

**Taxonomic Revision of the Rare South American Dung Beetle Genus
Holocanthon Martínez et Pereira, 1956 (Coleoptera: Scarabaeidae:
Scarabaeinae: Deltochilini)**

Authors: Lucas Sawaris, Mario Cupello, and Fernando Z. Vaz-de-Mello

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TAXONOMIC REVISION OF THE RARE SOUTH AMERICAN DUNG BEETLE GENUS *HOLOCANTHON* MARTÍNEZ ET PEREIRA, 1956 (COLEOPTERA: SCARABAEIDAE: SCARABAEINAE: DELTOCHILINI)

LUCAS SAWARIS^{1,2,5}, MARIO CUPELLO^{3,4} and
FERNANDO Z. VAZ-DE-MELLO^{2,4}

¹*Instituto Federal de Mato Grosso, Campus Avançado de Tangará da Serra, Rua 28, 980, Vila Horizonte, Tangará da Serra, MT, CEP 78300-000, Brazil; e-mail: lucas.sawaris@gmail.com*

²*Universidade Federal de Mato Grosso, Instituto de Biociências, Departamento de Biologia e Zoologia. Av. Fernando Correa da Costa, 2367, Boa Esperança, Cuiabá, MT, CEP 78060-900, Brazil; e-mail: vazdemello@gmail.com*

³*Universidade Federal do Paraná, Departamento de Zoologia, Laboratório de Sistemática e Bioecologia de Coleoptera, Centro Politécnico, Jardim das Américas, CEP 81.531-980, Curitiba, PR, Brazil; e-mail: mcupello@hotmail.com*

⁴*Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq)*

⁵*Corresponding author*

Abstract.— *Holocanthon* is a dung beetle genus distributed across South American open environments such as the Humid Chaco, the Brazilian Cerrado and the Argentinian Espinal, as well as some more forested localities in the southern Atlantic Forest and in the Bolivian and Argentinian Yungas. Considered monospecific for more than 60 years, the genus now includes two species: *H. fuscobruber* (Blanchard, 1846), **new comb.** (= *H. mateui* Martínez et Pereira, 1956, **new junior subjective synonym**), from Paraguay, Argentina and southern Brazil, and *H. giosilvai* Sawaris, Cupello & Vaz-de-Mello **sp. nov.**, known only from three distant localities in Bolivia and southern Brazil. The lectotype of *Canthon fuscobruber* is herein designated from the only known syntype, while the holotype and the rest of the type series of *H. mateui* is deemed to be lost.



Key words.— Neotropical, new species, identification key, description, synonymy

INTRODUCTION

Holocanthon Martínez et Pereira, 1956 was originally established as a monospecific genus for *H. mateui* Martínez et Pereira, 1956, from southern Brazil and Argentina. The genus belongs to Deltochilini (Tarasov and Dimitrov 2016) and is distinguished from other members of that exclusively New World tribe by having the mentum completely divided longitudinally into two independent parts (Martínez and Pereira

1956, Vaz-de-Mello *et al.* 2011). This characteristic, which may in some way even resemble the ancestral condition of the Insecta, for the insect labium evolved from the fusion of the second pair of maxillae typical of crustaceans (Snodgrass 1935, Brusca and Brusca 2002, Grimaldi and Engel 2005), is unique among dung beetles and we are not aware of its presence in any other Coleoptera. Studying its ontological development may help shed light into the evolution of the insect mouthparts.

The examination of specimens gathered over the past years in the CEMT raised some questions about the monospecificity of *Holocanthon*, which triggered this revision of the genus. After visiting some collections and examining the type material of some mysterious nominal species housed in European museums, we concluded that a small series of odd-looking specimens from Bolivia and Brazil initially identified by us as *H. mateui* actually does not belong to that species, but rather constitute a new species in the genus. Furthermore, the examination of Émile Blanchard's (1819–1900) type material in the Museum nationale d'Histoire naturelle, Paris, France, revealed that *Canthon fuscorubrus* Blanchard, 1846, a name that puzzled dung beetle specialists for more than 150 years, in reality refers to the same species as *H. mateui*, and that both names are, consequently, synonyms. Our purpose with this paper, therefore, is to present the results of our taxonomic study and discuss its implications for the taxonomy of South American Scarabaeinae.

MATERIAL AND METHODS

For the preparation of this work, the following 17 collections were searched for *Holocanthon* specimens (curators or contact in parentheses):

- BMNH – The Natural History Museum, London, United Kingdom (Maxwell V. L. Barclay);
- CEAH – Coleção Entomológica Adolph Hempel, Instituto Biológico, São Paulo, Brazil (Sergio Ide);
- CEIOC – Coleção Entomológica do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (Jane Costa);
- CEMT – Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil (Fernando Z. Vaz-de-Mello);
- CMNC – Canadian Museum of Nature, Ottawa, Canada (François Génier);
- DZUP – Coleção Entomológica Padre Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (Lucia Massutti de Almeida);
- FSCA – Florida State Collection of Arthropods, Gainesville, Florida, United States (Paul Skelley);
- INPA – Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (Marcio Luiz de Oliveira);
- MCNZ – Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil (Luciano de Azevedo Moura);
- MCZC – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, United States (Charles Farnum and Rachel Hawkins);
- MGAP – Museu Anchieta de Ciências Naturais, Colégio Anchieta, Porto Alegre, Brazil (Fernando Meyer);
- MNHN – Muséum national d'Histoire naturelle, Paris,

France (Olivier Montreuil and Antoine Man-tilleri);

- MNRJ – Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Miguel A. Monné and Marcela L. Monné);
- MPEG – Museu Paraense Emílio Goeldi, Belém, Brazil (Orlando Tobias Silveira);
- MZSP – Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Sonia Casari and Carlos Campaner);
- MZUFPA – Museu de Zoologia, Instituto de Ciências Biológicas, Universidade Federal do Pará, Belém, Brazil (Fernando A.B. Silva);
- TAMU – Texas A&M University, College Station, Texas, United States (Edward G. Riley).

Of these, only eight were found to hold specimens of *Holocanthon*: CEAH, CEMT, CMNC, DZUP, MCNZ, MNHN, MZSP and TAMU. In total, they house 85 individuals of two species.

The morphological terminology adopted here mostly follows standard references in dung beetle systematics such as Edmonds (1972). Exceptions are the terminology for the ventral sclerites of the beetle body, which follows Beutel and Lawrence (2005) and Lawrence *et al.* (2010), and that for the tegument microsculpture, which follows Cupello and Vaz-de-Mello (2018). The geographical distribution of each species is given also following the scheme established in Cupello and Vaz-de-Mello (2018). Type specimen's labels are transcribed verbatim with information of each separate label enclosed between quotation marks, slashes (“/”) indicating different lines on a same label, and italics referring to handwritten data. Finally, species taxa are here interpreted according to the Biological Species Concept (Mayr 1940, 1942, 1963, 1970, 1996, and elsewhere; see also Cupello and Vaz-de-Mello [2018] for a full discussion on this topic).

