



Systematics, Morphology and Biogeography

A revision of *Dichotomius (Homocanthonides)* Luederwaldt, 1929 (Coleoptera: Scarabaeidae: Scarabaeinae)



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ABSTRACT

The monospecific subgenus *Dichotomius (Homocanthonides)* is revised and its single species, *Dichotomius (H.) smaragdinus* (Perty, 1830) is redescribed and distinguished from other *Dichotomius* species. *Dichotomius (H.) smaragdinus* is a polymorphic species and its distribution comprises the Brazilian Cerrado. For the first time, morphological variation and male genital organ are described and illustrated. We believe that this species might be endangered due to extensive deforestation of Brazilian Cerrado by agricultural and pasture expansion. Thus, we highlight the importance of preserving this very unusual *Dichotomius* species.

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Introduction

Dichotomius Hope, 1838 is one of the most diverse genera of Neotropical Scarabaeinae comprising more than 170 described species (Nunes and Vaz-de-Mello, 2013; Maldaner et al., 2015; Nunes et al., 2016; Valois et al., 2017). Four subgenera are currently recognized: *Dichotomius* s. str.; *Homocanthonides* Luederwaldt, 1929; *Selenocoris* Burmeister, 1846; and *Luederwaldtinia* Martínez, 1951.

Among *Dichotomius*, the subgenus *Homocanthonides* is distinguishable by the presence of a single central clypeal tooth and green colored body with a green to red sheen. *Dichotomius (H.) smaragdinus* (Perty, 1830) is the only species assigned to the subgenus and was reviewed by Harold (1859, 1869a), Luederwaldt (1929) and Pessôa and Lane (1941). We present here an updated species description based on both sexes and all morphological variations encountered in its distributional range.

Materials and methods

Examined specimens belong to the following collections (curators in parenthesis):

CEMT – Setor de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Departamento de Biologia e Zoologia, Cuiabá, Mato Grosso, Brazil (Fernando Vaz-de-Mello)

CERPE – Coleção Entomológica da Universidade Federal Rural de Pernambuco, Recife, Brazil (Paschoal Grossi)

CMNC – Canadian Museum of Nature, Ottawa, Canada (François Génier)

CZMA – Coleção Zoológica do Maranhão, Universidade Estadual do Maranhão, Caxias, Maranhão, Brazil (Francisco Limeira-de-Oliveira)

MNRJ – Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Miguel Monné and Marcela Monné)

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

ZSM – Zoologische Staatssammlung München, Munich, Germany (Michael Balke and Lars Hendrich)

Terminology for the external structures used in descriptions follows Vaz-de-Mello et al. (2011), Valois et al. (2017) to aedeagus morphology and Tarasov and Génier (2015) to endophalllic sclerites. Type specimen labels are transcribed *ipsis litteris*. Labels are separated by slashes "/". Data from non-type material are

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presented as: country name written in capital letters (e.g. BRASIL), states or provinces written in italic (e.g. *Mato Grosso*), followed by localities and complementary information, such as coordinates, altitude, dates, method of collection, and collector. The number and sex of specimens plus the acronyms of collections or museums where they are deposited are located between brackets (e.g. [4♂ 2♀ CEMT]).

Taxonomy

Dichotomius (Homocanthonides) smaragdinus (Perty, 1830)

Copris smaragdina Perty, 1830: 42 (original description)

Copris (Chalcocoris) smaragdina Perty: Burmeister, 1846: (unpaginated)

Copris smaragdina Perty: Harold, 1859: 197–198 (redescription)

Pinotus smaragdinus (Perty, 1830): Harold, 1869a: 127–128; 1869b: 1011; Gillet, 1911: 62; Blackwelder, 1944–1957: 208 (checklist).

Pinotus (Homocanthonides) smaragdinus (Perty, 1830): Luederwaldt, 1929: 661–663, 59–61

Dichotomius (Homocanthonides) smaragdinus (Perty, 1830): Martínez, 1951: 140; Vaz-de-Mello, 2000: 193.

Type material

Male Lectotype [ZSM, designated by Scherer (1983)]: 30. Brasilia. *Pinotus smaragdinus*. Perty/HOLOTYPE *Copris smaragdina* Perty det. D.-Scherer 1981/*Pinotus smaragdinus* (Perty) det. G. Scherer, 1981//LECTOTYPE ♂ *Copris smaragdina* Perty des. F.Z. Vaz-de-Mello, 2014. Following articles 74.5 and 74.6 of the International Code of Zoological Nomenclature (ICZN), we agreed that Scherer (1983) unintentionally designated the lectotype of *Copris smaragdina* when he found a specimen in Spix's collection and published its labels' transcription mentioning the word "typus" before giving a brief description of this specimen (Fig. 1A).

