




Identification guide of dung beetle species (Coleoptera: Scarabaeidae: Scarabaeinae) of the Brazilian Pantanal

Adriana Andrade Mota^{1,5*} , Edrielly Carvalho², César M. A. Correa³ & Fernando Z. Vaz-de-Mello⁴

¹Universidade Rural Federal de Pernambuco, Departamento de Agronomia/Fitossanidade, 52171-900, Recife, PE, Brasil.

²Instituto Nacional de Pesquisas da Amazônia, Programa de Pós-Graduação em Entomologia, 69011-970, Manaus, AM, Brasil.

³Universidade Estadual de Mato Grosso do Sul, Laboratório de Bioecologia de Scarabaeoidea, 79200-000, Aquidauana, MS, Brasil.

⁴Universidade Federal de Mato Grosso, Instituto de Biociências, Departamento de Biologia e Zoologia, Av. Fernando Correia da Costa, Coxipó, 78060-900, Cuiabá, MT, Brasil.

⁵Universidade Federal do Paraná, Departamento de Zoologia, Setor de Ciências Biológicas, 81531-980, Curitiba, PR, Brasil.

*Corresponding author: adrianaandrademota@gmail.com

MOTA, A.A., CARVALHO, E., CORREA, C.M.A., VAZ-DE-MELLO, F.Z. **Identification guide of dung beetle species (Coleoptera: Scarabaeidae: Scarabaeinae) of the Brazilian Pantanal.** *Biota Neotropica* 23(2): e20221443. <https://doi.org/10.1590/1676-0611-BN-2022-1443>

Abstract: The Pantanal is the largest seasonal freshwater wetland on Earth, characterized by the seasonal flooding and complex mosaic vegetation, which determines its biodiversity. Among this biodiversity, dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are a group of insects that perform important ecological functions, such as: nutrient cycling, seed dispersion and parasite control. In order to mitigate the lack of information on dung beetle fauna of the Brazilian Pantanal, we conducted a bibliographic search of virtually all literature published until november-2020 on dung beetles sampled in the Pantanal. In addition, we had accessed to the records the largest collection of the dung beetle species from Brazilian Pantanal. We recorded 68 dung beetle species of 30 genera. The genera *Canthon* Holffmanseg 1847 is the most diverse with 13 species recorded. Although our knowledge about the dung beetle fauna in this ecosystem is still incipient, our results demonstrated a high richness of dung beetles in the Brazilian Pantanal. In addition, our study provides first list of dung beetle species and an illustrated dichotomy key to identify genera and some species occurring in the Brazilian Pantanal. Thus, the use of this guide for identification of dung beetle species and a list of species can be important tools to help researchers and provide incentive for new inventories on dung beetle fauna in the Brazilian Pantanal.

Keywords: Checklist; insect diversity; humid zones; dichotomous key; wetlands.

Guia de identificação de espécies de besouros rola-bostas (Coleoptera: Scarabaeidae: Scarabaeinae) do Pantanal Brasileiro

Resumo: O Pantanal é a maior área úmida sazonal de água doce Neotropical da Terra, caracterizada pelas inundações sazonais e pela complexa vegetação em mosaico, que determina sua biodiversidade. Dentre essa biodiversidade, os besouros rola-bosta (Coleoptera: Scarabaeidae: Scarabaeinae) são um grupo de insetos que desempenham importantes funções ecológicas, tais como: ciclagem de nutrientes, dispersão de sementes e controle de parasitas. A fim de mitigar a falta de informações sobre a fauna de besouros rola-bosta do Pantanal brasileiro, realizamos uma pesquisa bibliográfica de praticamente toda a literatura publicada até novembro de 2020 sobre besouros rola-bosta amostrados no Pantanal. Além disso, acessamos os registros da maior coleção da espécie de rola-bosta do Pantanal brasileiro. Registramos 68 espécies de besouros rola-bosta de 30 gêneros. O gênero *Canthon* Holffmanseg 1847 é o mais diverso com 13 espécies registradas. Embora nosso conhecimento sobre a fauna de rola-bostas neste ecossistema ainda seja incipiente, nossos resultados demonstraram uma alta riqueza de besouros rola-bosta no Pantanal brasileiro. Além disso, nosso estudo fornece a primeira lista de espécies de besouros rola-bosta e uma chave de dicotomia ilustrada para identificar gêneros e algumas espécies encontrados no Pantanal brasileiro. Assim, a utilização deste guia para identificação das espécies de besouros rola-bostas e uma lista de espécies podem ser ferramentas importantes para auxiliar pesquisadores e incentivar novos inventários sobre a fauna de besouros rola-bostas no Pantanal brasileiro.

Palavras-chave: Checklist; diversidade de insetos; áreas úmidas; chaves dicotômicas; áreas alagadas.

Introduction

The Pantanal is the largest seasonal freshwater wetland on Earth (ca. 160,000 km²), and also considered a World Heritage Site and Biosphere Reserve (UNESCO, 2000). This extensive wetland is located in Brazil (states of Mato Grosso and Mato Grosso do Sul) with approximately 130,000 km², 15,000 km² in Bolivia and 5,000 km² in Paraguay (Cunha et al. 2014) and has a vegetation system arranged in a mosaic (i.e., different plant communities scattered side-by-side across space) (Pott et al. 2011). Furthermore, two well-defined ecohydrology cycles can be identified in the Pantanal: dry and rainy. In the dry season, the surface water becomes scarce, being restricted to the perennial rivers (with defined beds) and large ponds (Alho & Sabino 2011; Nunes et al. 2014). Thus, the seasonal flooding and complex mosaic vegetation determine a biodiversity unique adapted to Brazilian Pantanal (Junk et al. 2006; Tomas et al. 2019).

Among this biodiversity, insects, such as dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), are essential for the maintenance of ecosystem functioning in the Brazilian Pantanal (Correa et al. 2020). Dung beetles are broadly distributed and highly diverse taxonomically and functionally (Halffter & Edmonds 1982; Hanski & Cambefort 1991). They are represented by more than 6,837 species worldwide which belong to 278 genera (Schoolmeesters 2023). Their feeding behavior is quite varied, most species being coprophagous, but there are also species that feed on decaying carcasses, fungi and fruits, and can even be predators or generalists (Halffter & Matthews 1966). They can be classified into three functional groups based on food allocation behavior and/or nesting behavior: (1) roller (telecoprid) species that remove portions of dung, which are rolled away from the food resource and then buried; (2) tunneler (paracoprid) species that construct tunnels below or adjacent to the food resource and transport dung into them; and (3) dweller (endocoprid) species that nest within a dung pad and do not exhibit resource allocation (Halffter & Matthews 1966; Hanski & Cambefort 1991).

When dung beetles bury food resources (e.g. feces, carcass and fruits), they provide important ecological functions and services in natural and anthropogenic ecosystems, such as: increased water infiltration and soil porosity, improved herbaceous plant growth, reduction of livestock gastrointestinal parasite and dung-fly availability (Nichols et al. 2008) and greenhouse gas emissions from dung pats (Slade et al. 2016; Piccini et al. 2017). In addition, these beetles have been widely used as both ecological and biodiversity indicators because they are sensitive to natural and anthropogenic changes (Halffter & Favila 1993; McGeoch et al. 2002; Nichols et al. 2007), are easily sampled with standardized protocols (Correa et al. 2018; Gardner et al. 2008; da Silva & Hernández 2015) and are diverse and relatively well characterized taxonomically (Vaz-de-Mello et al. 2011).

Although studies on dung beetle assemblages have been growing recently in the Brazilian Pantanal (Tissiani et al. 2015; Daniel & Vaz-de-Mello 2016, Pessôa et al. 2017; Correa et al. 2016, 2019, 2020, 2021, 2022a, b; Correa & da Silva 2022, Gonçalves et al. 2022), our knowledge on dung beetle fauna in this biome is incipient. Indeed, the Pantanal is one of the least known ecosystems in terms of biodiversity of Brazil (Lewinsohn et al. 2005). Therefore, new inventories of dung beetles in different localities are essential to increase new records of dung beetle species in the Brazilian Pantanal. In this study, we bring a

list of dung beetle species of the Brazilian Pantanal and an illustrated identification key.

Material and Methods

We used the Scopus and Web of Science databases to search for literature on the dung beetles in the Brazilian Pantanal, following the PRISMA methodology (Moher et al. 2009), which only considers indexed articles. The following search terms were used: (“Dung beetle*” OR “Scarabaeinae*” OR “coprophagous beetles*”) AND (“Wetland*” OR “Pantanal*” OR “humid zones”). We complemented the taxonomic diversity search by including articles published in Portuguese from the authors’ collection. The search window of time covered articles published between January 2007 to November 2020.

Our search returned 40 articles, regarding dung beetle species in wetlands. The relevant articles were selected using the following criteria: i) the study includes species from Scarabaeinae subfamily, ii) the study is based partly or entirely in Brazilian Pantanal (e.g., Mato Grosso and Mato Grosso do Sul states). Under these criteria, 10 articles were retained for data extraction (e.g. Louzada et al. 2007; Rodrigues et al. 2010; Tissiani et al. 2015; Daniel & Vaz-de-Mello 2016; Pessôa et al. 2017; Vaz-de-Mello et al. 2017; Correa et al. 2016, 2019, 2020), only species identified at a specific level were considered. In addition, 10 genera have been added to the identification key that have a good chance of being collected in the Brazilian Pantanal region (Vaz-de-Mello personal communication). The genera that are under taxonomic revision are not included in the identification keys with their respective species that occur in the Pantanal.

All previously existing records were reviewed for their identifications (when possible, we used specimen vouchers) for correct species identification. We also list the records of the Entomology Section of the Zoological Collection at the UFMT (CEMT, curator F. Z. Vaz-de-Mello). Currently, it is considered one of the most important collections of dung beetles in the world, with specimens from all regions of Brazil and across the globe, making it possible to assemble a list of species from the different Brazilian biomes (Tissiani et al. 2017). The dung beetle species mentioned in the present study are classified according to their nesting behavior, following the classification by Hanski & Cambefort (1991).

Finally, an identification key was constructed to identify the genera and species of dung beetles present in Brazilian Pantanal. Its main structure from Vaz-de-Mello et al. (2011), and this was refined based on the analysis of the external morphology of the species, including – where necessary – the secondary sexual characteristics.

Leica M205A stereomicroscope coupled with a Leica DMC4500 and a Leica Application Suite V4.10.0 Interactive Measurements, Montage was used for the photos.

Results

The dung beetle fauna of the Brazilian pantanal is composed of 68 species in 30 genera. The most diverse genera are: *Canthon Hoffmannsegg*, 1817 (13 species), *Dichotomius* Hope, 1838 (nine species) and *Ontherus* Erichson, 1847 (seven species) (Table 1). Paracoprid beetles correspond to 48.35% of all species recorded, whereas telecoprid and endocoprid accounted for 34.37% and 17.28% of all species recorded, respectively (Table 1).

Table 1. List of dung beetle species that occur in the Pantanal with bibliography data separated by their functional group.

Species	Functional group	References
<i>Canthidium angulicolle</i> Balthasar, 1939	Paracoprid	Vaz-de-Mello et al. 2017
<i>Canthidium barbaticum</i> Preudhomme de Borre, 1886	Paracoprid	Louzada et al. 2007; Pessôa et al. 2017; Vaz-de-Mello et al. 2017; Correia et al. 2020, 2022b
<i>Canthidium breve</i> (Germar, 1824)	Paracoprid	Louzada et al. 2007; Vaz-de-Mello et al. 2017
<i>Canthidium cuprinum</i> Harold, 1867	Paracoprid	Pessôa et al. 2017
<i>Canthidium kelleri</i> (Martinez, Halfter & Pereira)	Paracoprid	Daniel and Vaz-de-Mello 2015
<i>Canthidium viride</i> (Lucas, 1859)	Paracoprid	Pessôa et al. 2017; Vaz-de-Mello et al. 2017; Correia et al. 2022b
<i>Canthon conformis</i> (Harold, 1868)	Telecoprid	Correia et al. 2022b
<i>Canthon chalybaeus</i> Blanchard 1845	Telecoprid	Daniel and Vaz-de-Mello 2015
<i>Canthon curvodilatatus</i> Schmidt, 1922	Telecoprid	Tissiani et al. 2015; Correa et al. 2016, 2019, 2020; Vaz-de-Mello et al. 2017; Pessôa et al. 2017; Correia et al. 2022b
<i>Canthon daguerrei</i> Martínez, 1951	Telecoprid	Pessôa et al. 2017
<i>Canthon edentulus</i> Harold, 1868	Telecoprid	Daniel and Vaz-de-Mello 2015; Vaz-de-Mello et al. 2017; Correa et al. 2016, 2020
<i>Canthon histrio</i> (Lepelletier de Saint-Fargeau & Audinet-Serville, 1828)	Telecoprid	Louzada et al. 2010; Correa et al. 2016, 2019, 2020, 2022b; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Canthon mutabilis</i> Lucas, 1859	Telecoprid	Correa et al. 2016, 2020; Vaz-de-Mello et al. 2017
<i>Canthon maldonadoi</i> (Pereira & Martinez, 1960)	Telecoprid	Daniel and Vaz-de-Mello 2015; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Canthon ornatus ornatus</i> Redtenbacher, 1867	Telecoprid	Tissiani et al. 2015; Correa et al. 2016, 2020; Vaz-de-Mello et al. 2017
<i>Canthon quadratus</i> Blanchard, 1846	Telecoprid	Vaz-de-Mello et al. 2017
<i>Canthon quinquemaculatus</i> Castelnau, 1840	Telecoprid	Louzada et al. 2007; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Canthon substriatus</i> Harold, 1868	Telecoprid	Correa et al. 2016, 2020; Vaz-de-Mello et al. 2017
<i>Canthon unicolor</i> Blanchard, 1843	Telecoprid	Vaz-de-Mello et al. 2017; Correia et al. 2022b
<i>Canthon virens</i> (Mannerheim, 1828)	Telecoprid	Daniel and Vaz-de-Mello 2015
<i>Coprophanaeus bonariensis</i> (Gory, 1844)	Paracoprid	Correa et al. 2016, 2019, 2020; Pessôa et al. 2017
<i>Coprophanaeus cyanescens</i> (d'Olsoufieff, 1924)	Paracoprid	Vaz-de-Mello et al. 2017; Correa et al. 2019; Correa et al. 2022b
<i>Coprophanaeus ensifer</i> (Germar, 1824)	Paracoprid	Daniel and Vaz-de-Mello 2015; Correa et al. 2016, 2020
<i>Coprophanaeus spitzii</i> (Pessoa, 1935)	Paracoprid	Correia et al. 2022b
<i>Coprophanaeus milon</i> (Blanchard, 1846)	Paracoprid	Correa et al. 2016, 2020; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Dendropaemon nitidicollis</i> d'Olsoufieff, 1924	Unknown	Correa et al. 2022a
<i>Deltochillum cupreicolle</i> (Blanchard)	Telecoprid	Daniel and Vaz-de-Mello 2015
<i>Deltochillum silphoides</i> Balthasar, 1939	Telecoprid	Pessoa et al. 2017; Vaz-de-Mello et al. 2017
<i>Deltochillum icaroides</i> Balthasar, 1939	Telecoprid	Vaz-de-Mello et al. 2017
<i>Deltochillum pseudoicarus</i> Balthasar, 1939	Telecoprid	Daniel and Vaz-de-Mello 2015; Correa et al. 2016, 2019, 2020; Vaz-de-Mello et al. 2017
<i>Dichotomius carbonarius</i> (Mannerheim, 1929)	Paracoprid	Vaz-de-Mello et al. 2017
<i>Dichotomius bos</i> (Blanchard, 1845)	Paracoprid	Louzada et al. 2007; Rodrigues et al. 2010; Correa et al. 2016, 2019, 2020, 2022b; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Dichotomius cuprinus</i> (Felsche, 1901)	Paracoprid	Daniel and Vaz-de-Mello 2015; Correia et al. 2022b
<i>Dichotomius glaucus</i> (Harold, 1869)	Paracoprid	Correa et al. 2016, 2019, 2020; Vaz-de-Mello et al. 2017
<i>Dichotomius luctuosoides</i> (Harold, 1869)	Paracoprid	Vaz-de-Mello et al. 2017
<i>Dichotomius lycas</i> (Felsche, 1901)	Paracoprid	Pessôa et al. 2017
<i>Dichotomius nisus</i> (Olivier, 1789)	Paracoprid	Louzada et al. 2007; Rodrigues et al. 2010; Tissiani et al. 2015; Correa et al. 2016, 2019, 2020, 2022b; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Dichotomius opacipennis</i> (Luederwaldt, 1931)	Paracoprid	Tissiani et al. 2015; Correa et al. 2016, 2019, 2020, 2022b; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Dichotomius sexdentatus</i> (Luederwaldt, 1925)	Paracoprid	Daniel and Vaz-de-Mello 2015
<i>Digitonthophagus gazella</i> (Fabricius, 1787)	Paracoprid	Correa et al. 2016, 2019, 2020, 2022b
<i>Eurysternus aeneus</i> Génier, 2009	Endocoprid	Vaz-de-Mello et al. 2017; Correa et al. 2019
<i>Eurysternus caribaeus</i> (Herbst, 1789)	Endocoprid	Correa et al. 2016, 2019, 2020; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Eurysternus jessopi</i> Martinez, 1988	Endocoprid	Daniel and Vaz-de-Mello 2015

Continue...

