



## Systematics, Morphology and Biogeography

Redefinition and taxonomic revision of the “buqueti” species-group,  
*Dichotomius* Hope, 1838 (Coleoptera: Scarabaeidae: Scarabaeinae)Jorge Armando Arias-Buriticá <sup>a,\*</sup>, Fernando Z. Vaz-de-Mello <sup>b</sup><sup>a</sup> Universidad Pedagógica y Tecnológica de Colombia, Grupo de investigación Sistemática Biológica, Escuela de Ciencias Biológicas, Tunja, Colombia<sup>b</sup> Universidade Federal de Mato Grosso, Instituto de Biociências, Departamento de Biología e Zoología, Cuiabá, MT, Brazil

## ARTICLE INFO

## Article history:

Received 17 August 2018

Accepted 12 November 2018

Available online 23 November 2018

Associate Editor: Marcela Monné

## Keywords:

Taxonomy

Dung beetles

*Dichotomius sensu stricto*

Neotropical

Male genital organ

## ABSTRACT

On the basis of external morphology and genitalia of males, as well as a comparison between different species belonging to other groups of *Dichotomius*, we propose a redefinition of the “buqueti” species group separated by Luederwaldt (1929). Six species are excluded from this group and transferred to other groups: *D. ribeiroi* (Pereira, 1954) in the “cotopaxi” group; *D. camposeabrai* Martínez, 1974 in the “bitiensis” group; *D. reclinatus* (Felsche, 1901), *D. horridus* (Felsche, 1911), *D. quadrinodosus* (Felsche, 1901) and *D. nimuendaju* (Luederwaldt, 1925) (revalidated species) forming the newly defined “reclinatus” group. The other species kept in the “buqueti” group include *D. buqueti* (Lucas, 1857) from Brazil (lectotype here designated), *D. haroldi* (Waterhouse, 1891) from Argentina and *D. nutans* (Harold, 1867) from Brazil, Argentina and Uruguay. The taxonomic revision of the “buqueti” group are presented, including a history of the included species, a determination key, illustrations of the structures of external morphology, male genitalia and sclerites of the internal sac, and a distribution map.

© 2018 Sociedade Brasileira de Entomologia. Published by Elsevier Editora Ltda. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

## Introduction

*Dichotomius* Hope, 1838 is one of the most diverse and abundant genera of dung beetles (Scarabaeidae: Scarabaeinae) in neotropical ecosystems, with about 154 species, in which a taxonomic revision is urgently needed (Génier, 2000; Vaz-de-Mello et al., 2001; Kohlmann, 2003). Although, a few authors have worked in groups of species (Arias-Buriticá and Vaz-de-Mello, 2012, 2013; Maldaner et al., 2015; Nunes et al., 2016; Valois et al., 2017), the genus has not undergone a recent general taxonomic revision. The last researcher to study the group as a whole was Luederwaldt (1929). Based on external morphological characters, this author proposed the distinction of the species into sections (here presented as species-groups) to study the genus. Within the nominotypical subgenus, this author proposed the “buqueti” species-group for species with the following features: “triangular head, at least in the male, which is sometimes extremely long as in the *buqueti* species. Clypeal margin slightly emarginate, with transverse wrinkles. Head armor, in males, between the eyes or in front of them, with a medium horn, fully compressed, generally lamelliform and with a short spine

or tooth on each side of the base; in the female, in the posterior clypeal margin, transversely with three or four projections. Male thorax strong or very strongly excavated, in the female, the thorax excavation is smooth and without the presence of prominences. Usually black in color, rarely brown. Striae of elytra not evident with fine points. Spur of metatibiae usually emarginate. Medium to large body size”. *Sensu Luederwaldt (1929)* eight species are included in the group: *Dichotomius buqueti* (Lucas, 1857) (Minas Gerais, Brazil); *Dichotomius haroldi* (Waterhouse, 1891) (Chaco de Santiago, Argentina); *Dichotomius horridus* (Felsche, 1911) (Bucay, Ecuador); *Dichotomius nimuendaju* (Luederwaldt, 1925) (Amazonas, Brazil); *Dichotomius quadrinodosus* (Felsche, 1901) (southern Brazil in the states of Minas Gerais, Santa Catarina, Espírito Santo and Paraná); *Dichotomius verticalis* (Felsche, 1901) (Argentina); *Dichotomius reclinatus* (Felsche, 1901) (Colombia) and *Dichotomius gibbosus* Luederwaldt (1928) (Argentina).

Martínez (1951) proposes the synonymy of *D. gibbosus* with *Dichotomius triangulariceps* (Blanchard, 1846) and Pereira (1953) that of *D. haroldi* with *D. verticalis*. Pereira (1954) describes *Dichotomius ribeiroi* from the state of Amazonas in Brazil; raising the known species in the group to nine (including *D. haroldi* and *D. verticalis* as distinct species); however, he proposed that it has been little studied and that individuals are rare in collections: the females of at least five species are unknown. Finally, he elaborates

\* Corresponding author.  
E-mail: [joariasbu@gmail.com](mailto:joariasbu@gmail.com) (J.A. Arias-Buriticá).

a key for the species of the section based on body sculpture characteristics and for the first time the male genital organs of some of the species are illustrated.

**Martínez (1974)** describes *Dichotomius camposeabrai* from an individual collected in the state of Espírito Santo (Brazil) and proposes the exclusion of *D. triangulariceps* from the “buqueti” group and the incorporation of *Dichotomius nutans* (Harold, 1867), a species that had been located by Luederwaldt (1929) in a separate group (the “nutans” group). Assuming the synonymy of *D. haroldi* and *D. verticalis*, although with a different configuration, the group remains with nine species.

**Vulcano et al. (1976)** include within the section *Dichotomius calcaratus*, species described by Arrow (1913) from individuals found in the state of Mato Grosso (Brazil), which were included by Luederwaldt (1929) within the “assifer” group. Vulcano et al. (1976) comment that this situation occurs because Luederwaldt assumed as males the type specimens in the description of Arrow. Subsequently, through collections made in the type locality of the Arrow individuals, males and females of this species were found, the males being those described as *D. nimuendaju* by Luederwaldt (1925) and they propose *D. nimuendaju* as a synonym of *D. calcaratus*.

Consequently, the “buqueti” species group includes nine species: *D. buqueti*, *D. nutans*, *D. haroldi*, *D. quadrinodosus*, *D. reclinatus*, *D. horridus*, *D. calcaratus*, *D. ribeiroi* and *D. camposeabrai* (Pereira, 1954; Martínez, 1974; Vulcano et al., 1976).

