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Taxonomic revision of the *batesi* species group of *Dichotomius* Hope, 1838, with the description of three new Amazonian species (Coleoptera, Scarabaeidae, Scarabaeinae)

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Abstract

Dichotomius (*Selenocopris*) is amongst the most diverse subgenera of *Dichotomius* Hope, 1838. Due to the scarcity of material and logistical problems experienced by previous authors to access type specimens, the available taxonomic information for the *batesi* group is mainly the short and superficial original descriptions of its species. In this paper, we provide a revision for all the species assigned to the *batesi* group and a comparative study with species belonging to taxonomically related species groups, namely: *agenor*, *geminatus*, *inachus*, *carbonarius*, and *lucasi*. The *batesi* group is redefined to include five Amazonian species: *D. batesi*, *D. ziliolii*, *D. snethlageae* **sp. nov.**, *D. martavannucciae* **sp. nov.**, and *D. leopoldinae* **sp. nov.** . The *globulus* is proposed for the remaining species formerly included in the *batesi* group; these species occur from Costa Rica to northern Amazonia. *Dichotomius parcepunctatus* and *D. fortestriatus* are considered **new synonyms** of *D. batesi*. Distribution data and an identification key are provided for the species in the *batesi* group.

Keywords

Dichotomiini; dung beetles; new species; systematics

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Introduction

Dichotomius Hope, 1838 is the most diverse genus in the New World tribe Dichotomiini (Coleoptera: Scarabaeinae). It comprises approximately 190 species separated into four subgenera: *D.* (*Dichotomius*) Hope, 1838; *D.* (*Selenocopris*) Burmeister, 1846; *D.* (*Homocanthonides*) Luederwaldt, 1929; and *D.* (*Cephagonus*) Luederwaldt, 1929 (Luederwaldt 1929; Martínez 1951; Nunes & Vaz-de-Mello 2019). *Dichotomius* (*Selenocopris*) includes species with the following combination of characteristics: (1) clypeus bidentate with a distinct central emargination between the clypeal teeth; (2) junction between clypeus and the paraocular areas of the frons rounded, without angulation; (3) lateral lobes of metaventrite usually with abundant setae; (4) and female with sixth abdominal ventrite as long as fifth medially, lacking tubercles or carina (Luederwaldt 1929; Nunes & Vaz-de-Mello 2013). Species in this subgenus are widely distributed from Mexico to Argentina, and they have been sorted into 14 species groups (Luederwaldt 1929; Nunes & Vaz-de-Mello 2013; Nunes & Vaz-de-Mello 2019).

One of the most important taxonomic issues that needs to be properly revised in *Dichotomius* is the poorly defined species boundaries of early studies. The scarcity of taxonomic information has resulted in difficulties for modern biologists who seek to identify species accurately. Many recent papers dealing with taxonomic revisions on *Dichotomius* species groups have provided redescriptions and diagnoses after careful comparison of types and additional material deposited in collections (Nunes and Vaz-de-Mello 2013; Maldaner et al. 2015; Nunes et al. 2016; Valois et al. 2017; Arias-Boriticá & Vaz-de-Mello 2019; Nunes & Vaz-de-Mello 2019; Rossini & Vaz-de-Mello et al. 2020; Cassenote et al. 2020; Montoya-Molina & Vaz-de-Mello 2021). However, in *Dichotomius* (*Selenocopris*) such efforts have been concentrated in groups that have practical characteristics for identification, such as: 1) low diversity, with less than ten species; and (2) easy definition based on a distinctive character, such as the presence of metallic coloration (Maldaner et al., 2015), a pair of deep foveae on pronotum (Valois et al. 2017), or hairy depression on hypomera (Nunes et al. 2016). As a direct consequence of these identification procedures, the more diverse and poorly defined groups, such as the *batesi* group, continue to accumulate taxonomic problems.

Within *D.* (*Selenocopris*), the *batesi* species group includes 14 species occurring from Costa Rica to Bolivia (Luederwaldt 1929; Kohlmann & Solís 1997; Guandini & Aguilar 2009; Vaz-de-Mello & Nunes 2016). Species of this group have a small to medium body size, a single conical horn on the head, and a pronotum that is in general without deep excavations, horns, or projections. Because of that combination of characteristics, Luederwaldt (1929) referred to these species as having a "simple shape" in the genus. However, species in the groups *inachus*, *carbonarius*, *geminatus*, *agenor*, and *lucasi* also fit with these features and Luederwaldt (1929) usually had difficulties defining unambiguous taxonomic limits between some of these species groups. For instance, the *batesi* group was originally defined based on the presence of coarse punctures on the pronotum, and included ten species: *D. batesi* (Harold, 1869), *D. globulus* (Felsche, 1901), *D. fortepunctatus* (Luederwaldt, 1923), *D. parcepunctatus* (Felsche,

1901), *D. fortestriatus* (Luederwaldt, 1924), *D. geminatus* (Arrow, 1913), *D. taunayi* (Luederwaldt, 1922), *D. micans* (Luederwaldt, 1924), *D. muticus* (Luederwaldt, 1922), and *D. ocellatopunctatus* (Felsche, 1901). However, in a later work, Luederwaldt (1936) established a new group for *D. micans*, while *D. muticus* and *D. taunayi* were transferred to the *inachus* species group.

Pereira (1947) provided the first taxonomic revision of the *batesi* group after Luederwaldt's work. However, he added few contributions to its taxonomy since the author was not able to examine the type of many species names. Other species were described over time, mostly from Central America, which were assigned to the *batesi* group based on slight similarities with *D. globulus* (Howden & Young 1981; Kohlmann & Solís 1997). Vaz-de-Mello and Nunes (2016) described *D. benesi*, the most recent species to be included in the *batesi* group. They have also discussed the existence of two different patterns of pronotal punctuation that could be useful for distinguishing the Amazonian species from those occurring in Central America.

The aim of this paper is to perform a comprehensive comparative study of the species currently assigned to the *batesi* group. The hypothesis of Vaz-de-Mello and Nunes (2016) that the species in the batesi group could be divided into two subgroups based on the pattern of pronotal punctuation and geographic distribution is investigated in the light of a detailed morphological study. Descriptions, diagnoses, identification key, and illustrations are also included for all species. Furthermore, we provide a discussion on the diagnostic characteristics historically used to delimit the species groups that are taxonomically related to the *batesi* group. We also illustrate, for the first time, the components of the male genitalia of *D. fortepunctatus* (Luederwaldt, 1923), *D. lycas* (Felsche, 1901), *D. inachus* (Erichson, 1847), *D. agenor* (Harold, 1869), *D. geminatus* (Arrow, 1913), and *D. lucasi* (Harold, 1869).

Material and methods

Morphological study

A total of 426 dry-preserved specimens of *Dichotomius* were examined. The material was kindly provided by the curators of the institutions as listed below:

CEMT	Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Brazil (Fernando Z. Vaz-de-Mello).
DZUP	Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil (Lúcia Massutti de Almeida).
MNHN	Muséum national d'Histoire naturelle, Paris, France (Olivier Montreuil and Antoine Mantilleri).
MPEG	Seção de Entomologia da Coleção Zoológica, Museu Paraense Emílio Goeldi, Belém, Brazil (Orlando Tobias).
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Sônia Casari, via Carlos Campaner and Juares Fuhrmann).

MZUFPA Coleção de Scarabaeinae do Museu de Zoologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil (Fernando A. B. Silva).

SMTD Museum für Tierkunde, Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany (Olaf Jäger and Klaus-Dieter Klass).

The study was based on dry-preserved adult specimens of *Dichotomius*, including name-bearing types of all available names assigned to the *batesi* species group and taxonomically related species groups: *inachus*, *carbonarius*, *agenor*, *geminatus*, and *lucasi*. For species description, we followed the terminology of Beutel and Lawrence (2005) and Lawrence et al. (2010) for ventral and pleural ventrites, and Edmonds (1972) for the remaining external morphological structures. We provided a general section for describing sexual dimorphic characters in females of the *batesi* group to avoid redundancy in the species descriptions.

External morphological structures and male genitalia (tegmen and endophallites) were examined using a stereomicroscope Motic CMZ-168. Photos were taken using a Stereomicroscope Leica M205A with image stacking software (Leica Application Suite, version 4.2). To study the male genitalia, the tegmen was removed from the beetles's body through the pygidium opening and then illustrated in dorsal view. Accessory endophallites were named according to the terminology in Tarasov and Solodovnikov (2011) and Tarasov and Génier (2015). The shape of the medial endophallite (ME) of *Dichotomius* and allies is unique among Scarabaeinae genera. The ME was useful for diagnosing the species group and was illustrated according to the tegmen position in dorsal view and, when necessary, in lateral view. The terminology used to describe the ME follows Cupello et al. (2022), adapted as shown in Figs 3H–J.

Verbatim content of the labels of the name-bearing types is presented between quotation marks (“”). Different labels were separated by a double slash (//) and lines in the same label by a single slash (/). Labels of paratypes and non-type material examined were written as follows: COUNTRY (uppercase); *States or provinces* (in italic, separated by “:”); the number and sex of specimens examined (eg.: 1♂ 1♀); locality, coordinates, altitude, dates, collect method (separated by “,”); and abbreviations of collections or museums where they are deposited between parentheses (eg.: CEMT). When necessary, complementary information was provided between brackets “[]”. Map showing species distributions was made using QGIS “Lyon” 2.18 (Sherman et al. 2012).

Results

***Dichotomius* Hope, 1838 (type species: *Scarabaeus boreus* Olivier, 1789)**

Dichotomius (*Selenocopris*) Burmeister, 1846 (type species: *Copris bicuspis* Germar, 1823)

batesi species group

“Seção *Batesi*”; Luederwaldt 1929: 74

"*Dichotomius batesi* species group": Nunes & Vaz-de-Mello 2013

Diagnosis. As defined here, the *batesi* group is distinguished from other species groups in *D.* (*Selenocopris*) by the following combination of characteristics: medium-sized body (12–14 mm); pronotal disc covered with ocellate punctures, irregularly spaced (Figs 1A–1E); pronotum lacking deep fovea at each posterior angle; thoracic ventrites generally glabrous or with very short setae; protibial spur slightly curved at the apical fifth, not sickle-shaped; metatibial spur deeply emarginated at apex (Fig. 8I); basal portion of endophallus with a pair of strong sclerotized bristles ventrally (Figs 5G, 5J); lateral edges of paramera widened at the apical fifth (Figs 3A–3F); dorsal surface of paramera with a small, laterally directed teeth at the apical fifth (Figs 3A–F); medial endophallite (ME) twice longer than wide, midline and lateral edges forming longitudinal folds along their entire lengths (Figs 3G–J).

Redescription (♂). *Body.* Length: 12–14 mm. Black, opaque or shiny, usually with glossy bluish sheen on pronotum and elytra (Figs 1A–1E). *Head.* Surface sparsely to densely coated with ocellate punctures. Clypeal edge widely margined medially, bidentate, with rounded or acute median teeth separated by V-shaped emargination (Figs 1A–1E). Clypeal surface with slight transverse ridges anteriorly (Fig. 2C). Junction between clypeus and the paraocular areas of the frons rounded, lacking angulation. Clypeo-frontal region with low conical process. Antennae 9-segmented, antennal club slightly elongated, yellow to light brown integument, coated with long scattered yellow setae. *Thorax.* Pronotum twice as wide as long, as wide as elytra. Pronotal disc convex with shallow anterior declivity on anteromedial region. Posterior edge of pronotum with a band of ocellate punctures (Figs 2F–2G). Anterior pronotal angle acute, posterior angle obtuse. Mid-longitudinal sulcus of pronotum covered with ocellate punctures on basal half of disc. Anterior region of hypomera with dense ocellate punctures, usually setiferous; posterior region with ocellate punctures, or C-shaped punctures near posterior edge. Prosternum densely coated with ocellate punctures. Mesoventrite smooth medially, with dense ocellate punctures on lateral regions. Mesepisternum with ocellate and setiferous punctures, longitudinal ridges, or C-shaped punctures. Meso-metaventral suture feebly indicated, arcuate. Anterior lobe of metaventrite with ocellate and coarse punctures. Metaventral disc smooth, glabrous, mid-longitudinal sulcus feebly impressed, region between metacoxae with 1–2 rows of ocellate punctures. Lateral lobe of metaventrite with ocellate punctures spaced by the diameter of a puncture. Elytral striae well-impressed, usually carinate, punctate, punctures larger than striae (Figs 2J–L). Pseudoepipleuron not reaching elytral base. Surface of interstriae flat or convex, smooth. *Legs.* Protibiae with three distinct teeth at external margin. Inner apical angle of protibiae >90°. Protibial spur bent at apical third. Ventral surface of profemora covered with dense coarse and setiferous punctures. Ventral surface of meso– and metafemora with ocellate punctures at the apical region (Figs 8C–D). Posterior edge of mesofemora, in ventral view, with a longitudinal groove restricted to the apical half (Fig. 8C). Posterior edge of metafemora with groove usually present along the entire length of femora (Fig. 8D). Surface of longitudinal groove on meso– and metafemora with shagreened microsculpture.