Non-type material

[43 males, 54 females, 6 specimens unsexed] BRAZIL: *Mato Grosso*: Diamantino. Vale da Solidão. 14°22'14"S; 56°07'59"W. Light. 24.X.2006. E. Furtado [4♂ 2♀ CEMT]; same locality, but 31.x.2013. Collected burying *Attalea* fruits [1♂ 8♀ CEMT]; same data, but 20.X.2006 [1♀ CEMT]; same data, but 14°22'S; 56°07'W. 450m. XI.2012. [4♀ CEMT]; same data, but X.2012 [1♂ CEMT]; same municipality, but Alto Rio Arinos. Light. 09.IX.1998. E. Furtado [3♂ 2♀ CEMT]; Porto Estrela. Estação Ecológica Serra das Araras. 03–23.X.2011. Manual. M. Souza and F. Vaz-de-Mello. [1♂ CEMT]; Chapada dos Guimarães. Cidade de Pedra. 22.X.2009. Light trap. F.R. Fernandes. [1♀ CEMT]; Cuiabá. Fazenda Mutuca. Eucalipto. 25.X.2008. [1♀ CEMT]; Nova Xavantina, XI.1946 [1 specimen unsexed, MNRJ]; Rosário Oeste [1 specimen unsexed, MNRJ]; Rosário Oeste, XII.1975, A. Maller col. [1 specimen unsexed, MNRJ]; Conquista do Oeste, XI.2012. M.A. Carvalho. [3♂ CEMT]. *Mato Grosso do Sul*: Selvíria. UNESP farm. Carrion baited pitfall trap riparian forest - pasture transition area. 24.X.1992. C.A.H. Flechtmann. [1♀ CEMT]; same data, 03.X.1992. [1♂ CEMT]; Três Lagoas, X.1952, D. Sabetai col. [1 specimen unsexed, MNRJ]. Goiás: Mineiros. Parque Nacional das Emas. X.1999. F. Rodrigues [1♀ 1♂ CEMT]; Niquelândia. X.1993. [1♀ CEMT]; Campinaçu, 17.X.1985, L. C. Alvarenga col. [1 specimen unsexed, MNRJ]; Goiânia ("Campinas"), X.1935, lacking collector. [1 specimen unsexed, MNRJ]; Rio Verde, 07.XI.1945, H. Zellibor col. [3 specimens unsexed, MNRJ]; same data, but [no dates], Dr. Nick [1♂ 1♀ CMNC]; same data, but XII.1941 [1♂ 2♀ CMNC]; same data, but XII.1945, Zellibor leg. [2♀ CMNC]; same data, but Ribeirão Pires, XI.1956, P. Pereira leg. [1♀ CMNC]. Vianópolis, X.1968, N. Tangerini col. [1 specimen unsexed, MNRJ]. Distrito Federal: Planaltina. Embrapa Cerrados. Fragmento Cerrado.

15°36'20"S; 47°42'26"W. 03.XI.2005. Light. C. Oliveira. [6♂ 7♀ CEMT]; same data, 18.XI.2005. [2♂ 4♀ CEMT]; same data, but Cerrado Nativo. 15°36'20"S; 47°42'16"W. 03.XI.2006. [2♂ 1♀ CEMT]; same data, but 15°36'16"S; 47°44'16"W. 03.XI.2006. [2♂ 1♀ CEMT]; Brasília. XI.1989. C. Godinho. [2♂ 2♀ CEMT]; same locality, but 18.X.2002. Jorge and Ricardo [1♂ CEMT]; same locality, but Universidade de Brasília. 15.VIII.2010. Buckmann, H. M. [1♀ CEMT]. Minas Gerais: Cordisburgo. Fazenda Pontinha. I.1999. Falqueto and Vaz-de-Mello [1♀ CEMT]; same locality, XII.1997. Vaz-de-Mello [1♂ CEMT]; same locality, II.1996. Vaz-de-Mello. [1♂ CEMT]; Paracatu. XI.1997. S. Lourenço Jr. [1♀ CEMT]; same locality, XI.1992. C. Godinho. [1♀ CEMT]; Bocaiúva. Fazenda Corredor. 05.XI.1998. M.F. Vasconcelos and A.A. Azevedo. [1♀ CEMT]; same locality, 26.XI.1998. M.F. Vasconcelos. [1♂ CEMT]; Martinho Campos. XII.1988. [1♂ CEMT]; Águas Vermelhas. XII.1997. A. Bello and F. Vaz-de-Mello. [1♀ CEMT]; same locality, XI.1991. E. Grossi [1♂ CEMT]; Faz. Faceiro. 12–19.XII.2012. E. and P. Grossi. [2♂ 2♀ MZUFPA]; same locality. 16.XII.2012. [1♂ CERPE]; Três Marias. XI.1991. J.N.C. Louzada. [1♀ CEMT]; same locality XI.1991. J. C. Zanúcio. [3♀ CEMT] same location, but X.1989. [1♂ CEMT]; Divisa Alegre. XI.1977. C. Godinho [1♂ 1♀ CEMT]. Uberlândia. 18°45.494S; 048°18'.986W. XII.2106. Carvalho, R. [1♂ 1♀ CEMT]. São Paulo: Batatais. XII.1943 [1 specimen unsexed, MNRJ]; same data, but XII.1945, Ginástico S. José [1♂ CMNC]. Maranhão: Geraldina. 3.XII.2009. C.M. Meier [1♂ CEMT]; Mirador. Parque Estadual Mirador. Base da Geraldina. 06°37'25"S; 45°52'08"W. 12–20.X.2012. Light trap. F. Limeira-de-Oliveira, L. S. Santos and C.F. Barros. [1♂ CEMT]; same data but [1♂ 1♀ CERPE]. No data: [3♀ CEMT].