...Continuation

Species	Functional group	References
<i>Eurysternus nigrovirens</i> Génier, 2009	Endocoprid	Daniel and Vaz-de-Mello 2015; Correa et al. 2016, 2020, 2022b; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Eurysternus plebejus</i> Harold, 1880	Endocoprid	Vaz-de-Mello et al. 2017
<i>Genieridium cryptops</i> (Arrow, 1913)	Endocoprid	Daniel and Vaz-de-Mello 2015; Pessôa et al. 2017
<i>Genieridium bidens</i> (Balthasar, 1938)	Endocoprid	Correa et al. 2016, 2020
<i>Gromphas inermis</i> Harold, 1869	Paracoprid	Daniel and Vaz-de-Mello 2015; Correa et al. 2016, 2020; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Isocopris foveolatus</i> (Luederwaldt, 1931)	Paracoprid	CEMT
<i>Malagoniella astyanax</i> (Oliver, 1789)	Telecoprid	Daniel and Vaz-de-Mello 2015; Correa et al. 2016, 2020; Vaz-de-Mello et al. 2017
<i>Malagoniella punctatostrata</i> (Blanchard, 1846)	Telecoprid	Vaz-de-Mello et al. 2017; Correa et al. 2019; Correa et al. 2022b
<i>Malagoniella puncticollis</i> (Blanchard, 1846)	Telecoprid	Correa et al. 2016, 2019, 2020; Vaz-de-Mello et al. 2017
<i>Ontherus azteca</i> Harold, 1869	Paracoprid	CEMT
<i>Ontherus aphodioides</i> Burmeister, 1874	Paracoprid	CEMT
<i>Ontherus appendiculatus</i> (Mannerheim, 1829)	Paracoprid	Louzada et al. 2007; Rodrigues et al. 2010; Tissiani et al. 2015; Correa et al. 2016, 2019, 2020, 2022b; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Ontherus dentatus</i> Luederwaldt, 1930	Paracoprid	Vaz-de-Mello et al. 2017
<i>Ontherus digitatus</i> Harold, 1869	Paracoprid	Vaz-de-Mello et al. 2017; Pessôa et al. 2017
<i>Ontherus erosioides</i> Luederwaldt, 1930	Paracoprid	Vaz-de-Mello et al. 2017
<i>Ontherus sulcator</i> (Fabricius, 1775)	Paracoprid	Louzada et al. 2007; Tissiani et al. 2015; Correa et al. 2016, 2020; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Onthophagus hircus</i> Billberg, 1815	Paracoprid	Correia et al. 2022b
<i>Phanaeus kirbyi</i> Vigors, 1825	Paracoprid	Daniel and Vaz-de-Mello 2015
<i>Phanaeus palaeno</i> Blanchard, 1846	Paracoprid	Daniel and Vaz-de-Mello 2015; Vaz-de-Mello et al. 2017
<i>Pseudocanthon xanthurus</i> (Blanchard, 1845)	Telecoprid	Louzada et al. 2007; Vaz-de-Mello et al. 2017
<i>Sulcophanaeus menelas</i> (Castelnau, 1840)	Paracoprid	Vaz-de-Mello et al. 2017
<i>Trichillidium quadridens</i> Arrow, 1932	Endocoprid	Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Trichillum externepunctatum</i> Preudhomme de Borre, 1886	Endocoprid	Louzada et al. 2007; Tissiani et al. 2015; Correa et al. 2016, 2020, 2022b; Pessôa et al. 2017; Vaz-de-Mello et al. 2017
<i>Zonocopris gibbicollis</i> (Harold, 1868)	Endocoprid	Vaz-de-Mello et al. 2017
<i>Uroxys corporaali</i> Harold, 1868	Endocoprid	CEMT

Key to identification of dung beetle genera

1. Scutellum visible dorsally (**Figure 1A**).....2
 - Scutellum not visible dorsally (**Figure 1B**).....3
2. (1) Body flattened dorsally, elongated, with parallel sides. Labial palpi with two palpomeres; Mesocoxae parallel to the longitudinal axis of the body, positioned externally in relation to the metaventricle. Pronotum with basal margination (**Figure 2A;C**).....
 -*Eurysternus* Dalman, 1824
 - Body slightly convex dorsally, without parallel sides, usually oval. Labial palpi with more than two palpomeres; Mesocoxae perpendicular or oblique to the longitudinal axis of the body. Pronotum without basal margination (**Figure 2B;D**).....
 - *Malagoniella* Martínez, 1961
3. (1) Anterior leg with trochantofemoral fovea (**Figure 3A**).....4
 - Anterior leg without trochantofemoral fovea (**Figure 3B**).....11
4. (3) Last abdominal ventrite greatly expanded in the middle, covering the entire disc of the abdomen. The other ventrites visible only on the sides of the abdomen (**Figure 4A**).....5
 - Last abdominal ventrite not covering the entire disc, other ventrites visible and clearly distinguishable in the middle of the abdomen (**Figure 4B**).....9
5. (4) Pseudepipleuron forming two lateral sinuosities, posterior partially (which is at the height of the metacoxa) covers the epipleuron, which is sharply narrowed towards the apex (**Figure 5A**).....6
 - Pseudepipleuron not forming two lateral sinuosities, epipleura gradually narrowed to apex (**Figure 5B**).....8
6. (5) Straight or slightly curved edge of the clypeus on each side between the clypeal tooth and the clypeogenal suture (**Figure 6B**)*Trichillum* Harold, 1868
 - Edge of clypeus with strong rounded lobe or angulation between clypeal tooth and clypeogenal suture (**Figure 6A**).....7

7. (6) Clypeogenal margin with an incision over the suture, clypeus and gena appear separately rounded (**Figure 7A**).....
Eutrichilum Martínez, 1969
 – Clypeogenal margin straight to slightly sinuous (**Figure 7B**).....
Besourena Vaz-de-Mello, 2008
8. (5) Head with four clypeal teeth, rounded body (**Figure 8A**).....
Trichillidium Vaz-de-Mello, 2008
 – Head with two clypeal teeth (**Figure 8B**).....
Genieridium Vaz-de-Mello, 2008
9. (4) Side of pronotum with deep longitudinal sulcus. Absent lateral pronotal fossae or callus. (**Figure 9A**).....
Uroxys Westwood, 1842
 – Side of pronotum without deep longitudinal sulcus, with lateral pronotal fossae or callus (**Figure 9B**).....10
10. (9) Pygidium with deep transverse sulcus on disc. Last meso- and metatarsomere without dentiform process above claw insertion (**Figure 10A;B**).....
Agamopus Bates, 1887
 – Pygidium with disc without sulcus. Last meso- and metatarsomere with dentiform process above claw insertion (**Figure 10C;D**).....
Zonocoprís Arrow, 1932
11. (3) Length of the first metatarsomere greater than the combined length of the next three metatarsomeres, metatarsal with five tarsomeres (**Figure 11A**).....12
 – Length of the first metatarsomere less than the combined length of the next three metatarsomeres together; or metatarsi with less than five tarsomeres (**Figure 11B**).....13
12. (11) Propleuron with oblique carina that reaching lateral margin next to the anterior angle, forming an anterolateral tooth, rounded in males and acute in females; (African species introduced); size 7-13mm (**Figure 12A**).....
Digitonthophagus Balthasar, 1959
 – Propleuron without anterolateral tooth near the anterior angle, insertion of the longitudinal (hypomeral) propleural carina exactly under the anterior angle, or not reaching the pronotal edge; size 4-12mm (**Figure 12B**).....
Onthophagus Latreille, 1807
13. (11) Meso- and metatarsus lacking claws (**Figure 13A**).....14
 – Meso- and metatarsus with claws (**Figure 13B**).....20
14. (13) Meso- and metatarsus with two to four tarsomeres (**Figure 14A**).....
Dendropaemon Perty, 1830
 – Meso- and metatarsus with five tarsomeres (**Figure 14B**).....15
15. (14) Basal antennomere of antennal club not concave apically; apical two antennomeres clearly separated from basal antennomere (**Figure 15A**). Metepisternum simple, without posterior extension.....
Gromphas Brullé, 1838
 – Basal antennomere of antennal club large, strongly concave apically, receiving in the concavity the two apical lamellae (**Figure 15B**). Metepisternum with posterior extension covering lateral margin of elytra.....16
16. (15) Clypeal margin deeply, acutely emarginate medially, emarginations producing two acute teeth that are separated from adjacent clypeal border by external emargination (**Figure 16A**).....
Coprophanaeus d'Olsoufieff, 1924
 – Clypeal margin without deep and sharp emargination, with at most two conspicuous middle teeth (**Figure 16B**).....17
17. (16) Head with transverse frontal carina (sometimes raised as pair of horns in male), in addition to frontoclypeal carina (**Figure 16B**).....
Diabroctis Gistel, 1857
 – Head with single horn or carina, or bare.....18
18. (17) Metasternum with long, dorsally curved, acute spiniform process extending between apices of procoxae (**Figure 17A**).....
Oxysternon Laporte, 1840
 – Metasternum simply angled anteromedially, without spiniform process (**Figure 17B**).....19
19. (18) Anterior portion of circumnotal ridge entire, not interrupted behind each eye (**Figure 18A**).....
Sulcophanaeus Olsoufieff, 1924
 – Anterior portion of circumnotal ridge interrupted behind each eye (**Figure 18B**).....
Phanaeus Macleay, 1819
20. (13) Pronotum with two distinct, posteromedian fossae. Body metallic red color and length greater than 15mm (**Figure 19A**).....
Bolbites Harold, 1868
 – Posteromedian pronotal fossae absent. Body brownish to black and length smaller than 15mm (**Figure 19B**).....21
21. (20) Tarsal claws reduced, straight or only weakly curved (**Figure 20A**). Hypomeron convex or weakly concave, never strongly excavated. Head without transverse carina.....
Anomiopus Westwood, 1842
 – Tarsal claws large, strongly curved, falciform or angulate (**Figure 20B**); if only weakly developed, then either hypomeron deeply excavated anteriorly or head with transverse carina or both.....22
22. (21) Metatibia not enlarged toward apex, or only weakly and gradually (**Figure 21A**).....23
 – Metatibia, abruptly widened toward apex (**Figure 21B**).....27
23. (22) Elytral interstriae with short carina or tubercles at the apex (**Figure 22A**).....
Deltochilum Eschscholtz, 1822
 – Elytral interstriae without carina or tubercles at the apex, at most with a lateral carina that may be almost complete (**Figure 22B**).....24
24. (23) Posterior edge of head not margined between eyes (**Figure 23A**). Mesosternum relatively long, not narrowed medially, completely horizontal.....
Pseudocanthon Bates, 1887
 – Posterior edge of head completely margined between eyes (**Figure 23B**). Mesosternum shorter in the middle than laterally, or positioned vertically and weakly visible.....25
25. (24) Mentum completely divided longitudinally (**Figure 24A**).....
Holocanthon Martínez & Pereira, 1956
 – Mentum not completely divided, at most with deep U- or V-shaped emargination (**Figure 24B**).....26
26. (25) Pronotum with regular sculpturing, regularly convex, at most with posterior mean depression (scutellar impression) (**Figure 25A**).....
Canthon Hoffmannsegg, 1817
 – Pronotum with strong striated microsculpture, flat, and distributed depressions and elevations (**Figure 25B**).....
Anisocanthon Martínez & Pereira, 1956

27. (22) Hypomeron deeply excavated anteriorly, excavation delimited posteriorly by a vertical area separated from the unexcavated part by a transversal carina (**Figure 26A**). Apical internal angle of the tibia ~ 90° or acute, anterior edge of continuous apical tooth (without forming an angle) with apical truncation.....*Ateuchus* Weber, 1801
- Hypomeron weakly excavated anteriorly, excavation not clearly delimited posteriorly; Transverse carina absent (**Figure 26B**). Apical internal angle of the protibial obliquely truncated (>90°); if ~90° or weakly acute, then the anterior edge of the apical tooth forms an angle with margin of apical truncation.....28
28. (27) Apical internal angle of the protibiae ~90° or acute (**Figure 27A**). Mesosternum usually very short, vertically positioned; metasternum usually convex (**Figure 27B**).....*Canthididium* Erichson, 1847
- Apical internal angle of the protibiae clearly obtuse, apical edge in continuation with apical tooth (**Figure 27C**). Mesosternum very well developed, horizontal; metasternum usually flat (**Figure 27D**).....29
29. (28) Medial ventral carina of protibiae interrupted by punctures (**Figure 28A**). Body elongated, abdomen very short in relation to the body. Ventral clypeal process absent (**Figure 28B**).....*Ontherus* Erichson, 1847
- Medial ventral carina of protibiae complete (**Figure 28C**). Rounded body, abdomen not shortened. Ventral clypeal process, usually coniform and apically bifurcated, sometimes inserted into a longitudinal carina; rarely otherwise, but never with simple transverse carina (**Figure 28D**).....30
30. (29) Antennae with eight antennomeres (**Figure 29A**).....*Isocoprís* Pereira & Martínez, 1960
- Antennae with nine antennomeres (**Figure 29B**).....*Dichotomius* Hope, 1838.

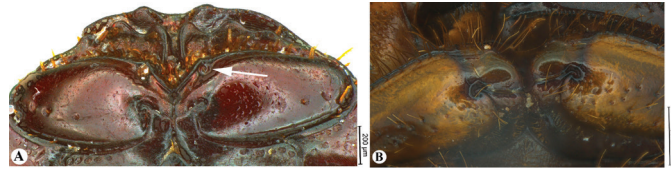


Figure 3. (A) *Trichillum* sp. anterior leg with anterior trochantofemoral fovea; (B) *Eurysternus* sp. anterior leg without anterior trochantofemoral fovea. Scale: A, 200µm; B, 1,19mm.

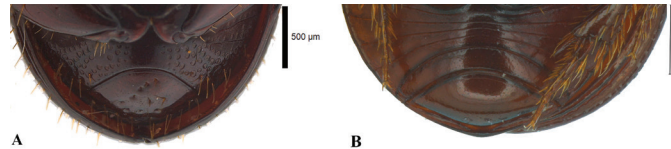


Figure 4. (A) *Trichillum* sp. view of sternites; (B) *Uroxys* sp. view of sternites. Scale: A, 500µm; B, 1,19mm.



Figure 5. (A) *Trichillum* sp. pseudopleuron forming two lateral sinuosities, posterior partially (white arrows); (B) *Genieridium* sp. pseudopleuron not forming two lateral sinuosities. Scale: A, 500µm; B, 1mm.

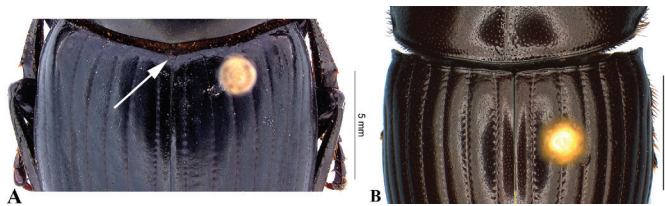


Figure 1. (A) *Eurysternus* sp. scutellum visible dorsally with the elytra closed; (B) *Malagoniella* sp. scutellum not visible dorsally with closed elytra. Scale: A, 5mm; B, 3mm.

