view of pygidium. **35)** Male genitalia. **a)** Apical view of parameres. **b)** Lateral view of genital capsule.

angle not depressed; circumnotal ridge entire, not serrate posteriorly. Hypomeral carina present. *Pterothorax*: Mesoventrite smooth; metaventrite finely, sparsely punctate on strong shagreen background. *Elytra*: Interstriae (Fig. 33) finely alutaceous, microspotting conspicuous; 2nd and 3rd slightly, if at all raised anteriorly. Striae (Fig. 33) fine, superficial, lateral margins weakly defined; subhumeral (8th) stria carinulate, sometimes only weakly so; epipleural (9th) stria usually obsolete, sometimes persisting as vague fragments. *Legs*: Inner protibial margin not offset, almost straight; spur sexually dimorphic, apex acute in female, bifurcate in male. Hind femur lacking anterior row of conspicuous setae. *Abdomen*: Pygidium (Fig. 34) densely alutaceous, slightly more convex apically. Last (6th) ventrite with sparse puncturing on weak shagreen background; remaining ventrites (1-6) smooth. *Genital capsule*: Compressed distal portion of parameres (Fig. 35b) shortened, triangular, ventral apical angles in form of elongated knobs (Fig. 35a). *General*: Black, sometimes with dark blue undertone. Length: 3.5 – 6.0 mm. *Geographic distribution* (Fig. 100). South Texas and adjacent northeastern Mexico. *Ecogeographic environment* (Fig. 2): Desert and Xeric Shrublands, and Tropical and Subtropical Grasslands, Savannas and Shrublands biomes (Western Gulf coastal grasslands, Tamaulipan mezquital and Tamaulipan matorral ecoregions). *Specimens examined*: 241.

Collection localities.

MEXICO — NUEVO LEON: *Mpio. Linares* ●8 mi S Linares [Aug]; *Mpio. Sabinas Hidalgo* ●Sabinas Hidalgo [Jun]. **SAN LUIS POTOSÍ**: *Mpio. Ciudad Valles* ●31 mi N Cd. Valles, 1000 ft [Aug]. **TAMAULIPAS**: *Mpio. Abasolo* ●Abasolo [May]; *Mpio. El Mante* ●Cd Mante [Jul]; *Mpio. Valle Hermoso* ●14 mi SW Santa Teresa [Aug].

UNITED STATES — TEXAS: *Atacosa Co.* ●Pleasanton [Jun]; *Bexar Co.* ●San Antonio, Salado Creek (Jun-Jul]; *Cameron Co.* ●Brownsville [Apr];●Port Isabel [Jun] ●1 mi N Laguna Vista [Oct] ●8.9 km N Los Fresnos, 26.15100° -97.46923° [Sep]●Sabal Palm Grove Sanctuary [Oct]; ●9 mi E Rio Hondo [Jun] ●11 km NE Rio Hondo, 26.31193° -97.51292° [Sep] ●14 mi E Rio Hondo ●Laguna Atascosa National Wildlife Refuge, 23.23291°N 97.35214°W [Sep-Nov]; *Comal Co.* ●(no data); *Duval Co.* ●5 mi S Realitos [Mar]; ●2.2 mi W Freer [Sep]; *Hidalgo Co.* ●Bentsen Rio Grande Valley State Park [Jun] ●Las Palomas Wildlife Management Area, Penitas Unit [Apr] ●Hidalgo [Aug] ●7 mi SE Alamo [May]; *Kerr Co.* ●Kerrville [Aug]; *Kleberg Co.* ●Kings Ranch at Kingsville [Oct]; *Live Oak Co.* ● 15 mi SW George West [Oct]; *McMullen Co.* ●6 mi SW Whitsett [Sep]; ●Calliham [Nov]; *Travis Co.* ●Austin; *Uvalde Co.* ●Uvalde [Jun-Jul] ●7 mi W Uvalde ●Garner State Park [Jun] ●Concan [May]; *Val Verde Co.* ●Del Rio [Nov]; *Starr Co.* ●14 mi E El Sauz [Oct]; *Webb Co.* ●Laredo [Apr] ●15 mi N Laredo [May]; *Williamson Co.* ●Taylor [Aug].

Comments. This species is easily recognizable by its pronotal sculpturing, which consists of a unique, double granulation. The primary (larger) granulation is very fine and densely coalescent, producing an even, rather finely granulorugose surface; the secondary (much smaller) granulation, responsible for the shagreen background characteristic of the genus, appears in small, isolated patches. Similar sculpturing also presents on the posterior portion of the head and pygidium, but does not extend to the elytra. I consider *B. lecontei* a taxonomic isolate with no close affinity to any other known congener. Its distribution (Fig. 100) completely overlaps that of *B. integricollis* but extends somewhat farther to the north.

Lindquist (1935) studied the life history of *B. lecontei* in Uvalde, Texas, where he found it to be attracted to carrion in addition to excrement. Blume (1970) recorded this species from the cattle dung community in Kerr County, Texas. Besides carrion and cattle dung, my records show it to be attracted also to swine and equine feces.

Boreocanthon ateuchiceps (Bates, 1887), restored generic combination

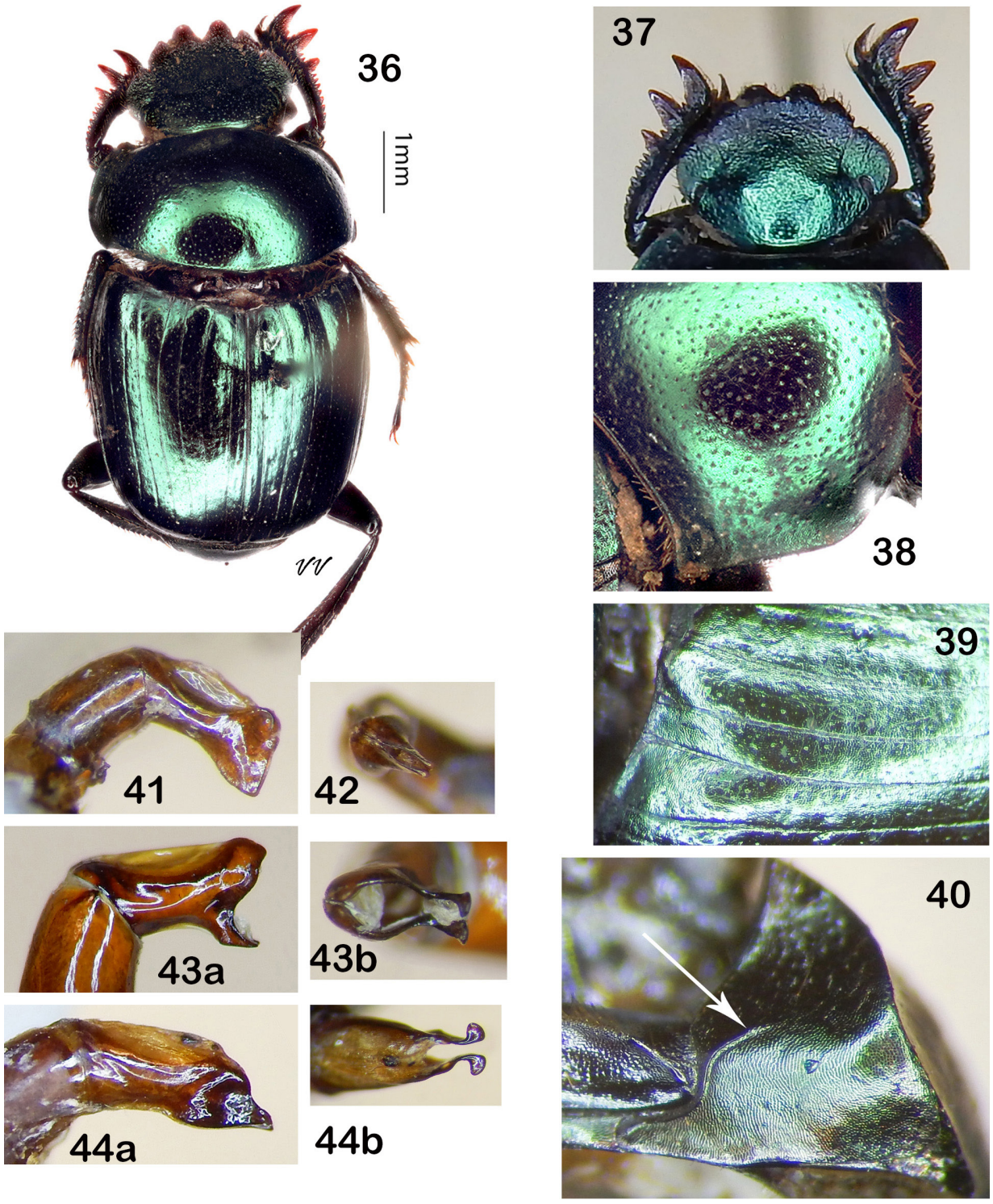
Fig. 36–45

Canthon ateuchiceps Bates 1887: 35.
Boreocanthon ateuchiceps (Bates) (new combination per Halffter 1961: 234).
Canthon (*Boreocanthon*) *ateuchiceps* Bates (new combination per Howden 1966: 727).
Boreocanthon ateuchiceps (Bates), **restored generic combination**.

Type material. Syntype (sex undetermined). The Natural History Museum, London. Not examined.

Type locality. Acapulco (Mexico).

Diagnosis. *Head*: Rugose anteriorly, coarsely punctured posteriorly, punctures denser centrally (Fig. 37). Clypeus quadridentate; paraocular notch conspicuous, setting off salient, rounded angle of paraocular area. Labio-gular



Figures 36–44. *Boreocanthon* and *Canthon* spp. **36–42)** *Boreocanthon ateuchiceps* (Bates). **36)** Habitus, dorsal view. **37)** Dorsal view of head and pronotal margin. **38)** Dorsolateral view of pronotum. **39)** Dorsolateral view of anterior portion of left elytron. **40)** Ventral view of left hypomeron (arrow indicates hypomeral carina). **41)** Lateral view of genital capsule. **42)** Apical view of parameres. **43**) *Canthon floridanus* Brown (= *Canthon imitator* auct.). **a)** Lateral view of genital capsule. **b)** Apical view of parameres. **44)** *Canthon* (*Bajacanthon*) *obliquus* (Horn). **a)** Lateral view of genital capsule. **b)** Apical view of parameres.

fimbria broadly, shallowly V-shaped, apex followed by loose field of coarse, setose punctures. *Prothorax*: Pronotum evenly covered by variable-sized, sharp, well-spaced punctures on highly shiny background, background shagreen largely effaced (Fig. 38); anterior angles only weakly upturned, posterior portion of circumnotal ridge entire, not serrate, posteromedian angle not depressed. Hypomeral carina present, reaching one-fifth distance to lateral prothoracic margin (Fig. 40). *Pterothorax*: Mesoventrite coarsely punctured medially, smooth laterally. Metaventrite evenly, sparsely covered by multi-sized, sharp, fine punctures. *Elytra*: Interstriae (Fig. 39) very shiny, smooth, bright, 2nd and 3rd not swollen anteriorly; discal interstriae with ill-defined, scattered, minute punctures, shagreen background largely effaced. Striae superficial, lateral margins weakly defined; subhumeral (8th) stria finely carinulate; epipleural (9th) stria usually weakly evident at least anteriorly. *Legs*: Inner margin of protibia

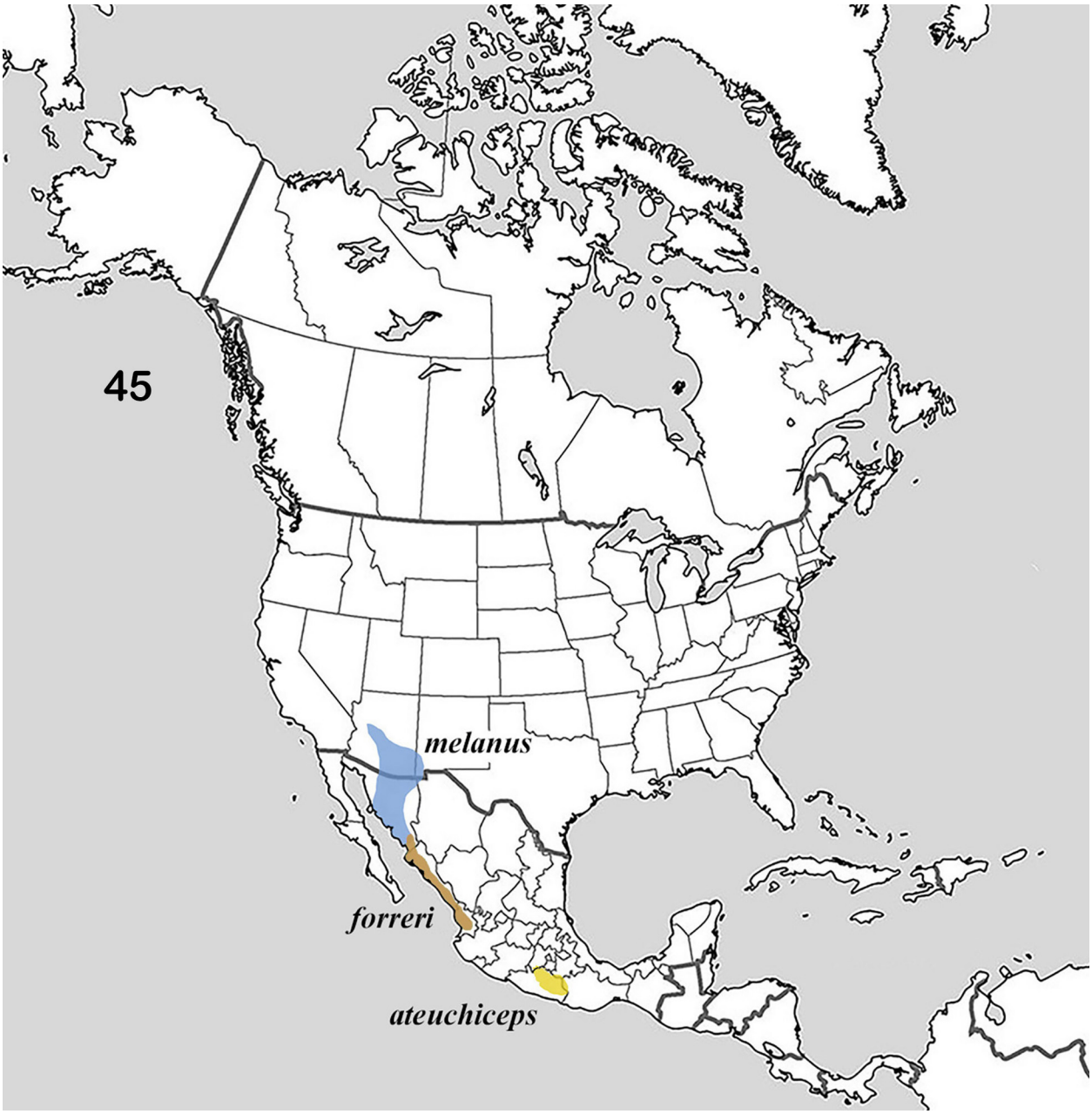


Figure 45. Approximate distributions of *Boreocanthon melanus* (Robinson), *B. forreri* (Bates) and *B. ateuchiceps* (Bates).

not offset; spur sexually dimorphic, acute apically in female, bifurcate in male. Hind femur lacking anterior row of conspicuous setae. *Abdomen*: Pygidium with sparse, shallow punctures on shagreen background. Last (6th) ventrite punctate medially; ventrites 1–5 smooth. *Genital capsule*: Distal portion of parameres triangular (Fig. 41), lower apical angles in form of elongate, rounded knobs (Fig. 42). *General*: Dorsum bright metallic green or yellow-green; venter colored similarly except ventrites 1–5, which are black. Length: 4.5–7.0 mm. *Geographic distribution*: Sierra Madre del Sur, Mexico? (Fig. 45, see Comments below). *Ecogeographic environment*: Tropical Dry Broadleaf Forest biome? *Specimens examined*: 4.

Collection localities. See Comments below.

Comments. Howden (1966) likened this species to *B. forreri*, while Bates (1887) placed it near *Canthon deyrollei* Harold. I do not consider it particularly close to *B. forreri*; it is an outlier species both morphologically and geographically, but, given especially the form of the clypeus and genital capsule, definitely a *Boreocanthon*. *Canthon deyrollei* is a Central American species only remotely related to *Boreocanthon*. *Boreocanthon ateuchiceps* is the only brightly metallic-colored member of the genus; the color of *B. forreri* (q.v.) is much darker, approaching black in some specimens.

My knowledge of this species is very limited. I have been able to directly examine only four specimens labeled "Matamoros Pue. Tlacotli 8-ix-43 F. Islas" collected almost 80 years ago by Federico Islas. I have not been able to identify "Tlacotli" nor confirm that "Pue" means Puebla, and I can only guess that Islas' reference to "Matamoros" is to the Pueblan city or municipality of Izúcar de Matamoros. Howden (1966) mentioned seeing specimens from the states of Guerrero and Mexico in The Natural History Museum (London); I have confirmed their presence there thanks to photographs provided by Max Barclay. Most are labeled "Tejupilco, Mex., Temascaltepec" and "Bejucos, Mex., Temascaltepec". Each of these two towns is the seat of its own eponymous municipality in the state of Mexico, and both are located on the same highway (No. 134) descending southwest from the city of Temascaltepec into the Balsas River basin in southern Mexico. The type, also in London, bears the label "Acapulco, Guerrero Höge." Others there bear the same Islas label as those accompanying specimens I have seen courtesy of Gonzalo Halffter. Islas (1942) himself cited it from "tierra caliente de Guerrero," with no mention of any Puebla locality or Acapulco. Given what little I know, my best guess is that this species is a scarce denizen of the Sierra Madre del Sur, perhaps descending into the Río Balsas valley.

Boreocanthon coahuilensis (Howden, 1966), new generic combination

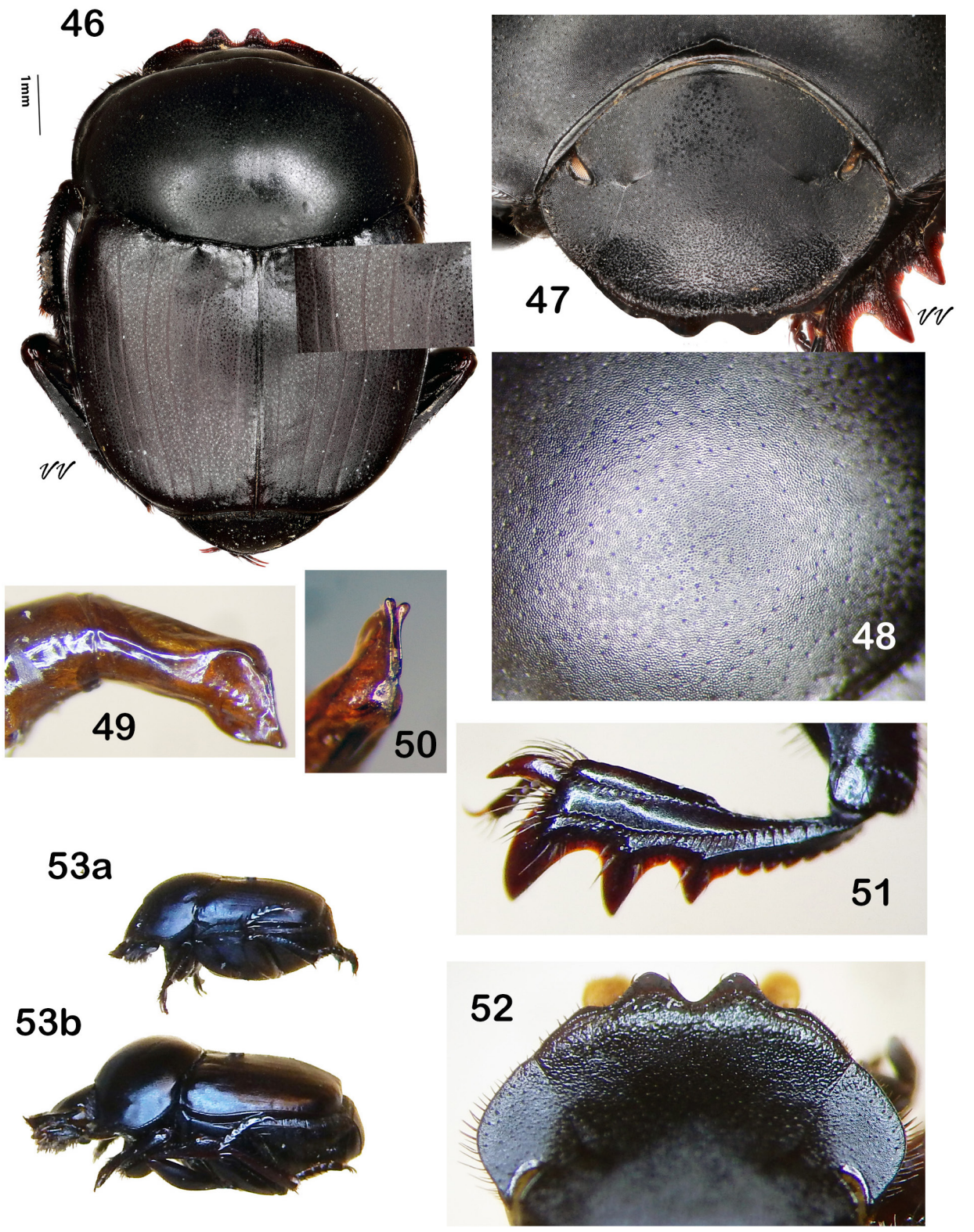
Fig. 46–53, 100

Canthon (Boreocanthon?) coahuilensis Howden 1966: 732.
Canthon (*Boreocanthon*) *coahuilensis* Howden (subgeneric confirmation per Halffter and Martínez 1977: 82).
Boreocanthon coahuilensis (Howden), **new generic combination**.

Type material. Holotype male, Canadian National Collection, Ottawa (CNC312445 = CNC Type No. 9143). Examined by photograph (https://www.cnc.agr.gc.ca/taxonomy/Specimen.php?id=3684).

Type locality. 21 mi SE Saltillo, Coahuila, Mexico, 6000 ft.

Diagnosis. Head: Apical one-third of clypeus very finely rugose, slightly shinier than rest of head; posterior portion of clypeus and frons with dense shagreen and widely spaced, small punctures (Fig. 47). Clypeus usually distinctly quadridentate, if only weakly so; middle teeth moderately developed, rounded apically, separated by broad, rounded emargination; lateral teeth small, weakly angular, sometimes obsolete such that head appears bidentate (Fig. 46–47). Paraocular notch virtually absent, lateral margin of head only very slightly curved inward. Labio-gular fimbria V-shaped, apex extending about one-third length of gula. *Prothorax*: Pronotum convex, elevated above elytral surface (viewed laterally, Fig. 53b), not depressed posteromedially; surface weakly lustrous, silky, with dense shagreen and widely spaced, inconspicuous punctures and numerous weak microspots (Fig. 46, 48); lateral margin very weakly upturned apically. Underside of lateral margin bearing a small rounded tubercle near anterior end, which can be very small or obsolete. Hypomeral carina absent. *Pterothorax*: Mesoventrite minutely punctured laterally. Metaventrite evenly, widely punctate on shagreen background. *Elytra*: Interstriae sculptured like pronotum, 2nd and 3rd not swollen apically, 2nd, 3rd and 5th usually bearing minute tubercle on anterior end (sometimes obscured by pronotal margin). Discal striae (1st–6th) weak, lacking well defined margins,



Figures 46–53. *Boreocanthon coahuilensis* (Howden). **46)** Habitus, dorsal view (inset magnifies elytral sculpturing). **47)** Frontal view of head and pronotal margin. **48)** Dorsal view of portion of pronotum. **49)** Lateral view of genital capsule. **50)** Apical view of parameres. **51)** Anterior view of protibia. **52)** Dorsal view of head. **53)** Comparison of body shape in profile. **a)** *Boreocanthon simplex*. **b)** *Boreocanthon coahuilensis*.

lateral striae (7th–9th) weaker, effaced anteriorly, subhumeral (8th) never carinulate, humeral area with scattered, fine punctures. *Legs*: Inner margin of protibia abruptly widened (offset) at level of basal tooth (Fig. 51); protibial spur sexually dimorphic, apically acute in female, bifurcate in male. Hind femur lacking conspicuous anterior row of long setae. *Abdomen*: Pygidium sculptured like pronotum. Last (6th) ventrite punctate, more strongly so than pygidium; other ventrites shagreened, with few lateral punctures. *Genital capsule*: Compressed apical portion of parameres narrowly triangular (Fig. 49); lower apical angles in form of elongate, rounded knobs (Fig. 50). *General*: Black, pronotum and venter weakly shiny. Length: 5.5–10.0 mm. *Geographic distribution* (Fig. 100): Sierra Madre Oriental in extreme SE Coahuila and neighboring Nuevo Leon, Mexico. *Ecogeographic environment* (Fig. 2): Desert Shrublands biome (Meseta Central matorral ecoregion). *Specimens examined*: 40.