Diagnosis

The current definition of Dichotomini (*sensu* Tarasov and Dimitrov, 2016) comprises four Neotropical/Neartic genera: *Dichotomius*, *Chalcocoris* Burmeister, 1846, *Holocephalus* Hope, 1838, and *Isocopris* Pereira and Martínez, 1960. *Dichotomius* (*H.*) *smaragdinus* is assigned to *Dichotomius* based on the following combinations of morphological characters: antenna with nine antennomeres; elongated antennal club; second labial palpomere triangular, not covering the third palpomere in ventral view; clypeal ventral process present (coniform to apically bifurcate). Within *Dichotomius*, the species has been isolated in a separated subgenus namely *Dichotomius (Homocanthonides)*. This subgenus (and its only species) has the following differences: it differs from the subgenus *D. (Dichotomius)* by having a body with a green metallic sheen and ventral thoracic sternites glabrous, lacking long dense setae; it differs from *D. (Selenocoris)* by clypeo-genal junction lacking angulation, ventral clypeal process pronounced into a small tubercle, not bifurcated, and sixth abdominal sternite of females not differentiated by the presence of tubercles, lobe or emarginations; and it differs from *D. (Luederwaldtinia)* by its single rounded tooth on clypeal margin, and all meso and metatarsomeres with a row of yellow setae on ventral surface.

Redescription Male: Length: 11–16 mm. Maximum width (pronotum): 6–9 mm. Body mainly green with metallic green, red or yellow sheen (Fig. 1). **Head:** surface finely punctated. Clypeal margin distinctly emarginated. Clypeal and genal margins with a single row of ventral orange setae. Ventral clypeal process pronounced into a short pointed tubercle. Clypeo-genal suture weakly impressed. Clypeo-frontal surface with a single, central tubercle [broken in the lectotype]. Antenna with nine antennomeres; club elongated, with orange and yellow setae. **Pronotum:** distinctly convex with a wide anterior declivity with two feeble excavations (Fig. 1A–E). Surface of anterior angles with ocellate punctures, punctures becoming weakly defined toward pronotal disc (Fig. 3B–E). Lateral portion of pronotum with coarse punctures. Posterior margin with coarse