RESULTS

Taxonomic treatment

Holocanthon Martínez et Pereira, 1956

Holocanthon Martínez and Pereira, 1956: 380–382; Pereira and Martínez 1956: 95, 108, 184; Martínez 1959: 58; Halffter 1961: 229–230, 253; Vulcano and Pereira 1964: 588; Halffter and Matthews 1966: 261; Halffter and Martínez 1966: 103; 1968: 210; Halffter 1974: 237; Halffter and Martínez 1977: 37–38, 46, 66; Halffter and Edmonds 1982: 139; Martínez 1987: 54; Hanski and Cambefort 1991: 468; Monteresino *et al.* 1996: 105, 111; Vaz-de-Mello 2000: 186, 193; Medina *et al.* 2003: 24, 40, 65; Hamel-Leigue *et al.* 2006: 3; Vaz-de-Mello 2008: 12–13; Scholtz *et al.* 2009: 563; Vaz-de-Mello *et al.* 2011: 5, 11, 19, 26, 34, 41, 44; Krajcik 2012: 126; Tarasov and Dimitrov, 2016: 15; Tissiani *et al.* 2017: 412, 414; Cupello and Vaz-de-Mello 2018: 18.

Canthon (*Holocanthon*): Krajcik 2006: 25 (tentatively classified as a subgenus of *Canthon*).

Type species. *Holocanthon mateui* Martínez et Pereira, 1956, by original designation (Martínez and Pereira 1956: 382).

Etymology. Probably from the Greek word *holos*, meaning “whole, entire, all” (Brown 1956) and the name of the genus *Canthon*. It is not clear what Martínez and Pereira (1956) were referring to when they chose that name. Gender masculine.

Diagnosis. *Holocanthon* is easily distinguished from the other deltochiline genera simply by its general appearance, having the body somewhat flatter than most other groups. The definitive character differentiating *Holocanthon* from the other Deltochilini, however, is one of its synapomorphies: the mentum completely divided into two halves, each bearing one of the labial palpi (Fig. 2C, red arrow). We are aware of no other dung beetle groups that possess such a condition in their labium. In a dried, pinned specimen, the separation between the two halves of the mentum is clearly indicated by the presence of a row of long setae on the internal edge of each half (see Vaz-de-Mello *et al.*'s [2011] fig. 98). Another peculiar characteristic of *Holocanthon* is the unique shape of the second labial palpomere, which is oddly transverse (Figs. 3C–D, blue arrows). Martínez and Pereira's (1956: 380–382) original description is so complete that we deem the redescription of the genus not to be necessary; readers are therefore referred to that work for the full characterization of *Holocanthon*.

Taxonomic history and phylogenetic relationships. *Holocanthon* is one of the many genera that is part of what Cupello and Vaz-de-Mello (2018) denominated as being the “*Canthon sensu lato*”; i.e., a group of genera that have their taxonomic history intimately associated with that of *Canthon* either because their species were originally described in that genus or because they were deemed to be closely related to *Canthon* at least in their original publication. Martínez and Pereira (1956) placed *Holocanthon* in Canthonini (= Deltochilini) and compared the genus to *Canthonidia* Paulian, 1939 and *Tetraechma* Blanchard, 1846. For the following 50 years, all authors agreed with their classification and maintained *Holocanthon* in Canthonini (Halffter and Martínez 1966, 1968, 1977; Halffter and Edmonds 1982; Martínez 1989; Hanski and Cambefort 1991; Monteresino *et al.* 1996; Medina *et al.* 2003), and Krajeck (2006) even considered *Holocanthon* as a subgenus under *Canthon* in his catalogue of the World Scarabaeoidea. Vaz-de-Mello (2008), however, proposed the transfer of *Holocanthon* from Canthonini to Coprini in reason of some supposed apomorphic characteristics shared with *Canthidium* Erichson, 1847 and *Parachorius* Harold, 1873 (*viz.*, the presence of 10 elytral striae, hypomera with transverse carina and just feebly excavated anteriorly, and protibiae with anterior edge angled).

Vaz-de-Mello's (2008) proposal would not last long, though, since Tarasov and Dimitrov (2016), based both on their own molecular phylogenetic analysis of the Scarabaeinae and on Tarasov and Génier's (2015) previous morphological study, concluded that *Holocanthon* is indeed part of the same group as *Canthon* and allied genera as firstly proposed by Martínez and Pereira (1956). As a result, Tarasov & Dimitrov (2016) retransferred the genus *Holocanthon* to its original tribe, which had by then been renamed to Deltochilini (an older synonym of Canthonini; see Bouchard *et al.* 2011). We agree with Tarasov and Dimitrov's (2016) decision and consider *Holocanthon* a member of Deltochilini, but its more intimal relationships within the tribe are still unclear.

Identification key to the species of *Holocanthon* Martínez et Pereira, 1956

1. Dorsal colouration coppery (Fig. 1A). Clypeus and genae strongly wrinkled near anterior edge. Antennal lamellae with greyish pubescence. Hypomeron not excavated anteriorly and with transverse carina incomplete, not reaching the external edge of hypomeron. Pronotal disc evenly micropunctate. Mesoventrite long; meso-metaventral carina visible, not hidden by the posterior edge of prothorax. Pygidium not margined basally (Figure 1B). Paramere apex not notched dorsally (Fig. 2A–B). Brazil (from Goiás to Rio Grande do Sul), Paraguay and Argentina (from Salta to Entre Ríos) (Fig. 4) *Holocanthon fusciorubrus* (Blanchard, 1846), new combination
- . Dorsal colouration dark green or bluish (Fig. 1C). Clypeus and genae smooth near anterior edge. Antennal lamellae with brownish to orange pubescence. Hypomeron deeply excavated anteriorly and with complete transverse carina, which reaches the external edge of hypomeron. Pronotal disc with tenuous, sparse micropunctuation. Mesoventrite short; meso-metaventral carina usually hidden beneath the posterior edge of prothorax in dry specimens. Pygidium with complete basal margin (Fig. 1D). Paramere apex deeply and broadly notched dorsally (Fig. 1C). Bolivia (La Paz and Santa Cruz) and Brazil (Rio Grande do Sul) (Fig. 4) . . . *Holocanthon giosilvai* Sawaris, Cupello & Vaz-de-Mello, sp. nov.

Holocanthon fusciorubrus (Blanchard, 1846),
new comb.
(Figs 1A–B, 2A–B, 3–4.)

Canthon fusco-rubrum Blanchard, 1846: 171.

Canthon fusciorubrus: Bruch 1911: 183; Bruch 1915: 543; Martínez 1959: 78.

Choeridium fusco-rubrum: Lacordaire 1856: 93.

Choeridium fuscorubrum: Gillet 1911: 52; Bruch 1915: 543; Balthasar 1939: 66; Blackwelder 1944: 204; Martínez 1959: 78.

Canthidium fuscorubrum: Harold 1869b: 1005; Gillet 1911: 55; Blackwelder 1944: 205; Martínez 1959: 78; Krajcik 2006 22; 2012: 62.

Ateuchus fuscorubrus: Martínez 1959: 78; Krajcik 2006: 14; 2012: 49.

Holocanthon mateui Martínez et Pereira, 1956: 382–387, fig. 21–28; Pereira and Martínez 1956: 108; Martínez 1959: 59; Vulcano and Pereira 1964: 589; Halffter and Martínez 1977: 66; Martínez 1989: 54; Monteresino *et al.* 1996: 105, 115, fig. 2D; Vaz-de-Mello 2000: 193; Medina *et al.* 2003: 65; Vaz-de-Mello 2008: 4, 12, 13; Vaz-de-Mello *et al.* 2011: 44, 59, fig. 97–98; Krajcik 2012: 126. **New subjective synonymy.**

Canthon mateui: Krajcik 2006: 28.