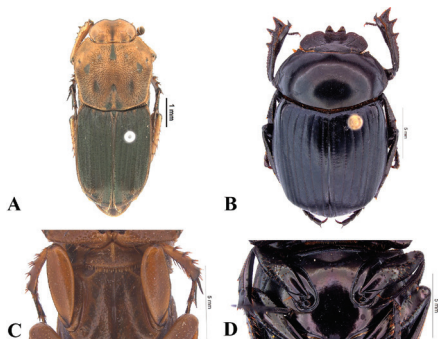


Figure 2. (A) *Eurysternus* sp. in dorsal view; (B) *Malagoniella* sp. in dorsal view; (C) Metasterno de *Eurysternus* sp; (D) Metasterno de *Malagoniella* sp. Scale: A, 1mm; B, 5mm; C, 5mm; D, 5mm.

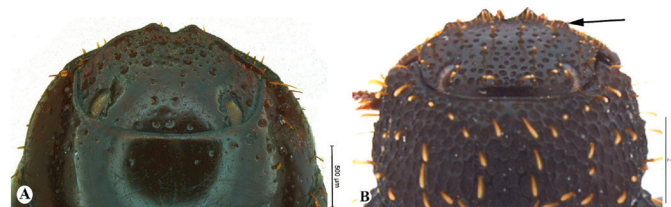


Figure 6. (A) *Trichillum* sp. the clypeal tooth and the clypeogenal suture; (B) *Eutrichilum* sp. the clypeal tooth and the clypeogenal suture. Scale: A, 500µm; B, 2mm.



Figure 7. (A) *Eutrichilum* sp. clypeogenal margin; (B) *Besourensa* sp. clypeogenal margin. Scale: A-B, 1mm.

Dung beetle species of the Brazilian Pantanal

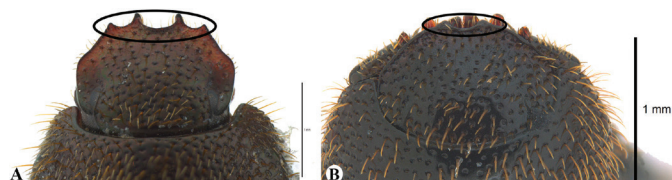


Figure 8. (A) *Trichillidium* sp. head with two or four clypeal teeth; (B) *Genieridium* sp. head with two or four clypeal teeth. Scale: A-B, 1mm.

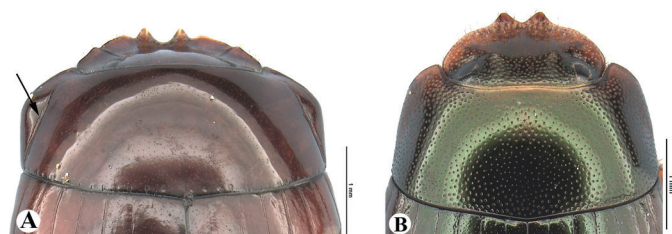


Figure 9. (A) *Uroxyis* sp. side of pronotum with deep longitudinal sulcus; (B) *Agamopus* sp. side of pronotum without deep longitudinal sulcus. Scale: A-B, 1mm.

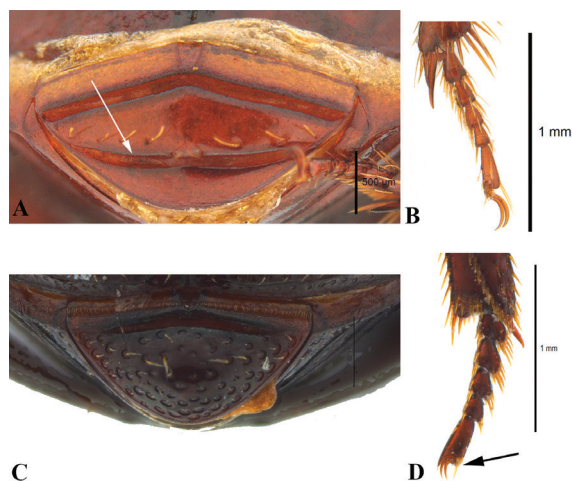


Figure 10. (A) *Agamopus* sp. pygidium with deep transverse sulcus on disc; (B) *Agamopus* sp. Last mesotarsomere and metatarsomere without dentiform process above claw insertion; (C) *Zonocopriss* sp. pygidium with disc without sulcus; (D) *Zonocopriss* sp. last mesotarsomere and metatarsomere with dentiform process above claw insertion. Scale: A, 500µm; B-D 1mm.

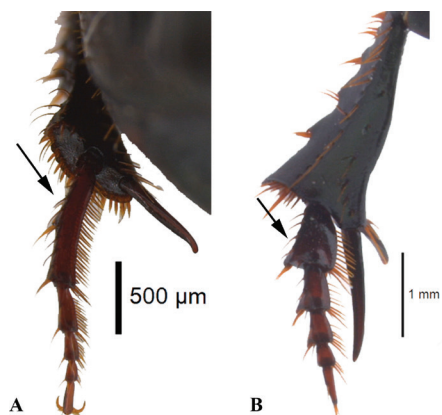


Figure 11. (A) *Digitonthophagus* sp. the first metatarsomere; (B) *Dendropaemon* sp. the first metatarsomere. Scale: A, 500µm; B, 1mm.

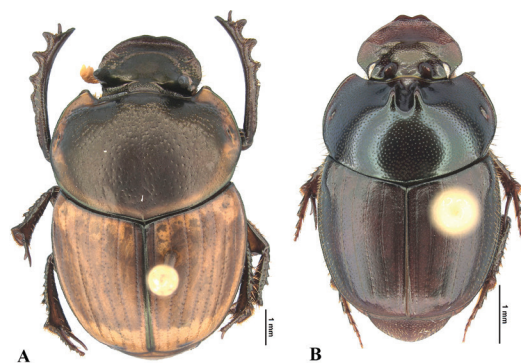


Figure 12. (A) *Digitonthophagus* sp.; (B) *Onthophagus* sp. Scale: A-B, 1mm.

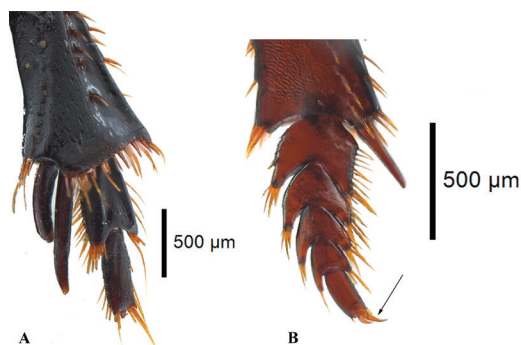


Figure 13. (A) *Dendropaemon* sp. mesotarsus and metatarsus lacking claws; (B) *Bolbites* sp. mesotarsus and metatarsus with claws. Scale: A-B, 500µm.

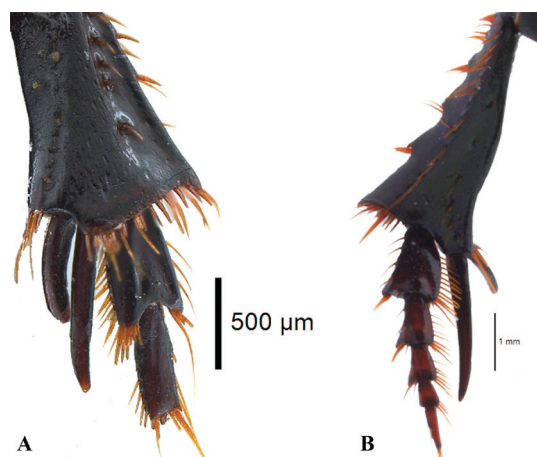


Figure 14. (A) *Dendropaemon* sp. mesotarsus and metatarsus with two to four tarsomeres; (B) *Bolbites* sp. mesotarsus and metatarsus with five tarsomeres. Scale: A, 500µm; B, 1mm.

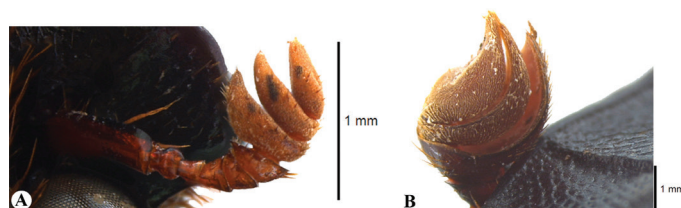


Figure 15. (A) *Gromphas* sp. basal antennomere of antennal club not concave apically; (B) *Coprophanaeus* sp. basal antennal club Lamela large, strongly concave apically. Scale: A-B, 1mm.

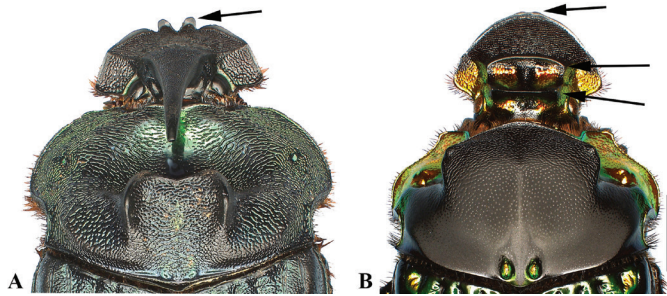


Figure 16. (A) *Coprophanaeus* sp. clypeal margin with two teeth; (B) *Diabroctis* sp. clypeal margin with two teeth conspicuous middle teeth. Scale: A-B, 9mm.

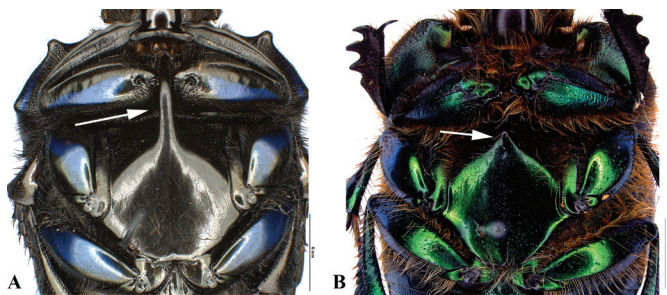


Figure 17. (A) *Oxysternon* sp. metasternum with long, dorsally curved, acute spiniform process; (B) *Phanaeus* sp. Metasternum simply angled anteromedially, without spiniform process. Scale: A-B, 6mm.

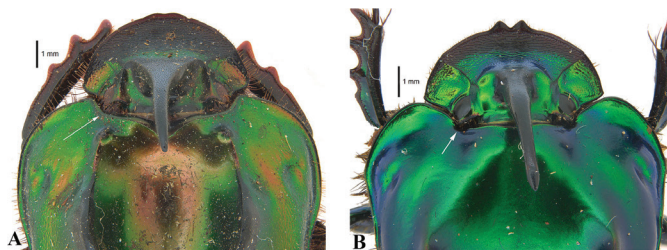


Figure 18. (A) *Sulcophanaeus* Anterior portion of circumnotal carina entire, not interrupted behind each eye; (B) *Phanaeus* Anterior portion of circumnotal ridge interrupted behind each eye. Scale: A-B, 1mm.



Figure 19. (A) *Bolbites* sp. pronotum with two distinct, posteromedian fossae white arrows; (B) *Anomiopus* sp. posteromedian pronotal fossae absent. Scale: A-B, 1mm.

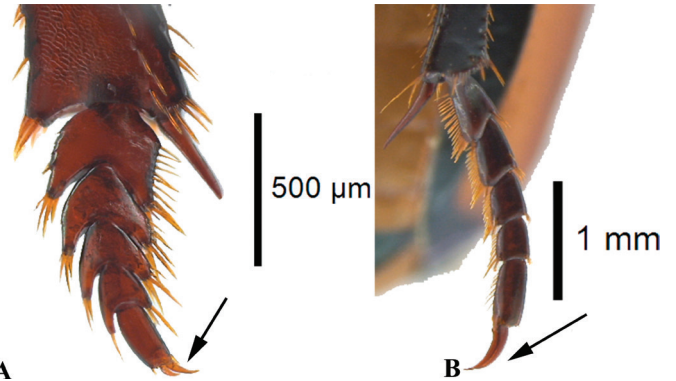


Figure 20. (A) *Anomiopus* sp. tarsal claws reduced, straight or only weakly curved; (B) *Deltochilum* sp. tarsal claws large, strongly curved, falciform or angulate. Scale: A, 500µm; B, 1mm.

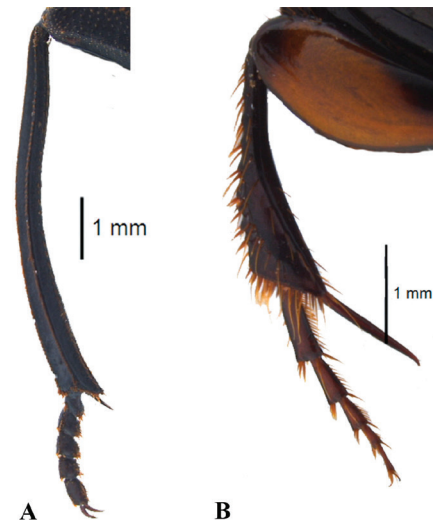


Figure 21. (A) *Deltochilum* sp. mesotibia and metatibia not enlarged to apex; (B) *Ateuchus* sp. mesotibia, and usually also metatibia, abruptly widened to apex. Scale: A-B, 1mm.

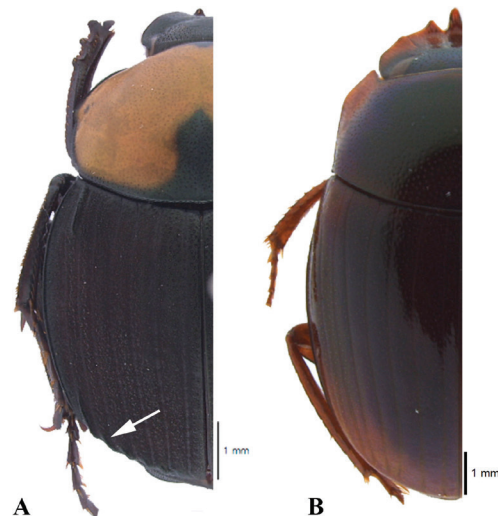


Figure 22. (A) *Deltochilum* sp. apex of some discal elytral interstriae with short carina or tubercles; (B) elytral interstriae without carina or tubercles. Scale: A-B, 1mm.

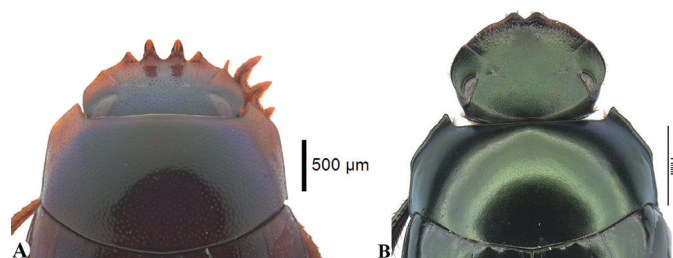


Figure 23. (A) *Pseudocanthon* sp. posterior margin of head not margined between eyes; (B) *Canthon* sp. posterior border of head completely margined between eyes. Scale: A, 500µm; B, 1mm.

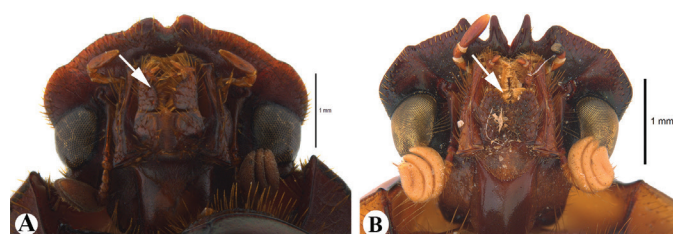


Figure 24. (A) *Holocanthon* sp mentum completely divided longitudinally; (B) *Canthon* sp. mentum not completely divided. (white arrows). Scale: A-B, 1mm.



Figure 25. (A) *Canthon* sp. pronotum with regular sculpturing, regularly convex, at most with posterior mean depression; (B) *Anisocanthon* sp. flat pronotum, with distributed depressions and elevations, and strong striated microsculpture. Scale: A-B, 1mm.