Collection localities.

MEXICO — COAHUILA: *Mpio. Saltillo* ●21 mi SE Saltillo, Coahuila, 6000 ft [Jul] ●Chapinque Mesa, 20 km SE Saltillo, 2050 m [Jul]. **NUEVO LEON**: *Mpio. Galeana* ●4 mi E San Roberto [Jul]; *Mpio. Montemorelos* ●Las Raíces [Aug].

Comments. In his original description, Howden (1966), with some doubt, assigned this species to *Canthon* using the heading "*Canthon* (*Boreocanthon*?) *coahuilensis* n. sp.". That his hesitancy applied to subgeneric rather than generic placement is certain as he expressly (p. 727) treated *Boreocanthon* as a subgenus: "I have treated all [generic and subgeneric] divisions [of *Canthon*] as subgenera, and my assignments of some species considered below are tentative." I gather that his hesitancy to assign *B. coahuilensis* to *Boreocanthon* derived especially from the variation in clypeal dentition that departed from the usual form in other *Boreocanthon*. Nevertheless, he was struck by obvious similarities to *B. simplex*. I agree with Howden's assessment. Indeed, its closest relative appears to be *B. simplex*, with which it shares several common features: moderately to weakly developed clypeal teeth; small paraocular notch; basally effaced 7th and 8th elytral striae, and truncated profile of the parameres. The abruptly offset profile of the inner protibial margin is shared only with *B. depressipennis* and *B. ebenus*. The pronotum of *B. coahuilensis* is rather strongly humped (Fig. 53b), a feature rarely seen in other *Boreocanthon*.

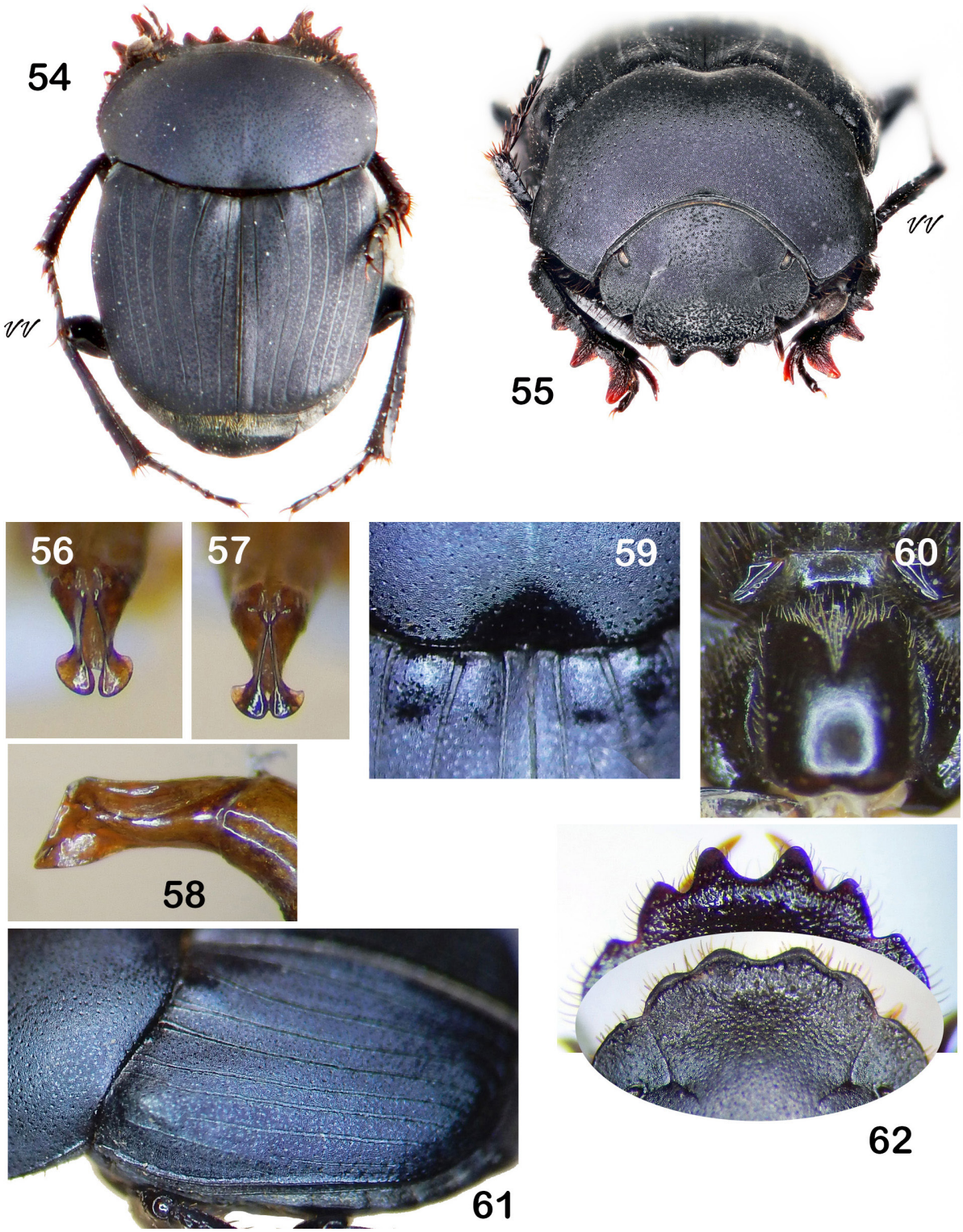
This species is so far known from but four nearby localities in far southern Coahuila and across the state border into the southwest corner of Nuevo Leon. My guess is that it extends farther to the south along the flanks of the Sierra Madre Oriental, at least as far south as southern San Luis Potosí, that is, along the length of the Meseta Central matorral ecoregion (Fig. 2). Its geographical isolation and sharp morphological distinctness bespeaks an early separation from *B. simplex*. Given that it is an arid land species, which regularly exhibit population explosions during sort-lived favorable conditions, I rather doubt that it is rare, or even uncommon, in spite of what appears might be a very localized distribution. Howden's description was based on a type series of 35 specimens collected near Saltillo, Coahuila. For this study, I was fortunate to examine two other series totaling 37 specimens collected from horse and cattle dung by Paul Lago from Chapinque Mesa, Coahuila, and San Roberto, Nuevo Leon, as well as three specimens from the Halffter collection from Las Raíces.

Boreocanthon puncticollis (LeConte, 1866), restored generic combination

Fig. 54–63

Canthon puncticollis LeConte 1866: 381.
Boreocanthon puncticollis (LeConte) (new combination per Halffter 1958: 210).
Canthon (*Boreocanthon*) *puncticollis* LeConte (new combination per Howden 1966: 727).
Boreocanthon puncticollis (LeConte), **restored generic combination**.
Canthon nyctelius Bates 1887: 31 (new synonymy per Schaeffer 1915: 50).
Canthon mixtus Robinson 1948: 91, **new synonymy**.

Type material. 1) *Canthon puncticollis* LeConte: syntype, female. Museum of Comparative Zoology, Harvard University, MCZ-ENT00003698. Examined by photograph (https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:3698). **2)** *Canthon nyctelius* Bates: Syntype (sex undetermined). The Natural History Museum, London. Not examined. **3)** *Canthon mixtus* Robinson: Holotype, male. National Museum of Natural History, Washington, D.C. Not examined.



Figures 54–62. *Boreocanthon puncticollis* (LeConte). **54)** Habitus, dorsal view. **55)** Habitus, frontal view. **56–57)** Apical views of parameres. **58**) Lateral view of genital capsule. **59)** Dorsal view of mid-body (note triangular, posteromedian depression of pronotum and swelling of interstriae). **60)** Ventral view of submentum and gula. **61)** Oblique dorsal view of pronotum and elytron. **62)** Comparison of unworn (above) and heavily worn (below) head margin (dorsal views).

Type localities. 1) *Canthon puncticollis* LeConte: Cape San Lucas, Lower California [Mexico]; **2)** *Canthon nyctelius* Bates: Santa Clara (Chihuahua), Chihuahua City, Durango City (Durango); **3)** *Canthon mixtus* Robinson: Marfa, Texas.

Diagnosis. *Head*: Clypeus (Fig. 55, 62) finely roughened, weakly shiny; remainder of head surface distinctly punctate on shagreen background with very weak microspotting. Sexdentate, clypeal teeth prominent, rounded apically, median pair separated by broadly rounded emargination, paraocular notch large, nearly right-angled, anterior angle of paraocular area obtusely dentate. Labio-gular fimbria broadly V-shaped, constricted apically and reaching about one-third length of gula. *Prothorax*: Pronotum (Fig. 59, 61) boldly, conspicuously punctate, punctures shallow, evenly distributed over entire surface shagreen, microspotting conspicuous. Anterior angles of pronotum only very slightly reflexed; postero-median angle depressed as dark, triangular declivity adjacent anterior ends of first elytral interstriae (Fig. 55, 59). Hypomeral carina absent. *Pterothorax*: Mesoventrite smooth, sometimes with few coarse, median punctures. Metaventrite shiny, evenly covered by small, sharp, evenly dispersed punctures. *Elytra*: Interstriae (Fig. 59, 61) alutaceous, microspotting dense, punctures absent. Striae bold, with crisp, sharply defined edges, especially anteriorly. Anterior ends of 2nd and 3rd interstriae swollen, those of 1st depressed, forming with the adjacent depression of the pronotum a rimless median "crater" or fossa (Fig. 55, 59). Subhumeral (8th) stria carinulate, usually strongly so; epipleural (9th) stria almost always distinct apically, occasionally weakly carinulate. *Legs*: Inner margin of protibia gently curved, not offset. Protibial teeth sexually dimorphic, apically acute in female, bifurcate in male. Metafemora lacking conspicuous anterior row of long setae. *Abdomen*: Pygidium weakly punctured on shagreen background, microspotting weak, apex sometimes more convex and shinier than rest of surface. Sixth ventrite with small median field of coarse punctures, remaining ventrites smooth, impunctate. *Genital capsule*: Compressed distal portion of parameres (Fig. 58) triangular, lower apical angles bearing lateral, ear-like flanges (Fig. 56–57). *General*: Black, usually with strong blue highlights, very rarely with green highlights. Length: 4.0 – 6.5 mm. *Geographic distribution* (Fig. 63): Southern Baja Peninsula and Central Mexico from the Transverse Volcanic Axis to far western Texas and southern Arizona. *Ecogeographic environment* (Fig. 2): Desert and Xeric Shrublands biome. *Specimens examined*: 833.

Collection localities.

MEXICO — AGUASCALIENTES: *Mpio. Aguascalientes* ●15 mi E Aguascalientes. **BAJA CALIFORNIA**: *Mpio. Ensenada* ●4.3 mi W El Rosario [Sep]. **BAJA CALIFORNIA SUR**: *Mpio*. *Los Cabos* ●5 mi N Cabo San Lucas [Oct] ● Santiago ●San José del Cabo ●11 km N Santa Anita [Aug] ●20 km NW Cabo San Lucas, 120 m [Sep] ●22 km NW Cabo San Lucas, 23°01.538′ N 110°04.895′ W, 30 m [Jul] ●4.3 mi SW Miraflores ●Miraflores [Jul]; *Mpio. Mulejé* ●San Venancio [Oct] ●Santa Rosalia; *Mpio. La Paz* ●2.5 mi SE La Huerta, 2200 ft [Oct] ●9.5 mi S San Pedro [Sep] ●3 mi N San Pedro [Jul] ●La Paz [Oct] ●8 mi SE La Paz, 1000 ft [Oct] ●17 mi S La Paz [Sep] ●15 mi W La Paz ●11 mi S Todos Santos, Playa Los Cerritos [Sep] ●2 mi W El Triunfo, 1900 ft [Oct] ●3 mi S El Triunfo [Aug-Sep] ●11.8 mi N El Triunfo [Sep] ●0.5 mi NW El Triunfo, 1800 ft [Oct] ●7 mi W El Triunfo, 1500 ft [Oct] ● Sierra de la Laguna, 3 mi W Cuadaño [Sep] ● Sierra de la Laguna, 5 mi S San Antonio [Sep] ●Sierra de la Laguna, 27 km W Hwy 1 on Ramal a Las Naranjas, 23°14′12″ N 109°57′15″ W, 2450 ft [Jul-Aug] ●3.5 mi W Los Barriles, 500 ft [Dec]; *Mpio. Loreto* ●Canipolé [Oct]. **CHIHUAHUA**: *Mpio. Chihuahua* ●12 km N Chihuahua [Aug]; *Mpio. Janos* ●45 mi NW Casas Grandes [Aug]. **COAHUILA**: *Mpio. Castaños* ●1 mi NE Junction Hwy 53 and Baján Rd.; *Mpio. Ocampo* ●35.5 mi W Ocampo, Laguna La Leche Flats, 27°17.0′ N 102°53.6′ W ●Sierra El Carmen (Maderas del Carmen), 28°59′54″ N 102°36′ 42″ W, 2310 m. [Jul] ●Boquillas del Carmen [Jul]; *Mpio. Saltillo* ●6 km E Saltillo [Jul]. **DISTRITO FEDERAL:** ●Tepeyac [Aug]. **DURANGO**: *Mpio. Cuencamé* ●Hwy 49, 20 km SE Cuencamé; *Mpio. Durango* ●Tapías, 6400 ft [Jun]; *Mpio. Lerdo* ●La Loma, 4100 ft [Aug]; *Mpio. Mapimí* ●Reserva de la Biósfera Mapimí [Jun, Sep]; *Mpio. Ocampo* ●173 mi N Durango [Aug]; *Mpio. Saucillo* ●Estación Conchos [Jun]. **HIDALGO**: *Mpio. Jacala de Ledezma* ●7 mi N Jacala [Jul]; *Mpio. Zimapán* ●Zimapán [Jun]. **OAXACA**: Mpio. Santiago Chazumba ●San Sebastián Frontera [Jul]. **PUEBLA**: Mpio. Tepeyahaulco ●Alchichica [Jun]. **SAN LUIS POTOSÍ**: *Mpio. Guadalcázar* ●19.6 mi N Huizache [Jul]; *Mpio. Matehuala* ●Matehuala [Jul]. **SONORA**: *Mpio. Naco* ●Naco, 5000 ft [Aug]. **ZACATECAS**: *Mpio*. *Villa de Cos* ●Tropic of Cancer marker, Hwy 54 (Zacatecas – Saltillo), ~ 23°26′12″ N 102°12′05″ W, 1958 m [Jul].

UNITED STATES — ARIZONA: *Apache Co*. ●White Mountains, Diamond Creek [Aug]; *Cochise Co*. ●10 mi N Portal [Sep] ●2 mi NE Portal [Jul] ●4 mi NNW Portal, 31°58′ N 109°09′ W, 4600 ft ●13 mi W Gleeson

[Aug] ●Dragoon Mountains, Cochise Stronghold [Jul] ●Dos Cabezas [Aug] ●Palominas [Aug] ●Guadalupe Canyon [Jul] ●Douglas [Jul] ●15 mi E Douglas [Aug] ●Turkey Creek Canyon, Chiricahua Mountains, 31.8657° N 109.4125° W, 1642 m [Jul] ●San Simon [Aug]; *Graham Co*. ●12 mi S Safford [May]; *Mojave Co*. ●17 mi S Wikieup [Aug]; *Pima Co*. ●Tucson [Sep] ●Saguaro National Park (West) [Aug] ●Green Valley [Sep] ●18 mi S Tucson [Jul]; *Santa Cruz Co*. ●Nogales [Aug] ●Santa Rita Mts [Aug]; *Yavapai Co*. ●4 mi N Clarkdale [Jul]. CALIFORNIA: *San Bernadino Co*., New York Mountains [Aug]. **NEW MEXICO**: *Catron Co*. ●5 mi NW Reserve [Jul]; *Doña Ana Co*. ●La Jornada Experimental Range, 15 mi N Las Cruces [Jul-Sep] ●6 km NW Mesilla Dam ●Las Cruces [Jul-Aug] ●1 mi SE Afton Pump Station [Jul] ●10 mi NE Las Cruces, 32.490206 -106.781367, 4523 ft; *Grant Co*. ●Silver City ●8 mi E Silver City [Jul]; *Hidalgo Co*. ●1 mi N Rodeo [Jul]●5 mi N Rodeo [Aug] ●13 mi NE Rodeo [Jul] ●1 mi S Rodeo; *Luna Co*. ●Deming [Jul-Aug] ●6 mi NW Columbus [Jul]; *Otero Co*. White Sands

Figure 63. Approximate distributions of *Boreocanthon puncticollis* (LeConte) and *B. integricollis* (Schaeffer).

National Park, Lake Lucero [Aug] ●Lake Holloman Camp, 32.811° N 106.121° W, 1230 m; *Quay Co*. ●1.1 mi N Tucumcari, 4100 ft [Aug]; *Sandoval Co*. ●4 km NE Sandia, Sandia Pueblo, 35.224547 -106.529917 [Jul]; *Sierra Co*. ●Elephant Butte [Oct] ●Eagles Point, Elephant Butte Reservoir [Aug]. **TEXAS**: *Brewster Co*. ●~17 km W Alpine (Paisano Baptist Encampment), 30°17′37″N 103°47′35″W, 1550 m (Jul) ●Chisos Mountains [Jul] ●15 mi S Marathon [Jun] ●20 mi E Marathon, 30°12′04″ N 102°54′47″ W [Jun] ●Boquillas [Jul] ●Tornillo Creek at Hwy 227, Big Bend National Park [Jul] ●Elephant Butte Wildlife Management Area, 26 mi S Alpine [Apr] ●Big Bend National Park, Buttrill Springs [Jul]; *Culberson Co*. ●17 mi E Van Horn [Jul, Sep] ●4 mi E Kent [Jun]; *Dickens Co*. ●2 mi E Dickens [May]; *Ector Co*. ●Odessa, 31.884°N 102.32°W [Jul]; *El Paso Co*. ●18.5 mi E El Paso, Hueco Mts. [Sep]; *Howard Co*. ●Big Spring; *Hudspeth Co*. ●8 mi W Sierra Blanca, 31.21° N 105.49° W, 1390 m [Aug]; *Jeff Davis Co*. ●Ft. Davis [Jul] ●16 km S Fort Davis (along TX 17), 30°27′48″N 103°58′59″W, 1600 m [Aug] ●Valentine [Jul] ●13 mi E Valentine [Aug] ●~16 km NE Valentine, Muerto Springs Ranch (Muerto Springs, near headquarters), 30°40′28″N 104°24′07″W, 1475 m [Jul] ●8 km SE Fort Davis (via TX 118), Chihuahuan Desert Research Institute (Visitor Center area), 30°32′32″N 103°50′11″W, 1555 m [Aug] ●Chihuahuan Desert Research Institute (Quarry Unit), 30°32′06″N 103°50′37″W, 1480 m [Aug–Sep]; *Pecos Co*. ●25 mi W Fort Stockton [Jul]; *Motley Co*. (no data) [May]; *Presidio Co*. ●C.E. Miller Ranch (~16 km W Valentine), 30°32′50″N 104°39′40″W (Camp Holland) 1410 m (Aug) ●~16 km W Valentine (Miller Ranch, near headquarters), 30°33′30″N 104°38′44″W, 1350 m [Jul–Aug] ●~6.5 km W Marfa (Hip-O Ranch), 30°21′54″N 104° 7′12″W, 1530 m [Aug–Sep] ●Pinto Canyon Ranch (~58 km SSW Marfa on FM 2810), 30°01′18″N 104°27′42″W (headquarters area), 1475 m [Aug] ●Dalquest Research Site, 29°33′30″N 103°47′30″, 1010 m [Sep]; ●37 km SSW Marfa (along FM 2810, Petan Ranch – Cherry Hills sector), 30°07′35″N 104°19′24″W, 1630 m [Jun] ●20–26 km SSE Marfa (along FM 169), 1355–1415 m [Jun] ●3 km NE Marfa (along FM 1112), Marfa Golf Course, 30°19′40″N 103°59′41″W, 1470 m [Jul, Sep] ●~30 km SSE Marfa (along FM 169), Humphreys Ranch, 30°02′30″N 104°01′00″W, 1285 m [Jul] ●~8km W La Viuda Peak, 29°42′30″N 103°54′30″, 1200 m [Sep] ●~19 km E Marfa (via US 90/67), 30°16′07″N 103°48′44″W, 1565 m [Jul] ●~3 km N Marfa (along TX 17), 30°20′27″N 104°01′7″W, 1500 m [Jul] ●near Plata (FM 169/Alamito Creek bridge) Kennedy Ranch (headquarters), 29°52′16″ N 103°59′28″ W, 1200 m [Jun] ●Pinto Canyon Ranch (~65 km SSW Marfa on FM 2810), 29°59′54″N 104°30′48″W (Pinto Canyon Creek), 1460 m [Aug] ●7 mi N Presidio [Oct] ●Big Bend Ranch State Park, La Cuesta Campground, 29.298° N 103.954° W [Aug] ●FM 170 (River Road) jct. Casa Piedra Rd., 8 mi NW Redford ●2.5 mi S Shafter [Jun]; *Terrell Co*. ●Sheffield [Jun] ●~15 mi W Sanderson, Hwy 90 at Longfellow Draw, 30°09.7′ N 102°38.2′ W, 3380 ft [Apr] ●Oasis Ranch, Independence Creek, 15 mi S Sheffield, 595 m, 30.4665° N 101.8008° W [May]; *Tom Green Co*. ●12.8 km N San Angelo [Oct]; *Ward Co*. ●1 mi SE Barstow [Jul].

Comments. *Boreocanthon puncticollis* is a common species in arid central Mexico and the southwestern United States as well the southern portion of the Baja Peninsula. It is sister species to *B. integricollis* (q.v.), with which it shares apically flanged parameres, strong ("crisp") dorsal sculpturing, and tumid 2nd and 3rd elytral striae. The apical flanges of the parameres vary somewhat in shape (Fig. 56–57), but the variation is subtle and appears continuous and taxonomically insignificant.

Besides its presence in the southern portion of the Baja California Peninsula, this species is widely distributed across the arid highlands (Altiplano) of Mexico between the Sierra Madre cordilleras flanking it on the east and west, from which it ranges into Arizona, New Mexico and the western portion of Texas. Whether or not the Baja California Sur distribution of *B. puncticollis* is truly disjunct from its distribution on the mainland remains an open question. My inclination is that it is, indeed, isolated as shown in Figure 63. The northern portion of the Sonoran Desert (i.e., the Yuma Desert portion of the Sonoran Desert) appears to produce a collective void in the distribution of the genus. (See biogeographical comments in the Introduction.) In their analysis of dung beetle ecology in Mexican arid zones, Halffter et al. (2012) pointed out that "… only few species … range across the expansive arid zones [of Mexico]. These species are widely distributed and co-occur in the dry habitats of the northern Mexican Altiplano and southwest of the United States … *Canthon* (*Boreocanthon*) *puncticollis* is distributed in the desert zones of Baja California, Arizona and Chihuahua, arid zones of the Mexican Altiplano (even near Barranca de Metztitlán [Hidalgo], with a southern limit in Tehuacán [Puebla-Oaxaca]." I have seen several specimens of *B. puncticollis* from the Tehuacán–Cuicatlán desert region of Puebla/Oaxaca, Mexico, and suspect

that this region marks the southernmost point of its distribution. I have seen a single specimen labeled Puente de Ixtla, Morelos, but its presence there needs confirmation.

