



## Taxonomic revision of the genus *Deltepilissus* Pereira, 1949 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini)

FERNANDO A. B. SILVA<sup>1,2\*</sup>, ANA B. M. FERREIRA<sup>2</sup> & FRANÇOIS GÉNIER<sup>3</sup>

<sup>1</sup>Universidade Federal Rural de Pernambuco, Unidade Acadêmica de Serra Talhada. Avenida Gregório Ferraz Nogueira, s/n. Serra Talhada, PE, 56909-535, Brazil.

✉ [fernandoabsilva@yahoo.com.br](mailto:fernandoabsilva@yahoo.com.br); <https://orcid.org/0000-0002-3894-4846>

<sup>2</sup>Universidade Federal do Pará, Instituto de Ciências Biológicas, setor de Zoologia, Campus Belém. Rua Augusto Corrêa, 01, Guamá. Belém, PA, 66075-110, Brazil.

✉ [abeatrizmf@gmx.com](mailto:abeatrizmf@gmx.com); <https://orcid.org/0000-0001-7661-9924>

<sup>3</sup>Beatty Centre for Species Discovery, Canadian Museum of Nature, 1740 Chemin Pink, Gatineau, Quebec, J9J 3N7, Canada.

✉ [fgenier@nature.ca](mailto:fgenier@nature.ca); <https://orcid.org/0000-0002-5399-8412>

\*Corresponding author

### Abstract

*Deltepilissus* Pereira, 1949 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini) is revised and consists of two valid species, both endemic to the Brazilian Atlantic Forest. *Deltepilissus diabolicus* (Harold, 1880), from Bahia, and *D. infernalis* (Harold, 1880), from Espírito Santo to São Paulo, are redescribed, including characters of the adult female and of the male genitalia, both described and illustrated here for the first time. Lectotypes are designated for *D. diabolicus* (Harold, 1880) and *D. infernalis* (Harold, 1880). A detailed literature review, synonymies, diagnoses, key for species identification, illustration of key morphological characters, as well as data of the studied material and geographic distribution are provided for each species. A discussion about their conservation status is also provided.

**Key words:** Dung beetles, Neotropical fauna, systematics, Brazilian Atlantic rainforest

### Introduction

In 1880, Edgar von Harold described the new species *Canthon infernalis* and *C. diabolicus*, both from Brazil. Though formally placing them in *Canthon* Hoffmannsegg, 1817, Harold informed that these closely-related species actually belonged to a new genus that he would soon describe. According to him, this new taxon was “intermediate”, in his words, between *Canthon* and *Deltochilum*. However, Harold never described the genus and died soon after in 1886 (Cupello 2020).

Sixty-three years later, Pereira (1949) described a new genus and species, *Deltepilissus travassosi*, from a single specimen collected in the city of Rio de Janeiro (Brazil). Four years later, however, Pereira (1953), with access to three additional specimens, realised that *D. travassosi* had already been described by Harold as *C. infernalis*. He then transferred *C. infernalis* to *Deltepilissus* and treated the species name as a senior subject synonym of the now invalid *D. travassosi*. Pereira (1953) also mentioned that, based on Harold’s comments, *Canthon diabolicus*, the other species from 1880, was likely a second *Deltepilissus*. This was later confirmed by Halffter & Martínez (1977), who transferred *C. diabolicus* to this genus. However, these authors did not provide diagnoses or an identification key to separate the two species. Since then, no other taxonomic work has been published on this group.

Tarasov & Dimitrov (2016) performed a molecular phylogenetic analysis to reconstruct the phylogeny of dung beetles. The study included a large dung beetle molecular dataset, with a global biogeographic coverage of phylogenetic lineages, and some enigmatic taxa. Therein, the tribe Deltochilini was formally redefined to include only New World dung beetle genera, and *Deltepilissus* was provisionally considered part of the tribe, even though not included in their molecular analyses. Thus, to date, the assignment of *Deltepilissus* to the tribe Deltochilini is purely based on putative morphological synapomorphies (Tarasov & Génier 2015) and diagnostic characters through specimen examination.

Within *Deltochilini sensu* Tarasov & Dimitrov (2016), *Deltepilissus* is characterized mainly by reduced tarsal claws; protibiae elongate, weakly widened apically, with three small and spaced lateral teeth; and metatibial spur short, apically widened, with a spiniform process on internal edge (Vaz-de-Mello *et al.* 2011).

Very few distribution records are available in the literature for the species of *Deltepilissus*. *Deltepilissus infernalis* and *D. diabolicus* were only recorded from the Brazilian Atlantic rainforest in Bahia and Rio de Janeiro states (Harold 1880; Pereira 1949, 1953; Vulcano & Pereira 1964). Furthermore, there are very few specimens in collections, and the last records are from the 1950s (Pereira 1949, 1953). Therefore, there are good reasons to consider these species as endangered due to the serious anthropic threats to the Atlantic rainforest areas in Brazil, as urbanization (residential and industrial development), illegal wood exploitation, and impacts associated with tourism (Vieira *et al.* 2008; Ribeiro *et al.* 2009; Vieira *et al.* 2011; Silva *et al.* 2020), to which these species seem to be endemic.

This paper aims to revise the taxonomy of *Deltepilissus*, and we provide information on the morphology of the species, including the first description of the anatomy of their endophalli, and an identification key. We also present new distributional data from the examination of several entomological collections. It is our hope that new specimens of these seldomly recorded species will come to light with more accurate locality data and natural history information.

## Material and methods

A total of 14 adult specimens of *Deltepilissus* were examined. The material was kindly provided by the curators of the institutions as listed below.

AMBC	Ayr Bello private collection, Rio de Janeiro, RJ, Brazil (Ayr de Moura Bello)
BMNH	The Natural History Museum, London, United Kingdom (Max Barclay).
CEMT	Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Brazil (Fernando Z. Vaz-de-Mello).
CERPE	Coleção Entomológica da Universidade Federal Rural de Pernambuco, Pernambuco, Brazil (Paschoal C. Grossi).
CMNC	Canadian Museum of Nature, Ottawa, Canada (François Génier).
MFNB	Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany (Johannes Frisch and Joachim Willers); only types examined.
MNRJ	Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Miguel A. Monné and Marcela L. Monné); information provided by Mario Cupello; specimen destroyed in the 2018 fire.
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Carlos Campaner and Sônia Casari); examined by Fernando A.B. Silva.

The following collections were also searched but do not appear to house any *Deltepilissus* specimens: Coleção Entomológica do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (Márcio Félix); Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (Lucia Massutti de Almeida, examined by Mario Cupello); Institut royal des Sciences naturelles, Brussels, Belgium (Alain Drumont); and University of Nebraska State Museum, Nebraska, United States of America (Brett C. Ratcliffe).

Label data of type specimens is presented verbatim. Labels are separated by a double slash (//) and line breaks on the same label with a single slash (/). Italic text indicates handwritten labels. The information on the labels of non-type material was organized as follows (when available): country name in capital letters, in bold; department or state name in capital letters; more specific municipality and locality; habitat information in square brackets ([]); geographic coordinates in square brackets ([]); elevation data; collection date; collection method; collector; number of females (♀) and / or males (♂); repository in parentheses.

According to Cupello (2020, 2021), the type specimens described by Edgar von Harold (1830–1886) are housed in several museums all over Europe and in the Museum of Comparative Zoology. Those from Harold's personal collection are indeed mostly housed in the Muséum national d'Histoire naturelle, Paris, France, via René Oberthür (1852–1944) collection. However, we know that the types of the two Harold names treated here (*Canthon diabolicus*

Harold, 1880 and *C. infernalis* Harold, 1880) are indeed the ones at the MFNB for the following reason: (1) Harold says in the introduction to his 1880 article that the species he was describing were mostly from the collection of the Berlin museum, where he held the post of curator for insects between 1879 and 1880 (Cupello 2020); (2) The identification label borne by each of the specimens indicated here as Harold types is marked with an asterisk (Figs 4B, 4D). This is the notation used by the curators at the Berlin museum in the late 19th century and early 20th century to indicate that the collection houses the type(s) of the name; (3) these specimens match Harold's descriptions of the respective species. The holotype of *Deltepilissus travassosi* Pereira, 1949 is housed in the Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Lectotypes are designated here in accordance with Article 74 (specifically 74.1.1 and 74.7) of the International Commission on Zoological Nomenclature (1999), with the purpose of maintaining nomenclatural stability. We found just one type specimen of *Canthon diabolicus* and *Canthon infernalis* in the collections studied. Analyzing the original descriptions (Harold 1880), no holotype was originally fixed, and we could not find any explicit mention that these species were described based on a single specimen. Following the International Commission on Zoological Nomenclature (1999) Recommendation 73F, we assume the type series were based on two or more individuals. Therefore, we designate here lectotypes rather than assume that the specimens we found are the holotypes.

