Insect systematics More and the systematics of the systematics of the systematics of the systematics of the systematic o

1014

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

> W. D. Edmonds 2625 SW Brae Mar Ct. Portland, Oregon 97201

Date of issue: October 27, 2023

Center for Systematic Entomology, Inc., Gainesville, FL

Edmonds WD. 2023. Taxonomic review of the North American dung beetle genus *Melanocanthon* Halffter, 1958 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). Insecta Mundi 1014: 1–28.

Published on October 27, 2023 by Center for Systematic Entomology, Inc. P.O. Box 141874 Gainesville, FL 32614-1874 USA http://centerforsystematicentomology.org/

INSECTA MUNDI is a journal primarily devoted to insect systematics, but articles can be published on any nonmarine arthropod. Topics considered for publication include systematics, taxonomy, nomenclature, checklists, faunal works, and natural history. Insecta Mundi will not consider works in the applied sciences (i.e. medical entomology, pest control research, etc.), and no longer publishes book reviews or editorials. Insecta Mundi publishes original research or discoveries in an inexpensive and timely manner, distributing them free via open access on the internet on the date of publication.

Insecta Mundi is referenced or abstracted by several sources, including the Zoological Record and CAB Abstracts. Insecta Mundi is published irregularly throughout the year, with completed manuscripts assigned an individual number. Manuscripts must be peer reviewed prior to submission, after which they are reviewed by the editorial board to ensure quality. One author of each submitted manuscript must be a current member of the Center for Systematic Entomology.

Guidelines and requirements for the preparation of manuscripts are available on the Insecta Mundi website at http://centerforsystematicentomology.org/insectamundi/

Chief Editor: David Plotkin, insectamundi@gmail.com
Assistant Editor: Paul E. Skelley, insectamundi@gmail.com
Layout Editor: Robert G. Forsyth
Editorial Board: Davide Dal Pos, M. J. Paulsen, Felipe Soto-Adames
Founding Editors: Ross H. Arnett, Jr., J. H. Frank, Virendra Gupta, John B. Heppner, Lionel A. Stange, Michael C. Thomas, Robert E. Woodruff
Review Editors: Listed on the Insecta Mundi webpage

Printed copies (ISSN 0749-6737) annually deposited in libraries

Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA The Natural History Museum, London, UK National Museum of Natural History, Smithsonian Institution, Washington, DC, USA Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia

Electronic copies (online ISSN 1942-1354) in PDF format

Archived digitally by Portico. Florida Virtual Campus: http://purl.fcla.edu/fcla/insectamundi University of Nebraska-Lincoln, Digital Commons: http://digitalcommons.unl.edu/insectamundi/ Goethe-Universität, Frankfurt am Main: http://nbn-resolving.de/urn/resolver.pl?urn:nbn:de:hebis:30:3-135240

This is an open access article distributed under the terms of the Creative Commons, Attribution Non-Commercial License, which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited. https://creativecommons.org/licenses/by-nc/3.0/

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

W. D. Edmonds

2625 SW Brae Mar Ct. Portland, Oregon 97201 wdedmonds@hotmail.com

Abstract. This paper presents a taxonomic review of the genus *Melanocanthon* Halffter, a group of ball-rolling (telocoprid) dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) endemic to eastern North America. The genus comprises five species, each keyed, diagnosed, illustrated and presented with information on distribution, relationships, and biology: *Melanocanthon punctaticollis* (Schaeffer), *M. granulifer* (Schmidt), *M. nigricornis* (Say), *M. bispinatus* (Robinson) and *Melanocanthon vulturnus* Edmonds, **new species**.

Key words. Genus and species diagnoses, key to species, new species.

ZooBank registration. urn:lsid:zoobank.org:pub:FA7D5D5E-CEB8-48ED-A442-74C315FCF5E4

Introduction

This paper is a sequel to the recent taxonomic study of *Boreocanthon* (Edmonds 2022). *Melanocanthon* and *Boreocanthon* are very closely related, distinct phylogenetic lineages with affinities to the pilularius species group of *Canthon* (Halffter 1961) and the monotypic taxon, *Bajacanthon obliquus* (Horn) (Halffter et al. 2022). The goal of this paper is a taxonomic review of the genus *Melanocanthon* and its constituent species. These two studies are contributions to the systematic background necessary for a future study of the historical biogeography of the native deltochiline fauna of the United States. *Melanocanthon* is virtually endemic to the United States, and *Boreocanthon* largely so. Remaining to complete the taxonomic picture is a re-examination and review of the pilularius species group of *Canthon* (sensu Halffter 1961), also mostly restricted to the United States.

Halffter (1958) created the genus *Melanocanthon* to accommodate four United States species of *Canthon: C. nigricornis* (Say, 1823), *C. granulifer* Schmidt, 1920, *C. punctaticollis* Schaeffer, 1915, and *C. bispinatus* Robinson, 1941. He designated *Canthon bispinatus* Robinson type species of the new genus. Among the features characteristic of the group, Halffter cited a) the presence of two apical spurs on the hind tibiae; b) a deeply V-shaped labio-gular fimbria; c) a spinate subclypeal process; and d) an otherwise very strong similarity to the genus *Boreo-canthon*, which he created at the same time as *Melanocanthon* (Halffter 1958).

The first de-facto taxonomic study of *Melanocanthon* was that published by Robinson (1941) as a review of the "nigricornis [species] group of *Canthon*," which he later incorporated into a broader study of *Canthon* inhabiting the United States (Robinson 1948). Halffter's (1958) study essentially formalized Robinson's view by creating the genus *Melanocanthon* to subsume the nigricornis species group. As considered here, the genus conserves the Robinson-Halffter taxon with the exception that Florida populations previously regarded as *M. granulifer* by Woodruff (1973) are here assigned to the new species, *Melanocanthon vulturnus*.

As observed by Edmonds (2022), cladistic studies that include *Melanocanthon*, as well as *Boreocanthon*, are very few. In those by Kohlmann and Halffter (1990) and Medina et al. (2003), the two resolved as sister groups; and, in that by Halffter et al. (2022), *Boreocanthon* (*Melanocanthon* was not considered) resolved as sister group to *Bajacanthon*, a monotypic group endemic to the southern tip of Baja California. Clearly much remains to be learned regarding the phylogenetic picture of these three groups, as well as the pilularius species group of *Canthon*, in the overall context of the history of the autochthonous deltochiline fauna of North America.

Materials and Methods

The methods employed for this study are essentially the same as those used for the similar treatment of *Boreocanthon* (Edmonds 2022). The present review is based on examination of approximately 3550 specimens, all of which were graciously provided by the caretakers of the institutional and private collections cited in the Acknowledgments.

Collection localities were gleaned almost exclusively from specimens seen by me. For each species, they 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 and followed in brackets by month(s) of collection, if known. The symbols are used to clearly punctuate locality lists, otherwise visually difficult to separate using more conventional marks. If a label cites only a United States 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. Geographical distributions depicted by county occurrence (Fig. 16–18) employ base maps available at https://gisgeography.com/us-county-map/.

As was for the case of *Boreocanthon*, a weakness of this study is the fact that I was unable to examine directly type material. In most cases, however, photographs of putative types were 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 (1999) 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 (1999: 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.

The morphological discussion presented in Edmonds (2022) is generally applicable here and supplemented in the section that follows.

Taxonomic characters in *Melanocanthon*. *Melanocanthon* is a tightly knit group of species sharing the rather extensive suite of characters presented in the diagnosis below. The separation of its species, as here defined, rests almost exclusively on variations in dorsal sculpturing, distributional data, and male genitalia. Dorsal sculpturing, while variable intraspecifically, is an important source of diagnostic characters that, with some experience, are reliable at least 75–80% of the time. While all five species exhibit characteristic features of dorsal sculpture, these often must be combined with the form of the parameres and distributional data to arrive at a confident identification. Robinson (1941) stressed the importance of the aedeagus, "Upon examining the genitalia ... I have found that four distinct species can be separated in the unique group [of *Canthon*] with two spurs on the posterior tibiae." Later Robinson (1948) reiterated his findings, "Some of our species [of *Canthon*] are quite variable in their external characters ... The male genitalia, while varying to a degree among some of the species, are the only single character found absolutely to segregate species in the [Boreocanthon] puncticollis and [*Melanocanthon*] nigricornis groups." In the context of this study, Robinson's conclusion still largely holds and I have concluded similarly that, without reference to parameres, species identification in *Melanocanthon* can be tenuous at best. To this observation I add the following comments:

Clypeal sculpturing—In *M. punctaticollis* and *M. granulifer*, the anterior portion of the clypeus immediately behind the clypeal teeth is usually populated by a loose, transverse array of 15–20 or so conspicuously large, shallow punctures producing a "freckled" visage (Fig. 20, 27). Such "freckling" can also appear in *M. bispinatus*, but in this case the number of conspicuous punctures is limited to fewer than ten. These large punctures are always in addition to other intermingled, less noticeable puncturing on the head surface.

Pronotal sculpturing—For all species, pronotal sculpturing is best assessed on the pronotal disk; the form of granulation, in particular, often varies from the elongate shape characteristic of granules on the discal area to more rounded in peripheral areas. In *M. granulifer* (Fig. 28–29) and *M. vulturnus* (Fig. 43–44) the pronotal disk is evenly and fairly densely covered by coarse, rounded or elongate granules that stand out from the shagreen background; any visible puncturing is very fine and widely scattered. In *M. bispinatus* (Fig. 52–53) and *M. nigricornis* (Fig. 34–35) the pronotal disk is rather densely granulate, but the granules are more elongate ("streaked") and much finer and more variable in intensity, from rather bold to nearly attenuated, but always accompanied by sharp, evenly distributed punctures. In *M. punctaticollis* (Fig. 22) granulation is virtually completely attenuated except near the lateral margins such that the surface assumes a smoother, velvety texture covered by a mélange of sharp punctures and, occasionally, shining microspots (presumed remnants of former granulation).

Elytral sculpturing—There are eight elytral striae, but to quote Halffter (1958), "[Elytral striae poorly marked and difficult to count]". I have not observed even the slightest indication of an abbreviated ninth stria, as seen in some *Boreocanthon*. The elytral interstriae always bear elevated, round granules, but there is significant variation among species in size, density, and distribution. In general, however, their configuration varies within fairly narrow limits within species. In *M. granulifer* (Fig. 28) and *M. vulturnus* (Fig. 46–47) the granulation is bold, rather densely and evenly distributed across the entire elytral surface. In the remaining three species, the granulation of the lateral interstriae (7th and 8th) is strong and evenly distributed, whereas on the discal interstriae, granules become much smaller, and more widely and unevenly distributed, especially centrally (interstriae 4–6). The extremes are manifested by *M. granulifer*, in which they are relatively large, prominent, closely packed and evenly dispersed over the entire elytral surface (Fig. 28), and *M. punctatcollis*, in which they vary considerably in size and density and distribution (Fig. 25).

Hind tarsus—Robinson (1941) was first to point out that, in *M. punctaticollis*, the metabasitarsus (Fig. 26) is longer by about one-half than the second tarsomere. The same feature is generally true for *M. bispinatus* (Fig. 55) and *M. vulturnus* (Fig. 45), although variation tends to render the character difficult to assess. In all three species, the length of the last (apical) tarsomere exceeds the combined lengths of tarsomeres 3–4, and the tarsus overall is what I term here as "slender." In both *M. nigricornis* (Fig. 39) and *M. granulifer* (Fig. 33) the length and width of tarsomeres 1–4 are about equal, lending the tarsus a distinctly "wider" profile where the length of the apical tarsomere is about equal to the combined lengths of tarsomeres 3–4. Shapes and proportions of tarsomeres is best assessed from an inner (mesal) view of the tarsus.

Distribution—The five species of *Melanocanthon* sort geographically into two groups separated roughly along the 88th meridian from the Gulf of Mexico to Lake Michigan, a line more-or-less coincident with the axis of the Mississippi River drainage system (Fig. 15). The historical, ecological or other factors that might explain this separation remain an open question. An intermediate area, indicated by the yellow box in Figure 19, is an area of potential, yet undemonstrated, sympatry between *M. nigricornis* (a western species) and *M. bispinatus* (an eastern species); definitive identification of specimens from localities in this area rests on examination of the parameres.

Systematics

Genus Melanocanthon Halffter, 1958

Melanocanthon Halffter 1958: 210.

Type species. Canthon bispinatus Robinson, 1941, by original designation.

Diagnosis. (presumed apomorphic features, in the context of the autochthonous US fauna of deltochilines, are *italicized*): • Small (length 5–10 mm), usually dull black, ball-rolling dung beetles ("tumblebugs") (Fig. 1–2). • Clypeal margin (Fig. 12) quadridentate, middle teeth large, acute apically, lateral teeth widely, obtusely angulate; clypeal teeth, combined with small, anterior prominences of the paraocular areas, produce a weakly sexdentate anterior head margin. • *Clypeal process spiniform* (Fig. 4–5), abraded to triangular tooth in worn specimens (Fig 6). • Anterior angle of paraocular area weakly produced, angulate (Fig. 12); paraocular notch obsolete. • Fronto-clypeal suture very fine, sometimes nearly effaced. • Posterior margin of head completely, very finely margined. • Labiogular fimbria (Fig. 8, arrow) narrowly V-shaped, apex extending posteriorly sometimes beyond middle of



Figures 1–8. Generic features of *Melanocanthon.* **1**) *M. bispinatus* (Robinson) habitus *in vivo*, New Hanover County, North Carolina. **2**) *M. nigricornis*, habitus *in vivo*, Lake County, Illinois. **3**) *M. granulifer* (Schmidt), right protibia-tarsus of male. **4**) Same, frontal view middle portion clypeus (square encloses area magnified in Figure 5). **5**) Same, spiniform clypeal process. **6**) Same, shape of clypeal process modified by wear. **7**) Same, lateral view of portion of head and prothorax. **8**) Same, ventral view of head (arrow indicates labio-gular fimbria).