Blume's (1972) reference to *B. puncticollis* in Kerr and Bexar counties, Texas, is likely incorrect and should probably read *B. integricollis.* As far as I know, *B. puncticollis* does not occur as far east as the Edwards Plateau of central Texas. This species is commonly collected along with *B. praticola* throughout the Texas–New Mexico–Arizona portion of its range. As with most other congeners, this species is poorly known biologically. Edmonds (2016) reported it to be diurnal and a generalist feeder (cattle, human, and equine feces) inhabiting grassland and open scrub habitats in the Big Bend region of west Texas; M. J. Paulsen (pers, comm.) reported collecting it from burrows (probably a species of ground squirrel) in Hudspeth County, Texas. Lobo (1996) collected specimens in low numbers from cattle dung in various desert habitats at Mapimí Biosphere Reserve in northern Durango, Mexico, where the dung beetle fauna was overwhelmingly dominated by two introduced scarabaeines, *Digitonthophagus gazella* (Fabricius) an *Euoniticellus intermedius* (Reiche) (see Edmonds 2018).

LeConte's (1866) original description of *Canthon puncticollis* was based on two specimens from "Cape San Lucas, Lower California." The description is somewhat ambiguous in several respects, but the photographs of the syntype I have examined clearly show the salient features used here to diagnose this common species. Bates (1887) distinguished his species, *Canthon nyctelius*, from *B. puncticollis* by its having a "… remarkable depression at the base of the thorax and elytra, and the corresponding elevation of the second and third elytral interstices at their base." Schaeffer (1915), in his argument supporting their synonymy, pointed out that *B. puncticollis* also shares this feature and noted that it was not clearly mentioned by LeConte (1866) in his description. Bates (1887) did not consider *B. puncticollis* in his work and probably did not have specimens on hand to compare with his species, prompting him to rely on LeConte's description for comparison. In addition to the syntype cited above, there is another probable syntype also present in the LeConte Collection at the Museum of Comparative Zoology, Harvard University (Crystal Maier, pers. comm), and the two specimens are almost certainly LeConte's original type series.

Robinson (1948) based his description of *Canthon mixtus* on three specimens. I was not able to examine the holotype, which resides in the USNM collection in Washington, D.C. However, I have examined the paratype referenced by Robinson from the Casselberry Collection, now deposited in the collection of the American Museum of Natural History. It lies well within the taxonomic limits I adopt here for *B. puncticollis*, which I here regard as senior synonym. My references (Edmonds 2018) to *Canthon mixtus* in western Texas should now be taken as *B. puncticollis*.

Boreocanthon integricollis (Schaeffer, 1915), restored generic combination

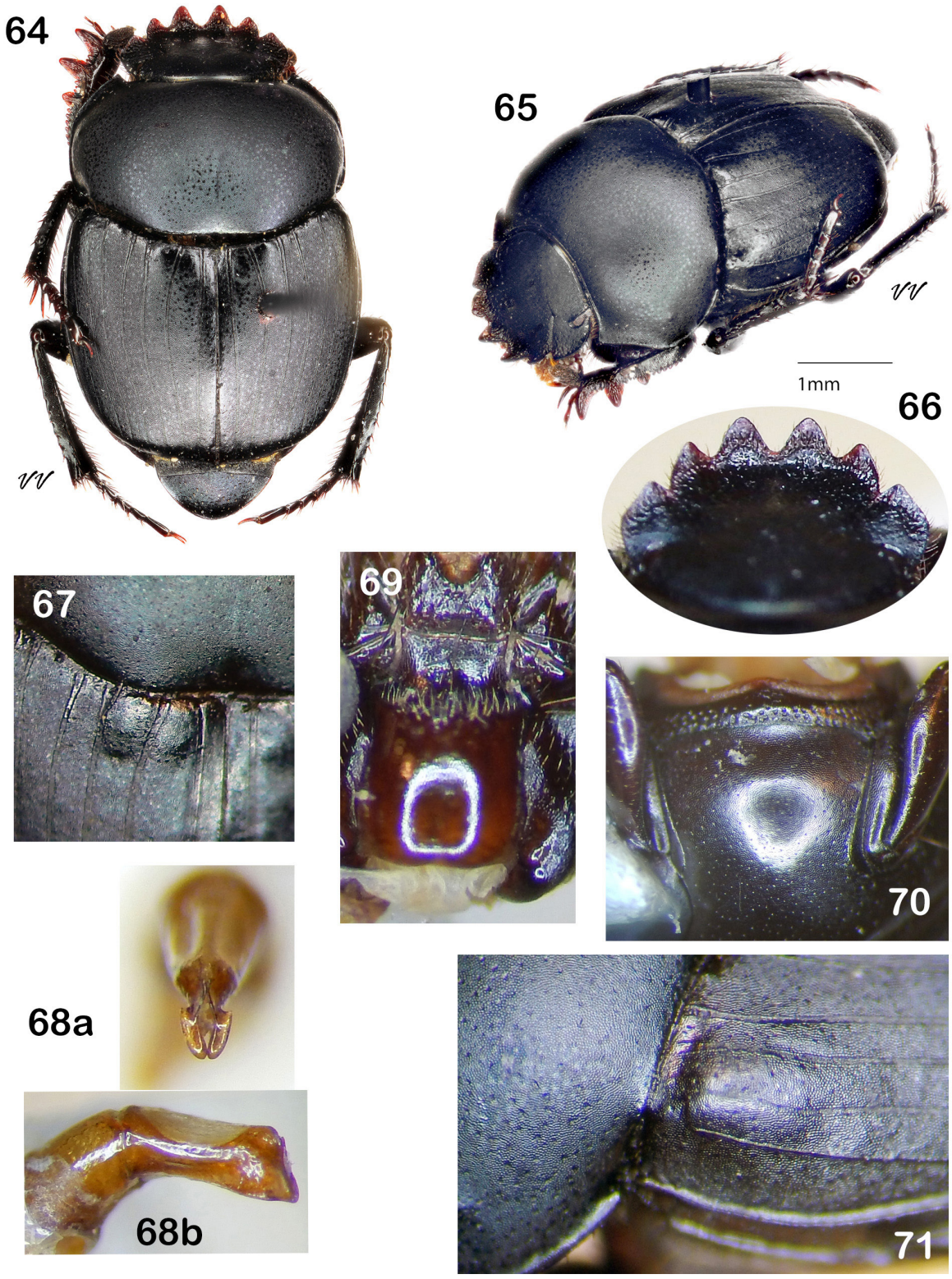
Fig. 63–71

Canthon puncticollis var. *integricollis* Schaeffer 1915: 50.
Canthon integricollis Schaeffer (new status per Robinson 1948: 90).
Boreocanthon integricollis (Schaeffer) (new combination per Halffter 1958: 210).
Canthon (*Boreocanthon*) *integricollis* Schaeffer (new combination per Howden 1966: 727).
Boreocanthon integricollis (Schaeffer), **restored generic combination**.

Type material. Syntype (sex undetermined). National Museum of Natural History, Washington, D.C. Not examined.

Type localities. Hidalgo and Brownsville, Texas; Santa Rita Mountains, Arizona (see Comments below).

Diagnosis. *Head*: Margin strongly sexdentate (Fig. 66), anterior one-half of clypeus rugose and moderately shiny; remainder of head surface flat, with fine, shallow punctures on dense shagreen. Paraocular notch strong, setting off angulate, anteriorly-directed, toothlike angle of paraocular area. Middle clypeal teeth narrowly rounded apically, separated by rounded, V-shaped emargination; lateral teeth strong, rounded apically. Labio-gular fimbria (Fig. 69) gently curved posteriorly, often interrupted medially by coarse punctures. *Prothorax*: Pronotum (Fig. 65, 71) covered by dense shagreen, punctured, punctures scattered, somewhat larger, deeper than those on head, microspots numerous; anterior angles weakly, narrowly reflexed; posteromedian angle at most only slightly impressed. Hypomeral carina vestigial. *Pterothorax*: Mesoventrite (Fig. 70) densely, coarsely punctured. Metaventrite (Fig. 70) with widely spaced, small punctures on dense shagreen. *Elytra*: Interstriae (Fig. 64, 67, 71) with



Figures 64–71. *Boreocanthon integricollis* (Schaeffer). **64)** Habitus, dorsal view. **65)** Habitus, anterodorsal view. **66)** Dorsal view of head. **67)** Dorsal view of mid-body. **68)** Genital capsule. **a)** Lateral view. **b)** Apices of parameres. **69)** Ventral view of labium and gula. **70)** Ventral view meso- and metaventrites. **71)** Dorsolateral view of pronotum and elytron.

dense shagreen and numerous microspots; anterior ends of 2nd and 3rd usually only weakly raised, 1st interstriae depressed. Striae well delineated, with sharp, carinulate lateral margins, especially anteriorly. Subhumeral (8th) stria sharply carinate basally; epipleural (9th) stria almost always visible at least posteriorly. *Legs*: Inner margin of protibia straight or only very gently curved; protibial spur sexually dimorphic, apex acute in female, bifurcate in male. Metafemora lacking row of long setae along anterior surface; ventral surface punctured, with few short setae. *Abdomen*: Pygidium weakly punctate, with dense shagreen; apex weakly tumid, shinier than base. Sixth ventrite punctured; remaining ventrites with dense shagreen, lacking distinct punctures. *Genital capsule*: Compressed apical portion of parameres narrowly triangular (Fig. 68b); lower apical angles in form of elongate flanges (Fig. 68a). *General*: Black, dull, sometimes with weak blue highlights. Length: 4.0 – 5.5 mm. *Geographic distribution*: Endemic to south Texas and adjacent Mexico along the Rio Grande (Fig. 63). *Ecogeographic environment*: Xeric Shrublands and Tropical Grassland biomes (Western Gulf coastal grasslands, Tamaulipan mezquital and Tamaulipan matorral ecoregions). *Specimens examined*: 55.

Collection localities.

MEXICO — NUEVO LEON: *Mpio*. *San Nicolás de los Garza* ●San Nicolás de los Garza [Sep].

UNITED STATES — TEXAS: *Bastrop Co*. ●Bastrop [Apr] ●6 mi N Bastrop, Camp Swift [Nov]; *Cameron Co*. ●7.4 mi ENE jct. hwys 48 & 511 [Aug] ●Laguna Atascosa National Wildlife Refuge [Oct]; *Dimmit Co*. ●Chaparral Wildlife Management Area [Mar-May]; *Duval Co*. ●2.2 mi W Freer [Sep] ●5 mi S Realitos [Mar]; *Frio Co*. ●US Hwy. 57, 20.6 mi W route I-35 [Apr]; *Hidalgo Co*. ●Santa Ana National Wildlife Refuge [Oct] ●Las Palomas Wildlife Management Area (Penitas Unit) [Apr]; ●Bentsen-Rio Grande Valley State Park [May]; *Jim Wells Co*. ●Ben Bolt [Jun]; *Lee Co*. ●Fedor [May]; *Kleberg Co*. ●Kingsville [Sep]; *La Salle Co.* ●Chaparral Wildlife Management Area, 8 mi W Artesia Wells [Oct]; *Live Oak Co*. ●8 and 12 mi S George West [May]; *McMullen Co*. ●20 mi N Freer (Duval Co.) [Oct]; *Starr Co*. ●6 mi S La Gloria [Jun] ●Falcon Woodlands, Falcon Dam [Apr] ●Falcon State Park, 26°35.22′ N 99°08.82′ W, 270 ft [Oct]; *Uvalde Co*. ●7 mi W Uvalde [Jun]; *Webb Co*. ●16 mi NW Freer [Aug].

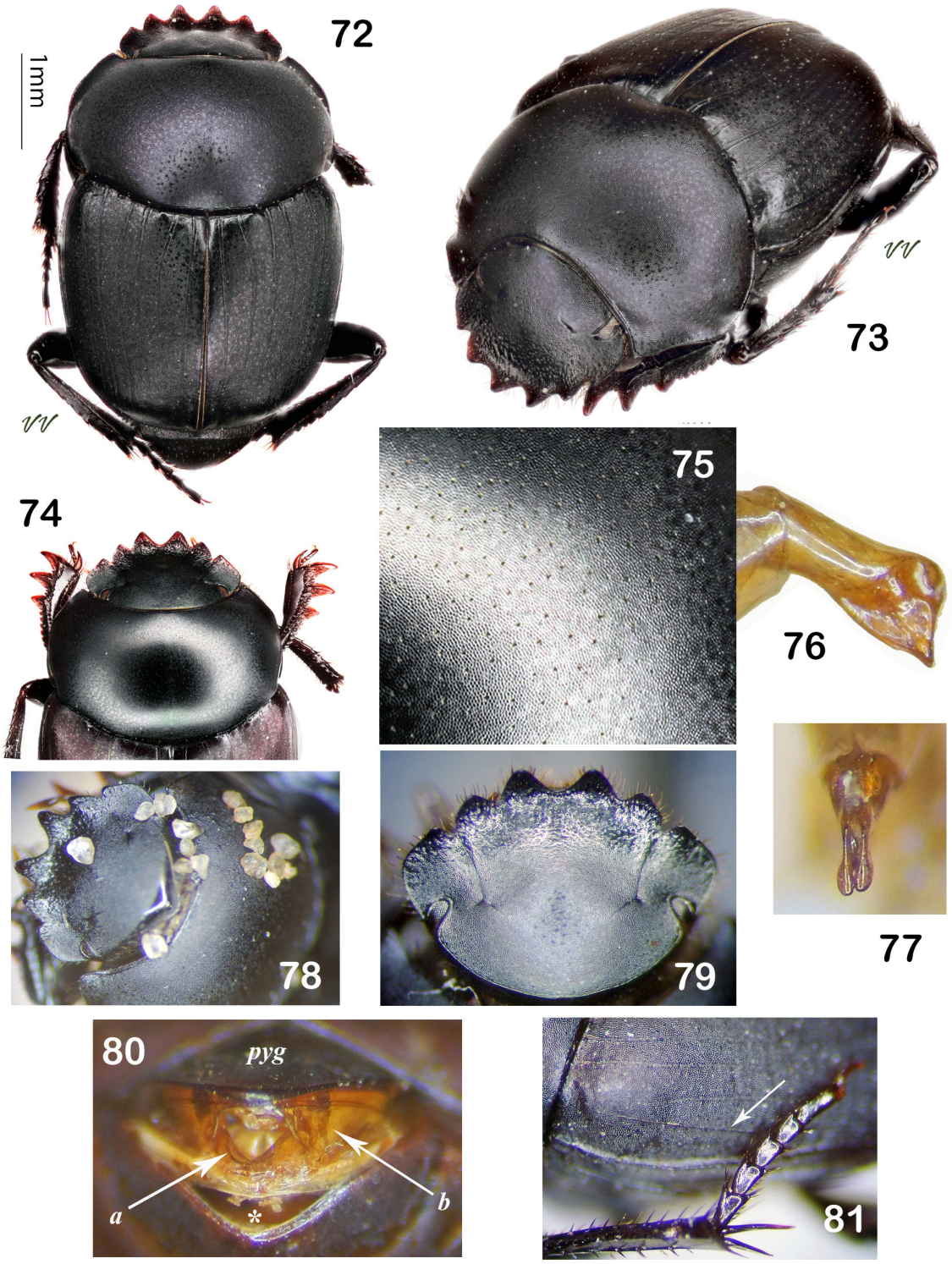
Comments. Schaeffer (1915) included specimens from the Santa Rita Mountains (Santa Cruz Co., Arizona) in his type series of "var. *integricollis*", which he distinguished from *B. puncticollis* by its lack of a mid-dorsal depression at the base of the elytra. I have not seen these specimens, but I suspect that they are assignable to *Boreocanthon melanus*, which occurs along with "good" *B. puncticollis* in the Santa Rita Mountains region. In any case, future designation of a lectotype from Schaeffer's syntypic series is in order to fix the species name to the concept of *Boreocanthon integricollis* presented here. I have seen two specimens from Hidalgo, Texas, from the Charles Schaeffer Collection currently housed at the California Academy of Science, which are definitely *B. integricollis* as defined here and possible syntypes.

I regard *B. integricollis* and *B. puncticollis* (q.v.) as sister species The former can be confused with *B. probus*, with which it can occur in scattered localities in southern Texas. Both have the head margin strongly sexdentate and an often shiny anterior portion of the clypeus, but they are clearly distinguished by pronotal and mesoventrite sculpturing and shape of the apical angles of the parameres. I have seen but one specimen from Mexico, from the environs of the city Monterrey about 125 miles south of Laredo, Texas; I would expect it to occur throughout northern Nuevo Leon and adjacent Tamaulipas. The biology of this species is essentially unknown. I have one rather tantalizing record of its capture in Cameron County, Texas, in a Berlese funnel at a pack rat nest.

Boreocanthon probus (Germar, 1823) restored generic combination

Fig. 72–82

Ateuchus probus Germar 1823: 98.
Canthon probus (Germar) (new combination per LeConte 1863: 36).
Boreocanthon probus (Germar) (new combination per Halffter 1958: 210).
Canthon (*Boreocanthon*) *probus* (Germar) (new combination per Howden 1966: 727).
Boreocanthon integricollis (Schaeffer), **restored generic combination**.
Coprobius minor Sturm 1843: 104 (new synonymy per Blanchard 1885: 165, as *Canthon minor* [Sturm]) **nomen nudum**.
Canthon abrasus LeConte 1859c: 11 (new synonymy per Horn 1870: 45).



Figures 72–81. *Boreocanthon probus* (Germar). **72)** Habitus, dorsal view. **73)** Habitus, oblique anterolateral view. **74)** Dorsal view forebody. **75)** Area of pronotal surface. **76)** Lateral view of genital capsule. **77)** Apical view of parameres. **78)** Dorsal view of forebody with adherent white sand grains. **79)** Dorsal view of head. **80)** Apical view of female abdomen (pyg = pygidium; arrow [a] indicates apex of paraproct; arrow [b] indicates flange of pygidial margin; asterisk marks breach in intersegmental membrane, not a natural orifice). **81)** Dorsolateral view of elytron (arrow marks carinulate 8th stria).

Type material. 1) *Ateuchus probus* Germar: Syntype (sex undetermined), Museum für Naturkunde, Berlin. Examined by photograph, courtesy Fernando Vaz-de-Mello. **2)** *Coprobius minor* Sturm: Unknown to me; **3)** *Canthon abrasus* LeConte: Unknown to me.

Type localities. 1) *Ateuchus probus* Germar: North America (Kentucky); **2)** *Coprobius minor* Sturm: America borealis; **3)** *Canthon abrasus* LeConte: Georgia.

Diagnosis. *Head*: Anterior one-half clypeus finely roughened and sometimes highly reflective (Fig. 79), forming bright band behind marginal teeth; remainder of surface dull, alutaceous, minutely punctured; head margin strongly sexdentate (Fig. 74, 79), clypeal teeth strong, rounded apically, paraocular notch acute, anterior angle of paraocular area produced as strong tooth. Labio-gular fimbria gently bowed posteriorly, often followed medially by elongate field of coarse, setose punctures. *Prothorax*: Anterior angles (Fig. 73) at most weakly upturned (more so in western populations). Surface (Fig. 75) alutaceous with dispersed puncturing and compact microspotting, appearing smooth, weakly shiny to dull (especially in western populations), not depressed posteromedially. Hypomeral carina either absent or only weakly indicated. *Pterothorax*: Mesoventrite smooth, at most with few punctures. Metaventrite moderately shiny, with very small, evenly dispersed, widely spaced punctures. *Elytra*: Interstriae shagreened, with dense field of microspotting; 2nd and 3rd intervals not distinctly raised, 3rd and 5th lacking distinct tubercle on anterior margin. Striae superficial, edges sharp, especially basally; subhumeral (8th) stria often carinulate (Fig. 81; especially western populations); epipleural (9th) stria effaced. *Legs*: Protibia gradually widened, inner margin not offset; apical spur sexually dimorphic, apex acute in female, bifurcate in male. Metafemur lacking conspicuous row of setae along anterior margin. *Abdomen*: Pygidium sculptured like elytra, sometimes noticeably more convex medially. Last visible (6th) ventrite punctate along posterior margin, sometimes with small, median bump. *Genital capsule*: Compressed distal portion of parameres abbreviated, in form of equilateral triangle (Fig. 76); ventral apical angles acute, capped by elongate knobs (Fig. 77). *General*: Length: 4.0 – 5.5 mm. Dorsum dull black, pronotum sometimes with weak, green luster. *Geographic distribution*: Broad southerly region of United States from Atlantic coast to Rocky Mountains (Fig. 82, and see Comments). *Ecogeographic environment* (Fig. 2): Temperate Grasslands, Savannas and Shrublands biome. *Specimens examined*: 719.

Collecting localities:

UNITED STATES — ALABAMA: *Dale Co*. ●Fort Rucker Military Reservation [Apr, Jun]; *Shelby Co*. ●Longview. **ARKANSAS**: *Little River Co*. ●11mi NE Texarkana. **COLORADO**: *Morgan Co*. ●12 mi E Brush, 4280 ft; *Yuma Co*. ●5 mi W Joes. **FLORIDA**: *Alachua Co*. ●Gainesville Airport [Sep] ●3.4 mi WNW mi W Archer [Aug] ●0.75 mi W Archer [Jun]; *Bay Co*., ●26.5 km NNW Panama City Beach, Pine Log State Forest, 30°24′17″ N 85°53′14″ W[Oct]; *Charlotte Co*. ●27°01.224′ N 81°57.573′ W [Mar]; *Dade Co*. Miami [Mar-Sep]; *Duval Co*. ●Jacksonville; *Gilchrist Co*. ●5 mi W Newberg [Jun]; *Hernando Co*. ●Brooksville [Jul]; *Highlands Co*. ●Archbold Biological Station [Feb-Jun] ●Hammock State Park [Jun] ●Sebring [May]; *Hillsborough Co*. ●Lutz [Feb-Apr] ●Hillsborough River State Park [Mar] ●Tampa [Apr]; *Indian River Co*. ●Vero Beach [Nov]; *Lafayette Co*. ●Picket Lake [Mar]; *Lake Co*. ●Forest Hills [Feb]; *Lee Co*. ●3.4 mi NW Koreshan State Park [Apr]; *Levy Co*. ●3.8 mi SW Archer [Mar]; *Liberty Co*. ●Apalachicola Bluffs & Ravines Preserve, Alum Bluff [Jun]; *Marion Co*. ●Citra [Apr]; *Martin Co*. ●Jonathan Dickenson State Park [Dec]; *Miami-Dade Co*. ●North Miami [Jul]; *Okaloosa Co*., ●Elgin Air Force Base (Range 51) [Mar]; *Osceola Co*. ●Kissimmee; *Orange Co*. ●Orlando [May] *Palm Beach Co*. ●Boca Raton [Aug]; *Pasco Co*. ●7 mi E Bayonet Point [Aug]; *Pinellas Co*. ●Dunedin [Feb-Mar]; *Polk Co*. ●Tiger Creek Preserve, 27°48′42″ N 81°29′24″ W [Jun]; *Putnam Co*. ●Interlachen [May] ●3 mi W Interlachen [Mar]; *St. Lucie Co*. ●(no data) [Jan]; *Suwannee Co*. ●Suwannee River [Aug] ●Branford [Aug]; *Taylor Co*. ●Blue Springs Lake [Jun] ●Steinhatchee. (See also Woodruff 1973 for additional Florida records.). **GEORGIA**: *Baker Co*. ●Newton, Ichauway Ecological Reserve [May]; *Burke Co*. ●10.2 km NW Girard, Yuchi Wildlife Management, 33°05′13″ N 81°48′17 W″ [Mar-Apr]; *Cobb Co*. [Aug]; *Decatur Co*. ●Spring Creek [Apr, Jun-Aug]; *Dougherty Co*. ●Albany [Sep]; *Emanuel Co*. ●Ohoopee Dunes, 32°31′51″ N 82°27′23″ W ●George L. Smith State Park, 32.5503° N 82.1261° W [Jun] ●Swainsboro [Jul-Aug]; *Glynn Co*. ●Brunswick [Jun]; *Haralson Co*. ●Bremen [May]; *Johnson Co*. ●1 mi E Kite [Aug]; *Lamar Co*. ●Milner [Aug, Nov]; *Lowndes Co*. ●Vidalia [Aug, Oct]; *McIntosh Co*. ●Sapelo Island, Nanny Goat Beach, 31.39065° -81.26533° [May]; *Monroe Co*. ●Bolingbroke [Aug]; *Montgomery Co*. ●Uvalda [Sep]; *Richmond Co*. ●Augusta [Mar] ●12.5 km SW Augusta, 33°20′20″ 82°09′25″**W**; *Spalding Co*. ●(no data) [Feb. Apr]; *Telfair Co*. ●McRae [Jul]; *Tift Co*. ●Tifton [Jul]; *Toombs Co*. ●Vidalia [Aug]; *Walker Co.*