Dissection of the male genitalia was executed following Zunino (1978). The terminology used to describe these structures followed Tarasov & Solodovnikov (2011), Tarasov & Génier (2015) and Génier (2019). The endophallus was removed from the tegmen through the basal foramen of the phallobase, and its endophallites were illustrated. The axial and subaxial (A+SA), the superior right peripheral (SRP), and the additional endophallites (AE) were illustrated in left lateral view. The frontolateral peripheral endophallite (FLP) was illustrated in right lateral view. The lamella copulatrix (LC) is absent. Standard criteria of homology (Wägele 2005) were applied to assess the hypotheses of primary homology between parts of the endophallites.

Photographs of *D. diabolicus* were taken with a Leica stereomicroscope M205A, using image stacking software (Leica Application Suite, version 4.2). Photographs of *D. infernalis* were taken with a Leica Z16 APO imaging system and images were processed with LAS software version 4.13. The images were edited using the Adobe Photoshop CS4 and distribution maps were in QGIS Lyon 2.12.1.

### ***Deltepilissus* Pereira, 1949**

*Deltepilissus* Pereira 1949: 231 (original description); Pereira & Martínez 1956: 96, 125, 184 (identification key, catalog); Halffter 1961: 231 (identification key); Vulcano & Pereira 1964: 660 (catalog); Halffter & Matthews 1966: 261 (distribution); Halffter & Martínez 1977: 37, 52, 66 (identification key, taxonomic remarks, checklist); Halffter & Edmonds 1982: 139 (distribution); Vaz-de-Mello 2000: 186, 192 (checklist); Krajcik 2006: 47 (checklist); Vaz-de-Mello *et al.* 2011: 5, 10, 18, 25, 32, 40, 55 (identification key); Krajcik 2012: 88 (checklist); Tarasov & Dimitrov 2016: 15 (new delimitation for Deltochilini); Cupello & Vaz-de-Mello 2018: 18 (taxonomic remarks); Schoolmeesters 2020 (catalog); Vaz-de-Mello 2021 (checklist).

**Type species.** *Deltepilissus travassosi* Pereira, 1949 by original designation (currently a junior subjective synonym of *Canthon infernalis* Harold, 1880).

**Diagnosis.** Among the genera included in the tribe Deltochilini (sensu Tarasov & Dimitrov 2016), *Deltepilissus* can be distinguished by reduced tarsal claws (Figs 1G–I, 2I–L); protibiae long, weakly widened apically, with three small and spaced, lateral teeth (Figs 1A–B, 2A–D); metatibial spur short, widened apically, with spiniform process at least on internal edge (Figs 1H–I, 2K–L).

**Redescription. Colour and tegument sculpture** (Figs 1A–B, 2A–D). Head, pronotum, elytra and ventral surface with black, copper or red coloration. Body densely punctate. **Length.** 9–15 mm. **Head** (Figs 1C, 2E). Surface with strong, deep and dense punctures. Clypeus with two widely spaced, small teeth. Eye comma shaped in dorsal view. Dorsal interocular space at least 10 times eye width. Lateral margin of head regularly curved outward. **Thorax** (Figs 1A, 2A, 2C). Pronotum convex; anterior angles acute, directed forward. Lateral edge of pronotum regularly curved outward; posterior angle obtuse. Pronotum with a longitudinal sulcus on midline posteriorly. Hypomera not excavated (Figs 1D, 2F). Mesometasternal suture slightly arched. Metaventrite punctures variable in size; smaller and denser medially (Figs 1B, 2B, 2D). **Elytra** (Figs 1A, 2A, 2C). Lateral margin slightly curved outward. Elytral striae visibly impressed. Pseudepipleural carina complete, visible on entire length of epipleuron.

Elytral lateral edge formed by the pseudepipleural carina. Interstriae flattened, without carinae or tubercles basally and apically. **Abdomen** (Figs 1E, 2B, 2D, 2G). Punctures denser on lateral surface of ventrites. Sixth ventrite longer than 2nd, 3rd, 4th and 5th. Pygidium rounded apically, densely punctate, separated from propygidium by carina (Figs 1F, 2H). **Legs**. Femora densely punctate (Figs 1B, 2B, 2D); anterior and posterior edges marginate. Protibiae long, thin and curved. Apical one-quarter of protibiae abruptly expanded along inner edge (Figs 1A–B, 2A–D). Apical one-third of protibiae with three distinct lateral teeth; medial lateral tooth closer to apical tooth than to basal tooth (Figs 1A–B, 2A–D). Meso- and metatibiae smoothly arched toward body, not abruptly expanded along inner edge (Figs 1A–B, 2A–D). Longitudinal carinae of meso- and metatibiae with row of setae. Metatibial spur short, sinuous and spatulate; bifurcate apically (Figs 1I, 2L), almost rounded (Fig. 1H), or with a conspicuous denticle (spiniform process) on inner edge (Fig. 2K). First meso- and metatarsomeres triangular; tarsomeres 2–4 trapezoidal, the last subrectangular (Figs 1H–I, 2K–L). Tarsal claws reduced (Figs 1G–I, 2I–L). **Secondary sexual characters**. Females can be distinguished from males, in general, by the last abdominal ventrite evenly wide (Fig. 2D); in males, the last abdominal ventrite is subtly narrower medially (Figs 1E, 2G). Females have the protibial spur bifurcate apically (Fig. 2J); in males, protibial spur is wide and rounded, lacking denticle apically (Fig. 1G), or with a denticle on external edge (Fig. 2I). Females have also sinuous and bifurcate apex of metatibial spur, with denticle (spiniform process) on internal and external edges (Figs 1I, 2L); in males, metatibial spur only have denticle on inner edge (Fig. 2K), or it is rounded apically, with inner denticle almost inconspicuous (Fig. 1H). Furthermore, females have the apical third of metatibiae almost straight (Figs 1I, 2L), whereas in males the apical third of metatibiae is distinctly curved inward (Figs 1H, 2K). **Tegmen**. Parameres symmetrical, subtriangular in lateral view (Figs 3C, 3F), pointed and curved inward apically (Figs 3A–F). **Endophallus**. Lamella copulatrix absent. Superior right peripheral endophallite circular, with curved handle-shaped extension and ring with thin border (Figs 3G–H). Frontolateral peripheral endophallite with irregular shape (Figs 3I–J). Complex of axial and subaxial endophallites elongate, with irregular shape (Figs 3M–N). There are also two short additional endophallites (Figs 3K–L) between the frontolateral peripheral endophallite and the axial and subaxial endophallites.

**Remarks**. Although none of the specimens with collecting data provide indications on the natural history of the genus, we suspect that species of *Deltepilissus* are inquiline. We base this assumption on the fact that none specimen was collected in dung traps or any other type of baited pitfall traps. The reduced tarsal claws is a common adaptation for inquiline, however no other obvious adaptations are present such as concealed mouthparts, highly modified legs or trichome. The rather dense, small swallow punctures with a minute seta present in *Deltepilissus* are eerly similar to those found in *Ateuchus (Lobidion) punctatissimus* (Génier, 2010), a documented ant inquiline species (Génier, 2010). Another possibility, considering its fully functional wings and rather elongate legs, would be a predatory behavior on social insects. Meliponine bees are common in the Atlantic rainforest and nests in trees. Flying higher in the canopy would explain the fact that species of *Deltepilissus* have also never been collected in flight interception traps set on the ground. This is purely speculative at the moment, but it would be interesting to verify these hypotheses.