Type material. *Canthon fuscorubrus* Blanchard, 1846: **Lectotype:** Female, here designated (“*C. fuscorubrum* / Blanch / Corrientes / M D’Orbigny”, “76 / 1995”, “MUSEUM PARIS / PROVINCE DE / CORRIENTES / D’ORBIGNY 1834”, “TYPE”, “*Canthon* / *fuscorubrum* / Blanch”, “LECTOTYPE ♀ / *Choeridium* / *fuscorubrum* / Blanchard / des. F.Z. Vaz-de-Mello, 2014”), MNHN. **Paralectotypes:** Unknown. *Holocanthon mateui* Martínez et Pereira, 1956: **Holotype:** Male, unknown to us. **Paratypes:** Six females, three unknown to us. 1. Female (“MISIONES –

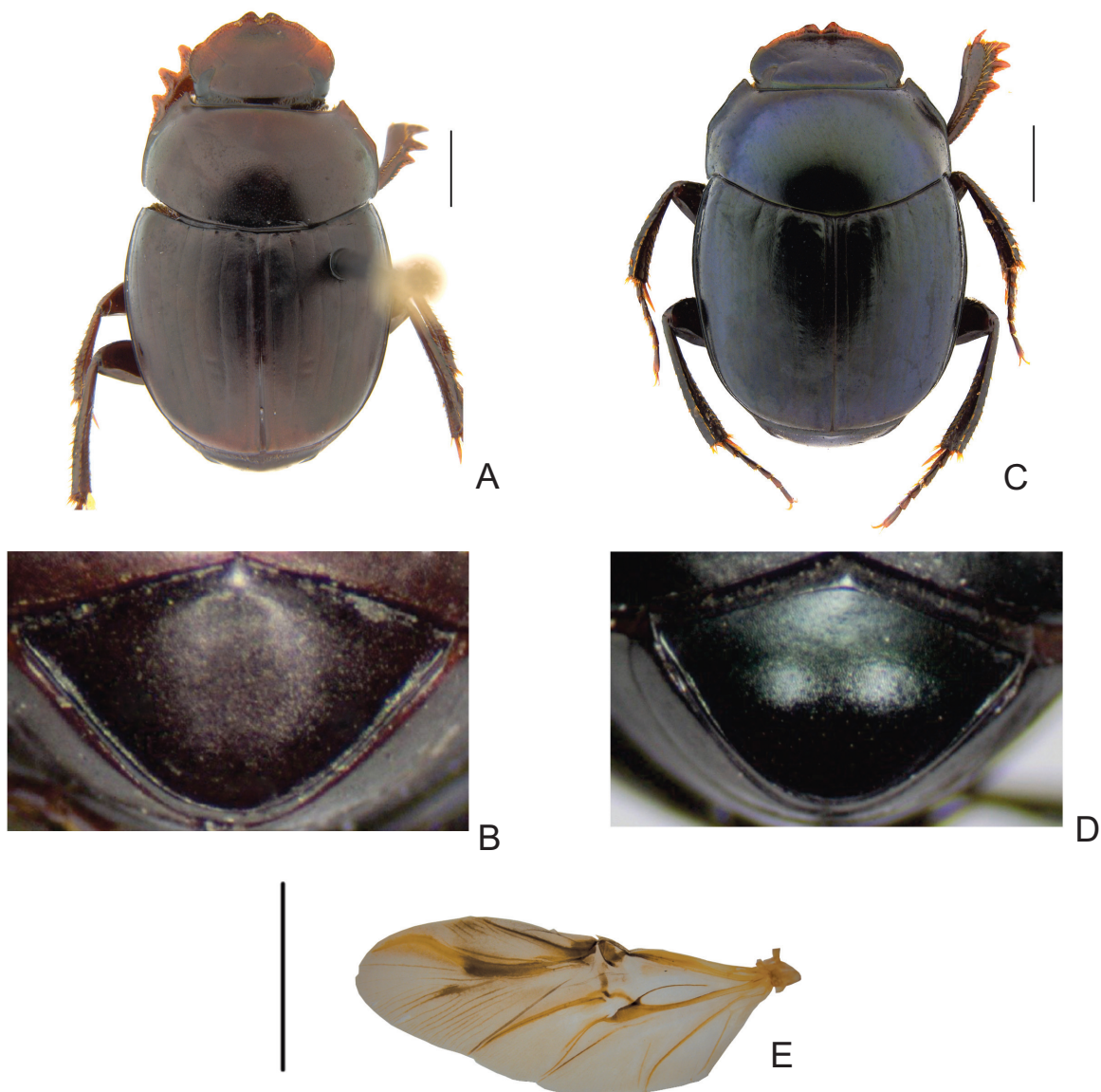


Figure 1. The two species of *Holocanthon*. (A–B) *Holocanthon fuscorubrus* (Blanchard, 1846): (A) Dorsal view. (B) Pygidium. Note that the basal margin is absent. (C–D): *Holocanthon giosilvai* Sawaris, Cupello & Vaz-de-Melo, sp. nov. (C) Dorsal view. (D) Pygidium. Note the presence of a complete basal margin. (E) Hind wing. Scale bars: 1 mm.

ARGENTINA / Dep. Concep. - Sta. Maria / M. J. Viana", "H. & A. HOWDEN / COLLECTION / ex. A. Martínez coll.", "PARATYPE", "PARATIPO", "*Holocanthon* ♀ / *mateui* gen et sp.n. / F.S. Pereira y / A. Martínez-DET-1955", "Canadian Museum of / Musée canadien de la / NATURE / CMNEN 00000160"), CMNC - ex A. Martínez and Henry & Anne Howden collections. 2. Female ("MISIONES - ARGENTINA / Dep. Concep. - Sta. Maria / M. J. Viana", "H. & A. HOWDEN / COLLECTION / ex. A. Martínez coll.", "PARATYPE", "PARATIPO", "*Holocanthon* ♀ / *mateui* / gen et sp.n. / F.S. Pereira y / A. Martínez-DET-1955", "Canadian Museum of / Musée canadien de la / NATURE / CMNEN 00000161"), CMNC - ex A. Martínez and Henry & Anne Howden collections. 3. Female ("ARGENTINA / MISIONES / PINDAPOY / Finca Bovino / Coll. Martínez / Nov.-945", "PARATYPE", "PARATIPO", "*Holocanthon* ♀ / *mateui* / gen et sp.n. / F.S. Pereira

y / A. Martínez-DET-1955", "Canadian Museum of / Musée canadien de la / NATURE / CMNEN 00000162"), CMNC - ex A. Martínez and Henry & Anne Howden collections.

Type locality. *Canthon fusciorubrus*: Argentina: Corrientes (originally cited as "la province de Corrientes"). ***Holocanthon mateui*:** Argentina: Misiones: Leandro N. Alem: Cerro Azul (originally cited as "Argentina, Misiones: Región de Oberá, Cerro Azul"). The paratypes were collected in other localities in Brazil (Santa Catarina: Seara: Nova Teutônia) and Argentina (Corrientes: "Santa Maria", and Misiones: San Ignacio and Pindapoy).