●Head River [Aug]; *Ware Co*. ●Waycross [Sep]; *Wheeler Co*. ●Alligator Creek Wildlife Management Area, 21.8 km SSE Alamo, 31.96704 N 82.68711 W [Oct]. **KANSAS**: *Phillips Co*. (no data); *Reno Co*. ●Medora [Jun-Jul]; *Republic Co*. (no data); *Seward Co*. (no data) [Jul]. **LOUISIANA**: *Natchitoches Par*. ●Vowells Mill. **MARYLAND**: *Anne Arundel Co*. ●Glen Burnie [Jul-Aug]; *Dorchester Co*. ●3 mi E Hurlock [May]; *Worcester Co*. ●Nassawango Iron Furnace Site [Aug]. **MISSISSIPPI**: *Forrest Co*. ●Hattiesburg [Aug]; *Lincoln Co*. ●Wesson [May]; *Oktibbeha Co*. ●Starkville [Apr]. **MISSOURI**: *Lewis Co*., ●7 mi S LaGrange, Wakonda State Park [Jun]. **NEBRASKA**: *Dundy Co*., Haigler [Jul]; **NEW JERSEY**: *Atlantic Co*. ●Weymouth [Jun]; *Burlington Co*. ●Masonville [Aug] ●Bridgeboro [Sep] ●Rancocas State Park [Jun-Jul] ●Woodland Township [Aug] ●Washington Township, Wharton State Forest [Aug] ●Bass River Township, East Plains [Jul] ●Warren Grove [Aug-Sep] ●Browns Mills [Aug]; *Camden Co*. ●Clementon [May]; *Ocean Co*. ●Manchester [Sep]; ●Lakehurst [Sep] ●Union Township [Aug]. **NEW MEXICO**: *Chavez Co*. ●38 mi E Roswell, Mescalero Sand Dunes [Jul]; *Curry Co*. ●19 mi N Clovis [Jun]; *DeBaca Co*. ●15 mi SE Fort Sumner [May]; *Eddy Co*. ●26 mi E Carlsbad [Jul]; ●Waste Isolation Pilot Plant, 32°21.4′ N 103°46.9′ W [Jul] ●Artesia [Jun-Jul]; *Guadalupe Co*. ●Santa Rosa [Jun]; *Lea Co*. ●Crossroads [Apr]; *Otero Co*. ●White Sands [Jun]; *Quay Co*. ●10.5 mi NE Logan, 3850 ft [Aug]; *Roosevelt Co*. ●Oasis State Park [Jul-Aug] ●8 mi NE Portales, ENMU Natural History Reserve, [Jun-Sep]. **NORTH CAROLINA**: *Moore Co*. ●Southern Pines [Jun-Aug]. OKLAHOMA: *Carter Co*. ●Ardmore [Jul]; *Logan Co*. ●Hwy I-35 at Cimarron River [Apr]; *Payne Co*. ●(no data) [May]; *Woods Co*. ●(no data) [Jul]. **SOUTH CAROLINA**: *Aiken Co*. ●5.3 mi E Montmorenci [Mar]; *Horry Co*. ●Myrtle Beach [Jun]; *Kershaw Co*. ●Cassatt [Nov]; *Pickens Co*. ●Clemson [Apr-May]. **TEXAS**: *Bexar Co*. ●3 mi S junction route 281 and Loop1604 [Nov]; *Brazos Co*. ●College Station [Apr]; *Comal Co*. ●(no data) *Crane Co*. ●junction routes 1053 and 1233 (sandhills) [Jun]; *Dallas Co*. ●Dallas; *Dimmit Co*. ●4 mi W Carrizo Springs [Sep]; *Erath Co*. ●Stephenville [Aug]; *Frio Co*. ●4 mi W Dilley [Oct]; ●8 mi S Moore; *Gillespie Co*. ●7 mi S Doss [Apr]; *Hall Co*. ●Memphis; *Harrison Co*. ●Karnack [Jun]; *Howard Co*. ●Big Spring [Aug]; *Kerr Co*. ●Kerrville [Aug]; *Kinney Co*. ●20 mi E Brackettville [Apr, Oct]; *Lee Co*. ●Fedor; *Tarrant Co*. ●Arlington [Sep]; *Uvalde Co*. ●Uvalde [Jun] ●7 mi W Uvalde [Jun]; *Val Verde Co*. ●Devils River at Dolan Falls [Jul]; *Ward Co*. ●1 mi E Monahans [Mar, Jul] ●Monahans Sandhills State Park [Aug]; *Willacy Co*. ●Point Mansfield [May] (see Comments); *Winkler Co*. ●10 mi NE Kermit, 31°56′24.6″ N 102°58′41.3″ W, 928 m [Jun] ●16 mi NE Kermit, 31°57′13″ N 102°58′15″ W [Oct].

Comments. Germar (1823) cited "America septentrionale (Kentucky)" as the type locality for his species, but I have seen no specimens from that state nor any bordering state. Dajoz' (1994; cited by Lobo 2000) reference to *Canthon probus* in the Peloncillo Mountains of southeastern Arizona likely refers to *B. puncticollis*.

Blanchard (1885) synonymized *B. probus* and *Coprobius minor* Sturm (as *Canthon minor*) without indicating the basis for his action or any reference to a description. The synonymy was noted by Woodruff (1973), Harpootlian (2001) and Ratcliffe and Paulsen (2008). Since Sturm's name was published without description, it is a nomen nudum. Horn (1870) synonymized *Canthon probus* and *C. abrasus* LeConte, and noted "I have no hesitation in uniting the species of LeConte to that of Germar, and although some slight differences exist between the description and LeConte's unique, it must be remembered that both species have been described from single specimens." I do not know if Horn's statement "single specimens" is accurate. Lacking any information to the contrary, however, I accept Horn's opinion taking into account that, in the context of this study, the type locality of *C. abrasus*, Georgia, is home to only two species of *Boreocanthon*: *B. depressipennis* and *B. probus*.

A somewhat reliable identification flag for *B. probus* is an strongly sexdentate head with the clypeal teeth usually followed by a band of shiny integument (Fig. 79). This glossy anterior portion of the clypeus contrasts markedly with the dull, shagreened expanse of the remaining head surface and marks specimens from throughout its range. Populations in eastern New Mexico and adjacent western Texas east of the Pecos River can closely resemble *B. halffteri* (q.v.), a similarity supporting the idea that it derives from *B. probus* (see below). Southwestern populations also tend to be darker and less lustrous than eastern populations and can lack the shiny clypeal band altogether; moreover, pronotal punctures tend to be larger, more conspicuous, anterior angles more prone to be upturned, as well as higher frequency finely carinate 8th elytral stria. It is intuitively tempting to recognize eastern and western populations of *B. probus* as separate species, and perhaps a future, more rigorous analysis will support such action. For the present, however, I have no basis for confidently doing so and accept the notion that observed variability is more clinal than punctuated. Populations of *B. probus* from the eastern limit of its distribution also show considerable variation. I have seen numerous specimens from Rancocas State Park in southern

New Jersey that are variable in ways similar to western populations; the dorsal surface from dull to lustrous and only 20–25% bear a shiny anterior band across the clypeus.

Figure 82 does not reflect several specimen records for *B. probus* in the far southern part of Texas, most notably Willacy County. Its presence there, while tenable, needs confirmation. It can be easily confused with *B. integricollis*, which is more common in that area. Likewise needing confirmation is its presence in Otero County, New Mexico (marked with a question mark in Fig. 82); I have seen a single specimen labeled White Sands.

Boreocanthon probus is very closely related to *B. halffteri* (q.v.), the latter so far known only from the Rio Grande basin in central New Mexico and very far west Texas. Specimens I have seen from Winkler and Ward

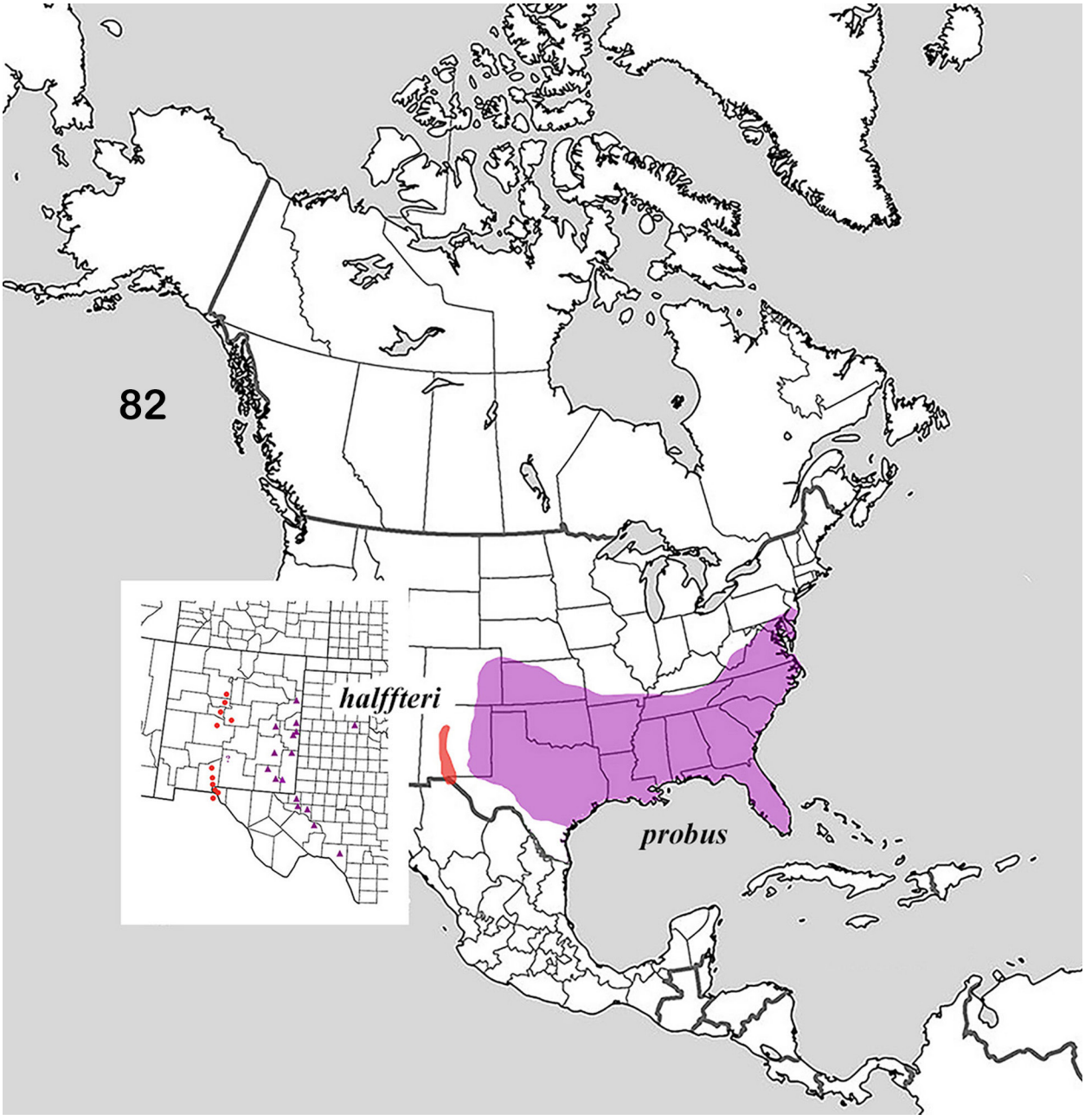


Figure 82. Approximate distributions of *Boreocanthon probus* (Germar) and *B. halffteri*, new species. Inset depicts recorded collection sites for *B. halffteri* (solid red circles) and in western Texas for *B. probus* (solid lavender triangles; ? = doubtful site for *B. probus,* q.v).

Counties (Monahans sand dune system), as well as dunes in Crane Co. (Texas) and southeastern NM — that is, west Texas sand dune habitat roughly east of the Pecos River — I have assigned to *B. probus*. These populations are somewhat problematic taxonomically but very interesting biogeographically as they represent (as I currently interpret the situation) western variants of *B. probus* of an ilk that could have given rise to *B. halffteri*. *Boreocanthon halffteri* appears to be restricted to the red sand dune habitats characteristic of the Rio Grande drainage of New Mexico from north of Albuquerque to the Samalayuca dunes just south of Cd. Juarez. The *probus-halffteri* nexus would doubtless be a good subject for further study as it begs a number of questions very amenable to molecular and spatial analyses that are beyond the scope of this study, such as, is this area a possible hybridization zone.

Ecological notes on *B. probus* are scattered and brief. Staines (1984), cited by Nemes and Price (2015), listed food sources for *B. probus* as cow, rabbit and deer droppings. Miller (1954) collected numerous *B. probus* in Georgia, of which 90% were nocturnal. Woodruff (1973) reported that it is active year-round and prefers sandy, wooded habitats. Brown's (1927) mention of *B. lecontei* as common on rabbit droppings in very sandy areas probably refers to *B. probus*. Halffter and Matthews (1966) reported *B. probus* as one of several dung beetle species inhabiting "… open forests of Eastern [U.S.] lowlands …" that "… [cannot] be considered to be a forest form … because of the nature of the woods they inhabit—generally open, with much insolation of the substrate—and because they are also found outside the forests." Indeed, *B. probus* is variable ecologically, inhabiting open forests in the eastern U.S. as well as open habitats west of the Mississippi River, including arid parts of western Texas. The common ecological denominator across these areas seems to be only that the substrate be sandy.

Boreocanthon halffteri Edmonds, new species

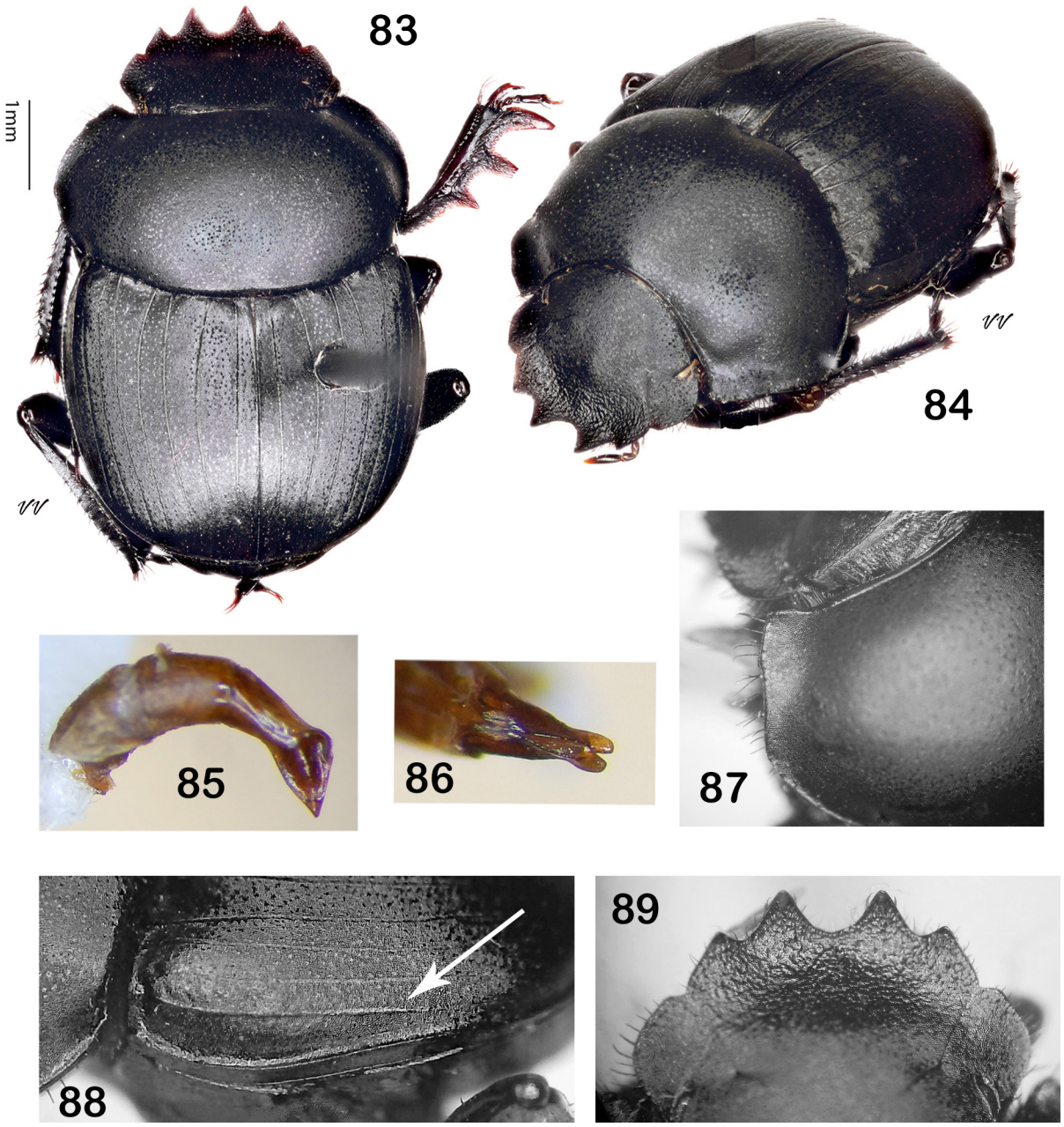
Fig. 82–89

Type material. Male holotype, Texas A&M University Insect Collection (TAMU-ENTO X0294090), TX: El Paso Co., red dunes 14 [sic] NE of Fabens, VII-11-96, C. Wolfe & D. Marqua.

Type locality. Texas: El Paso Co., red dunes, 14 [mi] NE Fabens.

Etymology. It is my great pleasure to dedicate this species to my late friend and colleague of almost 60 years, Gonzalo Halffter†, in honor of his distinguished career as a taxonomist, biogeographer, environmentalist, conservationist and dung beetle behaviorist, and founding father of the Instituto de Ecología, A.C., in Xalapa, Veracruz.

Diagnosis. *Head*: Anterior portion clypeus (Fig. 89) finely rugose, not strongly shinier than rest of head, posterior part of head finely, evenly punctate on weak shagreen background. Clypeal teeth (Fig. 83–84, 89) strong, acute apically, middle pair separated by broad, rounded emargination. Paraocular notch broad and shallow, setting off conspicuous, rounded anterior angle of paraocular area. Labio-gular fimbria bowed posteriorly, interrupted medially by broad, V-shaped field of coarse, setigerous punctures. *Prothorax*: Pronotum (Fig. 83, 87) very finely sculptured, minute puncturing and shagreen; anterior angles broadly explanate beginning at lateral angle, widening anteriorly; posteromedian angle not depressed. Hypomeral carina absent. *Pterothorax*: Mesoventrite weakly punctured medially, smooth laterally. Metaventrite weakly, sparsely punctate on shagreen background. *Elytra*: Interstriae (Fig. 83, 88) with strong shagreen and dense microspotting, more strongly sculptured than pronotum; 2nd and 3rd not swollen anteriorly, 3rd and 5th each with small tubercle in middle of anterior margin. Striae well marked, with sharply defined margins at least anteriorly; subhumeral (8th) stria (Fig. 88, arrow) strongly carinulate to point usually at least midway to elytral apex; epipleural (9th) stria obsolete. *Legs*: Protibia weakly, if at all, offset along inner margin; apical spur sexually dimorphic, apically acute in female, bifurcate in male. Hind femur lacking row of conspicuous setae along anterior margin. *Abdomen*: Pygidium sculptured as pronotum, flattened except for slightly swollen apex. Last (6th) ventrite punctured; other ventrites smooth. *Genital capsule*: Compressed distal portion of parameres (Fig. 85) triangular, ventral apical angles in form of elongate knobs (Fig. 86). *General*: Black, no hint of colorful undertones anywhere. Length: 4.5 – 6.5 mm. *Geographic distribution* (Fig. 82): Rio Grande basin of central New Mexico and far west Texas and adjacent Chihuahua (Fig. 82). Ecogeographic environment (Fig. 2): Desert and Xeric Shrublands biome (Chihuahuan Desert ecoregion). *Specimens examined*: 121.



Figures 83–89. *Boreocanthon halffteri*, new species. **83)** Holotype male, dorsal view. **84)** Holotype male, oblique anterolateral view. **85)** Lateral view of genital capsule. **86)** Apical view of parameres. **87)** Dorsal view of portion of pronotum. **88)** Dorsolateral view of elytron (arrow marks carinulate 8th stria). **89)** Dorsal view of head margin.

Notes on the holotype. The holotype male (Fig. 83–84) conforms with the diagnosis above annotated as follows: Left protibia-tarsus missing. Pronotal microspots dense, almost contiguous in some places. Edges of elytral striae 1–6 sharply defined by carinulate margins for almost entire length; 8th elytral stria with strong carinula extending from umbone to point even with first abdominal ventrite; 9th stria obsolete but vaguely indicated. Apex of pygidium distinctly convex, somewhat shinier than base, microspots virtually effaced, shagreen extremely fine (×50). Last abdominal ventrite with small, shiny bump at middle of posterior margin. Genital capsule not extracted. Length: 6.0 mm. The holotype was chosen because it conserves almost unblemished surface sculpturing. It carries

the following five labels: (1) TX: El Paso Co., red dunes 14 NE of Fabens, VII-11-96, C. Wolfe & D. Marqua. (2) ex. Charles S. Wolfe Collection, June 2006, TAMU Insect Collection. (3) TAMU-ENTO, X0294090. (4) [small light yellow circle]. (5) HOLOTYPE, *Boreocanthon halffteri* Edmonds, 2022. [*Label notes: Distance units not specified in label (1), presumed to be 14 miles. Small yellow circle is reference to habitus photographs, Fig. 83–84. All labels on white paper printed in black, HOLOTYPE in red*].

Collection localities.

MEXICO — CHIHUAHUA: Mpio. Juarez ●Samalayuca [Jun].

UNITED STATES — NEW MEXICO: Bernalillo Co. ●Albuquerque [Jun-Jul, Oct] ●Volcano Cliffs, Albuquerque [Aug]; Doña Ana Co. ●2.5 mi N Mesquite [Oct] ●USDA Jornada Experimental Range, 32.619590 -106.787845, 4356 ft [Jul-Aug] ●Anthony [Jun]; Sandoval Co. ●Coronado State Park, Bernalillo [Aug]; Socorro Co. ●Bosque de Apache NWR [Jul] ●Sevilleta NWR, Rio Salado [Jul] ●17 km SW/S Bernardo, 34.292° N 106.928° W [Jul] ●Sevilleta NWR, LTER Site 3,4 [Jul, Sep]; Torrance Co. ●Town of Gran Quivara, 6500 ft [Aug]; Valencia Co. ●5 mi N Belen [Jul]. **TEXAS**: El Paso Co.● red dunes on Montana Ave., 31.841°N 106.131°W, 1245 m [Aug-Sep] ●14 mi NE Fabens [Jul].