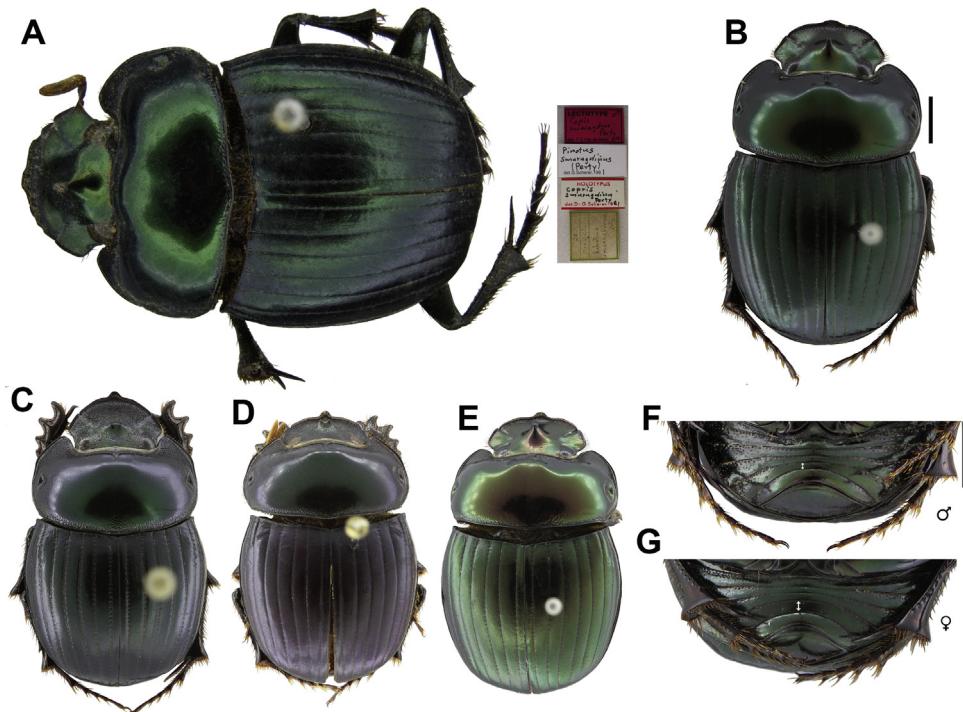


Fig. 1. *Dichotomius (Homocanthonides) smaragdinus* (Perty, 1830). (A) Lectotype of *Copris smaragdina* Perty, 1830 [ZSM]. (B) Male habitus, green variation. (C) Female habitus, green variation. (D) Female habitus, dark elytra variation. (E) Male habitus, green with red and yellow sheen variation. (F) Male abdominal sternites. (G) Female abdominal sternites.

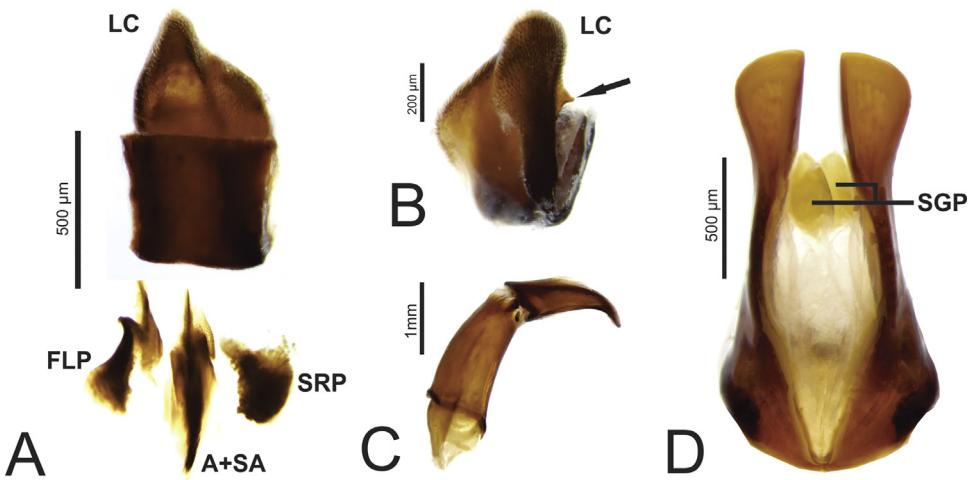


Fig. 2. Aedeagus of *Dichotomius (H.) smaragdinus*. (A) Endophallus and dissected sclerites, dorsal view. LC, lamella copulatrix; FLP, frontal lateral peripheral sclerite; A+SA, complex of axial and sub-axial sclerites; SRP, superior-right peripheral sclerite. (B) Lamella copulatrix, left view. (C) Aedeagus, lateral view. (D) Dorsal view of paramera. SGP: Subgenital plates.

irregular granules, preceded by a more or less wide band of coarse punctures. Glossy pronotal disc with weakly defined longitudinal sulcus. Anterior margin well defined throughout, with narrowly produced posterior along midline. Anterior angles rounded. Hypomeron: weakly excavated anterior. Anterior portion filled with dense setae, surface covered with irregular ocellate punctures; punctures spaced by approximately half or less their diameter on central portion of excavation. Lateral margins with a row of setae shorter than those on excavation. Central region slightly punctated and posterior portion with setose punctures. Prosternum: with ocellate punctures. Mesosternum: divided by smooth central area. Lateral portion with ocellate punctures irregularly spaced. Meso-metasternal suture almost straight, and medially obsolete. Mesepisternum: glabrous, with deep ocellate punctures.

Metasternum: anterior lobe coarsely punctated. Flat disc, that is finely punctated. Lateral, glabrous lobes, with dense ocellate punctures. **Elytra:** glossy, with green sheen. Interstriae convex, simply punctated. Punctures larger than striae, shallowly impressed and spaced by two times their diameter (Fig. 3C, E, F). Elytra with nine elytral striae; first to seventh striae broader basally; ninth stria not reaching base. **Legs:** with long orange pilosity. External margin of protibiae quadridentate. Apical spur of protibiae curved down, and pointed at the apex. Ventral surface of profemur is punctated on posterior half; apical portion with setose punctures, setae very short. Meso and metatarsomeres I-IV slightly enlarged toward the apex. Apical metatarsomere cylindrical, almost two times longer than IV. Apical spur of metatibia is truncated. **Abdomen:** sternites narrowed medially. Sternites with a row of punctures along