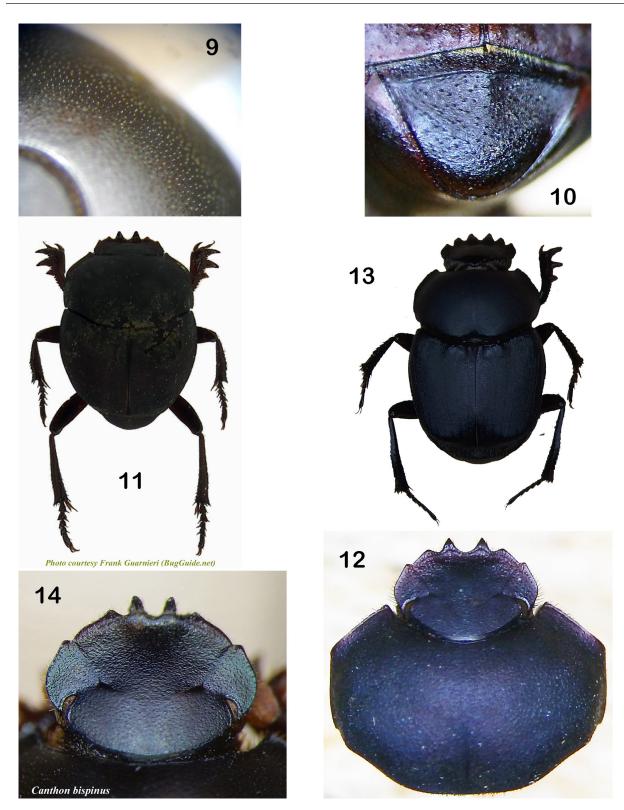
gula. • Lateral pronotal angles widely obtuse such that pronotum (viewed from above) appears "broad shouldered" (Fig. 12); lateral pronotal fossae obsolete, sometimes represented by a weak bump. • Anterolateral portion of pronotal margin (viewed dorsally, Fig. 12) almost straight, and (viewed laterally, Fig. 7) strongly bowed upwards to accommodate front leg; anterior end of bow followed by single coarse tubercle and row of smaller bumps reaching anterior angle. • Pronotum (viewed laterally) raised above level of elytra ("humped") and (viewed dorsally) slightly impressed along midline from posterior angle to near middle of disk. • Hypomeral carina absent. • Elytral profile (viewed dorsally, Fig. 11) more-or-less evenly curved from umbones to pygidium such that body appears gradually narrowed posteriorly; dorsal silhouette more or less acorn-shaped. • Eight elytral striae; striae very weak, superficial, and often difficult to discern, lateral striae (5-8) often mostly effaced; interstriae flat • Outer margin of protibia (Fig. 3) strongly tridentate, serrate basally and between large teeth; inner margin abruptly offset at level of third (basal) lateral tooth; inner apical angle sometimes produced as conical tubercle. • Protibial spur sexually dimorphic: apex acute in female, bifurcate in male (Fig. 3). • Ventral surfaces of femora completely, evenly punctured, punctures well defined, fairly dense. • Metafemur lacking carina along anterior margin. • Metatibia with two apical spurs (Fig. 26, 39, 55) • Pygidium (Fig. 10) completely margined, evenly covered with distinct granules on shagreen background; base impressed, sometimes only weakly so, on each side of raised midline; apex always strongly convex. • Parameres (Fig. 23, 31-32, 56-58) compressed laterally, apex (viewed laterally) truncate, lower apical lobes (viewed caudally) rounded knobs or flattened tabs. • Dorsum (including pygidium) often with distinct, raised granules on very fine shagreen background (50×) intermingled with minute, scattered, setose punctures especially on head and pronotum (Note: Setae readily perceptible only when viewed at very low, almost flat angle at high power [50×], Fig. 9). Granules can be rudimentary or reduced to shiny microspots on head and pronotum. • Virtually endemic to the United States, distributed from Atlantic coast to Rocky Mountains, with peripheral populations in far northeastern Mexico and Great Lakes region of southeastern Ontario (Fig. 15).

Comments. The species of *Melanocanthon* recognized here are very similar and comprise a cohesive taxonomic group most closely related to the *Boreocanthon ebenus-depressipennis* species-pair via *Melanocanthon granulifer*. Linking the two (*Boreocanthon ebenus+depressipennis* to *M. granulifer*) is the following set of characters: a) strongly, densely granulate dorsal surface essentially lacking punctures; b) base of pygidium impressed on each side of median convexity; c) abruptly widened anterior tibia (inner margin stepped, offset). Separating them are the apomorphic features listed in the diagnosis above.

Horn (1870) was first to report the presence of two apical metatibial spurs in *Canthon nigricornis*, a character that Robinson (1941) used to group the then known four species as the "nigricornis group of *Canthon*," now *Melanocanthon*. This feature is unique to *Melanocanthon* among known Scarabaeinae, although Horn erroneously attributed it also to *Canthon indigaceus* LeConte (corrected by Blanchard 1885). The mesotibia of *Melanocanthon* has two apical spurs, like all other known scarabaeine genera except one, the exception being the Brazilian genus *Atlantemolanum*, which has but one (González-Alvarado et al. 2019).

The shapes of the anterior margin of the head and margin of the pronotum of *Melanocanthon* (Fig. 12) are quite consistent among the species; that of the head margin is closely mimicked by the distantly related, South American species, *Canthon bispinus* Harold (Fig. 14) and very rarely subject to developmental anomaly (Fig. 21). Equally characteristic is the overall ship's bow-shaped elytral profile (Fig. 11), markedly different from the more evenly rounded shape found in its sister genus, *Boreocanthon* (Fig. 13).

Observations on the biology of *Melanocanthon* are scarce and mentioned in the species treatments below. Like *Boreocanthon*, they are undeniably psammophilous, as noted very early on by Hart (1907) and Vestal (1913), and quite common in open conifer and broadleaf habitats with sandy substrate. For *Melanocanthon* species, there does not yet exist enough precise ecological data to pursue an analysis of the effect of spatial distribution of sandy habitat on species distributions, such as that by Marshall et al. (2000) for *Geoglycosa* wolf spiders in the sand ridge system of peninsular Florida. Published comments, as well as my own findings from collection records, suggest an inclination toward fungus-feeding not observed in *Boreocanthon*; all species but *M. granulifer*, have been recorded from bolete basidiomycetes ("toadstools"). Otherwise, collectively the members of the genus exhibit acceptance of a wide variety of food sources, including excrement of many origins, decomposing fruit and carrion.



Figures 9–14. Generic features of *Melanocanthon.* **9**) *M. bispinatus* (Robinson), oblique frontal view of pronotum highlighting microsetae. **10**) Same, posterior view of pygidium. **11**) Same, dorsal profile of habitus (image darkened to enhance silhouette). **12**) Same, dorsal view of forebody. **13**) *Boreocanthon puncticollis* (LeConte), dorsal profile of habitus (image darkened to enhance silhouette). **14**) *Canthon bispinus* Harold, dorsal view of head.

Melanocanthon is virtually endemic to the continental United States and, in my opinion, unquestionably monophyletic. Known occurrences outside the US are limited to only two cases. I know of a single collection record of *M. nigricornis* from northern Nuevo Leon, Mexico, but it and *M. granulifer* are probably both to be found more widely in the far northeastern portion of Mexico. To the north, *M. bispinatus* is recorded from a few Canadian localities in the far southeastern, Great Lakes region of Ontario. The corporate distribution of the genus (Fig. 15) suggests an origin and diversification in the eastern United States in varied Pliocene-Pleistocene savanna and woodland habitats. The relatively localized distribution of *M. granulifer*, as well as its rather striking resemblance to *Boreocanthon ebenus*, begs the hypothesis of an origin from a *Boreocanthon*-like ancestor in the more arid western part of its range, where *Boreocanthon* currently reigns (see Edmonds 2022), and an eastward dispersal into the humid savannas and low forests, where, in the absence of significant competition from its sister genus, diversification occurred.

Mario Cupello (pers. comm.) suggests that the distribution of Melanocanthon (Fig. 15), especially in the light of its distribution patterns and the sometimes "fuzzy" lines of morphological distinction among its constituent species, supports the idea of recognizing the genus as a superspecies (sensu Mayr 1931, 1963) at a stage when geographical barriers separating allospecies are dissolving and contacts (zones of sympatry) are being established, as could well be the case in the Florida peninsula (see Neill 1957; Howden 1963, 1966 for related commentary). The notion is an attractive context for contemplating the taxonomic relationship between M. bispinatus and M. nigricornis in mid-continent, between M. bispinatus and M. vulturnus/M. punctaticollis in the southeast and between M. nigricornis and M. granulifer in Texas. In the first two cases, definitive identification of *M. bispinatus* from areas of contact or potential contact (Fig. 15, 19) rests primarily on the form of the parameres and secondarily, among other features, on the nature of cephalic and pronotal sculpturing. The case of the taxonomic differences between M. nigricornis and M. granulifer, is somewhat clearer as secondary characters are significantly less variable and, therefore, more reliable identifiers. Nonetheless, these two latter species are undoubtedly very closely related and perhaps should be considered sisters. An analysis of the historical biogeographical and cladistic context for the origin and diversification of Melanocanthon is beyond the scope of this study. Suffice it to say that, given a more robust data set (including molecular data) and more rigorous analytical tools, the genus and its relatives present an attractive opportunity for exploring diversification in North American dung beetles.

A total of five valid species-group names are here assigned to the genus *Melanocanthon*. They are listed below (original generic placement noted in parentheses). I know of no other available names assignable to the genus.

Melanocanthon nigricornis (Say, 1823) (Ateuchus)—valid name Melanocanthon punctaticollis (Schaeffer, 1915) (Canthon)—valid name Melanocanthon granulifer (Schmidt, 1920) (Canthon)—valid name Melanocanthon bispinatus (Robinson, 1941) (Canthon)—valid name Melanocanthon vulturnus Edmonds, 2023 (Melanocanthon)—**new species**

Key to the Species of Melanocanthon Halffter, 1958

Note: Reliability of the key below will be enhanced if target specimens are free or largely so of significant wear and soiling, especially to the dorsal surface, and if accurate locality data are available.

1.	Head and pronotum (25×) virtually lacking distinct granulation (Fig. 20, 22), surface uniformly cov-
	ered by mélange of fine, distinct punctures sometimes accompanied on pronotum by shiny, elongate
	microspotting; attenuated granulation sometimes perceptible marginally on pronotum. Anterior por-
	tion of clypeus with loose, transverse group of 20-25 large, shallow punctures, appearing "freckled"
	(Fig. 20). Metabasitarsus elongate (Fig. 26), length about 1.5 width at apex, clearly longer than second
	tarsomere. Peninsular Florida (Fig. 15–16) 1. Melanocanthon punctaticollis (Schaeffer)
_	Pronotum, and usually also head (25×) with at least some distinct, sometimes coarse granulation, with
	or without distinct puncturing (Fig. 29, 53). Metabasitarsus variable. Clypeal sculpture variable.
	Distribution variable

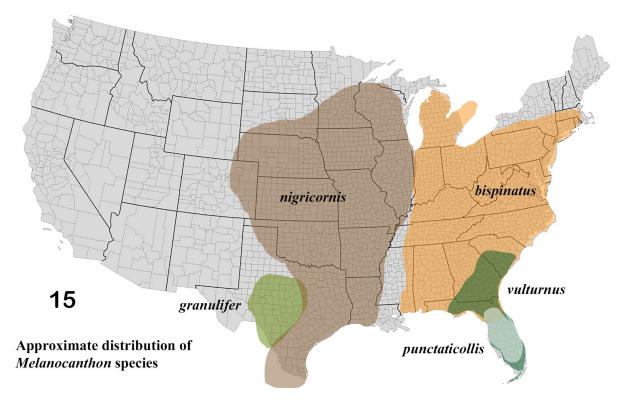


Figure 15. Approximate distributions of species of *Melanocanthon*.