### Key to adults of *Deltepilissus* Pereira, 1949 and similar genera in the tribe Deltochilini

(modified from Vaz-de-Mello *et al.* 2011)

1. Tarsal claws reduced, straight or only weakly curved (Figs 1G–I, 2I–L). Hypomera convex or weakly excavated anteriorly (Figs 1D, 2F). Head lacking transverse carina ..... 2
- Tarsal claws large, strongly curved, falciform or angulate; if only weakly developed, then either hypomera deeply excavated anteriorly or head with transverse carina or both ..... other Deltochilini genera (see Vaz-de-Mello *et al.* 2011, 2020)
2. Protibiae short, with lateral teeth large and contiguous. Metatibial spur spiniform ..... 3
- Protibiae long, with three small and spaced teeth (Figs 1A–B, 2A–D). Metatibial spur short, spatulate, with denticle (spiniform process) at least on inner edge (Figs 1H–I, 2K–L). ..... *Deltepilissus* Pereira, 1949... 4
3. Protibiae with lateral teeth set along apical third, at least apical two directed towards apex ..... *Scatonomus* Erichson, 1835
- Protibiae with lateral teeth set along apical half or more; at least second tooth directed laterally ..... *Anomiopus* Westwood, 1842
4. Punctures of central portion of pronotum spaced by at least twice their diameter (Figs 2A, 2C). Males with denticle on external edge of protibial spur (Fig. 2I). Males with a conspicuous denticle on inner edge of metatibial spur (Fig. 2K). Body length 9–11 mm. Apex of parameres slightly curved inward in dorsal and ventral views (Figs 3D–E). Brazil (Espírito Santo, Rio de Janeiro, and São Paulo) ..... *D. infernalis* (Harold, 1880)
- Punctures of central portion of pronotum closely set, spaced by less than their diameter (Fig. 1A). Males with wide and

rounded protibial spur, without denticle apically (Fig. 1G). Males with rounded metatibial spur apically, inner denticle almost inconspicuous (Fig. 1H). Body length about 15 mm. Apex of parameres distinctly curved inward in dorsal and ventral views (Figs 3A–B). Brazil (Bahia) . . . . . *D. diabolicus* (Harold, 1880)

***Deltepilissus diabolicus* (Harold, 1880)**

(Figs 1A–I, 3A–C, 3G, 3I, 3K, 3M, 4A–B, 5A–B)

*Canthon diabolicus* Harold 1880: 150 (original description); Gillet 1911: 29 (catalog); Schmidt 1922: 67, 74 (taxonomic remarks, distribution); Balthasar 1939: 201 (identification key); Blackwelder 1944: 199 (checklist); Vulcano & Pereira 1964: 611 (catalog).

*Deltepilissus diabolicus*: Halffter & Martinez 1977: 66 (transferred *C. diabolicus* to the genus *Deltepilissus*, checklist); Vaz-de-Mello 2000: 192 (checklist); Krajcik 2006: 47 (checklist); Krajcik 2012: 88 (checklist); Schoolmeesters 2020 (catalog); Vaz-de-Mello 2021 (checklist).

**Diagnosis.** *Deltepilissus diabolicus* can be distinguished from *D. infernalis* by the head approximately 1.2 times wider than long (Fig. 1C); punctures of central portion of pronotum closely set, spaced by less than their diameter (Fig. 1A); body length about 15 mm. Furthermore, males have wide and rounded protibial spur, lacking denticle apically (Fig. 1G); and rounded metatibial spur apically, with almost inconspicuous inner denticle (Fig. 1H). Apex of parameres are also distinctly curved inward in dorsal and ventral views (Figs 3A–B).

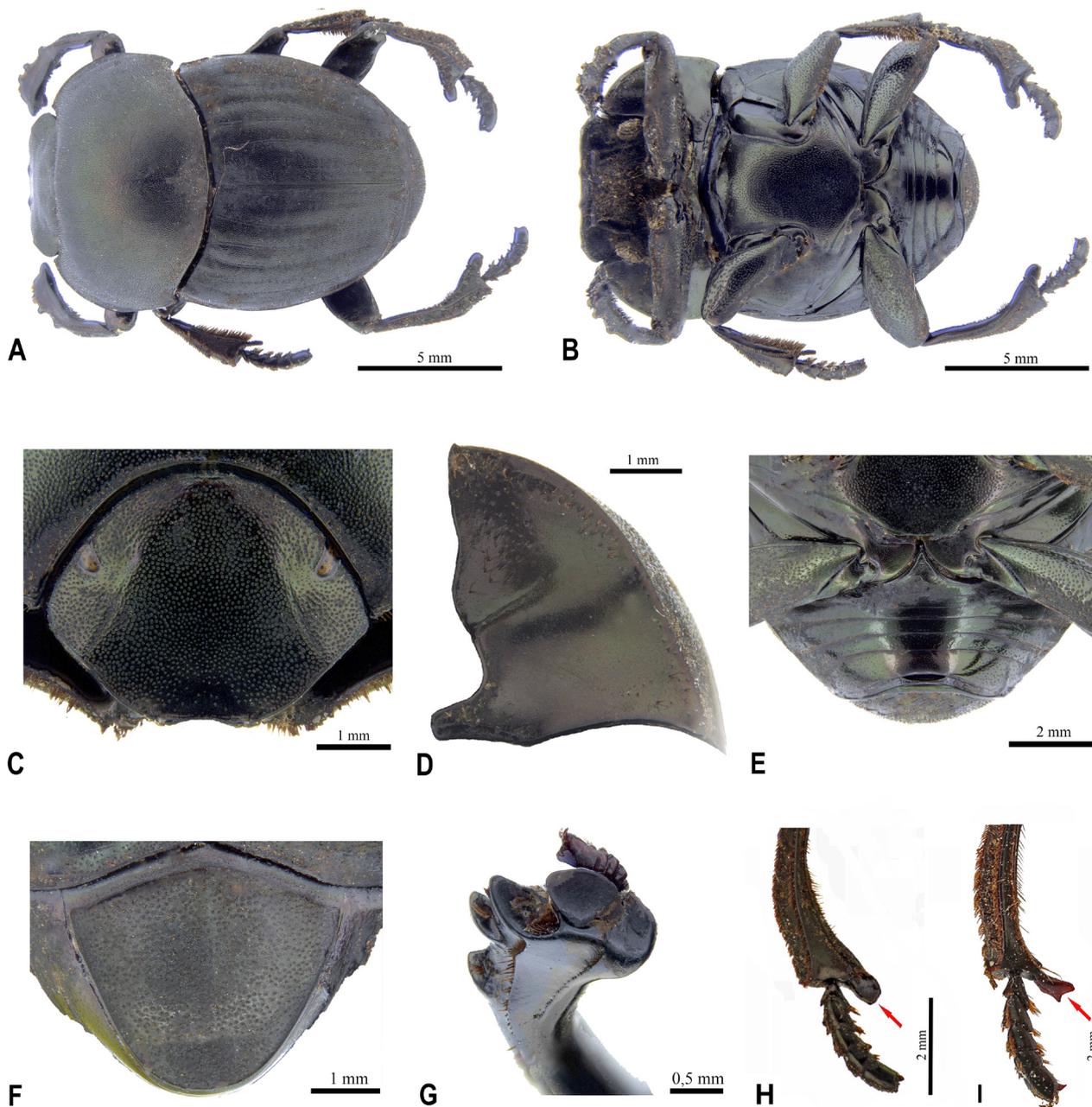
**Redescription. Colour and tegument sculpture** (Figs 1A–B). Body, in general, black. Head and pronotum with light copper or green sheen. Body surface densely punctate. **Length.** 15 mm. **Head** (Fig. 1C). Densely punctate. Foveiform punctures approximately equally spaced to their diameter; punctures around clypeal teeth shallower, more spaced and smaller. Clypeus with two widely spaced, small teeth. Surface slightly depressed behind clypeal teeth. Clypeo-genal suture visible. **Thorax.** Disc of pronotum with dense closely set foveiform punctures, approximately spaced by less than their diameter; punctures denser on posterocentral portion (Fig. 1A). Hypomera not excavate, with sparse setose punctures on anterior and posterolateral portions (Fig. 1D). Hypomera with oblique carina not reaching lateral margin; carina about half hypomeral width. Mesoventrite almost smooth, with sparse punctures. Metaventricle punctures variable in size, smaller and denser medially (Fig. 1B). **Elytra** (Fig. 1A). Punctures of elytral striae spaced by once or twice their diameter on 1st, 2nd and 3rd striae; punctures more spaced on lateral striae. Elytral striae wider, carinate margins clearly separated. Seventh stria effaced basally. Eighth and ninth striae almost fused, only visible on posterior half. Elytral interstriae with dense, close and foveiform punctures, generally spaced by less than their diameter. Pseudopleural carina complete, visible on entire length of epipleuron. **Abdomen** (Fig. 1E). Punctures denser on lateral surface of ventrites. Pygidium rounded apically, densely punctate, separated from propygidium by carina (Fig. 1F). Pygidium with sulcus on basal and apical edges (Fig. 1F). **Legs.** Metatibial spur spatulate, with lateral edges weakly sinuous; apex rounded, with inconspicuous inner denticle (Fig. 1H). First meso- and metatarsomeres triangular; tarsomeres 2–4 trapezoidal, apical tarsomere subrectangular (Fig. 1H). Tarsal claws reduced (Figs 1G–I). **Sexual dimorphism.** Females can be distinguished from males by last abdominal ventrite evenly wide. Last abdominal ventrite of males subtly narrower medially. Females with protibial spur slightly emarginate apically (bifurcate). Protibial spur of males wide and rounded, lacking denticle apically (Fig. 1G). Females with metatibial spur apically sinuous and bifurcate, with denticle (spiniform process) on internal and external edges (Fig. 1I). Males with metatibial spur rounded apically, inner denticle almost inconspicuous (Fig. 1H). Apical third of metatibiae almost straight in females (Fig. 1I), distinctly curved inward in males (Fig. 1H). **Aedeagus.** Parameres symmetrical, subparallel in lateral view, with abruptly pointing downward apically (Fig. 3C). Apex of parameres curved inward in dorsal and ventral views (Figs 3A–B). **Endophallus.** Lamella copulatrix absent. Superior right peripheral endophallite ring shaped; lateral projection arched, rounded apically (Fig. 3G). frontolateral peripheral endophallite elongate, irregular (Fig. 3I). Complex of axial and subaxial endophallites elongate, irregular (Fig. 3M). Additional endophallites short, comma shaped (Fig. 3K).