Etymology. *Canthon fusciorubrus*: From the Latin words *fuscus*, meaning dark, and *rubrus*, meaning red, in reference to the coppery dorsal colouration of the species. In Blanchard's (1846) words, "Canthon brun-rouge". ***Holocanthon mateui*:** A patronym after

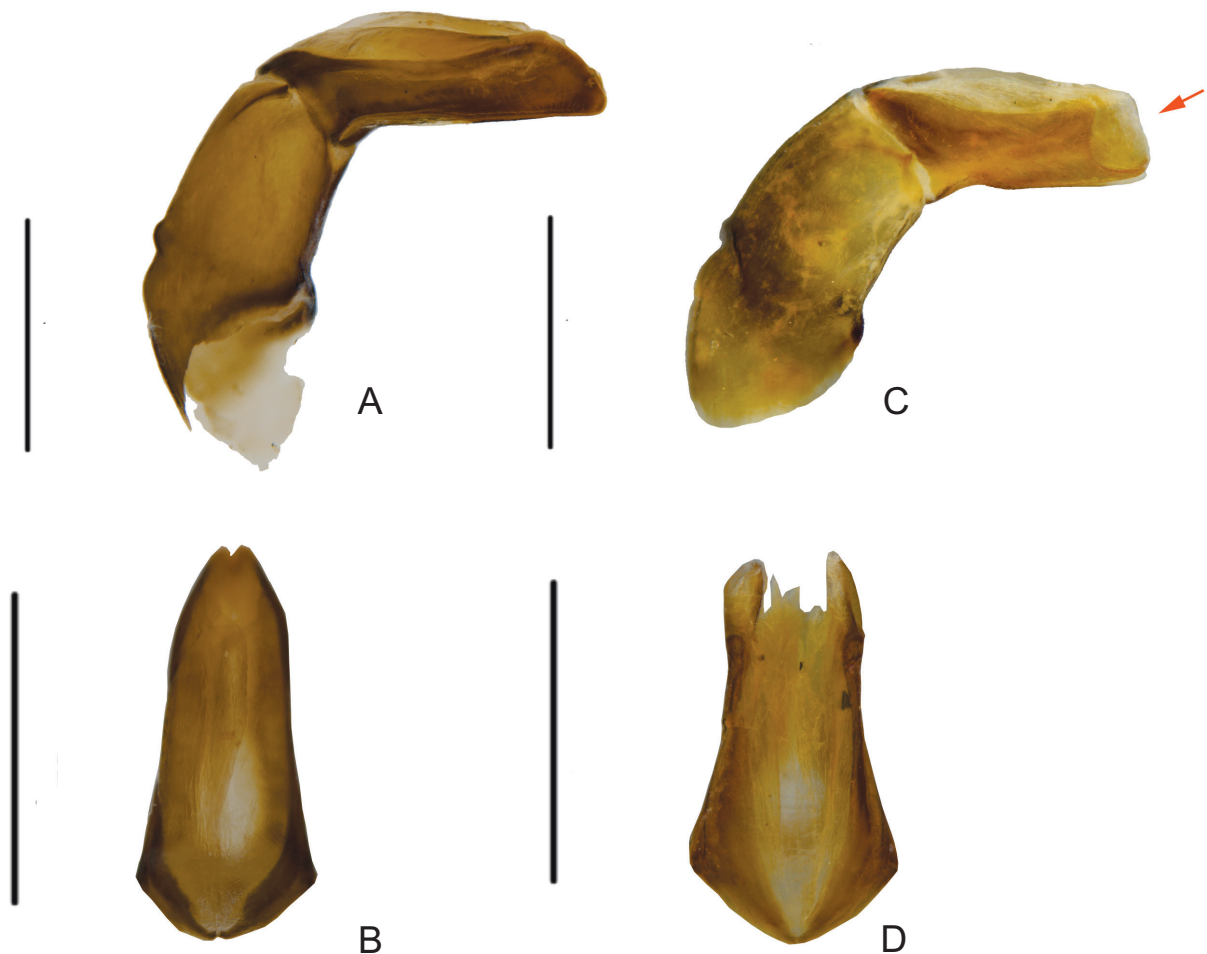


Figure 2. Aedeagus of the two species of *Holocanthon*. (A–B) *H. fusciorubrus*: (A) Lateral view of the genital capsule. (B) Dorsal view of the parameres. (C–D) *H. giosilvai* sp. nov.: (C) Lateral view of the genital capsule. Red arrow indicates the apical notch unique to the parameres of this species. (D) Dorsal view of the parameres. Scale bars: 1 mm.

the Spanish entomologist Joaquim Mateu Sanpere (1921–2015) (Martínez and Pereira 1956: 386). Bellés (2015) presents a short biography of Mateu.

Diagnosis. *Holocanthon fuscobrus* is distinguished from the new species by the characters presented in the key. The sexual dimorphism seen in *H. fuscobrus* is the same as for *H. giosilvai*: males have apically-bifid protibial spur and ventrite VI narrowed medially, while females have spiniform protibial spur and ventrite VI broad medially. For a full description of *H. fuscobrus*, see Martínez and Pereira's (1956: 382–386) detailed characterization of *H. mateui*.

Distribution. Widely distributed across open environments in central South America and some inland areas of the southern Atlantic Forest (Fig. 4). **Ecoregions.** Southern Andean Yungas, Humid Chaco, Espinal, Uruguayan Savannah, Cerrado, Alto Paraná Atlantic Forest. **Collecting sites:** **BOLIVIA:** Santa Cruz. **BRAZIL:** Goiás: Jataí. Mato Grosso do Sul: Bata-guassu. São Paulo: Botucatu. Santa Catarina: Seara (Nova Teutônia). Rio Grande do Sul: Santa Maria, São Jerônimo, Viamão. **PARAGUAY:** Canindeyú: Reserva Natural del Bosque Mbaracayú. Alto Paraná: Presidente Franco (Puerto Bertoni). Caazapá: Estero Cristal. Itapúa: Puerto Cantera. **ARGENTINA:** Salta: *General José de San Martín* (Salvador Mazza ["Pocitos"]). Tucumán. Córdoba: *Río Cuarto* (*Río Cuarto*). Misiones: Apóstoles (Pindapoy), Capital (Posadas), Concepción ("Santa María"), Eldorado, Iguazú (Puerto Iguazú), *Leandro N. Alem* (*Cerro Azul*), San Ignacio. Corrientes: Ituzaingó (Villa Olivari), Mburucuyá. Entre Ríos: Concordia. Salta: General José de San Martín (Tartagal)."

Remarks. As with other dung beetle nominal species established by Blanchard (1846) (see Cupello and Vaz-de-Mello [2018], for instance, for the convoluted taxonomic history of *Canthon xanthopus* Blanchard, 1846), the correct application of the name *Canthon fuscobrus* has puzzled scarab specialists over the last 170 years. Apart from the fairly superficial original description, which reports only general aspects of colouration and punctuation, a further confusing element for many authors who tried to decipher the identity of *C. fuscobrus* was that Blanchard (1846) presented the description of the species amid his new *Choeridium* Lepeletier de Saint-Fargeau et Audinet-Serville, 1828 (= *Ateuchus* Weber, 1801), not among the other *Canthon* Hoffmannsegg, 1817 he described, more precisely between *Choeridium viridicolle* Blanchard, 1846 and *C. viduum* Blanchard, 1846. These two factors – the very schematic original description and its confusing placement in Blanchard's book – would lead many authors to disagree on the generic placement of *C. fuscobrus*.