2.	Individuals from localities outside the rectangular area indicated in Figure 19
—	Individuals from localities within the area enclosed by yellow rectangle in Figure 19 6
3.	 Species occurring west of about the 88th meridian, in Illinois and Wisconsin and otherwise west of the Mississippi River (Fig. 15). Lower apical lobes of parameres flattened, oval tabs (Fig. 32, 41). Meta-tarsus wider, length of metabasitarsus about equal to that of second tarsomere, length of apical tarsomere about equal to combined lengths of tarsomeres 3–4 (Fig. 33, 39)
	triangular tabs (Fig. 56–58). Metatarsus slender, length of metabasitarsus usually clearly greater than that of second tarsomere, length of apical tarsomere greater than combined lengths of tarsomeres 3–4 (Fig. 45, 55)
4.	 Pronotum (15×) densely covered with strong, elongated granules on shagreen background (Fig. 29); punctures usually lacking but, if visible, minute (25×) and very widely scattered. Head, elytral interstriae, pteropleura and adjacent metaventrite evenly populated by round granules (Fig. 27–30). Clypeus bearing a loose, transverse array of 8–20 conspicuously large, shallow punctures extending into paraocular areas, appearing "freckled" (Fig. 27). Central Texas (Fig. 15, 17)
_	Pronotum (15×) with distinct puncturing, punctures fine, sharp and evenly dispersed among distinct, usually fine, elongate granules (Fig. 34–35), granules sometimes attenuated and clearly perceptible only when viewed obliquely. Dorsum of head (Fig. 34) finely punctate, almost always lacking conspicuous clypeal punctures and distinct granules except occasional weak granulation near eyes and on paraocular areas. Elytral interstriae 3–6 sparsely granulate, granules small, variable in size and unevenly distributed (Fig. 36); pteropleura and adjacent metaventrite (Fig. 38) finely, densely striate, lacking granules. Central United States from Gulf coast to Great Lakes region (Fig. 15, 17)

- Expansions (tabs) of lower apical lobes of parameres (viewed caudally) flattened, triangular, with prominent lateral angle, itself curved toward base of genital capsule (Fig. 56–58); apical margins strongly curved outwardly, producing pronounced oval gap between tips of parameres (Fig. 57, arrow). Pronotum black (Fig. 52), occasionally with faint green metallic undertones (15×), with distinct puncturing, punctures fine, sharp and evenly dispersed among distinct, usually fine, elongate granules (Fig. 53). Head evenly granulate (Fig. 51); elytral interstriae unevenly granulate, granules small, variable in size and unevenly distributed (Fig. 54). Eastern US north to Ontario, Canada (Fig. 15–16)

Species Treatments

1. Melanocanthon punctaticollis (Schaeffer, 1915)

Fig. 15-16, 20-26

Canthon nigricornis var. punctaticollis Schaeffer 1915: 50.

Canthon punctaticollis Schaeffer (new status per Blatchley 1927: 61).

Melanocanthon punctaticollis (Schaeffer) (new combination per Halffter 1958: 211).

Type material. Syntype, male. National Museum of Natural History, Washington, D. C. Not examined.

Type locality. Florida.

Diagnosis. *Head*: Dorsum (25×) sharply punctured on shagreen background (Fig. 20); granules and microspots either lacking or weak and perceptible only posteriorly. Clypeus weakly roughened, somewhat shinier anteriorly with transverse array of 10–15 large, shallow punctures (Fig. 20–21). *Pronotum*: Evenly covered by distinct (25×) puncturing (Fig. 22); granules and shiny spots usually absent, weak granulation sometimes present posteriorly. *Elytra*: Interstriae bearing widely and unevenly scattered, very small granules best observed in oblique view (Fig. 25); shagreen very fine, obscure. *Pygidium*: Covered by weak, irregularly shaped granules on shagreen background (Fig. 24), basal impressions weak, sometimes virtually absent. *Venter*: Generally smooth with some irregular wrinkling on sides of abdominal sternites; pteropleura and sides of metaventrite lacking any trace of granulation; central portion of metaventrite evenly, finely punctured. *Parameres*: Ventral apical lobes small, rounded tabs; apical margins usually only weakly curved outwardly at middle. *General*: Dull black, lacking any metallic undertones. Length 6.0–11.0 mm. *Geographic distribution*: Endemic to Florida peninsula (Fig. 15–16). Specimens examined: 634.

Collection localities. UNITED STATES — **FLORIDA**: *Alachua Co.* • 3.4 mi WNW Archer, Ashton Biological Preserve [Mar–Aug]; *Clay Co.* • Gold Head Branch State Park, 29.8475 –81.9617 [Feb, May] • Ordway Preserve [Sep]; *Collier Co.* • Old Hwy 41 at Sun Century Rd [Oct–Nov]; *DeSoto Co.* • Arcadia [May]; *Gilchrist Co.* • 5 mi W Newberry; *Highlands Co.* Lake June State Park 27°17′59″ N 81°25′28″ W [May–Jun] • Archbold Biological Station [Mar–Aug]; *Lake Co.* • Grasshopper Lake, Ocala National Forest [Mar] • Lake Delaney, Ocala National Forest

[Mar]; *Levy Co.* • 8 mi E Bronson [Mar] • 3.8 mi SW Archer [May] • 2 mi W Archer [Mar, Aug] • 4 mi W Archer [Mar] • Cedar Key [Mar]; *Marion Co.* • 3 mi E Eureka [Jun] • Ocala National Forest [Mar, May–Jun, Aug] • Juniper Springs [Apr] • Delancy [Aug] • Lake Marion Creek Estates [May]; *Okeechobee Co.* • 22 mi N Okeechobee [Jan–Apr]; *Orange Co.* • Wekiwa Springs State Park [Feb, Jun–Sep] • Orlando [Jul] • Central Florida University campus, 28°36'16" N 81°11'38" W [Feb, May–Sep]; *Osceola Co.* • Walt Disney World [Jul]; *Polk Co.* • Catfish Creek State Park, 27.98457 –81.49606 [Jun] • Lake Marion Estates [Apr–Jun]; *Putnam Co.* • 4 mi W Rodman, 0.8 mi E Deep Creek [Mar] • Welaka Research Station [Apr, Oct, Dec] • 1 mi W Georges Lake [Mar] • 3.2 mi NE Florahome [Jan] • Red Water Lake [Jun] • 3 mi S Melrose [Jun] • 3 mi E Melrose [Feb, Oct] • Interlachen [Apr]; *Seminole Co.* • Geneva Wilderness Area, 28.704738 –81.122344 [Oct] • Econ River Wilderness Area [Mar–Apr].

Comments. This species is endemic to the Florida peninsula, where it is sympatric with both *M. bispinatus* and *M. vulturnus*. Woodruff (1973) captured numerous specimens using malt traps in central Florida turkey oak (*Quercus laevis* Walter) scrub habitat. I have label records of capture from cattle, human and swine feces, fungi, yeast trap as well as from dead lubber grasshoppers (Orthoptera: Romaleidae) and in the soil pushup at the entrance to a gopher nest burrow (*Geomys*). Sandor Kelly (pers. comm.) routinely observes *M. punctaticollis* using various fleshy fungi, both fresh and desiccated, in Central Florida uplands, where it can occur along with *M. vulturnus*. Feeding aggregations are lively as individual beetles capture and roll away fungal pieces, which can be the object of energetic scuffles.

Schaeffer (1915) did not indicate the number of specimens on hand for his description of *M. punctaticollis*. The NMNH entomology database (https://collections.nmnh.si.edu/search/ento/) records a specimen designated as holotype, which was not available for this study. Moreover, I was unable to examine holdings there for other possible syntypes and, so, reserve opinion about the status of the putative holotype.

The uniquely smooth sculpture of the head and pronotum of this species makes for rather easy identification of *M. punctaticollis*. I have seen a single specimen from Ocala National Forest (Marion Co., Florida) with parameters similar to those of *M. bispinatus*, which I consider its nearest relative.

2. Melanocanthon granulifer (Schmidt, 1920)

Fig. 3-8, 15, 17, 27-33

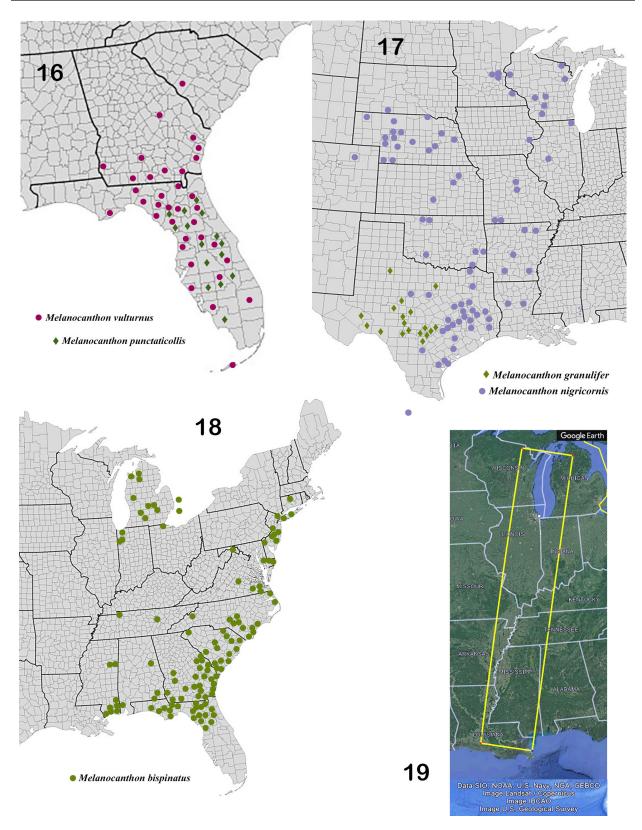
Canthon granulifer Schmidt 1920: 126.

Melanocanthon granulifer (Schmidt) (new combination per Halffter 1958: 211).

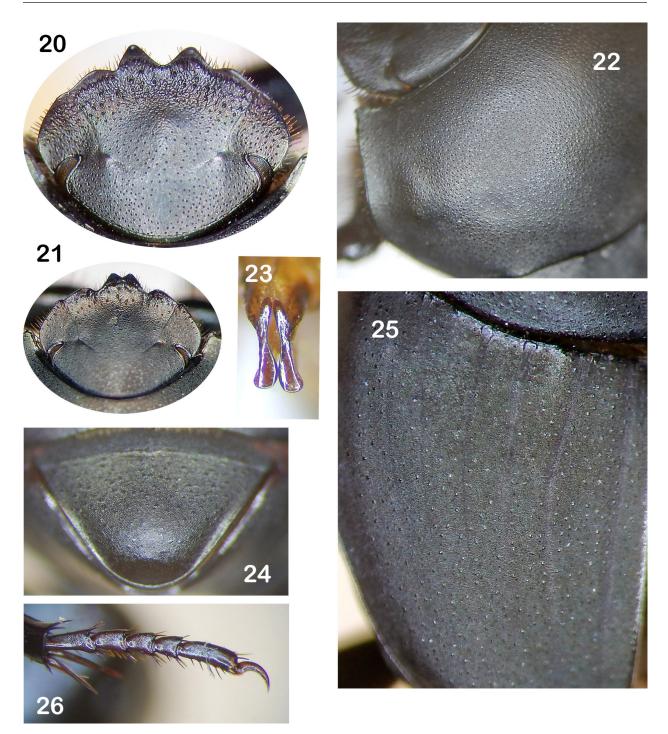
Type material. Syntype male (labeled "Typus", SMNH 9678 E92) and syntype female (labeled "Type/Allotypus", SMNH 9678 93), Swedish Museum of Natural History, Stockholm. Examined by proxy (see Comments below). Syntype male (labeled "Syntypus", DEI Müncheberg Col – 07658), Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany. Examined by photograph in Vaz-de-Mello and Cupello (2018).

Type locality. Texas.

Diagnosis. *Head*: Dorsum boldly granulate on shagreen background (Fig. 27) with interspersed, very small punctures; granules rounded, numerous, evenly distributed, rarely sparse; shiny microspots lacking. Clypeus bearing loose, transverse array of 5–15 conspicuous, large, flat punctures just behind clypeal teeth (Fig. 27). *Pronotum*: Completely, evenly covered by prominent granules on shagreen background (Fig. 28–29), sometimes with (50×) minute, interspersed punctures on sides and anterior angles; granules elongated on disk, becoming more rounded laterally. *Elytra*: Completely, usually evenly and densely covered by round granules on shagreen background with occasional micropunctures (Fig. 28); granules arranged in poorly organized, longitudinal rows, generally uniform in size and density over surface. *Pygidium*: Evenly, coarsely granulate. *Venter*: Granulation weaker than on dorsum, extending to pteropleura, lateral portions of metaventrite and abdominal sternites (Fig. 30); central portion of metaventrite completely, evenly and conspicuously punctured, usually lacking distinct granulation except for weakly rugose area behind mesosternite. *Legs*: Metatarsus (Fig. 33) wide, lengths of tarsomeres 1–4 about equal to width at apex; length of apical tarsomere (excluding claws) about equal to combined lengths of tarsomeres 3–4. *Parameres*: Ventral apical lobes flattened, ovoid (spoon-shaped) tabs (Fig. 32); apical margins usually strongly curved outward at middle, creating wide, oval gap. *General*: Length 5.5–10 mm. *Geographic distribution*: Central Texas (Fig. 15, 17). Specimens examined: 303.



Figures 16–19. Distributions of *Melanocanthon* species. **16**) By-county distributions of *M. vulturnus* and *M. punctaticollis*. **17**) Same, *M. granulifer* and *M. nigricornis*. **18**) Same, *M. bispinatus*. **19**) Central United States, rectangle demarcates area of potential sympatry between *M. bispinatus* and *M. nigricornis* (see text for explanation).



Figures 20–26. *Melanocanthon punctaticollis* (Schaeffer). **20**) Dorsal view of head. **21**) Same, deformed head margin. **22**) Dorsal view of pronotum. **23**) Apical view of parameres. **24**) Caudal view of pygidium. **25**) Dorsal view of left elytron. **26**) Lateral view of metatarsus.