Nevertheless, group inconsistencies between the external morphology of some of the species and the characteristics proposed by Luederwaldt (1929) were found. Therefore, based on other external morphological characters, the male genital organ and the comparison of the species with other species of the genus, this paper proposes the redefinition and taxonomic revision of the “buqueti” species-group.

## Materials and methods

This study was based on the examination of 383 specimens of nine species in the “buqueti” species-group and a pair from 37 species in other species-groups and *Dichotomius* subgenera. These specimens were deposited in the following entomological collections (name of each collection curator in parentheses):

**BMNH:** The Natural History Museum, London, England (Maxwell Barclay and Malcolm Kerley)

**CEMT:** Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Brazil (Fernando Vaz-de-Mello)

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

**IBSP:** Coleção Entomológica “Adolph Hempel”, Instituto Biológico, São Paulo, Brazil (Sergio Ide)

**MAPA:** Museu Anchieta, Porto Alegre, Brazil (Fernando R. Meyer)

**MNHN:** Muséum National d’Histoire Naturelle, Paris, France (Olivier Montreuil and Antoine Mantilleri)

**MZSP:** Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Sonia Casari and Carlos Campaner)

**SMTD:** Staatliches Museum für Tierkunde, Dresden, Germany (Olaf Jäger)

Species identification was performed using the original descriptions (Arrow, 1913; Felsche, 1901, 1911; Harold, 1867; Lucas, 1857; Luederwaldt, 1925; Waterhouse, 1891; Pereira, 1954) and specific keys (Luederwaldt, 1929; Pereira, 1954). For the preparation of specimens, the Medina et al. (2003) methodology was followed. Male genitalia (aedeagus) dissection and preparation was carried out under the Zunino methodology (1978).

Illustrations of the male *habitus* and differences within the pronotum and head of females, as well as illustrations of aedeagus in lateral, dorsal and ventral views and internal sac sclerites were produced. Terminology of the external morphology was assigned according to Vaz-de-Mello et al. (2011). For male genitalia, Zunino (1978) and López-Guerrero (2005) nomenclature was followed.

For each species, the taxonomic treatment developed shows the following information: Location of the type specimens, nomenclatural history, material examined, redescription of the male and female, comments and geographical distribution. For the latter, distribution maps were made with geographical data obtained from local labels of the specimens, using the software DIVA GIS Ver 7.5 (Hijmans et al., 2012).

## Results and discussion

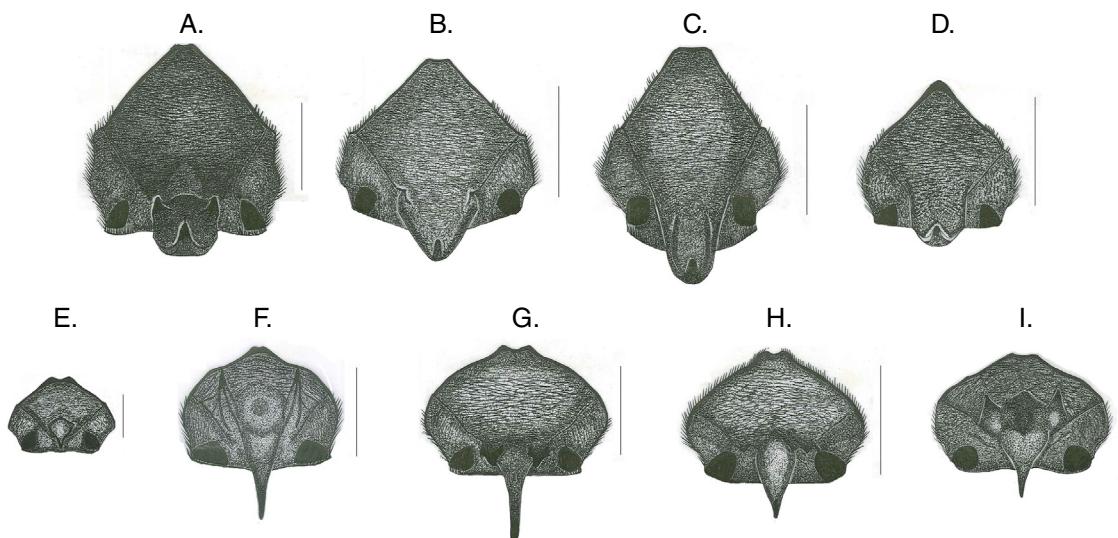
**Vulcano et al. (1976)** included *D. calcaratus* in the “buqueti” species-group. After revision of the holotype and due to the morphology of the head and the thorax of this species, it is concluded that it has no relationship with the “buqueti” species-group. In the same paper, these authors synonymized *Dichotomius nimuendaju* (Luederwaldt, 1925) with *D. calcaratus*, which was a mistake and, following the revision of the holotype of *D. nimuendaju*, this species is revalidated. Therefore, the “buqueti” species-group would consist of the following species: *D. buqueti*, *D. camposeabrai*, *D. nutans*, *D. haroldi*, *D. horridus*, *D. quadrinodosus*, *D. nimuendaju*, *D. reclinatus* and *D. ribeiroi*.

By studying the external morphology characteristics proposed by Luederwaldt (1929) for the “buqueti” species-group, it was noticed that the triangular shape of the head and the laminar cephalic horn in males were not related, features not exhibited by *D. nimuendaju*, *D. camposeabrai*, *D. quadrinodosus*, *D. horridus* and *D. reclinatus*. These species have an oval head with two defined clypeus teeth and a sub-cylindrical cephalic horn (Fig. 1).