Abdomen. Medial regions of ventrites with a single row of ocellate punctures along the anterior edge; lateral regions with ocellate punctures on anterior half. Sixth ventrite half the length of the fifth. Pygidium twice wider than long (as Fig. 2M). Pygidial disc with ocellate punctures more concentrated near the base. *Male genitalia.* Paramera with 2/3 of the phallobase length, symmetric, approximately triangularly shaped, slightly compressed medially in dorsal view (Figs 3A–F). Apex of paramera membranous (Figs 3A–F). Superior-right peripheral endophallite (SRP) semi-circular, right side thin (Fig. 3G). Complex of axial and subaxial endophallites (A+SA) elongate, apical fifth of subaxial endophallite reticulated (Fig. 3G). Medial endophallite (ME) with the dorsal projection of the inferior edge divided by V-shaped emargination (Figs 3G–H). Fronto-lateral peripheral endophallite (FLP) C-shaped at the inferior half, about two-thirds of the A+SA length (Fig. 3G). *Female.* Females of all species in the *batesi* group differ from males in the same characters. Females have a clypeal teeth acute, and separated by a deep V-shaped emargination (Fig. 2C). Anterior region of clypeus with well-defined transverse ridges. Sixth ventrite approximately twice as long as fifth. Pygidium short, approximately 2.5 times wider than long (as Fig. 2M).

Distribution. Species of the *batesi* group are widely distributed across the North and Midwest of South America reaching the southern borders between the Amazon basin and the dry habitats in Brazil and Bolivia (Fig. 9). According to the biogeografic regionalization of the Neotropical region by Morrone (2014), the distribution of the *batesi* group matches the Boreal Brazilian and the South Brazilian dominions, which encompass Brazil, Peru, Colombia, Ecuador and, Bolivia (Fig. 9).

Remarks. In *Dichotomius* (*Selenocopris*), seven of its14 species groups have species recorded in the Amazon rainforest (Table 1). However, none of these 14 Amazonian groups has so far had a modern taxonomic revision published. As demonstrated here, the new species of the *batesi* group are cryptic and, in the past, were frequently misidentified or unrecognized by researchers. Despite the efforts of ecologists in recent years to understand the susceptibility of dung beetles communities to landscape modification and fragmentation in different habitat types in the Amazon rainforest (Klein 1989; Feer 2000; Cajaiba et al. 2017a; Jacobs et al. 2018; Santos et al. 2018), studies on the taxonomy of the Amazonian *Dichotomius* (along with other dung beetles genera) have not advanced at the same way. The lack of taxonomic information has hampered the process of species identification in these ecological studies (Klein 1989; Feer 2000; Cajaiba et al. 2017b; Santos et al. 2018), which can lead to negative consequences to species conservation due to underestimation of local richness, and may also limit the inclusion of these species in wider comparative ecological studies.

Table 1. List of the species group of *Dichotomius* (*Selenocopris*) related to the *batesi* and *globulus* groups. Data of type localities were based on type labels or the original descriptions, quotation marks indicates that the information were transcribed *ipisis litteris*. Country abbreviations: BRA – Brazil; BOL – Bolivia; COL – Colombia; ECU – Ecuador; PER – Peru; VEN – Venezuela; GUF – French Guyana; SUR – Surinam; CRI – Costa Rica; PAN – Panama; NIC – Nicaragua; MEX – Mexico.

Taxon	Author and date	Type locality
***agenor* species group**		
Dichotomius agenor	(Harold, 1869)	"Columbia" (COL)
D. belus	(Harold, 1880)	"Columbia" and, "Medellin" (COL)
D. deyrollei	(Harold, 1869)	"Brasilia" (BRA)
D. inachoides	(Felsche, 1901)	"Merida" (VEN)
D. tristis	(Luederwaldt, 1923)	"Venezuela"
D. validipilosus	(Luederwaldt, 1931)	"Caracas" (VEN)
***batesi* species group**		
D. batesi	(Harold, 1869)	"Ega" [currently Tefé] (BRA)
D. fortestriatus **syn. nov.**	(Luederwaldt, 1923)	"Barcellos" (BRA)
D. parcepunctatus **syn. nov.**	(Felsche, 1901)	"Ega" [currently Tefé] (BRA)
D. leopoldinae	**sp. nov.**	Novo Progresso (BRA)
D. martavannucciae	**sp. nov**	Santarém (BRA)
D. snethlageae	**sp. nov**	Belém (BRA)
D. ziliolii	Gandini & Aguilar, 2009	"Jardin Botanico" (BOL)
***carbonarius* species group**		
D. carbonarius	(Mannerheim, 1829)	"Brasilia: Serra da Lapa" (BRA)
D. cuprinus	(Felsche, 1901)	"Sanga" (BOL)
D. glaucus	(Harold, 1869)	"Brasilia" (BRA)
D. luctuosus	(Harold, 1869)	"Brasilia" (BRA)
D. lycas	(Felsche, 1901)	"N. Brasilien" "Bahia" (BRA)
D. pseudocuprinus	(Gandini & Aguilar, 2009)	"Rondonia: Alto Senger" (BRA)
***globulus* species group**		
D. benesi	Vaz-de-Mello & Nunes, 2016	"Veraguas" (PAN)
D. danieli	Kohlmann & Solís, 1997	"Est. [ación] Pitilla" (CRI)
D. favi	Kohlmann & Solís, 1997	"Sector Cerro Cocori" (CRI)
D. femoratus	Howden & Young, 1981	"Barro Colorado Island" (PAN)
D. fortepunctatus	(Luederwaldt, 1923)	"Bucay" (ECU)
D. gamboaensis	Howden & Young, 1981	"Gamboa" (PAN)
D. globulus	(Felsche, 1901)	"Amazonas" (BRA)
D. ocellatopunctatus	(Felsche, 1901)	"Merida" (VEN)
D. rodrigoi	Kohlmann & Solís, 1997	"Puntarenhas" (CRI)
***geminatus* species group**		
D. geminatus	(Arrow, 1913)	"E. Brazil: Natal, Ceara" (BRA)
D. opacipennis	(Luederwaldt, 1931)	"Matto Grosso: Murtinho (BRA)"
D. mysticus	(Luederwaldt, 1935)	"Natal" (BRA)
D. vidaurrei	Nunes & Vaz-de-Mello, 2013	"Palmar de las Islas" (BOL)
***inachus* species group**		
D. apicalis	(Luederwaldt, 1931)	"Amazones" (BRA)
D. fallax	(Harold, 1880)	"Cararacas" "La Mesa" (VEN)
D. inachus	(Erichson, 1847)	"Peru" (PER)
D. planus	(Luederwaldt, 1923)	"Bolivia" (BOL)
D. problematicus	(Luederwaldt, 1923)	"Franz. Guyana" (GUF)

Table 1. List of the species group of *Dichotomius* (*Selenocopris*) related to the *batesi* and *globulus* groups. Data of type localities were based on type labels or the original descriptions, quotation marks indicates that the information were transcribed ipisis litteris. Country abbreviations: BRA – Brazil; BOL – Bolivia; COL – Colombia; ECU – Ecuador; PER – Peru; VEN – Venezuela; GUF – French Guyana; SUR – Surinam; CRI – Costa Rica; PAN – Panama; NIC – Nicaragua; MEX – Mexico. (*cont.*)

Taxon	Author and date	Type locality
D. simplex	(Taschenberg, 1870)	"Colomb." (COL)
D. yucatanus	(Bates, 1887)	"S. W. Yucatan" (MEX), "Chonta" (NIC)
***lucasi* species group**		
D. lucasi	(Harold, 1869)	"Brasilia" (BRA)
D. lucasi formosus	(Luederwaldt, 1931)	"Manaos" (BRA), "Cayenna" (GUF) and, Surinam (SUR)

Key to species of the batesi species group

Within *D.* (*Selenocopris*), species of the *batesi* and *globulus* groups can be distinguished from others by the following combined characters: median body size (11–14 mm); body black usually with a glossy bluish sheen on dorsum; fronto-clypeal region with a single conical process in both sexes (as Fig. 7A); pronotal disc covered with ocellate punctures (Figs 7A, F); metatibial spur deeply emarginated at apex (Fig. 8I); male protibial spur not sickle shaped; apex of paramera membranous (Figs 3A–F, 4A) and bent downwards (see the revision of the *globulus* group in Valois et al., 2022). The first couplet of our key is the diagnostic characters stated here to distinguish the *batesi* and *globulus* groups:

1. Pronotal disc with ocellate punctures irregularly spaced, more disperse on disc than on anterior and lateral regions (Fig. 7E). Surface of elytral interstriae smooth, finely punctated (Figs 2J–L). Metafemora slightly club-shaped (Fig. 8D). Ventral surface of meso– and metafemora with coarse punctures restricted to the apical region (Figs 8C–D). Posterior edges of meso– and metafemora with a longitudinal groove having fourth of the femora width; groove usually restricted to the apical half or apical third (Figs 8C–D). Dorsal surface of paramera with a small, laterally directed teeth at pre-apical region (Fig. 3F, arrow). Basal portion of endophallus with both a set of microbristles and a pair of strong sclerotized bristles ventrally (Figs 5G, J). Medial endophallite (ME) twice as long as wide (Figs 3G–J), inferior edge with two hook-like projections close each other, blade-shaped at the apex (Figs 3G–J). Lateral edges and midline of ME produced into well-developed longitudinal folds along its entire length (Figs 3G–J) (Brazil, Colombia, Bolivia, Peru, and Ecuador) ……..……..…***batesi* species group** 2
– Pronotal disc generally covered with umbilicate ocellate punctures (Fig. 7F). Surface of elytral interstriae dull, entirely shagreened or only shagreened along lateral regions. Metafemora not club-shaped, anterior and posterior edges almost

parallel along their lengths (Fig. 8F). Ventral surface of meso- and metafemora covered with dense coarse punctures at least on apical half (Figs 8E–F). Posterior edges of meso- and metafemora with a thin longitudinal groove along all femora lenght; groove usually wider on the apical half (Figs 8E–F). Dorsal surface of paramera smooth, with a longitudinal carina (as Fig. 4A, arrow) or a strong spine-like projection at pre-apical region (only *D. rodrigoi*). Basal portion of endophallus with a set of microbristles ventrally (Figs 5F, K). Medial endophallite (ME) as longer as wide (Fig. 6A), inferior edge with two hook-like projections widely separated from each other, not blade-shaped at the apex (as Fig. 6A). ME with a feeble longitudinal fold along its midline (as Fig. 6A)……..…..……
..….***globulus* species group** (from Costa Rica to Ecuador) (see Valois et al. 2022).