Paratype data (arranged by institutional/personal collection; all bear my determination labels printed in black on white paper with PARATYPE in blue and dated either 2021 or 2022; no allotype designated):

American Museum of Natural History. New York NY – 3 females, Samalayuca Chih[uahua] Mexico, vi-24-47, Rockefeller Exp[edition], [C.D.] Michener, Accession Codes 00011194–96. **Arizona State University, Hasbrouck Insect Collection, Tempe AZ** – 1 male, NM Doña Ana Co., Anthony, 24-vi-70, M. Cazier, sandy hills, depressions, *Atriplex* ASUHIC 0145853**. California Academy of Sciences, San Francisco CA** – 28: 12 males, 15 females, New Mex., Torrance Co., Town of Gran Quivara, 6500 ft. alt., 29-viii-1967, Hugh B. Leech, ex vertical tunnel in sandy soil; one female, New Mex., Torrance Co., Town of Gran Quivara, 29-viii-1967, Hugh B. Leech, with humus in burrow. **Carnegie Museum of Natural History, Pittsburgh PA** – 4: 2 males, one female, TX: El Paso Co. Red Sands, US 62, 180, Sept. 17, 1985, Col. G.A. Coovert, GAC 1254; one male, NM: Bernalillo Co., Albuquerque, X-18-1928, H. Klages Collection, CM Acc No. 11414. **Monte L. Bean Life Science Museum, Brigham Young University, Provo UT** – one male, NM: Sandoval Co., Coronado State Park, Bernalillo, 21 Aug 1985, Bauman, Huish, Nelson, Wells, Whiting. **Museum of Southwestern Biology, University of New Mexico, Albuquerque NM** – 29: one male, Socorro Co. NM, Jul 89, C. Blanco M.// MSB Cat. No. 8226; 3 females, one male, NM: Socorro Co., Sevilleta NWR, Rio Salado, vii-17-1995, D. Holiday; 3 females, 2 males, USA NM Socorro Co., 17 km SW/S Bernardo, N 34.292 W 106.928, 17 July 1998, coll. S.L. Brantley // MSB Cat. No. 17784–17790; 2 males, one female, Bernalillo Co., NM, Volcano Cliffs, Alb., 10 Aug 1979, C. S. Crawford // MSB Cat No. 7851–7854; 2 males, Valencia Co, NM, 5 mi N Belen, 21 July 1987, K. Flies // MSB Cat No. 7855 and 7857; 2 females, one male, Socorro Co., NM, Sevilletta [sic] sand dunes, 20 April 1982, C. S. Crawford; 3 females, one male, Socorro Co. NM, Sevilleta NWR, LTER Site 3, 4 Sept. 1992; 2 males, USA New Mexico, Dona Ana Co., USDA Jornada Experimental Range, 32.619590 -106.787845, 17 August 1989, 4356'elev., mesquite dunes, pitfall trap, D. C. Lightfoot collector; one male, Socorro Co. NM, Sevilleta NWR, LTER Site 3, 31 July 91; one male, N. Mex., Dona Ana Co., 2.5 mi N Mesquite, 2 Oct 1982, D. Lightfoot; one female, Socorro Co. NM, Bosque de Apache NWR, line A, trap #6, 14 July 1996; one female, Bernalillo Co, NW Albuquerque, 16-VI-93, Dick Fagerlund // MSB Cat. No. 8225; one female, N. Mex., Dona Ana Co., Jornada Range, 15 m N of Las Cruces, 24.VII.79, pit trap // David Richmond. **University of Nebraska State Museum, Lincoln NB** – 8: 1 male, 7 females, TX: El Paso Co, red dunes on Montana Ave., 31.841° N 106.131° W, 1245 m, rolling AM after PM rains, 22-VIII-2010, M. J. Paulsen. **New Mexico State University Arthropod Collection, Las Cruces NM** – 20: NMSUAC Accession Codes (yellow labels): Males (6): 0016583, 0020360, 0020364, 0020371, 0020375, 0020385. Females (14): 0016584, 0020357, 0020359, 0020361, 0020362, 0020365, 0020366, 0020368, 0020370, 0020377, 0020378, 0020384, 0020386, 0020389 Locality Data: 0016583 and 0016584: NM, Doña Ana Co., Jornada Exp. Range, pit trap, vii-14-1989, D. Richman; all others: N. Mex., Doña Ana Co., Jornada Range, 15 m N Las Cruces, 24-vii-79, D. Richman. **Paul K. Lago Collection, University MS** – 2: one male, one female, Red sands US [Hwy] 62,180, El Paso Co. Tex., Sept. 17, 1985, Coll. G.A. Covert//GAC 1254. **Snow Entomological Collections, University of Kansas, Lawrence KS** – one male, NM, Albuquerque, VII-5-41, E. L. Todd. **Richard A. Cunningham Collection, Show Low AZ** – 2 males, N. Mex., Doña Ana Co., Jornada Range, 15 m N of Las Cruces, pit trap, 24 vii 79.

Texas A&M University Insect Collection, College Station TX – 22: 7 males, 4 females (same data as holotype) database numbers TAMU-ENTO X 0295573, 0296014, 0296864, 0297061, 0297466, 1205379, 1212529, 1224107, 1224300, 1224163, 1224681; 2 males, 2 females [*ex CAS*], New Mex., Torrance Co., Town of Gran Quivara, 6500 ft. alt., 29-viii-1967, Hugh B. Leech, ex vertical tunnel in sandy soil, X 1224343, 1695095, 1699095, 1700596; one female [ex *MSB*], Socorro Co., NM, Sevilletta [sic] sand dunes, 20 April 1982, C. S. Crawford, X 1695695; one female [*ex MSB*], 17 km SW/S Bernardo, N 34.292 W 106.928, 17 July 1998, coll. S.L. Brantley, X 1698174; one male [*ex MSB*], Bernalillo Co., NM, Volcano Cliffs, Alb., 10 Aug 1979, C. S. Crawford, X 1570302; one female [*ex MSB*], NM, Bernalillo Co., Albuquerque, Aug. 2, 1974, B. Blake, X 0012317; one male, one female [*ex NMSUAC*], N. Mex., Doña Ana Co., Jornada Range, 15 m N Las Cruces, 24-vii-79, D. Richman, X 1699292, 1700581; one female [*ex UNSM*], TX: El Paso Co, red dunes on Montana Ave., 31.841° N 106.131° W, 1245 m, rolling AM after PM rains, 22-VIII-2010, M. J. Paulsen, X 1547783. Total paratypes: 120

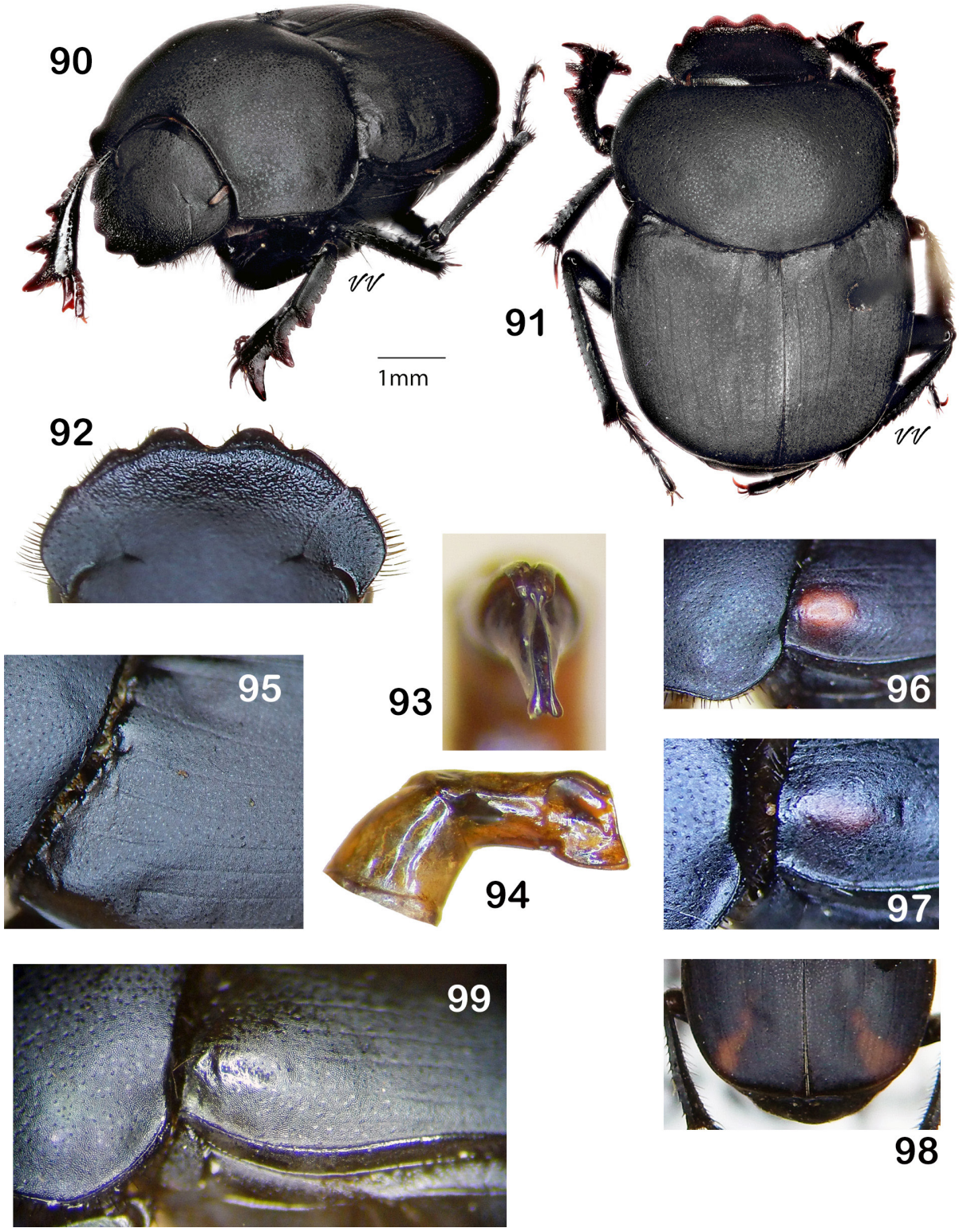
Comments. *Boreocanthon halffteri* is very closely related to *B. probus*, from which it differs by a) distribution; b) anterolateral pronotal angles conspicuously explanate; c) more elongate parameres; d) rounded shape of paraocular areas; d) somewhat more acute, narrower and widely spaced clypeal teeth. Some specimens of the latter species from eastern New Mexico and adjacent west Texas counties are intermediate between *B. halffteri* and more "typical" *B. probus*. They could be considered reasonable grounds for regarding the two taxa as subspecies. However, what I know now suggests that *B. halffteri*, in addition to being morphologically distinct, is restricted to the Rio Grande drainage and geographically isolated from *B. probus*, which to me weaken an assumption that they are conspecific. The most proximate populations between the two species are that of *B. halffteri* in El Paso (El Paso County) and that of *B. probus* near Monahans (Ward County), Texas, separated by about 200 miles (Fig. 82, inset). Of note is the fact that red sands characterize the El Paso site while white sands predominate in those near Monahans. Viewed on Google Earth, the intervening east-west gap between about 31°N and 32° N latitude, where neither species is yet known to occur, appears largely devoid of dune habitat. Whether or not the disjunction is real will be tested by the results of future sampling in that area. Of note is the fact that *B. ebenus* occurs at both the El Paso and Monahans locations. Schoenly's (1983) reference to *B. melanus* on the west slopes of the Hueco Mountains (El Paso County, 31°44′ N 106°04′ W) is likely assignable to this new species; however, his voucher specimens, collected along with *B. ebenus*, could not be located at Angelo State University, where Schoenly reported depositing them (Serina Brady, pers. comm.).

Boreocanthon simplex (LeConte, 1857), restored generic combination

Fig. 90–101

Canthon simplex LeConte 1857: 41.
Canthon corvinus Harold 1868:129 (new synonymy per Horn 1870: 46).
Canthon simplex var. *militaris* Horn 1870: 46 (new synonymy per Robinson 1948: 87).
Canthon simplex var. *humeralis* Horn 1870: 46 (new synonymy per Robinson 1948: 87).
Canthon simplex antiquus Pierce 1946: 120 (new synonymy per Miller et al. 1981: 626).
Boreocanthon simplex (LeConte) (new combination per Halffter 1958: 209).
Canthon (*Boreocanthon*) *simplex* (LeConte) (new combination per Howden 1966: 727).
Boreocanthon simplex (LeConte), **restored generic combination**.
Canthon bisignatus Balthasar 1939: 229, **new synonymy**.
Canthon (*Boreocanthon*) *bisignatus* Balthasar 1939 (new combination per Halffter and Martínez 1977: 82).

Type material. 1) *Canthon simplex* LeConte: syntype (male). Museum of Comparative Zoology, Cambridge, MCZ-ENT00003699. Examined by photograph (https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:3699); **2)** *Canthon corvinus* Harold: syntype (sex undermined), Museum für Naturkunde, Berlin. Examined by photograph courtesy F. V. Vaz-de-Mello; **3)** *Canthon simplex humeralis* Horn: syntype? (female). Museum of Comparative Zoology, Cambridge, MCZ-ENT00008108. Examined by photograph (https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:8108); **4)** *Canthon simplex militaris* Horn: syntype? (female). Museum of Comparative Zoology, Cambridge, MCZ-ENT00008109. Examined by photograph https://mczbase.mcz.harvard.edu/guid/MCZ:Ent:8109); **5)** *Canthon bisignatus* Balthasar: syntypes (two, sex undetermined), National Museum, Prague. Examined by photograph courtesy Jiří Hájek. **6)** *Canthon simplex antiguus* Pierce: holotype (sex undetermined). Los Angeles County Museum of Natural History, LACMIP 2594. Not examined.



Figures 90–99. *Boreocanthon simplex* (LeConte). **90)** Habitus, anterolateral view. **91)** Habitus, dorsal view. **92)** Dorsal view of anterior portion of head. **93)** Apical view of parameres. **94)** Lateral view of genital capsule. **95)** Dorsal view of base of left elytron. **96–97)** Maximum (96) and minimum (97) expression of orange/red elytral humerus. **98)** Anomalous orange elytral markings. **99)** Lateral view of base of pronotum and elytron.

Type localities. 1) *Canthon simplex* LeConte: Oregon and California. **2)** *Canthon corvinus* Harold: Sonora, California (see Comments); **3)** *Canthon simplex humeralis* Horn: California, Coast Mountains south; **4)** *Canthon simplex militaris* Horn: California, Tejon and Visalia; **5)** *Canthon bisignatus* Balthasar: California; **6)** *Canthon simplex antiguus* Pierce: Rancho La Brea, Tar Pits A and 81, Hancock Park, Los Angeles, California.

Diagnosis. *Head*: Anterior one-third of clypeus (Fig. 92) finely rugose, weakly shiny, posterior portion and paraocular areas minutely punctured on dense shagreen background, microspots very weak. Clypeus (Fig. 92) bearing four rather weak marginal teeth, median pair short, rounded apically, separated by rounded emargination, lateral pair small, angulate apically. Paraocular notch subtle, sometimes almost effaced, setting off very small, angular corner of the paraocular area. Labio-gular fimbria broadly triangular, apex extending about one-third length of gula. *Prothorax*: Pronotum (Fig. 95–97) evenly covered by dense shagreen and widely spaced punctures, microspots faint, denser than punctures. Anterior pronotal angles very weakly upturned, posteromedian angle at most only very weakly depressed; circumnotal ridge smooth posterolaterally. Hypomeral carina usually absent or only feebly developed, occasionally distinct. *Pterothorax*: Mesoventrite with few weak punctures on shagreen background; metaventrite with evenly distributed, widely spaced, small punctures. *Elytra (see also Comments below)*: Interstriae covered by dense shagreen, microspots small, faint, discal interstriae with few, very widely spaced micropunctures; 2nd and 3rd not usually swollen apically; anterior margin of some or all interstriae 2–5 bearing minute tubercle (sometimes obscured by pronotal margin). Humeral umbone dull black, sometime shiny (Fig. 99) or with orange/red spot (Fig. 96–97). Elytral striae weak, edges not sharply defined; lateral striae (7-9), especially anterior one-half, often effaced or nearly so, 8th stria never with any trace of carinula. *Legs*: Inner margin of protibia (Fig. 90) at most only gently widened at base of basal tooth. Protibial spur sexually dimorphic: strongly curved and apically acute in female, curved and apically bifurcate in male. Anterior margin of hind femora with conspicuous row of long setae, ventral surface punctate with few short setae. *Abdomen*: Pygidium evenly convex, uniformly dull; pygidium and 6th abdominal ventrite sculptured as elytra, remaining ventrites smooth. *Genital capsule*: Compressed distal portion of parameres broadly triangular (Fig. 94), ventral apical angles in form of slender, elongate knobs (Fig. 93). *General*: Black, rarely weakly shiny, rarely with green or blue undertone on head, pronotum; elytral umbone sometimes partially or completely orange or red. Length: 4.5 – 8.0 mm. *Geographic distribution* (Fig. 100–101). Widely distributed in United States west of the Rocky Mountains. *Ecogeographic environment*: Desert and Xeric Shrublands, Temperate Conifer Forests, and Mediterranean Forests, Woodlands and Scrub biomes. *Specimens examined*: 3196.

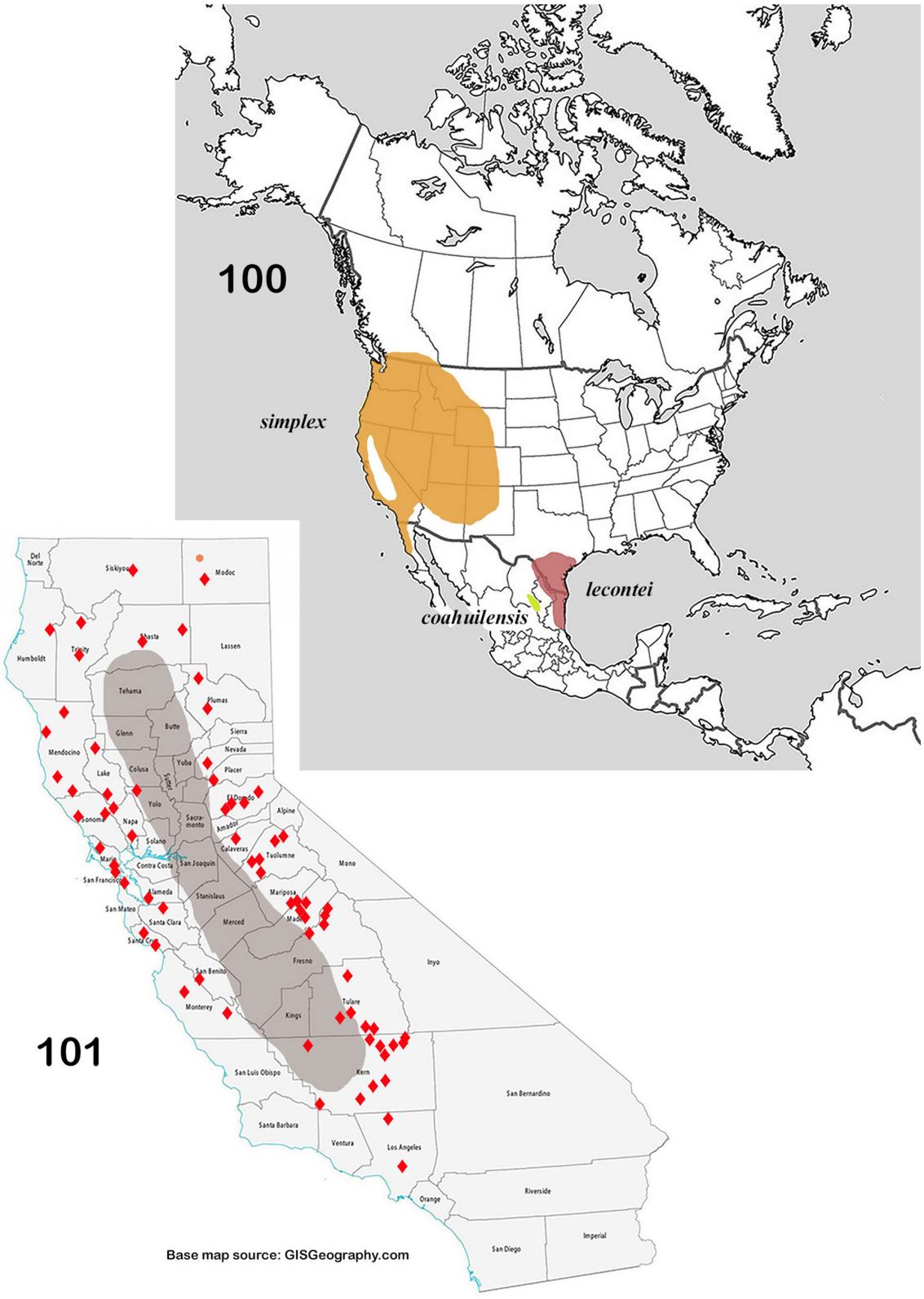
Collection localities.

Note. Red diamonds mark collection localities with at least one observed specimen bearing orange/red elytral umbones.

CANADA — BRITISH COLUMBIA: *Cariboo RD* ●Chilicotin; *East Kootenay RD* ●Roosville [Aug] ●Kimberley [Jun] ●Cranbrook [May]; *Columbia-Shuswap RD* ●Salmon Arm [Apr]; *Kootenay Boundary RD* ●Rock Creek [Jul]; *North Okanagan RD* ●Vernon [Apr, Aug]; *Thompson-Nicola RD* ●Aspen Grove [Jul].

MEXICO — BAJA CALIFORNIA: *Mpio. Ensenada* ●47 km E San Telmo (road to Parque Nacional San Pedro Mártir), 950 m [Jun] ●Rancho La Bellota, 32° 09.411′ N 116° 27.680′ W, 1863 ft [May] ●Mike′s Sky Rancho, 4000 ft [Jun] ●San Vicente, 200 m [May] ●43 mi E Ensenada, Santa Catarina, Sierra de Juarez, 3600 ft [Aug] ●Ensenada [Jun] ●7 mi N Ensenada ●Santo Domingo [May] ●Valle de las Palmas [Nov] ●20 mi S Santo Tomás [Aug] ●Punta Banda [Jun] ●40 mi S Tecate.

UNITED STATES — ARIZONA: *Apache Co*. ●Chuska Mountains, Wagon Wheel Forest Camp, 36.452° N 109.1704° W [Aug] ●White Mountains, Diamond Creek [Jun]; *Coconino Co*. ●Bear Canyon [Jun] ●Flagstaff [Sep] ●5 mi S Sedona, Red Rock Crossing Campground [Apr]; *Cochise Co*. ●Portal [Jul] ●Benson [Apr]; *Gila Co*. ●0.5 mi W Miami ●3 mi NE Gisela [Mar] ●13 mi S Globe [Aug] ●Globe [Apr, Jul] ●Lake Roosevelt ●base Pinal Mts., 4000 ft [May]; *Graham Co*. ●12 mi S Safford [May]; *Maricopa Co*. ●Tempe [Mar] ●Phoenix [Apr] ●Ft. McDowell [Apr-May] ●0.5 mi SE Sunflower [Apr] ●Rock Springs, Agua Fria River [Apr]; *Mojave Co*. ●Beaver Dam (near Littlefield), 36°53′41″ N 113°55′55″ W, 1916 ft [Apr]; *Pima Co*. ●Tucson [Mar-Apr, Jun] ●Santa Catalina Mountains [Jun]; *Pinal Co*. ●Superior [Mar] ●6 mi S Superior, 33.2162 N -111.0655 W, 990 m [Apr-Jul] ●3.5 mi W Superior, Boyce-Thompson Arboretum [Feb] ●Aravaipa Canyon [Apr]; *Yavapai Co*. ●Bumble Bee [May] ●12 mi S Camp Verde, 3000 ft [Jun] ●4 mi N Clarkdale ●4 mi S Sedona [Jun] ●34°13′23″ N 112°05′37″ W ●Hwy



Figures 100–101. *Boreocanthon* distribution. **100)** Approximate distributions of *Boreocanthon simplex* (LeConte), *B. lecontei* (Harold) and *B. coahuilensis* (Howden). **101)** Solid red diamonds mark California collection sites for *B. simplex* with red elytral humeri in one or more specimens; shaded area marks general limits of the Central Valley.