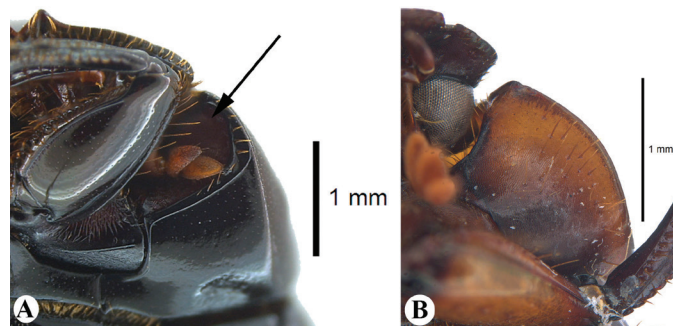


Figure 26. (A) *Ateuchus* sp. hypomere deeply excavated anteriorly (B) *Canthididium* sp. hypomere weakly excavated anteriorly. Scale: A-B, 1mm.

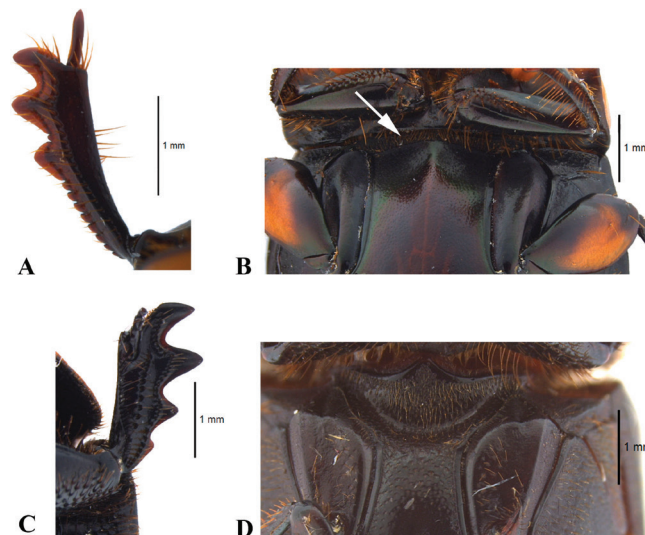


Figure 27. (A-B) *Canthididium* sp. apical internal angle of the protibia and mesosternum; (C-D) *Ontherus* sp apical internal angle of the protibia and mesosternum. Scale: A-D, 1mm.

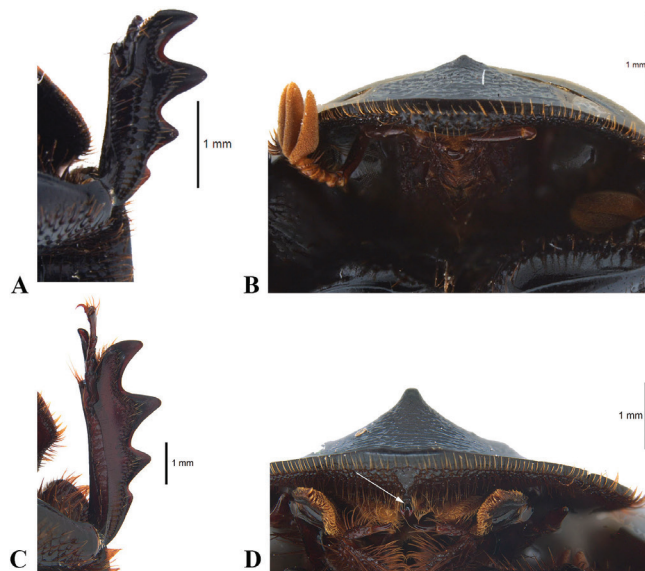


Figure 28. (A) *Ontherus* sp. carina of the protibia and transverse ventral clypeal process; (B) *Dichotomius* sp. carina of the protibia and transverse ventral clypeal process. Scale: A-B, 1mm.

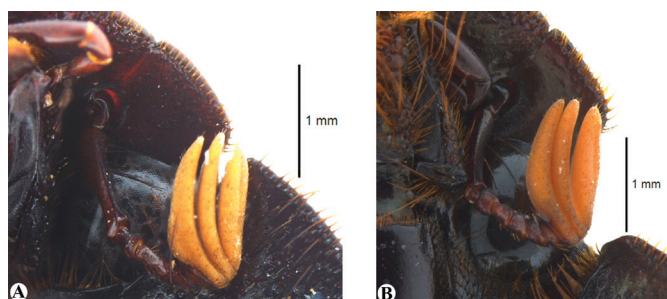


Figure 29. (A) *Isocopris* sp. antennas with eight antennomeres; (B) *Dichotomius* sp. antennas with nine antennomeres. Scale: A-B, 1mm.

Identification key for the species of *Eurysternus*

1. Metaventricle disc with round fovea in the middle. Pronotum dark with a light spot anteriorly, just behind the head. Size 6-10mm (**Figure 30A;B**).....*E. plebejus*
 - Metaventricle disc flat, wavy or with longitudinal sulcus, without round fovea in the middle. Pronotum totally dark or mostly light with dark spots. Size 9-20mm (**Figure 30C;D**).....2
2. (1) Light colored posterior femurs, at least in the apical half. Pronotum mostly lighter, with well-defined dark spots (**Figure 31A;C**)3
 - Posterior femurs totally dark like the pronotum (**Figure 31B;D**)4
3. (2) Posterior femurs with teeth at the posterior edge, darker at the base. Size 10-20mm (**Figure 31A**).....*E. caribaeus*
 - Posterior femurs without teeth at the anterior edge. Size 9-13mm (**Figure 31B**).....*E. jessopi*
4. (2) Middle and posterior femurs claviform. Dorsal body without any metallic luster. Elytra apex bristles straight. Size 9-14mm (**Figure 31B**)*E. parallelus* (**Figure 32A**).....
 - Middle and posterior femurs not claviform. Body dorsally with metallic sheen at least in the elytral sutural striae and anterior part of the clypeus. Bristles at apex of elytra strongly curved in apical half (**Figure 32B**).....5
5. (4) Head surface with most no metallic reflections, except for a narrow metallic green band anteriorly on the clypeus. Lateral edge of male hind tibia curved in half in dorsal view. (**Figure 33A;C**)*E. nigrovirens*
 - Head surface mostly glossy and with strong metallic reflections between ocellates. Lateral edge of male hind tibia almost straight or straight in the middle in dorsal view (**Figure 33B;D**)*E. aeneus*

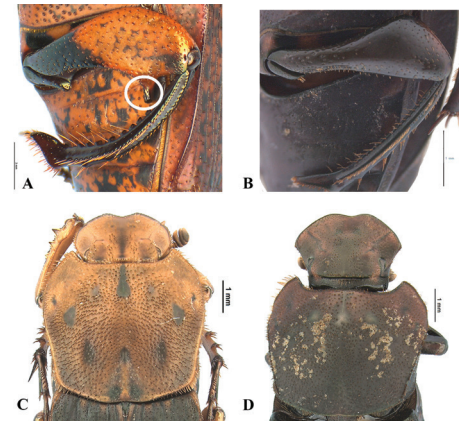


Figure 31. (A-C) *E. caribaeus*. Light colored posterior femurs, at least in the apical half, *E. jessopi* Pronotum mostly lighter, with well-defined dark spots; (B-D) *E. parallelus*. Posterior femurs totally dark like the pronotum. Scale: A, 3mm; B-D, 1mm.

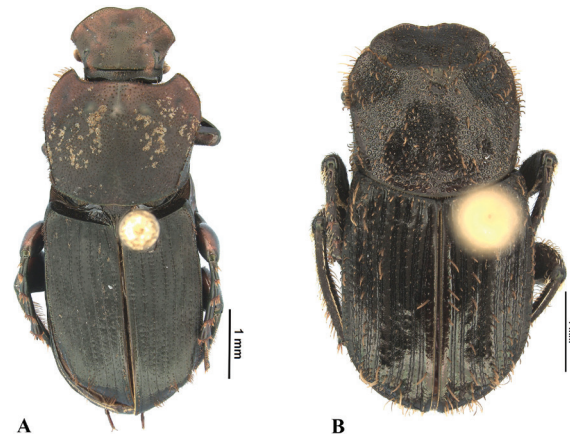


Figure 32. (A) *E. parallelus*. Dorsal body without any metallic luster. Elytra apex bristles straight. Size 9-14mm; (B) *E. aeneus*. Body dorsally with metallic sheen at least in the elytral sutural striae and anterior part of the clypeus. Bristles at apex of elytra strongly curved in apical half. Scale: A-B, 1mm.

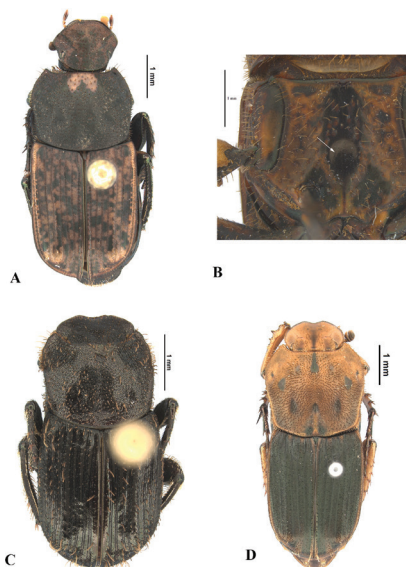


Figure 30. (A) *Eurysternus plebejus*. Pronotum dark with a light spot anteriorly, just behind the head. Size 6-10mm; (B) Metaventricle disc with round fovea in the middle; (C) *E. aeneus*. Pronotum totally dark or mostly light with dark spots. variable size; (D) *E. jessopi*. Pronotum totally dark or mostly light with dark spots variable size. Scale: A-C, 1mm.

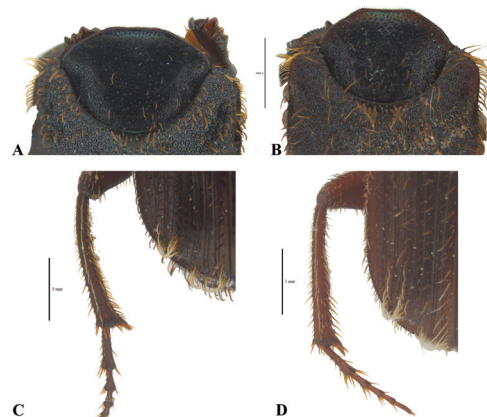


Figure 33. (A) *E. nigrovirens*. Head surface with most no metallic reflections, except for a narrow metallic green band anteriorly on the clypeus; (B) *E. aeneus*. Head surface mostly glossy and with strong metallic reflections between ocellates; (C) *E. nigrovirens*. Lateral edge of male hind tibia curved in half in dorsal view; (D) *E. aeneus*. Lateral edge of male hind tibia almost straight or straight in the middle in dorsal view. Scale: A-B, 1mm.

Identification key for the species of *Canthon*

1. Pygidium and propygidium separated by carina (**Figure 34A**).....2
 - Pygidium and propygidium not separated by carina (**Figure 34B**)8
2. (1) Head with quadridented clypeus (**Figure 35A**).....3
 - Head with bidented clypeus (**Figure 35B**).....4
3. (2) Pronotum, in dorsal view, with smooth lateral margin and serrated in ventral view. (**Figure 36A**).....*C. mutabilis* Lucas, 1859
 - Pronotum with smooth lateral margin, in dorsal and ventral view. (**Figure 36B**).....*C. curvodilatatus* Schmidt, 1920
4. (2) Gena anteriorly with visible tooth (**Figure 37A black arrow**)5
 - Gena anteriorly, prominent, but without tooth.....7
5. (4) Clypeus with two long teeth bulging, rounded, or subtriangular at apex, not acute (**Figure 37A**).....*C. substriatus* Harold, 1868
 - Clypeus with two long, triangular teeth, acute, not bulging or rounded at the apex (**Figure 37B**).....6
6. (5) Pronotum completely punctated, being more subtle on the disc than on the sides; shiny elytra with well-marked striations; subtly punctuated interstriae. Metafemora with complete anterior and incomplete posterior margination (**Figure 38A;C**).....*C. virens* (Mannerheim, 1829)
 - Pronotum with almost imperceptible punctation on the disc; opaque elytra, striae not as marked as in *C. virens*; interstriae with microreticulated punctation; metafemora with complete anterior and posterior margination (**Figure 38B;D**)*C. chalybaeus* Blanchard, 1845
7. (4) Short clypeal teeth; complete hypomeral carina; pronotum and elytra dark (**Figure 39A;B**).....*C. daguerrei* Martinez, 1951
 - Clypeal teeth not as short as above; incomplete hypomeral carina; light pronotum with black stain and green reflections and dark elytra (**Figure 39C;D**).....*C. ornatus* Redtenbacher, 1858
8. (1) Head with quadridented clypeus (**Figure 40A**).....*C. quinquemaculatus* Castelnau, 1840
 - Head with bidented clypeus, which can be very or poorly defined (**Figure 40B**).....9
9. (8) Central clypeal teeth separated by U-shaped emargination or poorly defined teeth (**Figure 40B black arrow**).....10
 - Central clypeal teeth separated by open V-shaped emargination. (**Figure 40C**).....12
10. (9) Central clypeal teeth separated by well-delimited U-shaped emargination; pronotum and elytra light with dark outline. (**Figure 41A**).....*C. maldonadoi* Martínez, 1951
 - Clypeal teeth are little delimited, pronotum and elytra dark. (**Figure 41B**).....11
11. (10) Clypeal teeth short and rounded; pygidium longer than wide and with thick punctation; size 5–6,5mm (**Figure 42A;B**).....*C. edentulous* Harold, 1868
 - Clypeal teeth only weakly indicated, not salient, separated by wide emargination; Pygidium wider than long and fine punctation compared to the previous one; size 10–12mm. (**Figure 42C;D**) *C. quadratus*

12. (9) Pronotum and elytra dark; metafemur with anterior and posterior margination. (**Figure 43A;C**).....*C. unicolor* Blanchard, 1845
 - Pronotum and elytra may be yellow with black spots; metafemur only with anterior margination. (**Figure 43B;D**).....*C. histrio* (Saint-Fargeau & Audinet-Serville, 1828)

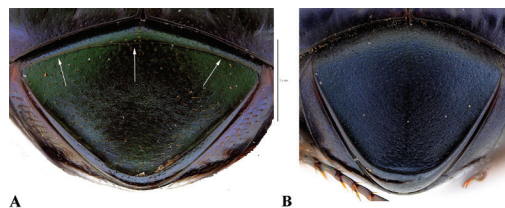


Figure 34. (A) *Canthon*. Pygidium and propygidium separated by carina; (B) *Canthon*. Pygidium and propygidium not separated by carina. Scale: A-B, 1mm.

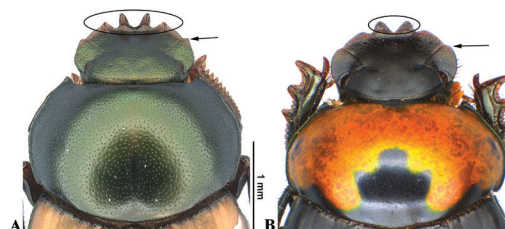


Figure 35. (A) *Canthon mutabilis*. Head with quadridented clypeus; (B) *Canthon (ornatus) ornatus*. Head with bidented clypeus. Scale: A, 1mm; B, 2mm.



Figure 36. (A) *C. mutabilis*. Pronotum in dorsal view, with straight lateral margin and serrated in ventral view; (B) *C. curvodilatatus*. Pronotum with straight lateral margin, in dorsal and ventral view. Scale: A-B, 1mm.

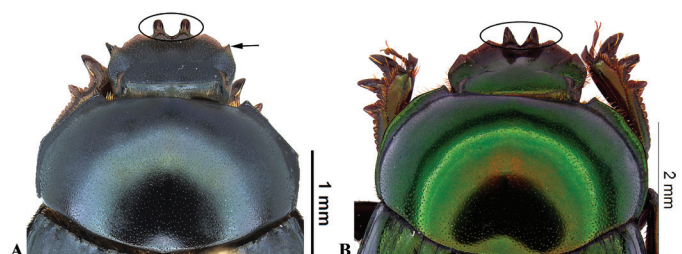


Figure 37. (A) *C. substriatus*. Gena anteriorly with visible tooth and clypeus with two long teeth bulging, rounded, or subtriangular at apex, not acute; (B) *C. virens*. Clypeus with two long, triangular teeth, acute, not bulging or rounded at the apex. Scale: A, 1mm; B, 2mm.