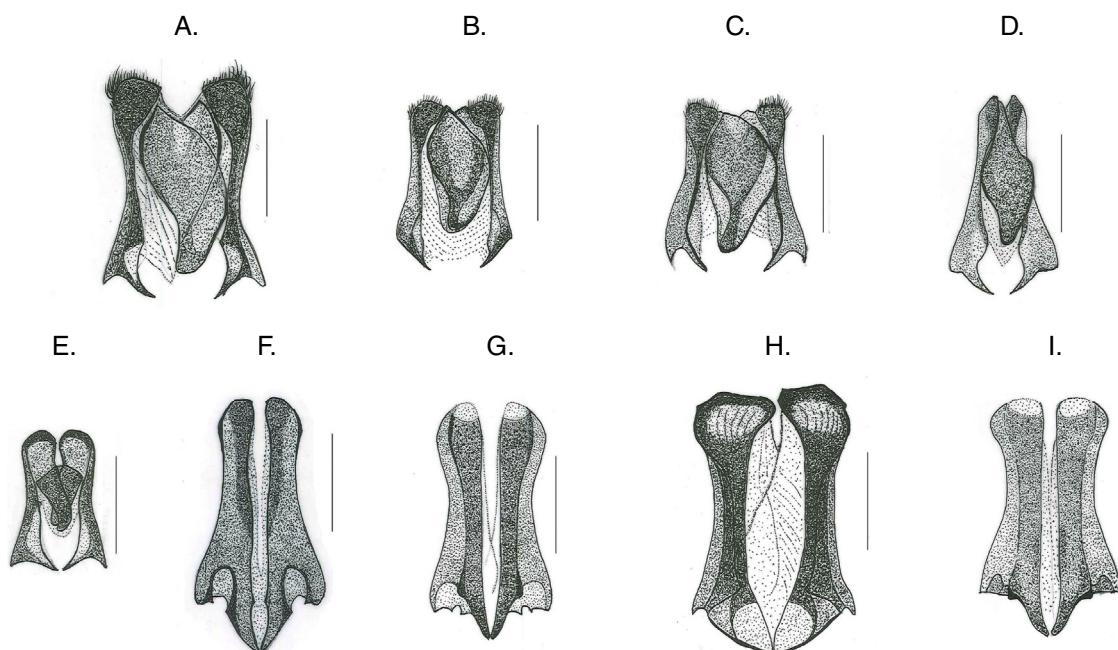
For this reason, the study was expanded to include male genitalia morphological characteristics, which have shown a greater consistency than intraspecific external morphology characteristics (Zunino, 1985; Zunino and Monteresino, 1990). However, inconsistencies in the “buqueti” species-group (*sensu* Luederwaldt) were higher and it is therefore concluded that this group consists of a mixture of species. The species in the “buqueti” species-group presented two morphologies in male genitalia, where *D. buqueti*, *D. haroldi*, *D. nutans*, *D. ribeiroi* and *D. camposeabrai* presented aedeagus with two laminar processes between parameres in ventral view and *D. nimuendaju*, *D. quadrinodosus*, *D. horridus* and *D. reclinatus* do not have this structure between parameres (Fig. 2).

The internal sac sclerites also show differences between species, mainly in the copulatrix lamella: the structure that according to López-Guerrero (2005) is where the biggest differences between *Dichotomius* species are found. In the “buqueti” species-group we found that *D. buqueti*, *D. haroldi*, *D. nutans* and *D. ribeiroi* have a sub-quadrangular copulatrix lamella with two projections on the right side and setae across the whole surface (Fig. 3A–D), while *D. nimuendaju*, *D. quadrinodosus*, *D. horridus* and *D. reclinatus* have a well sclerotized and irregular copulatrix lamella (Fig. 3F–I) and *D. camposeabrai* have a different lamella to those described above (Fig. 3E).

As a result of the aforementioned and according to a comparison of the external morphology and male genitalia with other *Dichotomius* groups, we propose the redefinition of the “buqueti” species-group, in which should be *D. buqueti*, *D. haroldi* and *D. nutans*, in the following terms: aedeagus with laminar processes between parameres, parameres with setae at apex, sub-quadrangular copulatrix lamella with two lateral projections and setae over the whole surface, triangular head, male cephalic



**Fig. 1.** Heads of “buqueti” species group. (A) *D. buqueti*; (B) *D. haroldi*; (C) *D. nutans*; (D) *D. ribeiroi*; (E) *D. camposeabrai*; (F) *D. horridus*; (G) *D. nimuendaju*; (H) *D. quadrinodosus*; (I) *D. reclinatus*. Line scale 1 mm.



**Fig. 2.** Ventral view of the parameres of “buqueti” species group. (A) *D. buqueti*; (B) *D. haroldi*; (C) *D. nutans*; (D) *D. ribeiroi*; (E) *D. camposeabrai*; (F) *D. horridus*; (G) *D. nimuendaju*; (H) *D. quadrinodosus*; (I) *D. reclinatus*. Line scale 1 mm.

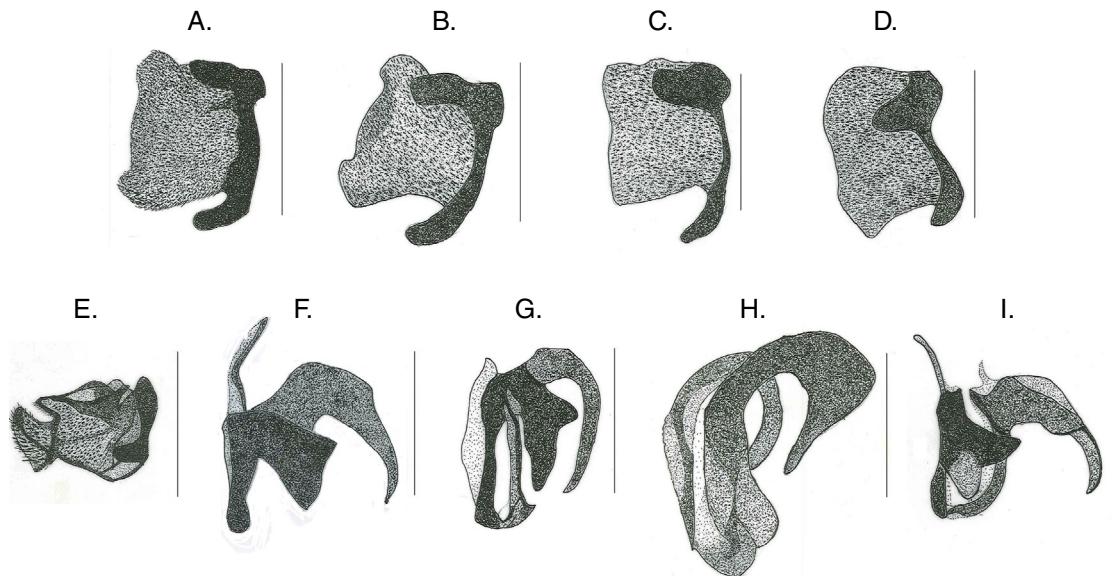
process at least two-thirds in laminar form ending in a conical process directed forward and pronotum with excavation at 1/3 of the anterior region.

We propose a new species group, which will be called “*reclinatus*”, in which *D. horridus*, *D. nimuendaju*, *D. quadrinodosus* and *D. reclinatus* are included, with the following features: males and females with rounded, wider than long heads, with a flange extension across clypeus, with two soft and emarginated teeth in the center, male with central cephalic process directed toward the back, long, sub-cylindrical and blunt ending and with two minor processes at the base (except *D. reclinatus* and *D. horridus*, which are in the clypeus). Pronotum with sharp antero-lateral angle, the males have a middle excavation which continues up to two-thirds of its length. Aedeagus in ventral view, without laminar processes between parameres. Parameres with straight inner edge, with basal area extended to the phallobase and single invagination on either

side of this projection. Irregular and well sclerotized copulatrix lamella.