**Type material.** *Canthon diabolicus* Harold. **Lectotype** ♀ (**here designated**; MFNB) (Figs 4A–B): “HOLOTYPE // Bahia, / Sello // 9004 // Type // *diabolicus* / Har // SYNTYPUS / Canthon / diabolicus Harold, 1880 / labelled by MNHUB 2013”

**Additional material.** BRAZIL: BAHIA, no date and collector – 1 sex undetermined (BMNH – ex Fry collection); Ilhéus, 11.IX.1968, Guy V. Santos – 1 ♂ (CEMT).

**Habitat.** Most likely from Atlantic coastal rainforest. The type specimen of *D. diabolicus* was collected by the

Prussian naturalist Friedrich Sellow (1789–1831). He travelled through Brazil, Uruguay and Argentina between 1814 and 1831. We were able to check Sellow’s itinerary in Bahia (Papavero 1971, map 8). Therein, he only visited areas in the Atlantic coastal forest between Salvador and southern Bahia. Furthermore, the only specimen studied here with a precise locality was collected from Ilhéus, which is a coastal city located in southern Bahia. The predominant ecosystem surrounding the area is the Atlantic coastal forest, which hosts a high number of endemic species. In addition to this vegetation, there are areas of restinga (tropical rainforest close to coastal, sandy areas) and mangroves on the coastal line, and large cocoa-growing areas planted among the natural Atlantic rainforest (Cabruca = ecological system of cultivation agroforestry). The specimen might have been collected from any of these different habitats.



**FIGURE 1.** Details of the external morphology of *Deltepilissus diabolicus*. **A**, Body, male, dorsal view; **B**, body, male, ventral view; **C**, head, male; **D**, hypomeron, male; **E**, abdominal ventrites, male; **F**, pygidium, male; **G**, detail of protibial spur, male; **H–I**, left metatibia, ventral view, male and female, respectively (arrows indicate apex of metatibial spur).

**Distribution.** Known only from Brazil (Bahia). **Literature records. BRAZIL:** Bahia (Harold 1880) (Fig. 5).

**Conservation status.** Based on available data, this species seems to be endemic to the state of Bahia, Brazil. The last known record for this species was from Ilhéus in 1968. Therefore, we do not have information about the

conservation status of populations of this species. We know at least two cases of apparently rare species along the range of the two species of *Deltepilissus* (southern Bahia and Espírito Santo) that when the number of collectors in the area increased, a great number of specimens have been collected. These cases can be verified with *Streblopus opatroides* Van Lansberge, 1874 (Cupello *et al.* 2020) and some species of *Aphengium* Harold, 1868 (Silva & Vaz-de-Mello 2015). However, despite many collecting efforts with pitfalls and/or flight interception traps in Atlantic rainforest remnants throughout that region and neighboring areas (F. Silva and F. Vaz-de-Mello, personal communication) no specimens of *D. diabolicus* have been recently collected. The rarity of *D. diabolicus* in natural history collections can be due to its unknown natural history and/or some unusual ecological specialization. The baits used for collecting – usually, human feces – might not be attractive for this species. Even so, flight interception traps would have likely collected specimens were the populations substantial, suggesting that population densities are indeed quite low or that the specimens flying higher in the canopy.

Based on its supposed endemism, the extent of occurrence of this species is being estimated as up to 100 km<sup>2</sup>, with large surrounding areas of unsuitable habitat. The Atlantic rainforest is probably the most extinction-prone ecosystem of Brazil. Its ecosystems have been suffering intense degradation early during European colonization. The major threats for the southern Bahia region are urbanization (residential and industrial development), illegal wood exploitation, and impacts associated with tourism (Vieira *et al.* 2011; Silva *et al.* 2020). Therefore, we evaluated this species using the International Union for Conservation of Nature (2012) criteria and found that it could be assessed as Critically Endangered (CR) under criterion B1ab(iii)+B2ab(iii), mainly due to high fragmentation and destruction of the Atlantic rainforest, and its apparent restricted distributional range, and also due to the low number of individuals historically collected. Sellow died in 1831 (Papavero 1971), therefore the specimen studied by Harold was certainly collected at least 190 years ago, and after that date few specimens were recorded.

### ***Deltepilissus infernalis* (Harold, 1880)**

(Figs 2A–L, 3D–F, 3H, 3J, 3L, 3N, 4C–H, 5A–B)

*Canthon infernalis* Harold, 1880: 150 (original description); Gillet 1911: 30 (catalog); Schmidt 1922: 62, 73 (taxonomic remarks, distribution); Balthasar 1939: 181 (identification key); Blackwelder 1944: 199 (checklist).

*Deltepilissus travassosi* Pereira, 1949: 231, 232, fig. 1 (original description); Pereira 1953: 393 (synonymized *Deltepilissus travassosi* with *Canthon infernalis*).

*Deltepilissus infernalis*: Pereira 1953: 393 (distribution; transferred *C. infernalis* to the genus *Deltepilissus*); Pereira & Martínez 1956: 125 (catalog); Vulcano & Pereira 1964: 660 (catalog); Halfpeter & Martínez 1977: 66 (checklist); Vaz-de-Mello 2000: 192 (checklist); Krajcik 2006: 47 (checklist); Vaz-de-Mello *et al.* 2011: 55, fig. 59 (figure); Krajcik 2012: 88 (checklist); Schoolmeesters 2020 (catalog); Vaz-de-Mello 2021 (checklist).

**Diagnosis.** *Deltepilissus infernalis* can be distinguished from *D. diabolicus* by head approximately 1.4 times wider than long (Fig. 2E); punctures of central portion of pronotum spaced by at least twice their diameter (Figs 2A, 2C); body length 9–11 mm; males with denticle on external edge of protibial spur (Fig. 2I), and a conspicuous denticle on inner edge of metatibial spur (Fig. 2K); apex of parameres slightly curved inward in dorsal and ventral views (Figs 3D–E).

**Redescription. Colour and tegument sculpture** (Figs 2A–D). Body, in general, black. Head and pronotum with light copper or blue sheen. Body surface densely punctate. **Length.** 9–11 mm. **Head** (Fig. 2E). Densely punctate. Foveiform punctures approximately equally spaced to their diameter; punctures shallower, more spaced and smaller adjacent to clypeal teeth. Clypeus with two widely spaced, small teeth. Surface slightly depressed behind to clypeal teeth. Clypeo-genal suture visible. **Thorax.** Disc of pronotum with dense foveiform punctures spaced by at least twice their diameter; punctures denser on postero-central portion (Figs 2A, 2C). Hypomera not excavate, with sparse setose punctures on anterior and posterolateral portions (Fig. 2F). Hypomera with oblique carina not reaching lateral margin; carina about half hypomeral width. Mesoventrite almost smooth, with sparse punctures. Metaventrite punctures variable in size, smaller and denser medially (Figs 2B–D). **Elytra** (Fig. 2A, 2C). Punctures of elytral striae spaced by once or twice their diameter on 1st, 2nd and 3rd striae; punctures more spaced on lateral striae. Elytral striae wider, carinate margins clearly separated. Seventh stria effaced basally. Eighth and ninth striae almost fused, only visible on posterior half. Elytral interstriae with foveiform punctures spaced at least by once or twice their diameter. Pseudepipleuron complete, visible on entire length of epipleuron. **Abdomen** (Fig. 2G). Punctures denser on lateral surface of ventrites. Pygidium rounded apically, densely punctate, separated from propygidium