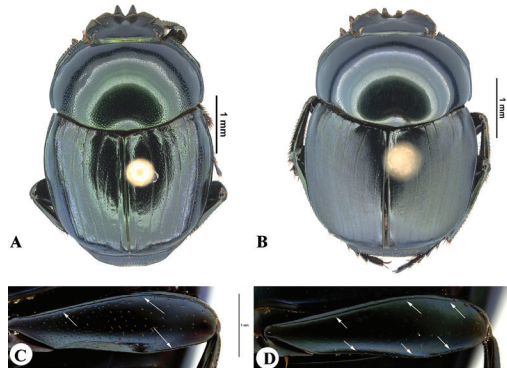


Figure 38. (A) *C. virens*. Pronotum is completely punctuated, being more subtle on the disc than on the sides; shiny elytra with well-marked striations; subtly punctuated interstriae; (B) *C. chalybaeus*. Pronotum with almost imperceptible punctuation on the disc; opaque elytra, striae not as marked as before; (C) *C. virens*. Metafemur with complete anterior and incomplete posterior margination; (D) *C. chalybaeus*. interstria with micro reticulated punctuation; metafemur with complete anterior and posterior margination. Scale: A-D, 1mm.

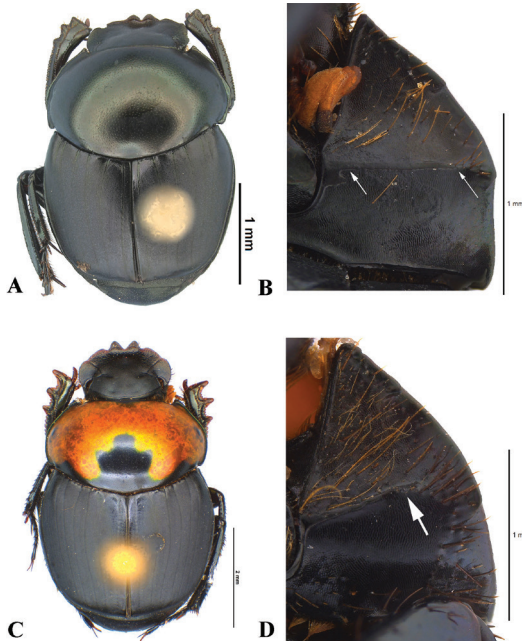


Figure 39. (A-B) *C. daguerrei*. Short clypeal teeth; complete hypomeral carina; pronotum and elytra dark; (C-D) *C. ornatos* Clypeal teeth not as short as before; incomplete hypomeral carina; light pronotum with black stain and green reflections and dark elytra. Scale: A-D, 1mm.

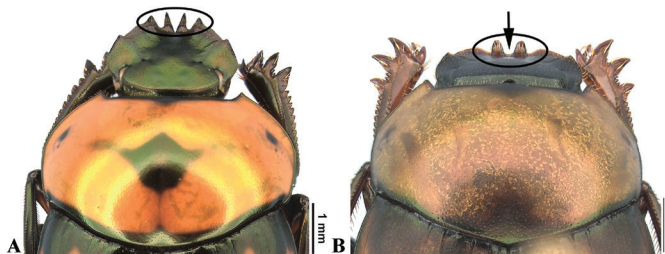


Figure 40. (A) *C. quinquemaculatus*. Head with quadrident clypeus; (B) *C. maldonadoi*. Head with bident clypeus, can be very or poorly defined; (C) *C. edentulus*. Clypeal teeth are short and rounded; "V" shape. Scale: A-B, 1mm.

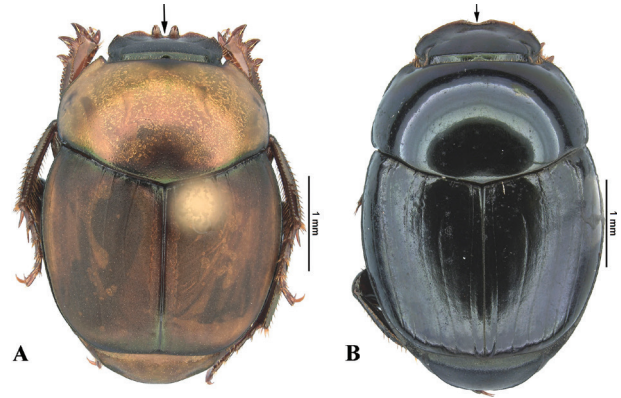


Figure 41. (A) *C. maldonadoi*. Central clypeal teeth separated by well-delimited U-shaped emargination; pronotum and elytra light with dark outline; (B) *C. edentulus* Clypeal teeth are little delimited, pronotum and elytra dark. Scale: A-B, 1mm.

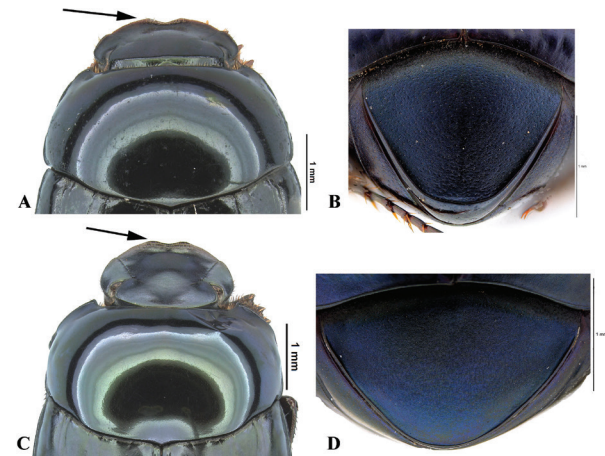


Figure 42. (A-B) *C. edentulus*. Clypeal teeth are short and rounded; pygidium longer than wide and with thick punctuation; size 5-6,5mm; (C-D) *C. quadratus*. Clypeal teeth only weakly indicated, not salient, separated by wide emargination; Pygidium wider than long and fine punctuation compared to the previous one; size 10-12mm. Scale: A-D, 1mm.

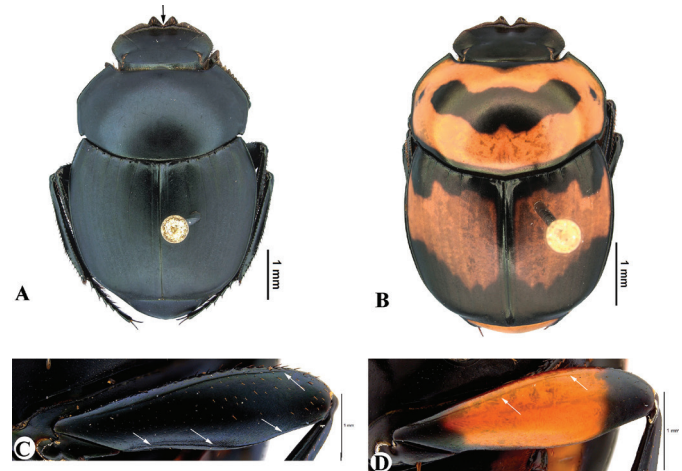


Figure 43. (A-C) *C. unicolor*. Pronotum and elytra dark; metafemur with anterior and posterior margination; (C-D) *C. histrio*. Pronotum and elytra may be yellow with black spots; metafemur only with anterior margination. Scale: A-D, 1mm.

Identification key for the species of *Coprophanæus*

1. Elytral striae smooth; interstriae with subtle punctation (**Figure 44A**)2
 - Elytral striae sculpted; rugopunctated interstriae (**Figure 44B**).....3
2. (1) Anterior portion of circumnotal ridge interrupted behind eyes (**Figure 45A**).....*C. milon* (Blanchard, 1845)
 - Anterior portion of circumnotal ridge entire, not broken behind eyes (**Figure 45B**).....*C. cyanescens* (d’Olsoufieff, 1924)
3. (1) Elytral striae 2–4 only slightly wavy; width of striations at narrowings at least three-quarters of that at widest points; size 25–35 mm (**Figure 46A**).....*C. bonariensis* (Gory, 1844)
 - Elytral striae strongly wavy; width of striations at narrowest points not more than half (often much less than half) that at widest points; size 30–55mm (**Figure 46B**).....*C. ensifer* (Germar, 1824)

Identification key for the species of *Dichotomius*

1. Clypeal margin rounded or weakly emarginated; if bidentate, small, non-margined teeth (**Figure 47A**).....2
 - Clypeus distinctly bidentate, teeth usually margined (**Figure 47B**)3
2. (1) Elytra with smooth striations and no punctation. Pronotum with median longitudinal sulcus (**Figure 48A;B**).....*D. bos* (Blanchard, 1845)
 - Elytra with punctiform striations. Pronotum without median sulcus (**Figure 49A;B**).....*D. luctuosoides* (Luederwaldt, 1922)
3. (1) Metallic elytra (satin gloss), coloration green, reddish or almost burgundy brown (**Figure 50A**).....4
 - Pronotum and elytra staining black, opaque or glossy (**Figure 50B**)6
4. (3) Pronotum mesoanteriorly not flattened; base of the pronotum without evident punctation in the central region (**Figure 51A**)5
 - Pronotum mesoanteriorly flattened; base of pronotum with two rows of ocellar punctation evident (**Figure 51B**).....*D. lycas* (Felsche, 1901)
5. (4) Dorsal surface monochromatic, glossy greenish satin; teeth margined, triangular and pointed; pronotum with flat anterior lateral edge; anterior tibia spur, spiniform (**Figure 52A**).....*D. glaucus* (Harold, 1869)
 - Dorsal surface bicolor, black pronotum and glossy satin burgundy elytra; rounded and flat teeth; pronotum with anterior lateral edge forming an almost triangular tip; protibial spur quadrangular (**Figure 52B**).....*D. cuprimus* (Felsche, 1901)
6. (3) Sides of metaventrite and hypomeron with dense and long setae, red to yellowish-brown (**Figure 53A**).....7
 - Sides of metaventrite and hypomeron without setae as described above (**Figure 53B**).....*D. opacipennis* (Luederwaldt, 1931)
7. (6) Clypeus with six teeth; pronotum with median anterior slope with ocellated punctations (**Figure 54A**).....*D. sexdentatus* (Luederwaldt, 1925)

- Clypeus with two teeth; posterior margin of the pronotum with ocellated punctations (**Figure 54B**).....*D. nisus* (Olivier, 1789)

Identification key for the species of *Ontherus*

1. Frontoclypeal suture without carina and/or tubercles (**Figure 55A**)*O. digitatus* Harold, 1869
 - Frontoclypeal suture with carina and/or tubercles (**Figure 55B**).....2
2. (1) Abdominal ventrites medially set, bristles similar to those on the lateral aspect of the metasternum (**Figure 56A**).....3
 - Abdominal ventrites glabrous medially, with at most one row of short bristles along the posterior border of the metacoxa (**Figure 56B**).....4
3. (2) Posterior border of metacoxa smooth. Metaventrite with most of the punctation of the oval lateral edges, with little defined edges (**Figure 57A;B**).....*O. appendiculatus* (Mannerheim, 1829)
 - Posterior edge of metacoxa slightly serrated. Metaventrite with most of the punctation of the lateral edges rounded, clearly delimited (**Figure 57C;D**).....*O. azteca* Harold, 1869
4. (2) Median metaventral lobe length less than twice its width (**Figure 58A**).....5
 - Median metaventral lobe length twice its maximum width (**Figure 58B**).....6
5. (4) Pygidium wider than long, punctures of moderate size and deeply impressed; space between glossy scores; smaller than 12mm (**Figure 59A**).....*O. aphodioides* Burmeister, 1874
 - Pygidium as wide as long, punctures small and weakly impressed; greater than 12mm (**Figure 59B**).....*O. sulcator* (Fabricius, 1775)
6. (4) Posterior edge of the metatrochanter complete with sulcus; pygidium with subtle punctation (**Figure 60A;B**).....*O. dentatus* Luederwaldt, 1930
 - Posterior edge of metatrochanter partially with sulcus; pygidium with well-marked punctation (**Figure 60C;D**).....*O. erosioides* Luederwaldt, 1930

Identification key for the species of *Deltotichilum*

1. Bidentate clypeus (**Figure 61A**).....2
 - Clypeus quadridentate, medial teeth stronger and longer than others (**Figure 61B**).....*D. pseudoicarum* Balthasar, 1939
2. (1) Head longer than wide (**Figure 62A**).....3
 - Head much wider than long (**Figure 62B**).....*D. silphoides* (Balthasar, 1939) (and possibly other species of the *irroratum* group)
3. (2) Pronotum and elytra of the same color, dark with greenish reflections (**Figure 63A**).....*D. icaroides* Balthasar, 1939
 - Pronotum yellow with dark spot in the center, elytra of uniform dark coloration (**Figure 63B**).....*D. cupreicoile* (Castelnau, 1840)

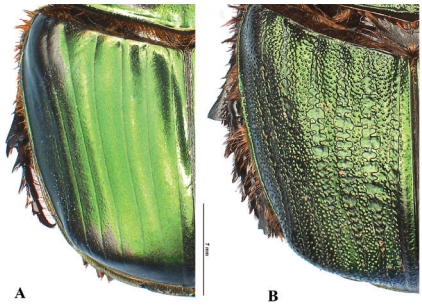


Figure 44. (A) *C. milon*. Elytral striae smooth; interstriae with subtle punctation; (B) *C. cyanescens*. Elytral striae sculpted; rugopunctate interstriae. Scale: A, 7mm; B, 10mm.

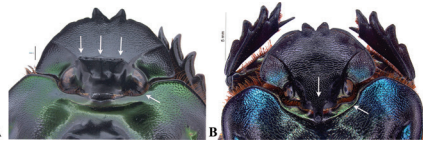


Figure 45. (A) *C. milon*. Margin behind eye absent; head with horn trident laminated; (B) *C. cyanescens*. Margin behind the eye present; head with cylindrical horn. Scale: A, 1mm; B, 5mm.

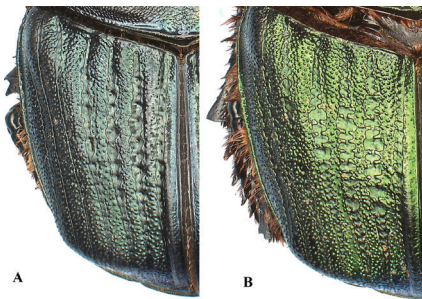


Figure 46. (A) *C. bonariensis*. Elytral striae 2-4 only slightly wavy; width of striations at narrowings at least three-quarters of that at widest points; size 25-35mm; (B) *C. ensifer*. Elytral striae strongly wavy; width of striations at narrowest points not more than half (often much less than half) that at widest points; size 30-55mm. Scale: A-B, 10mm.

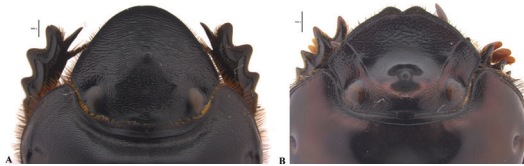


Figure 47. (A) *D. bos*. Clypeal margin rounded or weakly emarginated; if bidentate, small, non-margined teeth; (B) *D. luctuosioides*. Clypeus distinctly bidentate, teeth usually margined. Scale: A-B, 1mm.

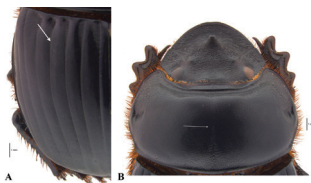


Figure 48. (A-B) *D. bos*. Elytra with smooth striations and no punctuation; pronotum with median longitudinal sulcus. Scale: A-B, 1mm.

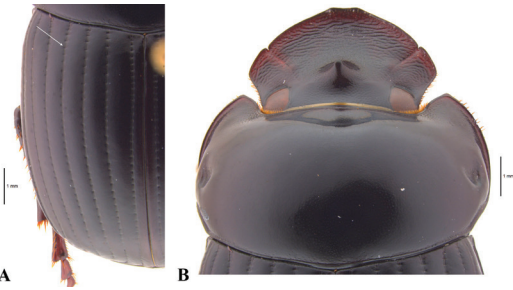


Figure 49. (A-B) *D. luctuosioides*. Elytra with punctiform striations; pronotum without median sulcus. Scale: A-B, 1mm.

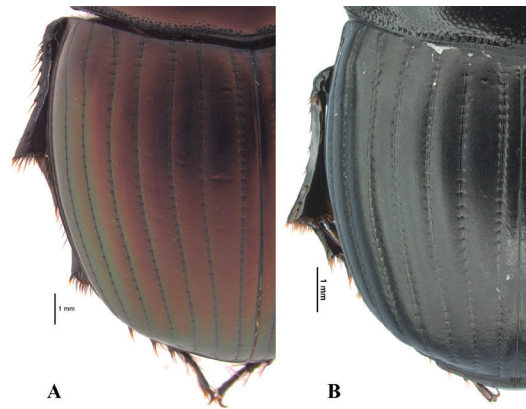


Figure 50. (A) *D. lycas*. Metallic (satin gloss) coloration in green, reddish or almost burgundy brown; (B) *D. opacipennis*. Pronotum and elytra staining black, opaque or glossy. Scale: A-B, 1mm.