I-17, 2 mi S jct Hwy 179 [Apr] ●2.1 mi NW Moctezuma Well, Moctezuma Castle National Monument, 3984 ft [May] ●8 mi NE Yarnell [Jun] ●Prescott [Mar]. **CALIFORNIA**: *Alameda Co.* ♦Oakland [Apr, Jun]; *Alpine Co.* ●Monitor Pass 8300 ft [Jun, Aug] ●38.4504° N 119.5979° W, 8100 ft [Jun-Jul] ●Ebbett's Pass, 8950 ft [Jun] ●Bloods [Jul] ●Hope Valley, 7000ft [May]; *Amador Co.* ●El Dorado National Forest, Panther Creek Road [Jun]; *Butte Co.* ●Butte Meadows [Jun] ●Richardson Springs [May]; *Calaveras Co.* ●13 mi E Dorrington [Jun] ♦Mokelumne Hill [Jul] ●5 mi NE Tamarack [Jun]; *El Dorado Co.* ●Kyburz [Jul] ●Caldor [Jun] ♦Somerset [Jun] ♦13 mi E Georgetown, Blodgett Forest [Jun] ♦Pacific House [Sep] ●Ice House [May] ●3 mi N Wrights Lake [Jun] ●Camino [Jun] ●Twin Bridges, Pyramid Creek [Jun] ♦White Hall [Jun] ●Mt. Ralston [Aug] ♦Riverton [Jun-Jul] ●Placerville [Jun]; *Fresno Co.* ♦Squaw Valley [Apr, Aug] ♦6 mi S Shaver Lake [May] ♦Stevenson Creek, Sierra National Forest [May] ♦Camp Greeley, 2800 ft [Jun] ♦Huntington Lake, 7000 ft [Jul] ♦Kings Canyon National Park [Jun, Aug] ♦Lost Lake [Apr] ●Wishon Reservoir [Jul]; *Humboldt Co.* ♦Willow Creek [Jun]; *Kern Co.* ♦Tehachapi ♦Grapevine [Apr] ♦Lake Isabella [Jul] ♦Kelso Valley Road [Apr] ♦2.5 mi NW Canebrake [Apr] ●9 mi E Onyx ♦Onyx [May] ♦9 mi N Onyx ●Frazier Park [Apr] ♦Rancheria Creek, Walker Basin [Jun] ♦Ft. Tejon ♦Tejon Canyon [May] ♦Deer Creek [Apr] ●Lebec (Dutchman's Camp) [Apr] ♦5 mi S Alta Sierra [Apr] ♦Weldon [Mar]; *Lake Co.* ♦Anderson Springs [May] ♦Bartlett Springs [Jun]; *Lassen Co.* ●Hallelujah Junction [Jul] ●Norval Flats, 5500 ft [May, Jul] ●Hayden Hill [Aug]; *Los Angeles Co.* ●Los Angeles [May] ♦Pasadena [Feb Apr-May] ●Claremont ●Big Tijunga Canyon [May] ♦Fairmont [Apr] ●Azusa [May] ●Chilao Recreational Area, 5300 ft [May]; *Madera Co.* ♦Oakhurst [May] ♦Coarsegold [May] ♦Bass Lake, 5000 ft [Jun-Jul] ●Sugar Pine ♦Southfork [Jul]; *Marin Co.* ♦Fairfax [Jul] ♦Stinson Beach [Apr] ♦Mill Valley [Aug] ♦Inverness [Aug]; *Mariposa Co.* ●Yosemite Valley [Jun] ●Glacier Point, 7214 ft ♦Fish Camp [May] ♦Miami [Mountain] Ranger Station, 37°25′09.62″ N 119°44′41.15″ W [May]; *Mendocino Co.* ♦Yorkville [May–Jun] ♦Jumpoff Creek [Aug] ♦2 mi NW Philo, Navarro River [Jul] ♦Newport; *Modoc Co.* ♦Hackamore [Apr] ●Warner Mountains, near Lost Lake, 8000 ft [May-Aug]; *Mono Co.* ●2 mi E Tioga Pass, 9500 ft [Jun] ●Mammoth Lake, 8000 ft [May-Jun] ●Hwy 108, Sonora Pass, 9700 ft [Jun-Jul] ●Saddleback Lake, 10000 ft [Jul] ●Bodie, 8500 ft [Aug]; *Monterey Co.* ●Stone Canyon [Apr] ●Paraiso Springs [Jun] ●Tassajara Hot Springs [May] ●Bradley [Apr] ●Carmel Valley [Jul] ●Bryson [Apr] ●Pacific Grove [Jun]; *Napa Co.* ♦Napa [Jun-Jul] ♦Mt. St Helena [May-Jun] ●Deer Park [Jul]; *Nevada Co.* ♦Grass Valley [May] ●5 mi N Hobart Mills [Jun] ●Sagehen Creek [Jun] ●Truckee, 5800 ft [Jun, Aug]; *Orange Co.* ●Anaheim [Jun] ●Laguna Beach [Jun] ●Temple Hills [Mar] ●Laguna Beach [Jun] ●Laguna Niguel [Jun]; *Placer Co.* ●Tahoe City [Jul] ●Morongo Valley [May] ♦Sugar Pine [Aug] ●Cisco [Jun] ●Colfax [Jun]; *Plumas Co.* ●Quincy ●Lake Almanor [Jun] ♦Chester [Jul] ♦Meadow Valley, 6000 ft [Jul]; *Riverside Co.* ●Cabazon [Apr] ●Riverside [Mar] ●Aguanga [May] ●0.5 mi SE Aguanga [Apr] ●8 mi SE Hemet, Bautista Canyon, 33°41′ N 116°50′ W, 2300 ft [Apr] ●Coahuilula Creek [May] ●6 mi E Temecula [Mar] ●San Jacinto [Mar] ●Idyllwild [Jun-Jul] ●Palm Springs [May] ●5 mi W Sage [Jul] ●Gavilan Hills [Apr] ●Goff Flats Campground, San Jacinto Mountains [Jul]; *San Benito Co.* ♦Pinnacles National Monument [Apr, Jun]; *San Bernadino Co.* ●2.9 mi N Cedar Springs [Jul] ●0.9 mi NE Cedar Springs ●Colton [Mar] ●San Bernadino [May] ●Glenwood Springs [Aug] ●Deep Creek Campground [Jun] ●Big Bear Lake [May] ●Fawnskin [Jul]; *San Diego Co.* ●Campo [May] ●Scissors Crossing [Apr] ●10 mi N Scissors Crossing [Jun] ●Lake Cuyamaca [Apr] ●Pamo Valley [Jun] ●Indian Flats Campground, Warner Springs [Jun-Jul] ●Dulzura [Apr] ●Boulevard [Jul] ●Mason Valley [Jun] ●Poway, 500 ft [Apr] ●Lake Moreno [Mar] ●Bonsall, Gopher Canyon Rd. [May] ●Camp Pendleton, 5 mi E I-5, Mateo Creek ●6 mi E Banner [Jul] ●San Felipe Valley, 3000 ft [May] ●Murray Dam [May] ● Mt. Palomar [Jun] (See also McPeak et al. 2014 for additional San Diego Co. records.); *San Francisco Co.* ♦San Francisco; *Santa Barbara Co.* ●Clear Creek, Cuyama Canyon [Mar] ●Santa Maria [Mar] ●Buellton [May] ●Santa Barbara ●10 mi E Santa Maria, Cuyama River [Jul]; *Santa Clara Co.* ♦30 mi SE Livermore (Alameda Co.) [Jun]; *Santa Cruz Co.* ♦Ben Lomond [Jun] ♦Santa Cruz [Apr]; *Shasta Co.* ♦Cayton [Jul] ●Old Station [May-Jun] ♦Hat Creek (May-Jun) ●Shingletown [Jun]; *Sierra Co.* ●Sierraville [Aug] ●10 mi S Sierraville [Jun]; *Siskiyou Co.* ●Yreka ●Walker [Jun] ●McCloud [Jun] ●Bartle [Jul] ●Cole [Jul] ●Klamath River [May] ♦Taylor Lake, 5600 ft [Aug] ●Castle Lake, 5200 ft [Jul] ●Burney Valley [Aug] ●Mt. Hebron [Aug]; *Sonoma Co.* ♦Mark West Springs [May] ●Mt. St Helena [Jun] ♦Rio Nido [Aug]; *Tehama Co.* ●South Fork Battle Creek [Aug]; *Trinity Co.* ♦Carrville, 2500 ft [Jun] ♦Zenia [Jun] ●Plummer Spring [Jun] ♦Hayfork [May] ●Mountain Meadows Ranch, head Coffee Creek, 5100 ft [Jul]; *Tulare Co.* ♦Kaweah ♦California Hot Springs [Jun-Jul] ●Sequoia National Park, Kings River Canyon [May] ♦2 mi E Johnsondale ●Shake Camp Campground [Jun] ♦Porterville [May] ♦Springville; *Tuolumne Co.* ●Tuolumne Meadows ●Sonora Pass, 38.3281° -119.6371°, 2950 m ●Spring Gap [Jun]

♦Strawberry [Aug] ♦Twain Harte [Mar] ♦17 mi S Sonora [May] ♦Pinecrest [Jun-Jul] ♦Hardin Flats [May] ♦6 mi E Groveland, 2800 ft [Jul]; *Ventura Co.* ●Lake Piru [Jun] ●Ventura [May] ●Sespe Canyon [Apr] ●Santa Paula [Nov]; *Yolo Co.* ♦Rumsey [May]; *Yuba Co.* ●Strawberry Valley [Sep]. **COLORADO**: *Boulder Co.* ●8mi SW Boulder, 8400 ft [Jul]; ●Ward ●Gold Hill [Jul]; *El Paso Co.* ●Cascade [Jul]; *Fremont Co.* ●Coal Creek [May]; *Garfield Co.* ●Glenwood Springs [Jul]; *Gunnison Co.* ●8 mi NE Almont, One Mile Canyon, 8200 ft [Jul] *Jackson Co.* ●Walden [Aug]; *Larimer Co.* ●Estes Park, 40°21′11″N 105°28′45″ W, 2500 m [Aug] ●Red Feather Lake [Jun]; *Mineral Co.* ●Creede [Jul]; *Moffat Co.* ●10 mi W Maybell [Jun]; *Ouray Co.* ●Ouray [Jul]; *Routt Co.* ●Steamboat Springs [Jun]; *Teller Co.* ●Florissant Canyon, 8500 ft [Jul]. **IDAHO**: *Ada Co.* ●Boise, 2690 ft [May]; *Adams Co.* ●Packer Johns Cabin State Park [Jun] ●6 mi E New Meadows [Jun]; *Bear Lake Co.* ●Montpelier ●Georgetown [May] ●Paris [May]; *Bannock Co.* ●Pocatello [May, Jul] ●Lava Hot Springs; *Benewah Co.* ●St. Maries [Aug]; *Blaine Co.* ●Prairie Creek [Jul] ●Frenchman Creek, Hwy 75 below Galena Summit ●10 mi S Bellevue [May] ●Clarendon Hot Springs [Jul]; *Boise Co.* ●Thorn Creek [Jul] ●Gardena [Jun] ●8.5 mi NE Gardena [Jun]; *Bonner Co.* ●Sagle [Jun] ●Sandpoint, 2085 ft [May-Jul] ●Priest River Experimental Forest [Jun] ●Granite [Jun]; *Bonneville Co.* ●Gray's Lake [Apr] ●Willow Creek [Jun]; *Butte Co.* ●Craters of the Moon National Monument, Little Cottonwood Creek [Jun-Jul]●6 mi S Howe [May]; *Caribou Co.* ●Diamond Point [Aug] ●6 mi SW Soda Springs [Apr] ●3 mi E Wayan [Jun]; *Clark Co.* ●Dubois [Jun] ●Camp Creek, 5 mi S Humphrey [Jul]; *Clearwater Co.* ●Elk River [May] ●1 mi N Elk River [May]; *Custer Co.* ●Double Springs Ranch [Jun]; *Elmore Co.* ●11 mi S Pine [Jun] ●8.5 mi E Featherville [Jun] ●Little Camas Reservoir [Jun]; *Fremont Co.* ●St Anthony [Jul] ●Coal Creek [May]; *Gem Co.* ●Sweet [Jul]; *Kootenai Co.* ●Worley [May] ●Chilco [May] ●Coeur d'Alene, 2150 ft [May-Jun] ●6 mi W Athol [Jun]; *Latah Co.* ●Moscow, 2560 ft [Apr, Jun-Jul] ●Bovill [Apr] ●5 mi N Troy [May] ●Spring Valley Reservoir [Apr, Jul]; *Lewis Co.* ●Winchester [May]; *Lincoln Co.* ●Shoshone [Jul]; *Madison Co.* ●Driggs [Jun]; *Nez Perce Co.* ●Gifford [May]; *Oneida Co.* ●Sublette Canyon [Apr]; *Owyhee Co.* ●17 mi W Silver City; *Shoshone Co.* ●Wallace [Jun, Aug] ●3.4 mi N Clarkia; *Teton Co.* ●Tetonia [Jul]; *Twin Falls Co.* ●Timber Canyon [Jul] ●Steamboat Rock [Jun]; *Valley Co.* ●Bear Valley [Jul] ●Cascade [May] ●Donnelly [May]; *Washington Co.* ●7 mi NW Midvale [Apr]. **MONTANA**: *Beaverhead Co.* ●Centennial Valley [May] ●Dillon [Jul] ●Birch Creek [Aug]; *Broadwater Co.* ●Limestone Hills (near Townsend), 46°17.54′ N 111°36.45′ W; *Flathead Co.* ●Big Creek, Flathead National Forest ●Glacier National Park, Colby Meadow [Jun-Sep]; *Gallatin Co.* ●7 mi S Logan, Madison Buffalo Jump State Park [May] ●Willow Creek [Jun]; *Hill Co.* ●Beaver Creek, 6300 ft; *Lake Co.* ●Ronan [Jul-Aug]; *Lewis and Clark Co.* ●Helena [Jul]; *Madison Co* ●9 mi S Alder, Ruby Reservoir [Jul]; *Meagher Co.* ●Ringling [Apr]; *Missoula Co.* ●Salmon Lake, 7.5 mi N jct. hwys 200 & 83 [Jul]; *Park Co.* ●Crazy Mountains, 5000 ft [Jun]; *Ravalli Co.* ●Hamilton [Jun] ●Camp Creek [Jul] ●Gird Creek [Jul] ●Flathead Lake [May] ●Darby [Aug]; *Sanders Co.* ●Thompson Falls [Jun]; *Sheridan Co.* ●Sheridan [Aug]. **NEVADA**: *Clark Co.* ● 10 mi N Paradise [Jun] ● *Elko Co.* ●Elko [Jul] ●Wildhorse Crossing State Park [Sep] ●Jarbidge [Jul]; *Lander Co.* ●18 mi S Austin [Jun]. **NEW MEXICO**: *Catron Co.* ●Luna [Apr]; *Sandoval Co.* ●Valles Caldera National Preserve, Valle Grande, 35°53′ N 106°30′ W [Jul]. **OREGON**: *Baker Co.* ●Whitman National Forest, Eagle Mountains, Skookum Creek ●Pine Creek, Blue Mts, 4000 ft [Aug] ●Baker [Apr, Jul]; *Benton Co.* ●Monroe [Jun] ●Corvallis [May-Aug] ●McDonald Forest, Oak Creek [Apr]; *Deschutes Co.* ●16 mi SE LaPine [May] ●7 mi NW LaPine, Pringle Butte, 4000 ft [Apr] ●Paulina Creek [Aug]; *Douglas Co.* ●Riddle [May]; *Grant Co.* ●Graylock Butte [Jul] ●Dixie Pass, 5200 ft ●Silvies [Jun]; *Harney Co.* ●Steens Mountain, 6500 ft [Jun-Jul] ●Hwy 20, mile marker 156, near Buchanan [Mar-Jun] ●Steens Mt., above Fish Lake, 8000-9000 ft [Jun]; *Hood River Co.* ●4 mi W Oak Grove [May-Jun]; *Jackson Co.* ●Medford [Apr-May] ●Colestin [Jul] ●Gold Hill [Apr]; *Jefferson Co.* ●0.3 mi E Horseshoe Lake [Jul-Aug] ●Santiam Pass, 5000 ft [Jun]; *Josephine Co.* ●Grants Pass [Jul]; *Klamath Co.* ●Worden [Jul] ●Collier State Park [Jul] ●Klamath Lake [Jun] ♦Fremont National Forest [Jun] ●Crater Lake [Jul] ● Bly, Meryl Lake [Jun] ●7 mi NE Bly, Deming Creek [Jul] ●8 mi N Bly, Preacher Creek [May] ●Spencer Creek [Jun] ♦Algoma [Apr]; *Lake Co.* ●15 mi E Lakeview [Jun] ♦Warner Canyon, near Lakeview [Jun-Jul] ●12 mi SW Silver Lake [Aug]; *Lane Co.* ●10 mi NNW Junction City [Sep] ●11 mi NE Blue River, H.J. Andrews Experimental Forest [Jun]; *Marion Co.* ●Pratum; *Multnomah Co.* ●Portland [Jun]; *Umatilla Co.* ●Tollgate [Jun] ●Meacham, 4300 ft [May-Jun] ●Cold Springs [Jun]; *Union Co.* ●28 mi SE Union 4280 ft [Jul] ●La Grande [Jun] ●0.2 mi N Rd. 77 on Rd. 600, 5550 ft [Jun] ●Kamela [Jun]; *Wallowa Co.* ● Hwy 3 at Day Ridge Road, 25 mi N Enterprise, 4700 ft [Sep] ●Zumwaldt Prairie Reserve [Jun] ●Blue Creek, 4170 ft; *Wasco Co.* ●16.5 mi E Hwy 35 on Hwy 44, 2800 ft [Jun-Jul]; ●6.4 mi E Rd. 1720 on Upper Fivemile Rd.; 14.8 mi E Hwy 35 on Hwy 44, Hood River National Forest [Apr] ●10.1 mi W Dufur Road on Hwy 44, 45°24.882′ N

121°19.524′ W, 2732 ft [May] ●Mt. Hood National Forest, Clear Creek Campground [Jun]; *Washington Co*. ●Forest Grove [May]; *Wheeler Co*. ●Walton Lake [Jun]; *Yamhill Co*. ●McMinnville [Apr-May]. **UTAH**: *Box Elder Co*. ●Rosevere Creek, Raft River Mountains [Jun]; *Cache Co*. ●Logan Canyon, 7200 ft [May] ●Bear Lake, summit Logan Canyon [Jun] ●Tony Grove [Jul] ●Sardine Canyon ●Wellsville Canyon [Jun]; *Carbon Co*. ●8 mi NE Castlegate [Jun] ●Scofield Reservoir [Jun]; *Duchesne Co*. ●Hanna [Jul]; *Juab Co*. ●Nephi Canyon [Jun] ●Chicken Creek Campground, 5 mi E Levan [Sep]; *Morgan Co*. ●Cottonwood Canyon, Cache National Forest [Jul] ●Lost Creek, above Lost Creek Reservoir [Jul]; *Rich Co*. ●Logan Canyon [May-Jun] ●Birch Creek Reservoir [Jul] ●Otter Creek Spring, 12 mi W Randolph [Jun] ●Laketown Canyon; *Salt Lake Co*. ●Little Cottonwood Canyon, Wasatch Mountains [Jul]; *Sanpete Co*. ●Boulger Lake, Wasatch Plateau [Jun] ●Indianola [May]; *San Juan Co*. ●Blanding [Jul] ●Ute Mountains (Colorado state line) [Jun]; *Tooele Co*. ●Oquirrh Mountains, Settlement Creek Canyon [Jul]; *Utah Co*. ●Timpanogos, Wasatch Mountains [Jun] ●Aspen Grove, 7000 ft [May, Aug] ●Provo [Apr, Sep]●Provo Canyon [Sep] ●American Fork Canyon, 9500 ft [Aug] ●Payson Canyon [Jul] ●Payson Lakes [Jun] ●Sundance [May] ●Timpanogos Lodge [May] ●Squaw Peak [Aug] ●Alpine [May]; *Wasatch Co*. ●Strawberry Reservoir [Jun-Jul] ●Provo River [Jun] ●Silver Lake [Jul]; Wasatch Mt. State Park [May] ●Cascade Springs [Apr-May] ●Daniels Canyon, 8000 ft [Jul]; *Washington Co*. ●St. George ●Leeds Canyon [Apr] ●Lytle Preserve, 37.14490° N 114.02283° W, 836 m [Sep] ●Lytle Ranch, Welcome Spring [Jun] ●Snow Canyon Dunes [Mar-Apr] ●Red Cliffs Recreation Area, Red Cliffs Campground [Apr] ●Toquerville. **WASHINGTON**: *Asotin Co*. ●8 mi SE Clearwater Ranger Station (near Mt. Misery); *Benton Co*. ●Prosser [May]; *Chelan Co*. ●Riverhead Campground, Wenatchee National Forest [Jun]; *Ferry Co*. ●10 Mile Creek Campground, 48.515 -118.739, 1800 ft [Jun]; *Klickitat Co*. ● Spearfish [Jul] ●Glenwood, 0.2 mi N jct. Ladiges Rd on Bird Creek Road., 46°01.955′ N 121°18.255′ W, 1993 ft [May]; *Kittitas Co*. ●13 mi NE Kittitas [May] ●Easton ●Lake Cle Elum [Jun]; *Pend Oreille Co*. ●5.8 mi SW Tiger, Nile Lake, 3400 ft [Aug] ●Leo Lake, 3150 ft [Jun]; *Snohomish Co*. ●Lewis Peak, Blue Mts. [Jun]; *Spokane Co*. ●Mt. Spokane, 5000-5800 ft; *Stevens Co*. Northport [Jun] ●Pleasant Valley [May, Oct]; *Walla Walla Co*. ●Lowden [May] ●Walla Walla [Apr-May]; *Whitman Co*. ●Pullman [Mar-May, Jul] ●Palouse, Kamiak Butte [Apr-May]; *Yakima Co*. ●Bird Creek Ford, Yakima Indian Reservation, 2500 ft [Jun] ●5 mi W, 2 mi N Wenas Lake ●Toppenish [May]. **WYOMING**: *Albany Co*. ●5 mi W Garrett [Jul] ●Medicine Bow National Forest, Curtis Gulch Campground [Jul]; *Big Horn Co*. ●Trout Creek [Jun]; *Fremont Co*. ●Sweetwater Station [Jun]; *Natrona Co*. ●Bates Creek, 22 mi S Casper, 7000 ft [Aug]; *Park Co*. ●Lake Creek Camp, 13 mi SE Cooke City, MT, 7200 ft [Jul]; *Sublette Co*. ●Fremont Lake [Jul] ●Half Moon Lake [Jun]; *Sweetwater Co*. ●Burntfork [Jun] ●Green River [Jul]; *Teton Co*. ●43.61735° N 110.42963° W, 7300 ft [Aug] ●Yellowstone National Park, Lamar Valley [May] ● Yellowstone National Park, Trumpeter Swan Lake, 6080 ft [Sep] ●Jackson Lake, Teton National Park [May] ●Jackson Hole, 6300 ft [Jul, Sep] ●Jenny Lake [Jun]; *Washakie Co*. ●12.5 mi ESE Ten Sleep, Ten Sleep Preserve (The Nature Conservancy) [Jun].

Comments. There is potential confusion regarding the date of publication (1857 or 1860) of this LeConte species. Moore (1986) pointed out that the various parts of the Steven's survey were published hastily and piecemeal and only later grouped and formally published in book form in 1860 — making it, in Moore's words, a "collater's nightmare." LeConte, and perhaps other contributors, evidently opted to commission a private "preprint" of his results, which he distributed to colleagues years in advance of the issue of the complete report. I have not seen a copy of LeConte's "preprint" but, in the light of Moore's commentary and the fact that the 1857/1860 duality is of no nomenclatorial consequence, I accept the long-standing reported date of publication as 1857.

Thanks to Dr Jiří Hájek of the Czech National Museum, Prague, I have examined photographs of the two syntypes there of *Canthon bisignatus* Balthasar. In his study of *Canthon*, Balthasar (1939) considered eleven species here assigned to *Boreocanthon*, including *B. simplex* and a new species, *Canthon bisignatus*. The latter he separated from the remaining species, including *B. simplex*, in couplet 77(232) of his identification key (p. 190), ["Clypeus bidentate, lateral teeth either completely absent or indicated at most only by a weakly angulate thickening of the clypeal margin."], terminating at couplet 146(147). Both syntypes are clearly highly worn individuals of *B. simplex* whose originally quadridentate clypei have been rendered weakly bidentate by severe abrasion; moreover, both have bright red/orange elytral umbones. One bears the label, *Canthon simplex humeralis* Horn, Det. B. D. Gill '96. Since, to my knowledge, the synonymy of *Canthon bisignatus* Balthasar with *Boreocanthon simplex* has not heretofore been established formally, I do so here.

In addition to the syntype for *Canthon simplex* LeConte cited above (labeled by blue disk as Oregon/ Washington), there are two additional likely syntypes also present in the LeConte Collection at the Museum of Comparative Zoology (Crystal Maier, pers. comm). These are labeled (brown disk) as "Russian America", a possible reference to Fort Ross in present day Sonoma County, or other colonial outpost in California operated by the Russians until 1841 (Ballard 1997). Potential syntypes of Horn's (1870) varieties *humeralis* and *militaris* also reside in the MCZ collection. But in each case, the specimen depicted in the MCZ database (see photographs referenced above) as putative type material was, for an unknown reason, drawn from the LeConte Collection (Crystal Maier, pers. comm.) and, therefore, not strictly attributable to Horn. For this reason, I have added "?" to the syntype designations above.