The first author to mention *C. fuscobrus* after Blanchard (1846) was Lacordaire (1856), who listed it

amongst the species of *Choeridium*, not along with those of *Canthon*. A decade later, Harold (1869b) included *C. fuscobrus* among the *Canthidium* in his catalogue of the World Scarabaeinae; as with many other such generic transfers present in the catalogue, no argument was provided to support that decision. Indeed, it is worth mentioning that Harold had not mentioned *C. fuscobrus* either in his previous revisions of *Canthon* (Harold 1868a), *Choeridium* (Harold 1868b) and *Canthidium* Erichson, 1847 (Harold 1867a, b) or in his study of the Blanchard type material housed in the MNHN (Harold 1869a). The species would be cited again only four decades later, when it was included in two 1911 catalogues: Gillet (1911), in his updated version of the Harold catalogue, listed *C. fuscobrus* in combination with both *Canthidium* (p. 55) and *Choeridium* (p. 52), but not with *Canthon*, while Bruch (1911), in a catalogue of the Argentinian scarabaeoid, did exactly the opposite, citing the species only in its original combination with *Canthon*. Four years later, however, in a corrigenda to his catalogue, Bruch (1915) corrected himself and deemed *Choeridium fuscobrum* the proper combination instead. Blackwelder (1944), then, in his list of the Neotropical Coleoptera, repeated Gillet (1911) and cited *C. fuscobrus* under *Canthidium* (p. 205) and *Choeridium* (p. 204) only. Finally, the last mention to *C. fuscobrus* found in the 20th-century literature is that of Martínez (1959), who in a new catalogue of the Argentinian dung beetles cited the species in combination with *Ateuchus* (which had been revalidated by Chapin [1946] after being put aside in favour of its junior synonym *Choeridium* for more than a century). Even though Martínez (1959) himself recognized that generic placement as just tentative, it seems that ever since the publication of his work the placement of *C. fuscobrus* in *Ateuchus* has been accepted, as the species was cited in the lists of neither the *Canthon* (Vulcano and Pereira 1964, Halffter and Martínez 1977) nor the *Canthidium* (Martínez and Halffter 1986, Cupello 2018) species published thereafter, and it is in combination with that nominal genus that the species appears in the Catalogue of Life (Schoolmeesters 2018). The only 21st-century exceptions were the Krajcik (2006, 2012) catalogues of the World Scarabaeoidea, which followed Gillet (1911) and Blackwelder (1944) and listed *C. fuscobrus* as a species of both *Canthidium* and *Ateuchus*.

Therefore, it is clear that it would be necessary to re-examine the type material of *C. fuscobrus* in order to figure out its real identity. During a year-long stay at the MNHN between 2013 and 2014 (see Vaz-de-Mello and Cupello [2018] for more details), the third author located a single specimen (Fig. 3A–B) that we judge to be one of the specimens studied by Blanchard for his description of *C. fuscobrus*. This specimen,

therefore, is here considered to be one of the syntypes of *C. fuscoviridis* (following the International Code of Zoological Nomenclature's (ICZN 1999) Recommendation 73F, we assume Blanchard's description was based on a series of syntypes, not on a single specimen). That specimen, a female, bears a label indicating it was collected by the French naturalist and explorer Alcides d'Orbigny (1802–1807) in Corrientes, Argentina, and has the year of 1834 written on it. Indeed, Blanchard (1846) remarked his specimens were brought by

d'Orbigny from Corrientes ("*M. d'Orbigny a trouvé cette espèce dans la province de Corrientes*"), and d'Orbigny indeed collected in that Argentinian province, although the year stated on the label certainly does not refer to the date when the specimen was caught, since d'Orbigny visited Corrientes at different moments between March 1827 and April 1828, not in 1834 (Papavero 1971). In fact, 1834 was the year when d'Orbigny returned to France after spending eight years in South America (Papavero 1971) and the insect

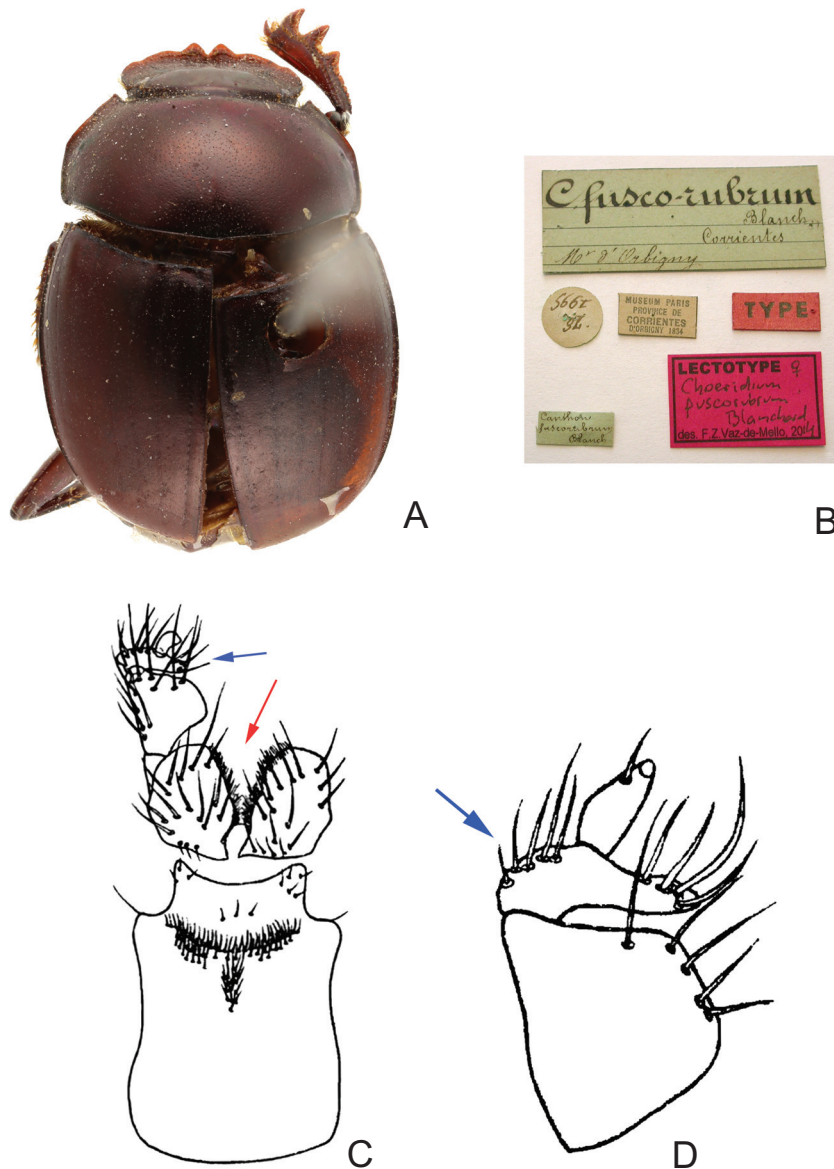


Figure 3. *Holocanthon fuscoviridis*. (A–B) Lectotype of *Canthon fuscoviridis*: (A) Dorsal view. (B) Its labels. (C–D) Two of the most unique characteristics of *Holocanthon* among the dung beetles and synapomorphies of the genus: (C) Ventral view (aboral surface) of the labium. Note how the mentum is completely divided into two halves (red arrows points to the separation between them). It is possible to see also that the second labial palpomere is highly transversal (blue arrow). (D) Labial palpus. Observe the transversal shape of the second palpomere in more detail (red arrow). Figures C and D modified from Pereira and Martínez (1956).

material he collected was deposited in the MNHN (Horn and Kahle 1936). Thus, it is likely that the 1834 information on the syntype's label refers to the date when that specimen was incorporated into the MNHN. Besides that, we can infer that that specimen is indeed one of the syntypes of *C. fuscrobustus* because the type specimens of Blanchard are known to be housed in the MNHN (Horn and Kahle 1935), as well as most of the d'Orbigny material (Horn and Kahle 1936; but see Cupello and Vaz-de-Mello [2016] for a putative d'Orbigny specimen in the BMNH). In conclusion, therefore, we judge we have good evidence indicating that that female is one of the syntypes of *C. fuscrobustus*, and herein we designate it as the name's lectotype.