2. Ocellate punctures on posterior pronotal edge larger than those on pronotal disc (Fig. 2F). Elytral striae widened, densely punctated, punctures spaced by the diameter of a puncture or less (Figs 2J–K). …...……..…..3
– Ocellate punctures on posterior pronotal edge with similar size than those on pronotal disc (Fig. 2G). Elytral striae thin, sparsely punctate, punctures spaced by more than their diameter (Fig. 2l). ……..…….....5
3. Clypeal surface densely covered with ocellate punctures (Fig. 2A). Surface of pronotal sides densely punctated near lateral pronotal fovea (Fig. 2D). Brazil (Pará and Maranhão)…….…...….***D. snethlageae* sp. nov.**
– Clypeal surface with ocellate punctures concentrated on posterior half (Fig. 2B). Surface of pronotal sides sparsely punctate near lateral pronotal fovea (Fig. 2E)…….……...….4
4. Body oval, shiny on dorsum (Fig. 1C). Clypeal teeth acute, separated by a deep V-shaped emargination. Pre-apical edge of paramera as long as apical edge in dorsal view; inner apical edge straight at the apical eighth (Fig. 3C, arrow). Brazil (Pará)……..……...***D. martavannucciae* sp. nov.**
– Body elongate, opaque on dorsum (Fig. 1B). Clypeal teeth rounded, separated by a narrow V-shaped emargination. Pre-apical edge of paramera as long as the apical edge in dorsal view (Fig. 3B). Inner edge of paramera oblique at the apical eighth (Fig. 3B, arrow). Brazil (Pará, Mato Grosso, Acre, and Rondônia)…..... *D. leopoldinae* sp. nov.**
5. Clypeal surface finely punctated medially. Clypeal median teeth rounded, separated by a shallow V-shaped central emargination. Elytral interstriae slightly convex. Apex of paramera acuminate, pre-apical edge longer than apical edge in dorsal view (Fig. 3A). Brazil, Colombia, Ecuador and Peru …..…….***D. batesi* (Harold)**
– Clypeal surface coarsely punctate medially. Clypeal median teeth acute, separated by a V-shaped central emargination. Elytral interstriae flat. Apex of paramera rounded, pre-apical edge as long as apical edge in dorsal view (Fig. 3E). Bolivia (Santa Cruz)…….……..……*D. ziliolii* Gandini & Aguilar.**

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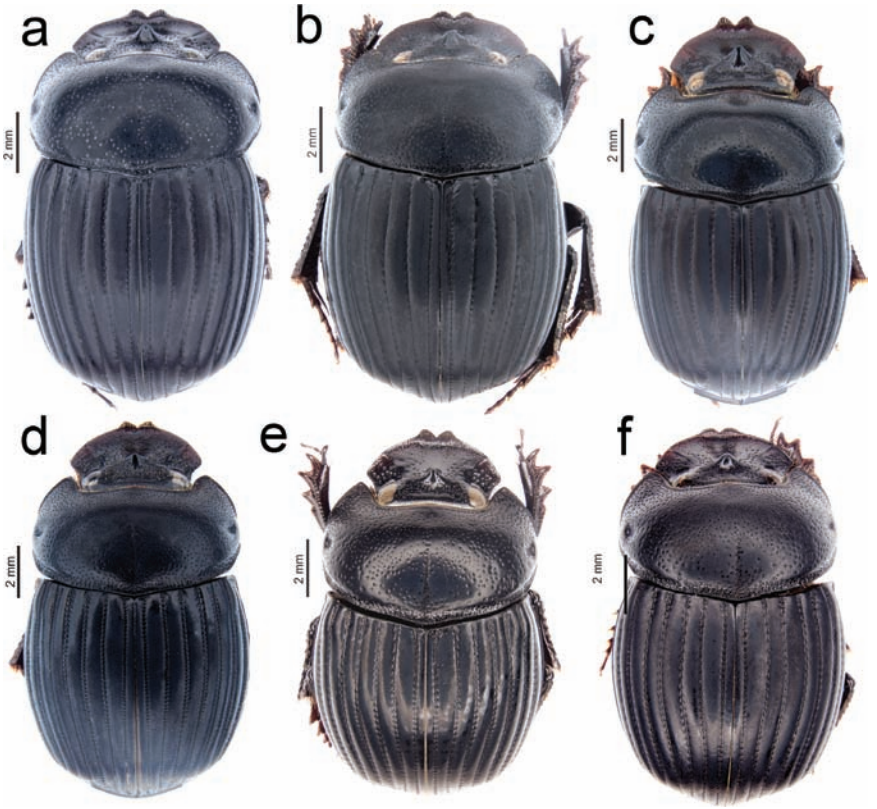

Fig. 1. Species of the *batesi* species group, dorsal view. (A) *D. batesi*; (B) *D. leopoldinae* **sp. nov.**; (C) *D. martavannucciae* **sp. nov.**; (D) *D. snethlageae* **sp. nov.**; (E) *D. ziliolii*.

***Dichotomius (Selenocopris) batesi* (Harold, 1869)**
(Figs 1A, 2G, 3A, 5A, 5J, 9)
Pinotus batesi Harold, 1869: 98
Dichotomius (*Luederwaldtinia*) *batesi*: Vaz-de-Mello, 2000: 193
Pinotus parcepunctatus Felsche, 1901: 140 **syn. nov.**
Dichotomius (*Luederwaldtinia*) *parcepunctatus*: Vaz-de-Mello, 2000: 193
Pinotus fortestriatus Luederwaldt, 1923: 14 **syn. nov.**
Dichotomius (*Luederwaldtinia*) *fortestriatus*: Vaz-de-Mello, 2000: 193

Type material examined. HOLOTYPE (*Pinotus batesi* Harold): BRAZIL: ♀, ("*Amaz.*" // "*38*" // "*Ega* / *P.* / *Batesi* / *Harold*" // "Ex-Musaeo / E. Harold" // "Museum Paris / ex Coll. R. Oberthur" (MNHN) [approximate coordinates of the type locatity: 3°20'16.3"S; 64°42'50.1"W]. LECTOTYPE (*Pinotus parcepunctatus* Felsche; **here designated**): BRAZIL: ♀, ("Ega" // "Typus." // "Coll. C. Felsche / kauf 20. 1918" // "parcepuncta / tus. Felsche [illegible handwritten]" // "Staatl. Museum fur / Tiekunde Dresden" // "LECTOTYPE ♀ / *Pinotus* / *parcepunctatus* / *Felsche* / des. F. Z. Vaz-de-Mello" (SMTD). PARALECTOTYPES: BRAZIL: 2♀♀, ("*Ega*" // "Coll. C. Felsche /

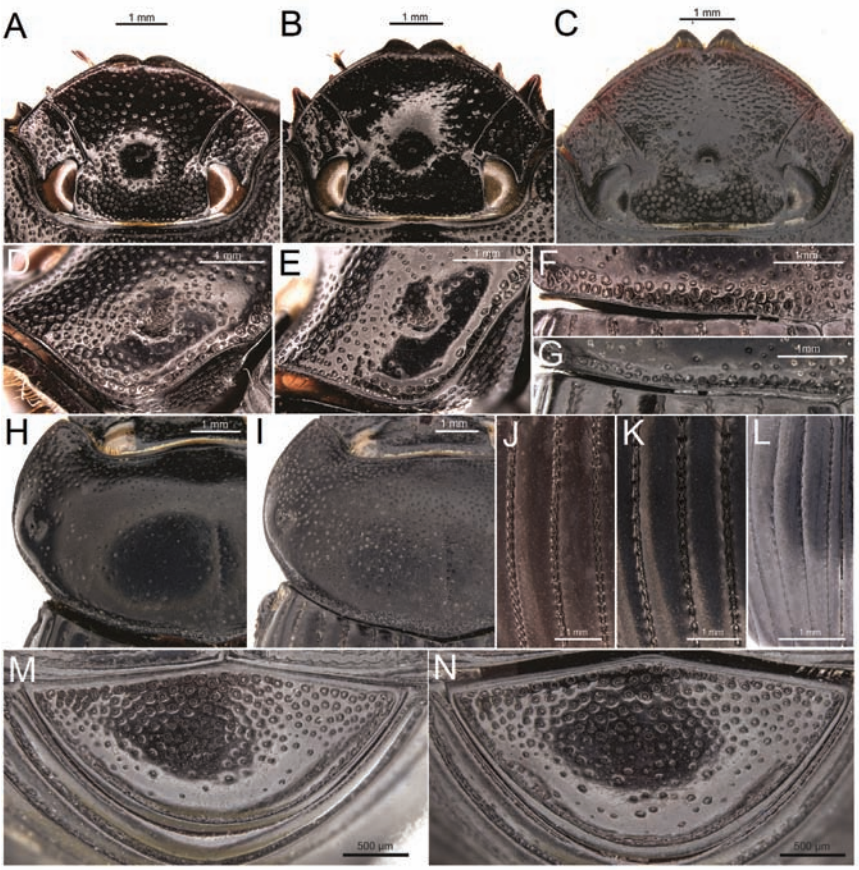

Fig. 2. Details of external morphology in the *batesi* species group. (A) *D. snethlageae* **sp. nov.**, male head; (B) *D. martavannucciae* **sp. nov.**, male head; (C) *D. leopoldinae* **sp. nov.**, female head; (D) *D. snethlageae* **sp. nov.**, lateral view of pronotum; (E) *D. martavannucciae* **sp. nov.**, lateral view of pronotum; (F) *D. snethlageae* **sp. nov.**, posterior margin of pronotum; (G) *D. batesi*, posterior margin of pronotum; (H) *D. batesi*, pronotal disc; (I) *D. leopoldinae* **sp. nov.**, pronotal disc; (J) *D. snethlageae* **sp. nov.**, elytral striae; (K) *D. martavannucciae* **sp. nov.**, elytral striae; (L) *D. ziliolii*, elytral striae; (M) *D. leopoldinae* **sp. nov.**, female, pygidial disc; (N) *D. leopoldinae* **sp. nov.**, male, pygidial disc.

kauf 20. 1918" // "Staatl. Museum fur / Tiekunde Dresden" // "PARALECTOTYPE / *Pinotus* / *parcepunctatus* ♀ / Felsche / des. F. Z. Vaz-de-Mello") (SMTD). HOLOTYPE (*Pinotus fortestriatus* Luederwaldt): BRAZIL: ♀, ("*Barcellos* / *28–VI–1905* / *Ducke*" // "HOLOTIPO" // "*Pinotus forte*" / *striatus Lud.* / *Lud. det. 23*" // ♀ // 17726") (MZSP) [approximate coordinates of the type locatity: 0°58'23.7"S; 62°55'39.2"W].

On the type material of *D. batesi* and *D. fortestriatus*. Based on the original description of *Dichotomius batesi*, one can conclude that Harold (1869) relied on a single specimen as he provided an accurate length measurement of 11 millimeters. When examining the type series of Scarabaeinae hosted in the MNHN, we found a specimen

identified as *Pinotus batesi* (= *Dichotomius batesi*) with a set of labels that clearly indicate that it belongs to Harold's collection. One of the labels reads "Ega, *P. batesi*, Harold" [handwriting]. In addition to Harold's signature on the label, the locality mentioned on the label is the same as that indicated by Harold in the original description of *D. batesi*: "Ega", currently Tefé in the State of Amazonas, Northern Brazil. This evidence allows us to consider the specimen hosted at the MNHN as the holotype of *D. batesi*, by monotypy.

Luederwaldt (1923) based on a single female to describe *D. fortestriatus*. This was explicitly informed by the author in the original description of the species. The identity of the name bearing type can also be corroborated by the locality data provided in the original description of *D. fortestriatus*, which is the same found in one of the label attached to the holotype (see labels descriptions on "type material examined" section).

Additional material examined. BRAZIL: *Amazonas*: 1♀, Benjamin Constant, Guanabara II, Forest, 10-III-2004 (CEMT); 1♀, 2♀♀, same locality but, III-42 (DZUP); 1♂, 1♀, no data (MZSP); 3♀♀, Rio Javari, IV1941 (MZSP); 1♀, same data but 15-III to 15-IV–1942 (MZSP); 1♀, Rio Itui, VIII-1942 (MZSP); 1♀, Manicoré, Rio Madeira, no date (CEMT); 2♂♂, same data but (MZSP); 1♂, same locality but, BR-319, Km 350, 61°50'22, 6"W, 5°12'56,4"S, 30-VII-2007 (CEMT); 4♀♀, Teffé (Ega), 3º semester 1878 (CEMT); 1♂, 2♀♀, same data but Ega (MZSP); 7♂♂, 8♀♀, [Maués], Rio Parauarí, III-1937 (MZSP). 1♀, Coari, no date (MZSP). *Pará*: 2♀♀, Jacareacanga, XII-1968 (DZUP). *Acre*: 20♂♂, 20♀♀, Xapuri, Reserva Chico Mendes, 25-X-2006, W6841.608 S10 28.250 (CEMT). *Rondônia:* 6♂♂, 5♀♀, ESEC Cuniã [Cuniã Ecological Station], 10-12-XI-2013, 8°4'11.82"S, 63°28'34.64"W, 83m (CEMT). COLOMBIA: *Amazonas*: 1♂, Leticia, X-2005, wet forest, 70 m (CEMT). *Vaupés*: 2♂♂, Caparú igapó, 100m (CEMT); 2♀♀, same locality but, Caparú Colina, XI-1995, 100m (CEMT). ECUADOR: *Napo*: 4♂♂ 3♀♀ 6 [unsexed], Scyasuni, 25-27-X-1997, 200m (CEMT). PERU: *Loreto*: 2♂, [between Rio Tigre and Nanay], 15–25-I-2009 (CEMT); 1♂, Rio Pucacura, Bosque de terra firme, 0420668E, 9761968N, 213m, 01-XII-2007 (CEMT); 1♀, Iquitos, 09-IX-2005 (CEMT); 1♂, same locality but, 21-I-2008 (CEMT); 1♂, same locality but, 13-xii-2007 (CEMT); 1♀, same locality but, 11-IX-2005 (CEMT). *Ucayali*: 2♀♀, Pucallpa, Rio Ucayali, no date (MZSP). *Huánuco:* 1♀, Puerto Inca, Rio Pachitea (MNHN).