anterior margin. Fifth sternite approximately two times shorter than sixth medially (Fig. 1F). Pygidium: wider than long. Shiny, with spars and feeble punctures. Phalobase: almost as long as parameres. Parameres: subgenital plates (SGP) of aedeagus reduced, weakly sclerotized (Fig. 2D). In lateral view, apex dorso-ventrally flattened, strongly curved ventrally. In dorsal view, apex laterally expanded, external margins rounded (Fig. 2C, D). Inner margin straight on apical fourth, remaining parts of margin curved outward, converging at the base (Fig. 2D). Endophallus [in the dorsal view]: as in Fig. 2A. Lamella copulatrix (LC) with a square-shaped dorsal projection (Fig. 2A); in left view with a pointed projection (Fig. 2B, arrow). Female: Length: 11–16 mm. Maximum width (pronotum): 6–9 mm. Clypeal surface transversally ridged; posterior portion coarsely punctated. Genal surface wrinkled. Clypeofrontal surface with a short notched tubercle. Interocular surface with coarse elongated punctures except for posteromedian with smooth surface. Fifth sternite is as long as sixth medially (Fig. 1G).

Morphological variation

Dichotomius (Homocanthonides) smaragdinus is a widespread species in Brazilian Cerrado with considerable chromatic variation (Figs. 1 and 3). Some specimens have the pronotal disc with yellow or red sheen; or elytra entirely black, lacking green reflections (see Discussion section).

Taxonomic remarks

Copris smaragdina Perty, 1830 and *C. hesperus* (Olivier, 1789) were originally characterized by their colored body with green, red or yellow coloration. Burmeister (1846) described the subgenus *Copris (Chalcocoris)* for *C. hesperus* and *C. smaragdina* based on the presence of eight antennal segments and metallic body coloration. Ten years later, Lacordaire (1856) argued that *C. smaragdina* was a synonym of *C. hesperus* describing nine antennal segments to *Copris*, except for *C. hesperus* which had only eight antennal segments (as he explained in a footnote). Harold (1859) stated eight antennal segments for *C. smaragdina*, but corrected it to nine segments later (Harold, 1969a). Additionally, Harold (1859) examined and redescribed Perty's specimen of *C. smaragdina* concluding that this species is completely different from *C. hesperus*. Later, Cupello et al. (2016) designated *C. hesperus* as the type-species of *Chalcocoris*. In 1869, Harold transferred *C. smaragdina* to *Pinotus* Erichson. Luederwaldt (1929) described the new subgenus *Homocanthonides* and redescribed *Pinotus (Homocanthonides) smaragdinus*, its single and then type-species, based on a female specimen. Martínez (1951) made the new, currently valid combination *Dichotomius (Homocanthonides) smaragdinus* (Perty, 1830), considering the precedence of *Dichotomius* Hope, 1838 over *Pinotus* Erichson, 1847.

Distribution

Brazilian Cerrado, in the states of Mato Grosso, Mato Grosso do Sul, Goiás, Distrito Federal, Maranhão, Minas Gerais and São Paulo (Fig. 3A).

Collecting information

Nine specimens were found burying seeds of *Attalea* palm (Arecaceae) in the municipality of Diamantino, Mato Grosso state (Eurides Furtado, collector notes). Other species of *Dichotomius* have been reported from fruits (Halffter and Halffter, 2009). However, apart of this single report of *D. (H.) smaragdinus* in *Attalea* fruits, the species has been known to be captured only at light,

flight interception traps, and rarely in pitfall traps, independent of bait type or even of being baited (our observation).

Discussion

Here we were concerned with the taxonomy of the monospecific subgenus *Dichotomius (Homocanthonides)*, describing morphological variations, and providing a redescription and diagnosis for its single species *D. (H.) smaragdinus*. In early classifications, *D. (H.) smaragdinus* was closely related to *Chacolcopris hesperus* based on their body color (metallic green) and antenna supposedly with eight antennomeres. Harold (1869a) correctly described nine antennal segments for *D. (H.) smaragdinus* and transferred it from *Copris* Geoffroy, 1762 to *Dichotomius* (cited as *Pinotus* Erichson, 1847). In revising *Dichotomius*, Luederwaldt (1929) treated *D. (H.) smaragdinus* in a separated subgenus based on its single tooth on clypeal margin.

Among *Dichotomius* subgenera, the colored body of *D. (H.) smaragdinus* resembles some *D. (Luederwaldtinia)* species in the *D. (L.) speciosus* and *D. (L.) carbonarius* species-groups, *D. (L.) glaucus* (Harold, 1869b) and *D. (L.) lycas* (Felsche, 1901). Plus, the two subgenera have very similar sexual dimorphic characters, such as the clypeal surface of female with transversal ridges, and the male's sixth abdominal sternite being two times longer than fifth. For the first time, the aedeagus and the endophalic sclerites of *D. (H.) smaragdinus* are described and illustrated (Fig. 2). In this species, the subgenital plates (SGPs) of aedeagus are small and weakly sclerotized, contrasting with large and well-sclerotized SGPs found in most *Dichotomius* species. The Lamella copulatrix (LC) is well-developed and bears a square-shaped dorsal projection resembling the basic plan of LC in the *D. sericeus* species-group (Valois et al., 2017). Previous studies have demonstrated the high taxonomic and phylogenetic value of the endophalic sclerites in dung beetle evolution (Tarasov and Solodovnikov, 2011; Rossini et al., 2018), however these structures are still poorly known in most *Dichotomius* species.