by carina (Fig. 2H). Pygidium with sulcus on basal and apical edges. **Legs.** Metatibial spur spatulate; apex acutely angular on inner edge (Fig. 2K). First meso- and metatarsomeres triangular; tarsomeres 2–4 trapezoidal, the apical subrectangular (Fig. 2K–L). Tarsal claws reduced (Figs 2I–L). **Sexual dimorphism.** Females can be distinguished from males by last abdominal ventrite evenly wide (Fig. 2D); last abdominal ventrite of males slightly narrower medially (Fig. 2G). Females with protibial spur slightly emarginated apically (bifurcate), with a denticle (spiniform process) on inner and external edges (Fig. 2J); protibial spur of males with denticle on external edge only (Fig. 2I). Females with metatibial spur apically sinuous and bifurcate, inner and external edges with denticles (Fig. 2L); males only with a conspicuous denticle on apical inner edge of metatibial spur (Fig. 2K). Apical third of metatibiae almost straight in females (Fig. 2L), distinctly curved inward in males (Fig. 2K). **Aedeagus.** Parameres symmetrical, subparallel in lateral view, abruptly pointing downward apically (Fig. 3F). Apex of parameres curved inward in dorsal and ventral views (Figs 3D–E). **Endophallus.** Lamella copulatrix absent. Superior right peripheral endophallite ring shaped; lateral projection arched, rounded apically (Fig. 3H). Frontolateral peripheral endophallite elongate, irregular (Fig. 3J). Complex of axial and subaxial endophallites elongate, irregular (Fig. 3N). Additional endophallites short, comma shaped (Fig. 3L).

**Type material.** *Canthon infernalis* Harold. **Lectotype** ♂ (here designated; MFNB) (Figs 4C–D): ‘HOLOTYPE // *Brasil Besuxe* // 9005 // Type // *infernalis* / *Har* // SYNTYPUS / *Canthon* / *infernalis* Harold, 1880 / labelled by MNHUB 2013. *Deltepilissus travassosi* Pereira. **Holotype** ♂ (MZSP) (Figs 4E–H): Rio de Janeiro, Paineiras, IV-1934, Dr. L. Travassos.

**Additional material.** BRAZIL: no specific locality [Brasil – inter], no date and collector, – 1 unsexed specimen (BMNH). ESPÍRITO SANTO, Mimoso do Sul, 05.IX.1986, R.L.C. Baptista – 1 ♀ (CEMT). RIO DE JANEIRO, no date and collector – 1 unsexed specimen (BMNH – ex Fry collection); Itaguaí, Serra da Caveira, 800 m, 25.II.1948, W. Zikán – 1 unsexed specimen (MNRJ); Itaguaí, Serra da Caveira, 600 m, 25.II.1948, W. Zikán – 1 ♀ (CEMT); Nova Friburgo, XII.1999, E. & P. Grossi – 1 ♀ (CEMT); Nova Friburgo, XII.1999, E. & P. Grossi – 1 unsexed specimen (CERPE); Rio de Janeiro, Jacarepaguá, 1956, no collector – 1 ♂ (CMNC – ex. H. & A. Howden collection, ex. A. Martínez collection). SÃO PAULO, Guarujá, Forte dos Andradas, XII.1971, Ayr Bello – 1 ♂ (AMBC).

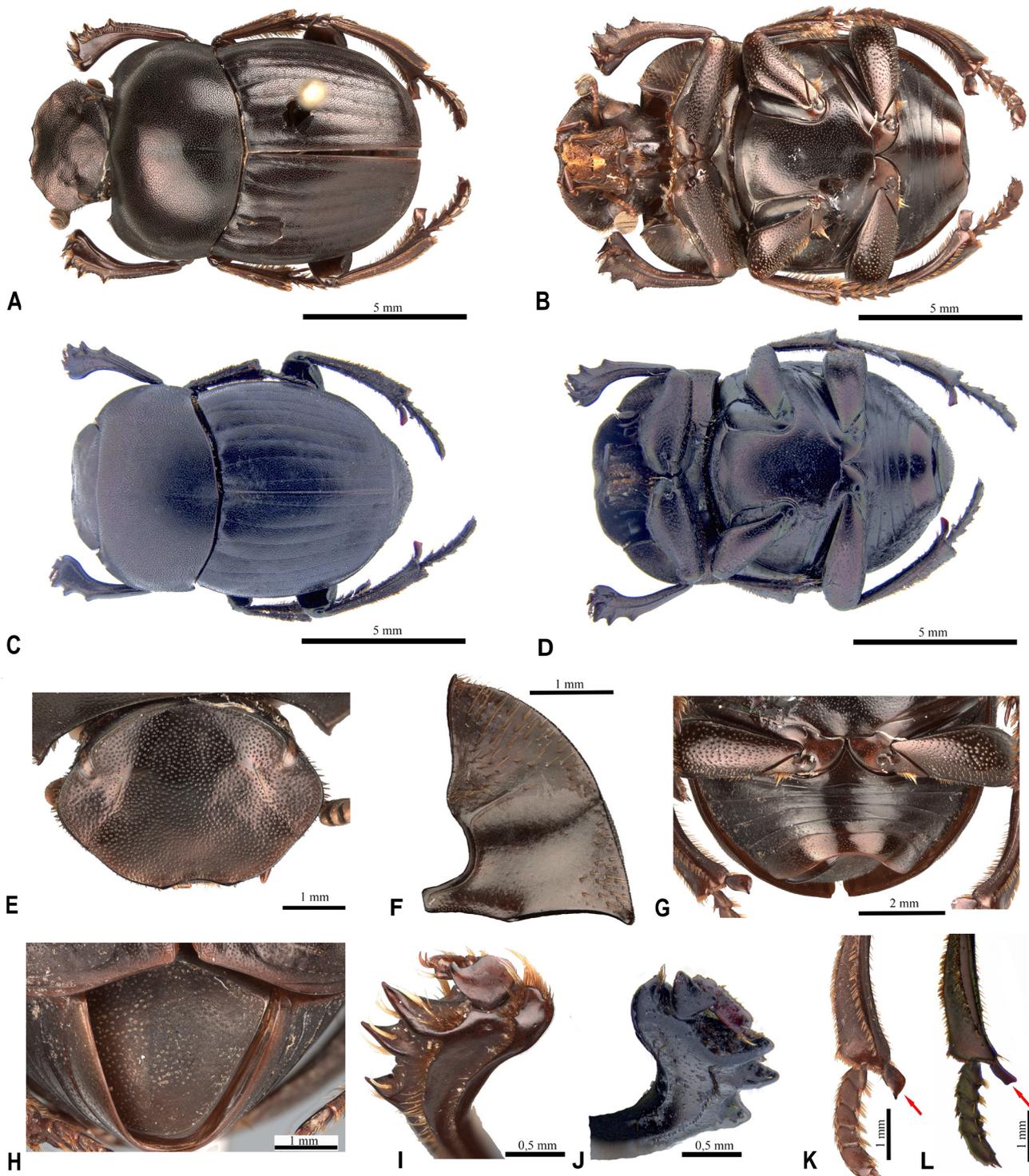
**Habitat.** This species inhabits the Brazilian Atlantic rainforest from southern Espírito Santo to São Paulo states, mainly at low elevation along the coastal parts of the Atlantic rainforest, from 0–800 m. A single specimen was collected by Renner Baptista in a soil block (manure and roots) dug up in a cattle ranch in Espírito Santo, Brazil. A specimen was also collected within debris (leaves, seaweed, broken shells, insects and some plastic garbage) deposited on beach sand in Guarujá, São Paulo, Brazil (Ayr Bello, personal communication). All those records were made from manual collect method. However, the data presented above are not enough to define the food habits of *D. infernalis*. As already mentioned for *D. diabolicus*, the baits traditionally used for collecting dung beetles did not attract *D. infernalis*.

**Distribution.** Known from southeastern Brazil (Espírito Santo, Rio de Janeiro and São Paulo). **Literature records.** BRAZIL: RIO DE JANEIRO, Itaguaí (Pereira 1953), Rio de Janeiro [Paineiras] (Pereira 1949, 1953), Rio de Janeiro [cited as “Guanabara”, the state-level name by which the city was known between 1960 and 1975] (Vulcano & Pereira 1964) (Fig. 5).