Collection localities. UNITED STATES — **TEXAS:** *Bexar Co.* • San Antonio, 29.48708, -98.69572 [May]; *Blanco Co.* • Pedernales State Park, 30.33° N 98.25° W [Oct]; *Briscoe Co.* • Quitaque [Jun]; *Brown Co.* • 6.6 mi km SE Brownwood, Camp Bowie National Guard, 31.628° N 98.906° W [Jun–Jul]; *Comal Co.* • Bulverde [Apr] • Landa Park [Nov]; *Crockett Co.* • Ozona [Jun]; *Dickens Co.* • White River Reservoir [May–Jun]; *Hays Co.* • 6 mi NW Dripping Springs, 30°13.589' N 98° 11.096' W, 30°13.554' N 98° 11.039' W, 1340 ft [Jun]; *Kendall Co.* • Boerne [Apr] • Sisterdale [Jul] • Cave Without a Name [Jul]; *Kerr Co.* • Kerrville [May]; *Kimble Co.* • I-10 at N. Llano River, 4.2 mi NW Junction [Jun]; • Junction, Texas Tech University Center [Apr–May] • 2 mi S Junction [May]; *McColloch Co.* • 2 mi SE Brady [Sep]; *Menard Co.* • 30 mi W Menard [Jul]; *Parker Co.* • Dennis; *Pecos Co.* • 5 mi W Sheffield [Jun]; *Real Co.* • 27 mi N Leakey [Oct]; *Runnels Co.* • 4 mi N Ballinger [Jun]; *Sutton Co.* • Sonora [Oct]; *Terrell Co.* • 15 mi S Sheffield, Oasis Ranch, 30.4665° N 101.8008° W; *Tom Green Co.* • Christoval [Jun]; *Travis Co.* • Austin, 30.312° N 97.808° W [May, Oct]; *Uvalde Co.* (no data) [May]; *Val Verde Co.* • 23.6 mi N Comstock [Jun] • Devils River Preserve, Texas Nature Conservancy, Dolan Falls [Feb, Apr–Jun].

Comments. Vaz de Mello and Cupello (2018) recorded three syntypes of Schmidt's species, one in Munich and two in Stockholm. Mattias Forshage of the Swedish Museum of Natural History has very kindly compared photographs provided by me with the two Schmidt syntypes under his care; thanks to his efforts, I am confident that the name *M. granulifer* is used here in the exact sense of its describer.

This species has previously been cited from Florida (Robinson 1948; Woodruff 1973; Gordon and Cartwright 1974; Kaufman and Wood 2012). These references likely refer to the new species, *Melanocanthon vulturnus*, described below.

The distribution of *M. granulifer* is evidently largely restricted to the oak-juniper scrub habitat common to the Edwards Plateau of central Texas. This area is sometimes recognized as the Balconian Biotic Province, one of the principal bioregions of the state (Smith and Buechner 1947; Blair 1950). The granulation characteristic of this species varies little in texture and density. I have noted only one instance (in a population from Dickens Co.) of pronotal sculpturing with distinct punctures in addition to granules.

Biological data on the habits of *M. granulifer* are scarce. The few records I have include cattle and human dung as well as one instance of attraction to dead land snails in Bexar Co. It is the only species of the genus lacking any record of association with fungi.

3. Melanocanthon nigricornis (Say, 1823)

Fig. 2, 15, 17, 34–42 *Ateuchus nigricornis* Say 1823: 207. *Canthon nigricornis* (Say) (new combination per Melsheimer 1853: 53). *Melanocanthon nigricornis* (Say) (new combination per Halffter 1958: 209).

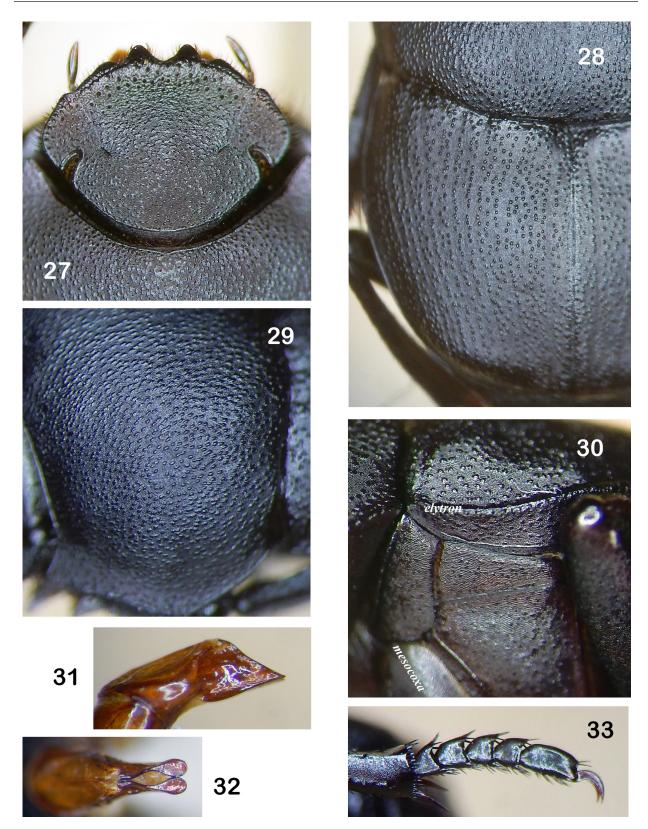
Type material. Unknown to me.

Type locality. Cape Gerardeau [now Cape Girardeau, Missouri]; New Jersey (See Comments below).

Diagnosis. *Head*: Dorsum lacking distinct granulation except for few weak granules near eyes and on paraocular areas, otherwise distinctly, evenly covered by mixture of very small punctures and shiny microspots on shagreen background (Fig. 34). Anterior portion of clypeus weakly roughened, bearing few somewhat larger punctures (Fig. 34); lacking any conspicuously large, flat punctures. *Pronotum*: Evenly covered by mélange of attenuated, very fine, elongate shiny granules and very fine, but conspicuous puncturing (25×) on shagreened background (Fig. 35); granules weaker, shinier, less well defined on disk, usually more distinct and less shiny laterally and posteriorly. *Elytra*: Interstriae weakly granulate on shagreene background with interspersed, very fine punctures (Fig. 36); granules small, round, varying in size, and scattered, seldom forming loose rows, weakest and least numerous on middle portions of discal interstriae (3–6). *Pygidium*: Evenly granulate. *Venter*: Dorsal granulation not extending to venter; pteropleura (Fig. 38) covered by dense microstriation, abdominal sternites (Fig. 37) smooth, metaventrite evenly, densely punctate. *Legs*: Metatarsus (Fig. 39) wider; lengths of tarsomeres 1–4 about equal to width at apex; length of apical tarsomere (excluding claws) about equal to combined lengths of tarsomeres 3–4. *Parameres*: Ventral apical lobes (Fig. 41) flattened, oval tabs; apical margins usually somewhat curved outwardly at middle, creating narrow, oval gap. *General*: Black. Length 4.0–8.5 mm. *Geographic distribution*: Central United States (Fig. 15, 17). Specimens examined: 938.

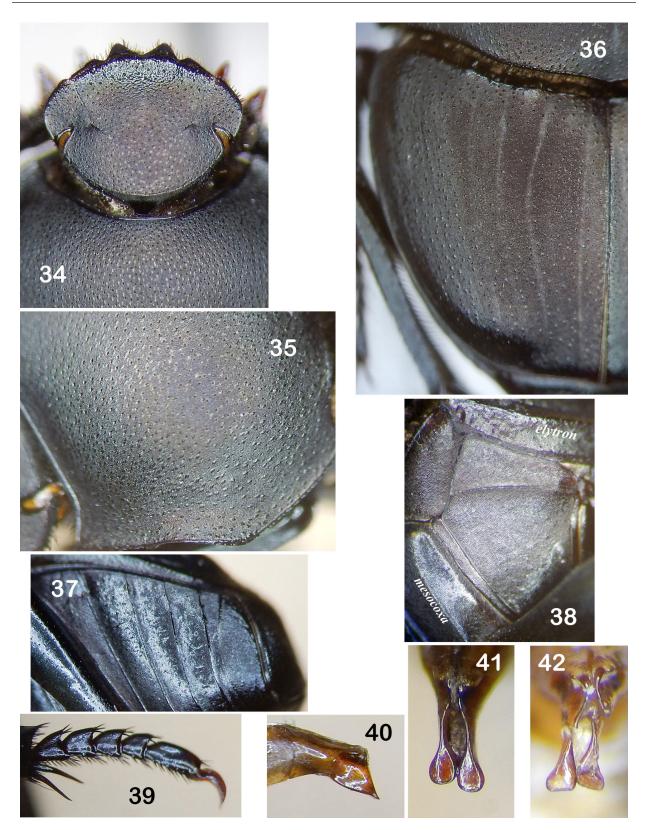
Collection localities. MEXICO – NUEVO LEON: Mpio. Monterrey • Monterrey [Jun].

UNITED STATES — ARKANSAS: Drew County • Hunger Run West (County Road 12), 33°41.75' N 91°53.52' W [Aug]; Izard Co. • Devil's Knob, 36°00.19' N 92°03.05' W [Apr]; Lawrence Co. • Imboden [Aug];



Figures 27–33. *Melanocanthon granulifer* (Schmidt). 27) Dorsal view of head. 28) Dorsal view of left elytron. 29) Dorsal view of pronotum. 30) Lateral view of midbody. 31) Lateral view of parameters. 32) Apical view of parameters. 33) Lateral view of metatarsus.

Nevada Co. • White Oak Lake State Park [Apr] • 2.4 mi SSE Bluff City [Mar]; Saline Co. • Middle Fork Barrens Natural Area, 34°38'16" N 92°50'31" W [Sep]. COLORADO: Morgan Co. • 3 mi N Orchard [Jun]. ILLINOIS: Lake Co. • Zion, Illinois Beach State Park [Jul]; Mason Co. • Sand Ridge State Forest, 5 mi W Manito [Jul]. IOWA: Muscatine Co. • Big Sand Mound Prairie Preserve, 41.341015 -91.086545 [Jun]. KANSAS: Geary Co. • Fort Riley, Macomb Hill [May]; Pottawatomie Co. • 5 mi S Olsburg, Little Gobi Desert; Reno Co. • Sand Dunes State Park, 38°07'00" W 97°50'40" W [Oct]. LOUISIANA: La Salle Par. • Olla [Mar]; Natchitoches Par. • Kisatchie National Forest, Red Dirt Wildlife Management Area [Apr] • Kisatchie National Forest, Lotus Campground [Sep-Oct] • Vowells Mill. MINNESOTA: Anoka Co. [Jun-Aug] • Cedar Creek Natural History Area; Isanti Co. [Jun-Aug] • Cedar Creek Natural History Area; Sherburne Co. • Elk River [Jun] • Sand Dune State Forest [Jun]; Wabasha Co. • McCarthy Lake, Weaver Dunes, 44°16' 26.85" N 91°56' 55.08" W [Jul]. MISSOURI: Barry Co. • Roaring River State Park [Aug]; Boone Co. • Columbia [Jul]; Cole Co. • 4 mi W Jefferson City [Aug]; Stone Co. (no data) [May]. NEBRASKA: Arthur Co. (no data) [Jul]; Boyd Co. (no data); Cherry Co. • 25 mi N Valentine [Sep]; Custer Co. • Anselmo [Jun] • Milburn [Aug]; Dawes Co. • Whitney [Sep] • Pine Ridge [Jul]; Dodge Co. • Dead Timber State Recreation Area, 3.5 mi N Scribner, 41.7236° –96.6971° [Apr]; Dundy Co. • Max [Jul] • 2 mi E Benkelman [Jum]; Hall Co. • Mormon Island State Recreation Area [Aug]; Hitchcock Co. (non data) [Apr]; Hooker Co. (no data [Aug]; Keith Co. • 7 mi E Cedar Point Biological Station, 41.18° -101.52° [Jul] • Cedar Point Biological Station [Jul]; Lincoln Co. • 14 mi NW North Platte; Madison Co. • Meadow Grove [Jun]; McPherson Co. • Tyron [Jun] • Sandhills Agricultural Laboratory [Jul]; Merrick Co. • 1.5 mi E Silver Creek [Aug]; Thomas Co. • Nebraska National Forest, Whitetail Camp, Dismal River, 41.792° -100.267°, 820 m [Jun] • Nebraska National Forest, 1.3 km SSW Bessey Bee Campground, 41.88937° N 100.30676° W [Sep] • Halsey, 41.9033° -100.2686° [Jul-Aug] • 2.5 mi W Halsey, Nebraska National Forest [Jun] • Thedford [Aug] • 10.5 mi S Thedford. OKLAHOMA: Alfalfa Co. • Salt Plains National Wildlife Reserve [Apr]; Choctaw Co. • Schooler Lake [Aug]; Comanche Co. • Wichita Mountains Wildlife Refuge [Apr, Jul]; Latimer Co. (no data) [Apr-Sep]; Le Flore Co. • Ouachita National Forest [Jul]; Woods Co. • 14mi N, 7 mi W Alva [Nov]. SOUTH DAKOTA: Bennett Co. • 10 mi E Martin, La Creek National Wildlife Refuge [May]. TEXAS: Anderson Co. • 2 mi W Blackfoot, Engeling Wildlife Area [May, Aug–Sep] • 7 mi E Palestine 31°45'N 95°29' W [Jun] • 14 mi E Palestine, 31°45'N 95°23' W [Jun]; Angelina Co. • Angelina National Forest, ~3 mi NE Rockland, 31°03'19" N 94°22'06" W; Aransas Co. • 7 mi N Fulton [Mar]; Atascosa Co. • 8 mi NW Poteet [Apr-May] • 8 mi E Rossville; Bastrop Co. • 6mi N Smithville, Stengl Biological Station, 30°05'10.2" N 97°09'44.3" W [Jun] • 7.3 mi S Rosanky [Apr] • ~2.5 mi E jct. Hwy 95 on Hwy 21 [Mar] • Lake Bastrop [Apr] • Bastrop [Apr] • Bastrop State Park [Apr-Jul] • Bastrop [Mar-Apr] • 8.6 km N Bastrop, Camp Swift National Guard, 30.300° N 97.294° W [Jun-Sep] • Sayersville [Jul]; Brazos Co. 12 mi NE Bryan [Jul] • College Station, Lick Creek Park [Jan-Feb, Jul, Sep-Oct] • 10 mi W Kurten [Jul]; Burleson Co. • 30°30.713' N 96°47.911' W, 2.5 mi N jct. Hwy 21 on FM 908; Callahan Co. • Baird [Apr]; Colorado Co. • Rock Island [Jun]; Erath Co. • Stephenville [Apr]; Freestone Co. Buffalo [Mar] • 5 mi E Donie, Old Spring Seat Church [May]; Hardin Co. • Roy E. Larson Sandyland Sanctuary, 5 mi W Silsbee [Mar] • 1 mi W Silsbee [Sep]; Houston Co. • 12 mi NNW Ratcliff, 31°33' N 95°09' [Jun] • 11 mi WNW Crockett, 31°23' N 95°36' W [May] • 4 mi NNE Kennard, 31°24' N 95°09' W [Jun] • 2 mi SW Kennard, 31°20' N 95°13' W [May] • 17 mi NE Crockett, 31°30' N 95°16' W [May] • 19 mi NE Crockett, 31°29' N 95°13' W [May]; Lamar Co. • 3.5 mi S Powderly, Camp Maxey National Guard, 33.801° N 95.554° W; Lee Co. • Fedor [May]; Leon Co. • Marquez [May] • 9 mi ENE Buffalo, 31°32' N 95°55' W [May] • 5 mi SSW Buffalo, 31°23' N 95°05' W [Sep] • 1 mi SSE Jewett, 31°20' N 96°07' W [Apr-May] • 5 mi N Jewett, 31°26' N 96°08' W [Apr-May] • 4 mi NNW Normangee, 31°04' N 96°09' W [Sep-Oct] • 7 mi SW Centerville, 31°11' N 96° 04' W [Apr] • 5 mi E Centerville, 31°15' N 96°52' W [Sep] • 3 mi N Centerville, 31°16' N 96°57' W [Sep] • 4 mi S Centerville, 31°15' N 96°52' W [Sep] • 2 mi NW Centerville, 31°16' N 96°52' W [Sep] • 7 mi SSW Centerville, 31°16' N 96°11' W [Apr] • 8 mi NNE Centerville, 31°10' N 96°00' W [Sep] • 9mi SSE Oakwood 31°26' N 95°48' W [May] • 5 mi N Flynn [May] • 4 mi WNW Leona, 31°09' N 96°02' W [Sep]; Limestone Co. • 7 mi E Kosse [May]; Madison Co. • 4 mi W North Zulch [Apr] • 9 mi ESE Madisonville, 30°54' N 95°46' W [Sep-Oct]; Milam Co. • 4 mi N Gause, Sugarloaf Mountain, 300 ft [Apr, Aug-Oct]; Montgomery Co. • Conroe [Apr] • Willis [Apr]; Refugio Co. • Austwell; San Patricio Co. • 8 mi NE Sinton, Welder Wildlife Refuge [May-Jun]; Trinity Co. • Davy Crockett National Forest, 31°01' N 94°00' W [Jun]; Tyler Co. • Kirby State Forest, 30°34'30" N 94°25'03" [Apr, Jun]; Victoria Co. • Victoria [Apr]; Walker Co. • 12 mi SSW Huntsville, Lake Stubblefield [Jul] • Huntsville, Sam Houston State University Center for Biological Field Studies [Jun] • 11 mi NNW Huntsville [Apr]; Wood Co. • 18



