



# New records of relictual populations of dung beetle species (Coleoptera, Scarabaeidae) in the Atlantic Forest of the Brazilian Northeast

Josival Francisco Araújo<sup>1</sup>, Fernando Augusto Barbosa Silva<sup>2</sup>, Rita de Cássia de Moura<sup>1</sup>

**1** Universidade de Pernambuco, Instituto de Ciências Biológicas, Campus Santo Amaro, Laboratório de Biodiversidade e Genética de Insetos, Rua Arnóbio Marquês 310, Santo Amaro, CEP 50.100-130, Recife, PE, Brazil. **2** Universidade Federal do Pará, Instituto de Ciências Biológicas, Campus Belém, Rua Augusto Corrêa 01, Guamá, CEP 66.075-110, Belém, PA, Brazil.

**Corresponding author:** Josival F. Araújo, [araujojosi.f@gmail.com](mailto:araujojosi.f@gmail.com)

## Abstract

The diversity of dung beetles is still underestimated in northeastern Brazil. Recent collections have revealed new records of the following species: *Canthon histrio* (Lepeletier de Saint-Fargeau & Audinet-Serville, 1828), *Coprophanæus acrisius* (MacLeay, 1819), *Coprophanæus dardanus* (MacLeay, 1819), *Deltochilum alpercata* Silva et al., 2015, *Deltochilum brasiliense* (Castelnau, 1840), *Dichotomius gilletti* Valois et al., 2017, *Dichotomius iannuzziae* Valois et al., 2017, *Eurysternus calligrammus* Dalman, 1824, *Eurysternus parallelus* Castelnau, 1840, *Oxysternon silenus* Castelnau, 1840, and *Phanaeus splendidulus* (Fabricius, 1781). These records are discussed in light of the known biogeography of each species.

## Keywords

Faunistic inventories, geographical distribution, Scarabaeinae, species conservation.

**Academic editor:** Rafael Benzi Braga | Received 12 March 2020 | Accepted 13 September 2020 | Published 29 September 2020

**Citation:** Araújo JF, Silva FAB, Moura RC (2020) New records of relictual populations of dung beetle species (Coleoptera, Scarabaeidae) in the Atlantic Forest of the Brazilian Northeast. Check List 16 (5): 1289–1303. <https://doi.org/10.15560/16.5.1289>

## Introduction

The Atlantic Forest shelters distinct fauna and flora in comparison with other biomes (Rodrigues et al. 2004; Santos et al. 2007; Morrone 2014). However, the distribution of this biodiversity along the Atlantic Forest is not homogeneous. This biome encompasses regional endemisms and different physiognomies, which represent distinct biogeographical units (Silva et al. 2012b; Morrone 2014). The Atlantic Forest present in northeastern Brazil is mainly composed of isolated patches of lowland forests along the coast (Dense Ombrophilous Forest, Open Ombrophilous Forest), forest enclaves in the

Brazilian semiarid (Submontane Seasonal Semideciduous Forest, Montane Seasonal Semideciduous Forest), and associated ecosystems, such as mangroves and restingas (IBGE 1985).

This biome is widely threatened along the Northeast region, with its remaining 2.21% area reduced to small, isolated fragments, some smaller than 10 ha (Tabarelli et al. 2006). In addition, some parts of this biome are considered a refuge of the Late Quaternary, whose fauna and flora were influenced by the South American and Amazonian forests (Andrade-Lima 1960, 1982; Prance 1982).

For example, the altitudinal Atlantic Forests are “islands” of humid forest on plateaus in the semiarid region, surrounded by Caatinga vegetation (Andrade-Lima 1982). According to Andrade-Lima (1982), these ecosystems would be transitory corridors that promoted biodiversity interchange between the Amazon and the Atlantic Forest under favorable environmental conditions.

The beetles of the subfamily Scarabaeinae, commonly known as dung beetles, comprise approximately 6,200 valid species grouped into 267 genera (Tarasov and Génier 2015). In Brazil, 64 genera and 728 species have been documented so far, with 64 species being endemic (González-Alvarado et al. 2019; Pacheco and Vaz-de-Mello 2019; Vaz-de-Mello 2020). Among all terrestrial ecosystems, tropical forests contain the greatest diversity of these beetles, and are some of the biomes most threatened by anthropic activities such as fragmentation, defaunation, logging and agricultural expansion (Halffter and Favila 1993; Foley et al. 2005; Dirzo et al. 2014). Owing to their sensitivity to the destruction and loss of their habitat, scarabs are considered parameters to analyze, inventory and monitor the biodiversity in tropical forests (Halffter and Favila 1993).

The diversity of the subfamily Scarabaeinae is still underestimated in northeastern Brazil. Until the year 2000, 137 species had been recorded for this region (Vaz-de-Mello 2000). Since then, 26 studies have been published reporting data on this group from the region (Hernández 2003, 2005, 2007; Lopes et al. 2003, 2006; Endres et al. 2007; Silva et al. 2007, 2010; Costa et al. 2009, 2013, 2014; Gillett et al. 2010; Silva 2011; Filgueiras et al. 2011a, 2011b; Liberal et al. 2011; Vieira and Silva 2012; Lima et al. 2013; Mayer and Vasconcelos 2013; Medina and Lopes 2014; Filgueiras 2015; Pergentino 2015; Salomão and Iannuzzi 2015; Vieira et al. 2017; Leite et al. 2018; Salomão et al. 2019). However, the lack of modern taxonomic studies for some genera and species groups holds back the understanding about dung beetle diversity in this region. In addition, there are some genera with many species still to be described.

Fortunately, recent taxonomic reviews have allowed an accurate identification of several species belonging to the following genera addressed in the present work: *Canthon* Hoffmannsegg, 1817 (Nunes et al. 2018, 2020; Vieira et al. 2019; Vaz-de-Mello et al. 2020), *Coprophanæus* d’Olsoufieff, 1924 (Edmonds and Zidek 2010), *Deltochilum* Eschscholtz, 1822 (Génier 2012; González-Alvarado and Vaz-de-Mello 2014; Silva et al. 2015), *Dichotomius* Hope, 1838 (Nunes and Vaz-de-Mello 2013, 2016, 2019; Maldaner et al. 2015, 2018; Valois et al. 2017; Arias-Buriticá and Vaz-de-Mello 2019; Rossini and Vaz-de-Mello 2020; Silva et al. 2020), *Eurysternus* Dalman, 1824 (Génier 2009), *Phanaeus* MacLeay, 1819 (Edmonds and Zidek 2012), and *Oxysternon* Castelnau, 1840 (Edmonds and Zidek 2004).

*Canthon* Hoffmannsegg, 1817 is currently the largest genus of the tribe Deltochilini, with 75 species recorded for Brazil (Vaz-de-Mello 2020). The specimens are

preferentially coprophagous, but some species are copro-necrophagous, necrophagous, predators of ants from the genus *Atta* Fabricius, 1804, or may be attracted by volatile defensive secretions of millipedes (Halffter and Matthews 1966; Bedoussac et al. 2007; Araújo et al. 2015).

The genus *Deltochilum* Eschscholtz, 1822 presents 61 species recorded for Brazil (Vaz-de-Mello 2020). It currently comprises eight valid subgenera: *Aganhyboma* Kolbe, 1893; *Calhyboma* Kolbe, 1893; *Deltochilum* Eschscholtz, 1822 s. str.; *Deltohyboma* Lane, 1946; *Euhyboma* Kolbe, 1893; *Hybomidium* Shipp, 1897; *Parahyboma* Paulian, 1938; and *Rubrohyboma* Paulian, 1938 (Vaz-de-Mello 2020). Its specimens have preferably necrophagous feeding habits. In addition, predatory behavior has also been described in specimens of the subgenus *Deltochilum* (*Aganhyboma*) on millipedes (Halffter and Matthews 1966; Silva et al. 2012a).

The genus *Dichotomius* Hope, 1838 belongs to the tribe Dichotomiini, and presents 101 species recorded for Brazil (Vaz-de-Mello 2020). The species of *D. sericeus* group are often the dominant component of local communities in the Atlantic Forest, restinga and Caatinga. This group was recently revised, being composed of nine species (Valois et al. 2017; Silva et al. 2020); of these, eight occur in northeastern Brazil, namely *Dichotomius catimbau* Valois, Vaz-de-Mello & Silva, 2017, *D. guaribensis* Valois, Vaz-de-Mello & Silva, 2017, *D. gilletti* Valois, Vaz-de-Mello & Silva, 2017, *D. iannuzziae* Valois, Vaz-de-Mello & Silva, 2017, *D. irinus* (Harold, 1867), *D. laevicollis* (Felsche, 1901), *D. schiffleri* Vaz-de-Mello, Louzada & Gavino, 2001, and *Dichotomius valoisae* Silva, Moura, Araújo & de Moura, 2020.

*Eurysternus* Dalman, 1824, the only genus of the tribe Eurysternini, was revised by Génier (2009) and contains 53 valid species. Of these, only six have been recorded in northeastern Brazil: *E. nanus* Génier, 2009, *E. hirtellus* Dalman, 1824, *E. cyanescens* Balthasar, 1939, and *E. caribaeus* (Herbst, 1789) in the Atlantic Forest domain; and *E. jessopi* Martínez, 1988 and *E. nigrovirens* Génier, 2009 in the northeastern Cerrado.

The genera *Coprophanæus* d’Olsoufieff, 1924, *Phanaeus* MacLeay, 1819, and *Oxysternon* Castelnau, 1840 belong to the tribe Phanaeini. *Coprophanæus* was revised by Edmonds and Zidek (2010), who recognized 38 species distributed into three subgenera (*Megaphanaeus* d’Olsoufieff, 1924, *Metallophanæus* d’Olsoufieff, 1924; and *Coprophanæus* s. str. d’Olsoufieff, 1924). The genus has a Neotropical distribution, with 28 species recorded in Brazil (Edmonds and Zidek 2010; Vaz-de-Mello 2020), and there are several species of forensic importance owing to their preference for animal carcasses (Almeida et al. 2015).

*Phanaeus* was revised by Edmonds and Zidek (2012), currently presenting 61 valid species (Moctezuma et al. 2019). Of these, only 10 occur in Brazil (Vaz-de-Mello 2020). The genus *Oxysternon* Castelnau, 1840 inhabits the tropical forests of the Amazon, Guyana, and Chaco, as well as Brazilian extra-Amazon areas in the Cerrado

and Atlantic Forest; it is widely distributed in northern and northwestern South America (Edmonds and Zidek 2004; Filgueiras et al. 2011b; Gigliotti et al. 2011). The genus has 11 species, all occurring in Brazil (Edmonds and Zidek 2004; Vaz-de-Mello 2020).