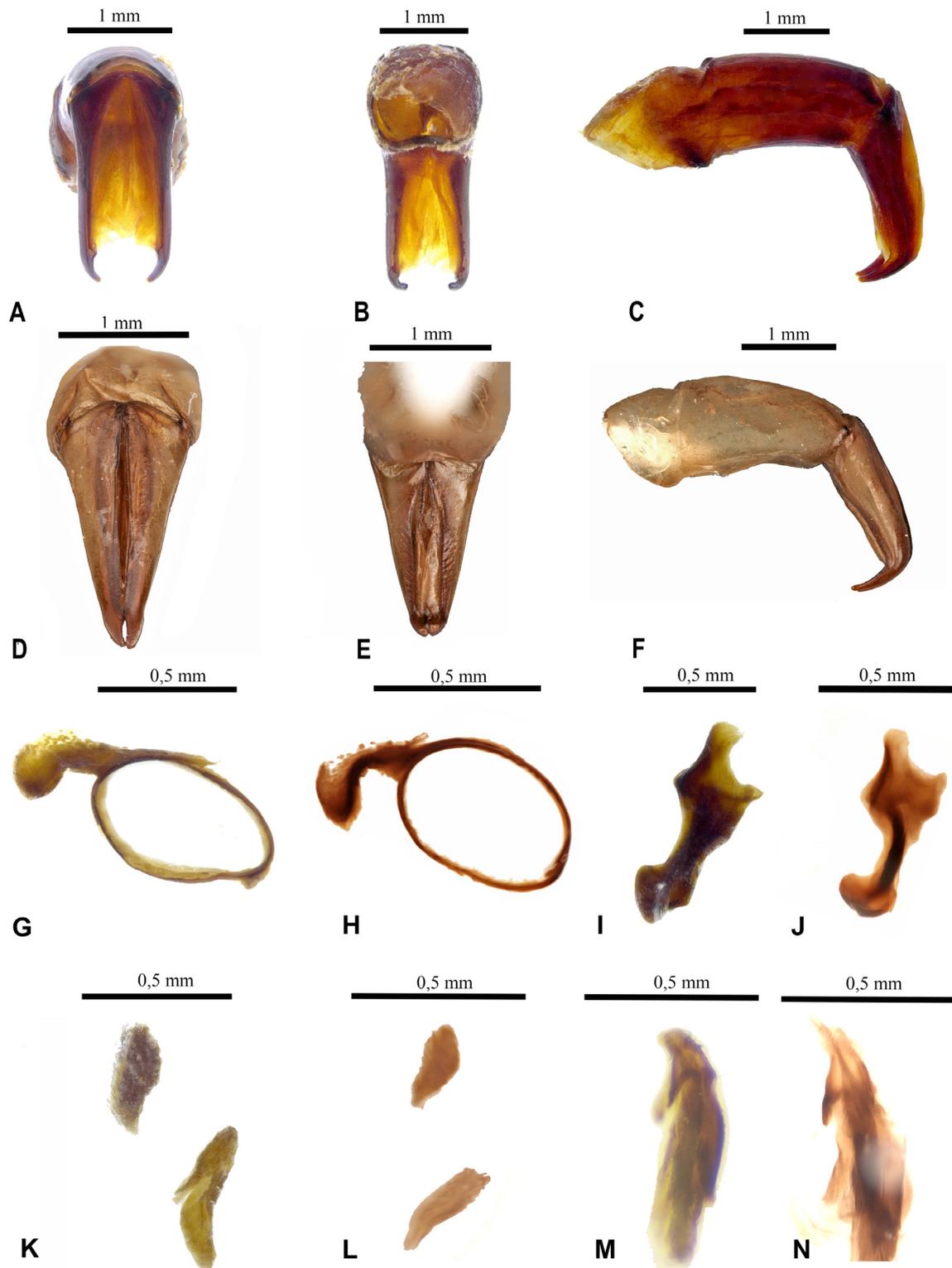
**Remarks.** Harold (1880) described *Canthon infernalis* from one or more specimens collected by von Olfers, a German naturalist, in Brazil. A type specimen was found and photographed by Fernando Vaz-de-Mello in MFNB (see material and methods section). Pereira (1949) described *Deltepilissus travassosi* on a specimen from Rio de Janeiro, Brazil [holotype from Parque Nacional da Tijuca, Paineiras, Rio de Janeiro, Brazil; housed in MZSP]. Later, Pereira (1953) considered *D. travassosi* a junior subjective synonym of *Canthon infernalis* and transferred the latter to the genus *Deltepilissus*. In this study, we examined the holotype of *D. travassosi* and compared it with the photographs of the type of *Canthon infernalis*, and we did not find significant differences in their external morphology. Unfortunately, we could not examine the genitalia of the holotype of *D. travassosi*, as the current policies of the MZSP do not allow the dissection of name-bearing type specimens (*i.e.*, holotypes, lectotypes) if there are no other available types in that collection (*i.e.*, paratypes, paralectotypes). However, because *D. travassosi* Pereira was synonymized with *Canthon infernalis* Harold by its author (Pereira 1953), we agree with Pereira (1953) to consider *D. travassosi* as synonym of *D. infernalis*.

**Conservation status.** Over the past 25 years, the several collecting events in Atlantic rainforest remnants yielded only two specimens of *D. infernalis* (see “additional material”). Other known records for this species are older, with specimens collected between the early 19<sup>th</sup> century (1818–1819 by von Olfers, see Papavero 1971) and the 1980s.

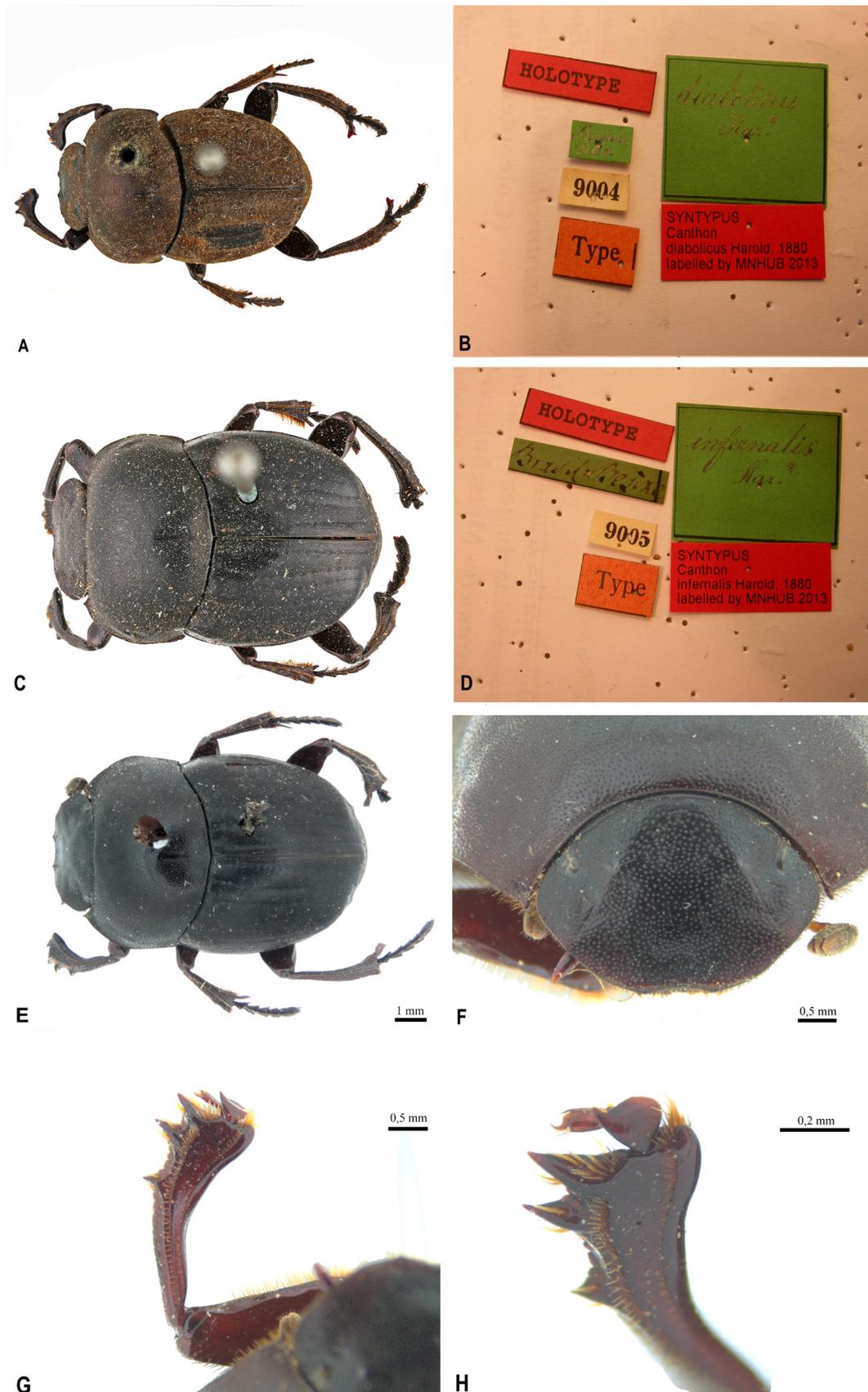
The extent of occurrence of this species was estimated as up to 100 km<sup>2</sup>, with large surrounding areas of unsuitable habitat in southeastern Brazil. According to the International Union for Conservation of Nature (2012) criteria, *D. infernalis* may be assessed as Critically Endangered (CR) under criterion B1ab(iii)+B2ab(iii), mainly due to high fragmentation and destruction of the Atlantic rainforest and low number of specimens collected over more than 140 years since its description.