Diagnosis. Dichotomius batesi and *D. ziliolii* have ocellate punctures on posterior pronotal edge with similar size to those on pronotal disc (Fig. 2G), and elytral striae thin, with punctures spaced by more than two times their diameter (Fig. 2L). However, *D. batesi* have clypeal surface with ill-defined transverse ridges rather than rows of punctures as in *D. ziliolii*. Regarding the male tegmen, in *D. batesi* the apex of paramera are elongated and pre-apical edge is longer than apical edge in dorsal view (Fig. 3A).

Redescription (♂). *Body.* Length: 12–14 mm. Oval, tegument black, barely glossy with bluish sheen on dorsum and elytra (Fig. 1A). *Head.* Surface with dense ocellate punctures on interocular space, paraocular areas of the frons, and posterior half of clypeus. Clypeal edge with two median rounded teeth, separated by a shallow V-shaped emargination. Surface of anterior region of clypeus lacking ocellate punctures, with ill-defined transverse ridges. Clypeo-frontal region with a short central knob, acute

at apex. *Thorax.* Pronotum with slight anterior declivity and a shallow anteromedial excavation (Fig. 1A). Pronotum with ocellate and minute punctures irregularly distributed. Mid-longitudinal sulcus present on basal half of the disc, covered with ocellate punctures. Anterior region of metaventrite with ocellate punctures spaced by their diameter. *Elytra*. Interstriae slightly convex, shiny, and finely punctated. *Legs.* Ventral surface of profemora with coarse setiferous punctures spaced by their diameter. Longitudinal groove on posterior edge of mesofemora restricted to the apical two-thirds. Longitudinal groove of metafemora present along all posterior edge; groove fourth as wider as femora. *Abdomen.* Sixth ventrite twice longer than fifth. Pygidium subtriangular, twice wider than long. Pygidial disc slightly convex, basal half covered with dense ocellate punctures, apical half smooth, usually with some scattered ocellate punctures.

Distribution. Amazon rainforest in Brazil (States of Pará, Mato Grosso, Acre, and Rondônia), Colombia (Amazonas and Vaupés), Ecuador (Napo) Peru (Loreto, Ucayali, and Huánuco) (Fig. 9).

Morphological variation and the taxonomic status of D. parcepunctatus and D. fortestriatus

Based on the material of *D. batesi* examined here, specimens vary in size, dorsal coloration, pronotal punctuation, and elytral striae punctuation. The body length vary from 12 to 14 mm. One male from Xapuri (Acre State, Brazil) has the pronotal disc with punctures spaced by more than four times their diameter (Fig. 2H). Some specimens have the dorsum black lacking a glossy bluish sheen. One female from Manicoré (Amazonas State, Brazil) and the type series of *Pinotus parcepunctatus* have the dorsum with a glossy bluish sheen, elytral striae larger, and the elytral punctures deeply impressed. Some specimens have a more densely punctated pronotal disc, but this is likely to be related to the state of preservation of these specimens. The pronotal disc tends to have more distinct ocellate and fine punctures in well-preserved specimens than in the pronotal discs of poorly preserved specimens.

Among the Amazonian species that were originally assigned to the *batesi* group, there is considerable confusion in the taxonomic literature concerning the identities of *D. batesi*, *D. parcepunctatus*, *D. fortestriatus*, and *D. globulus*. Much of this confusion is likely due to the lack of taxonomic tools to distinguish one species from another. *Dichotomius batesi* was the first described of those species. It was described by Harold (1869) based on a female from "Ega" (currently Tefé) in Amazonas State, Brazil (see on the type material of *D. batesi* and *D. fortestriatus* section). Felsche (1901) described *D. parcepunctatus* from the same type locality ("Amazonas, Ega"), and *D. globulus* from "Amazonas" without a specific locality. Finally, Luederwaldt (1923) described *D. fortestriatus* based on a female from "Barcellos" (also Amazonas state in Brazil). Luederwaldt (1929) allocated the four species in the "section *batesi*" and included an identification key for the group, but did not provide a redescription for any of them. Pereira (1947) provided detailed redescriptions for those species, except for *D. globulus* for which he only transcribed the original diagnosis.

Pereira's (1947) redescriptions for *D. fortestriatus* and *D. parcepunctatus* are very similar, as pointed out by the author himself. To distinguish the two species, he used only the presence of an iridescent glow on the dorsum of *D. parcepunctatus*. Interestingly, Pereira listed specimens having the same label data in the examined material of both supposed species ("Rio Parauarí, III-1937"). During our study, we examined the type series of all species names and additional material, which included specimens from localities near the type localities of *D. batesi*, *D. fortestriatus*, and *D. parcepunctatus* (including Pereira's and Luederwaldt's specimens deposited in the MZSP collection). Our study showed that dorsal coloration varies within local populations. We were not able to find any significant morphological differences in the punctuation pattern of the body, in the shape of the paramera or endophallites. Regarding *D. parcepunctatus*, we examined the type series deposited in the SMTD collection, and a series of 28 specimens identified with this name and whose external characteristics fit that of the types. The type series of *D. parcepunctatus* is composed of three females having the elytral striae wider than those usually found in *D. batesi* and the punctures on the striae are deeply impressed. However, in comparing the male tegmen of these specimens found in Pereira's collection with those identified as *D. batesi*, we could not found any significant morphological difference to separate the two species. According to the similarities in the male genitalia and geographic distribution, we reinterpreted the differences in dorsal coloration and in the punctures of the elytral striae as intraspecific variation. Therefore, we proposed here *D. parcepunctatus* and *D. fortestriatus* as **new subjective synonyms** of *D. batesi*.

In the redescription of *D. batesi*, Pereira's (1947) observations were based on specimens from Villavicencio (Colombia). According to the author, the species shows a strong sexual dimorphism expressed in the male's cephalic ornamentation and pronotum. Large males of *D. batesi* were described by Pereira (1947) as having a long, plate-like cephalic horn on the fronto-clypeal region, and the pronotum with a high anterior declivity. Meanwhile, smaller males and females were described as having shorter cephalic process and the pronotum with a feeble anterior declivity. Pereira (1947) realized the differences between the specimens from Villavicencio and that stated by Harold (1869) in the original description of *D. batesi*, arguing that Harold (1869) was likely to have based his identification on a less developed male to describe the species; for that reason his specimens would not have the extravagant sexual characteristics observed by Pereira (1947) in the large males of Villavicencio. On examining the type material of *D. batesi*, we found that Harold (1869) actually based his description on a female (rather than a less developed male as presumed by Pereira (1947)). In addition, Harold's holotype and additional males identified by us as *D. batesi* do not fit Pereira's redescription. In studying Pereira's specimens from Villavicencio we concluded that they belong to a new species here assigned to the *globulus* group. This new species will be properly described in a future paper that group.

Since the unique source of taxonomic information concerning *D. globulus* is the original description, both Luederwaldt (1929) and Pereira (1947) used the same original diagnostic characteristic (body rounded, as long as wide) to distinguish it among others in the *batesi* group. In fact, *D. globulus* is easily distinguished by having the

pronotal disc covered with umbilicate punctures, which approximates it to the Central American species formerly included in the *batesi* group. Based on differences in the pattern of pronotal punctuation and male genitalia, the group *globulus* was proposed for *D. globulus* and its closely related species (Table 1) (see the revision of the *globulus* group in Valois et al., 2022).

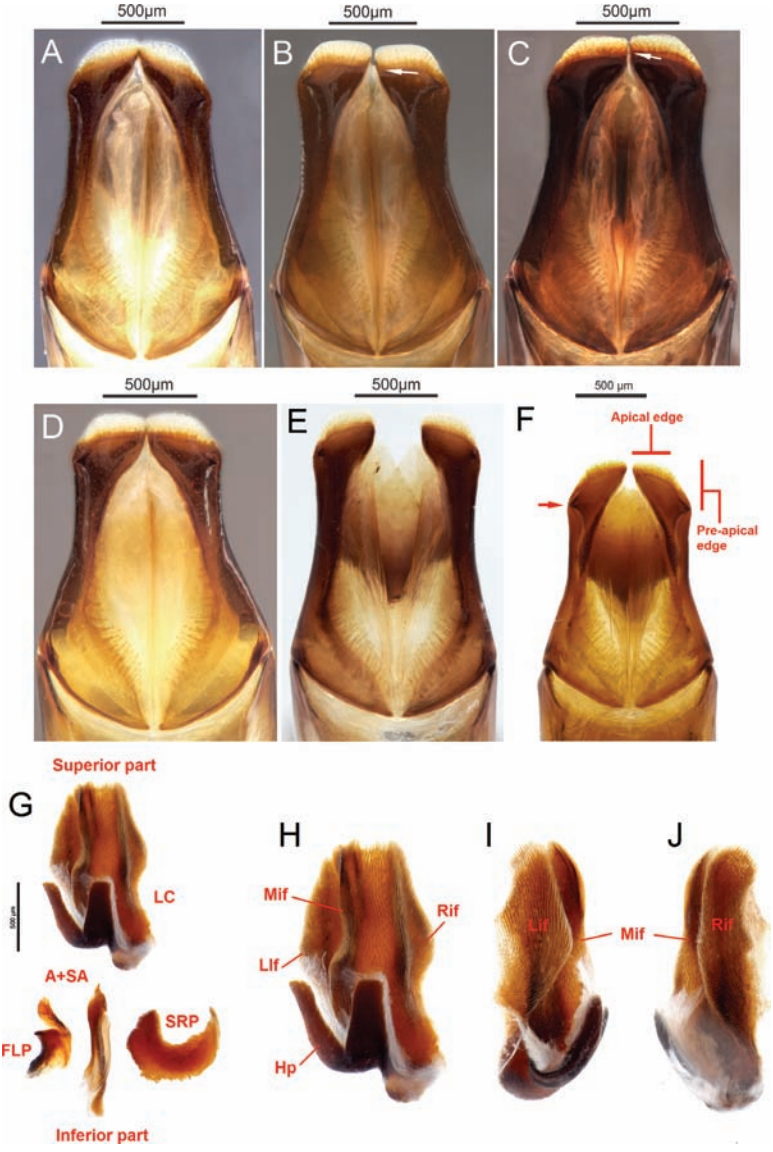

Fig. 3. Tegmen and endophallites of the *batesi* species group. (A) *D. batesi*; (B) *D. leopoldinae* **sp. nov.**; (C) *D. martavannucciae* **sp. nov.**; (D) *D. snethlageae* **sp. nov.**; (E) *D. ziliolii*; (F) *D. batesi*, terminology used to describe the apex of the paramera; (G) endophallites of *D. batesi*; (H–J) Medial endophallite (ME) of *D. batesi*. Terminology used here to indicated parts of the ME: (Mlf) median longitudinal fold; (Llf) left longitudinal fold; (Rlf) right longitudinal fold; (Hp) hook-like projection.