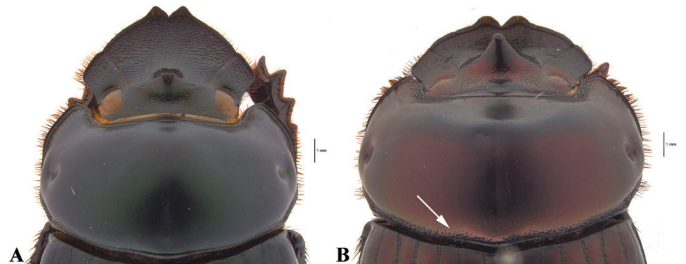


Figure 51. (A) *D. glaucus*. Pronotum mesoanteriorly not flattened; base of the pronotum without evident punctuation in the central region; (B) *D. lycas*. Pronotum mesoanteriorly flattened; base of pronotum with two rows of ocellar punctuation evident. Scale: A-B, 1mm.

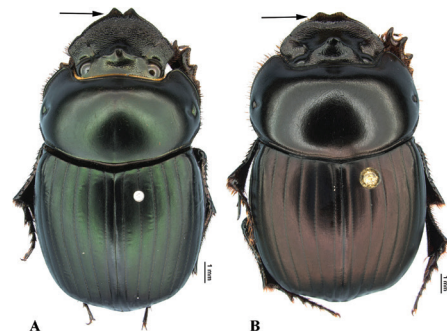


Figure 52. (A) *D. glaucus*. Dorsal surface monochromatic, glossy greenish satin; teeth margined, triangular and pointed; pronotum with flat anterior lateral edge; (B) *D. cuprinus*. Dorsal surface bicolor, black pronotum and glossy satin burgundy elytra; rounded and flat teeth; pronotum with anterior lateral edge forming an almost triangular tip. Scale: A-B, 1mm.

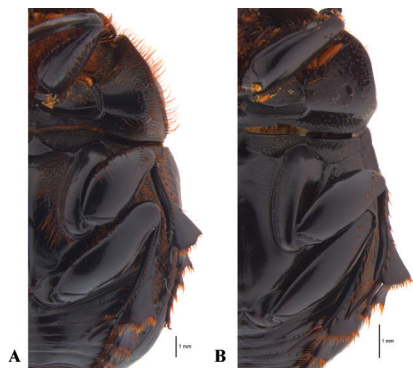


Figure 53. (A) *D. sexdentatus*. Sides of metasternum and hypomere with dense and long setae, red to yellowish-brown; (B) *D. opacipennis*. Sides of metasternum and hypomerus without setae as described above. Scale: A-B, 1mm.



Figure 54. (A) *D. sexdentatus*. Clypeus with six teeth; pronotum with median anterior slope with ocellated punctuations; (B) *D. nisus*. Clypeus with two teeth; posterior margin of the pronotum with ocellated punctuations. Scale: A-B, 1mm.

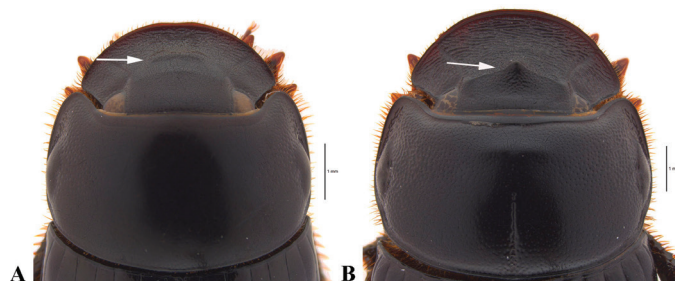


Figure 55. (A) *O. digitatus*. Fronto clypeal suture without carina and/or tubercles; (B) *O. appendiculatus*. Posterior border of metacoxa smooth. Metasternum with most of the punctuation of the oval lateral edges, with little defined edges. Scale: A-B, 1mm.



Figure 56. (A) *O. appendiculatus*. Abdominal sternites medially set, bristles similar to those on the lateral aspect of the metasternum; (B) *O. aphodioides*. Abdominal sternites glabrous medially, with at most one row of short bristles along the posterior border of the metacoxa. Scale: A-B, 1mm.

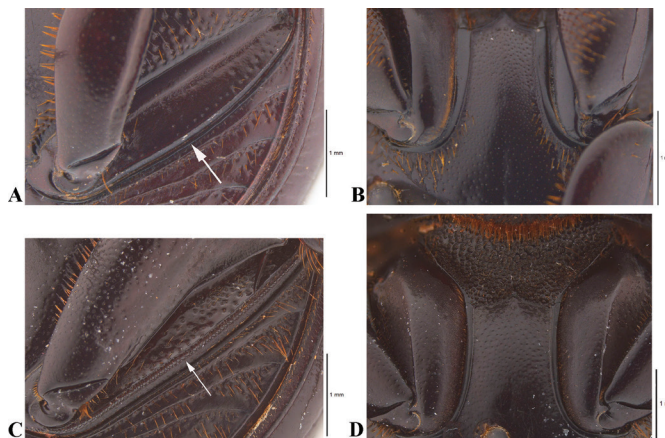


Figure 57. (A-B) *O. appendiculatus*. Posterior border of metacoxa smooth. Metasternum with most of the punctuation of the oval lateral edges, with little defined edges; (C-D) *O. azteca*. Posterior edge of metacoxa slightly serrated. Metasternum with most of the punctuation of the lateral edges rounded, clearly delimited. Scale: A-D, 1mm.

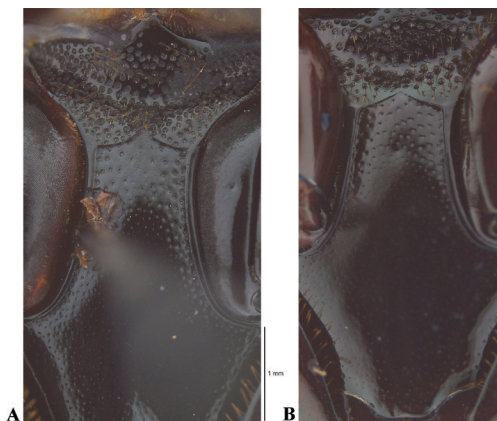


Figure 58. (A) *O. aphodioides*. Median metasternum lobe length less than twice its width; (B) *O. dentatus*. Median metasternum lobe length twice its maximum width. Scale: A-B, 1mm.

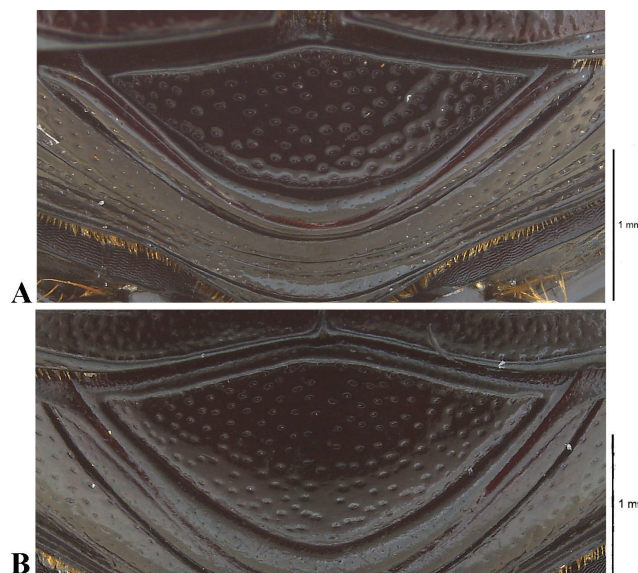


Figure 59. (A-B) *O. aphodioides*. Pygidium wider than long, pits of moderate size and deeply imprinted; space between glossy scores; (C-D) *O. sulcator*. Pygidium as wide as long, punctuations small and weakly printed. Scale: A-B, 1mm.

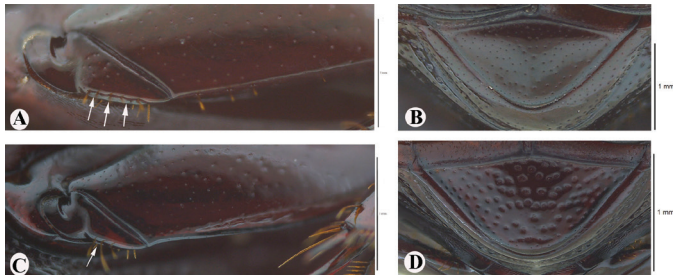


Figure 60. (A) *O. dentatus*. Posterior edge of the metatrochanter complete with sulcus; pygidium with final score; (B) *O. erosioides*. Posterior edge of metatrochanter partially with sulcus; pygidium with thick score. Scale: A-B, 1mm.

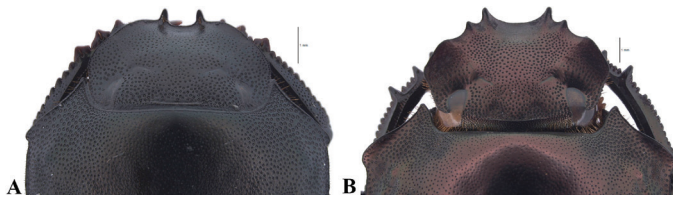


Figure 61. (A) *D. silphoides*. Bidentate clypeus; (B) *D. pseudoicaricus*. Clypeus quadridentate, medial teeth stronger and longer than others. Scale: A-B, 1mm.

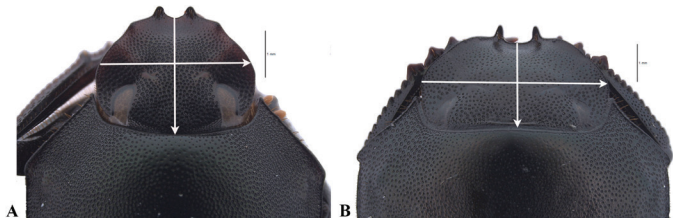


Figure 62. (A) *D. icaroides*. Head much wider than long; (B) *silphoides*. Pronotum and elytra of the same color, dark with greenish reflections. Scale: A-B, 1mm.

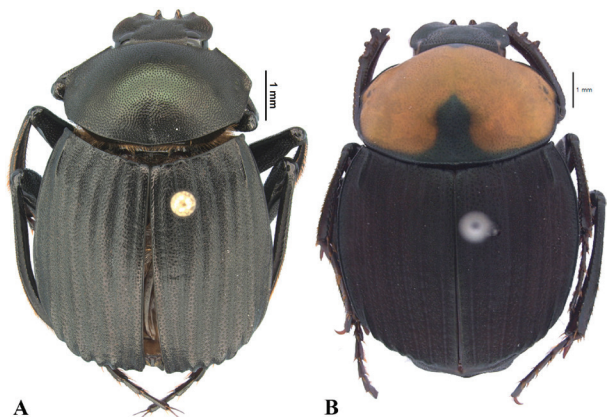


Figure 63. (A) *D. icaroides*, Pronotum and elytra of the same color, dark with greenish reflections; (B) *D. cupreicoile*, Pronotum yellow with dark spot in the center, elytra of uniform dark coloration. Scale: A-B, 1mm.

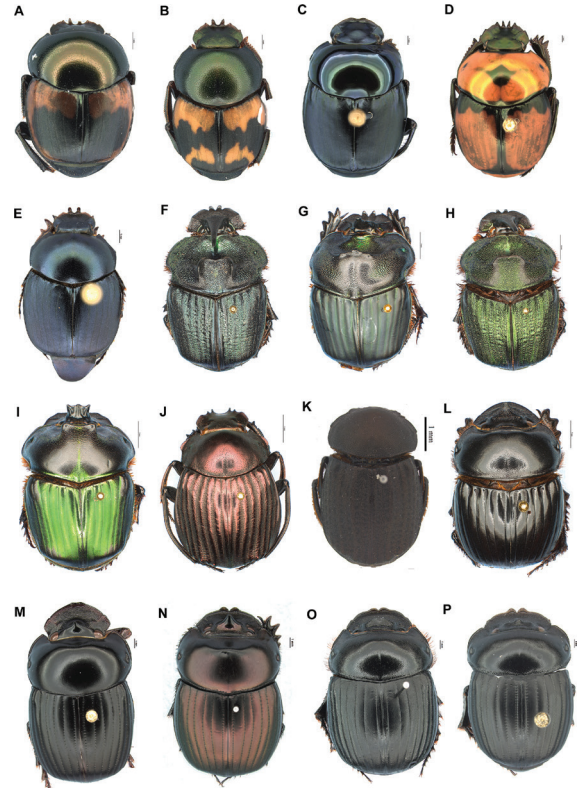


Figure 64. Habitus. (A) *Canthon curvodilatatus*; (B) *C. mutabilis*; (C) *C. quadratus*; (D) *C. quinquemaculatus*; (E) *C. substriatus*; (F) *Coprophanaeus bonariensis*; (G) *C. cyanescens*; (H) *C. ensifer*; (I) *C. milon*; (J) *Deitchler pseudoicaricus*; (K) *D. silphoides*; (L) *Dichotomius bos*; (M) *D. luctuosoides*; (N) *D. lycas*; (O) *D. nisus*; (P) *D. opacipennis*. Scale bar: A-E; M-P 1mm; G, I-L 7mm; H 10mm.

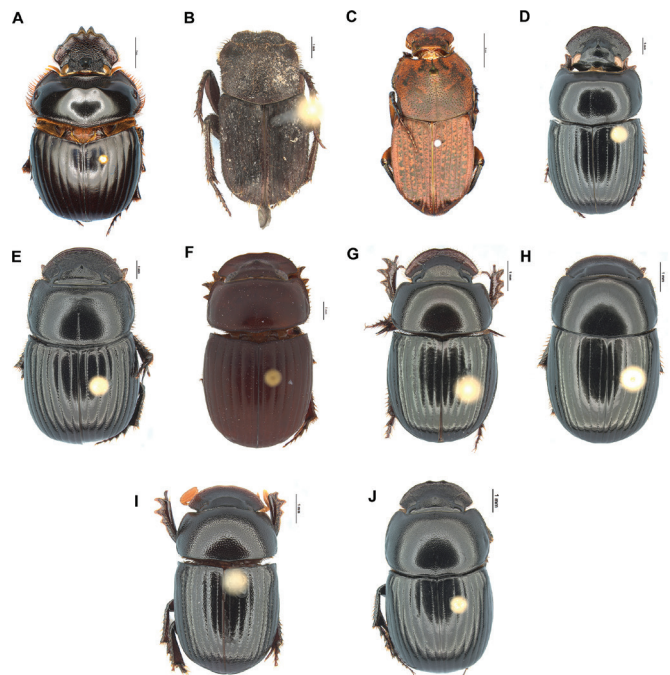


Figure 65. Habitus. (A) *D. sexdentatus*; (B) *Eurysternus aeneus*; (C) *E. caribaeus*; (D) *Ontherus aphodioides*; (E) *O. appendiculatus*; (F) *O. azteca*; (G) *O. dentatus*; (H) *O. digitatus*; (I) *O. erosioides*; (J) *O. sulcator*. Scale bar: B, D-J, 1mm; C, 5mm; A, 7mm.

Discussion

In this study, we provide an updated list of species of dung beetles of the Brazilian Pantanal. No such list had hitherto been published. The closer parallel had been Vaz-de-Mello et al.'s (2017) list of the species of Mato Grosso do Sul state, which indicated those which were present in its Pantanal area. Our study mitigates the lack of information on dung beetles species of the Brazilian Pantanal as a whole, increasing the number of species recorded from 43 (see Vaz-de-Mello et al. 2017) to 68 species (**Figure 64A-P** and **Figure 65A-J**). Below is an up-to-date commentary on the taxonomic status of the genera that occur in the Pantanal.

Ateuchus Weber, 1801: Genus with paracoprid representatives and 101 species currently recognized as valid distributed in the Americas (Schoolmeesters 2023). Except for some regional works, the genus was last revised by Harold (1868) and identifying its South American species is currently unfeasible relying on published information. During the data survey for this work, these species were reported: *Ateuchus carbonarius* (Harold, 1868) (Pessôa et al. 2017), *Ateuchus latus* (Boucomont, 1928) (Vaz-de-Mello et al. 2007), and *Ateuchus prunus* (Boucomont, 1928) (Correia et al. 2022b). However, this genus is under revision and only one species could be confirmed as present in the Brazilian Pantanal: *Ateuchus* aff. *viduus* (Blanchard, 1846), a species with wide distribution in the Pantanal and southern Cerrado regions (Mario Cupello, personal communication).