*D. ribeiroi* has a triangular head, the pronotum anterior excavation and the copulatrix lamella is as species of the “buqueti” species-group. However, this species is here transferred to “cotopaxi” species-group based on the following characteristic: head, pronotum and elytra with callosity, dimpled elytral striae, base of striae 1–5 with depressions, invagination in the posterior area of the lateral portion of the pronotum, the shape of the parameres and internal sac sclerites. Pereira (1954) proposed the similarity of this species with *Dichotomius cotopaxi* owing to characteristics of the body calluses but placed it in the “buqueti” species-group based only on the triangular shape of the head.

Finally, *D. camposeabrai*, it seems to be a species near *Dichotomius nemoricola* (Pereira, 1942) because of characteristics such as the shape of the parameres, typical meaty copulatrix



**Fig. 3.** Copulatrix lamellae of “buqueti” species group. (A) *D. buqueti*; (B) *D. haroldi*; (C) *D. nutans*; (D) *D. ribeiroi*; (E) *D. camposeabri*; (F) *D. horridus*; (G) *D. nimuendaju*; (H) *D. quadrinodosus*; (I) *D. reclinatus*. Line scale 1 mm.

lamella process with long bristles on the left, as well as the shape of the pronotum, pronotal punctuation, elytral striae and elytral interstriae. Therefore, this species should be included in the “bitiensis” species-group to which *D. nemoricola* belongs (Arias-Buriticá and Vaz-de-Mello, 2012).

#### Redefinition of “buqueti” species-group

The species of the “buqueti” species-group are recognized by the following characteristics: (1) males and females with triangular head. (2) Clypeus in most widely emarginated and flat, with strong transverse wrinkles. (3) Males with lamelliform cephalic process, sub-quadrangular at the base and ending at the apical conical process directed forward; with a smaller process on each side at the base of the leading edge at the eye. (4) Females with a four-pointed process between the eyes (except in *D. haroldi*). (5) Males and females with excavated pronotum in anterior third, with two central tubercles, being stronger in males than in females. (6) Pygidium with incomplete posterior ridge in the middle. (7) Aedeagus with basal area of parameres ending in a strong constriction giving the appearance of spina and lamelliform process between parameres. (8) Parameres with setae at apex. (9) Sub-quadrangular copulatrix lamella with two extensions on the right and setae present throughout the surface.

#### Key for the species of the “buqueti” species-group and species that may be confused\*

1. Males and females with calluses on head, elytra and pronotum giving a corrugated appearance ..... ***D. ribeiroi*** \*
- Males and females without calluses on head, elytra and pronotum ..... 2
2. Males and females with elytral striae of one through five widened in the basal area (Fig. 7A) ..... ***D. nutans*** (Fig. 7)
  - Males and females without widened elytral striae (Figs. 5A–6A) ..... 3
  - 3. Large size (27–37 mm), elytra with blue overtones. Males with long, acute cephalic lateral processes (2 mm or more), females with four point process ..... ***D. buqueti*** (Fig. 5)



**Fig. 4.** *Dichotomius buqueti*. Labels of Lectotype here designated.

- Medium size (18–28 mm), black elytra. Males with small lateral cephalic processes (less than 1 mm), females with cephalic process similar to the processes of the male ..... ***D. haroldi*** (Fig. 6)

#### *Dichotomius buqueti* (Lucas, 1857)

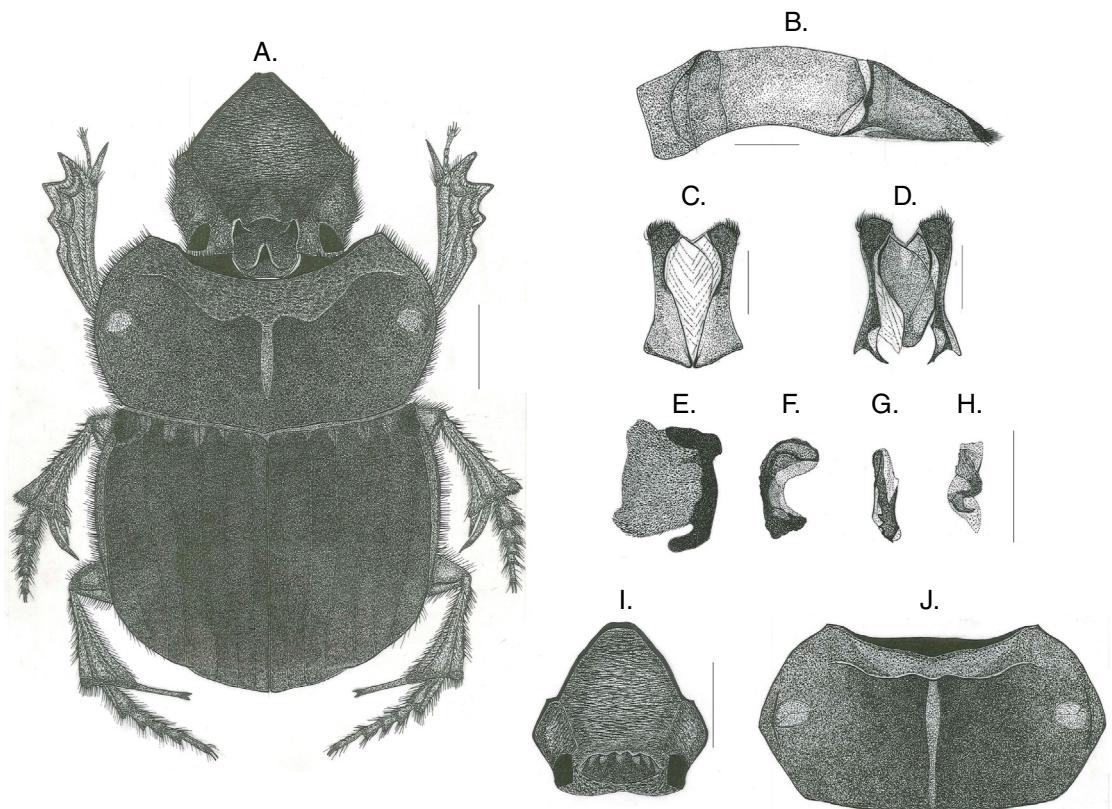
(Figures 4, 5A–J, 8A)

*Copris buqueti* Lucas, 1857: Page 105 (original description).

*Pinotus buqueti* (Lucas, 1857): Page 1009; Gemminger, M., Harold, E., 1869. (Transfer to *Pinotus*).

**Type Material: Lectotype male (here designed):** [1, quadrangular and red label, handwritten] Buqueti mihi, Tridens, Buquet, [2, quadrangular and yellow label, handwritten] 5089. 1♂. [BMNH] (Fig. 4).