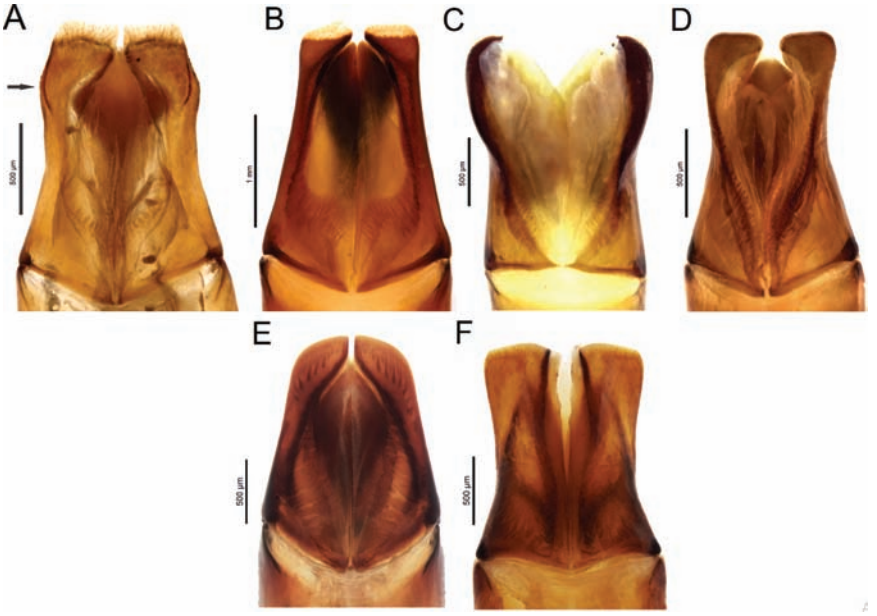

Fig. 4. Tegmen in *Dichotomius* species. (A) *D. fortepunctatus* (*globulus* group); (B) *D. lycas* (*carbonarius* group); (C) *D. inachus* (*inachus* group); (D) *D. agenor* (*agenor* group); (E) *D. geminatus* (*geminatus* group); (F) *D. lucasi* (*lucasi* group).

***Dichotomius* (*Selenocopris*) *snethlageae* sp. nov.**
(Figs 1D, 2A, D, F, J, 3D, 7E, 9)
ZooBank: https://zoobank.org/C3D46A6E-992A-49F5-B4E7-BE94813775C9

Etymology. Named after the German naturalist and ornithologist Emilie Snethlage (1868–1929), for her pioneering studies as a woman scientist of the Amazon biodiversity in the early 20th century.

Type material examined. HOLOTYPE. BRAZIL: ♂, ("Brazil Pará Belém IPEAN / XI.1984 / N. Degallier") (CEMT) [approximate coordinates of the type locatity: 1°26'09.4"S; 48°26'56.8"W. PARATYPES. BRAZIL: 1♂ 2♀, no data (MNHN). *Pará*: 3♂♂ 3♀♀, Belém, IPEAN, XI-1984 (CEMT); 1♂ 1♀, Paragominas, Fazenda Cachoeira do Rio Vermelho, 18-I-1991 (MPEG); 1♂ 3♀♀, Marajó, Breves, Japixaua river, 05-XII-1987 (MPEG); 2♂♂ 1♀, Tucuruí, Rio Tocantins, Base 4, 5-18-XII-1985 (MPEG); 7♂♂ 8♀♀, Carajás, Serra Norte, 13-XI to 2-XII-1987 (MPEG); 4♂♂ 5♀♀, same locality, Estação Manganês (MPEG); 2♂♂ 1♀, same locality, 4-6-II-1986 (MPEG); 1♂ 2♀♀, same locality, 18-20-X-1984 (CEMT); 1♂ 3♀♀, same locality, XI-1984 (CEMT); 1♀, Redenção, Pinkaiti AiK, 07°46'S, 51°58'W, X-1999 (CEMT); 1♀, Serra do Cachimbo, X-2010 (CEMT); 1♀, Acará, 08-XII-1977 (MPEG); 5♂♂ 3♀♀ Bragança, no date (MNHN); 1♂ 4♀♀, São Miguel do Guamá, I-1963 (MZSP). *Maranhão*: 3♂♂, Bom Jardim, REBIO Gurupi [Gurupi Biological Reserve], 17 to 27-I-2010 (CEMT); 2♂ 4♀♀, Aldeia Araçu, Iguarapé Gurupi 50Km FC de Canindé, V-1968 (MZSP).

Diagnosis. Dichotomius snethlageae **sp. nov.** seems to be related to *D. martavannucciae* **sp. nov.** and *D. leopoldinae* **sp. nov.** by having the ocellate punctures on pronotal disc smaller than those on the posterior pronotal edge (as Fig. 2F), as well as, the elytral striae widened and densely punctated, with punctures spaced by the diameter of a puncture (Figs 2J-K). However, *D. snethlageae* **sp. nov.** can be distinguished by the following combination of characters: punctures on elytral striae spaced by half their diameter (Fig. 2J); clypeal surface with dense ocellate punctures (Fig. 2A). Sides of pronotum with dense ocellate punctures near lateral pronotal fovea (Fig. 2D); apical edge of paramera as long as the pre-apical edge in dorsal view (Fig. 3D).

Description (♂). *Body*. Length: 11–13 mm. Oval, tegument black with glossy bluish sheen (Fig. 1D). *Head.* Surface with dense ocellate punctures, more spaced on clypeus and paraocular areas of the frons. Clypeal edge with two median rounded teeth, separated by shallow V-shaped emargination. Clypeo-frontal region with a short conical horn or tubercle. *Thorax.* Pronotum with a feeble central declivity anteriorly. Pronotal surface glossy, with bluish sheen; filled with ocellate and minute punctures (Fig. 1D). Punctures on anterior pronotal angle as dense as those on disc. Posterior edge of pronotum with 1–2 irregular rows of large ocellate punctures (Fig. 2F). Mid-longitudinal sulcus present on pronotal disc, filled with punctures on basal two-thirds. Surface around median pronotal sulcus less punctate than the rest regions of the disc. *Elytra*. Striae coarsely punctate. Punctures on striae spaced by half their diameter. Interstriae convex, shiny and finely punctated. *Legs.* Ventral surface of mesofemora coarsely punctate at apical third. Ventral surface of metafemora with ocellate punctures at apical half. Longitudinal groove of metafemora present along all the posterior edge. *Abdomen.* Sixth ventrite approximately as long as fifth. Pygidium twice wider than long. Pygidial disc slightly convex, ocellate punctures more concentrated on basal half.

Morphological variation. In some specimens, the mid-longitudinal sulcus of the pronotum is restricted to the central region of the disc. The groove on the posterior edge of the metafemora can be absent on its basal half. The pygidial disc has dense ocellate punctures on its apical half in some specimens.

Distribution. Amazon rainforest northern of Brazil (States of Pará and Maranhão) (Fig. 9).

***Dichotomius (Selenocopris) martavannucciae* sp. nov.**
(Figs 1C, 2B, 2E, 2K, 3C, 9)
ZooBank: https://zoobank.org/79FD93EB-43B4-4966-805A-53055E9D4B4D

Etymology. Named after the Italian zoologist Marta Vannucci (1921−2021), for her contributions to the Brazilian oceanography.

Type material examined. HOLOTYPE: BRAZIL: ♂, ("Brasil Pará Santarém / Alter do Chão -54. 93384, -2.47996 [2°28'47.9"S; 54°56'01.8"W] / Ilha de Mata Estação Seca 24-XII-2002 / A. P. Lima & E. Vasconcelos.") (MPEG). PARATYPES. BRAZIL: 4 [unsexed], same locality as the holotype (MPEG); 1♀, Santarém, III-90 (MNHN); 1♀, same but 1920 (CEMT); 1♀, Curuá-Una, XII-1996 (MPEG); 1♂, Reserva Tapajós, 7-I-2009, S2 36 662, W55 36 513 (CEMT).

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DOI 10.1163/1876312X-bja10046

Fig. 5. Endophallus in *Dichotomius* species. (A) *D. batesi*; (B) *D. fortepunctatus* (*globulus* group); (C) *D. lycas* (*carbonarius* group); (D) *D. inachus*; (E) *D. geminatus*; (F) *D. gamboaensis* (*globulus* group), set of microbristles on the ventral part of the endophallus; (G) *D. batesi*, set of microbristles and a pair of C-shaped set of strongly sclerotized bristles on the ventral part of the endophallus; (H) *D. lycas*, C-shaped set of strongly sclerotized bristles on the ventral part of the endophallus; (I) *D. geminatus*, set of strongly sclerotized bristles on the dorsal part of the endophallus; (J) *D. batesi*, partially everted endophallus; (K) *D. gamboaensis* (*globulus* group), partially everted endophallus.

Diagnosis. Dichotomius martavannucciae **sp. nov.** resembles *D. snethlageae* **sp. nov.** and *D. leopoldinae* **sp. nov.** by having the ocellate punctures on pronotal disc smaller than those along posterior pronotal edge (as Fig. 2F), the elytral striae widened and densely punctated, with punctures spaced by the diameter of a puncture (as Figs 2J-K). *Dichotomius martavannucciae* **sp. nov.** can be distinguished by the following combination of characters: body oval, shiny (Fig. 1C); clypeal teeth acute, separated by a deep V-shaped emargination; punctures on elytral striae spaced by their diameter; lateral

region of pronotum with sparse ocellate punctures near lateral pronotal fovea (Fig. 2E); apical edge of paramera as long as pre-apical edge in dorsal view, inner apical edge straight at the apical eighth (Fig. 3C, arrow).

Description (♂). *Body.* Length: 11–13 mm. *Head.* Surface with ocellate and minute punctures. Clypeal surface with sparse ocellate punctures on lateroposterior regions; anterior edge with transverse ridges (Fig. 2B). Clypeo-frontal region with a conical, central tubercle, acute at apex (Fig. 2B). *Thorax.* Anterior region of pronotum with a feeble central declivity (Fig. 1C). Pronotal surface glossy, with bluish sheen; filled with dense ocellate and minute punctures (Fig. 1C). Punctures on anterior angle of the pronotum denser than those on disc. Posterior edge of pronotum with 1–2 irregular rows of large ocellate punctures. Mid-longitudinal sulcus of pronotum conspicuous, covered by ocellate punctures on basal two-thirds of the disc. Surface around mid-longitudinal sulcus less punctate than the rest regions of the disc. *Elytra*. Striae well-impressed, closely punctate. Interstriae convex, finely punctated. *Legs.* Ventral surface of metafemora with sparse ocellate punctures at the apical half. Longitudinal groove of metafemora present on 2/3 of apex. *Abdomen.* Sixth ventrite as long as fifth. Pygidium approximately triangular shaped, twice wider than long. Pygidial disc slightly convex, ocellate punctures concentrated on basal half.

Morphological variation. Dorsum black, lacking glossy sheen. Some females have the clypeal teeth separated by a deep U-shaped emargination.

Distribution. Only known from the Amazon rainforest of Santarém (Pará State, Brazil) (Fig. 9).

***Dichotomius* (*Selenocopris*) *leopoldinae* sp. nov.**
(Figs 1B, 2C, 2I, 2M, 2N, 3B, 8D, 8I, 9)
ZooBank: https://zoobank.org/5D73B86E-9EBA-40D1-8274-098DEE151E80

Etymology. Named after the Brazilian first empress consort Maria Leopoldina of Austria (1797−1826), a lover of the Brazilian biodiversity and an enthusiast of science.