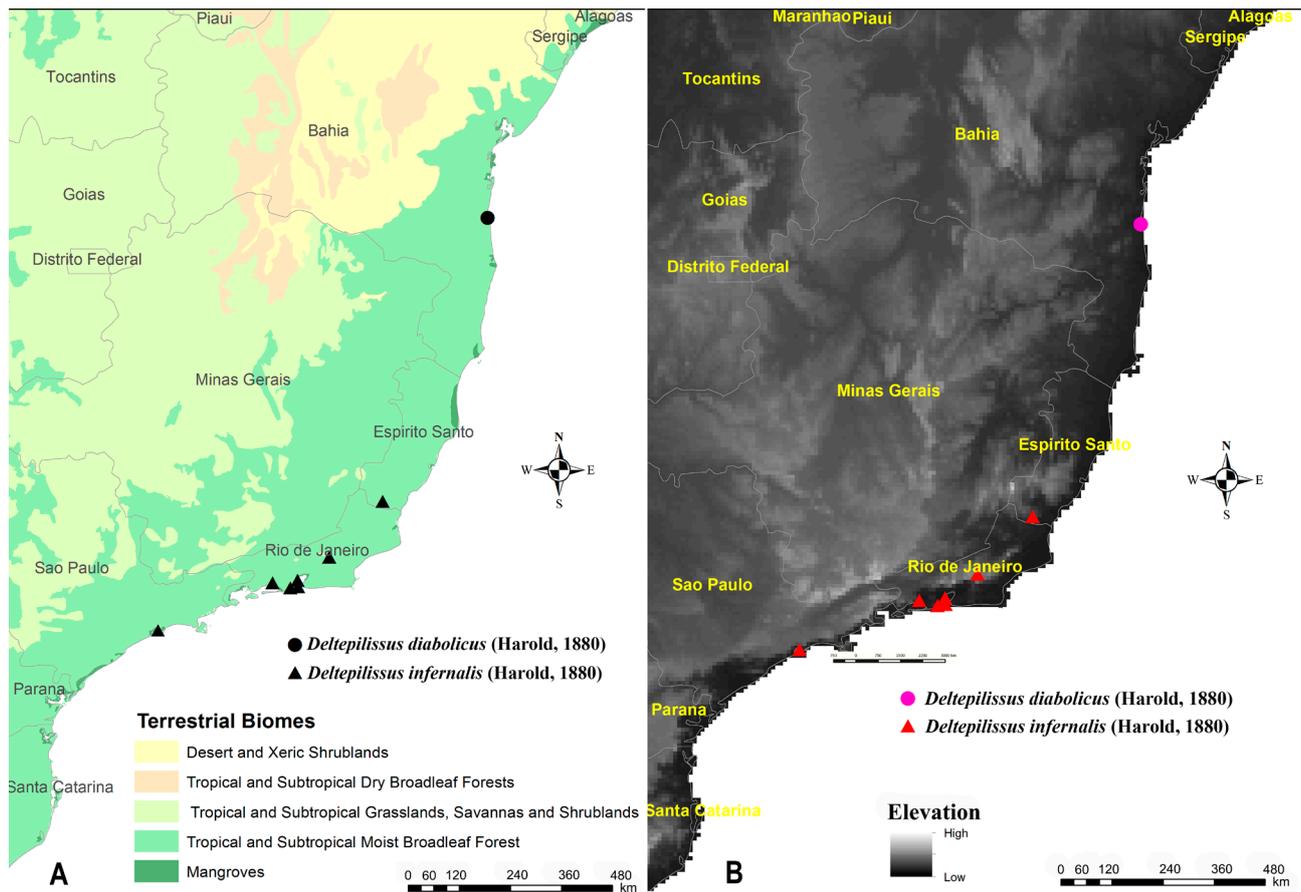
**FIGURE 2.** Details of the external morphology of *Deltepilissus infernalis*. A–B, Body, male, dorsal and ventral views, respectively; C–D, body, female, dorsal and ventral views, respectively; E, head, male; F, hypomeron, male; G, abdominal ventrites, male; H, pygidium, male; I–J, detail of protibial spur, male and female, respectively; K–L, right metatibia, ventral view, male and female, respectively (arrows indicate apex of metatibial spur).



**FIGURE 3.** Details of the male genitalia in *Deltepilissus*. **A–C**, *Deltepilissus diabolicus*: **A**, parameres, dorsal view; **B**, parameres, ventral view; **C**, aedeagus, lateral view. **D–F**, *Deltepilissus infernalis*: **D**, parameres, dorsal view; **E**, parameres, ventral view; **F**, aedeagus, lateral view. **G**, *Deltepilissus diabolicus* superior right peripheral (SRP) endophallite. **H**, *Deltepilissus infernalis* superior right peripheral (SRP) endophallite. **I**, *Deltepilissus diabolicus* frontolateral peripheral (FLP) endophallite. **J**, *Deltepilissus infernalis* frontolateral peripheral (FLP) endophallite. **K**, *Deltepilissus diabolicus* additional endophallites (AE). **L**, *Deltepilissus infernalis* additional endophallites (AE). **M**, *Deltepilissus diabolicus* complex of axial and subaxial (A+SA) endophallites. **N**, *Deltepilissus infernalis* complex of axial and subaxial (A+SA) endophallites.



**FIGURE 4.** Type specimens in *Deltepilissus* and respective label data. **A–B**, Lectotype of *Canthon diabolicus* Harold, 1880: **A**, body, dorsal view; **B**, labels. **C–D**, Lectotype of *Canthon infernalis* Harold, 1880: **C**, body, dorsal view; **D**, labels. **E–H**, holotype of *Deltepilissus travassosi* Pereira, 1949: **E**, body, dorsal view; **F**, head; **G**, left protibia, dorsal view; **H**, protibial and tarsal claws. Photographs A–D provided by Fernando Z. Vaz-de-Mello.



**FIGURE 5.** Known distribution of species of *Deltepilissus*. **A**, Records plotted on terrestrial biomes layer; **B**, records plotted on elevational range layer.

## Acknowledgements

We thank Fernando Z. Vaz-de-Mello for kindly allowing us to access and reproduce his photographs of the type specimens of *Deltepilissus* housed in the MFNB and for the loan of the CEMT specimens. We also thank the other curators and collection managers mentioned in the Material section for granting us access to material under their care, and Mario Cupello for providing the label data of the now-destroyed MNRJ specimen and tips on the BMNH specimens. Mario Cupello and other anonymous referee provided thoughtful comments that helped improve the manuscript. CAPES/Pro-equipments provided the photographic equipment used in this work, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided research grants for Fernando Silva (444020/2014-4). Fernando Silva is a CNPq fellow.

## References cited

- Balthasar, V. (1939) Eine Vorstudie Zur Monographie der Gattung *Canthon* Hffsg. *Folia Zoologica et Hydrobiologica*, 9, 179–238.
- Blackwelder, R. (1944) Checklist of the coleopterous insects of Mexico, Central America, the West Indies and South America. Part 2. *Bulletin of the United States National Museum*, 185, 189–341. <https://doi.org/10.5479/si.03629236.185.2>
- Cupello, M. (2020) The discovery of Edgar von Harold type material in the Museum of Zoology, Dresden. *Scarabaeus*, 1, 15–24.
- Cupello, M. (2021) Addenda and corrigenda to ‘The discovery of Edgar von Harold type material in the Museum of Zoology, Dresden’. *Scarabaeus*, 2, 18–25.