**Additional specimens (20♂♂, 24♀♀):** BRAZIL: 1♂. [MZSP]. **Minas Gerais:** Passa Quatro, Fazenda Dos Campos, 6/IV/1914, J.F. Zikan 1♀ [MZSP]; IX/1917 1♀. [MZSP]; XI/1918 1♀. [MZSP]; 1919 1♂. [MZSP]. Vila Monte Verde, 15/IV/1960, J. Halik. 1♂. [MZSP]; 17/III/1966 1♂. [MZSP]; 18/III/1966, 3♂. [MZSP]; 18/IV/1966, 1♀. [MZSP]; 18/IV/1966 1♂. [MZSP]; 21/XI/1966 1♀. [MZSP]; 23/II/1969 1♀. [MZSP]; 26/VII/1968 1♀. [MZSP]. Monte verde, 16/VII/1959, Reichard Col. 1♀. [MZSP]. Passa Quatro, 915m, 2/IV/1922, J.F. Zikan 2♂. [1♂. MZSP; 1♂. IBSP]. **Rio de Janeiro:** Itatiaia, 16/III/1989, Godinho, C. 1♂. [CEMT]; IV/1992, 1♀. [CEMT]; II/1993, 1♂. [CEMT]; 1/III/1993, Celso, J. 1♂. [CEMT]. Nova Friburgo, Campo Coelho,



**Fig. 5.** *Dichotomius buqueti*. (A) Dorsal habitus of the male. (B) Lateral view of aedeagus. (C) Dorsal view of parameres. (D) Ventral view of the parameres. (E) Copulatrix lamellae. (F) Central accessory lamella. (G) Left lateral accessory lamella. (H) Right lateral accessory lamella. (I) Head of female. (J) Thorax of female. Line scale 1 mm.

I/1996, Penna, F. 1♂. 1♀. [CEMT]. Petrópolis, 22/I/1899. 1♀. [MZSP]; **São Paulo:** Campos [do] Jordão, 5/I/1960, J. Halik. 1♀. [MZSP]; Campos do Jordão, I/2004, Almeidaneta, G.P. 1♀. [CEMT]; 19/I/2004, Pereira, E. 1♀. [CEMT]; 5/II/2004, Pereira, E. 1♂. 1♀. [CEMT]; 1800m, I/2005, Pereira, E. 2♀. [CEMT]. Serra da Bocaina, San Jose do Barro, I-II/1960, M.A. Vulcano. 3♂. 8♀. [MZSP].

**Males:** Length 27–37 mm; width 17–21 mm. Black color. Elytra with blue overtones (Fig. 5A).

**Head:** Longer than wide, with prolonged anterior margin giving the appearance of a blunt triangle. Clypeus with a bright flange, without clypeal teeth. Surface of clypeus with strong, parallel wrinkles. Genae with curved and pronounced anterior edge, lateral edge straight and then curved, surface with strong wrinkles. Clypeo-genal suture evident, reaching the cephalic process. Frons with three horns; the central and most close to back edge looking like a prolonged “C”, dorsoventrally flattened in the basal region at lateral view, in the second-third getting compressed and ending with a cylindrical, brilliant and blunt tip; in frontal view it shows a central keel. The lateral horns are conical, with 2 mm or more, wide base and ending with cylindrical, brilliant and blunt tips, directed upwards and diagonal to the base of the central horn, reaching its middle.

**Thorax:** Pronotum twice as wide as long. Surface with circular punctures, elongated toward the lateral margins and are separated by twice or three times their length. Anterior region with a wide and smooth edge, which gets compressed toward the anterior angles. The anterior angle is curved forming an angle of approximately 90°. In side view of pronotum, the anterior region is vertical to the dorsal region, straight in the central region and curved toward the lateral region. Pronotum with two short and curved tubercles on the central region; from these tubercles come two protuberances like humps toward the lateral zones giving the appearance of an excavation at the anterior area of the pronotum. Behind and

between both tubercles, there is an elongated and deep fovea that reaches the posterior region of the pronotum. Both lateral foveae are big, deep and dorsiventrally enlarged. Hypomere with shagreened surface and dense setigerous punctures; lateral edges with erect, long and brown setae which can be seen at dorsal view and less dense at the central region where they are separated by twice their diameter. At the central region under the femur, the surface is smooth and brilliant. Shagreened prosternum with setigerous punctures prolonged from its medium region until covering the antero-medial zone of the mesosternum. From the posterior edge of the prosternum emerge many yellow setae directed toward the mesosternum. Elytra with soft and bicarinate striae, with ocellated punctures spaced by about five times their diameter; the base of the first five striae has an irregular fovea. Interstriae with shagreened surface with very soft punctures separated between them by seven times their diameter observed at 20×. In some specimens there are transverse wrinkles near to the striae. Mesosternum strongly narrowed medially, on which there is a brilliant and smooth process that precludes seeing the meso-metasternal suture, there is a shagreened surface toward the sides with setigerous punctures and yellow setae. Mesepisternum with the same surface as the lateral edges of the mesosternum. The meso-metasternal suture is erased in the central area by a mesosternum process, lateral margins are evident and brilliant. Metasternum with shagreened, shiny central area without setae; strong carina from 1/3 of metasternum to the back ending in a deep fovea. Side edges of the anterior area shagreened with dense setigerous punctures, posterior area shagreened with large setigerous punctures. Metepisternum equal to mesepisternum.

**Abdomen:** Sternites shagreened with some soft and separated punctures, evident in the 5th and 6th sternites. Lateral edges of all sternites with dense ocelated punctures. 6th sternite very narrowed medially. Pygidium shagreened with elongated and

separated punctures at least twice its diameter, incomplete margin in the middle inferior region.

**Male genital organ:** Side view of aedeagus with sub-quadrangular phallobase, basal zone with a medium bulge at both sides, apex with a constriction of approximately 115°. Sub-triangular parameres with a thin prolongation at the inferior base, which continues with an invagination toward the middle zone; apex thin, blunt, with a flat surface where long and yellow setae emerge (Fig. 5B). Dorsally symmetric with enlarged base and becoming thinner toward apical zone at which ending with a blunt tip; in this view setae can be seen too. Internal region with a convex invagination toward the middle until the apical region of each paramere (Fig. 5C). In the ventral view, parameres are thin at the basal zone with an acute prolongation described in the lateral view: apex blunt and flat where setae can be seen. Between parameres and inserted from the apical to the basal zone by a membrane, there are two lamellated and overlapped processes, that of the left paramere over that of the right paramere in a characteristic way which goes from the apical zone to beyond two-thirds of the parameres (Fig. 5D). Internal sac tubular with raspules at basal 1/3; at the center one big, sub-quadrangular, brown color copulatrix lamellae with two lateral tubular and darker prolongations, whole surface covered by bristles which become longer toward lateral margins (Fig. 5E). Apical zone with three accessory lamellae, one long and central with undefined form, more sclerotized in the central area with a surrounding semi-quitinized membrane (Fig. 5F). Left lateral lamella has "C" form, with a flat base, well sclerotized with irregular borders (Fig. 5G). Right lateral lamella has "N" form, enlarged, sclerotized in the center and surrounded by a semi-quitinized membrane (Fig. 5H).