All these previous inventories and taxonomic studies have contributed significantly to knowledge on Brazilian scarabs. However, recent collections have revealed new records of dung beetles from the northeastern region. In this paper, these records are presented and discussed in light of the biogeography of each species, which increases significantly their known geographical range, and contributes to the conservation of the Atlantic Forest.

## Methods

The collections were carried out in remnants of northeastern Brazil with vegetation of Atlantic Forest *stricto sensu*, restinga and transition forest (Table 1). The specimens were collected in the years 2009, 2017, 2018, and 2019 with the use of pitfall traps, most of which were baited with human feces. Pitfall trap consists of a plastic container buried at the ground level and covered with a disk supported with three wooden sticks to protect the baits from rain or drying. In each locality, we installed at least 30 traps 200 m distant from the fragment edge and from each other. The traps remained in the field for 48 hours. Wounded millipedes were only used as bait in the Mata de Jaguarana and in the Environmental Protection Area (EPA) Aldeia-Beberibe. These collections were performed with authorization of the National System of Biodiversity Information (SISBIO; no. 16278-1), with a permanent license for zoological material of the class Insecta. The specimens are deposited at the Entomological Collection of the University of Pernambuco (CEUPE), Laboratory of Biodiversity and Genetics of Insects (LBGI), Institute of Biological Sciences, University of Pernambuco, PE, Brazil.

For identification at genus level, the key to genera and subgenera of Vaz-de-Mello et al. (2011) was used. Some of the identifications at species level were accomplished with the aid of taxonomic reviews (Edmonds and Zidek 2004, 2010, 2012; Génier 2009; Silva et al. 2015; Valois et al. 2017).

## Results

Twelve new accounts of dung beetle species were made in the northeastern Brazil, listed and described as follows:

### Tribe Deltachilini

#### *Canthon histrio* (Lepeletier de Saint-Fargeau & Audinet-Serville, 1828)

Figures 1A, 3A

**New record.** BRAZIL • 1 ♂; Sergipe, Santa Luzia do Itanhi municipality, Mata do Crasto; 11°22'11.11"S, 037°25'12.8"W; 84 m a.s.l.; 21–23 June 2017; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C2698.

**Identification.** Within Deltachilini (sensu Tarasov and Dimitrov 2016), *Canthon* can be distinguished by the following combination of characters: posterior margin of head completely margined between eyes; mentum not completely divided medially; pronotum not explanate at sides, lacking denticle anteriorly, and surface with evenly distributed sculpturing, lacking tubercles; elytral interstriae lacking carinae or tubercles at apex; meso and metatibiae lacking transverse carinae; metatibia with one spur at apex; second meso- and metatarsomeres with external margin approximately 1.5 times the length of the first tarsomere, or shorter; lateral margins of meso- and metatarsomeres 2–4 divergent apically, not forming a continuous border for all tarsi; dorsal/internal surface of mesotibiae with setae arranged in rows; tarsal claws not reduced, curved, lacking basal tooth; and base of pygidium completely exposed, not covered by elytra (Vaz-de-Mello et al. 2011; Silva and Valois 2019).

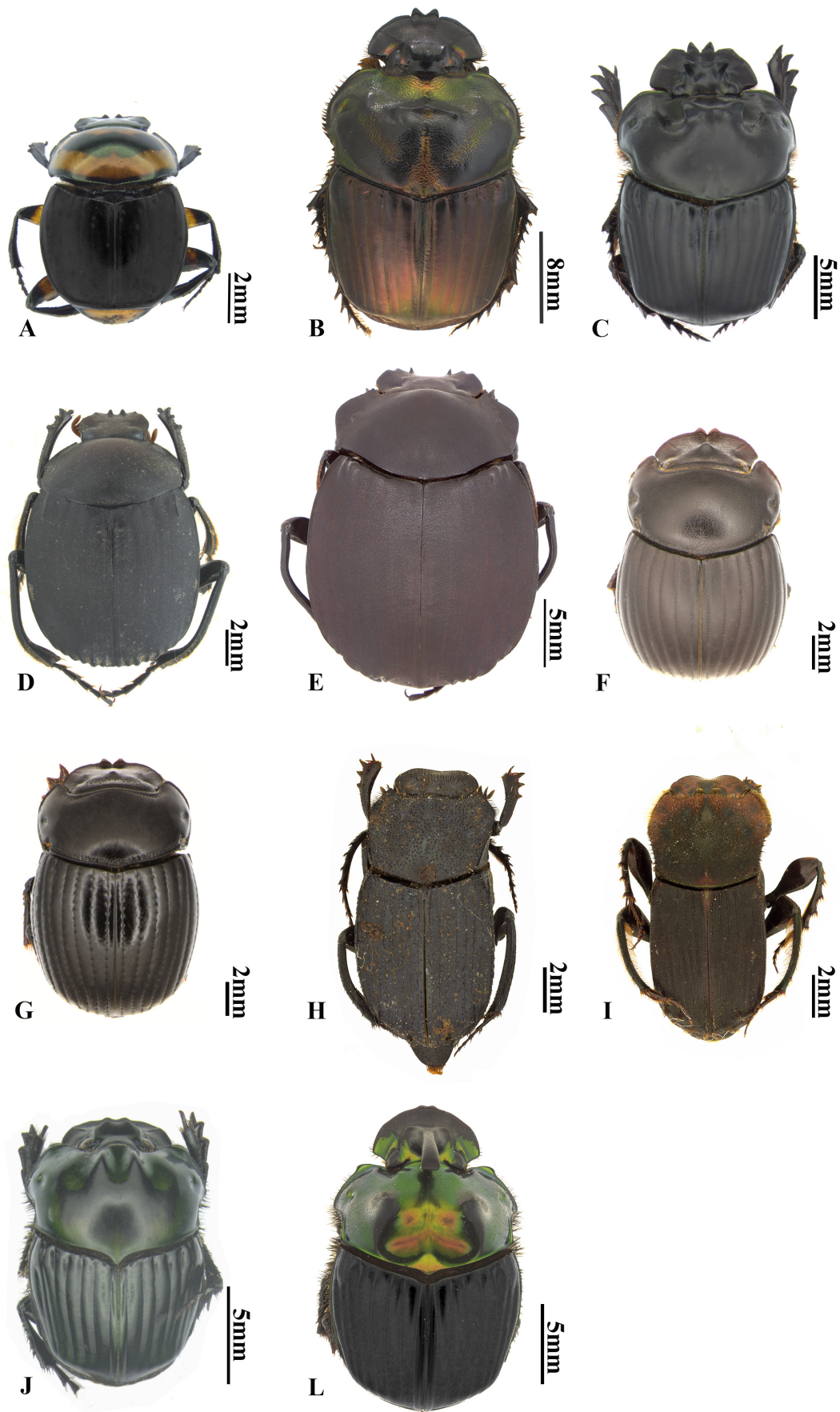
*Canthon histrio* is distinguished by the clypeus with two triangular and short teeth with tapered apex; pronotum with transverse black spot, butterfly or bat shaped; elytra completely black, or yellow at disc and black at edges; ninth elytral interstria not carinated; metafemur margined anteriorly; ventral surface of metafemur with posterior margin complete, not effaced; mesotibiae without lateral tooth, lateral keel or excavation on the outer edge; metatibiae with apical edge sinuous; and pygidium not separated from propygidium by carina (Nunes 2015).

**Remarks.** In Brazil, the species *C. histrio* has been reported in the states of Bahia, Ceará, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Pernambuco, Rio Grande do Sul, Rondônia, São

**Table 1.** Localities of recent collections carried out in northeastern Brazil, with the respective vegetation, coordinates and area. Abbreviations: AL, Alagoas; PE, Pernambuco; SE, Sergipe.

Localities	State	Vegetation	Latitude	Longitude	Area (ha)
Mata do Crasto in Santa Luzia do Itanhi	SE	Forest of transition	11°22'11.11"S	037°25'12.80"W	1,000
Murici Ecological Station	AL	Dense Ombrophilous Forest	09°12'50.56"S	035°52'20.82"W	3,788
Muro Alto Beach	PE	Restinga	08°25'37.00"S	034°58'48.00"W	24
Urban Forest Reserve Mata de Jangadinha	PE	Dense Ombrophilous Forest	08°05'30.15"S	034°58'40.57"W	84.68
Urban Forest Reserve Mata de Jaguarana	PE	Dense Ombrophilous Forest	07°55'13.47"S	034°52'52.79"W	332.28
EPA Aldeia-Beberibe	PE	Dense Ombrophilous Forest	07°57'09.03"S	034°59'13.24"W	31,634





**Figure 1.** Species of dung beetles, dorsal view. **A.** *Canthon histrio*. **B.** *Coprophanaeus acrisius*. **C.** *Coprophanaeus dardanus*. **D.** *Deltochilum alpercata*. **E.** *Deltochilum brasiliense*. **F.** *Dichotomius gillettei*. **G.** *Dichotomius iannuzziae*. **H.** *Eurysternus calligrammus*. **I.** *Eurysternus parallelus*. **J.** *Oxysternon silenus*. **L.** *Phanaeus splendidulus*.

Paulo, and Tocantins (Nunes 2015). Besides its broad distribution, the species shows color variations throughout its occurrence areas (Nunes 2015). For instance, one individual collected at the Mata do Crasto, state of Sergipe, presented black elytra, a variation also found in the Atlantic Forest of Bahia and Minas Gerais (Nunes 2015). In the Charles Darwin Ecological Refuge in Pernambuco, specimens with yellow elytra and black margins were identified both in open fields as well as in forest areas (Silva et al. 2010). In the EPA Aldeia-Beberibe in Pernambuco, one collected specimen, found perched on a leaf in the forest understory, showed black elytron and dark-green pronotum, both shiny, which is an atypical melanic variation in this species.