Despite the morphological similarities between species of *D. (Luederwaldtinia)* and *D. (H.) smaragdinus* we decided to maintain its current taxonomic status since its diagnostic characters contrast with those used to define all other *Dichotomius* subgenera (see Diagnosis). However, the phylogenetic value of these characters was not tested since the phylogenetic relationships among *Dichotomius* species remain unclear. Therefore, we believe that a possible close relation between *D. Luederwaldtinia* and *D. (H.) smaragdinus* should first be tested in a phylogenetic study before taxonomic changes are proposed.

We have not examined specimens from Bahia, Piauí and Tocantins states, but we believe that *D. (H.) smaragdinus* may occur in its Cerrado habitats and it may be collected using light or flight interception traps. The color variation illustrated here is present in specimens from all localities and does not show exclusive regional variations. However, we found two distinct patterns of sculpture and punctuation on pronotum and elytra for *D. (H.) smaragdinus* specimens. Populations from western Cerrado (comprising localities as Diamantino and Barra do Garças, Mato Grosso State) exhibit strong sculpturing on pronotal lateral declivities (Fig. 3B), elytral striae and interstriae (Fig. 3C). As opposed to populations from extreme eastern Cerrado, which have pronotal lateral declivities that are almost smooth, and with indistinct punctures or impressions, thin and sparsely punctated elytral striae and an interstrial surface that is finely punctated (Fig. 3F–G). These patterns are linked by intermediate sculptural forms from localities in Distrito Federal and Minas Gerais State (Fig. 3D–E). The east-west cline of sculpturing variation, combined with the lack of definite genital differences among populations studied, led us to believe that these phenotypes represent variations of a single species.