**Female:** length 26.5–37 mm; width 16.8–21.1 mm. It differs from males by presenting a more defined clypeus edge. Frons with a four pointed cephalic process; both central tips higher and attached, lateral ones conical and smaller (Fig. 5I). Central tubercles of pronotum are softer (Fig. 5J). 6th abdominal sclerite not shortened medially.

**Commentaries:** The species is distinguished from the others of the group “buqueti” because the males present a process of three horns in the front where the two lateral horns have two or more mm and the females with four pointed cephalic process, pronotum with two short and curved tubercles on the central region and elytra with blue overtones. The species is associated with areas of Atlantic forest with altitudes of between 900 m and 1200 m in the mountains of Mantiqueira and Órgãos in Brazil.

**Distribution:** This species is distributed in Brazil in the São Paulo, Rio de Janeiro and Minas Gerais states (Fig. 8).

#### *Dichotomius haroldi* (Waterhouse, 1891)

(Figs. 6A–J, 8B)

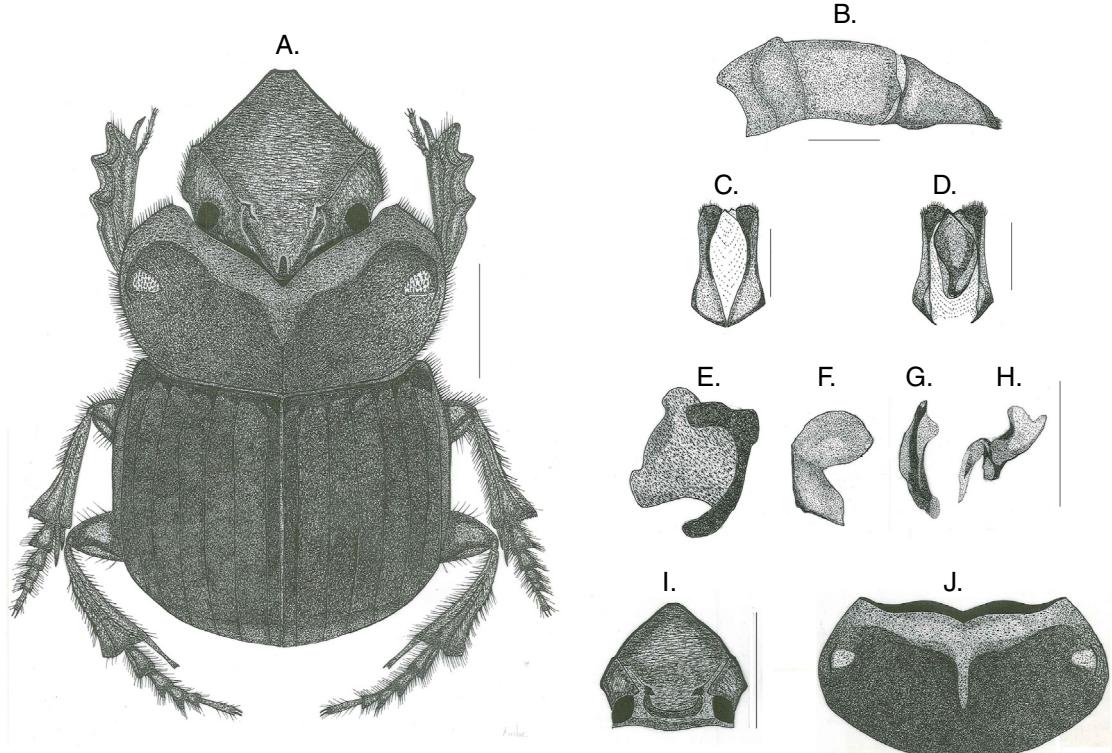
*Pinotus haroldi* Waterhouse, 1891: page 359 (original description).

*Pinotus verticalis* Felsche, 1901: page 136 (original description).

*Dichotomius verticalis* (Felsche, 1901): page 389. Pereira, F.S. 1953 (synonym).

**Type Material:** *Pinotus haroldi* Waterhouse. **Holotype.** (♂) [1,circle label with red border] Type [2,square label with green line, handwritten] Cordova 18./3 [3,square label, handwritten] Pinotus haroldi (Type) Waterh [4,quadrangular and red label with black borders] HOLOTYPE 1♂. [BMNH]. *Pinotus verticalis* Felsche. **Holotype.** (♂) [1,quadrangular label, second word handwritten] Bahia Blanca [2,quadrangular orange label] Typus. [3,quadrangular green label] Coll. C. Felsche Kauf 20, 1918 [4,square label with doble purple line, handwritten] verticalis Felsche [5,quadrangular red label with black borders] HOLOTYPE 1♂. [SMTD].

**Additional specimens.** (27♂♂. 25♀♀.): ARGENTINA: Cerro Corta Pie, II/1942, 2♀. [MZSP]. **Buenos Aires:** II/1942, 4♂. 4♀. [MZSP]; XI/1942, 1♂. 2♀. [MZSP]; III/1950, 3♂. [CEMT]. Partido Puán, Felipe Solá, I/1948, Martínez, A. 2♀. [CEMT] Dto. Puán, Felipe Solá, XI/1959, Martínez, A. 1♂. [MZSP]. Felipe Solá, II/1942, 8♂. 2♀. [MZSP];



**Fig. 6.** *Dichotomius haroldi*. (A) Dorsal habitus of the male. (B) Lateral view of aedeagus. (C) Dorsal view of parameres. (D) Ventral view of the parameres. (E) Copulatrix lamellae. (F) Central accessory lamella. (G) Left lateral accessory lamella. (H) Right lateral accessory lamella. (I) Head of female. (J) Thorax of female. Line scale 1 mm.

Martínez, A., II/1942, 2♂. 5♀. [MZSP]; Martínez, A. X/1942, 1♂. 1♀. [MZSP]; X/1942, Pohl, B. 1♀. [MZSP]. XII/1961, Martínez, A. 1♀. [MZSP]. **[Buenos Aires]:** Saavedra, Goyena I, 1960, Martínez, A. 1♂. 2♀. [MZSP]. **Córdoba:** 1♀. [MZSP]. San Francisco, X/1961. 1♀. [CEMT]. **Santiago del Estero:** Pinto, I/2006, Abadie, E. 1♂. [CEMT]. Río Salado Wagner Col. 1♂. [MZSP] decembre Collection Wagner 1♂. [MZSP]. Ojo de Agua, Coll. Martínez, Feb[rero]. [1]974 1♂. 1♀. [CMNC]. Ojo de Agua, 17.II.1982, H. & A. Howden. 1♂. [CMNC].