Having found part of the type material of *C. fuscrobustus*, we could finally know its actual identity: it does not belong to any of the genera which it has been placed in combination with over the years (namely, *Canthon*, *Canthidium* and *Choeridium/Ateuchus*), but rather to *Holocanthon*, and what is more, it represents the same species as *Holocanthon mateui* Martínez et Pereira, 1956. Both nominal species, therefore, are subjective synonyms, with Blanchard's name being valid. Hence, *Holocanthon mateui* is a **new junior subjective synonym** of *Holocanthon fuscrobustus*, **new combination**.

Unfortunately, we were not able to trace the whereabouts of the holotype of *H. mateui*. Martínez and Pereira (1956) stated that the holotype male and three paratype females (including the allotype) were deposited in Martínez's collection, whereas two other female paratypes would be housed in the MZSP and a last female paratype had been sent to the personal collection of the Argentinian entomologist Manuel J. Viana (1916–1997). As explained in Cupello and Vaz-de-Mello (2018), after his death, Martínez's collection was divided into two parts, one containing the holotypes and allotypes of the nominal species he established, the other composed of his paratypes and the rest of the ordinary material of his collection; the first part was, then, incorporated into the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, Argentina, whereas the second part was bought by Henry and Anne Howden and later deposited in the Canadian Museum of Nature (CMNC), Ottawa, Canada. The second author visited the MACN in October 2014, but he found neither the holotype nor the allotype of *H. mateui* housed there (and those were not the only type specimens supposed to be there that were not found by MC; see Cupello and Vaz-de-Mello [2018] for another example). Since they are neither in the CMNC (MC, personal observation, 2019) nor in the MZSP (MC, personal observation, 2018), we deem the holotype and the allotype lost. As for the other paratypes, we found three of them in the CMNC, where it was supposed to be only two (i.e., those that

were said to have been deposited in the Martínez collection). The paratypes allegedly deposited in the MZSP were not found by MC in that museum, while the female deposited in the Viana collection is now possibly housed in the Museo de La Plata (MLPA), La Plata, Argentina, where the Viana collection is currently preserved (Lanteri and Hernández 2017), or is the "extra" paratype found in the CMNC. Unfortunately, we did not have the opportunity to visit the MLPA during the course of this project to check that out.

But despite not having examined the holotype of *H. mateui*, we are confident the synonymy between that name and *C. fuscrobustus* is correct because the three paratypes studied by us – as well as several other specimens collected at the same localities (viz., those from Nova Teutônia and San Ignacio) – do belong to the same species as the lectotype of *C. fuscrobustus*. Furthermore, Martínez and Pereira's (1956) description, contrary to Blanchard's (1846), is extremely detailed and leaves no doubt about the identity of their species." Of particular importance, their description of the coppery colouration along with that of the incomplete hypomeral carina show that *H. mateui* does not refer to *H. giosilvai* sp. nov., the second species of *Holocanthon*. Finally, the type locality of *H. mateui* (Cerro Azul, Misiones) and that of *C. fuscrobustus* (the province of Corrientes) are close to one another, both lying in the region known as the Argentinian Mesopotamia, in the interfluvium of the Paraná and the Uruguay Rivers. All these data together give us confidence that our proposed synonymy is correct.

Ecology. Almost nothing is known on the biology of *H. fuscrobustus*. With a single exception, the specimens examined here were all collected in the months from September to March, indicating that adults of the species are active only during the rainy season (i.e., during spring and summer); the only exception was an Argentinian female caught in July 1982. The specimens collected by D. Link in Rio Grande do Sul were caught in a light trap, which indicates the species probably has a nocturnal flight activity (as inferred by Monteresino *et al.* [1996]). No food or reproductive habits have been recorded, but we assume *H. fuscrobustus* should be coprophagous and a roller, belonging to Halffter and Edmonds' (1982) Pattern IV of their classification of the dung beetle nesting behaviour, like most of the other Delftochilini. Finally, it should be noted that *H. fuscrobustus* inhabits a wide variety of open habitats in southern South America, including some dry areas such as the Cerrado, the Pampas (Uruguayan Savannah ecoregion) and the Argentinian Espinal, as well as some wetter areas like the Humid Chaco and the more forested environments of the Southern Andean Yungas and the Alto Paraná Atlantic Forest. But the fact remains that we know very little about the distribution of *H. fuscrobustus* in those regions, neither do

we know if, in the Cerrado, for instance, they live in more humid gallery forests or in the dry open grasslands. Only more fieldwork will allow us to answer these questions.

Material examined. 33 males and 39 females.

ARGENTINA: CORRIENTES: Ituzaingó, III.1976, no collector – 4 males (CMNC – ex A. Martínez and Henry & Anne Howden collections); Ituzaingó, Villa Olivari, VII.1982, no collector – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections); Ituzaingó, Villa Olivari, IX.1982, no collector – 1 male and 1 female (CMNC – ex A. Martínez, Henry & Anne Howden and François Génier collections); Ituzaingó, Upper Paraná River, XI.1975, no collector – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections); Mburucuyá, 27°58'S, 57°59'W, 04.III.2004, G. Rubio leg. – 1 male (DZUP, ex TAMU) and 1 male (TAMU). ENTRE RÍOS: no specific locality, XII.1989, Liebig leg. – 1 female (CEMT); Concordia, no date, Viana leg. – 3 males and 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections); Concordia, “Salto Grande”, I.1975, no collector – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections); Concordia, “Salto Grande”, I.1981, no collector – 1 male (CMNC – ex A. Martínez and Henry & Anne Howden collections). MISIONES: Capital, Posadas, “Maembemirí”, X.1985, no collector – 1 male (CMNC – ex A. Martínez and Henry and Anne Howden collections); Eldorado, XI.1969, no collector – 1 female (TAMU); Iguazú, XII.1957, no collector – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections); Iguazú, Puerto Iguazú, XII.1957, no collector – 1 male (CMNC – ex A. Martínez and Henry & Anne Howden collections); San Ignacio, no date, Bade leg. – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections); San Ignacio, no date, B. Bade and W. Bade leg. – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections); San Ignacio, “Villa Lutecia”, 1910, E.R. Wagner leg. – 1 female (CEMT). **SALTA:** General José de San Martín, Tartagal, XI.1957, no collector – 1 male (CMNC – ex A. Martínez and Henry & Anne Howden collections). **BOLIVIA:** SANTA CRUZ: no specific locality (later label says Santa Cruz de la Sierra, but original label does inform that), 500 m, 10.XI.1955, Zischka leg. – 1 male (CMNC – ex A. Martínez and Henry & Anne Howden collections). **BRAZIL:** GOIÁS: Jataí, Fazenda Nova Orlandia, I.1964, Martins, Morgante and Silva leg. – 1 male [dissected] (MZSP) and 1 male (CEAH). MATO GROSSO DO SUL: Bataguassu, “Rio Caraguatá”, 400 m, 21°48'S, 52°27'W, III.1953, Fritz Plaumann leg. – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections). RIO GRANDE DO SUL: Santa Maria, 14.XII.1971 [light trap], D. Link leg. – 1 female (MCNZ); Santa Maria, 12.I.1972 [light trap], D. Link leg. – 1 female (MCNZ); Santa Maria, 05.II.1972 [light