***Deltochilum alpercata* Silva, Louzada & Vaz-de-Mello, 2015**

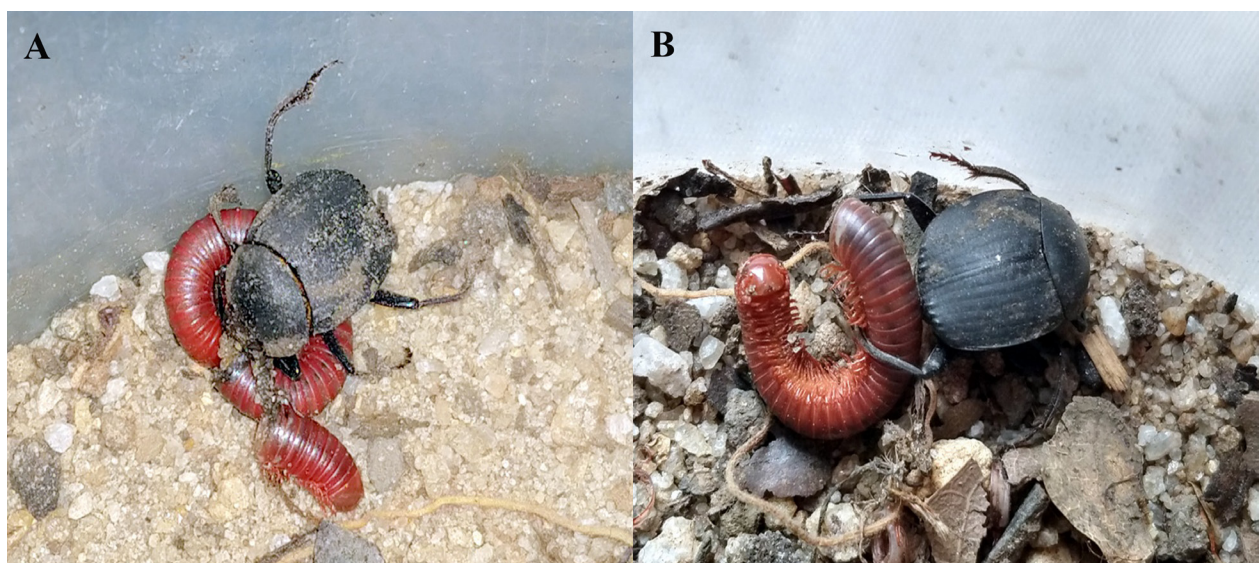
Figures 1D, 3B

**New records.** BRAZIL • Pernambuco • 1 ♂; Paulista municipality, Urban Forest Reserve Mata de Jaguarana; 07°55'13.47"S, 034°52'52.79"W; 15 m a.s.l.; 14–16 April 2018; Josival Araújo, Júlio Silva leg.; urban Atlantic Forest, *pitfall* with millipede reviled; CEUPE C1948. • 1 ♂, 3 ♀; same locality; 19–21 May 2018; Josival Araújo, Júlio Silva leg.; urban Atlantic Forest, *pitfall* with millipede reviled; CEUPE C1951 to C1955. • 4 ♂, 5 ♀; same locality; 16–18 June 2018; Josival Araújo, Júlio Silva leg.; urban Atlantic Forest, *pitfall* with millipede reviled; CEUPE C1956 to C1964. • 2 ♀; same locality; 10–12 July 2018; Josival Araújo, Júlio Silva leg.; urban Atlantic Forest, *pitfall* with millipede reviled; CEUPE C1949 to C1950. • 1 ♂; Camaragibe municipality, Aldeia dos Camarás, Chã de Peroba; 07°57'09.03"S, 034°59'13.24"W; 75 m a.s.l.; 23–25 November 2018; Josival Araújo, Bruno Pereira leg.; periurban Atlantic Forest, *pitfall* with millipede reviled; CEUPE C1965.

**Identification.** Within *Deltochilini* (sensu Tarasov and Dimitrov 2016), the genus *Deltochilum* is characterized by the head lacking tubercles at front; elytral interstriae with short carinae or tubercles at apex (Vaz-de-Mello et al. 2011: fig. 67); and tarsal claws not reduced, curved (Vaz-de-Mello et al. 2011).

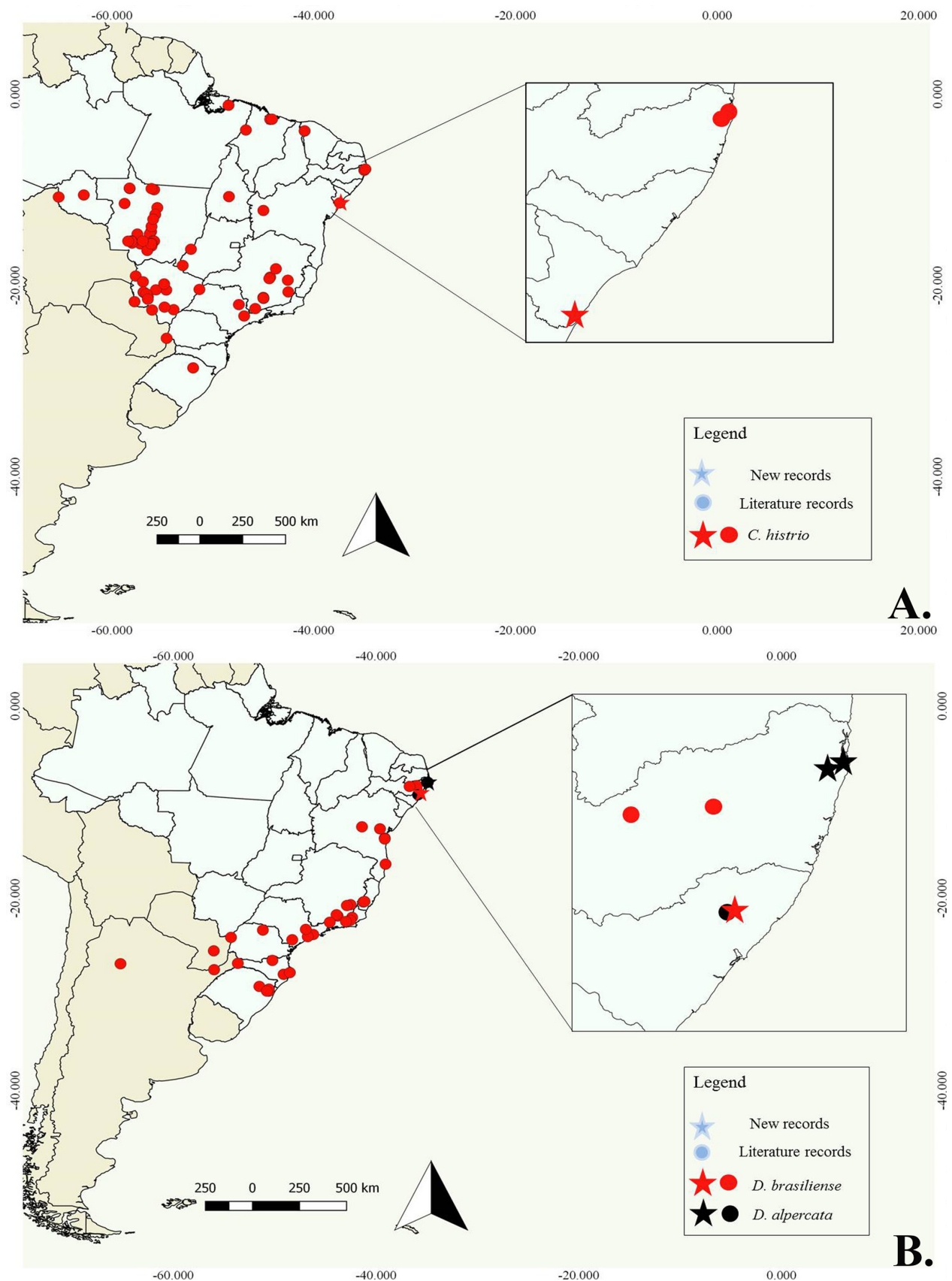
According to Silva et al. (2015), specimens of the *D. alpercata* can be distinguished from other *Deltochilum* by having the anterior part of head (between clypeogenal sutures) prolonged, similar to a small ‘muzzle’ (Silva et al. 2015: figs 60, 61); head with small clypeal teeth external to central teeth (Silva et al. 2015: fig. 61); dorsal interocular distance three to four times eye width (Silva et al. 2015: fig. 61); punctures on anteromedial surface of hypomera separated by less than one diameter (Silva et al. 2015: fig. 79); pronotum with opaque sheen or weak luster; elytra rounded, sides bulging outward; elytral striae narrow, carinate margins close and almost touching (Silva et al. 2015: fig. 74); and elytral microtubercles well delimited (Silva et al. 2015: fig. 77).

**Remarks.** In the fragments sampled in Pernambuco, specimens of *D. (Aganhyboma) alpercata* were collected in traps baited with injured millipedes. Thus far, this species only had a single known specimen, the holotype, collected in 1984 in a fragment at the municipality of Murici, Alagoas (Silva et al. 2015). Individuals of this subgenus are rare in collections because traps baited with millipedes are not frequently used in studies of fauna inventory. In the fragment of Chã de Peroba, Aldeia dos Camarás, Pernambuco, through active search during the rainy period, a specimen was observed in the field on March 29, 2019 at 10:00 p.m. initiating the predation of an uninjured millipede. A specimen was also observed by the first author attacking and transporting an injured millipede at 9:00 p.m. in a terrarium (Fig. 2A, B).



**Figure 2.** Different stages of predatory behaviour of *Deltochilum (Aganhyboma) alpercata*. **A.** On-site feeding stage. **B.** Millipede allocation stage.





**Figure 3.** Known distribution of species of dung beetles. **A.** *Canthon histrio*. **B.** *Deltochilum brasiliense* and *D. alpercata*.

***Deltochilum brasiliense* (Castelnau, 1840)**

Figures 1E, 3B

**New record.** BRAZIL • 4 ♂, 6 ♀; Alagoas, Murici municipality, Murici Ecological Station; 09°12'50.56"S, 035°

52°20.82"W; 613 m a.s.l.; 3–5 August 2018; Aline Félix, Igor Amorim, Geyner Cruz leg.; submontane Atlantic Forest, *pitfall* with feces; CEUPE C2115 to C2123.

**Identification.** According to Silva (2017), *D. brasiliense*

differs from other species in having an obtuse angle between the clypeogenal suture and the clypeal teeth; fourth, fifth, and sixth elytral interstriae with tubercles or elevations at base; seventh interstria with thin, short carina at base; basal carina of ninth interstriae extending at most to midway along elytra; pseudopipleural carina incomplete, effaced basally; apex of elytra with carina at third, fourth, fifth, sixth, and seventh interstriae; and body size longer than 20 mm.

**Remarks.** *Deltochilum (Euhyboma) brasiliense* is known from Bahia, Espírito Santo, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo (Vaz-de-Mello et al. 2014). The species is widely distributed in the Atlantic Forest, and accounts are frequent in forest areas of moderate temperature (Vaz-de-Mello et al. 2014). This is the first record of *D. (E.) brasiliense* from the state of Alagoas. In the Atlantic Forest north of the São Francisco river, this species was only previously recorded in an altitudinal Atlantic Forest at the municipality of Caruaru, Pernambuco (Vaz-de-Mello et al. 2014), with moderate temperatures in comparison to the lowland Atlantic Forest of the coast.

Tribe Dichotomiini

***Dichotomius gilletti* Valois, Vaz-de-Mello & Silva, 2017**

Figures 1F, 4A

**New record.** BRAZIL • 456 ♂, 533 ♀; Alagoas, Murici municipality, Murici Ecological Station; 09°12'50.56"S, 035°52'20.82"W; 613 m a.s.l.; 3–5 August 2018; Aline Félix, Igor Amorim, Geyner Cruz leg.; submontane Atlantic Forest, *pitfall* with feces; CEUPE C2701 to C3690.