- Cupello, M. & Vaz-de-Mello, F. (2018) A monographic revision of the Neotropical dung beetle genus *Sylvicanthon* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltophilini), including a reappraisal of the taxonomic history of 'Canthon sensu lato'. *European Journal of Taxonomy*, 467, 1–205.  
<https://doi.org/10.5852/ejt.2018.467>
- Cupello, M., Ribeiro-Costa, C.S. & Vaz-de-Mello, F.Z. (2020) Systematics of the enigmatic South American *Streblopus* Van Lansberge, 1874 dung beetles and their transatlantic origin: a case study on the role of dispersal events in the biogeographical history of the Scarabaeinae (Coleoptera: Scarabaeidae). *European Journal of Taxonomy*, 603, 1–85.  
<https://doi.org/10.5852/ejt.2020.603>
- Génier, F. (2010) A review of the Neotropical dung beetle genera *Deltorhinum* Harold, 1869, and *Lobidion* gen. nov. (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 2693 (1), 35–48.  
<https://doi.org/10.11646/zootaxa.2693.1.3>
- Génier, F. (2019) Endophallites: a proposed neologism for naming the sclerotized elements of the insect endophallus (Arthropoda: Insecta). *Annales de la Société entomologique de France*, 55, 482–484.  
<https://doi.org/10.1080/00379271.2019.1685907>
- Gillet, J.J.E. (1911) *Coleopterorum Catalogus. Pars 38: Scarabaeidae: Coprinae I*. W. Junk, Berlin, Germany, 100 pp.
- Halffter, G. (1961) Monografía de las especies norteamericanas del género *Canthon* Hoffsg. (Coleopt., Scarab.). *Ciencia*, 20, 225–320.
- Halffter, G. & Edmonds, W.D. (1982) *The Nesting Behavior of Dung Beetles (Scarabaeinae): an Ecological and Evolutionary Approach*. Instituto de Ecología, Mexico City, Mexico, 176 pp.
- Halffter, G. & Martínez, A. (1977) Revisión monográfica de los Canthonina Americanos, IV parte. Clave para géneros y subgéneros. *Folia Entomológica Mexicana*, 38, 29–107.
- Halffter, G. & Matthews, E.G. (1966). The natural history of dung beetles of the subfamily Scarabaeinae. *Folia Entomológica Mexicana*, 12–14, 1–312.
- Harold, E. (1880) Einige Neue Coleopteren. *Mitteilungen des Münchener Entomologischen Vereins*, 4, 148–171.
- International Commission on Zoological Nomenclature. (1999) *International Code of Zoological Nomenclature. 4th Edition*. International Commission on Zoological Nomenclature, The Natural History Museum, London, United Kingdom, 306 pp.
- International Union for Conservation of Nature (2012) *IUCN Red List Categories and Criteria: Version 3.1. 2nd Edition*. International Union for Conservation of Nature, Gland, Switzerland, iv + 32 pp.
- Krajcik, M. (2006) Checklist of Scarabeoidea of the World. 1. Scarabaeinae (Coleoptera: Scarabaeidae: Scarabaeinae). *Animma. X*, Supplement 3, 1–189.
- Krajcik, M. (2012) Checklist of the World Scarabaeoidea. *Animma.X*. Supplement 5, 1–278.
- Papavero, N. (1971) *Essays on the history of Neotropical dipterology: with special reference to collectors: 1750–1905: Volume I*. Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil, 216 pp.  
<https://doi.org/10.5962/bhl.title.101715>
- Pereira, F. (1949) Escarabeídeos americanos II (Coleopt.-Scarabaeidae). *Arquivos do Museu Paranaense*, 7, 231–246.
- Pereira, F. (1953) Notas sinonímicas (Col. Scarabaeidae). *Dusenía*, 4, 387–402.
- Pereira, F. & Martínez, A. (1956) Os gêneros de Canthonini americanos. *Revista Brasileira de Entomologia*, 6, 91–192.
- Ribeiro, M.C, Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, 142, 1141–1153.  
<https://doi.org/10.1016/j.biocon.2009.02.021>
- Schmidt, A. (1922) 1. Bestimmungstabelle der mir bekannten *Canthon*-Arten. 2. Verbreitungsgebiete der *Canthon*-Arten. 3. Neubeschreibungen von *Canthon*, *Saprositis*, *Mendidius*, *Euparia* und *Ataenius*. *Archiv für Naturgeschichte Abteilung A*, 88 (3), 61–103.
- Schoolmeesters, P. (2020) Scarabs: world Scarabaeidae database (version 2019-11-02). In: Roskov Y. et al., (Eds.), *Species 2000 & ITIS Catalogue of Life, 2020-02-24*. ISSN 2405-8858. Species 2000: Naturalis, Leiden, the Netherlands. Available from: <http://www.catalogueoflife.org/col> (accessed 12 January 2022)
- Silva, F.A.B & Vaz-de-Mello, F. (2015) A revision of the genus *Aphengium* Harold, 1868 (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini). *Zootaxa*, 3955 (4), 505–520.  
<https://doi.org/10.11646/zootaxa.3955.4.3>
- Silva, F.A.B., Moura, A.B.G., Araújo, J.F. & Moura, R.C. (2020) Brazilian Atlantic rainforest endangered biodiversity: a new species of the *Dichotomius sericeus* (Harold, 1867) species group (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa*, 4834 (3), 434–442.  
<https://doi.org/10.11646/zootaxa.4834.3.6>
- Tarasov, S. & Dimitrov, D. (2016) Multigene phylogenetic analysis redefines dung beetles relationships and classification (Coleoptera: Scarabaeidae: Scarabaeinae). *BMC Evolutionary Biology*, 16 (257), 1–19.  
<https://doi.org/10.1186/s12862-016-0822-x>
- Tarasov, S. & Génier, F. (2015) Innovative Bayesian and parsimony phylogeny of dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) enhanced by ontology-based partitioning of morphological characters. *PLoS One*, 10, 1–86. <https://doi.org/10.1371/journal.pone.0116671>
- Tarasov, S. & Solodovnikov, A. (2011) Phylogenetic analyses reveal reliable morphological markers to classify mega-diversity

- in Onthophagini dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Cladistics*, 27, 490–528.  
<https://doi.org/10.1111/j.1096-0031.2011.00351.x>
- Vaz-de-Mello, F. (2000) Estado atual de conhecimento dos Scarabaeinae s. str. (Coleoptera: Scarabeoidea) do Brasil. In: Martín-Piera, F., Morrone, J. & Melic, A. (Eds.), *Hacia un Proyecto CYTED para el inventario Y Estimación de la Diversidad Entomológica en Iberoamérica: PrIBES-2000*. Monografías Tercer Milenio & Sociedad Entomológica Aragonesa, Zaragoza, Spain, pp. 183–195.
- Vaz-de-Mello, F. (2021) Scarabaeinae. In: Catálogo Taxonômico da Fauna do Brasil. Available from: <http://fauna.jbrj.gov.br/fauna/faunadobrasil/127498> (accessed 5 March 2021)
- Vaz-de-Mello, F., Edmonds, W., Ocampo, F. & Schoolmeesters, P. (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa*, 2854 (1), 1–73.  
<https://doi.org/10.11646/zootaxa.2854.1.1>
- Vaz-de-Mello, F., Nunes, L.G.O.A. & Costa-Silva, V. (2020) A new species of the genus *Canthon* Hoffmannsegg (Coleoptera, Scarabaeidae, Scarabaeinae, Deltochilini) from central Brazil. *Papeis Avulsos de Zoologia*, 60, 1–6.  
<https://doi.org/10.11606/1807-0205/2020.60.special-issue.04>
- Vieira, L., Louzada, J.N.C. & Spector, S. (2008) Effects of degradation and replacement of southern Brazilian coastal sandy vegetation on the dung beetles (Coleoptera: Scarabaeidae). *Biotropica*, 40, 719–727.  
<https://doi.org/10.1111/j.1744-7429.2008.00432.x>
- Vieira, L., Louzada, J., Vaz-de-Mello, F.Z., Lopes, P.P. & Silva, F.A.B. (2011) New records, threatens and conservation status for *Dichotomius schiffleri* Vaz-de-Mello, Louzada & Gavino (Coleoptera: Scarabaeidae): an endangered dung beetle species from Brazilian atlantic forest ecosystems. *Neotropical Entomology*, 40, 282–284.  
<https://doi.org/10.1590/S1519-566X2011000200020>
- Vulcano, M.A. & Pereira, F. (1964) Catalogue of the Canthonini (Col. Scarab.) inhabiting the Western Hemisphere. *Entomologische Arbeiten aus dem Museum G. Frey*, 15, 570–685.
- Wägele, J. (2005) *Foundations of phylogenetic systematics*. Dr. Friederich Pfeil, Munich, Germany, 365 pp.
- Zunino, M. (1978) L'armatura genitale negli Onthophagini: tecniche di preparazione e criteri di studio. *Bollettino della Società Entomologica Italiana*, 90, 21–26.