Canthon simplex antiquus was one of two fossil taxa described by Pierce (1946) from asphalt deposits at Rancho La Brea in Los Angeles, California. It, along with *C. praticola vetustus* Pierce, are both considered conspecific with modern species (Miller et al. 1981; see Comments for *B. praticola*).

Horn (1870) recognized four varieties of *B. simplex*, viz., *simplex*, *corvinus*, *militaris* and *humeralis*. The second, *corvinus*, was in reference to Harold's (1860) species, which he explicitly rejected as deserving species status ("I cannot agree with Harold in separating *corvinus* as distinct."). Similarly, it is reasonable to assume that his "var. simplex" was a direct reference to LeConte's species. Only the remaining two varieties, var. *humeralis* and var. *militaris*, are here considered Horn taxa and, in accordance with ICNZ Article 45.6.4, are to be treated as subspecific names. Horn's (1870: 46) estimation of his varieties was blunt: "My own series is large, and my observation in California leads me to consider all these forms as mere local varieties and not distinct species." Robinson (1948: 88) later came to a similar conclusion, although he went farther by rejecting Horn's notion of local varieties altogether: "I think *simplex* is just a very variable species without any correlation between the internal and external variations and geographic localities, and therefore see no reason for continuing to split it into several varieties." I agree with Robinson's viewpoint.

I am inclined to believe that my taxonomic view of this species could be too simplistic — *Boreocanthon simplex* is anything but "simplex." As for morphological features, its only real constant is the shape of the head margin, with reduced clypeal teeth and weak paraocular notch (Fig. 92). Most specimens also show weakly expressed lateral elytral striae (7th and 8th), which, especially viewed obliquely from the side (Fig. 95), appear almost effaced basally. A common variable is the conspicuousness ("crispness") of pronotal puncturing, which varies continuously from nearly effaced to clearly expressed; the latter state figures in Harold's definition of his "var. *corvinus*." The elytral umbones, while dull black (Fig. 95) over most of its range, can be colored (Fig. 96–97, see below). I have not been able to sort these variables and others in any useful taxonomic way, and thus I, like previous observers (see below), have concluded that it is but a very common, widely distributed, highly variable species. A future student of the group might find it to be a complex array of populations with greater or lesser connections *inter se* — in other words, with other data (e.g., molecular) it might be possible to delimit multiple species, or semispecies or subspecies. Halffter (1958) fittingly recognized *B. simplex* as the most variable species in the genus and suggested that it could represent a "… [a Rassenkreiss or polytypic species with geographic subspecies … or {several} well-defined species]".

Perhaps the best known manifestation of variation in *B. simplex* is the color and luster of the elytral umbones. The most common condition throughout its range is the combination of dull, black umbones (Fig. 90, 95). Umbone luster varies irregularly but can be weakly shiny in contrast to the dull surrounding elytral surface in certain populations (Fig. 99). In some places, preponderantly in the mountainous zones surrounding the Central Valley of California (see Fig. 101 and collection localities listed above marked with red diamond ♦) a portion of the population bears umbones marked by an orange (reddish/red) spot. In most of these places, the colored umbones vary in size and intensity and occur along with all-black specimens. The types of the "varieties" *militaris*, *humeralis* and *corvinus*, as well as that of *Canthon bisignatus*, all bear orange markings, but only in the case of *militaris* are they cited in Horn's formal descriptions (1870:46). However, Harold (1868) does say, in his comments on *corvinus*, "[The number of individuals with red umbones is almost more than the solid black form.]" Moreover, he cites "Sorona, California" as type locality for his species, which I regard as a typographical error meaning Sonora, California (Tuolumne Co.). Individuals with orange umbones almost always occur with black individuals and are absent outside of California and southern Oregon. Among the 3000+ specimens examined for this study, I have seen only one outlier specimen with orange umbones; it is labeled LaGrande (Union Co.)

in far northeastern Oregon, a record I consider in need of corroboration. Robinson (1948) reported red/orange umbones in specimens from California, Oregon, Colorado and Arizona, but I have seen none from either of the latter two states. I have seen one unusual specimen of *B. simplex* (Pinnacles National Park, California) in which the orange color of the umbones, which are black, has "slipped" to the apices of the elytra (Fig. 98). Mario Cupello (pers. comm.) reports similar variability in umbone color in several South American scarabaeines, including *Ateuchus globulus* (Boucomont) and *Pseudocanthon xanthurus* (Blanchard).

I have examined a single, unusual specimen of *B. simplex* that I take as a sign of latent variability of this species in addition to that expressed across its range. It is from among numerous specimens collected at the Miami Ranger Station, Mariposa County, California. It is striking because it conserves distinct, but attenuated granules on the elytra, which normally present only shiny microspots. In addition, unlike "typical" *B. simplex*, the elytral striae are strongly accentuated. The pronotum of this specimen presents microspotting and conspicuous puncturing.

Given its morphological variability, it is not surprising that *B. simplex* is also highly variable from other points of view. Recorded food sources include the excrement of cattle, horses, humans, elk, deer, goat, rabbit, bear, and unidentified carnivores, as well as snake and porcupine carcass and other carrion. Its geographical range embraces widely disparate ecological settings, from conifer forests through desert steppe and scrub (cf. Fig. 2 and 100). Richard Cunningham (pers. comm.) reports collecting it from woodrat nests in Arizona. The recorded elevational spread of *B. simplex* is the widest of any *Boreocanthon* (and perhaps any other native U.S. dung beetle): from below 1,000 ft along the coastal ranges of the western U.S., to the summit of several mountain passes over the Sierra Nevada ranges in California (Sonora Pass, Mono County, 9,700 ft; Saddlebag Lake, 10,100 ft) and Utah (summit of American Fork Canyon, Utah County, 9,500 ft.). The distribution of *B. simplex* is not entirely blocked by a Rocky Mountain barrier; I have seen a few specimens from points east, mostly in the region of the Teton Mountains in Wyoming.

Occurrence of this species in the Great Basin is very poorly known – Figure 100 is presumptuous in showing it to occupy the entire region. I have seen fewer than 10 specimens from that enormous area and I assume that its rareness is result of poor collecting. It is noticeably absent or at least very scarce, or appears to be, from the Central Valley of California – confined largely to the surrounding mountains, and Pacific coastal region west of the coastal ranges as far south as northwestern Baja California (see Horn 1894: 304). The northern limit of the distribution of this species is far southern British Columbia (McNamara 2013; Macqueen and Beirne 1974). McNamara (2013) recorded *B. simplex* from British Columbia and Alberta; the latter record, while not out of the question, needs confirmation.

The collection at Carnegie Museum of Natural History (Pittsburgh) includes a single specimen of *B. simplex* bearing the label "Santa Fe Canon [sic], 7000 ft, Aug. 1880, Snow," presumably collected outside the city of Santa Fe by F. H. Snow. However, the report of the results of Snow's 1880 collecting trip to Santa Fe (Snow 1880), however, mentions only three scarabaeines, *Canthon praticola* and two species of *Onthophagus*, the new species *O. coproides* Horn, 1881, and *O. hecate* (Panzer, 1794). I am strongly inclined to conclude that it was mislabeled by Snow or by someone else. Robinson (1948) reported this species from Sonora, Mexico, which I am unable to corroborate.

Boreocanthon forreri (Bates, 1887), restored generic combination

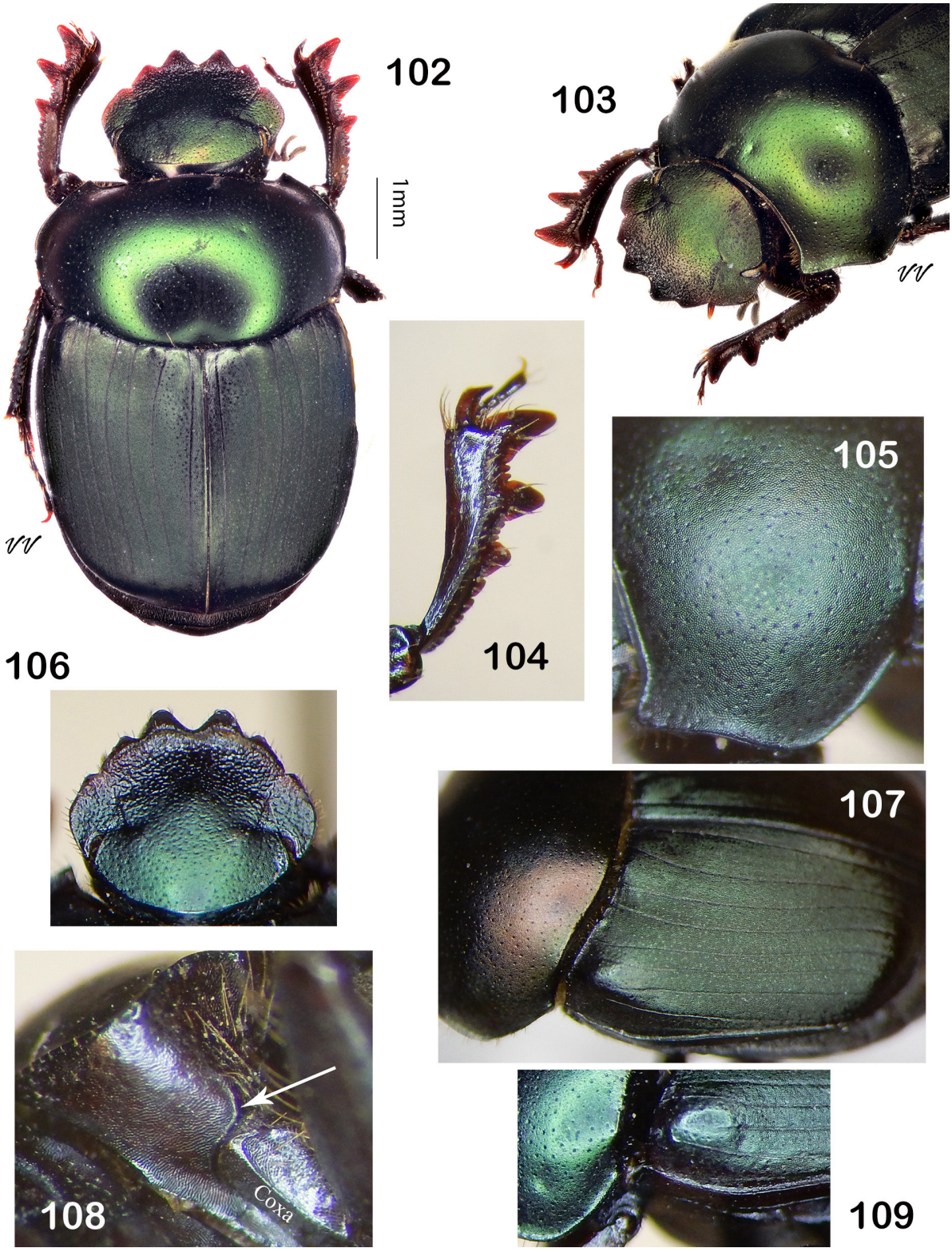
Fig. 45, 102–109

Canthon forreri Bates 1887: 31.
Boreocanthon forreri (Bates) (new combination per Halffter 1961: 234).
Canthon (*Boreocanthon*) *forreri* Bates (new combination per Howden 1966: 727).
Boreocanthon forreri Bates, **restored generic combination**.

Type material. Syntype (sex undetermined), The Natural History Museum London. Examined by photograph courtesy of Fernando Vaz-de-Mello.

Type locality. Mexico, Presidio (see Comments below)

Diagnosis. *Head*: Clypeus (Fig. 106) lightly roughened, weakly glistening anteriorly; bearing four marginal teeth; posteriorly, along with remainder of head, densely alutaceous, conspicuously punctate. Paraocular notch slight, setting off small, angulate corner of paraocular area (Fig. 106). Labio-gular fimbria curved posteriorly,



Figures 102–109. *Boreocanthon forreri* (Bates). **102)** Habitus, dorsal view. **103)** Anterolateral view of forebody. **104)** Anterior view right male tibia. **105)** Dorsolateral view of pronotum. **106)** Dorsal view of head. **107)** Laterodorsal view of pronotum and elytra. **108)** Ventral view of right hypomeron (arrow indicates hypomeral carina). **109)** Lateral view of humeral region.

interrupted medially by short V-shaped extension bearing coarse, setose punctures (as in Fig. 117). *Prothorax*: Pronotum (Fig. 102–103, 105) rather boldly, evenly punctate on weakly alutaceous background; anterolateral angles at most only very weakly upturned, posteromedian angle not noticeably impressed. Circumnotal ridge smooth, not serrate posteriorly. Hypomeral carina (Fig. 108) usually present, curving laterad to point one-eighth to one-fourth distance to outer margin. *Pterothorax*: Mesoventrite smooth; metaventrite evenly, sharply punctate. *Elytra*: Striae (Fig. 107, 109) lacking crisp margins (Fig. 107). Umbone distinctly shinier than disk (Fig, 109). Interstriae densely alutaceous, weakly microspotted; anterior ends of interstriae 2 and 3 not swollen, interstriae 3 and 5 with minute, acute tubercle in middle of anterior margin. Subhumeral (8th) stria carinulate basally, usually strongly so (Fig. 109); epipleural (9th) stria often visible, occasionally carinulate. *Legs*: Protibia (Fig. 104) evenly dilated, inner margin not offset; apical spur sexually dimorphic, apex acute in female, bifurcate in male. Hind femora lacking anterior row of longer setae, distal end bearing several conspicuous setae. *Abdomen*: Pygidium weakly punctured (as in Fig. 119), apex sometimes distinctly more convex and shinier than remainder of surface. Sixth ventrite punctate medially; other sternites smooth, impunctate. *Genital capsule*: Laterally compressed distal portion of parameres shortened, truncate ("snub nosed"), almost right-angled (as in Fig. 113); ventral apical angles in form of rounded knob (as in Fig. 114). *General*: Pronotum dark, shiny green, yellow-green or coppery, elytra and pygidium darker than pronotum with less pronounced color. Length: 4.5 – 6.0 mm. *Geographic distribution* (Fig. 45): NW coast of Mexico from Sonora to Nayarit. *Ecogeographic environment*: Tropical and Subtropical Dry Broadleaf Forests biome (Sonoran-Sinaloan Subtropical Dry Forest and Sinaloan Dry Forest ecoregions). *Specimens examined*: 88.

Collection localities.

MEXICO — NAYARIT: *Mpio. Del Nayar* ●Jesus Maria [Jun-Jul]. **SINALOA**: *Mpio. Culiacan* ●Altata [Jul-Aug] 14 mi N Culiacan [Aug]; *Mpio. Salvador Alvarado* ●11mi S Guamúchil [Aug]; *Mpio. San Ignacio* ●Rio Piaxtla, 1 mi W Hwy 15. **SONORA**: *Mpio. Alamos* ●Alamos [Jul-Aug] ●2 mi E Alamos ●La Aduana [Sep]; *Mpio. Etchojoa* ●Rio Mayo [Aug]; *Mpio. Huatabampo* ●53 mi S Navojoa [Jul]; *Mpio. Navojoa* ●Bacabachi [Sept] ●Tesopaco [Sep] ●5 mi E Navojoa [Aug] ●3 mi N Navojoa [Aug]; *Mpio. Santa Ana* ●6 mi S Benjamin Hill [Aug] ●11 mi S Benjamin Hill [Sep]; *Mpio. Ures* ●30 mi E Ures, 2700 ft [Aug].

Comments. The stated type locality of *B. forreri* is "Mexico, Presidio," which Selander and Vaurie (1962) identified as either the river, Rio Presidio, or the small village of Presidio east of Mazatlán, Sinaloa. Bates' specimens were collected in "N.W. Mexico" by Alphonse Forrer, one of the collectors who supplied material for the production of *Biologia Centrali-Americana* (Godman 1915). Besides work on the mainland, Forrer also collected on Islas Tres Marias, offshore from the small port of San Blas, Nayarit, which, like Mazatlán, could have been a point of embarkation to the islands. This port is close to another possible candidate for type locality, Presidio de los Reyes, a small town in Ruíz Municipality, Nayarit, about 65 km to the northeast. For present purposes, the choice remains moot as both "Presidios" are clearly within the range of *forreri* as considered here.

I regard this species as sister to *B. melanus*. Except for color, they are very similar and apparently overlap along the far northern coast of Sonora. Specimens assignable to both species occur in the area of Alamos, Sonora, begging the question of conspecificity, but I have not seen enough material from southern Sonora that I would want to resolve the question. Whether regarded as distinct species or not, the twosome comprises a distinct taxonomic entity.

I know nothing about the biology of *B. forreri* other than one record on fox excrement and another at blacklight.

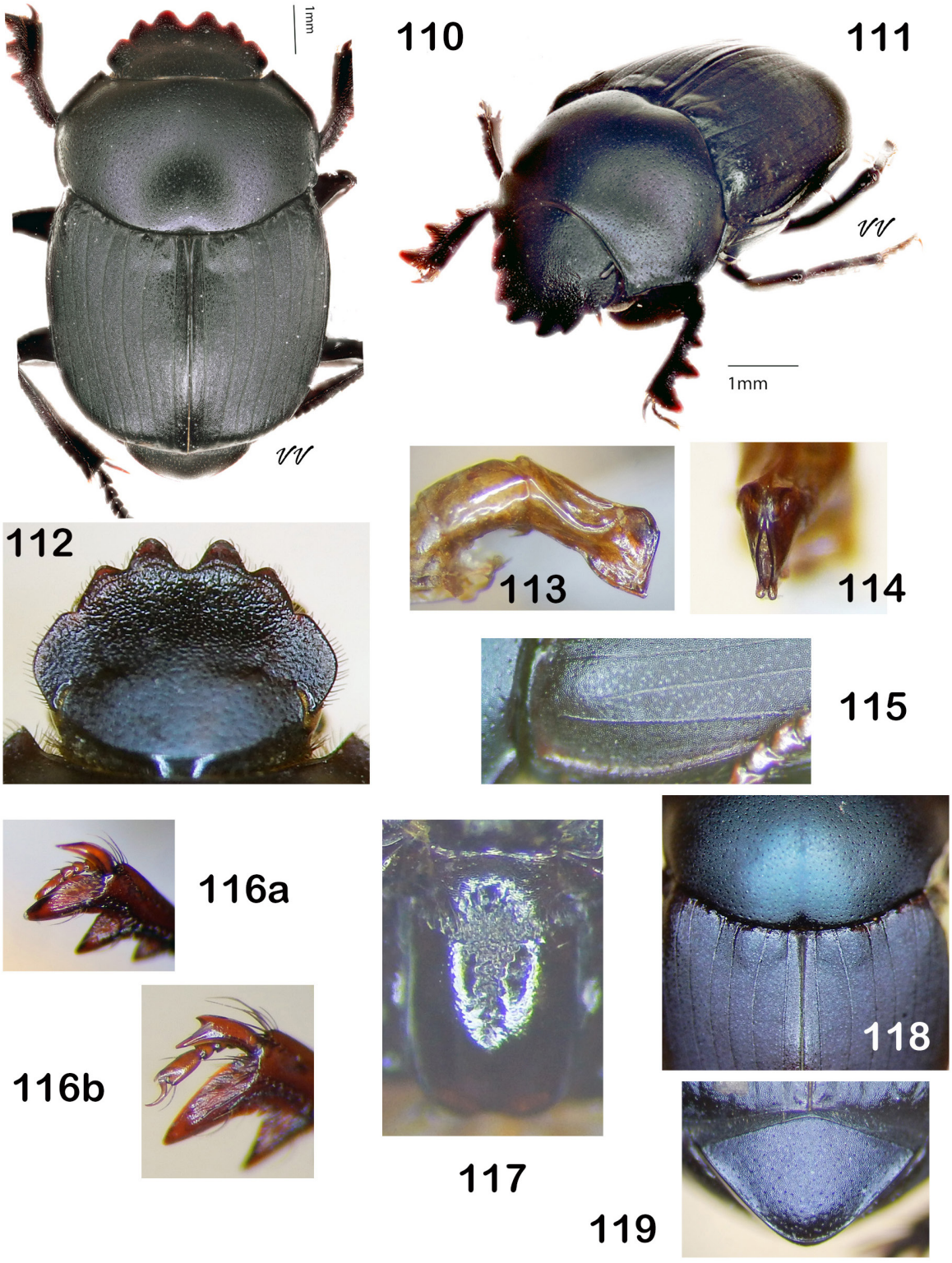
Boreocanthon melanus (Robinson, 1948), restored generic combination.

Fig. 45, 110–119

Canthon melanus Robinson 1948: 88.
Boreocanthon melanus (Robinson) (new combination per Halffter 1958: 209).
Canthon (*Boreocanthon*) *melanus* Robinson (new combination per Howden 1966: 727).
Boreocanthon melanus Robinson, **restored generic combination**.

Type. Syntype (sex undetermined). National Museum of Natural History, Washington, D.C. Not examined.

Type locality: Arizona, base of Pinal Mts.



Figures 110–119. *Boreocanthon melanus* (Robinson). **110)** Habitus, dorsal view. **111)** Habitus, oblique dorsolateral view. **112)** Dorsal view of head. **113)** Lateral view of genital capsule. **114)** Apical view of parameres. **115)** Dorsolateral view of lateral striae. **116)** Apex of protibia and tarsus. **a)** Female. **b)** Male. **117)** Ventral view of submentum and gula. **118)** Dorsal view of pronotum and elytra. **119)** Posterior view of pygidium.

Diagnosis. *Head*: Clypeus (Fig. 112) lightly roughened, weakly glistening anteriorly; bearing four strong marginal teeth; posteriorly, along with remainder of head, densely alutaceous, conspicuously punctate. Paraocular notch small, setting off small, angulate corner of paraocular area. Labio-gular fimbria (Fig. 117) curved posteriorly, followed medially by V-shaped field of coarse, setose punctures. *Prothorax*: Pronotum evenly punctate on shagreen background (Fig. 110, 118); anterolateral angles at most only very weakly upturned, posteromedian angle not noticeably impressed. Circumnotal ridge smooth, not serrate posteriorly. Hypomeral carina usually present, curving laterad to point one-eighth to one-fourth distance to outer margin (as in Fig. 108). *Pterothorax*: Mesoventrite smooth; metaventrite evenly, sharply punctate. *Elytra*: Striae (Fig. 115) lacking carinulate margins. Interstriae densely alutaceous, weakly microspotted; anterior ends of interstriae 2 and 3 weakly swollen (Fig.110–111, 118), interstriae 3 and 5 with minute, acute tubercle in middle of anterior margin. Subhumeral (8th) stria carinulate, usually strongly so (Fig. 115); epipleural (9th) stria effaced. *Legs*: Protibia evenly dilated, inner margin not offset; apical spur sexually dimorphic, apically acute in female (Fig. 116a), bifurcate in male (Fig. 116b). Hind femora lacking anterior row of longer setae, distal end bearing several conspicuous setae. *Abdomen*: Pygidium (Fig. 119) weakly punctured, apex sometimes distinctly more convex and shinier than remainder of surface. Sixth ventrite punctate medially; other ventrites smooth. *Genital capsule*: Laterally compressed distal portion of parameres shortened, truncate ("snub nosed"), almost right-angled (Fig. 113); ventral apical angles in form of rounded knobs (Fig. 114). *General*: Black, sometimes with green or blue highlights. Length: 4.0 – 6.5 mm. *Geographic distribution* (Fig. 45): Southern Arizona and northern Sonora, Mexico. *Ecogeographic environment* (Fig. 2): Deserts and Xeric Shrublands biome (Sonoran Desert ecoregion). *Specimens examined*: 645.

Collection localities.

MEXICO—CHIHUAHUA: *Mpio. Janos* ●Colonia Dublán ●45 mi N Casas Grandes. **SONORA**: *Mpio. Alamos* ●Alamos [Feb]; *Mpio. Altar* ●Llano Blanco [Jul]; *Mpio. Agua Prieta* ●10 mi SE Agua Prieta [Sep] ●15 mi SW Agua Prieta [Aug]; *Mpio. Hermosillo* ●Hermosillo [Sep]; *Mpio. Naco* ●Naco, 5000 ft [Aug]; *Mpio. Santa Ana* ●6 mi S Benjamin Hill [Aug] ●4mi, 17 mi S Santa Ana [Aug].