**Identification.** Within Dichotomiini (sensu Tarasov and Dimitrov 2016), the genus *Dichotomius* can be distinguished by the antenna with nine antennomeres; antennal club elongate; and second labial palpomere triangular, not covering the third palpomere in ventral view (Vaz-de-Mello et al. 2011).

*Dichotomius gilletti* belongs to *D. sericeus* species group which may be easily distinguished from other *Dichotomius* groups in having a deep fovea on pronotum posterior angles (Valois et al. 2017). *Dichotomius gilletti* differs from other species of the *sericeus* group in having the disc of pronotum with distinct ocellate punctures, at least near anterior angles; disc of pygidium smooth, ocellate punctures restricted at the margins (Valois et al. 2017: fig. 11h); and surface of elytral interstriae wrinkled, with conspicuous longitudinal ridges (Valois et al. 2017: fig. 7e).

**Remarks.** According to Valois et al. (2017), *D. gilletti* has records in Ceará, Paraíba and Pernambuco, being frequently verified in areas of Atlantic Forest *stricto sensu* and altitudinal Atlantic Forest. In a study performed by Silva et al. (2010) at the Charles Darwin Ecological Refuge, Igarassu, Pernambuco, *D. gilletti* represented 85% of the collected specimens, being dominant in the dung

beetle community of that region (Valois et al. 2017).

***Dichotomius iannuzziae* Valois, Vaz-de-Mello & Silva, 2017**

Figures 1G, 4A

**New record.** BRAZIL • 6 ♂, 14 ♀; Sergipe, Santa Luzia do Itanhi municipality, Mata do Crasto; 11°22'11.11"S, 037°25'12.8"W; 84 m a.s.l.; 21–23 June 2017; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C3691 to C3711. • 12 ♂, 21 ♀; same locality; 19–21 June 2019; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C3712 to 3745.

**Identification.** *Dichotomius iannuzziae* is distinguished from other species of the *sericeus* group in having the disc of pronotum with simple and sparse punctures, visible at high magnification; elliptical ocellate punctures closer to posterior margin of pronotum (Valois et al. 2017: fig. 8e); and lateral margin of pronotum with a row of ocellate punctures on anterior half (Valois et al. 2017: fig. 4e).

**Remarks.** *Dichotomius iannuzziae* has accounts in the states of Alagoas, Bahia, Minas Gerais and Pernambuco, occurring in areas of Atlantic Forest *stricto sensu* and altitudinal Atlantic Forest (Valois et al. 2017).

Tribe Eurysternini

***Eurysternus calligrammus* Dalman, 1824**

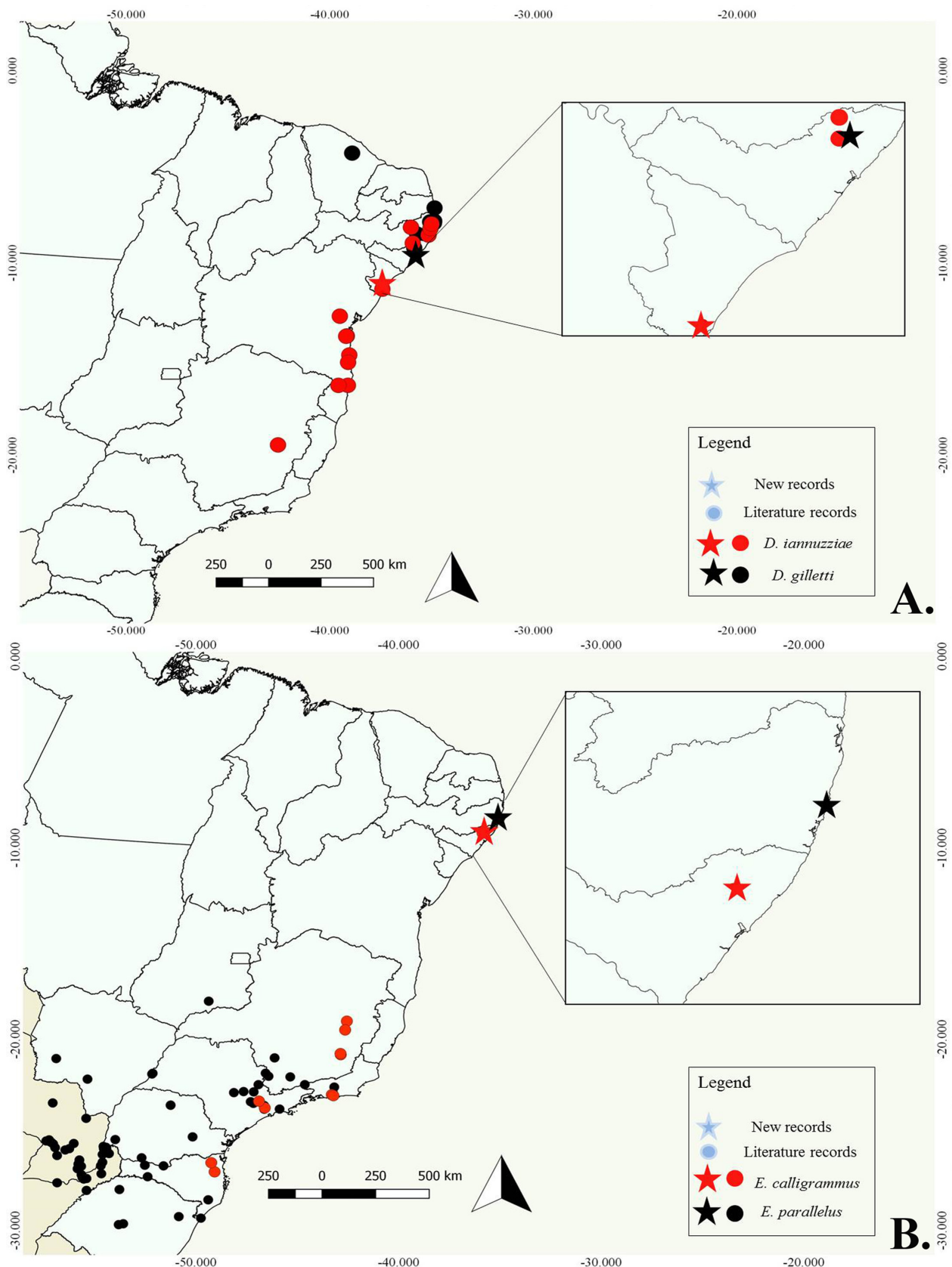
Figures 1H, 4B

**New record.** BRAZIL • 7 ♂, 3 ♀; Alagoas, Murici municipality, Murici Ecological Station; 09°12'50.56"S, 035°52'20.82"W; 613 m a.s.l.; 3–5 August 2018; Aline Félix, Igor Amorim, Geyner Cruz leg.; submontane Atlantic Forest, *pitfall* with feces; CEUPE C2649 to C2650, C3746 to C3753.

**Identification.** *Eurysternus* is easily distinguished from all other Neotropical dung beetles in having the body elongate, with parallel lateral margins; labial palpi with two palpomeres; mesocoxae widely separated, parallel to the body axis; tip of mesoscutellum clearly visible; and elytra flat (Génier 2009; Vaz-de-Mello et al. 2011).

*Eurysternus calligrammus* belongs to *calligrammus* species group which differs from other *Eurysternus* groups in having larger specimens (greater than 8.0 mm in length); eyes almost inconspicuous in dorsal view (Génier 2009: fig. 55); dorsum with short setae, usually uniform in size; surface of pronotum with uniform ocellate punctures on disc (Génier 2009: fig. 63); metacoxa unicolored laterally; third abdominal segment truncate at anterior part between metacoxae (Génier 2009: fig. 54); pseudopipleural carina higher than adjacent interstria at midway along elytra; protarsus present; and spur of metatibia fused in male (Génier 2009: fig. 46).

*Eurysternus calligrammus* is distinguished from other species of the *calligrammus* group in having elytra with short and scattered setae on disc; mesometasternal



**Figure 4.** Known distribution of species of dung beetles. **A.** *Dichotomius iannuzziae* and *D. gilletti*. **B.** *Eurysternus calligrammus* and *E. parallelus*.

suture carinate laterally (Génier 2009: fig. 119); protibia weakly recurved distally in male; surface of metacoxa glossy, without ocellate puncture internally to trochanter insertion (Génier 2009: fig. 114); and metafemur without

tooth at posterior margin in female (Génier 2009).

**Remarks.** *Eurysternus calligrammus* Dalman, 1824 had only been verified in low-altitude forests (0–700 m) in the states of Minas Gerais and Rio de Janeiro (Génier 2009).



It is the only species from the *calligrammus* group with reports of forensic importance (Almeida et al. 2015).

***Eurysternus parallelus* Castelnau, 1840**

Figures 1I, 4B

**New record.** BRAZIL • 1 ♂; Pernambuco, Ipojuca municipality, Muro Alto Beach; 08°25'37.00"S, 034°58'48.00"W; 10 m a.s.l.; 6–8 June 2009; Cristiane Costa, Igor Amorim leg.; restinga forest, *pitfall* with feces; CEUPE C2651.

**Identification.** *Eurysternus parallelus* belongs to the *deplanatus* species group which differs from other *Eurysternus* groups in having larger specimens (greater than 8.0 mm in length); dorsum with short setae, usually uniform in size; surface of pronotum lacking large, confluent, ocellate punctures on disc (Génier 2009: fig. 50); anterior portion of pronotum with three glabrous and glossy calluses (Génier 2009: fig. 50); metafemur club-shaped (Génier 2009: fig. 51); and spur of metatibia articulated in male (Génier 2009: fig. 43).

*Eurysternus parallelus* differs from the other species (*E. deplanatus* (Germar, 1824)) which composes the *deplanatus* group in having a dull surface of pronotum between punctures on the disc (Génier 2009: fig. 83); and body size greater than 11.0 mm in length (Génier 2009).

**Remarks.** *Eurysternus parallelus* was documented in various environments, such as the Cerrado, Atlantic Forest, borders of transition forests, and pasture matrices (Génier 2009). These individuals seem to be adapted to degraded habitats, occurring in altitudes that vary from 70 to 1,000 m a.s.l. in Argentina, Paraguay, and Brazil. In the latter, they are widely distributed in the states of Goiás, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, and São Paulo. In the south of Brazil, *E. parallelus* is abundant in forest fragments and occurs less profusely in pasture areas (Medri and Lopes 2001; Lopes et al. 2011). Here, specimens are reported for the first time in restinga environments. In the fragment of Muro Alto, Pernambuco, this species is rare, and was sampled in traps baited with feces in a conserved area. This was the only species from the genus *Eurysternus* reported in the study by Costa et al. (2014), where it was treated as a morphospecies.