trap], D. Link leg. – 1 female (CEMT); Santa Maria, 04.III.1972, D. Link leg. – 1 female (MCNZ); Santa Maria, 29.III.1972 [light trap], D. Link leg. – 1 male (MCNZ); São Jerônimo, 17.X.1982, H.A. Gastal leg. – 1 female (MCNZ); São Jerônimo, 06.XI.1982, C.J. Becker leg. – 1 female (MCNZ); Viamão, Águas Belas, 11–13.I.1980, H.A. Gastal leg. – 1 male (MCNZ). **SANTA CATARINA:** Seara, Nova Teutônia, II.1972, no collector – 1 female (CMNC); Seara, Nova Teutônia, XII.1972, F. Plaumann leg. – 1 female (CMNC); Seara, Nova Teutônia, III.1973, F. Plaumann leg. – 1 male and 2 females (CMNC); Seara, Nova Teutônia, XII.1973, F. Plaumann leg. – 1 female (CMNC); Seara, Nova Teutônia, XII.1974, F. Plaumann leg. – 2 males and 1 female (CMNC); Seara, Nova Teutônia, 14.I.1975, F. Plaumann leg. – 2 females (CMNC); Seara, Nova Teutônia, III.1977, no collector – 1 male and 1 female (CMNC); Seara, Nova Teutônia, IX.1977, no collector – 1 male (CMNC); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, XI.196(?), Fritz Plaumann leg. – 1 female (DZUP); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, III.1964, Fritz Plaumann leg. – 1 male (MZSP); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, IX.1964, Fritz Plaumann leg. – 1 male (CEAH); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, III.1972, Fritz Plaumann leg. – 1 female (CEAH); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, XII.1972, Fritz Plaumann leg. – 1 male and 1 female (CEAH); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, I.1975, Fritz Plaumann leg. – 1 female (DZUP); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, X.1975, Fritz Plaumann leg. – 1 female (TAMU, ex DZUP); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, X.1976, Fritz Plaumann leg. – 1 female (DZUP); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, XI.1976, Fritz Plaumann leg. – 1 male (DZUP); Seara, Nova Teutônia, 27°11'S, 52°23'W, 300–500 m, III.1981, Fritz Plaumann leg. – 1 male (DZUP). **SÃO PAULO:** Botucatu, X.1963, W. Zikán leg. – 1 male [dissected] (MZSP). **PARAGUAY:** ALTO PARANÁ: Presidente Franco, Puerto Bertoni, no date or collector – 1 female (MZSP). CAAZAPÁ: Estero Cristal, XI.1998, J. Jensen leg. – 1 female (CEMT); Estero Cristal (“Est. Cristal”), XI.1999, G. Arriagada leg. – 1 male and 1 female (DZSP, ex CEMT); Estero Cristal, 20.IX.1999, no collector – 2 males (CEMT). **CANYNDEYÚ:** Reserva Natural del Bosque Mbaracayú, Jejuími River, 13.I.1997, Carlos Aguilar Jr. leg. – 1 female (CMNC – ex François Génier collection). **ITAPÚA:** Puerto Cantera (“Cantera”), XI.1955, Walz leg. – 1 female (CMNC – ex A. Martínez and Henry & Anne Howden collections). **Dubious data.** “Serro Azul / 12.42” [the Cerro Azul municipality in the Argentinian province of Misiones, the homonymous municipality in the Brazilian state of Paraná, or the municipality of Cerro Largo, in the Brazilian state of Rio Grande do Sul, whose former name was also Cerro Azul?] – 1 female (MZSP).

Holocanthon giosilvai Sawaris, Cupello and Vaz-de-Mello, sp. nov.
(Figs 1C–E, 2C–D, 4)

Type material. **Holotype:** Male, here designated (“Coroico / Bolivia”, “*HOLOCANTHON / MATEUI / MARTÍNEZ Y PEREIRA / G.H. y A.M. DET. 76*”, “MUSÉUM PARIS / 1936 / COLL. A. BOUCOMONT”), CEMT. **Paratypes:** 2 males and 6 females. **ARGENTINA:** **CORRIENTES:** Ituzaingó, Villa Olivari, IX.1982, no collector – 1 male (CMNC – ex A. Martínez and Henry & Anne Howden collections). **BOLIVIA:** **SANTA CRUZ:** Cordillera, Cabezas, Cerro Parabanó, no date or collector – 2 females (CEMT). **BRAZIL:** **RIO GRANDE DO SUL:** Ijuí, 19.IX.2012, J. Lima. leg. – 1 male and 4 females (CEMT).

Type locality. Bolivia: La Paz: Nor Yungas: Coroico.

Etymology. The species is named after Pedro Gió-

vani da Silva, a Brazilian biologist specialist in the ecology of Scarabaeinae, particularly of the dung beetle communities of southern Brazil, of which *H. giosilvai* is part. The new specific name, thus, is a noun in the genitive case.

Diagnosis. *Holocanthon giosilvai* differs from *H. fuscrobustus* by the characters presented in the key. See the diagnosis of *H. fuscrobustus* for other comments.

Description. Measurements: Body length: ranges from 5.0 to 5.4 mm. Width of pronotum: ranges from 2.5 to 3.3 mm. **Colouration:** Dorsal surface dark green, shiny. **Head:** Triangular and semicircular at base. Clypeus with two rounded teeth apically with weak emargination separating them (Fig. 1C). Clypeo-genal junction with shallow incision; clypeo-genal suture well-marked. Anterior margin of clypeus almost smooth, with few rugosities near genae. Antennal apical lamellae with brownish to orange pubescence. **Pronotum:**