**Males:** Length 18–28 mm; width 11–14.5 mm. Black color with brown setae at both sides of head and pronotum (Fig. 6A).

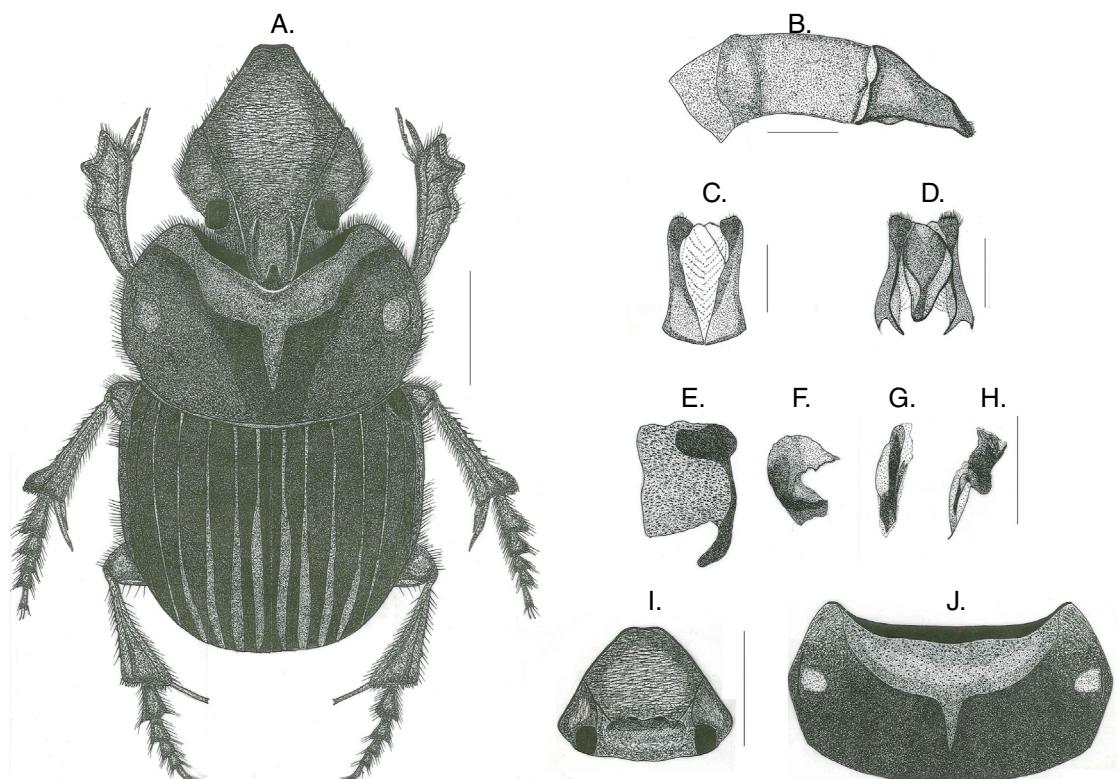
**Head:** As long as it is wide with prolonged anterior margin giving the appearance of a blunt triangle. Clypeus with a brilliant flange, without clypeal teeth. Surface of clypeus with strong and parallel wrinkles. Genae with curved and pronounced anterior edge, lateral edge straight and then curved, surface with strong wrinkles. Clypeus-genal suture evident, reaching the cephalic process. Frons with three horns, the central is long, sub-quadrangular and directed backwards, dorsoventrally flattened at the basal area, surface with softer wrinkles than the clypeus and compressed on the apical zone at which it ends with a cylindrical, blunt and brilliant tip that continues to the anterior region. The two lateral horns are triangular, small (less than 1 mm), directed upwards and diagonal to the base of the central horn. In small males the three cephalic processes are less developed.

**Thorax:** Pronotum twice as wide as it is long. Surface with elongated punctures separated by once their length or diameter across the whole surface. Anterior region with a wide and smooth edge; there is an acute angle behind the cephalic horn, then this edge gets compressed toward the anterior angles. The anterior angle is curved. In the side view, the anterior region of the pronotum is vertical to the dorsal region, excavated in the central region and curved toward the lateral zones, giving the appearance that the central horn of the head fits into this excavation. In the anterior-dorsal view the thorax has a deep excavation, formed

around to the two long humps that reach the anterior angle of the pronotum, in the central zone there is a small continuous invagination with an elongated fovea to the back region of the pronotum. Both lateral foveae are big, deep and elongated. Hypomere with shagreened surface and ocelated punctures rounded on anterior edges and elongated on the posterior edges on which being separated by one time their diameter. All punctures with erect, long brown setae, which can be seen on dorsal view and less dense at the central region. The central region under the femur surface is brilliant with the same puncture pattern. Shagreened prosternum, prolonged from its middle region until covering the antero-medial zone of the mesosternum. From the posterior edge of the prosternum many yellow setae emerge directed toward the mesosternum.

Elytra with soft and bicarinate striae, with medium and ocelated punctures spaced by about three times their diameter. Interstriae with shagreened surface with small and bright punctures separated by five times their diameter. Mesosternum strongly narrowed medially, on which there is a brilliant and smooth process that avoids the meso-metasternal suture, there is a shagreened surface toward the sides with soft and ocellated punctures and dense yellow setae. Mesepisternum with big and ocellated punctures, separated by about one time its diameter, with a seta out of each one. Metasternum with shagreened, shiny central area without setae; strong carina from 1/3 of metasternum to the back ending in a deep fovea. Side edges of the anterior area shagreened with dense setigerous punctures, posterior area shagreened with large setigerous punctures. Metepisternum equal to mesepisternum.

**Abdomen:** Sternites shagreened with small punctures separated by seven times their diameter, denser in the 5th and 6th sternites. Lateral margins of sternites 1–5 with dense ocelated punctures. 6th sternite very narrowed medially. Pygidium shagreened with elongated punctures separated by one time their diameter, incomplete margin in the middle inferior region.



**Fig. 7.** *Dichotomius nutans*. (A) Dorsal habitus of the male. (B) Lateral view of aedeagus. (C) Dorsal view of parameres. (D) Ventral view of the parameres. (E) Copulatrix lamellae. (F) Central accessory lamella. (G) Left lateral accessory lamella. (H) Right lateral accessory lamella. (I) Head of female. (J) Thorax of female. Line scale 1 mm.