Tribe Phanaeini

***Coprophanaeus acrisius* (MacLeay, 1819)**

Figures 1B, 5A

**New record.** BRAZIL • 1 ♂; Sergipe, Santa Luzia do Itanhi municipality, Mata do Crasto; 11°22'11.11"S, 037°25'12.80"W; 84 m a.s.l.; 21–23 June 2017; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C2699. • 1 ♂; same locality; 19–21 June 2019; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C2700.

**Identification.** Within Phanaeini tribe, the genus *Coprophanaeus* can be immediately distinguished by the

clypeal margin deeply, narrowly emarginate medially, with two prominent, acute median teeth that are separated from adjacent clypeal border by external emarginations; basal antennomere of antennal club strongly concave, embracing second and third antennomeres; protibiae quadridentate, with strong and acute dentition; and mesotarsus and metatarsus with five tarsomeres (Edmonds and Zidek 2010; Vaz-de-Mello et al. 2011).

*Coprophanaeus acrisius* can be distinguished by the following combination of characters: medium-sized specimens (less than 25 mm); clypeal margin rounded lateral to median teeth, not angulate or explanate; circumnotal ridge continuous, not effaced behind eyes (Edmonds and Zidek 2010: fig. 7); paraocular area straight at posterior margin, ending at middle of eye; prosternal ridge with acute tubercle at anterior part (Edmonds and Zidek 2010: fig. 112); pronotal carina of large male with three tubercles, middle tubercle larger than lateral ones (Edmonds and Zidek 2010: fig. 98); pronotal ridge of female trapezoidal, summit with three tubercles (Edmonds and Zidek 2010: fig. 107); swollen black areas around rugose median depression of pronotum, densely punctate or completely rugose; basal pronotal fossae distinct; elytral striae inconspicuously carinulate (Edmonds and Zidek 2010: fig. 100); hind wing with rounded notch in posterior margin near base; and protarsus lacking in females (Edmonds and Zidek 2010).

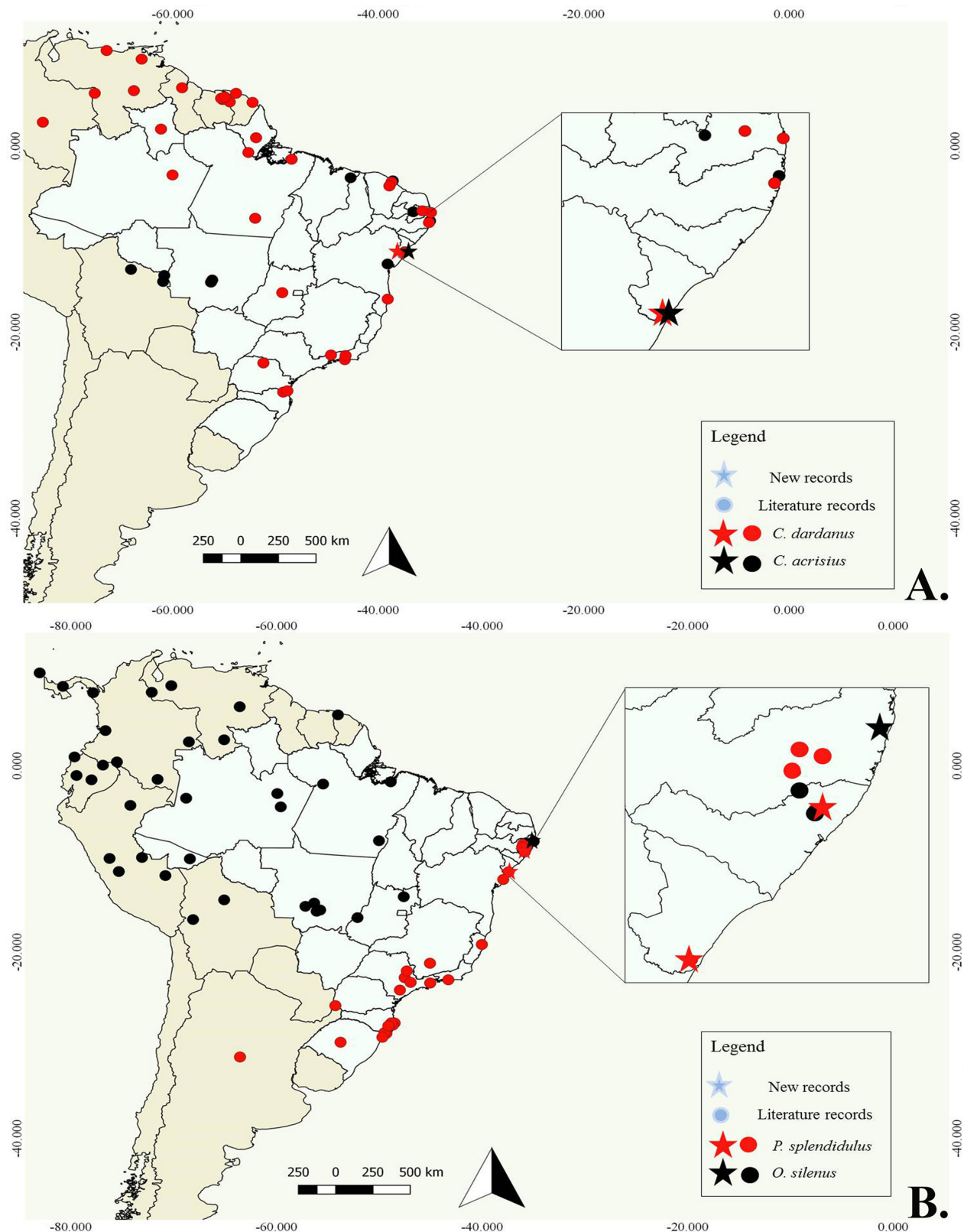
**Remarks.** *Coprophanaeus acrisius* occurs in the northern part of the Cerrado and Caatinga in the states of Bahia, Ceará, Maranhão, Mato Grosso, Paraíba, and Pernambuco (Edmonds and Zidek 2010; Gillett et al. 2010). It has also been recorded in lowland Atlantic Forest in the Pernambuco endemism center (Edmonds and Zidek 2010).

***Coprophanaeus dardanus* (MacLeay, 1819)**

Figures 1C, 5A

**New record.** BRAZIL • 2 ♀; Sergipe, Santa Luzia do Itanhi municipality, Mata do Crasto; 11°22'11.11"S, 037°25'12.8"W; 84 m a.s.l.; 21–23 June 2017; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C1857 to C1858. • 3 ♂, 5 ♀; same locality; 19–21 June 2019; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C1859 to C1867.

**Identification.** *Coprophanaeus dardanus* can be distinguished by the length of clypeus about equal to that of frons; clypeal margin usually strongly angulate adjacent to median teeth (Edmonds and Zidek 2010: fig. 235); circumnotal ridge effaced behind each eye (Edmonds and Zidek 2010: fig. 8); male cephalic process with strongly produced, horn-like lateral angles separated by deep curve in apical margin (Edmonds and Zidek 2010: figs 213, 214); female process produced in a carina with small denticle at each end separated by broad elevation (Edmonds and Zidek 2010: fig. 216); pronotal prominence of large male cleat-shaped, produced laterally into acute



**Figure 5.** Known distribution of species of dung beetles. **A.** *Coprophanaeus dardanus* and *C. acrisius*. **B.** *Phanaeus splendidulus* and *Oxysternon silenus*.

lobes (Edmonds and Zidek 2010: fig. 242); surface of pronotal disk smooth midlongitudinally; prosternal ridge simple, lacking tubercle anteriorly; and elytral striae not distinctly carinulate (Edmonds and Zidek 2010).

**Remarks.** The species *C. dardanus* has wide distribution in Brazil, occurring in Amapá, Amazonas, Bahia,

Ceará, Goiás, Pará, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Roraima, and Santa Catarina (Edmonds and Zidek 2010), in ecosystems of the Amazon region as well as of the Atlantic Forest on the Brazilian coast. In Ceará, the species inhabits the Atlantic Forest at altitudes above 200 m and may occur in areas above 500 m

in the Brazilian southeast (Gillett et al. 2010).

### *Oxysternon silenus* Castelnau, 1840

Figures 1J, 5B

**New record.** BRAZIL • 1 ♀; Pernambuco, Jaboatão dos Guararapes municipality, Urban Forest Reserve Mata de Jangadinha; 08°05'30.15"S, 034°58'40.57"W; 50 m a.s.l.; 21–23 June 2017; Aline Félix leg.; urban Atlantic Forest, *pitfall* with feces; CEUPE C1664.

**Identification.** Within Phanaeini tribe, the genus *Oxysternon* can be immediately distinguished by the metasternum acutely produced in a long, upwardly curved spiniform process extending between apices of procoxae (Vaz-de-Mello et al. 2011: fig. 140); and posteromedian angle of pronotum acutely produced between bases of elytra (Edmonds and Zidek 2004; Vaz-de-Mello et al. 2011).

*Oxysternon silenus* can be distinguished from its congeners by the following characters: body size usually greater than 15 mm; clypeal process forming transverse ridge (Edmonds and Zidek 2004: fig. 2); large male with erect, shot head horn (Edmonds and Zidek 2004: figs 24, 25, 90, 91); and metatibial spur acute. The pronotum shape is unique between species from *Oxysternon*. It has processes which consist of closely set pair of thick ridges, never horn-like (Edmonds and Zidek 2004).

**Remarks.** *Oxysternon silenus* has Amazonian distribution in the states of Acre, Amazonas and Pará, and extra-Amazonian occurrence in Alagoas, Goiás and Mato Grosso (Edmonds and Zidek 2004; Filgueiras et al. 2011b; Gigliotti et al. 2011). Filgueiras et al. (2011b) collected four females with emerald-green coloration in Serra Grande, Alagoas. In the present study, we collected one female with blue coloration at the Murici Ecological Station, Alagoas, on August 3–5, 2018, and one emerald-green female specimen in the Urban Forest Reserve Mata de Jangadinha, Pernambuco, on June 21–23, 2017.

### *Phanaeus splendidulus* (Fabricius, 1781)

Figures 1L, 5B

**New records.** BRAZIL • 60 ♂, 33 ♀; Alagoas, Murici municipality, Murici Ecological Station; 09°12'50.56"S, 035°52'20.82"W; 613 m a.s.l.; 3–5 August 2018; Aline Félix, Igor Amorim, Geyner Cruz leg.; submontane Atlantic Forest, *pitfall* with feces; CEUPE C2241 to C2334. • 30 ♂, 29 ♀; Sergipe, Santa Luzia do Itanhi, Mata do Crasto; 11°22'11.11"S, 037°25'12.80"W; 84 m elev.; 21–23 June 2017; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C2335 to C2394. • 6 ♂, 10 ♀; same locality; 19–21 June 2019; Igor Amorim, Aline Félix leg.; transitional Atlantic Forest, *pitfall* with feces; CEUPE C2395 to C2411.