Type material examined. HOLOTYPE. BRAZIL: ♂, ("Novo Progresso Fazenda Florentino / 55°29'23, 26"W 6°51'58.61"S / 12-I-2011 Amazon Forest / T.D. Pelissari") (CEMT). PARATYPES. BRAZIL: *Pará*: 1♀, Novo Progresso, Fazenda Florentino, 55°29'23, 26"W, 6°51'58,61"S, 12-I-2011, Amazon Forest (CEMT); 1♂ 1♀, same locality but, 55°30'26, 25"W, 6°53'18, 18"S, 2-I-2011 (CEMT). *Acre*: 1♂, Rio Branco, 09-IV-1996 (CEMT); 1♂, same locality, XI-2000 (CEMT); 1♂, same locality but, Restinga Humaitá, 11-IV-1996 (CEMT); 4♂♂, same locality, Sec, For, PZ - UFAC, II-1997 (CEMT); 1♂ 1♀, Senador Guiomard, Fazenda [Experimental] Catuaba, Primary Forest, II-1997 (CEMT). *Mato Grosso*: 2♀♀, Cotriguaçu, borders of Jurema river, 9°52'47,67"S, 58°14'7,09"W, X-2010 (CEMT); 1♀, 4 [unsexed specimens] Cotriguaçu, Fazenda São Nicolau, Matinha, 9°50'19"S, 58°15'03"W, 08-X-2009 (CEMT); 2♂♂ 2♀♀, same locality, horse faeces, XII-2009 (CEMT); 4♀♀, same locality but, Mata Norte, 9°49'9"S, 58°15'47"W, 08-10-XII-2009 (CEMT); 2♀♀, same locality but, Matinha, Fruta dossel, 9°50'53"S, 58°14'36"W, 11-XII-2009 (CEMT); 3♀♀, same locality, Prainha, 9°51'36"S, 58°12'53"W, 11-13-XII-2009 (CEMT); 2♂♂ 2♀♀, same locality, 15-XII-2009 (CEMT); 14♂♂ 5♀, same locality,

9°51’36”S, 58°12’53”W, X-2009 (CEMT); 2 [unsexed], same locality but, secondary forest, 58°13’20”W, 9°51’18”S, 200m (CEMT); 2♂♂ 1♀, same locality but, Matinha, X-2009 (CEMT); 4♂♂ 2♀♀, same locality but, Prainha, X-2009 (CEMT); 3♂♂ 9♀♀, same locality but, Matinha, forest borders, 9°50’19”S, 58°15’03”W, 13-XII-2009 (CEMT); 1♀, primary forest, Sherman trap, 9°49’17”S, 58°16’09”W, 13-XII-2009 (CEMT); 2♂♂, São Nicolau, 9°48’49”S, 58°18’14”W, 13-XII-2010 (CEMT); 4♂♂ 14♀♀, same locality but, 9°49’8”S, 58°15’40”W, 19-24-X-2012 (CEMT); 11♂♂ 7♀♀ 3[unsexed], same locality but, 22-X-2012 (CEMT); 1♀, Alta Floresta, Fragment 114, 09°45’19”S, 55°58’19”W, IV-2008 (CEMT); 5♂♂ 2♀♀, same locality but, Fragment 150, 09°35’54”S, 55°56’09”W (CEMT): 1♂, same locality, Fragment 151, 09°44’55”S, 56°1’41”W (CEMT); 3♂♂ same locality but, Fragment 153, 56°00’21”W, 09°50’22”S, IV-2008 (CEMT), 1♀, same locality, Fragmento FAH, 56°6’12”W, 09°52’52”S, III-2008 (CEMT); 3♂♂ 3♀♀, same locality, Fragment 154, 09°49’27”S, 55°53’34”W (CEMT); 1♂, same locality but, Fragment156, 09°54’24”S, 56°1’41”W, III-2008 (CEMT); 1♂, Aripuanã, 10°3’10”S, 59°29’42”W, 26-I-2012 (CEMT); 1♂ 1♀ Claúdia, Fazenda Continental (CEMT); 3♂♂ 2♀♀, same locality, 11°36’29”S, 55°15’01”W, 20-II-2010 (CEMT); 1♂, same locality but, 11°35’39”S, 55°17’07”W, 20-II-2011 (CEMT); 18♂♂ 23♀♀ 1[unsexed specimen], Nova Mutum, 13°48’07”S, 56°05’22”W, 23-I-2011 (CEMT); 2♂♂ 1♀, same locality but, Trivelato, 15-XII-1995 (CEMT); 1♂ 2♀, same locality, 56°05’22”W, 13°48’07”S, 25-I-2011 (CEMT); 8♂♂ 18♀♀, Novo Mundo, Parque Estadual Cristalino [Cristalino State Park], 9°28’9”S, 55°48’15”W, V-2003 (CEMT); 1♂ 1♀, Paranaíta, Rio Teles-Pires, 24-X-2009 (CEMT); 2♀♀, same locality, Módulo “Cajueiro”, 09°28’32,8”S, 56°28’20,0”W, V-2005 (CEMT); 1♀, same locality, Fazenda Hygino, X-XI-2009 (CEMT). *Rondônia*: 1♂ 4♀♀, Itapuã do Oeste, Floresta Nacional Jamari [Jamari Nacional Forest], *Mazama americana* dung, 09°11’33”S, 63°06’47”W, 20-ii-2013 (CEMT); 1♂♂, same locality but, *Mazama americana* dung, 09°05’37”S, 63°08’55”W, 24-ii-2013 (CEMT); 1♂, *Mazama gouazoubira* dung, 09°11’32”S, 63°06’35”W, 20-ii-2013 (CEMT); 1♂, same locality but, *Mazama gouazoubira* dung, 09°11’27”S, 63°06’36”W, 20-ii-2013 (CEMT); 2♂♂, same locality but, *Mazama nana* dung, 09°11’31”S, 63°06’35”W, 20-ii-2013 (CEMT); 2♀♀, same locality but, *Mazama nana* dung, 09°11’29”S, 63°06’35”W, 20-ii-2013 (CEMT); 1♂ 1♀, same locality but, *Mazama nemoagari* dung, 09°11’33”S, 63°06’47”W, 20-ii-2013 (CEMT); 1♀, *Mazama nemorivaga* dung, 09°11’26”S, 63°06’47”W, 20-ii-2013 (CEMT); 1♀, same locality but, *Mazama nemorivaga* dung, 09°05’41”S, 63°08’54”W, 20-ii-2013 (CEMT); 2♀♀, Ouro Preto do Oeste, 12-XI-1984 (CEMT); 2♂♂ 2♀♀, same locality but, mangrove right to the Santa Helena River, 30-III-1985 (CEMT); 1♂ 2♀♀, Porto Velho, 1-12-VI-2012 (CEMT); 1♂ 1♀, Mutum, 9°34’49”S, 65°03’13”W, 03-VI-2012 (CEMT); 1♂, same locality, 9°35’4”S, 65°3’10”W, 22-VI-2010 (CEMT); 1♀, Porto Velho, Caiçara, 9°26’S, 64°49’W, 1-III-2019 (CEMT); 1♂, same locality, 9°26’10”S, 64°49’59”W, 19-IX-2011 (CEMT); 1♂ 1♀, same locality, 28-II-2010 (CEMT); 5♂♂ 2♀♀, same locality, 9°26’52”S, 64°50’5”W, 29-II-2009 (CEMT); 1♂ 1♀, same locality, 9°35’4”S, 65°3’10”W, 8-I-2011 (CEMT); 1♀, ESEC Cuniã [Cuniã Ecological Station], 8°4’11,82”S, 63°28’34,64”W, 10-12-XI-2013 (CEMT); 4♂♂ 2♀♀, Nova Mutum Paraná, 09°26’31”S, 60°12’44”W, 27-28-II-2010 (CEMT);

4♂♂ 2♀♀, same locality, 9°35'46"S, 65°02'27"W, i-2012 (CEMT); 1♂, same locality, 9°35'4"S, 65°3'10"W, xi-2012 (CEMT).

Diagnosis.Dichotomius leopoldinae **sp. nov.** resembles *D. snethlageae* **sp. nov.** and *D. martavannucciae* **sp. nov.** by having the ocellate punctures on pronotal disc smaller than the punctures along posterior pronotal edge (as Fig. 2F), the elytral striae widened and densely punctated, with punctures spaced by the diameter of a puncture (as Figs 2J-K). However, *D. leopoldinae* **sp. nov.** can be distinguished from its relatives by the following combination of characters: body elongate, opaque (Fig. 1B); clypeal teeth rounded, separated by a shallow V-shaped emargination; punctures on elytral striae spaced by their diameter; lateral region of pronotum with sparse ocellate punctures near lateral fovea of pronotum (as Fig. 2E); apical edge of paramera as long as preapical edge in dorsal view (Fig. 3B); inner edge of paramera oblique at the apical eighth (Fig. 3B, arrow).

Description (♂). *Body.* Length: 11–13 mm. *Head.* Posterior half of clypeus with sparse ocellate punctures, anterior region transversally ridged. Clypeal median teeth rounded, separate by a V-shaped emargination. Clypeo-frontal region with a conical knob, apically truncated. *Thorax.* Pronotal disc with a feeble central declivity at anterior region. Pronotal surface with dense, irregularly spaced ocellate punctures. Posterior edge with ocellate punctures, punctures larger than those on disc. Mid-longitudinal sulcus present on posterior half, filled with ocellate punctures. *Elytra*. Interstrial surface convex, opaque, and smooth. *Legs.* Ventral surface of profemora with sparse setiferous ocellate punctures. *Abdomen.* Sixth ventrite as long as fifth. Pygidium twice larger than long, disc slightly convex near apex, surface filled with dense ocellate punctures more concentrated on basal half.

Morphological variation. Some females have the clypeal teeth separated by a deep U-shaped emargination and a clypeo-frontal region with a feeble central knob. Specimens from Cotriguaçu (Mato Grosso State, Brazil) have the head and pronotum more densely punctated.

Distribution. Amazon rainforest in Brazil (Fig. 9).

***Dichotomius* (*Selenocopris*) *ziliolii* Gandini & Aguilar, 2009**
(Figs 1E, 2L, 3E, 9)
Dichotomius ziliolii Gandini & Aguilar, 2009: 147

Type material examined. HOLOTYPE (*Dichotomius ziliolii* Gandini & Aguilar): BOLIVIA: ♂, Santa Cruz ("Bolivia / Dpto. Santa Cruz. Jardin Botanico / XI-2004 // Holotype ♂") (CEMT) [coordinates of the type locatity: 17°46'00"S; 63°04'13"W]. PARATYPES: BOLIVIA: 1♀, *Santa Cruz*: Ciudad de Santa Cruz, XI-2014 (CEMT); 1♂, Santa Cruz de la Sierra, Jardín Botánico, 17°46'00"S; 63°04'13"W, 420m (CEMT).

Additional material examined. BOLIVIA: 2♀♀, *Santa Cruz*: Santa Cruz de la Sierra, Jardín Botánico. Bosque Chiquitano. 17°46'S, 63°03'W. 398m. 25-I-2010 (CEMT); 3♂♂, 1♀, same data but 17°47'02"S; 63°03'47"W, 400m, 7–8-XI-2006 (CEMT); 1♀, same data but XI-2004 (CEMT).

Diagnosis. Dichotomius ziliolii has the pronotal disc densely punctated (Fig. 1E). Ocellate punctures on the posterior pronotal edge with similar size than those on disc

(as Fig. 2G). Elytral striae thin, with punctures spaced by more than their diameter (Fig. 2L). Anterior region of clypeus with transverse rows of ocellate punctures. Apex of paramera rounded, apical edge as long as pre-apical edge in dorsal view (Fig. 3E).

Redescription (♂). *Body.* Length: 11–13 mm. *Head.* dorsal surface with ocellate and minute punctures (Fig. 1E). Anterior region of clypeal surface with transverse rows of ocellate punctures near edge. Interocular space impressed medially. *Thorax.* Pronotal surface barely shiny, with glossy bluish sheen. Anterior region of pronotum with a slight declivity. *Elytra*. Elytral striae thin, punctate, punctures spaced by twice their diameter. Interstriae smooth, not distinctly convex. *Legs.* Ventral surface of profemora with sparse, coarse punctures. Ventral surface of meso and metafemora shallowly punctate at apical half. Longitudinal groove of meso and metafemora restricted at the apical half. *Abdomen.* Sixth ventrite 1.5× longer than fifth. Pygidium subtriangular, twice wider than long. Pygidial disc with dense ocellate punctures concentrated on basal half.

Distribution. Dry semi-deciduous Chiquitano Forest in Bolivia (Santa Cruz) (Fig. 9).

Notes on D. vidaurrei *Nunes & Vaz-de-Mello, 2013*

Nunes & Vaz-de-Mello (2013) described the brachypterous species *D. vidaurrei* based on specimens from Santa Cruz, Bolivia. The species was assigned to the *batesi* species group based on the presence of ocellate punctures on pronotal disc. After examining specimens of *D. vidaurrei*, we concluded this species should be transferred to the *geminatus* species group since it has a metatibial spur truncate, the paramera distinctly convex in dorsal view, and inner edge of paramera deeply excavate near apex. Within the *geminatus* group, *D. vidaurrei* seems to be closely related to *D. opacipennis*, which also has the inner edge of paramera deeply excavate near apex.

Discussion

Herein, the *batesi* group was redefined and its current diagnosis includes features from external morphology and male genitalia, some of them being exclusive for its species, such as the presence of a pair of small spine-like projections on the dorsal surface of the paramera (as Fig. 3F, arrow); and the ME twice as long as wide, with three well-defined longitudinal folds (Figs. 3G–J). Within *Selenocopris*, seven of its 14 species groups have been recorded in the Amazon rainforest (Table 1), but only the *batesi* species group seems to be exclusive to this biome (Fig. 9).