Figures 34–42. *Melanocanthon nigricornis* (Say). **34**) Dorsal view of head. **35**) Dorsal view of pronotum. **36**) Dorsal view of left elytron. **37**) Lateral view of abdomen. **38**) Lateral view of midbody. **39**) Lateral view of metatarsus. **40**) Lateral view of parameres. **41**) Apical view of parameres. **42**) Apical view of deformed parameres.

mi N Hawkins, 32°48′55″ N 95°10′00″ W [May].. **WISCONSIN**: *Adams Co.* (no data) [Jun]; *Iowa Co.* • 1 mi NW Arena [Jul]; *Monroe Co.* • 2.4 mi SW Mather {Juneau Co.} [Jun] • 2.8 mi S Warrens [Jun]; *Oconto Co.* (no data); *Polk Co.* • Trade River [Jun] • Fort McCoy, Alderwood Dunes [May]; *Sauk Co.* • Spring Green Preserve State Natural Area, 43.2031° N 90.0568°W [Jun].

Comments. To my knowledge, type specimens of Melanocanthon nigricornis are missing. Much of Say's collection was lost or destroyed many years ago (Weiss and Ziegler 1931; Mawdsley 1993). No specimens attributable to A. nigricornis 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.). Nor are specimens attributable to Say known in the collections of his foreign correspondents (Mario Cupello, Fernando Vaz-de-Mello, Stéphane Boucher, pers. comm.). About M. nigricornis Say (1823: 207) wrote, "I have observed this species near Cape Gerardeau [sic], and in the intermediate country between that town and the Rocky Mountains; and as I formerly obtained two specimens in New Jersey, I think it probable that it inhabits a principal portion of our country; but it does not seem to be common any where [sic] ..." It is obvious that, for his description of Ateuchus nigricornis, Say had at hand specimens representing two modern species, an unknown number of *M. nigricornis* and two of *M. bispinatus*, both of which conform equally well with his original description. Moreover, it is clear, given the very title of Say's 1823 paper ("... coleopterous insects collected in the late expedition to the Rocky Mountains ..." that specimens of *M. nigricornis* were the main basis of his description. Since New Jersey is home to only a single here-recognized species, M. bispinatus, I find it reasonable to assume, for present purposes, that Say's New Jersey specimens, if extant, would today be assignable to Melanocanthon bispinatus (Robinson), and that the remainder of his type series would remain M. nigricornis as here defined, with the type locality of Cape Girardeau, Missouri. For purposes of this review, the conditions favoring designation of a neotype for Ateuchus nigricornis Say as set forth in Article 75 of the International Code of Zoological Nomenclature (ICNZ 1999) are not satisfied as the name nigricornis, as used here, conforms with long-standing usage unrelated to any complex nomenclatorial problem.

The pronotal granulation of *M. nigricornis* is routinely rather fine and may be almost effaced on the disk so as to resemble the velvety texture of *M. punctaticollis*. Only rarely are the granules strongly raised on the central portion of the disk (Custer Co., Nebraska). The central portion of the dorsal surface of the head is smooth and distinctly punctate, only rarely with distinct granules (Bennett Co., South Dakota). There are scattered instances hinting of hybridization between *M. nigricornis* and *M. bispinatus* in Michigan. Occasional specimens of the latter species resemble the former in lacking well defined granules on the central portion of the head. Moreover, I have seen a single specimen from Nevada Co., Arkansas, with abnormal parameres reminiscent of *M. bispinatus* (Fig. 42).

Except for that portion occupying eastern Texas, the distribution of *M. nigricornis* is more-or-less congruent with the expansive western portion of the drainage system of the Mississippi River as well as that northern portion of the drainage embracing Illinois and Wisconsin. To what extent it might overlap with that of *M. bispinatus* is very much open to question. The depiction presented in Figure 15 is based on data gathered for this study; it suggests a barrier of some sort, perhaps ecological. I strongly suspect that careful collecting, especially in the zone indicated in Figure 19, will reveal that the two species are, in fact narrowly sympatric in places, but I presently have no evidence that they are.

Blatchley's (1910) reference to *M. nigricornis* from Starke Co., Indiana, is likely referable to *M. bispinatus*, as is that of Rounds and Floate (2012) for Missaukee Co., Michigan. The collection locality record above for Morgan Co., Colorado, while certainly reasonable, needs confirmation. *Melanocanthon nigricornis* is not recorded for Colorado by Krell (2010), but he points out records from bordering Nebraska. I have seen one specimen labeled Lucedale [George Co.], Mississippi; Paul Lago (pers. comm.) considers this record doubtful and in need of confirmation.

Vestal (1913) observed *M. nigricornis*, along with *Canthon pilularius* (L.) and *Canthon vigilans* LeConte in sandy, bunchgrass habitat along the Illinois River valley between Peoria and Meredosia. Fincher et al. (1986) reported it to be diurnal in wooded habitat Burleson Co., Texas; however, King (1914) found it attracted to electric lights. Williams and Kriska (2001) observed a group of a dozen individuals of *M. nigricornis* in Iowa County, Wisconsin, as they cut up, rolled away and buried pieces of "gill mushroom", as well as direct feeding on a dead

lizard and rolling carrion in neighboring Grant County. Freese et al. (2020) reported this species from deer and dog feces in various sandy and loess habitats in Iowa. Wagner et al. (2020) found *M. nigricornis* to be among the scarce species in a Nebraska Sandhills pasture ecosystem dominated mostly by native species of *Onthophagus*. I have label data recording attraction of *M. nigricornis* to cattle, pig, and human dung as well as to carrion (fish), fungi and rotting fruit. Whipple and Hoback (2012) reported that *M. nigricornis* was attracted to a wide variety of dung sources in food-choice trials utilizing excrement from native and exotic mammals.

4. Melanocanthon vulturnus Edmonds, new species

Fig. 15–16, 43–50

Type material. Holotype, male. Florida State Collection of Arthropods, Gainesville, Florida.

Type locality. Florida: Alachua Co., near Gainesville Regional Airport (GNV).

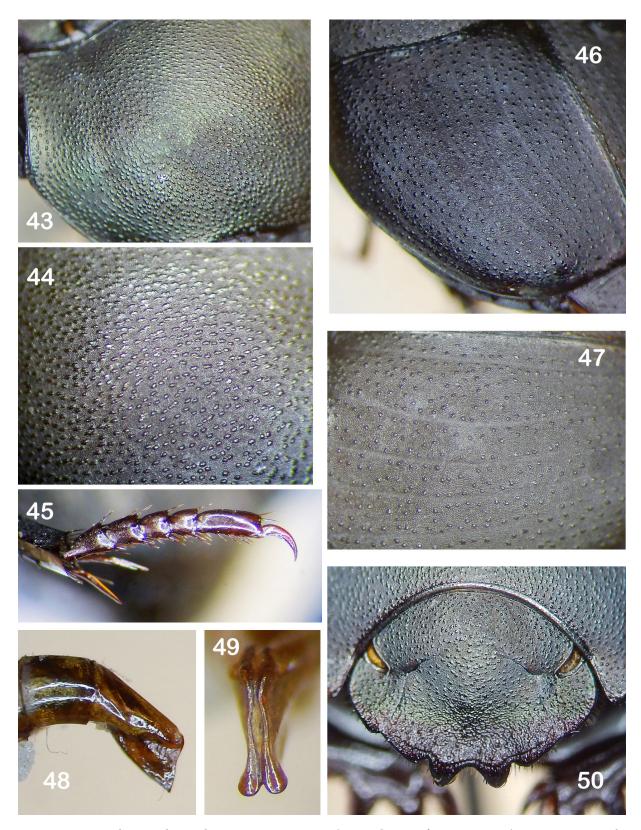
Diagnosis. *Head*: Evenly covered with coarse granulation (Fig. 50); anterior portion usually lacking an array of larger, prominent punctures, which, if present, number fewer than 5. *Pronotum*: Densely covered by distinct granulation (Fig. 43–44), granules elongate on disk, becoming more rounded peripherally, rarely accompanied by sparse punctures. *Elytra*: Interstriae bearing generally uniformly distributed, coarse granulation (Fig. 46–47). *Pygidium*: Evenly, rather densely covered with coarse granules. *Venter*: Granulation seldom extending to venter, and then very weak with vestiges confined to anterior portion of metaventrite and 6th abdominal ventrite. *Legs*: Metatarsus (Fig. 45) slender, basitarsus usually longer than second tarsomere, length of apical tarsomere (excluding claws) greater than combined lengths of tarsomeres 3–4. *Parameres*: apical margins only weakly separated at middle, lower apical lobes small, rounded knobs (Fig. 48–49). *General*: Black, head and pronotum often with dull, metallic green undertone (Fig. 43). Length: 6–10 mm. *Geographic distribution*: Southern South Carolina and Georgia, Florida peninsula and Big Pine Key (Fig. 15–16). Specimens examined: 231.

Notes on holotype and allotype: Holotype male; length 9.5 mm; aedeagus (Fig. 48–49) removed and pointed; head and pronotum dull, metallic green; bears two labels, printed in black on white paper—(1) FLORIDA: Alachua Co./nr Gainesville/ Airport14-vii-83/M.C. Thomas/pitfall trap yeast; (2) *Melanocanthon vulturnus* Edmonds 2023 HOLOTYPE. Allotype female; length 9.0 mm, head and pronotum dull metallic green; bears two labels, printed in black on white paper—(1) same as holotype; (2) *Melanocanthon vulturnus* Edmonds 2023 PARATYPE [printed in blue]/ALLOTYPE [handwritten in red]. Holotype and allotype are intact and very good condition with negligible wear and soiling, drawn from topotypic series of 13 individuals with same label data as holotype. Holotype and allotype are deposited in the Florida State Collection of Arthropods, Gainesville, Florida.