**Identification.** Within Phanaeini tribe, the genus *Phanaeus* can be distinguished by the following combination of characters: clypeus without deep, acute emarginations; head bare, or with single horn or carina, never with two parallel horizontal carinae; basal antennomere of antennal club concave, embracing second and third

antennomeres; anterior portion of circumnotal ridge effaced behind each eye; mesotarsus and metatarsus with five tarsomeres; and first meso- and metatarsomere elongate, much longer than wide (Vaz-de-Mello et al. 2011).

*Phanaeus splendidulus* belongs to *splendidulus* species group which differs from other *Phanaeus* groups in having the clypeus at most only weakly bidentate; clypeal process tooth-like (Edmonds and Zidek 2012: fig. 98); surface of anterolateral portions of pronotum with distinct punctures, or almost completely smooth; sculpture of pronotum never granulate, granulorugose or rugose; pronotum of larger males concave in dorsal view, with a pair of spinate horns arising from near posterior margin (Edmonds and Zidek 2012: fig. 116, 120); hind wing not notched basally; and protibial spur curved (Edmonds 1994; Edmonds and Zidek 2012).

*Phanaeus splendidulus* is immediately distinguished from other congeners species within the *splendidulus* group in having the anterior prominence of metasternum, in lateral view, acuminate, produced anteriorly as a minute, acute tubercle (Edmonds and Zidek 2012: fig. 56).

**Remarks.** *Phanaeus splendidulus* has wide distribution in the Atlantic Forest of the Brazilian coastline, with records extending from the altitudinal Atlantic Forest of Pernambuco to the Atlantic Forest in the south coast of the country (Gillett et al. 2010; Silva et al. 2011). In the Atlantic Forest of the northeast, it was verified in the state of Bahia (Edmonds and Zidek 2012) and in the altitudinal Atlantic Forest from the municipality of Bonito, Pernambuco (Cunha 2011).

## Discussion

From the species recorded in this study, *Deltotrichum brasiliense*, *Eurysternus calligrammus*, *E. parallelus*, *Oxysternon silenus*, and *Phanaeus splendidulus* possibly presented broader distribution in northeastern Brazil when the Atlantic Forest was continuous along its latitudinal extension, and/or when it was connected in the past with the eastern portions of the Amazon Rainforest. Currently, these species have relictual populations along the northeastern region, as verified to *Coprophanaeus bellicosus* (Olivier, 1789) recorded from altitudinal Atlantic Forest in Pernambuco (Silva 2011).

According to Camero and Lobo (2012), which carried out a modeling of potential distribution for species from the genus *Eurysternus*, *E. calligrammus* may occur in sites of the northeast that present favorable environmental conditions, despite being fragmented (Camero 2011). It is likely that this species has a wider distribution to the north of the São Francisco river when the Atlantic Forest was continuous (Camero and Lobo 2012). The historical process of exploitation, defaunation and fragmentation of the Atlantic Forest in the northeast may have isolated *E. calligrammus* in refuges with favorable environmental and climatic conditions. Since this species inhabits sites with strict climatic conditions (Camero and Lobo 2012),



only small population nuclei should be currently found in the region. The populations from the southeast are separated by at least 2,600 km from that newly recorded in Murici, state of Alagoas.

*Eurysternus parallelus* was documented in various environments, such as the Cerrado, Atlantic Forest, borders of transition forests, and pasture matrices (Génier 2009). According to the study of potential distribution carried out by Camero and Lobo (2012), *E. parallelus* has few favorable environmental areas in the northeast region, with some spots verified in Alagoas; a single small, isolated patch in Paraíba; and another on the southern coast of Pernambuco. The populations from the southeast are distant from those of Muro Alto, Pernambuco, by at least 3,200 km. Therefore, we believe that *E. parallelus* may have occupied restinga areas in the northeast coast, possibly owing to its generalist behavior towards feeding and habitats, tending to tolerate a wider range of climatic conditions such as high temperatures characteristic of lowland Atlantic Forests in the restinga domain.

*Oxysternon silenus* is a typical Amazonian species, with most of records from states of Acre, Amazonas and Pará (Edmonds and Zidek 2004). The Atlantic Forest to the north of the São Francisco river has rare accounts of *O. silenus* (Filgueiras et al. 2011b). The populations of Alagoas and Pernambuco are relictual and reinforce the hypothesis of a strong recent connection between the eastern Amazon and the Atlantic Forest of the northeast region (Ledo and Colli 2017). Previous records of species originating from the Amazon in altitudinal Atlantic Forest in the northeast are already relatively well-known (Prance 1982; Cavalcanti and Tabarelli 2004; Filgueiras et al. 2011b; Santos et al. 2019). However, it was not expected to find dung beetles from the Amazon fauna in the lowland Atlantic Forest from the far east of the northeast. The population from the Urban Forest Reserve Mata de Jangadinha in Pernambuco is isolated from the Amazonian populations by at least 3,300 km.

During the Pleistocene, climate changes with periods of low temperatures on Earth were prominent. The localities that did not suffer direct interference from glaciations underwent climate alterations with more moderate temperatures or dry periods (Barnosky 2005). In this context, the Atlantic Forest of the northeast would have presented climate conditions favorable to some species typical of regions with moderate temperature to the south (Sobral-Souza and Lima-Ribeiro 2017), such as *C. bellicosus*, *D. brasiliense*, *E. calligrammus*, and *P. splendulus*. These climate oscillations promoted fluctuations in the size and distribution of the populations, but when the climate became less favorable, these populations may have regressed and decreased in size, leading to local extinctions. Phylogenetic and biogeographic studies that address the theory of Pleistocene refuges with insects are scarce. Boucher (2005) was one of the few studies that considered Pleistocene refuges in the taxonomic revision of the genus *Veturius* Kaup, 1871 (Scarabaeoidea, Passalidae).

This study allowed to record some dung beetle species that inhabit refuges in the Brazilian northeast, and which may become locally extinct due to climate changes, and the destruction and fragmentation of the Atlantic Forest in this region. Owing to the presence of relictual populations of scarab species in the different analyzed fragments, we consider the maintenance of these ecosystems to be of great relevance. It is essential to expand the information on the distribution of dung beetle species in the Brazilian northeast, as these are parameters for biodiversity studies and environmental indicators of anthropic activity (Halffter and Favila 1993). Therefore, efforts towards the conservancy of these areas are urgent, and this work provides a contribution to the preservation of these refuges in the Brazilian northeast.

## Acknowledgements

We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for providing research grants for FABS (#444020/2014-4) and RCM (#305298/2014-3), and fellowships for JFA. We also thank the Fundação de Amparo à Ciência e Tecnologia de Pernambuco (FACEPE APQ – 0777-2.02/15) for financial support. Thanks go to those responsible for the reserves and the owners of the forest remnants for their support during the collections, especially the family of Dr Filipe Martins Aléssio. We also thank the members of the LBGI-ICB-UPE, Dr Igor Amorim, Aline Félix, Bruno Pereira, and Júlio Silva for their contribution in the fieldwork.

## Authors' Contributions

JFA performed some collections, identified species, and wrote the manuscript. FABS confirmed the identification of the species and contributed to the writing and revision of the manuscript. RCM organized the field activities, contributed to, and revised the manuscript.

## References

- Almeida LM, Corrêa RC, Grossi PC (2015) Coleoptera species of forensic importance from Brazil: an updated list. *Revista Brasileira de Entomologia* 59 (4): 274–284. <https://doi.org/10.1016/j.rbe.2015.07.008>
- Andrade-Lima D (1960) Estudos filogeográficos de Pernambuco. Arquivo do Instituto de Pesquisas Agronômicas de Pernambuco 5: 305–341.
- Andrade-Lima D (1982) Present day forest refuges in Northeastern Brazil. In: Prance GT (Ed.) *Biological diversification in the tropics*. Columbia University Press, New York, 245–254.
- Araújo MS, Rodrigues CA, Oliveira MA, Jesus FG (2015) Controle biológico de formigas-cortadeiras: o caso da predação de fêmeas de *Atta* spp. por *Canthon virens*. *Revista de Agricultura Neotropical* 2 (3): 8–12. <https://doi.org/10.32404/rean.v2i3.273>
- Arias-Buritica JA, Vaz-de-Mello FZ (2019) Redefinition and taxonomic revision of the “buqueti” species-group, *Dichotomius* Hope, 1838 (Coleoptera: Scarabaeidae: Scarabaeinae). *Revista Brasileira de Entomologia* 63 (1): 43–52. <https://doi.org/10.1016/j.rbe.2018.11.002>