Canthidium Erichson, 1847: Genus with paracoprids representatives and reported exclusively for the Neotropical region. It is one of the most speciose scarabaeine genera in the continent, with about 178 described species (Schoolmeesters 2023), and at least another 150 awaiting to be described (Vaz-de-Mello personal observation). This genus is divided into two subgenera: *Canthidium* s. str. and *Neocanthidium* Martínez et al., 1964, equally diverse (80 and 70 species, respectively), with 31 species deemed *incertae sedis* (not assigned to any subgenus). All of these taxa need urgent taxonomic revision. In this study, we recorded six species: *Canthidium angulicole* Balthasar, 1939, *C. barbaticum* Preudhomme de Borre, 1886, *C. breve* (Germar, 1823), *C. cuprinum* Harold, 1867, *C. kelleri* (Martínez et al., 1964), *C. viride* (Lucas, 1859). Currently, the genus is under review, with new species being described singly or being grouped into species groups (Cupello 2018; Kohlmann et al. 2018; Moctezuma et al. 2019; Carvalho de Santana et al. 2019).

Canthon Hoffmannsegg, 1817: It is one of the most diverse genera among the Scarabaeinae, exclusive to the Americas, with currently 163 recognized species (Schoolmeesters 2023). Its distribution ranges from the United States to Uruguay and central-west Argentina, with representatives in all biomes along this range. This genus is divided into nine subgenera, some of which are under revision (Cupello & Vaz-de-Mello 2018 and references cited therein). Overall, their representatives are telecoprids, and may be generalists and predators. In this study, we recorded 13 species: *C. chalybaeus* Blanchard, 1846, *C. curvodilatatus* Schmidt, 1920, *C. daguerrei* Martínez, 1951, *C. edentulus* Harold, 1868, *C. histrio* (LePeletier de Saint-Fargeau & Audinet-Serville, 1828), *C. maldonadoi* Martínez, 1951, *C. mutabilis* Lucas, 1859, *C. ornatus* Redtenbacher, 1868, *C. quadratus* Blanchard, 1846, *C. quinque maculatus* Castelnau, 1840, *C. substriatus* Harold, 1868, *C. unicolor* Blanchard, 1846 and *C. virens* (Mannerheim, 1829). Nunes &

Vaz-de-Mello (2022), in the revision of the genus *Tetraechma* Blanchard, 1842, two species of *Canthon* that were reported for the Brazilian Pantanal were transferred to the genus *Tetraechma*. They are: *Canthon apicalis* Lucas, 1859 and *Canthon lituratus solutus* Schmidt, 1920.

Coprophanaeus d'Olsoufieff 1924: Genus exclusive to the Americas, with 50 described species (Schoolmeesters 2023). This genus is divided into three subgenera: *Coprophanaeus* s. str. (38 species), *Metallophanaeus* d'Olsoufieff, 1924 (eight species) and *Megaphanaeus* d'Olsoufieff, 1924 (four species). The species are easily identifiable with the recent review by Edmonds & Zidek (2010), and further descriptions and revalidations (Kohlmann & Solís 2012, Cupello & Vaz-de-Mello 2013, 2014). Here, we recorded four species: *Coprophanaeus* (*Megaphanaeus*) *ensifer* (Germar, 1823), *C. (Megaphanaeus) bonariensis* (Gory, 1844), *C. (C.) cyanesens* (d'Olsoufieff, 1924), *C. (C.) milon* (Blanchard, 1845). Usually, the representatives are paracoprids and in dissonance of their name, they are usually necrophagous.

Deltochilum Eschscholtz, 1822: Genus endemic to the Americas, with approximately 114 described species (Schoolmeesters 2023), divided into eight subgenera, some of which are under revision (namely, *Deltohyboma* Paulian, 1938, with 42 species, and *Calhyboma Kolbe*, 1893, with 13), some with recent reviews completed (Génier 2012; González-Alvarado & Vaz-de-Mello 2014; Silva et al. 2015; Nazaré-Silva & Silva 2021). The species are telecoprid. *Deltochilum* is here represented by four species belonging to three different subgenera: *Deltochilum* (*Deltochilum*) *silphoides* Balthasar, 1939, *D. (Hybomidium) pseudoicarus* Balthasar, 1939, *Deltochilum* (*Aganhyboma*) *cupreicolle* (Blanchard, 1846) and *Deltochilum* (*A.*) *icarioides* Balthasar, 1939.

Dichotomius Hope, 1838: Genus with exclusive distribution in the Americas, with 200 described species, divided into four subgenera; *Dichotomius* s. str. (74 species), *Selenocopris* Burmeister, 1846 (85 spp.), *Cephagonus* Luederwaldt, 1929 (40 spp.) and *Homocanthonides* Luederwaldt, 1929 (1 sp.) (Schoolmeesters 2023), all under revision or recently revised (Arias-Buriticá et al. 2013, Maldaner et al. 2015, Nunes et al. 2016a-b, Vaz-de-Mello et al. 2016, Arias-Buriticá et al. 2019, Montoya-Molina et al. 2019, Cassenote et al. 2020, Boilly et al. 2021, Montoya-Molina et al. 2021, Valois et al. 2022, Maldaner et al. 2022, Valois et al. 2023, Arias-Buriticá et al. 2023). We recorded eight species from two subgenera: *Dichotomius* (*Dichotomius*) *bos* (Blanchard, 1846), *D. (D.) luctuosoides* (Harold, 1869), *Dichotomius* (*Selenocopris*) *cuprinus* (Felsche, 1901), *D. (S.) glaucus* (Harold, 1869), *D. (S.) lycas* (Felsche, 1901), *D. (S.) nisus* (Olivier, 1789), *D. (S.) opacipennis* (Luederwaldt, 1931) and *D. (S.) sexdentatus* (Luederwaldt, 1925).

Digitonthophagus Balthasar, 1959: An Afro-Asian genus, with 16 species (Genier & Moretto 2017). A species of African origin, *Digitonthophagus gazella* (Fabricius, 1787), was introduced in Brazil in the 1980s and is currently present in almost the entire national territory (Tissiani et al. 2017; Génier & Moretto 2017). This species is mainly associated with exotic pastures (e.g., African grasses; *Urochloa* spp.). It benefits from the presence of cattle ranching (Correa et al. 2020), and its occurrence is rare in areas of native vegetation. This species has a high rate of dispersal and fertility and is rapidly established in environments with high solar incidence, including savanna environments and pastures in the Amazon region (Matavelli & Louzada 2008).

Eurysternus Dalman, 1824: Genus with a Neotropical distribution, with 53 described species (Schoolmeesters 2023), recently revised by Génier (2009). Its representatives have endocoprid behavior. We

recorded five species: *Eurysternus caribaesus* (Herbst, 1789) with distribution from Mexico to and almost all of South America, *E. aeneus* Génier, 2009, *E. jessopi* Martínez, 1988, *E. nigrovirens* Génier, 2009, and *E. plebejus* Harold, 1880.

Genieridium Vaz-de-Mello, 2008: This genus has seven described species, frequently found in pastures in the Cerrado and Chaco areas. Other species are also associated with natural grasslands and non-forest phytophysionomies (Vaz-de-Mello 2008). Here represented by two species: *Genieridium bidens* (Balthasar, 1938) and *G. cryptops* (Arrow, 1913).

Gromphas Brullé, 1838: This genus has six species and the last revision of this genus was made by Cupello & Vaz-de-Mello (2013b, 2015). Here, it is represented by only one species, *Gromphas inermis* Harold, 1869. This species occurs in Brazil, Bolivia, Paraguay, Argentina and Uruguay.

Isocoprís Pereira & Martínez, 1960: This genus has seven species and the last revision of this genus was made by Rossini & Vaz-de-Mello (2017). In this study, we recorded only *Isocoprís foveolatus* (Luederwaldt, 1931).

Malagoniella Martínez 1961: This genus needs taxonomic revision, since the last was performed by Hallfater & Martínez (1966). It is currently divided into two subgenera *Malagoniella* s. str. and *Megatophomima* Martínez, 1961, with 16 described species (Schoolmaster 2023).

Ontherus Erichson, 1847: Genus with Neotropical distribution and 60 species, divided into three subgenera, *Ontherus* s. str. (34 species), *Caelontherus* Génier, 1996 (24 species) and *Planontherus* Génier, 1996 (two species) (Schoolmeesters 2023), revised by Génier (1996, 1998; see also González & Medina 2015). Its representatives present paracoprid habits. We recorded six species: *Ontherus appendiculatus* (Mannerheim, 1829), *O. aphodioides* Burmeister, 1874, *O. dentatus* Luederwaldt, 1930, *O. digitatus* Harold, 1868, *O. erosioides* Luederwaldt, 1930, and *O. sulcator* (Fabricius, 1775).

Phanaeus MacLeay, 1819: A genus with 82 species (Edmonds & Zidek 2012; Schoolmeesters 2023), two of which are inhabitants of grassland and savanna formations in Brazil and are occasionally collected in cultivated pastures (Edmonds 1994). Here represented by two species: *Phanaeus kirbyi* Vigors, 1825 and *Phanaeus palaeno* Blanchard, 1846.

Pseudocanthon Bates, 1887: Genus with ten described species present on continental America and the Antilles. Among these species, five occurring in South America, *P. perplexus* (LeConte, 1847), *P. xanthurus* (Blanchard, 1847), *P. vazdemelloi* Nazaré-Silva & Silva, 2021, *P. pantanensis* Nazaré-Silva & Silva, 2021 and *P. chaquensis* Nazaré-Silva & Silva, 2021.

Sulcophanaeus d'Olsoufieff, 1924: Genus exclusive to the Americas, with 15 valid species (Schoolmeesters 2023), its representatives are paracoprids. The last revision is by Edmonds (2000), and it was represented here by only one species, *Sulcophanaeus menelas* (Castelnau, 1840).

Trichillidium Vaz-de-Mello, 2008: Genus with four species, usually found in the Amazon, Chaco and Central America and with coprophagous diet (Vaz-de-Mello 2008). Here represented by *Trichillidium quadridens* (Arrow, 1932).

Trichillum Harold, 1868: Genus with Neotropical distribution, with 11 described species (Schoolmeesters 2023). Its representatives are

probably endocoprids. Here represented by only one species, *Trichillum externepunctatum* Preudhomme de Borre, 1886.

Zonocoprís Arrow, 1932: Genus with two described species associated with large gastropods of the genera *Strophocheilus* (Müller, 1774) and *Megalobulimus* (Müller, 1774). This genus is found in Brazil, northern and northeastern Argentina, southern Bolivia and Paraguay (Vaz-de-Mello 2007). In the Brazilian Pantanal, it is represented by *Zonocoprís gibbicollis* (Harold, 1868).

Uroxys Westwood, 1842: Genus with 59 recognized species (Schoolmasters 2023), which are present in forested areas. The last revision was carried out by Arrow (1933). It has size and ecological functions similar to those of the genus *Trichillum*. Here represented by one species: *Uroxys corporaali* Balthasar, 1940.

Although not recorded in our study, species of the genera *Agamopus* Bates, 1887, *Anomiopus* Westwood, 1846, *Besourenza* Vaz-de-Mello, 2008, *Dendropaemon* Perty, 1830, *Diabroctis* Gistel, 1857 and *Eutrichillum* Martínez, 1969 are also expected to occur in the Brazilian Pantanal, due to the record of species of these genera in regions close to the Pantanal (Vaz-de-Mello, personal observation). Indeed, species of the genus *Anomiopus* (Correa et al. 2022b) and *Dendropaemon* were recently reported from the Pantanal region in Aquidauana and Miranda – Mato Grosso do Sul, Brazil (see Correa et al. 2022a; Gonçalves et al. 2022).

Conclusions

This study provides an updated list and identification key for the identification of species of dung beetles occurring in the Brazilian Pantanal, except for species belonging to genera that are under taxonomic revision. We recorded high richness of dung beetles in the Brazilian Pantanal, with 68 dung beetle species of 30 genera. This underscores the importance of studies on this ecosystem in which the dung beetle fauna is still poorly known (Correa et al. 2022a). The bibliographical survey and the construction of the identification keys were carried out in 2020, and some species were updated (Table 1) according to new updates: *Coprophanaeus spitzii* (Pêssoa, 1935), *Dendropaemon nitidicollis* d'Olsoufieff, 1924, e *Onthophagus hircus* Billberg, 1815 (Correa et al. 2022b). With new inventories carried out in the Pantanal region, this species list will probably increase. Finally, the use of this guide for identification of dung beetle species can be an important tool to help researchers and provide incentive for new studies on the dung beetle fauna in the Brazilian Pantanal.

Acknowledgments

AAM thanks Universidade Federal de Mato Grosso for financing this project (Process number: 148/2017). AAM thanks A Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) for financial support (Process number: IBPG-0545-2.04/21) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) (Process 140194/2023-1).

EC thanks CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brazil) (Process 88887.654514/2021-00) and the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) – POSGRAD/scholarship/ for financing this study. CMAC thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior 'Bolsista CAPES/Brasil' for postdoctoral grant (Process 88887.603414/2021-00).

We also thank the Invertebrate Collection of INPA for allowing the use of photographic equipment. We also thank Vinicius Costa-Silva, Emanuel Ribas Gama and Arturo Gonzalez for providing some of the photos. We thanks to Mário Cupello for english revision.

FZVM, a CNPq PQ1A fellow, thanks Instituto Nacional de Ciencia e Tecnologia em Áreas úmidas (INAU), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) Process number: 431760/2018-7, and Fundação de Amparo a Pesquisa do Estado de Mato Grosso (FAPEMAT): Process number: 0147956/2017; PRONEM: 568005/2014. The authors thank Instituto Nacional de Ciência e Tecnologia em Áreas Úmidas (INAU) for the financial support.

Associate Editor

José Mermudes

Author Contributions

Adriana Andrade Mota: specimens identification; photo production; elaboration of the keys and writing of the manuscript.

Edrielly Carvalho: photo production and editing; elaboration of the keys and writing of the manuscript.

César Murilo de Albuquerque Correa: manuscript writing and review.

Fernando Vaz-de-Mello: specimens identification.

Conflicts of Interest

All authors have seen and agree with the contents of the manuscript and there is no conflict of interest, including specific financial interest and relationships and affiliations relevant to the subject of manuscript.

Data Availability

Supporting data are available at <<https://doi.org/10.48331/scielodata.HJNGV1>>.