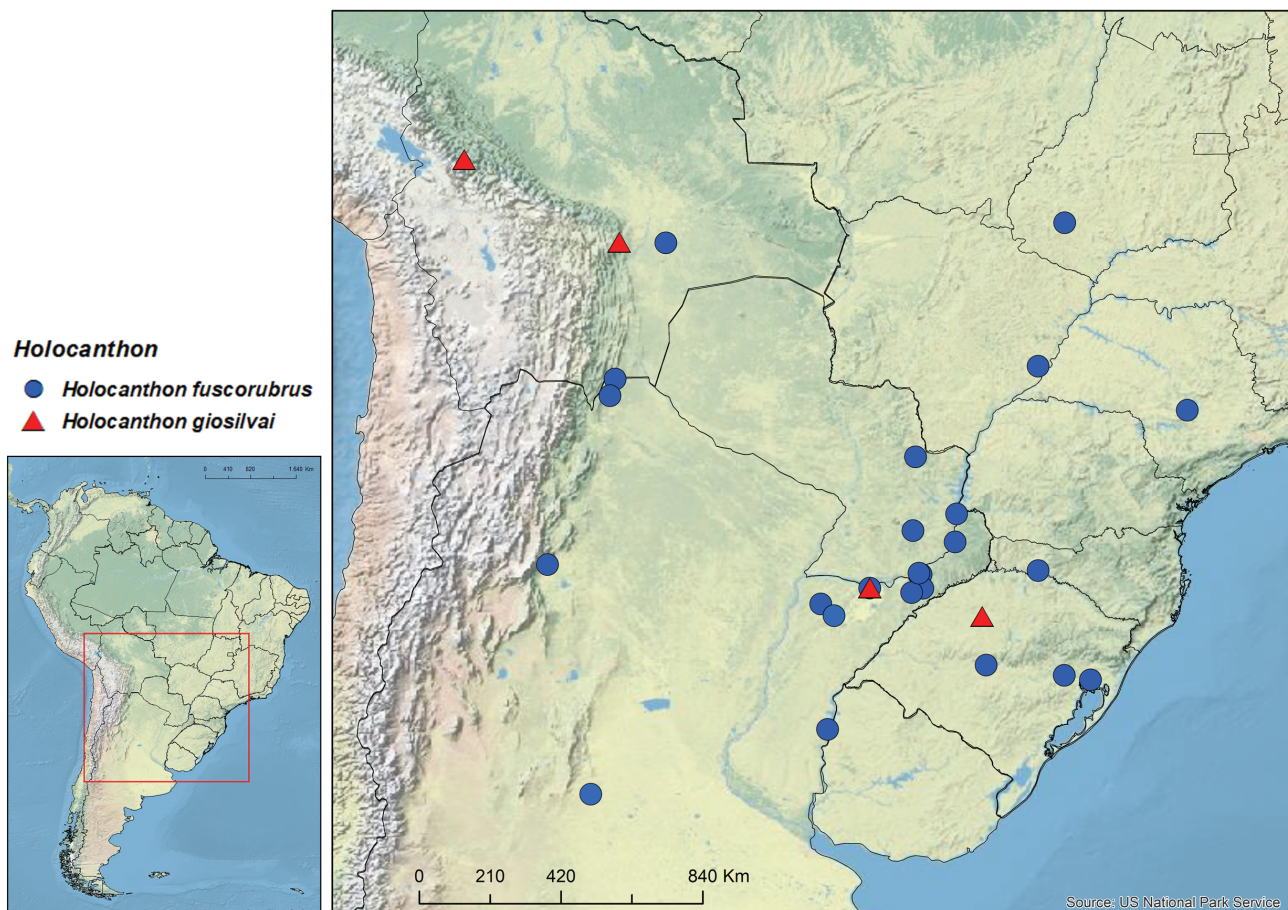


Figure 4. Distribution of *Holocanthon*. As discussed in the text, we assume that *H. fuscrobustus* and *H. giosilvai* have their distributions largely overlapped, although they have never been collected together. They seem, therefore, not to be syntopic. Across their geographical range, both species occupy a wide variety of open environments, such as the Humid and Dry Chaco, Brazilian Cerrado and the Argentinian Espinal, as well as some more forested habitats in the Southern Atlantic Forest and in the Bolivian and Argentinian Yungas.

Wider than long and narrower than elytra. Disc with tenuous, sparse micropunctuation. Anterior angles acute. Lateral margin angulate. **Hypomera:** Anterior region excavated; excavation with sparse and short setae and delimited posteriorly by a complete hypomeral carina, which reaches the external edge of hypomeron. **Prosternum and mesoventrite:** Glabrous, tegument similar to that of pronotum and metaventrite; mesoventrite short; meso-metaventral carina usually hidden beneath the posterior edge of prothorax in dry specimens. **Metaventrite:** Glabrous, covered by tenuous and sparse micropunctuation similar to that of the pronotum, anterior lobe expanded (wider than long). **Elytra:** Shiny. 10 striae slightly impressed. Scutellar impression tenuous, but present. **Legs:** Protibiae with three large lateral teeth. Mesofemora with anterior region strongly microsculptured. **Abdomen:** All ventrites with tegument covered by tenuous and sparse micropunctuation similar to that of metaventrite and pronotum. Pygidium wider than long, basal margin complete, micropunctuation as sparse and tenuous as that of the rest of the body. **Aedeagus:** Phallobase as long as parameres. Parameres symmetrical, apex deeply and broadly notched dorsally (Fig. 1C–D). **Secondary sexual characters:** **Males:** Protibial spur elongate and apically bifurcated. Ventrite VI strongly narrowed at middle by emargination on its posterior edge. **Females:** Protibial spur spiniform, with no apical bifurcation. Ventrite VI broad at middle, without any emargination.

Distribution. Known from only three distant localities in central South America (Fig. 4). **Ecoregions:** Bolivian Yungas, Dry Chaco, Humid Chaco, Alto Paraná Atlantic Forest. **Collecting sites:** **BOLIVIA:** **La Paz:** Nor Yungas (Coroico). **Santa Cruz:** Cordillera (Cabezas: Cerro Parabanó). **BRAZIL:** **Rio Grande do Sul:** Ijuí. **ARGENTINA:** **CORRIENTES:** Ituzaingó (Villa Olivari)."

Ecology. As for *H. fuscrobustus*, we are almost completely ignorant as to the biology of *H. giosilvai*. The nine specimens known to us come from four localities separated one another by about 340 km (the distance between Villa Olivari, Argentina, and Ijuí, Brazil) up to more than 1,300 km (the approximate distance between the southernmost Bolivian locality and Villa Olivari). Those four localities lie in four quite distinct environments: the Bolivian Yungas (Coroico), Dry Chaco (Cerro Parabanó), Humid Chaco (Villa Olivari) and the Atlantic Forest (Ijuí) (although the specimens of the latter biome may have been collected in artificial grasslands such as pastures). Therefore, like its sole congeneric, *H. giosilvai* seems to be very plastic in relation to the kind of environment in each it lives, although nothing is known about the specific habitats the species occupies in those biomes. The only specimens with a recorded month of collection are those from Ijuí, which were caught in November, and the

male from Villa Olivari, which was found in September, indicating that adults of *H. giosilvai*, like those of *H. fuscrobustus*, may be active only during the rainiest and hottest period of the year.

CONCLUDING REMARKS

With the discovery of the new species described herein, *Holocanthon* is no longer monospecific as considered to be for the last 63 years since its original description by Martínez and Pereira (1956). It is interesting to note that other South American dung beetle genera that had been considered to include a single species for a long time during their taxonomic history had a second or even more species described for them over the past few years, namely *Zonocopriss* Arrow, 1932 (Vaz-de-Mello 2007), *Chalcocopriss* Burmeister, 1846 (Rossini and Vaz-de-Mello 2015), *Paracryptocanthon* Howden et Cook, 2002 (Pacheco and Vaz-de-Mello 2017) and *Hansreia* Halffter et Martínez, 1977 (Valois *et al.* 2015), the latter now including six species. These remarkable findings show vividly how much we still have to learn about the diversity of the Scarabaeinae in the Neotropics.

As for the two species of *Holocanthon*, several gaps exist in our knowledge about their distribution, habitat preferences and behaviour. *Holocanthon giosilvai*, in particular, is known from just four localities distant from one another by at least 340 km; yet, no noticeable morphological variation was observed among the populations studied (although it is fair to say that we examined a rather small number of specimens per population, which may have hidden some subtle differences). In the same way, no geographical variation was observed for *H. fuscrobustus*, including in the morphology of the internal sac, despite the wide distribution range of the species. It is worth noting that despite their clear overlapping distribution (Fig. 4), *H. fuscrobustus* and *H. giosilvai* may not be syntopic, since they have apparently never been collected together (the specimens from the only locality where both species have been recorded from, the Argentinian municipality of Villa Olivari, do not have precise locality and date information and it is possible that they were not collected at the same exact place and date). These supposed differences in habitat preferences may be at least one of the isolating mechanisms preventing a widespread interbreeding between *H. fuscrobustus* and *H. giosilvai* and the merger of the two taxa. This is so because these names clearly represent two independent species and no potential hybrids have been found even though the geographical barrier that once divided their ancestral species and isolated their populations clearly already collapsed. More fieldwork will be necessary to solve these questions.

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