UNITED STATES—ARIZONA: *Cochise Co*. ●Dragoon [Aug]●12 mi NE Douglas [Aug] ●Palominas [Aug] ●Tombstone [Aug] ●6 mi E Tombstone [Aug] ●Texas Pass (hwy I-10) [Aug]●1 mi E Douglas [Aug] ●Apache, 5000 ft [Aug] ●Douglas [Jul-Aug] ●12 mi E Douglas [Aug] ●28 mi E Douglas, Guadalupe Canyon [Jul, Sep] ●Sierra Vista [Aug] ●Sunsites [Jul] ●5 mi SW Portal, Southwest Research Station [Jul, Sep] ●Willcox Dry Lake [Jul-Sep] ●San Pedro Riparian National Conservation Area [Oct] ●Coronado National Forest, Parker Canyon, 4800 ft [Sep] ●Courtland [Jul] ●Gleeson [Jul] ●Chiricahua Mountains, El Dorado, 5600 ft [Aug]; *Gila Co*. ●Globe [May]; *Graham Co*. ●Gila Valley/Safford [Aug]; *Maricopa Co*. ●Seven Springs Camp [Jun] ●El Dorado [Jul]; *Pima Co*. ●Hwy 89, 1 mi W Continental [Sep] ●11 mi E Continental [Sep] ●2 mi N Continental, 932 m, 31°50′19″ N 110°56′56″ W [May] ●Tumacacori [Aug] ●Rio Rico [Jul] ●Santa Rita Mountains, Madera Canyon, 16 km SE Green Valley, 4454 ft [Aug] ●Arivaca [Sep] ●Proctor Ranch, Madera Canyon [Jul] ●Green Valley [Sep-Oct] ●Jct. Hwy 86 and 386, entrance to Kitt Peak National Observatory [Sep] ●Hwy 286, 8 mi S. Three Points [Aug] ●Tucson [Aug-Sep]; *Santa Cruz Co*. ●Pajarito Mountains, Peña Blanca Canyon [Aug] ●Amado [Jul] ●7 mi E Sonoita [Aug] ●2.5 mi E Lochiel [Sep] ●Peña Blanca Lake [Jul] ●Duquesne Road, 2 mi E jct. Hwy 82 [Aug] ●4 mi N Nogales [Jul] ●10 mi NE Nogales [Jul] ●Nogales [Aug-Sep] ●Patagonia [Aug-Sep] ●10 mi W Patagonia ●Box Canyon, Santa Rita Mts. [Aug]; *Yavapai Co*. ●Yarnell [Sep] ●20 mi W Prescott [Aug].

Comments. *Boreocanthon melanus* is a common species south of the Colorado Plateau in southern Arizona, where it is sympatric with *B. puncticollis* and, less frequently, *B. simplex*. Its range extends to southern Sonora, where it apparently contacts its sister species, *B. forreri* (q.v.). There is a specimen in the Snow Entomological Collection (University of Kansas) labeled "S. Fe Canon [sic] 7000ft Aug 1880 (Snow)" presumably from F. H. Snow's trip to area in the summer of 1880; it is not referenced in Snow's report on the trip (Snow 1880). It, like a similar record for *B. simplex* (q.v.), I regard as a labeling error.

Label data record *Boreocanthon melanus* from human and cattle excrement. William Warner (pers. comm.) has collected it at blacklight and in flight intercept traps.

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Literature Cited

Balthasar V. 1939. Eine Vorstudie zur Monographie der Gattung *Canthon* Hffsg. 10. Beitrag zur Kenntnis der Scarabaeiden der neotropische Region. Folia Zoologica et Hydrobiologica 9: 179–238.

Ballard H. 1997. Ethnicity and chronology at Metini, Fort Ross State Historic Park, California. Kroeber Anthropological Society Papers 81: 116–140.

Barber HS. 1928. Thomas Say's unrecorded journey in Mexico. Entomological News 39: 15– 20.

Bates HW. 1887. Tribe Lamellicornia. p. 25–160. In: Bates HW. 1886–1890. Biologia Centrali-Americana, vol. 2, pt. 2. Taylor and Francis; London. 432 p. (Published serially: 1886: 1–24; 1887: 25–160; 1888: 161–336; 1889: 337–416; 1890: 417–432.).

Blackwelder RE. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 2. United States National Museum Bulletin 185: 189–341.

Blanchard F. 1885. On the species of *Canthon* and *Phanaeus* of the United States with notes on other genera. Transactions of the American Entomological Society 12: 163–169.

Blatchley WS. 1910. An illustrated descriptive catalogue of the Coleoptera or Beetles (exclusive of the Rhynchophora) known to occur in Indiana, with bibliography and descriptions of new species. The Nature Publishing Co.; Indianapolis. 1386 p.

Blume RR. 1970. Insects associated with bovine droppings in Kerr and Bexar Counties, Texas. Journal of Economic Entomology 63: 1023–1024.

Blume RR. 1972. Additional insects associated with bovine droppings in Kerr and Bexar Counties, Texas. Journal of Economic Entomology 65: 621.

Bousquet Y. 2016. Litteratura coleopterologica (1758–1900); a guide to selected books related to the taxonomy of Coleoptera with publication dates and notes. ZooKeys 583: 1–776.

Brown WJ. 1927. An annotated list of the coprophagous Scarabaeidae known to occur in Oklahoma. Proceedings of the Oklahoma Academy of Science 7: 24–28.

Cristóvão JP, Vaz-de-Mello FZ. 2020. The terminalia of the superfamily Scarabaeoidea (Coleoptera): specific glossary, dissecting methodology, techniques and previously unrecorded sexual dimorphism in some difficult groups. Zoological Journal of the Linnean Society 20: 1–43.

Cupello M, Vaz-de-Mello FZ. 2018. A monographic revision of the Neotropical dung beetle genus *Sylvicanthon* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini), including a reappraisal of the taxonomic history of '*Canthon* sensu lato'. European Journal of Taxonomy 467: 1–205.

Dajoz R. 1994. Les coléoptères coprophages du sud-est de l'Arizona (États-Unis). Composition spécifique, biogéographie et structure des peuplements. Annales de la Société Entomologique de France (N. S.) 30(2): 159–167.

Dawson RW. 1922. A synopsis of the Scarabaeidae of Nebraska (Coleoptera). University [of Nebraska] Studies 22: 163– 244.

Dejean AP. 1833. Catalogue des coléoptères de la collection de M. le Comte Dejean. Méquignon-Marvis Père et Fils; Paris. 443 p.

Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, Hansen M, Locke H, Ellis EC, Jones B, Barber CV, Hayes R, Kormos C, Martin V, Crist E, Sechrest W, Price L, Baillie JEM, Weeden D, Suckling K, Davis C, Sizer N, Moore R, Thau D, Birch T, Potapov P, Turubanova S, Tyukavina A, De Souza N, Pintea L, Brito JC, Llewellyn OA, Miller AG, Patzelt A, Ghazanfar SA, Timberlake J, Klöser H, Shennan-Farpón Y, Kindt R, Lillesø J-PB, van Breugel P, Graudal L, Voge M, Al-Shammari KF, Saleem M. 2017. An ecoregion-based approach to protecting half the terrestrial realm. BioScience 67: 534–545.

Edmonds WD. 1972. Comparative skeletal morphology, systematics and evolution of the phanaeine dung beetles (Coleoptera: Scarabaeidae). The University of Kansas Science Bulletin 49: 731–874.

Edmonds WD. 1994. Revision of *Phanaeus* Macleay, a New World genus of scarabaeine dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). Contributions in Science, Natural History Museum of Los Angeles County 443: 1–105.

Edmonds WD. 2018. The dung beetle fauna of the Big Bend region of Texas (Coleoptera: Scarabaeidae). Insecta Mundi 0642: 1–30.

Fincher GT, Blume RR, Hunter III JS, Beerwinkle KR. 1986. Seasonal distribution and diel flight activity of dung-feeding scarabs in open and wooded pasture in east-central Texas. Southwestern Entomologist, Supplement 10: 1–35.

Fincher GT, Stewart TB, Davis R. 1970. Attraction of coprophagous beetles to feces of various animals. Journal of Parasitology 56: 378–383.

Floate KD, Gill BD. 1998. Seasonal activity of dung beetles (Coleoptera: Scarabaeidae) associated with cattle dung in southern Alberta and their geographic distribution in Canada. Canadian Entomologist 130: 131–151.

Fuller HM, Hafen LR (eds.) 1973. The journal of Captain John R. Bell, official journalist for the Stephen H. Long expedition to the Rocky Mountains, 1820 (2nd edition). The Arthur H. Clark Company; Glendale, California. 349 p. + folding map.

Gámez N, Hihei SS, Schienvar E, Morrone JJ. 2016. A temporally dynamic approach for cladistic biogeography and the processes underlying the biogeographic patterns of North American Deserts. Journal of Zoological Systematics Evolutionary Research 55: 11–18.

Génier F. 2019. On the identity of *Canthon imitator floridanus* Brown, 1946 (Coleoptera: Scarabaeidae: Scarabaeinae). The Coleopterists Bulletin 73: 300–306.

Germar EF. 1823*. Coleopterorum species novae et minus cognitae, descriptionibus illustratae. Vol. 1, Coleoptera. Hendel and Sons; Halle, Germany. 624p. [*The publication date of this work is often cited as 1824; see Bousquet 2016.]

Gillet JJE. 1911. Coleopterorum catalogus, pars. 38, Scarabaeidae: Coprinae I. Junk; Berlin. 100 p.

Godman FD. 1915. Biologia Centrali-Americana. Zoology, Botany and Archaeology. Introductory volume. R. H. Porter; London. 149 p.

Gordon RD, Cartwright OL. 1974. Survey of food preferences of some North American Canthonini. Entomological News 85: 181–185.

Halffter G. 1958. Dos nuevos géneros de Canthonini (Col. Scarabaeidae). Ciencia (Mexico) 17: 207–212.

Halffter G. 1961. Monografía de las especies norteamericanas del género *Canthon* Hoffsg. (Coleopt. Scarab.). Ciencia (Mexico) 20: 225–320.

Halffter G. 2017. La zona de transición mexicana y la megadiversidad de México: del marco histórico a la riqueza actual. Dugesiana 24: 77–89.

Halffter G, Espinoza de los Monteros A, Nolasco-Soto J, Arriaga-Jiménez A, Rivera-Gasperín S. 2022. *Bajacanthon*, a new subgenus for the Mexican Deltochilini (Coleoptera: Scarabaeidae: Scarabaeinae) fauna. Diversity 14(109): 1–13.

Halffter G, Martínez A. 1977. Revisión monográfica de los Canthonini americanos, IV. Parte. Clave para géneros y subgéneros. Folia Entomológica Mexicana 38: 29–107.

Halffter G, Matthews EG. 1966. The natural history of dung beetles of the subfamily Scarabaeinae. Folia Entomológica Mexicana, Números 12–14: 1–312.

Halffter G, Morrone JJ. 2017. An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. Zootaxa 4226: 1–46.

Halffter G, Verdú JR, Moreno CE, Halffter V. 2012. Historical and ecological determinants of dung beetle assemblages in two arid zones of central Mexico. Journal of Arid Environments 76: 54–60.

Harold E von. 1868. Monographie der Gattung *Canthon*. Berliner Entomologische Zeitschrift 12: 1–144.

Harold E von. 1869. Vol. 4, Scarabaeidae. p. 979–1346. In: Gemminger M, Harold E von. 1869. Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Gummi; Munich. 3822 p.

Harpootlian PJ. 2001. Scarab beetles (Coleoptera: Scarabaeidae) of South Carolina. Biota of South Carolina, vol. 2. Clemson University; Clemson, South Carolina. 157 p.

Harris RA. 1979. A glossary of surface sculpturing. California Department of Food and Agriculture Occasional Papers in Entomology 28: 1–31.

Horn GH. 1870. Notes on some genera of coprophagous Scarabaeidae of the United States. Transactions of the American Entomological Society 3: 41–51.

Horn GH. 1894. The Coleoptera of Baja California. Proceedings of the California Academy of Sciences (series 2) 4: 302–449.

Howden HF. 1966. Notes on the Canthonini of the "Biologia Centrali-Americana" and description of new species (Coleoptera: Scarabaeidae). The Canadian Entomologist 98: 725–741.

Howden HF, Scholtz CH. 1986. Changes in a Texas dung beetle community between 1975 and 1985 (Coleoptera: Scarabaeidae, Scarabaeinae). The Coleopterists Bulletin 40: 313–316.

ICZN [International Commission on Zoological Nomenclature]. 1999. International Code of Zoological Nomenclature. Fourth Edition. The International Trust for Zoological Nomenclature; London. 306 p.

Islas F. 1942. Las especies mexicanas de los géneros *Canthon* Hffsg. y *Phanaeus* Mc'leay (Col. Scarabaeidae). Anales del Instituto de Biología 13: 301–340.

Kohlmann B, Halffter G. 1990. Reconstruction of a specific example of insect invasion waves: The cladistic analysis of *Canthon* (Coleoptera: Scarabaeidae) and related genera in North America. Quaestiones Entomologicae 26: 1–20.

Krajcik M 2006. Checklist of Scarabaeoidea of the World. 1. Scarabaeinae (Coleoptera: Scarabaeidae: Scarabaeinae). Animma.X, Supplement 3. Plzen; M. Krajcik. 190 p.

Krell F-T. 2010. Catalogue of Colorado scarab and stag beetles (Coleoptera: Scarabaeoidea), based on literature records. DMNS Technical Report 2010–4. Denver; Denver Museum of Nature and Science. 84 p.

Lawrence JF, Beutel RG, Leschen RAB, Slipinski A. 2010. Glossary of morphological terms. p. 9–20. In: Leschen RAB, Beutel RG, Lawrence JF (eds.). Coleoptera, beetles volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). Handbook of zoology Arthropoda: Insecta. De Gruyter; Berlin. 786 p.

LeConte JL. 1857 (1860). Report upon insects collected on the survey. Report No. 1, Zoological Report, Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean, Route near the forty-seventh and forty-ninth parallels , explored by I. I. Stevens, Governor of Washington Territory, in 1853–'55. Vol. 12, part 3. War Department; Washington, D.C. 72 p. [Note: The 1857 date is that of a privately distributed preprint of the report officially published in 1860; see Comments under *B. simplex*.]

LeConte JL. 1858. Catalogue of Coleoptera of the regions adjacent to the boundary line between the United States and Mexico. Journal of the Academy of Natural Sciences of Philadelphia (Series 2) 4: 9–42.

LeConte JL. 1859a (ed.). The complete writings of Thomas Say on the entomology of North America. Vol. 1. Bailliere Brothers; New York. 412 p.

LeConte JL. 1859b (ed.). The complete writings of Thomas Say on the entomology of North America. Vol. 2. Bailliere Brothers; New York. 814 p.

LeConte JL. 1859c. The Coleoptera of Kansas and eastern New Mexico. Smithsonian Contributions to Knowledge 2(6): 1–58.

LeConte JL. 1863. List of the Coleoptera of North America, prepared for the Smithsonian Institution. Part 1. Smithsonian Miscellaneous Collections No. 140. Smithsonian Institution; Washington, DC. 50 p.

LeConte JL. 1866. Additions to the coleopterous fauna of the United States. No. 1. Proceedings of the Academy of Natural Sciences of Philadelphia 1866: 361–394.

Leng CW. 1920. Catalogue of the Coleoptera of America, north of Mexico. John D. Sherman; Mount Vernon, NY. 470 p.

Lindquist AW. 1935. Notes of the habits of certain coprophagous beetles and methods of rearing them. United States Department of Agriculture Circular No. 351: 1–9.

Lobo JM. 1996. Diversity, biogeographical considerations and spatial structure of a recently invaded dung beetle (Coleoptera: Scarabaeoidea) community in the Chihuahuan Desert. Global Ecology and Biogeography Letters 5: 342–352.

Lobo JM. 2000. Species diversity and composition of dung beetle (Coleoptera: Scarabaeoidea) assemblages in North America. The Canadian Entomologist 132: 307–321.

Macqueen A, Beirne BP. 1974. Insects and mites associated with fresh cattle dung in the southern interior of British Columbia. Journal of the Entomological Society of British Columbia 71: 5–9.

McNamara J. 2013. Scarabaeidae. *In* Canadian National Collection of Insects, Arachnids and Nematodes, Checklist of beetles of Canada and Alaska. Available at http://www.canacoll.org/Coleo/Checklist/checklist.htm (Last accessed January 8, 2022.)

Majka CG, Chandler DS, Donahue CP. 2011. Checklist of the beetles of Maine, USA. Empty Mirrors Press; Halifax, Nova Scotia. 328 p.

Martínez A. 1948a. Insectos nuevos o poco conocidos — IV (Col. Scarabaeidae). Revista de la Sociedad Entomológica Argentina 14: 3–11.

Martínez A. 1948b. Notas coleopterológicas, I. Anales de la Sociedad Científica Argentina 146: 41–51.

Martínez A, Pereira FS. 1956. Dois gêneros novos de Canthonini americanos (Col. Scarabaeoidea, Scarabaeidae). Papéis Avulsos do Departamento de Zoologia 12: 363–388.

Martínez-Morales I, Morón MA. 2015. Los sistemas reproductivos en hembras de Melolonthinae, Rutelinae, y Dynastinae (Coleoptera: Scarabaeoidea, Melolonthidae). Southwestern Entomologist 40: 369–385.

Mawdsley JR. 1993. The entomological collection of Thomas Say. Psyche 100: 163–171.

McPeak RH, Lago PK, Hanley GA. 2014. The scarabaeoid beetles of San Diego County, California Part II. Diagnosis of families Lucanidae and Scarabaeidae (Subfamilies Aphodiinae and Scarabaeinae) with comments on Part I. Proceedings of the San Diego Society of Natural History No. 44: 1–39.

Medina CA, Scholtz CH, Gill BD. 2003. Morphological variation and systematics of *Canthon* Hoffmannsegg 1817, and related genera of New World Cathonini dung beetles (Coleoptera, Scarabaeinae). Deutsche Entomologische Zeitschrift 50: 23–68.

Melsheimer FE. 1853. Catalogue of the described Coleoptera of the United States [revised by S. S. Haldeman and J. L. LeConte]. Smithsonian Institution; Washington DC. 174 p.

Miller A. 1954. Dung beetles (Coleoptera: Scarabaeidae) and other insects in relation to human feces in a hookworm area of southern Georgia. The American Journal of Tropical Medicine and Hygiene 3: 372–389.

Miller SE. 1983. Late Quaternary insects of Rancho La Brea and McKittrick, California. Quaternary Research 20: 90–104.

Miller SE, Gordon RD, Howden HF. 1981. Reevaluation of Pleistocene scarab beetles from Rancho La Brea, California (Coleoptera: Scarabaeidae). Proceedings of the Entomological Society of Washington 83: 625–630.

Moore JA. 1986. Zoology of the Pacific Railroad surveys. American Zoologist 26: 331–341.

Morrone JJ. 2015. Halffter's Mexican transition zone (1962–2014), cenocrons and evolutionary biogeography. Journal of Zoological Systematics and Evolutionary Research 53: 249–257.

Nealis VG. 1977. Habitat associations and community analysis of South Texas dung beetles (Coleoptera: Scarabaeinae). Canadian Journal of Zoology 55: 138–147.

Nemes SN, Price DL. 2015. Illustrated keys to the Scarabaeinae (Coleoptera: Scarabaeidae) of Maryland. Northeastern Naturalist 22: 318–344.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR. 2001. Terrestrial ecoregions of the world: A new map of life on earth. BioScience 51: 933–938.

Parmenter RR, Brantley SL, Brown JH, Crawford CS, Lightfoot DC, Yates TL. 1995. Diversity of animal communities on southwestern rangelands: Species patterns, habitat relationships, and land management. Natural Resources and Environmental Issues 4(7): 1–22.

Pereira FS, Martínez A. 1956. Os gêneros de Canthonini americanos. Revista Brasileira de Entomologia 6: 91–192.

Pierce WD. 1946. Fossil arthropods of California. 11. Descriptions of the dung beetles (Scarabaeidae) of the tar pits. Bulletin of the Southern California Academy of Sciences 45: 119–131.

Pollock DA, Lavigne RJ. 2019. Records of Coleoptera as prey of robber flies (Diptera: Asilidae) in eastern New Mexico and west Texas. Proceedings of the Entomological Society of Washington 121: 81–102.

Ratcliffe BC, Paulsen MJ. 2008. The scarabaeoid beetles of Nebraska (Coleoptera: Scarabaeoidea). Bulletin of the University of Nebraska State Museum, Vol. 22. University of Nebraska State Museum; Lincoln, Nebraska. 569 p.

Riley EG, Wolfe CS. 2003. An annotated checklist of the Scarabaeoidea of Texas (Coleoptera). Southwestern Entomologist, Supplement No. 26: 1–37.

Robinson M. 1948. A review of the species of *Canthon* inhabiting the United States. Transactions of the American Entomological Society 74: 83–99.

Say T. 1823. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. Journal of the Academy of Sciences of Philadelphia 3: 139–216.

Schaeffer C. 1915. New Coleoptera and miscellaneous notes. Journal of the New York Entomological Society 23: 47–55.

Schmidt A. 1922. 1. Bestimmungstabelle der mir bekannten *Canthon*-Arten. 2. Verbreitungsgebiete der *Canthon*-Arten. 3. Neubeschreibungen von *Canthon*, *Saprositis*, *Mendidius*, *Euparia*, und *Ataenius*. Archiv für Naturgeschichte 88: 61–103.

Schoenly K. 1983. Arthropods associated with bovine and equine dung in an ungrazed Chihuahuan Desert ecosystem. Annals of the Entomological Society of America 76: 790–796.

Selander RB, Vaurie P. 1962. A gazetteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana." American Museum Novitates No. 2099: 1–70.

Snow FH. 1880. List of Coleoptera collected in Santa Fe Canon, New Mexico, by the Kansas University Expedition of 1880. Transactions of the Kansas Academy of Science 7: 67–71.

Staines CL. 1984. An annotated checklist of the Scarabaeoidea (Coleoptera) of Maryland. Maryland Entomologist 2: 79–89.

Sturm J. 1843. Katalog der Kaefer-Sammlung von Jacob Sturm. J. Sturm; Nuremberg. 386 p.

Tonelli M. 2021. Some considerations on the terminology applied to dung beetle functional groups. Ecological Entomology 46: 772–776.

Townsend CHT. 1902. Contribution to a knowledge of the coleopterous fauna of the lower Rio Grande valley in Texas and Tamaulipas, with biological notes and special reference to geographical distribution. Transactions of the Texas Academy of Science 5: 51–101.

Ulke H. 1874. List of species of Coleoptera, collected by Lieut. W. L. Carpenter, United States Army, for the United States Geological Survey of Colorado, 1873. Annual Report of the United States Geological and Geographical Survey of the Territories 1873: 567–570.

Vaz-de-Mello, FZ, Edmonds WD, Ocampo FC, Schoolmeesters P. 2011. A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World. Zootaxa 2854: 1–73.

Vulcano MA, Pereira FS. 1964. Catalogue of the Canthonini (Col. Scarab.). Entomologischen Arbeiten aus dem Museum G. Frey, Tutzing 15: 570–685.

Weiss HB, Ziegler GM. 1931. Thomas Say, early American naturalist. Charles C. Thomas; Springfield, Illinois. 260 p.

Wickham HG. 1902. A catalogue of the Coleoptera of Colorado. Bulletin from the Laboratories of Natural History of the State University of Iowa 5: 217–310.

Wolcott GN. 1922. Insect parasite introduction in Porto Rico. Journal of the Department of Agriculture of Porto Rico 6: 5–20.

Woodruff RE. 1973. The scarab beetles of Florida (Coleoptera: Scarabaeidae). Part I. The Laparosticti (Subfamilies: Scarabaeinae, Aphodiinae, Hybosorinae, Ochodaeinae, Geotrupinae, Acanthocerinae). Arthropods of Florida and neighboring land areas, Vol. 8. Florida Department of Agriculture and Consumer Services; Gainesville, Florida. 220 p.

Zachos FE. 2014. Taxonomic inflation, the Phylogenetic Species Concept and lineages in the Tree of Life – a cautionary comment on species splitting. Journal of Zoological Systematics and Evolutionary Research 53 (2): 180–184.

Zunino M, Halffter G. 2007. The association of *Onthophagus* Latreille, 1802 beetles (Coleoptera: Scarabaeinae) with vertebrate burrows and caves. Elytron 21: 17–55.

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