The diagnosis of the *batesi* group had not changed much since its original description by Luederwaldt (1929). The *batesi* group originally included the *Selenocopris* species with medium body size (12–14 mm), having a single conical process on head, posterior pronotal angles without deep fovea, and pronotal disc covered with ocellate punctures (Luederwaldt, 1929). The main contributions to the taxonomy of the group after 1929 were made by Luederwaldt (1936), Pereira (1947), Howden and Young (1981), and Kohlmann and Solís (1997). In those previous papers, some new species

were described and *D. muticus*, *D. taunayi,* and *D. micans* were placed in other species groups.

None of those previous studies proposed new taxonomic boundaries for the *batesi* group and Luederwaldt's diagnosis continued to be used. However, Maldaner et al. (2015) described *D. malyi* from São Paulo (southeastern Brazil), which fits into the diagnostic characteristics stated for the *batesi* group, including the pronotal surface covered with ocellate punctures. Despite the external similarities with the species of the *batesi* group, the authors concluded, based on the male falciform protibial spur, blue ventral coloration, and abundant setae on abdominal ventrites, that *D. malyi* belongs to the *speciosus* group which has other species from Atlantic rainforest. As a consequence, these distinctive characteristics were used to separate species of the *batesi* group from those of the *speciosus* group. Therefore, if new species having ocellate punctures are described in other groups whose features complicates the identification of the *batesi* group, then its diagnosis need to be amended. Based on our comparative study of these groups, the male genital characteristics can be a valid source of diagnostic characteristics rather than the exclusive use of external characteristics to define *Dichotomius* species groups, since they seem to have a homogeneous shape within each species group.

To demonstrate this alternative diagnosis we compared the male genitalia of the group *speciosus*, *batesi* and *globulus* in order to identify new distinctive characteristics for these groups. According to the illustrations provided by Maldaner et al. (2015), all the species in the *speciosus* group share similar paramera, which are short and approximately one third as long as the phallobase (Maldaner et al., 2015, as figs. 2c–d), while in the *batesi* and *globulus* groups the paramera are approximately twice as long as the phallobase (Figs 3A–F, 4A). After a more detailed examination of the male genitalia of *D. speciosus* (Waterhouse, 1891) and *D. opalescens* (Felsche, 1910), both included in the *speciosus* group, we found additional characteristics to separate them from the *batesi* and *globulus* groups, such as the lower sclerotized membrane between paramera being truncate basally, and the ventral membrane connecting the phallobase and paramera covered with small protuberances similar to sensory or glandular organs.

With regard to the endophallites, the two species of the *speciosus* group examined by us have a very similar morphology, but showed remarkable differences in comparison not only with the species of the *batesi* and *globulus* groups, but also to those in other Amazonian species groups of *D.* (*Selenocopris*). The shape of the ME showed the more significant differences among the groups. From the dorsal view of the tegmen, the ME of *D. speciosus* and *D. opalescens* is triangular shaped, the inferior projections are reduced, and, between these two projections, the ME has an additional plate-like projection.

As defined here, the group *batesi* only comprises Amazonian species that have pronotal punctuation irregularly spaced. The distinctive ground plan of the ME and the modification on the dorsal surface of the tegmen were useful for characterizing species of the *batesi* and *globulus* groups. Among the species of the *batesi* group, the shape of the pre-apical and apical edges of the paramera, pronotal punctation and elytral striae were more taxonomically relevant. In addition to the characteristics of the male genitalia, we

provided several new diagnostic characteristics to clearly distinguish the *batesi* and the newly proposed *globulus* group from any other *Dichotomius* species group.

The dichotomy between species having pronotal punctures equally or irregularly spaced, as suggested by Vaz-de-Mello and Nunes (2016), has practical advantages but it was not entirely compatible either with other external characteristics or with genitalia characteristics. *Dichotomius globulus* and *D. ocellatopunctatus* were included by Vaz-de-Mello and Nunes (2016) in the "Amazonian subgroup", which accommodates the species with the pronotal surface covered with irregularly spaced punctures. However, despite of *D. globulus* occurring in the Amazonian region, our type examination revealed that it has the pronotal surface covered with equally spaced punctures. In addition, the absence of spine-like projection on the dorsal surface of the paramera, the presence of shagreneed microsculpture on the elytral interstriae, and the cylindrical shape of the metafemora indicate that *D. globulus* could be more closely related to the species of the group having pronotal punctures equally spaced. On the other side, *D. ocellatopunctatus* has the pronotum covered with irregularly spaced punctures similar to *D. batesi*, however, elytral interstriae microsculpture and the shape of metafemora also relates *D. ocellatopunctatus* with the Central American subgroup.

Many of the taxonomic problems concerning the boundaries of species groups in *D*. (*Selenocopris*) are related with imprecise species descriptions and absence of distinctive and reliable morphological characters in literature. On revising *Dichotomius*, Luederwaldt (1929) dealt with groups that could be easily distinguished from others by a unique diagnostic external characteristic, but he also dealt with groups whose definition was not so straightforward at that time. As a consequence, some diagnoses, such as those of the *carbonarius*, *batesi,* and *inachus* groups, were based on the combination of characteristics taken from the cephalic armature, pronotal punctation, and body size. To understand the distribution of these characteristics and their applicability in the definitions of the *batesi* and *globulus* groups, we conducted a comparative study between these two groups and at least one species (the oldest described or those where a male was available for study) belonging to the *carbonarius*, *agenor*, *geminatus*, *inachus,* and *lucasi* groups. All these groups included species that may be considered to be "simple shaped" within the subgenus *D.* (*Selenocopris*) and some of them include species that are taxonomically related to the *Dichotomius* of the *batesi* group.

The male cephalic process has been often evoked to define species groups in *D*. (*Selenocopris*). In studying the morphological variability of this structure among the groups examined in this research, we found significant variation in the shape of cephalic process within the groups *carbonarius* and *inachus* as reported by Luederwaldt (1929) (Table 2). Only large males of the *agenor* group have a tribuberculate carina on the head (Fig. 7D). The more common type of cephalic process presented by the other groups is the single conical process, usually referred to by authors as horn, tubercle, or knob (Table 2) (Figs. 7A–B). When present, the cephalic process of the species of the *carbonarius* and *inachus* group vary from a conical tubercle (as Fig. 7A) to a high transverse carina apically emarginated (as Fig. 7C). In the *batesi*, *globulus*, and *geminatus* groups, the cephalic process is usually represented by a low conical tubercle, being

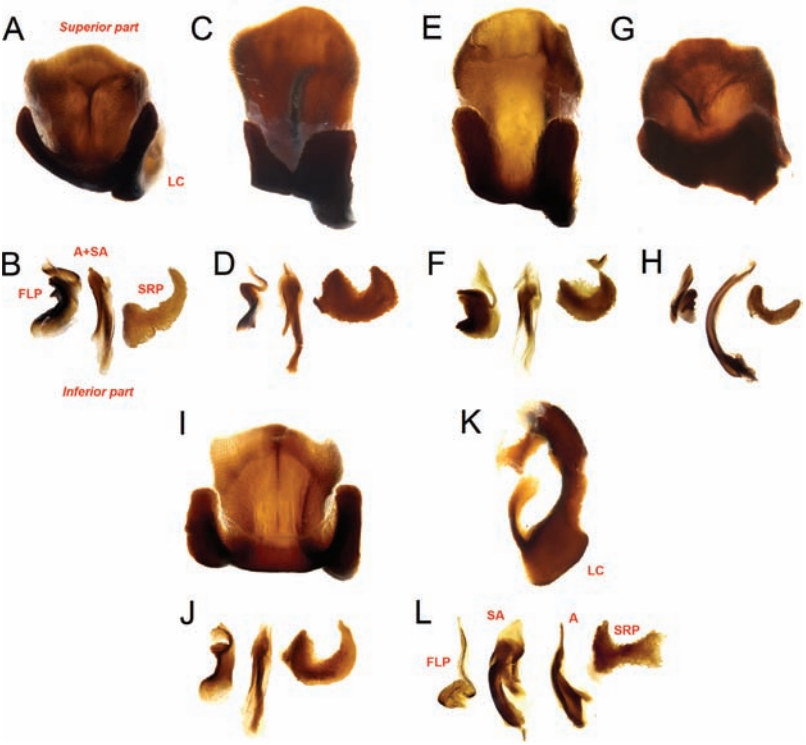

Fig. 6. Endophallites in *Dichotomius* species. (A–B) *D. fortepunctatus*; (C–D) *D. carbonarius*; (E–F) *D. inachus*; (G–H) *D. geminatus*; (I–J) *D. agenor*; (K–L) *D. lucasi*.

higher only in large males of *D. geminatus*. Luederwaldt (1929) used the shape of the cephalic process and pronotal punctation to include *D. geminatus* in the *batesi* group. At that time, the author did not distinguish between the type of punctures and the punctation patterns on the pronotum of the species. Unlike the species in the *batesi* and *globulus* groups, *D. geminatus* has the pronotum covered with coarse punctures (Fig. 7H).

In the absence of other morphological characteristics but mainly those of male genitalia, the inclusion of a species having punctures on the pronotum in the *batesi* or *geminatus* groups depends on the authors' interpretation concerning what is a coarse or an ocellate puncture. For example, Nunes and Vaz-de-Mello (2013) have described *D. vidaurrei* for the *batesi* species group based on the presence of ocellate punctures on the pronotal surface. However, in examining the species, we concluded that the pronotum of *D. vidaurrei* have coarse punctures. Also, the shape of the paramera and endophallites of *D. vidaurrei* suggest that it is more related with *D. opacipennis*, which also has coarse punctures on the pronotum and is currently included in the *geminatus* group.

Within the *geminatus* group, the pronotal punctures can be of two types: on the anterior angles and in the center of the pronotum (pronotal disc) are the coarse punctures (Fig. 7H); on the posterior pronotal edge, the punctures are elliptical. In the *batesi* and *globulus* groups, the pronotal punctures on the center of the pronotum are

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Table 2. Comparison of external characters of the *batesi*, *globulus* and related species groups.

Species group	Male cephalic process*	Pronotal surface	Shape of metafemura	Apex of metatibial spur
batesi	low conical tubercle (Fig. 7A)	covered with irregularly spaced ocellate punctures (Fig. 7E)	slightly club shaped (Fig. 7D)	deeply emargined (Fig. 8I)
globulus	low conical tubercle	covered with umbilicate ocellate punctures (Fig. 7F)	cylindrical (Fig. 7F)	deeply emargined
carbonarius	either a conical tubercle, transverse carina apically emargined (Fig. 7C) or pair of tubercles	covered with fine punctures (Fig. 7G)	club shaped (Fig. 7A)	deeply emargined
inachus	either flat, low conical tubercle or a transverse carina apically emargined	covered with fine punctures	club shaped	shallowly or deeply emargined*
agenor	trituberculate transverse carina (Fig. 7D)	covered with fine punctures	club shaped	shallowly emargined*
geminatus	high to low conical tubercle (Figs 7A-B)	covered with dense coarse punctures (Fig. 7H)	club shaped	Acute
lucasi	absent or a low central knob	covered with fine punctures	club shaped	Acute (Fig. 7G)

*Also based on Luederwaldt's (1929) descriptions.

ocellate punctures, the posterior pronotal edge has the same type of punctures, which in some species are larger than those on the other pronotal parts (Fig. 7F).

The presence of a deep apical emargination in the metatibial spur is among the diagnostic characteristics of the *carbonarius* group (Luederwaldt, 1929). However, the same character is present in species of the *batesi*, *globulus,* and *inachus* groups (Table 2). All the species of the *batesi* and *globulus* groups have a deep emarginated metatibial spur, whereas in the *inachus* group the metatibial spur is deeply emarginated in *D. fallax* and *D. yucatanus* (as Fig. 8I), and is feebly emarginated in *D. inachus*, *D. problematicus* and *D. apicalis* (as Fig. 8H). Therefore, the use of the emarginated metatibial spur as a diagnostic characteristic works only when it is taken in combination with other characteristics.

In contrast to the *batesi* and *globulus* groups, the species in the *carbonarius* and *inachus* groups have a smooth or finely punctate pronotal surface (as Fig. 7G). The latter two groups are currently under revision and these studies should provide the diagnostic characteristics for each one.