Distribution of remaining paratypes (by collection and number of specimens). *Institutional collections*: American Museum of Natural History [5]; California Academy of Sciences [3]; Canadian Museum of Nature [9]; Carnegie Museum of Natural History [8]; Clemson University Arthropod Collection [2]; Cornell University Insect Collection [2]; Enns Entomology Museum, University of Missouri [1]; Field Museum of Natural History [4]; Florida State Collection of Arthropods [128]; Georgia Museum of Natural History, University of Georgia [4]; Mississippi Entomological Museum [1]; Snow Entomological Collections, University of Kansas [22]; Texas A&M University Insect Collection [20]; University of Central Florida Collection of Arthropods [3]; University of Nebraska State Museum [5]. *Private collections*: Paul K. Lago, University, Mississippi [1]; Edward G. Riley, College Station, Texas [6]; Kyle E. Schnepp, Gainesville, Florida [5].

Etymology. Latin adjective *vulturnus* (masculine), meaning southeast (southeastern or southeasterly) in reference to distribution restricted to far southeastern United States.

Collection localities. UNITED STATES — **FLORIDA**: *Alachua Co.* • County Road 17B [Apr] • Gainesville [Feb, Apr–Oct] • 5mi W Hawthorn • Newmans Lake [Apr] • 9.5 mi N Alachua, Santa Fe River Ranch, Beef Unit [Oct] • 3.5 mi NE Gainesville [Jul] • 4 mi N High Springs [Mar] • High Springs, Oelfke Dairy • Co. Rd. 178, 0.4 mi S junction Co. Rd. 38 [Apr] • Archer [Apr]; • 2.5 mi SW Archer [Jul] • San Felasco Hammock [Jul]; *Baker Co.* • Glen St. Mary [Apr–May, Sep] • Trail Ridge; *Citrus Co.* • Inverness [Apr]; *Clay Co.* • 2 mi NE Gold Head Branch State Park [May]; *Columbia Co.* (no data); *Dixie Co.* • Old Town [May, Jul] • 4 mi N Old Town [May] • 10 mi N Old Town [Jul] • Suwannee [Jun]; *Franklin Co.* • St. Vincents Island [Jul]; *Gilchrist* Co. • 5 mi NNW Newberry, Watson Dairy [Apr, Oct]; *Hernando Co.* • Withalacoochee State Forest, Goat Road [May]; *Highlands Co.* • Archbold



Figures 43–50. *Melanocanthon vulturnus*, new species. **43**) Dorsal view of pronotum. **44**) Same, augmented to emphasize granulation. **45**) Lateral view of metatarsus. **46**) Dorsal view of left elytron. **47**) Dorsal view of interstriae 1–6. **48**) Lateral view of aedeagus. **49**) Apical view of parameres. **50**) Frontal view of head.

Biological Station, Lake Placid [Apr]; *Hillsborough Co.* • Lutz [Apr]; *Jefferson Co.* • Monticello [Aug] • Lamont [Jul]; *Lafayette Co.* • 5 mi E Mayo [May]; *Lake Co.* • Leesburg [May] • Tavares [Jan]; *Lee Co.* • Hwy. 41, 3.4 mi NW Koreshan [Apr]; *Levy Co.* • Cedar Key • 3.8 mi S Archer {Alachua Co.} [Mar, Jun]; *Marion Co.* • Ocala [Jul] • 14.3 mi E Ocala [Mar] • Romeo [Apr]; *Monroe Co.* • Big Pine Key, Key Deer Refuge, Watson Hammock [May–Jun, Aug]; *Orange Co.* • Orlando, Central Florida University campus [Jul] • Wekiwa Springs State Park [Apr, Aug]; *Osceloa Co.* • Disney Wilderness Preserve, 19 mi SE Kissimmee, 28.07° N 81.26° W [Jun]; *Palm Beach Co.* • Jupiter [Apr]; *Putnam Co.* • Red Water Lake [Jun]; *Sarasota Co.* • Sarasota [Apr]; *Suwannee Co.* • Suwannee Springs [Jul]; *Taylor Co.* • Blue Springs Lake [Jun]. **GEORGIA**: *Charlton Co.* • Okefenokee Swamp [Jul–Sep]; *Clinch Co.* • Fort Stewart [Jun]; *Lowndes Co.* (no data); *McIntosh Co.* • Harris Neck National Wildlife Refuge [Aug]; *Thomas Co.* (no data). **SOUTH CAROLINA**: *Aiken Co.* • Savannah River Site [Jun].

Comments. Woodruff (1973) treated this new species as *M. granulifer*, with some reservation (p. 45): "I have seen only a few specimens from Texas (type locality), and they seem to differ slightly from those from Florida. Further study of additional material will be necessary to determine if the two disjunct populations are distinct." I have no reservation about regarding these Florida populations as a separate, but closely related species to *M. granulifer*, but the structural differences between the two are as much in degree as in substance. The pronotal granulation of *M. vulturnus* is equally dense but finer in texture than of its Texas relative. They lack the generous array of conspicuously large clypeal punctures characteristic of *M. granulifer*, or at most present only very few. The shape of the lower apical lobes of the parameres of *M. vulturnus* never approaches the robust, spoon shape characteristic of *M. granulifer*. Moreover, while the head and pronotum of the new species are often have a dark metallic green undertone, *M. granulifer* is always dull black. At first glance, distinctly green specimens resemble *Boreocanthon depressipennis*, and occasional specimens in collections are so labeled. Differences in metatarsal structure are ordinarily distinct on close examination, but they can also be subtle. By far the most distinctive feature of *M. vulturnus* is its southeastern US distribution far from that of *M. granulifer*, roughly 1000 miles due west in Texas.

The range of *M. vulturnus* is overlapped by those of *M. punctaticollis* and *M. bispinatus*. From the former species it is reliably separated by head and pronotal sculpturing. In reference to *M. bispinatus*, Woodruff (1973) observed in his diagnosis of "*granulifer*" (p. 45): ".. this species [*vulturnus*] is ... often difficult to separate from *bispinatus* without comparative material. In general, everywhere the granules are more dense and with greater relief ... Punctures of head and pronotum, although perhaps no less numerous, [are] not as noticeable because of the density of the granules." To Woodruff's observation I add the obvious difference in the form of the lower apical lobes of the parameres (cf. Fig. 49, 56) and that *M. vulturnus* often presents a rather strong green color on the head and pronotum. The distributional picture of these three closely related species begs the question of habitat, behavioral and life cycle attributes that might promote their co-existence at a local scale.

Robinson's (1948) reference to *M. granulifer* from Romeo (Marion Co.), Florida (cited by Gordon and Cartwright 1974), probably refers to *M. vulturnus*. Kaufman and Wood (2012) referenced *M. vulturnus* (also cited as *M. granulifer*) among the uncommon members of the very diverse cattle pasture fauna in Alachua County, Florida. Fincher (1975) reported this species (also as *M. granulifer*) on Blackbeard Island, McIntosh County, Georgia, where the much commoner *M. bispinatus* outnumbered it 30:1. Miller's (1954) report of *M. granulifer* in Ware Co., Georgia, is undoubtedly also referable to *M. vulturnus*. Label data I have indicate its attraction to human, cattle, snake, and pig dung, snake carrion (decomposed cottonmouth, *Agkistrodon piscivorus* [Lacépède]), fungi and rotting fruit.

Peck and Howden (1985) were first to report *M. vulturnus* on Big Pine Key, although they listed it as *M. bispinatus*. A voucher specimen collected by Peck in the collection of the Canadian Museum of Nature confirms its new identity. I have also seen specimens collected on Big Pine Key by Kyle Schnepp and by Ed and Tom Riley. I have no records of *M. bispinatus* south of the Florida flatwoods ecoregions (i.e., roughly south of Highlands County). As suggested by Peck and Howden, the Big Pine population is a relic enclave isolated from the mainland during the post-glacial rise in sea level that formed the Florida Key archipelago within the last 10,000 years. Before that time, the archipelago was a corridor of land continuous with the peninsula (Neill 1957). Once isolation of the keys was underway, and the terrain of the southern tip of the peninsula became permeated by waterways and lakes, intervening populations became extinct, and a previously continuous range of *M. vulturnus*

became the naturally disjunct one it is today, a disjunction also seen in many other organisms (Neill 1957). The known Florida Keys scarabaeine fauna includes ten species, all of which also occur on mainland Florida (Wood-ruff 1973; Peck and Howden 1985). As reported by Peck and Howden, of these ten, *Pseudocanthon perplexus* (LeConte) occupied the most islands (11 of 19 sampled keys). Of the 19 keys sampled, Big Pine Key had the most diverse fauna (8 of 10 species known from the keys). Of the eight scarabaeine species known from Big Pine Key, *Melanocanthon vulturnus* was the only one confined to that island.

5. Melanocanthon bispinatus (Robinson, 1941)

Fig. 1, 9–12, 15, 18, 51–58

Canthon bispinatus Robinson 1941: 128.

Melanocanthon bispinatus (Robinson) (new combination per Halffter 1958: 211).

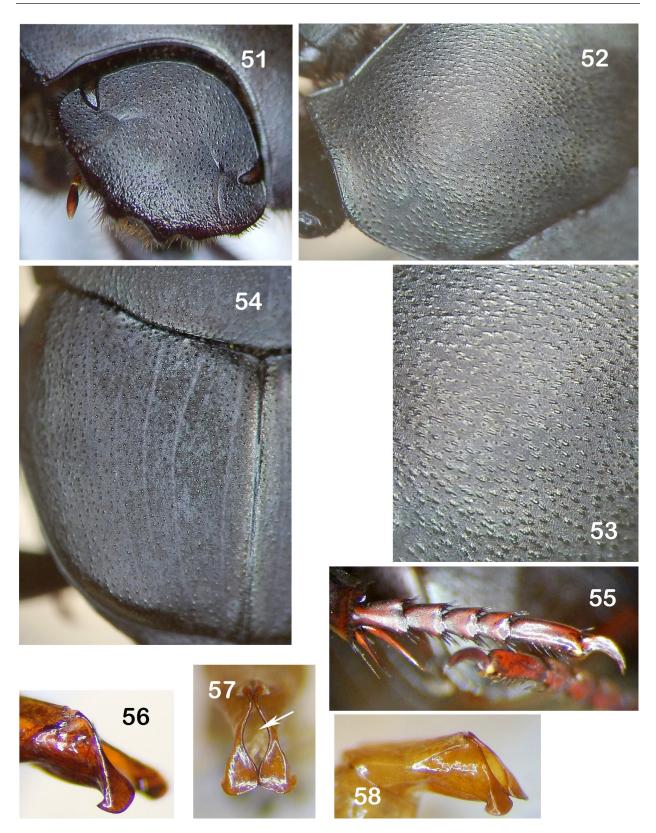
Type material. Holotype male. National Museum of Natural History, Washington, DC. Not examined. See Comments below.

Type locality. Warren Grove, Burlington County, New Jersey.

Diagnosis. *Head*: Dorsum usually completely covered by small, round granules interspersed with very small punctures on shagreen background (Fig. 51); usually lacking shiny microspots and any conspicuous larger, flat punctures along anterior portion of clypeus. *Prothorax*: Disk completely covered by elongate ("streaked") granules and fine, but conspicuous, sharp punctures on shagreen background (Fig. 52–53); granules becoming rounder laterally and posteriorly; shiny microspots usually absent. *Elytra*: Discal interstriae bearing widely scattered, unevenly distributed, small round granules on shagreen background (Fig. 54); granules vary in size but tend to be larger, more conspicuous and more numerous on lateral interstriae. *Pygidium*: Evenly covered by variable sized, round granules. *Venter*: Generally without granulation except for occasional vestigial granules on sides of abdominal sternites 1–5 and across 6. Pteropleura and lateral portions of metasternite completely covered by very fine, dense striation; median portion of metasternite completely, evenly punctured. *Legs*: Metatarsus narrow, basitarsus longer than second tarsomere, apical tarsomere longer than combined lengths of tarsomeres 3–4 (Fig. 55). *Parameres*: Ventral apical lobes of parameres expanded, triangular tabs with sharp, curved lateral angles (Fig. 56–58); apical margins strongly curved outward medially, creating wide, oval gap (Fig, 57, arrow). General: Black. Length 6.0–10.0 mm. Geographic distribution: Eastern US from Mississippi to Michigan to Atlantic coast and northern Florida (Fig. 15, 18). Specimens examined: 1450.

Collection localities. CANADA—ONTARIO: *Chatham-Kent Co.* • Rondeau Provincial Park [Jun]; *Lambton Co.* • Pinery Provincial Park, 43°14'15" N 81°52'31", 43°18' N 81°50' W, 43°13' N 81°54' W, [May–Jul, Sep–Oct].