- Barnosky AD (2005) Effects of Quaternary climatic change on speciation in mammals. *Journal of Mammalian Evolution* 12: 247–264. <https://doi.org/10.1007/s10914-005-4858-8>
- Bedoussac L, Favila ME, López RM (2007) Defensive volatile secretions of two diploid species attract the carrion ball roller scarab *Canthon morsei* (Coleoptera: Scarabaeidae). *Chemoecology* 17 (3): 163–167. <https://doi.org/10.1007/s00049-007-0375-y>
- Boucher S (2005) Évolution et phylogénie des coléoptères Passalidae (Scarabaeoidea). Les taxons du groupe famille la tribu néotropical des Proculini et son complexe Veturius. *Annales de la Société entomologique de France* 41 (3–4): 239–604. <https://doi.org/10.1008/00379271.2005.10697444>
- Camero RE (2011) Biogeografía, Relaciones Filogenéticas y Adaptaciones Ambientales de La Tribu Eurysternini (Coleoptera: Scarabaeidae). PhD dissertation, Universidad Autónoma de Madrid, Madrid, 365 pp.
- Camero RE, Lobo J (2012) The distribution of the species of *Eurysternus* Dalman, 1824 (Coleoptera: Scarabaeidae) in America: potential distributions and the locations of areas to be surveyed. *Tropical Conservation Science* 5 (2): 225–244. <https://doi.org/10.1177/194008291200500210>
- Cavalcanti D, Tabarelli M (2004) Distribuição das plantas amazônicas nordestinas no centro de endemismo Pernambuco: brejos de altitude vs. florestas de terras baixas. In: Pôrto KC, Cabral JJP, Tabarelli M (Eds) Brejos de altitude em Pernambuco e Paraíba. Ministério do Meio Ambiente, Brasília, 285–296.
- Costa CMQ, Barretto JW, Moura RC (2014) Changes in the dung beetle community in response to Restinga forest degradation. *Journal of Insect Conservation* 18 (5): 895–902. <https://doi.org/10.1007/s10841-014-9697-6>
- Costa CMQ, Silva FAB, Farias ÂI, Moura RC (2009) Diversity of Scarabaeinae (Coleoptera, Scarabaeidae) collected with flight intercept trap in the Charles Darwin Ecologic Refuge, Igarassu–PE, Brazil. *Revista Brasileira de Entomologia* 53 (1): 88–94. <https://doi.org/10.1590/S0085-56262009000100021>
- Costa FC, Pessoa KK, Liberal CN, Filgueiras BK, Salomão RP, Iannuzzi L (2013) What is the importance of open habitat in a predominantly closed forest area to the dung beetle (Coleoptera, Scarabaeinae) assemblage? *Revista Brasileira de Entomologia* 57 (3): 329–334. <https://doi.org/10.1590/S0085-56262013000300012>
- Cunha JCS (2011) Escarabeíneos (Coleoptera: Scarabaeidae) coprófagos em remanescentes de Brejo de Altitude, no estado de Pernambuco, Brasil. Bachelor final paper, Universidade de Pernambuco, Pernambuco, 61 pp.
- Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. *Science* 345 (6195): 401–406. <https://doi.org/10.1126/science.1251817>
- Edmonds WD (1994) Revision of *Phanaeus* MacLeay, a New World genus of scarabaeine dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Natural History Museum of Los Angeles County, Contributions in Science* 443: 1–105.
- Edmonds WD, Zidek J (2004) Revision of the Neotropical dung beetle genus *Oxysternon* (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Folia Heyrovskyana* 11: 1–58.
- Edmonds WD, Zidek J (2010) A taxonomic review of the Neotropical genus *Coprophanaeus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). *Insecta Mundi* 129: 1–111.
- Edmonds WD, Zidek J (2012) Taxonomy of *Phanaeus* revisited: revised keys to and comments on species of the New World dung beetle genus *Phanaeus* MacLeay, 1819 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Insecta Mundi* 274: 1–108.
- Endres AA, Creão-Duarte AJ, Hernández MIM (2007) Diversity of Scarabaeidae (Coleoptera) in the Reserva Biológica Guaribas, Mamanguape, Paraíba, Brazil: a comparison between Atlantic Forest and Northeast's Tabuleiro. *Revista Brasileira de Entomologia* 51 (1): 67–71. <https://doi.org/10.1590/S0085-56262007000100012>
- Filgueiras BKC (2015) Resposta dos besouros escarabeíneos (Scarabaeidae) e borboletas frugívoras (Nymphalidae) à modificação de habitat na floresta atlântica nordestina. PhD dissertation, Universidade Federal de Pernambuco, Pernambuco, 157 pp.
- Filgueiras BKC, Iannuzzi L, Leal IR (2011a) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. *Biological Conservation* 144 (1): 362–369. <https://doi.org/10.1016/j.biocon.2010.09.013>
- Filgueiras BKC, Iannuzzi L, Vaz-de-Mello FZ (2011b) First report of *Oxysternon silenus* Castelnau (Scarabaeidae, Scarabaeinae, Phanaeini) in the Brazilian Atlantic Forest. *Revista Brasileira de Entomologia* 55 (2): 283–284. <https://doi.org/10.1590/S0085-56262011005000010>
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. *Science* 309 (5734): 570–574. <https://doi.org/10.1126/science.1111772>
- Génier F (2009) Le genre *Eurysternus* Dalman, 1824 (Scarabaeidae: Scarabaeinae: Oniticeellini). Révision taxonomique et clés de détermination illustrées. *Pensoft Series Faunistica* 85. Pensoft, Sofia, 430 pp. <https://doi.org/10.13140/RG.2.1.1627.9129>
- Génier F (2012) A new species and notes on the subgenus *Deltochilum* (*Deltochilum*) Eschscholtz, 1822 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). *Zootaxa* 3357: 25–36. <https://doi.org/10.11646/zootaxa.3357.1.2>
- Gigliotti MS, Nunes R V, Vaz-de-Mello F Z (2011) Distribuição extra-amazônica brasileira de *Oxysternon* (*Oxysternon*) *conspicillatum* (Weber, 1801) e *Oxysternon* (*Oxysternon*) *silenus* Castelnau, 1840 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). In: I Simpósio de Entomologia do Rio de Janeiro (Ed.) Anais do I Simpósio de Entomologia do Rio de Janeiro. Museu Nacional, UFRJ, Rio de Janeiro, 35–36.
- Gillett CP, Gillett MP, Gillett JE, Vaz-de-Mello FZ (2010) Diversity and distribution of the Scarab Beetle Tribe Phanaeini in the northern states of the Brazilian Northeast (Coleoptera: Scarabaeidae: Scarabaeinae). *Insecta Mundi* 118: 1–19.
- González-Alvarado A, Vaz-de-Mello FZ (2014) Taxonomic review of the subgenus *Hybomidium* Shipp 1897 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilum). *Annales de La Société Entomologique de France (N.S.)* 50 (3–4): 431–476. <https://doi.org/10.1080/00379271.2014.989178>
- 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 (27–28): 1751–1765. <https://doi.org/10.1080/00222933.2019.1660429>
- Halffter G, Favila ME (1993) The Scarabaeinae (Insecta: Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. *Biology International* 27: 15–21.
- Halffter G, Matthews EG (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomológica Mexicana* 12: 1–312.
- Hernández MIM (2003) Riqueza de besouros escarabeídeos em duas áreas de Floresta Atlântica no Estado da Paraíba. In: Claudino-Sales V, Tonini IM, Dantas EWC (Eds) Anais de trabalhos completos do VI Congresso de Ecologia de Brasil, Simpósio Floresta Pluvial Tropical Atlântica, 9 a 14 de novembro de 2003. Editora da Universidade Federal do Ceará, Fortaleza, 300–302.
- Hernández MIM (2005) Besouros Scarabaeidae (Coleoptera) da área do Curimataú, Paraíba. In: FC Araújo, MJN Rodal, MRV Barbosa (Eds) Análise das variações de biodiversidade do bioma Caatinga: suporte a estratégias regionais de conservação. Ministério do Meio Ambiente, Brasília, 370–380.
- Hernández MIM (2007) Besouros escarabeíneos (Coleoptera: Scarabaeidae) da Caatinga Paraíba, Brasil. *Oecologia brasiliensis* 11 (3): 356–364. <https://doi.org/10.4257/oeco.2007.1103.06>