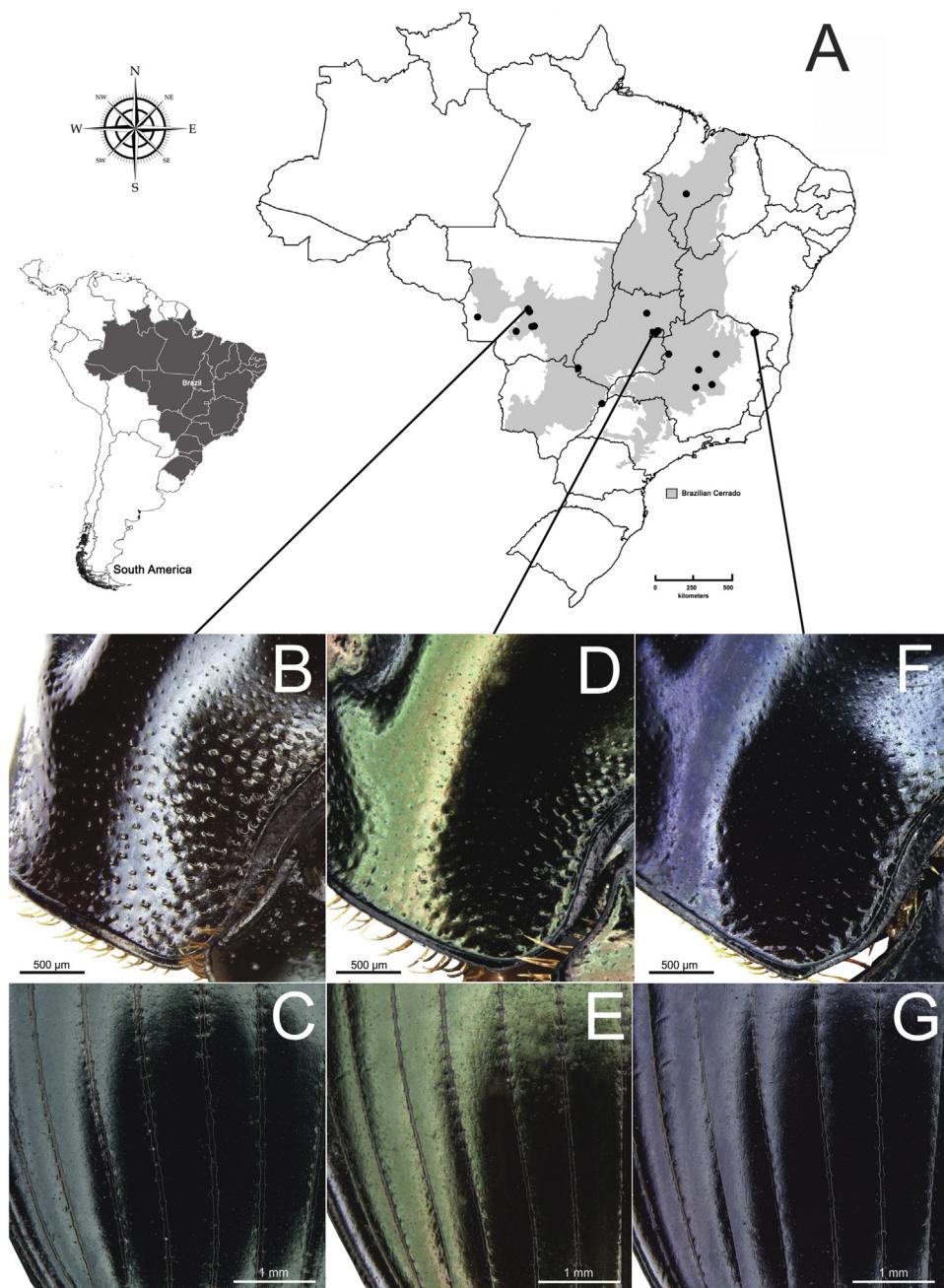


Fig. 3. (A) Known distribution of *Dichotomius (H.) smaragdinus*. Anterior angle of pronotum and elytra variations, respectively: (B) and (C) Diamantino, Mato Grosso State, western Cerrado. (D) and (E) Planatina, Federal District, central Cerrado. (F) and (G) Águas Vermelhas, Minas Gerais State, eastern Cerrado.

Dichotomius (H.) smaragdinus has not been assessed by IUCN Red List, and information solely in its distribution associated to the lack of ecological and tropical preferences would probably lead it to Data Deficient (IUCN, 2012). However, *D. (H.) smaragdinus* inhabits Brazilian Cerrado and because of that we believe that this species might be threatened in consequence of the severe deforestation of native Cerrado vegetation (Machado et al., 2004). In this context, the preservation and maintenance of native vegetation on Conservation Units (Brasil, 2000) and Legal Reserves (Brasil, 2012) shall be the most effective strategies on the conservation of this and other threatened Brazilian Cerrado species.

Conflicts of interest

The authors declare no conflicts of interest.