The tegmen of all groups studied have the paramera gradually flattened dorso-ventrally toward the apex except for *D. lucasi*, which has the paramera flattened antero-posteriorly (Fig. 4F). The species belonging to the *batesi*, *carbonarius*, and *globulus* groups share the apical edge of paramera weakly sclerotized and bent downwards (Table 3) (Figs. 3A–F, 4A–B). However, only species of the *batesi* and *globulus* groups have ornamentations on the paramera such as spines or longitudinal carina (Table 3).

Table 3. Comparison of male genitalic characters of the *batesi*, *globulus* and related species groups.

Species group	Paramera apex	Dorsal surface of paramera	LC shape	Inferior projections of LC	Mlf of LC
batesi	weakly-sclerotized (Figs 3A-F)	spine-like projections	twice longer than wide (Figs 3G-J)	separated by a V-shaped emargination	strong, present along the mid-line (Figs 3G-J)
globulus	weakly-sclerotized (Fig. 4A)	longitudinal carina	appx. as long as wide (Fig. 6A)	separated by a wide U-shaped emargination	weak, restricted to the median-superior portion (Fig. 6A)
carbon-arius	weakly-sclerotized (Fig. 4B)	smooth	twice longer than wide (Fig. 6C)	separated by a V-shaped emargination	strong, restricted to the median-superior portion (Fig. 6C)
inachus	sclerotized (Fig. 4C)	smooth	twice longer than wide (Fig. 6E)	separated by a wide U-shaped emargination	Absent (Fig. 6E)
agenor	sclerotized (Fig. 4D)	smooth	appx. as long as wide (Fig. 6J)	separated by a wide U-shaped emargination	weak, restricted to the median superior portion (Fig. 6I)
geminatus	Sclerotized (Fig. 4E)	smooth	appx. as long as wide (Fig. 6G)	separated by a shallow V-shaped emargination	Angulate, restricted to the median portion (Fig. 6G)
lucasi	sclerotized (Fig. 4F)	smooth	wider than long (Fig. 6K)	inferior projection reduced	Absent

In general, *D. geminatus* and *D. lucasi* showed the more distinctive genitalic characteristics among the species studied. The complex of A+SA endophallites of *D. geminatus* is thin and elongated (with approximately one third of the length of the endophallus) (Fig. 6H). In *D. lucasi*, the axial endophallite is significantly wider in the superior part than in the inferior part (Fig. 6L), and the subaxial endophallite is wider in the inferior part (Fig. 6L). The species of the *agenor, batesi*, *carbonarius*, *globulus*, and *inachus* groups showed a very similar morphology for the complex of A+SA endophallites (Figs. 3G, 6B, D, F, J): the axial endophallite is thin and elongated (with approximately a quarter of the endophallus length) and the superior part is only slightly wider than the inferior part; the subaxial endophallite is a set of folds in the more developed superior part that surrounds the axial endophallite.

The similarities between the species of the *agenor*, *batesi*, *carbonarius*, *globulus*, and *inachus* groups are also demonstrated by the shape of the SRP and FPL endophallites. In species of these groups, the SRP is C-shaped with one side usually truncated or wider than its opposite side, which is acute and thin (Figs. 3G, 6B, D, F, J). The FLP is usually C-shaped having an inferior blade-like projection in these groups and in *D. geminatus*. On the other hand, as observed for the complex of A+SA endophallites, *D. lucasi* largely differs in the shape of the FLP endophallite. In this species, the

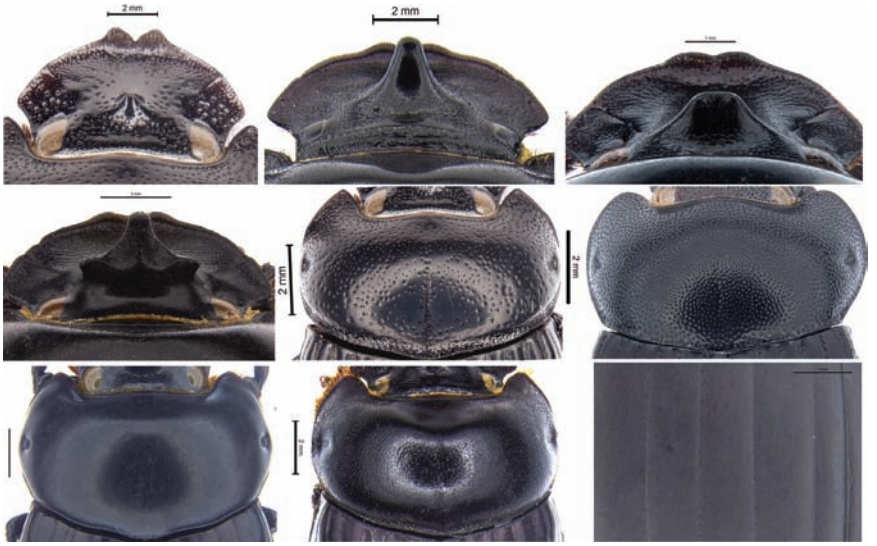

Fig. 7. Details of external morphology in *Dichotomius* species. (A) *D. snethlageae* **sp. nov.,** low conical process,; (B) *D. geminatus*, high conical process; (C) *D.* aff. *carbonarius*, transverse carina apically emargined; (D) *D. agenor*, tribuberculate carina; (E) *D. snethlageae* **sp. nov.**, pronotal surface covered with irregular ocellate punctures; (F) *D. fortepunctatus*, pronotal surface covered with umbilicate ocellate punctures; (G) *D.* aff. *carbonarius*, smooth pronotal surface; (H) *D. geminatus*, pronotal surface covered with coarse punctures; (I) *D.* aff. *carbonarius*, shagreened interstriae surface.

FLP endophallite has a thin and elongated inferior plate-like projection and instead of being C-shaped the inferior part is globose (Fig. 6L).

The ME morphology also suggested a close relationship between the *agenor, batesi*, *carbonarius*, *globulus*, and *inachus* groups when compared with *D. geminatus* and *D. lucasi*. In these five groups, the ME has two inferior projections separated by a V or U-shaped emargination (Table 3) (Figs. 3G, 6A, C, E, I). The inferior part of the ME of *D. geminatus* also seems to have a homologous projection at the inferior part, but it is not widely separated into two projections (Fig. 6G). The ME of *D. lucasi* appears to be widely reduced having only the inferior part sclerotized, and the inferior projection is present but is strongly reduced (Fig. 6K). The ME of *D. batesi*, *D. fortepunctatus* (*globulus* group), *D. lycas* (*carbonarius* group), *D. agenor*, and *D. geminatus* have a longitudinal fold in the medial region. In the *batesi* group, this fold is well developed and is extended throughout the entire length of the ME (Fig. 3G). Among the other species with this fold, it is restricted to the midline of ME or the inferior part (Figs. 6A, C, G, I).

Species belonging to the *batesi* and *globulus* groups seem to be more related each other since they have bodies covered with ocellate punctures, including the pronotum; the presence of a longitudinal groove on the posterior margin of the meso- and metafemora; an apical edge of paramera weakly sclerotized; and the presence of modifications on the dorsal surface of the paramera, such as spines and carinae. The two groups also demonstrate a similar pattern of geographic distribution, both being found

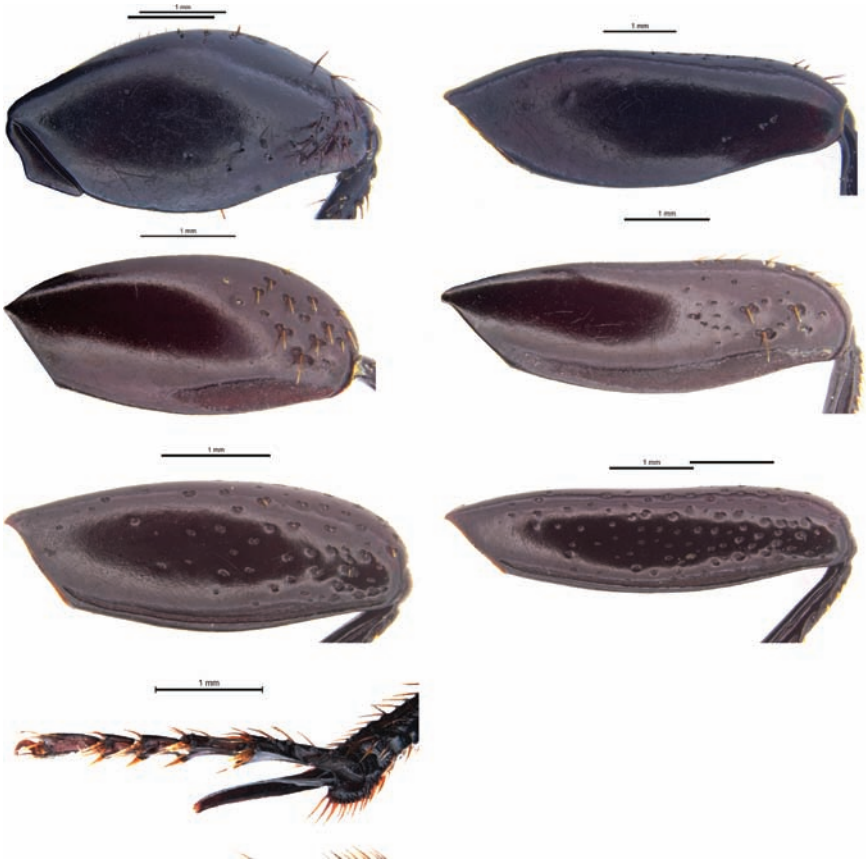

Fig. 8. Leg morphology in *Dichotomius* species. Meso– and metafemora, respectively: (A–B) *D. lycas* (*carbonarius* group); (C–D) *D. leopoldinae* **sp. nov.**; (E–F) *D. fortepunctatus* (*globulus* group). Metatibial spur: (G) *D. lucasi* (*lucasi* group); (H) *D. planus* (*inachus* group); (I) *D. leopoldinae* **sp. nov.**

in tropical rainforest in northern South America, and the subtropical forest of Central America. However, the shape of the ME, the paramera bended downwards in lateral view and the presence of a pair of strongly sclerotized bristles on the ventral portion of the endophallus approximates the *batesi* group to the species of the *carbonarius* group. In *D. lycas* (*carbonarius* group, for example, and in the species of the *batesi* group, the ME is twice as long as wide, the inferior projections are separated by a V-shaped emargination and have a well-developed median longitudinal fold (Figs. 3G–J, 6C).

Although testing these proposed phylogenetic hypotheses under a computational parsimony or statistical analysis is out of the scope of this paper, based on our comparative study of both external characteristics and male genitalia, it is possible to suggest that the species in the groups *agenor*, *batesi*, *carbonarius*, *globulus*, and *inachus* are likely more closely related to each other than to the other groups of *D.* (*Selenocopris*). Whereas the shape of the ME varies considerably between these species groups, the accessory endophallites have a more conserved anatomy, especially in the case of the complex of A+SA and SRP endophallites.

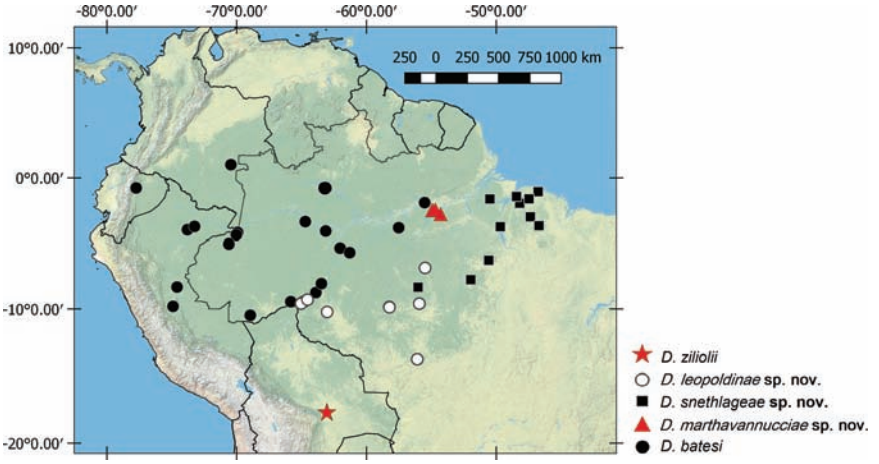

Fig. 9. Known distribution of the *batesi* species group.

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