- IBGE (1985) Atlas nacional do Brasil: região Nordeste. IBGE, Rio de Janeiro, 114 pp.
- Ledo RMD, Colli G R (2017) The historical connections between the Amazon and the Atlantic Forest revisited. *Journal of Biogeography* 44 (11): 2551–2563. <https://doi.org/10.1111/jbi.13049>
- Leite CMP, Mariano-Neto E, Rocha PLB (2018) Biodiversity thresholds in invertebrate communities: the responses of dung beetle subgroups to forest loss. *PloS ONE* 13 (8): e0201368. <https://doi.org/10.1371/journal.pone.0201368>
- Liberal CN, Farias ÂMI, Meiado MV, Filgueiras BK, Iannuzzi L (2011) How habitat change and rainfall affect dung beetle diversity in caatinga, a Brazilian semi-arid ecosystem. *Journal of Insect Science* 11 (1): 114. <https://doi.org/10.1673/031.011.11401>
- Lima MGA, Almeida Silva RP, Sousa MDF, Costa EM (2013) Diversidade de Scarabaeinae (Coleoptera: Scarabaeidae) no Parque Botânico do Ceará, Caucaia-CE, Brasil. *Revista Agro@mbiente On-line* 7 (1): 89–94. <https://doi.org/10.18227/1982-8470ragro.v7il.970>
- Lopes J, Korasaki V, Catelli LL, Marçal VVM, Nunes MPBP (2011) A Comparison of Dung Beetle Assemblage Structure (Coleoptera: Scarabaeidae: Scarabaeinae) between an Atlantic Forest fragment and adjacent abandoned pasture in Paraná, Brazil. *Zoologia* 28 (1): 72–79. <https://doi.org/10.1590/S1984-46702011000100011>
- Lopes PP, Louzada JNC, Vaz-de-Mello FZ (2006) Organization of dung beetle communities (Coleoptera: Scarabaeidae) in areas of vegetation re-establishment in Feira de Santana, Bahia, Brazil. *Sistentibus Séries Ciências Biológicas* 6 (4): 261–266.
- Lopes PP, Vaz-de-Mello FZ, Reis VPGS, Rebouças PLO (2003) Besouros detritívoros (Coleoptera: Scarabaeidae) de uma reserva de Mata Atlântica no litoral Norte da Bahia (Reserva da Sapiranga, município Mata de São João). In: XIV Encontro de Zoologia do Nordeste: A Zoologia no Desenvolvimento Sustentável (Ed.) Livro de Resumos 14. Editora da Universidade Federal de Alagoas (EDUFAL), Maceió, 247–247.
- Maldaner ME, Nunes RV, Vaz-De-Mello FZ (2015) Taxonomic revision of the *Dichotomius speciosus* (Waterhouse, 1891) species group (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 3986 (5): 549–560. <https://doi.org/10.11646/zootaxa.3986.5.2>
- Maldaner ME, Valois MC, Vaz-de-Mello FZ (2018) A revision of *Dichotomius* (Homocanthionides) Luederwaldt, 1929 (Coleoptera: Scarabaeidae: Scarabaeinae). *Revista Brasileira de Entomologia* 62 (3): 237–242. <https://doi.org/10.1016/j.rbe.2018.05.001>
- Mayer AC, Vasconcelos SD (2013) Necrophagous beetles associated with carcasses in a semi-arid environment in Northeastern Brazil: implications for forensic entomology. *Forensic Science International* 226 (1–3): 41–45. <https://doi.org/10.1016/j.forsciint.2012.11.019>
- Medina AM, Lopes PP (2014) Resource utilization and temporal segregation of Scarabaeinae (Coleoptera, Scarabaeidae) community in a Caatinga fragment. *Neotropical entomology* 43 (2): 127–133. <https://doi.org/10.1007/s13744-014-0198-9>
- Medri ÍM, Lopes J (2001) Scarabaeidae (Coleoptera) do Parque Estadual Mata Dos Godoy e de área de pastagem, no norte do Paraná, Brasil. *Revista Brasileira de Zoologia* 18: 135–141. <https://doi.org/10.1590/S0101-81752001000500011>
- Moctezuma V, Deloya C, Sánchez-Huerta JL, Halfiter G (2019) A new species of the *Phanaeus endymion* species group (Coleoptera: Scarabaeidae: Scarabaeinae), with comments on ecology and distribution. *Annales de la Société entomologique de France (N.S.)* 55: 1–6. <https://doi.org/10.1080/00379271.2019.1577170>
- Morrone JJ (2014) Biogeographical regionalisation of the Neotropical region. *Zootaxa* 3782: 1–110. <https://doi.org/10.11646/zootaxa.3782.1.1>
- Nunes, LGOA (2015) Revisão taxonômica das espécies de *Canthon* Hoffmannsegg do grupo *septemmaculatus* Latreille (Coleoptera: Scarabaeidae: Scarabaeinae: Deltotilini). MSc thesis, Universidade Federal de Mato Grosso, Cuiabá, 67 pp.
- Nunes LGOA, Nunes RV, Vaz-De-Mello FZ (2018) Taxonomic revision of the South American subgenus *Canthon* (Goniocanthon) Pereira & Martínez, 1956 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltotilini). *European Journal of Taxonomy* 2018 (437): 1–31. <https://doi.org/10.5852/ejt.2018.437>
- Nunes LGOA, Nunes RV, Vaz-de-Mello FZ (2020) Taxonomic revision of the South American subgenus *Canthon* (*Peltecanthon*) Pereira, 1953 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltotilini). *European Journal of Taxonomy* 594: 1–27. <https://doi.org/10.5852/ejt.2020.594>
- Nunes RV, Vaz-de-Mello FZ (2013) New brachypterous species of *Dichotomius* Hope, with taxonomic notes in the subgenus *Luederwaldtinia* Martínez (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 3609 (4): 411–420. <https://doi.org/10.11646/zootaxa.3609.4.3>
- Nunes RV, Vaz-de-Mello FZ (2016) New brachypterous species of *Dichotomius* (Selenocoprini) Burmeister (Coleoptera: Scarabaeidae: Scarabaeinae) with the definition of species groups and taxonomic in the subgenus. *Zootaxa* 4139 (1): 76–92. <https://doi.org/10.11646/zootaxa.4139.1.4>
- Nunes RV, Vaz-de-Mello FZ (2019) Taxonomic revision of *Dichotomius* (*Cephagonus*) Luederwaldt 1929 and the taxonomic status of remaining *Dichotomius* Hope, 1838 subgenera (Coleoptera: Scarabaeidae: Scarabaeinae: Dichotomiini). *Journal of Natural History* 53 (37–38): 2231–2351. <https://doi.org/10.1080/00222933.2019.1692088>
- Pacheco TL, Vaz-de-Mello FZ (2019) New dung beetle genus and species from a cave in the Espinhaço mountain range, Brazil (Coleoptera: Scarabaeidae: Scarabaeinae). *Journal of Natural History* 53 (19–20): 1247–1253. <https://doi.org/10.1080/00222933.2019.1640907>
- Pergentino HES (2015) Qual a contribuição dos escarabeíneos (Coleoptera: Scarabaeidae: Scarabaeinae) no processo de dispersão de sementes na caatinga? Bachelor final paper, Universidade Federal do Vale do São Francisco, Petrolina, 56 pp.
- Prance GT (1982) Forest refuges: evidence from woody angiosperms. In: Prance GT (Ed.) *Biological diversification in the tropics*. Columbia University Press, New York, 158 pp.
- Rodrigues ASL, Andelman SJ, Bakarr MI, Boitani L, Brooks TM, Cowling RM, Fishpool LDC, Fonseca GAB, Gaston KJ, Hoffmann M, Long JS, Marquet PA, Pilgrim JD, Pressey RL, Schipper J, Sechrest W, Stuart SN, Underhill LG, Waller RW, Watts MEJ, Yan X (2004) Effectiveness of the Global Protected Area Network in representing species diversity. *Nature* 428 (6983): 640–643. <https://doi.org/10.1038/nature02422>
- Rossini M, Vaz-de-Mello FZ (2020) Taxonomic review of the *Dichotomius* *macillatus* group (Coleoptera: Scarabaeidae), with a description of a new species, *Dichotomius* (*Dichotomius*) *gandini* sp. nov., from western Amazonia. *Austral Entomology* 59 (1): 52–73. <https://doi.org/10.1111/aen.12443>
- Salomão RP, Iannuzzi L (2015) Dung Beetle (Coleoptera, Scarabaeidae) assemblage of a highly fragmented landscape of Atlantic Forest: from small to the largest fragments of Northeastern Brazilian region. *Revista Brasileira de Entomologia* 59 (2): 126–131. <https://doi.org/10.1016/j.rbe.2015.03.008>
- Salomão RP, Alvarado F, Baena-Díaz F, Favila ME, Iannuzzi L, Liberal CN, Santos BA, Vaz-de-Mello FZ, González-Tokman D (2019) Urbanization effects on dung beetle assemblages in a tropical city. *Ecological Indicators* 103: 665–675. <https://doi.org/10.1016/j.ecolind.2019.04.045>
- Santos AMM, Cavalcanti DR, Silva JMC, Tabarelli M (2007) Biogeographical relationships among tropical forests in North-Eastern Brazil. *Journal of Biogeography* 34 (3): 437–446. <https://doi.org/10.1111/j.1365-2699.2006.01604.x>
- Santos VM, Cáceres MES, Lücking R (2019) Diversity of foliicolous lichens in isolated montane rainforests (brejos) of northeastern Brazil and their biogeography in a Neotropical context. *Ecological Research* 35: 182–197. <https://doi.org/10.1111/1440-1703.12071>



- Silva EEN (2017) Revisão taxonômica de *Deltochilum* (*Euhyboma*) Kolbe 1893, *D. (Parahyboma)* Paulian 1938 e *D. (Rubrohyboma)* Paulian 1939 (Coleoptera: Scarabaeidae: Scarabaeinae). BSc, Universidade Federal do Pará, Pará, 44 pp.
- Silva FAB (2011) First Record of *Coprophanaeus Bellicosus* (Olivier) (Coleoptera, Scarabaeidae) in a “brejo de altitude” forest in Northeastern Brazil: a historical biogeographical approach. *Revista Brasileira de Entomologia* 55 (4): 615–617. <https://doi.org/10.1590/S0085-56262011000400020>
- Silva FAB, Valois M (2019) A taxonomic revision of the genus *Scyb-alocanthon* Martínez, 1948 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini). *Zootaxa* 4629 (3): 301–341. <https://doi.org/10.11646/zootaxa.4629.3.1>
- Silva FAB, Louzada J, Vaz-de-Mello FZ (2015) A revision of the *Deltochilum* subgenus *Aganhyboma* Kolbe, 1893 (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 3925 (4): 451–504. <https://doi.org/10.11646/zootaxa.3925.4.1>
- Silva FAB, Hernández MIM, Ide S, Moura RC (2007) Comunidade de escarabeíneos (Coleoptera, Scarabaeidae) copro-necrófagos da região de Brejo Novo, Caruaru, Pernambuco, Brasil. *Revista Brasileira de Entomologia* 51 (2): 228–233. <https://doi.org/10.1590/S0085-56262007000200014>
- Silva FAB, Costa CMQ, Moura RC, Farias AI (2010) Study of the dung beetle (Coleoptera: Scarabaeidae) community at two sites: Atlantic Forest and clear-cut, Pernambuco, Brazil. *Environment Entomology* 39 (2): 359–367. <https://doi.org/10.1603/EN09180>
- Silva FAB, Vidaurre T, Vaz-de-Mello F, Louzada J (2012a) Predatory behaviour in *Deltochilum*: convergent evolution or a primitive character within a clade? *Journal of Natural History* 46 (21–22): 1359–1367. <https://doi.org/10.1080/00222933.2012.658584>
- Silva FAB, Moura ABG, Araújo JF, de Moura RC (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>
- Silva PG, Vaz-de-Mello FZ, Mare RAD (2011) Identification handbook of the Scarabaeinae species (Coleoptera: Scarabaeidae) of the city of Santa Maria, Rio Grande do Sul, Brazil. *Biota Neotropica* 11 (4): 329–345. <https://doi.org/10.1590/S1676-06032011000400027>
- Silva SM, Moraes-Barros N, Ribas CC, Ferrand N, Morgante JS (2012b) Divide to conquer: a complex pattern of biodiversity depicted by vertebrate components in the Brazilian Atlantic Forest. *Biological Journal of the Linnean Society* 107: 39–55. <https://doi.org/10.1111/j.1095-8312.2012.01919.x>
- Sobral-Souza T, Lima-Ribeiro MS (2017) De volta ao passado: revisitando a história biogeográfica das florestas neotropicais úmidas. *Oecologia Australis* 21 (2): 93–107. <https://doi.org/10.4257/oeco.2017.2102.01>
- Tabarelli M, Melo MDVC, Lira OC (2006) A Mata Atlântica do nordeste. Mata Atlântica: uma rede pela floresta. Atthaláia Gráfica e Editora Ltda, São Paulo, 149–164.
- 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 (3): 1–86. <https://doi.org/10.1371/journal.pone.0116671>
- 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>
- Valois MC, Vaz-de-Mello FZ, Silva FA (2017) Taxonomic revision of the *Dichotomius sericeus* (Harold, 1867) species group (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 4277 (4): 503–530. <https://doi.org/10.11646/zootaxa.4277.4.3>
- Vaz-de-Mello F (2000) Estado atual de conhecimento dos Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) do Brasil. *Monografias Tercer Milenio* 1: 183–195.
- Vaz-de-Mello FZ (2020) Scarabaeinae in Catálogo Taxonômico da Fauna do Brasil. PNUD. <https://fauna.jbrj.gov.br/fauna/faunado-brasil/127498> Accessed on: 2020-1-14.
- Vaz-de-Mello FZ, Nunes LGDOA, Costa-Silva VD (2020) A new species of the genus *Canthon* Hoffmannsegg (Coleoptera, Scarabaeidae, Scarabaeinae, Deltochilini) from central Brazil. *Papéis Avulsos de Zoologia* 60: 1–6. <https://doi.org/10.11606/1807-0205/2020.60.special-issue.04>
- Vaz-de-Mello FZ, Edmonds WD, Ocampo FC, Schoolmeesters P (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* 2854 (1): 1–73. <https://doi.org/10.11646/zootaxa.2854.1.1>
- Vaz-de-Mello FZ, Larsen T, Silva F, Gill B, Spector S, Favila M (2014) *Deltochilum brasiliense*. The IUCN Red List of threatened species 2014. <https://doi.org/10.2305/iucn.uk.2014-1.rlts.t138098a536070.en> Accessed on: 2020-1-14.
- Vieira L, Silva FAB (2012) Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) of the Floresta Nacional Contendas do Sincorá, Bahia, Brazil. *Check List* 8 (4): 733–739. <https://doi.org/10.15560/8.4.733>
- Vieira L, Silva FAB, Louzada J (2017) Dung beetles in a Caatinga natural reserve: a threatened Brazilian dry-forest with high biological value. *Iheringia, Série Zoologia* 107: 1–6. <https://doi.org/10.1590/1678-4766e2017045>
- Vieira MK, Vaz-de-Mello FZ, Silva FA (2019) A taxonomic revision of the *Canthon* subgenus *Pseudepilissus* Martínez, 1954 (Coleoptera: Scarabaeidae: Scarabaeinae). *Insect Systematics & Evolution* 51 (4): 696–752. <https://doi.org/10.1163/1876312X-00001023>