References

- ALHO, C.J.R. & SABINO, J. 2011. A conservation agenda for the Pantanal's biodiversity. *Braz. J. Biol.* 71:327–335.
- BALTHASAR, V. 1939. Megathoposoma n.Gen. und neue Arten der Gattung Deltochilum Eschz. 59. Beitrag zur Kenntnis der Scarabaeiden (Col.). *Cas. Ces. Spol. Entomol* 36:5–19.
- CARVALHO DE SANTANA, E.C., PACHECO, T.L. & VAZ-DE-MELLO, F.Z. 2019. Taxonomic revision of the *Canthidium* Erichson, 1847 species of the gigas group (Coleoptera, Scarabaeidae, Scarabaeinae). *Eur. J. Taxon.* 530:1–24.
- CORREA, C.M.A., AUDINO, L.D., HOLDBROOK, R., BRAGA, R.F., MENÉNDEZ, R. & LOUZADA, J. 2020. Successional trajectory of dung beetle communities in a tropical grassy ecosystem after livestock grazing removal. *Biodivers. Conserv.* 29:2311–2328.
- CORREA, C.M.A., AUDINO, L.D., VAZ-DE-MELLO, F.Z. & LOUZADA, J. 2022a. Diversity and structure of dung beetle (Coleoptera: Scarabaeidae) assemblage in natural grasslands of the Brazilian Pantanal. *Int. J. Trop. Insect Sci.* 42:3253–3261.
- CORREA, C.M.A., FERREIRA, K.R., ABOT, A.R., LOUZADA, J. & VAZ-DE-MELLO, F.Z. 2022b. Ivermectin impacts on dung beetle diversity and their ecological functions in two distinct Brazilian ecosystems. *Ecol. Entomol.* 47:736–748.
- CORREA, C.M.A., BRAGA, R.F., LOUZADA, J. & MENÉNDEZ, R. 2019. Dung beetle diversity and functions suggest no major impacts of cattle grazing in the Brazilian Pantanal wetlands. *Ecol. Entomol.* 44:524–533.
- CORREA, C.M.A., BRAGA, R.F., PUKER, A., ABOT, A.R. & KORASAKI, V. 2018. Optimising methods for dung beetle (Coleoptera: Scarabaeidae) sampling in Brazilian pastures. *Environ. Entomol.* 47:48–54.
- CORREA, C.M.A. & da SILVA, P.G. 2022. Environmental drivers of taxonomic and functional diversity of dung beetles across a chronosequence of tropical grasslands with different cattle grazing removal ages. *Austral Ecol.* 47:928–938.
- CORREA, C.M.A., da SILVA, P.G., PUKER, A. & ABOT, A. 2021. Spatiotemporal patterns of taxonomic and functional β -diversity of dung beetles in native and introduced pastures in the Brazilian Pantanal. *Austral Ecol.* 46:98–110.
- CORREA, C.M.A., PUKER, A., FERREIRA, K.R., CRISTALDO, C.M., FERREIRA, F.N.F., ABOT, A.R. & KORASAKI, V. 2016. Using dung beetles to evaluate the conversion effects from native to introduced pasture in the Brazilian Pantanal. *J. Insect Conserv.* 20:447–456.
- CUNHA, C.N., PIEDADE, M.T.F. & JUNK, W.J. 2014. Classificação e delineamento das áreas úmidas brasileiras e de seus microhabitats. EdUFMT, Cuiabá, p.1–156.
- CUPELLO, M. 2018. On the types species of the New World dung beetle genus *Canthidium* Erichson, 1847 (Coleoptera: Scarabaeidae: Scarabaeinae), with an annotated checklist of species. *Zootaxa* 4388:451–486.
- CUPELLO, M. & VAZ-DE-MELLO, F.Z. 2013a. New evidence for the validity of *Coprophanæus* (C.) *terrali* Arnaud, 2002 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini), a dung beetle from Brazil. *Zootaxa* 3717:359–368.
- CUPELLO, M. & VAZ-DE-MELLO, F.Z. 2013b. Taxonomic revision of the South American dung beetle genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini: Gromphadina). *Zootaxa* 3722:439–482.
- CUPELLO, M. & VAZ-DE-MELLO, F.Z. 2014. Revalidation of the Brazilian Atlantic Forest dung beetle species *Coprophanæus* (*Metallophanæus*) *machadoi* (Pereira & d-Andretta, 1955) (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini) based on morphological and distributional evidence. *Zootaxa* 3869:435–451.
- CUPELLO, M. & VAZ-DE-MELLO, F.Z. 2015. A new species and the phylogeny of the South American genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Journal of Natural History* 50(15-16): 943-969.
- CUPELLO, M. & VAZ-DE-MELLO, F.Z. 2018. A monographic revision of the Neotropical dung beetle genus *Sylvicanthon* Halffter & Martínez, 1977 (Coleoptera: Scarabaeidae: Scarabaeinae: Deltochilini), with a reappraisal of the taxonomic history of “*Canthon sensu lato*”. *European Journal of Taxonomy* 467: 1–205.
- DANIEL, G.M. & VAZ-DE-MELLO, F.Z. 2016. Biotic components of dung beetles (Insecta: Coleoptera: Scarabaeidae: Scarabaeinae) from Pantanal – Cerrado Border and its implications for Chaco regionalization. *J. Nat. Hist.* 50:1159–1173.
- da SILVA, P.G. & HERNÁNDEZ, M.I.M. 2015. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PLoS ONE* 10:e0126112.
- EDMONDS, W.D. 1994. Revision of *Phanaeus* Macleay, a new world genus of Scarabaeinae dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contrib. Sci.* 443:1–105.
- EDMONDS, W.D. 2000. Revision of the Neotropical dung beetle genus *Sulcophanæus* (Coleoptera: Scarabaeidae: Scarabaeinae). *Folia Heyrovskyana* 6:1–60.
- EDMONDS, W.D. & ZÍDEK, J. 2010. A taxonomic review of the neotropical genus *Coprophanæus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). *Insecta Mundi* 129:1–111.
- EDMONDS, W.D. & ZÍDEK, 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*, v.274, p.1–108.

- GARDNER, T.A., BARLOW, J., ARAUJO, I.S., ÁVILA-PIRES, T.C., BONALDO, A.B., COSTA, J.E. et al. 2008. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecol. Lett.* 11:139–150.
- GÉNIER, F.A. & MORETTO, P. 2017. *Digitonthophagus Balthasar*, 1959: taxonomy, systematics, and morphological phylogeny of the genus revealing an African species complex (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 4248:1–110.
- GÉNIER, F. 2012. A new species and notes on the subgenus *Deltochilum* (*Deltochilum*) Eschscholtz, 1822 (Coleoptera: Scarabaeidae: Scarabaeinae: *Deltochilini*). *Zootaxa* 3357:25–36.
- GÉNIER, F. 1996. A revision of the Neotropical genus *Ontherus* Erichson (Coleoptera, Scarabaeidae, Scarabaeinae). *Mem. Ent. Soc. Can.* 128:3–170.
- GÉNIER, F. 1998. A revision of the Neotropical genus *Ontherus* Erichson (Coleoptera: Scarabaeidae: Scarabaeinae), supplement 1. *The Coleopterists Bulletin* 52(3):270–274.
- GÉNIER, F. 2009. Le genre *Eurysternus* Dalman, 1824 (Scarabaeidae: Scarabaeinae: Oniticellini), révision taxonomique et clés de détermination illustrées. Sofia: Pensoft, (Pensoft series faunistica, 85), p.1–430.
- GONÇALVES, T.F., CORREA, C.M.A., AUDINO, L.D., VAZ-DE-MELLO, F.Z., FONTOURA, F.M. & GUEDES, N.M.R. 2022. Quantifying the post-fire recovery of taxonomic and functional diversity of dung beetles in the Brazilian Pantanal. *Ecol. Entomol.* 47:601–612.
- GONZÁLEZ-ALVARADO, F.A. & MEDINA, C.A. 2015. The genus *Ontherus* Erichson 1847 (Coleoptera: Scarabaeidae: Scarabaeinae): description of a new species, and notes on the genus in Colombia. *Zootaxa* 3949(1):82–90.
- GONZÁLEZ-ALVARADO, A. & VAZ-DE-MELLO, F.Z. 2021. Towards a comprehensive taxonomic revision of the Neotropical dung beetle subgenus *Deltochilum* (*Deltohyboma*) Lane, 1946 (Coleoptera: Scarabaeidae: Scarabaeinae): Division into species-groups. *PLoS ONE* 16:e0244657.
- GONZÁLEZ, F.A. & VAZ-DE-MELLO, F.Z. 2015. Taxonomic review of the subgenus *Hybomidium* Shipp 1897 (Coleoptera: Scarabaeidae: Scarabaeinae: *Deltochilum*). *Ann. la Soc. Entomol. Fr.* 50:431–476.
- HALFFTER, G. & EDMONDS, W.D. 1982. Nesting Behavior of Dung Beetles (Scarabaeinae). *Man and Biosphere Program – UNESCO, Mexico*, p.1–176.
- HALFFTER, G. & FAVILA, M.E. 1993. The Scarabaeinae (Insecta, Coleoptera), an animal group for analyzing, inventorying, and monitoring biodiversity in tropical rain forest and modified landscapes. *Biol. Int.* 27:15–21.
- HALFFTER, G. & MARTINEZ, A. 1966. Revision monographica de los *Canthonina* americanos (Coleoptera, Scarabaeidae) (1a. parte). *Rev. Soc. Mex. Hist. Nat.* 27:89–177.
- HALFFTER, G. & MARTÍNEZ, A. 1977. Revisión monográfica de los *Canthonina* americanos, IV parte. Clave para géneros y subgéneros. *Folia Entomol. Mex.* 38:29–107.
- HALFFTER, G. & MATTHEWS, E.G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomol. Mex.* 12:1–312.
- HANSKI, I. & CAMBEFORT, Y. (1991) *Dung beetle ecology*. Princeton, NJ: Princeton University Press, p.1–481.
- HAROLD, E. 1868. Die arten der gattung *Choeridium*. *Coleopterologische Hefte* 4, 32–76.
- JUNK, W.J., CUNHA, C.N., WANTZEN, K.M., PETERMANN, P., STRÜSSMANN, C., MARQUES, M.I. et al. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquat. Sci.* 69:278–309.
- KOHLMANN, B., ARRIAGA-JIMÉNEZ, A. & RÖS, M. 2018. An unusual new species of *Canthidium* (Coleoptera: Scarabaeidae: Scarabaeinae) from Oaxaca, Mexico. *Zootaxa* 4378:273–278.
- KOHLMANN, B. & SOLÍS, Á. 2012. New species and revalidations of scarab beetles (Coleoptera: Geotrupidae: Athyreini and Coleoptera: Scarabaeidae: Scarabaeinae) from Costa Rica and Panama. *Zootaxa* 3193:28–52.
- LEWINSOHN, T.M., FREITAS, A.V.L. & PRADO, P.I. 2005. Conservation of terrestrial invertebrates and their habitats in Brazil. *Conserv. Biol.* 19:640–645.
- LOUZADA, J.N.C., LOPES, F.S. & VAZ-DE-MELLO, F.Z. 2007. Structure and composition of a dung beetle community (Coleoptera, Scarabaeinae) in a small forest patch from Brazilian Pantanal. *Rev. Bras. Zoociencias* 9:199–203.
- MATAVELLI, R.A. & LOUZADA, J.N.C. 2008. Invasão de áreas de savana intra-amazônicas por *Digitonthophagus gazella* (Fabricius, 1787) (Insecta: Coleoptera: Scarabaeidae). *Acta Amaz.* 38:153–158.
- McGEOCH, M.A., van RENSBURG, B.J. & BOTES, A. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *J. Appl. Ecol.* 39:661–672.
- MOCTEZUMA, V., SÁNCHEZ-HUERTA, J.L. & HALFFTER, G. 2019. New species of *Canthidium* (Coleoptera: Scarabaeidae: Scarabaeinae) from Mexico. *Can. Entomol.* 151:432–441.
- MOHER, D., LIBERATI, A., TETZLAFF, J., ALTMAN, D.G., & PRISMA GROUP. 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *Ann. Intern. Med.* 151:264–269.
- NAZARÉ-SILVA, E.E. & SILVA, F.A.B. 2012. A revision of the subgenera *Euhyboma* Kolbe, 1893, *Parahyboma* Paulian, 1938, and *Rubrohyboma* Paulian, 1939 of *Deltochilum* Eschscholtz, 1822 (Coleoptera: Scarabaeidae: Scarabaeinae). *Revista Brasileira de Entomologia* 65(3):1–19.
- NICHOLS, E., LARSEN, T., SPECTOR, S., DAVIS, A.L., ESCOBAR, F., FAVILA, M. & VULINEC, K. 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biol. Conserv.* 137:1–19.
- NICHOLS, E., SPECTOR, S., LOUZADA, J.N.C., LARSEN, T., AMEZQUITA, S. & FAVILA, M.E. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* 141:1461–1474.
- PESSÔA, M.B., IZZO, T.J. & VAZ-DE-MELLO, F.Z. 2017. Assemblage and functional categorization of dung beetles (Coleoptera: Scarabaeinae) from Pantanal. *PeerJ* 5:e3978.
- PICCINI, I., ARNIERI, F., CAPRIO, E., NERVO, B., PELISSETTI, S., PALESTRINI, C., ROSLIN, T. & ROLANDO, A. 2017. Greenhouse gas emissions from dung pats vary with dung beetle species and with assemblage composition. *PLoS ONE* 12:e0178077.
- POTT, A., OLIVEIRA, A., DAMASCENO-JUNIOR, G. & SILVA, J.S.V. 2011. Plant diversity of the Pantanal wetland. *Braz. J. Biol.* 71:265–273.
- RODRIGUES, S.R., BARROS, A.T.M., PUKER, A. & TAIRA, T.L. 2010. Diversidade de besouros coprófagos (Coleoptera, Scarabaeidae) coletados com armadilha de interceptação de voo no Pantanal Sul-Mato-Grossense, Brasil. *Biota Neotrop.* 10:123–127.
- ROSSINI, M. & VAZ-DE-MELLO, F.Z. 2017. A taxonomic review of the genus *Isocoprís* Pereira and Martínez, 1960 (Coleoptera: Scarabaeidae: Scarabaeinae), with description of a new Brazilian species. *J. Nat. Hist.* 51:1091–1117.
- SCHOOLMEESTERS, P. 2023. World Scarabaeidae Database. *In*: Bánki O., Roskov Y., Döring M., Ower G., Vandepitte L., Hobern D., Remsen D., Schalk P., DeWalt R.E., Keping M., Miller J., Orrell T., Aalbu R., Abbott J., Adlard R., Adriaenssens E.M., Aedo C., Aeschl E., Akkari N., et al. (eds) *Catalogue of Life Checklist* (Version 2023–03-06). Available from <https://www.catalogueoflife.org/data/dataset/1027> [last accessed 03 Apr 2023].
- SILVA, F.A.B., LOUZADA, J. & VAZ-DE-MELLO, F. 2015. A revision of the *Deltochilum* subgenus *Aganhyboma* Kolbe, 1893 (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 3925: 451–504.
- SLADE, E.M., RIUTTA, T., ROSLIN, T. & TUOMISTO, H.L. 2016. The role of dung beetles in reducing greenhouse gas emissions from cattle farming. *Sci. Rep.* 6:1–8.
- TARASOV, S. & DIMITROV, D. 2016. Multigene phylogenetic analysis redefines dung beetle relationships and classification (Coleoptera: Scarabaeidae: Scarabaeinae). *BMC Evol. Biol.* 16:219–257.
- TISSIANI, A.S.O., SOUSA, W.O., SANTOS, G.G., IDE, S., BATTIROLA, L. & MARQUES, M.I. 2015. Environmental influence on coprophagous Scarabaeidae (Insecta, Coleoptera) communities in the Pantanal of Mato Grosso. *Braz. J. Biol.* 75:136–142.

Dung beetle species of the Brazilian Pantanal

- TISSIANI, A.S.O., VAZ-DE-MELLO, F.Z. & CAMPELO-JÚNIOR, J.H. 2017. Besouros rola-bostas das pastagens brasileiras e chave para identificação dos gêneros (Coleoptera: Scarabaeidae). *Pesq. Agropec. Bras.* 52:401–418.
- TOMAS, W.M., DE OLIVEIRA, R.F., MORATO, R.G., MEDICI, P.E., CHIARAVALLI, R., TORTATO, F. et al. 2019. Sustainability agenda for the Pantanal wetland: perspectives on a collaborative interface for science, policy, and decision-making. *Trop. Conserv. Sci.* 12:1940082919872634.
- UNESCO. 2000. World heritage. United Nations Educational, Scientific and Cultural Organization, Cairns.
- VAZ-DE-MELLO, F.Z. 2000. Estado atual de conhecimento dos Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) do Brasil. In: MARTÍN-PIERA, F., MORRONE, J.J., MELIC, A. (Ed.). *Hacia un Proyecto CYTED para el inventario y estimación de la diversidad entomológica en Iberoamérica: PrIBES-2000*. Zaragoza: Sociedad Entomológica Aragonesa, (Monografías tercer milenio, 1), p.183–195.
- VAZ-DE-MELLO, F.Z. 2007. Revision and phylogeny of the dung beetle genus *Zonocopriss* Arrow 1932 (Coleoptera: Scarabaeidae: Scarabaeinae), a phoretic of land snails. *Ann. Soc. Entomol. Fr.* 43:231–239.
- VAZ-DE-MELLO, F.Z. 2008. Synopsis of the new subtribe *Scatimina* (Coleoptera: Scarabaeidae: Scarabaeinae: Ateuchini), with descriptions of twelve new genera and review of *Genieridium*, new genus. *Zootaxa* 1955:1–75.
- VAZ-DE-MELLO, F.Z., EDMONDS, W.D., OCAMPO, F.C. & SCHOOLMEESTERS, P. 2011. A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa* 2854:1–73.

Received: 18/01/2023

Accepted: 16/05/2023

Published online: 30/06/2023