UNITED STATES — ALABAMA: Clay Co. • Springhill [Aug]; Dale Co. • Fort Rucker Military Reserve [Mar-May, Sep]; Geneva Co. • Geneva [Mar]; Mobile Co. • Chickasaw [Apr] • Mobile [May, Jul-Aug] • Dauphin Island [Jun]. CONNECTICUT: Hartford Co. • Suffield. DELAWARE: New Castle Co. • Wilmington. FLORIDA: Alachua Co. O'Leno State Park [May-Jun, Oct] • Austin Cary Memorial Forest [May] • 9.5 mi N Alachua [Aug] • 4 mi N High Springs [Mar] • 6 mi SW Gainesville [Apr] • 3.5 mi NE Gainesville [Sep]; Baker Co. • Glen St. Mary [Apr]; Bay Co. • 3 mi S Fountain [Jun] • Pine Log State Forest, 4.9 km SSE Ebro, 30.40464° N 85.88691° W [Oct] • Pine Log State Forest, 26.5 km NNW Panama City Beach, 30°24'17" N 85°53'14" W, 26 ft [Oct]; Calhoun Co. • Clarksville [Mar]; Citrus Co. • Withalacoochee State Forest, Citrus Wildlife Management Area [Jul]; Clay Co. • Bayard Conservation Area [May] • 9 mi NE Keystone Heights [Mar] • Ordway Preserve [Sep]; Columbia Co. • Lake City [Jun-Aug]; Dixie Co. • 3,5 mi N Old Town [Apr]; Franklin Co. • St. Vincents Island [Jul] • Apalachicola National Forest, Wright Lake [Apr] • St. Vincents Island [Jul]; Gadsden Co. (no data) [Apr]; Gilchrist Co. • 5 mi NNW Newberry[Oct]; Hamilton Co. • 12 mi E Madison [Sep]; Hernando Co. • Withalacoochee State Forest, Chinsegut Conservation Center [Apr]; Lafayette Co. • Picket Lake [Mar]; Leon Co. • Bradfordville [May] • Tall Timbers Research Station [Apr] • Apalachicola National Forest, 30°19'34.34" N 84°29'34.34" W; Levy Co. • 4.5 km S Archer, 29°30'31" N 82°33'53" W, 26 m [Mar] • 5.5 mi SW Williston, 29°21.586' N 82°31.089' W [Mar]; Liberty Co. • Bristol [May] • 9 mi N Bristol [Apr] • Torreya State Park [Apr, Jul-Aug, Oct-Nov] • Apalachicola Bluffs and Ravines Preserve, 30°29'42.66" N 84°58'42.46" W, 183 ft [Mar, May, Jul]; Marion Co. • Ocala Silver Springs State Park, 29°11.84' N 82°02.03' W, 23 m [Feb-Mar]; Putnam Co. • 1 mi W Georges Lake [Mar] • Gold Head Branch State Park [Jul]; Suwannee Co. • Branford [Jun-Aug]; Walton Co. • Defuniak Springs [Mar] • 7.2 mi



Figures 51–58. *Melanocanthon bispinatus* (Robinson). **51)** Dorsal view of head. **52)** Dorsal view of pronotum. **53)** Dorsal view pronotal disk. **54)** Dorsal view of left elytron. **55)** Lateral view of metatarsus. **56)** Oblique lateral view parameres. **57)** Apical view of parameres (arrow indicates oval gap). **58)** Lateral view parameres.

S Defuniak Springs [Jun] • Elgin Air Force Base [Jun] • County road 283, 0.3 mi S jct. US 90 [Jan]. GEORGIA: Bacon Co. • Alma (Nov); Baker Co. • Newton, Emory University Field Station [Mar]; Bulloch Co. • Statesboro [Jul]; Burke Co. • 0.2 km NW Girard, Yuchi Wildlife Management Area, 30°05'14" N 81°48'17" W, 218 ft [Apr], 33°05.104' N 81°46.593' W [Mar]; Camden Co. • Cumberland Island [Jul]; Charlton Co. • Folkston [Aug]• Suwannee Canal Recreation Area, Camp Cornelia [May] • Okefenokee Swamp [Aug]; Chatham Co. • Savannah [Jun] • 12 km NNW Richmond Hill, 32°02'41" N 81°20'13" W [May]; Clinch Co. (no data) [Apr]; Coffee Co. • 5 mi E Douglas [Jun]; Decatur Co. • Spring Creek [Jun-Jul]; Early Co. (no data) [Aug]; Emanuel Co. • 3.3 mi N Swainsboro, 32°40'37" N 82°23'08" W [Aug] • 9 mi SW Swainsboro [May] • 9.8 km WSW Swainsboro, 32.57174° N 82.43416° W • 4.5 km NE Norristown, Ohoopee Dunes Natural Area, 32.5285° N 82.4569° W [Jun-Jul]; Glynn Co. • Jekyll Island [Jun-Jul] • Brunswick [Jul]; Jefferson Co. • 15 mi SW Wadley [Mar]; Liberty Co. • Fort Stewart [Jun] • St. Catherines Island [Apr]; McIntosh Co., Blackbeard Island [Feb, Sep] • Sapelo Island, 31.40895° N 81.26634° W [May]; Richmond Co. • 12 km SW Augusta, 33°20'20" N 89°09'25" W [Oct] • 8 mi NE Wrens {in Jefferson Co.}; Screven Co. • Junction State Hwy 24 and US 301; Sumpter Co. • 1.9 mi W Americus [Mar]; Tattnall Co. • 3mi E Rte 147, along Ohoopee River [May-Jun] • 5 mi SW Reidsville [Sep-Nov]; Taylor Co. • 3 mi N Butler, 32.5998° N 84.2530° W [May-Jun]; Thomas Co. • Thomasville [Apr] • 10 km S Thomasville, 30°45.35' N 83°59.93' W, 7 m [Mar] • 4.5 mi S Thomasville [Jun] • Melrose Plantation [Apr] • Greenwood Plantation, 30°51'15" N 84°01'01" W [Sep-Oct]; Tift Co. • Coastal Plains Research Station [Jun] • Tifton [Jul]; Ware Co. • Waycross [Jul, Sep]; Wheeler Co. • Bells Ferry Road, Ocmulgee River [Apr, Aug] • 3.2 km NNE McRae, 32.09528° N 82.89099° W [May-Jun]. INDIANA: Jasper Co. • Jasper-Pulaski Fish and Wildlife Area [Jun]; Newton Co. • Beaver Lake Prairie Chicken Refuge, Kankakee Sands Preserve, 41°05′01″ N 87°24′22″ W [Jun–Jul], 41°04′56″ N 87°25′31″ W [Jun] • Conrad Savanna Nature Preserve [Jun]; Porter Co. • Indiana Dunes State Park, 41.6776 –87.0098, 190 m [May-Jun, Oct]. MARYLAND: Dorchester Co. • 2mi N Eldorado[May] • 3 mi W Hurlock [May] • 3 mi E Hurlock [May]; Wicomico Co. • Pemberton Historical Park, 38°20'53.58" N 75°38'26.29" W, 6 m [Apr] • Pemberton Historical Park, 38°20'49.79" N 75°38'50.70" W, 5 m [Jul]; Worcester Co. • Pokomoke State Forest, 38°11.406' N 75°30.241' W [Jun-Jul] • Pokomoke State Forest, 38°11'47.06" N 75°30'15.35" W, 12 m [Jun-Jul] • Pokomoke State Forest, 38.18845°N 75.49200°W, 10 m [Sep] • Pokomoke State Forest, 38.21900°N 75.52299°W, 10 m [Ju]. MICHIGAN: Antrim Co. • Grass River Natural Area [Jun-Jul]; Barry Co. • Barry Game Area [May]; Calhoun Co. • Ft. Custer; Clinton Co. • Rose Lake Conservation Area [Jul]; Leelanau Co. • Bingham [Jun]; Kalkaska Co. (no data) [Jun, Aug]; Livingston Co. • E. S. George Reserve, near Pinckney [Jul]; Newaygo Co. • 10 mi NE Newaygo [Aug]; Shiawassee Co. • Rose Lake Wildlife Experiment Station [Jun]. MISSISSIPPI: George Co. • Lucedale [Apr-Jun] • 4.5 mi NNW Lucedale [Jul]; Greene Co. • Leaf [Aug] • Avera [Apr]; Hancock Co. • Kiln; Harrison Co. • 3.5 mi SE Sancier [Apr-May, Jul]; Jackson Co. • Ocean Springs [Apr]; Lowndes Co. • 2.5 mi S Forreston, 33°18'02" N 88°18'30" W; Oktibbeha Co. (no data); Stone Co. • Wiggins [Jun] • 6.5 mi SE Wiggins • 6.5 mi ESE Perkinston [May]. NEW JERSEY: Atlantic Co. • 3.5 km SSE Weekstown, 39°33'49.7" N 74°35'05.8" W [May] • Cecil [May]; Bergen Co. • Wallington; Burlington Co. • Green Bank [Jun] • 7 mi W New Gretna [May] • Wharton State Forest [May] • Browns Mills [Sep] • Pemberton Township, Buffins Meadows [Jun]; Camden Co. • Atco [Jul]; Mercer Co. • Quaker Bridge (Sep]; Ocean Co. • Lakehurst [Jun] • East Plains [Aug-Sep] • West Plains [Jun-Sep] • Lacey Township, Cedar Bridge Fire Tower [Apr] • Whitesbog [May, Sep] • Bass River State Forest [Jul] • Warren Grove [Sep] • 1 mi W Warren Grove [Jun] • Lebanon State Park, Mt. Misery [May, Sep] • Ocean City [Jun]. NEW YORK: Suffolk Co. (no data) [Aug]; Nassau Co. • Long Beach [Jul]. NORTH CAROLINA: Bladen Co. Singletary Lake State Park, 34°35'00" N 78°27'30" W [May]; Brunswick Co. • Long Beach [May]; Cumberland Co. (no data); Currituck Co. • Knotts Island [May]; Dare Co. • Cape Hatteras, Buxton [Jun] • Nags Head; Hartnett Co. • Raven Rock State Park, 35.46207° N 78.91082° W; Hoke Co. • 1.5 mi SW McCain [Jun]; Moore Co. • Southern Pines [Apr, Sep]; New Hanover Co. • Carolina Beach State Park, 34.04688° N 77.91112° W [Jun]; Onslow Co. • Camp Lejuene [Jul]; Pender Co. • Holly Shelter Game Land [Apr, Sep]; Yancey Co. • Black Mountains. OHIO: Lucas Co. (no data) [Jun]. SOUTH CAROLINA: Aiken Co. • 1 mi S Windsor [Mar] • Aiken Gopher Tortoise Preserve, 10.7 km NE White Pond, 33°30'15" N 81°24'22" W, 259 ft [Apr], 33°29.350' N 81° 26.311' W • 10 km NE White Pond, Christmas Tree Road, 33°29'24" N 81°23' 23" W, 327 ft [Apr] • 3 mi E Montmorenci [Mar]; Beaufort Co. • Beaufort [Aug]; Berkeley Co. • Jamestown [Jun]; Calhoun Co. • St. Matthews; Charleston Co. • McClellanville, Bull's Island, 32°52' N 79°37' W [May, Aug]; Chesterfield Co. • McBee [Jul] • Cheraw State Park, 34°37'16" N 79°56'40" W, 34°38.010" N 79°53.421" W [Oct] • Carolina Sand Hills National Wildlife Refuge, 34.5855° N 80.2690° W, 34.5745° N 80.2232° W, 34.5626° N 80.2016° W, 34.5973° N 80.2400° W, 34.5476° N 80.2433° W [Mar, May]; *Colleton Co.* • Walterboro [Apr]; *Darlington Co.* • Pee Dee Recreation Area, 34.3070° N 79.7343° W [Jul]; *Florence Co.* • The Country Club of South Carolina [Apr]; *Georgetown Co.* • Baruch/Hobcaw, Belle Baruch Marine Field Station, 33°21′46″ N 79°13′33″ W [Apr–May] • Baruch/Hobcaw Barony, 33.3625° N 79.270° W [May] • Baruch/ Debidue Island, 33.3567° N 79.1526° W [May] • Georgetown [May]; *Hampton Co.* • Yemassee [Jul] • Scotia [Apr] • Hampton [Aug]; *Horry Co.* • Myrtle Beach [Apr, Jun]; *Jasper Co.* • Tillman [Aug]; *Richland Co.* • 6 mi E Columbia [Apr]; *Pickens Co.* • Clemson. **TENNESSEE**: *Cumberland Co.* • Black Mountain [May–Aug]; *Stewart Co.*, Ft. Campbell Military Reservation, Site 6, 36.59527° N 87.71574° W [Sep]. **VIRGINIA**: *City of Suffolk* • 6 mi SSE Franklin, South Quay Natural Area, 36.92019 –76.00423 [Jul–Aug]; *Cumberland Co.* • 2–5.5 km SW Columbia [Jun–Sep]; *Isle of Wight Co.* • Antioch Pines Natural Area Preserve [Sep] • Blackwater Ecological Reserve, 36.822749 –76.855168 [Aug] • Zuni Pine Barrens, Blackwater Ecological Preserve, 36.82466 –76.85519 [Jul–Aug] • 7 km S Zuni; *Sussex Co.* • Chub Sandhills Natural Area Preserve, 36.874 –77.184. **WEST VIRGINIA**: *Morgan Co.* • 7 km E Paw Paw, 39.5224 –78.3641 [Jul].

Comments. The holotype cited above is assumed to be Robinson's holotype male. Robinson's original description of *Canthon bispinatus* was based on 46 specimens. Robinson retained the holotype, allotype and an unspecified number of paratypes in his own collection (now at the National Museum of Natural History) and distributed remaining paratypes among the collections of the Academy of Natural Sciences of Philadelphia, the United States National Museum (National Museum of Natural History), the American Museum of Natural History, and the private collection of R. C. Casselberry.

Melanocanthon bispinatus is a wide-ranging species and common in all collections examined for this study. Mario Cupello (pers comm) likened its distribution to that of *Ateuchus lecontei* (Harold). As far as I know, *M. bispinatus* and *M. nigricornis* are allopatric. I have no reliable records placing them in the same state, although I harbor no serious doubt that they will ultimately be discovered in close proximity in the zone of potential sympatry depicted in Figure 19. There is no potential barrier I can imagine that would prevent encounters in, for example, Illinois, Indiana and Mississippi. Especially in that zone, occasional specimens of *M. bispinatus* from Michigan and northern Indiana can express a weakened dorsal sculpturing very similar to that of *M. nigricornis*, especially on the head where granules can be almost effaced.