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References

- Blackwelder, R.E., 1944–1957. Checklist of the Coleopterous Insects of Mexico, Central America, The West Indies and South America. Parts I through part 6. U.S. Nat. Mus. Bull. 185, Parts 1–6.
- Brasil, 2000. Ministério do Meio Ambiente. Sistema Nacional de Unidades de Conservação da Natureza: Lei N° 9.985, 18 de Julho de 2000 (accessed 16.04.18) http://www.mma.gov.br/images/arquivos/areas_protegidas/snuc/Livro%20SNUC%20PNAP.pdf.
- Brasil, 2012. Ministério do Meio Ambiente. Sistema Nacional de Unidades de Conservação da Natureza: Lei N° 12.651, 25 de Maio de 2012 (accessed 17.07.17) http://www.planalto.gov.br/ccivil_03/_Ato2011-2014/2012/Lei/L12651.htm#art83.
- Burmeister, H., 1846. *Genera Quaedam Insectorum*, Band III. H. Burmeister, Berlin.
- Cupello, M., Rossini, M., Vaz-de-Mello, F.Z., 2016. On the type species of the South American dung beetle genus *Chalcocoris* Burmeister, 1846 (Coleoptera: Scarabaeidae: Scarabaeinae), with some comments on the type locality of *C. hesperus* (Olivier, 1789). Zootaxa 4061 (3), 274–276.
- Gillet, J.J.E., 1911. Scarabaeidae: Coprinae I. In: Junk, W., Schenkling, S. (Eds.), *Coleopterorum Catalogus Pars 38*. W. Junk, Berlin.
- Halfpter, G., Halfpter, V., 2009. Why and where coprophagous beetles (Coleoptera: Scarabaeinae) eat seeds, fruits or vegetable detritus. Bol. SEA 45, 1–22.
- Harold, E.von, 1859. Beiträge zur Kenntniss einger coprophagen Lamellicornien. Dtsch. Entomol. Z. 3, 193–224.
- Harold, E. von, 1869a. Révision des espèces qui rentrent dans le genre *Pinotus* Erichs. L'Abeille 6, 123–144.
- Harold, E. von, 1869b. In: Gemminger, M., Harold, E.von. (Eds.), Catalogus coleopterorum. Hucusque descriptorum, synonymicus et systematicus. Tom. IV. Scarabaeidae. Sumptu E. H. Gummi, Munich, Germany, pp. 979–1346.
- Hope, F.W., 1838. The Coleopterists Manual Containing the Insects of Linneus and Fabricius. Henry G. Bohn, London.
- IUCN, International Union for Conservation of Nature, 2012. IUCN Red List Categories and Criteria, Version 3.1, 2nd edition (accessed 17.01.17) <http://www.iucnredlist.org/technical-documents/categories-and-criteria>.
- Lacordaire, J.T., 1856. Histoire naturelle des insectes. Genera des coléoptères, ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome troisième. Librairie Encyclopédique de Roret, Paris, France.
- Luederwaldt, H., 1929. As espécies brasileiras do gênero *Pinotus*. Rev. Mus. Paul. 16, 603–775, offprint: 1–177.
- Machado, R.B., Ramos Neto, M.B., Pereira, P.G.P., Caldas, E.F., Gonçalves, D.A., Santos, N.S., Tabor, K., Steininger, M., 2004. Estimativas de perda da área do Cerrado brasileiro. Conservation International do Brasil, Brasília.
- Maldaner, M.E., Nunes, R.V., Vaz-de-Mello, F.Z., 2015. Taxonomic revision of the *Dichotomius speciosus* (Waterhouse, 1891) species group (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 3986 (5), 549–560.
- Martínez, A., 1951. Notas Coleopterologicas V. An. Soc. Cient. Argent. 92, 138–142.
- Nunes, R.V., Vaz-de-Mello, F.Z., 2013. New brachypterous species of *Dichotomius* Hope, with taxonomic notes in the subgenus *Luederwaldtinia* Martínez (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 3609 (4), 411–420.
- Nunes, R.V., Carvalho, M.S., Vaz-de-Mello, F.Z., 2016. Taxonomic review of the *Dichotomius* (*Luederwaldtinia*) *assifer* (Eschscholtz) species-group (Coleoptera: Scarabaeidae). Zootaxa 4078 (1), 230–244.
- Pereira, F.S., Martínez, A., 1960. Notas escarabeídológicas – II. Rev. Bras. Entomol. 9, 37–55.
- Pessôa, S.B., Lane, F., 1941. Coleópteros necrófagos de interesse médico-legal: ensaio monográfico sobre a família Scarabaeidae de S. Paulo e regiões vizinhas. Arq. Zool. São Paulo, II (Tomo XXV da Revista do Museu Paulista), 389–504.
- Perty, J.A.M., 1830. De Insectorum in America Meridionali habitantum vitae genere, moribus ac distributione geographicâ, observationes nonnullae. In: Spix, J., Martius, C. (Eds.), *Delectus animalium articulatorum, quae in itinere per Brasiliam annis MDCCXVII–MDCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi peracto collegerunt Dr. J. B. de Spix, et Dr. C. F. Ph. de Martius. Digessit, descripsit, pingenda curavit Dr. Maximilianus Perty, praefatus est editid Carol. Frederic. Philip. de Martius, accedit dissertatione of insectorum in America Meridionali habitantum vitae genere, moribus et distributione geographicâ. (fasc. 1)*. Frid. Fleischer, Monachii, pp. 1–44.
- Rossini, M., Vaz-de-Mello, F.Z., Zunino, M., 2018. A taxonomic revision of the New World *Onthophagus Latreille*, 1802 (Coleoptera: Scarabaeidae: Scarabaeinae) of the osculatii species-complex, with description of two new species from South America. J. Nat. Hist. 52 (9–10), 541–586.
- Scherer, G., 1983. Die von J. B. v. Spix und C. F. Ph. v. Martius in Südamerika gesammelten Coleopteren. Spixiana 9, 295–305.
- Tarasov, S., Génier, F., 2015. Innovative Bayesian and parsimony phylogeny of dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) enhanced by ontology-based partitioning of morphological characters. PLOS ONE 10 (3), e0116671.
- Tarasov, S.I., Solodovnikov, A.Y., 2011. Phylogenetic analyses reveal reliable morphological markers to classify megadiversity in *Onthophagini* dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). Cladistics 27 (5), 490–528.
- Tarasov, S., Dimitrov, D., 2016. Multigene phylogenetic analysis redefines dung beetles relationships and classification (Coleoptera: Scarabaeidae: Scarabaeinae). BMC Evol. Biol. 16, 257.
- Valois, M.C., Vaz-de-Mello, F.Z., Silva, F.A.B., 2017. Taxonomic revision of the *Dichotomius sericeus* (Harold, 1867) species group (Coleoptera: Scarabaeidae: Scarabaeinae). Zootaxa 4277 (4), 503–530.
- 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. (Eds.), *Hacia un Proyecto CYTED para el inventario y Estimación de la Diversidad Entomológica en Iberoamérica: PriBeS-2000*. SeA, Zaragoza, pp. 183–195.
- Vaz-de-Mello, F.Z., Edmonds, W.D., Ocampo, F., Schoolmeesters, P., 2011. A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). Zootaxa 2854, 1–73.