The distribution of *Melanocanthon bispinatus* depicted in Figure 15 is presumptuous in that it includes the entire Ohio River Valley, from western Pennsylvania to the Mississippi River. In fact, I have not seen specimens nor reliable reports of this species from at least 90% of this vast area, including all, or virtually all, of the states of Indiana, Ohio, Kentucky, Pennsylvania, and West Virginia (see Fig. 18). I think it reasonable to predict that it is indeed found there, even if only in widely scattered patches of suitable habitat. Alternatively, the populations clustered in Michigan and adjacent sites in far northern Indiana and Ohio, and in southeastern Ontario, might well be regarded as a widely disjunct Great Lakes enclave of this species. The latter alternative (absence from the Ohio River valley) begs the question of why it has not populated that area, an explanation for which I presently have no reasonable conjecture.

This species occurs sympatrically with *M. punctaticollis* in north central Florida and with *M. vulturnus* in northern Florida and adjacent southern Georgia and South Carolina (Fig. 15), where it (especially females) can be difficult to separate. In general, however, the pronotal granulation of *M. vulturnus* is coarser and denser than that of *M. bispinatus* and often exhibits a metallic, greenish color never seen in this species. The parameres, however, are very distinctive (Fig 56–58) and will readily separate *M. bispinatus* from both of its sympatric congeners.

Label data indicate that this very common, widespread species is attracted to a wide variety of food types, including human, pig, coyote, and cattle dung, rotting fruit, fruit mixtures (such as banana, beer, sugar mashup), fungi, as well as an isolated record of rolling a dead melolonthine beetle (Scarabaeidae). Harpootlian (1995, 2001) reported *M. bispinatus* as common in South Carolina sand hills and coastal plains habitats, on dead carabid and cicindelid beetles and fungi, as well as rolling deer and rabbit pellets. Robinson (1941) reported *M. bispinatus* on old, partly dried toadstools in New Jersey pine barrens. Nemes and Price (2015), Price et al. (2012), and Price and Ratcliffe (2023) have reported *M. bispinatus* to be a common eastern Maryland species in coastal habitats where it exploits dung, dry fungi, carrion and rotting fruit. Löding's (1945) reference to *M. nigricornis* as common on fungi in Alabama probably referred to *M. bispinatus*. Young (2021) reported *M. bispinatus* to be the overwhelmingly

dominant dung beetle in a long leaf pine habitat community in southwest Georgia (Baker Co.); it could be, however, that a portion of specimens sampled for the study were *M. vulturnus*, which was not recognized at the time but is now known from adjacent counties. Hinson (2011) found *M. bispinatus* to be among the scarcer species in scarabeoid communities sampled with flight-intercept traps in various habitats in South Carolina.

I have examined one specimen of *M. bispinatus* labeled Palm Beach Co., Florida, far to the south of its known range in the northern part of the state. I regard this record as doubtful pending confirmation. I have examined a Peck-collected voucher specimen from the Canadian Museum of Nature and confirmed that Peck and Howden's (1985) reference to *M. bispinatus* on Big Pine Key (Monroe Co., Florida) refers to *M. vulturnus* (qv). Robinson (1948) listed *M. bispinatus* from Rhode Island and Pennsylvania, but I have seen no specimens from either state. Rounds and Floate's (2012) reference to *M. nigricornis* in Missaukee County, Michigan, is probably referable to *M. bispinatus*, which I have seen from several nearby counties. I have no reliable records of *M. nigricornis* from Michigan.

Acknowledgments

I am much indebted to the following colleagues whose gracious assistance has made this study possible:

To the following, who facilitated loans of specimens from the collections under their care: Robert Androw, Carnegie Museum of Natural History, Pittsburgh, PA; Jason Dombroskie, Cornell University, Ithaca, NY; Zachary Falin, University of Kansas, Lawrence KS; Michael Ferro, Clemson University, Clemson, SC; François Génier, Canadian Museum of Nature, Ottawa, Ontario; Chris Grinter, California Academy of Sciences, San Francisco, CA; Lee Herman, American Museum of Natural History, New York, NY; E. Richard Hoebeke, The University of Georgia, Athens, GA; Sandor Kelly, University of Central Florida, Orlando, FL; Paul Lago, University of Mississippi, University, MS; Steven Paiero, University of Guelph, Guelph, Ontario; M. J. Paulsen, University of Nebraska, Lincoln, NE; Gareth Powell, Florida State Collection of Arthropods, Gainesville, FL; Dana Price, Salisbury University, Salisbury, MD; Ed Riley, Texas A&M University, College Station, TX; D. Christopher Rogers, University of Kansas, Lawrence, KS; Terence Schiefer, Mississippi State University of Missouri, Columbia, MO; Sarah Smith, Michigan State University, East Lansing, MI; Robin Thomson, University of Minnesota, St, Paul, MN; Jessica Wadleigh, Field Museum of Natural History, Chicago, IL; Alex Wild, University of Texas, Austin, TX; Karen Wright, Texas A&M University, College Station, TX.

To the following who afforded valuable information, advice, consultation, field observations, photographs, key testing and personal insight: Eric Chapman, University of Kentucky, Lexington, KY; Patrick Coin, Durham, NC; Mario Cupello, Universidade Federal do Paraná, Curitiba, PR, Brazil; Mattias Forsage, Swedish Museum of Natural History, Stockholm; Frank Guarnieri, Waterville, ME; Kaloyan Ivanov, Virginia Museum of Natural History, Martinsville, VA; Sandor Kelly, University of Central Florida, Orlando, FL; Paul Lago, University of Mississippi, University, MS; Crystal Maier, Museum of Comparative Zoology, Cambridge, MA; Matthew Pintar, Florida International University, Miami, FL; D. Christopher Rogers, University of Kansas, Lawrence, KS; Andrew B. T. Smith, Canadian Museum of Nature, Ottawa, Ontario; Mark Swanson, Swannanoa, NC.

And to the following, for their careful, insightful reviews of the submission manuscript: Paul Lago, University of Mississippi, University, MS, and Ed Riley, Texas A&M University, College Station, TX.

Literature Cited

Blair WF. 1950. The biotic provinces of Texas. The Texas Journal of Science 2: 93–117.

- 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: 163–172.
- **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.

Blatchley WS. 1927. The Scarabaeidae of Florida. The Florida Entomologist 11: 55–62. (Note: Blatchley's work was published piecemeal under the same title in volumes 11–14 [1927–1930] of The Florida Entomologist, collated as follows by

- Woodruff (1973): **1927** [vol. 11: 44–46, 55–62]; **1928** [vol.12: 9–14, 22–30, 44–46, 63–65]; **1929** [vol. 13: 33–37, 52–56, 69–77]; **1930** [vol. 14: 13–17, 25–35].)
- **Edmonds WD. 2022.** Taxonomic review of the North American dung beetle genus *Boreocanthon* Halffter, 1958 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). Insecta Mundi 0952: 1–65.

Fincher GT. 1975. Dung beetles of Blackbeard Island (Coleoptera Scarabaeidae). The Coleopterists Bulletin 29: 319–320.

- 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.
- **Freese EL, Veal DA, Lago PK. 2020.** The Scarabaeoidea (Coleoptera) of Iowa: An annotated checklist. Insecta Mundi 0787: 1–83.
- González-Alvarado A, Molano-Rendón F, Vaz-de-Mello FZ. 2019. A new genus of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) endemic to the Brazilian Atlantic Forest. Journal of Natural History 53: 1751–1765.
- 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, Espinosa 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(2): 109.
- Harpootlian PJ. 1995. Notes and records of Scarabaeidae from the southeastern United States. The Coleopterists Bulletin 49: 280.
- Harpootlian PJ. 2001. Scarab beetles (Coleoptera: Scarabaeidae) of South Carolina. Biota of South Carolina, vol. 2. Clemson University; Clemson, South Carolina. 157 p.
- Hart CA. 1907. Zoological studies in the sand regions of the Illinois and Mississippi River valleys. Bulletin of the Illinois State Laboratory of Natural History 7:195–272.
- Hinson K. 2011. Species diversity and seasonal abundance of Scarabaeoidea at four locations in South Carolina. All Theses 1082. 113 p. Clemson University; Clemson, SC. Available at https://tigerprints.clemson.edu/all_theses/1082 (Last accessed August 3, 2023.)
- Horn GH. 1870. Notes on some genera of coprophagous Scarabaeidae of the United States. Transactions of the American Entomological Society 3: 41–51.
- Howden HF. 1963. Speculations on some beetles, barriers, and climates during the Pleistocene and pre-Pleistocene periods in some non-glaciated portions of North America. Systematic Zoology 12: 178–201.
- Howden HF. 1966. Some possible effects of the Pleistocene on the distributions of North American Scarabaeidae (Coleoptera). The Canadian Entomologist 98: 1177–1190.
- **ICZN** [International Commission on Zoological Nomenclature]. 1999. International Code of Zoological Nomenclature. Fourth edition. The International Trust for Zoological Nomenclature; London. 306 p.
- Kaufman PE, Wood LA. 2012. Indigenous and exotic dung beetles (Coleoptera: Scarabaeidae and Geotrupidae) collected in Florida cattle pastures. Annals of the Entomological Society of America 105: 225–231.
- King IN. 1914. The Coleoptera of Henry County, Iowa. Bulletin of the Iowa Academy of Sciences 21: 317–339.
- 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.
- 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.
- Löding HP. 1945. Catalogue of the beetles of Alabama. Geological Survey of Alabama 11: 1–172.
- Marshall SD, Hoeh WR, Deyrup MA. 2000. Biogeography and conservation biology of Florida's *Geolycosa* wolf spiders: threatened spiders in endangered ecosystems. Journal of Insect Conservation 4: 11–21.
- Mawdsley JR. 1993. The entomological collection of Thomas Say. Psyche 100: 163–171.
- Mayr E. 1931. Birds collected during the Whitney South Sea expedition. XII. Notes on *Halcyon chloris* and some of its subspecies. American Museum Novitates 469: 1–10.
- Mayr E 1963. Animal species and evolution. The Belknap Press of Harvard University Press; Cambridge, Massachusetts. 797 p.
- 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.

- Neill WT. 1957. Historical biogeography of present-day Florida. Bulletin of the Florida State Museum, Biological Sciences 2: 175–220.
- Nemes SN, Price DL. 2015. Illustrated keys to the Scarabaeinae (Coleoptera: Scarabaeidae) of Maryland. Northeastern Naturalist 22: 318–344.
- **Peck SB, Howden HF. 1985.** Biogeography of scavenging scarab beetles in the Florida Keys: post-Pleistocene land-bridge islands. Canadian Journal of Zoology 63: 2730–2737.
- **Price DL, Brenneman LM, Johnston RE. 2012.** Dung beetle (Coleoptera: Scarabaeidae and Geotrupidae) communities of eastern Maryland. Proceedings of the Entomological Society of Washington 114: 142–151.
- Price DL, Ratcliffe B. 2023. The scarabaeoid beetles of Maryland (Coleoptera). Bulletin of the University of Nebraska State Museum 33: 1–330.
- Robinson M. 1941. Studies in the Scarabaeidae of North America. Parts I and II. Transactions of the American Entomological Society 67: 127–136.
- Robinson M. 1948. A review of the species of *Canthon* inhabiting the United States. Transactions of the American Entomological Society 74: 83–99.
- **Rounds RJ, Floate KD. 2012.** Diversity and seasonal phenology of coprophagous beetles at Lake City, Michigan, USA, with a new state record for *Onthophagus taurus* (Schreber) (Coleoptera: Scarabaeidae). The Coleopterists Bulletin 66: 169–172.
- 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. 1920. Beitrag zur Kenntnis der Gattungen *Canthon* Hffsg., *Sybax* Boh., *Aphodius* Ill., *Simogenius* Har., *Ataenius* Har., Archiv für Naturgeschichte 86: 114–147.
- Smith HM, Buechner HK. 1947. The influence of the Balcones Escarpment on the distribution of amphibians and reptiles in Texas. Bulletin of the Chicago Academy of Sciences 8: 1–16.
- Vaz de Mello F, Cupello M. 2018. The type specimens of South American dung beetles. Part I: On the species described in the genus *Canthon* Hoffmannsegg, 1817 by the German entomologist Adolf Schmidt (1856–1923) (Coleoptera: Scarabaeidae, Scarabaeinae). Spixiana 41: 33–76.
- **Vestal AG. 1913.** An associational study of Illinois sand prairie. Bulletin of the Illinois State Laboratory of Natural History 10: 1–96.
- Wagner PM, Abagandura GO, Mamo M, Weissling T, Wingeyer A, Bradshaw JD. 2020. Abundance and diversity of dung beetles (Coleoptera: Scarabaeoidea) as affected by grazing management in Nebraska sandhills ecosystem. Environmental Entomology 50: 222–231.
- Weiss HB, Ziegler GM. 1931. Thomas Say, early American naturalist. Charles C. Thomas; Springfield, Illinois. 260 p.
- Whipple SD, Hoback WW. 2012. A comparison of dung beetle (Coleoptera: Scarabaeidae) attraction to native and exotic mammal dung. Environmental Entomology 41: 238–244.
- Williams AH, Kriska NL. 2001. Notes on the biology of *Melanocanthon nigricornis* (Coleoptera: Scarabaeidae). The Great Lakes Entomologist 34: 129–131.
- 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.
- Young KL. 2021. In the pines: dung beetle community composition in longleaf pine habitat. All Theses 3640. 34 p. Clemson University; Clemson, SC. Available at https://tigerprints.clemson.edu/all_theses/3640 (Last accessed August 2023.)

Received August 10, 2023; accepted October 15, 2023. Review editor Kyle Schnepp.