**Male genital organ:** Side view of aedeagus with sub-quadrangular phallobase, basal region with a medium bulge on both sides, apex with a constriction of approximately 115°. Sub-triangular parameres with a thin at the inferior base, which continues with an invagination toward the middle zone; thin and blunt apex, with a flat surface from which emerge short setae (Fig. 6B). Dorsally symmetric with enlarged base and becoming thinner toward the apical zone in which ending with a blunt tip; setae can be seen in lateral view. Internal region with a convex and soft invagination in the first third of the apical area of parameres (Fig. 6C). In ventral view, parameres are thin at basal zone with an acute prolongation described in the lateral view: blunt and flat apex where setae can be seen. Between parameres, and inserted from the apical to basal zone, there are two lamellated and overlapped processes: the left paramere process over the right one. These processes go from the apical zone for two-thirds of parameres (Fig. 6D). Internal sac is tubular with raspules on the basal two-thirds; there is a big, sub-quadrangular and brown copulatrix lamellae, with two darker lateral prolongations, the entire surface of the lamellae covered by bristles which become longer toward the lateral margins (Fig. 6E). Apical zone with three accessory lamellae; the central one is long with undefined form, more sclerotized in the central area surrounded by a semi-quitinized membrane (Fig. 6F). Left lateral lamellae has "C" form, with enlarged and sclerotized superior margin with defined edges (Fig. 6G). Right lateral lamella has "N" form, enlarged, sclerotized in the middle with surrounding semi-quitinized membrane that makes it look wider than the apical region of the sclerite (Fig. 6H).

**Female:** length 19–20 mm; width 12–13.1 mm. It differs from males due to having a softer anterior edge of the gena and frons with two lateral horns (Fig. 6I). The excavation of the pronotum is softer, so that the back central fovea is stronger and longer (Fig. 6J). 6th abdominal sclerite not shortened medially.

**Commentaries:** The species is distinguished from the others of the group "buqueti" because the males present a process of three horns in the front where the two lateral horns have less than 1 mm and the females only have the lateral horns in the front. Thorax with a deep excavation in the central area, which continues as an elongated fovea in the posterior area of the pronotum. Black elytra with soft and bicrenate striae. This species is preferentially associated to areas adjacent to the Chaco dry forests and grasslands of the Pampa.

**Distribution:** This species is distributed in Argentina in the Buenos Aires, Córdoba and Santiago de Estero provinces (Fig. 8).

#### *Dichotomius nutans* (Harold, 1867)

(Figs. 7A–J, 8C)

*Pinotus nutans* Harold, 1867: page 97 (original description).

**Type material:** *Pinotus nutans* Harold **Holotype** (♂): [1, square label with red border, handwritten] Uruguay P. nutans Harold. [2, square label with black line] Ex-Museo E. Harold [3, quadrangular and green label] Museum Paris ex Coll. R. Oberthur [4, quadrangular label, handwritten] Rio Parana [5, quadrangular label, handwritten] Uruguayanus o Reich. 1♂. [MNHN].

**Additional specimens.** (21♂♂. 15♀♀): ARGENTINA: **Buenos Aires:** Tandil, 20/I/1917, Bruch, C. 1♀. [MZSP]. Tandil, André-legit. Coll. Martínez, Ene[ro], [1]954, 1♂. [CMNC]. Tandil, Bolle-legit. Coll. Martínez, 23.I.[19]54. 1♀. [CMNC]. **Cordoba:** Colón, N of Cordoba W of Ascochinga Sierra de Cordoba N. 7.1.2010 1♀. [CEMT]. BRAZIL:

**Rio Grande do Sul:** U.S. Anna, IX/1927, P. Buck, 1♂. 1♀. [MZSP]. Porto Alegre, 12/VIII/1931, 1♂.; 13/X/1927, 1♂. 1♀.; 15/IX/1937, 1♀.; 21/VI/1928, 1♂.; 27/VI/1935, 1♂.; 3/IX/1941, 1♂.; 3/V/1938, 1♀.; 3/VIII/1931, 1♂.; 7/IX/1927, 4♂. 5♀.; 7/VI/1928, 4♂. 4♀.; 23/X/1935, 1♂. [MAPA]. VII/1928, 1♂. [MZSP]. VII/1928, Buck, P. 1♂. 1♀. [MZSP].

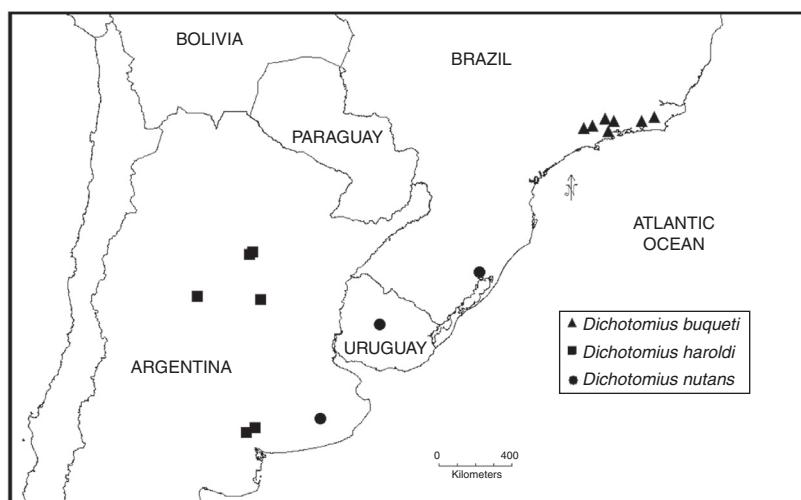
URUGUAY: Rocha, Cerro de Lechihuana, Castillos 25 agosto 1995. Leg: J.R. Verdú (00023405, 000234409) 2♂ (00023407) 1♀. [CEMT].

**Males:** Length 18.5–26.1 mm; width 11–16.3 mm. Black color with brown setae on both sides of head and pronotum (Fig. 7A).

**Head:** As long as it is wide with prolonged anterior margin giving the appearance of a blunt triangle. Clypeus with a brilliant flange, without clypeal teeth. Surface of clypeus with strong and parallel wrinkles. Genae with curved and pronounced anterior edge, lateral edge straight and then curved, surface with strong wrinkles. Clypeus-genal suture evident, reaching the cephalic process. Frons with a long, sub-quadrangular central cephalic process directed backwards, dorsoventrally flattened at basal area, and compressed on the apical zone where ending with a cylindrical blunt and brilliant tip; horn surface with softer wrinkles than those of clypeus from basal to mid-region. In smaller males the horn is short and without evident final process. Posterior region of the head with elongated holes separated by one time their length.

**Thorax:** Pronotum twice as wide as it is long. Surface with circular punctures elongated toward the lateral edges and are separated by one time their length. Anterior region with a wide and smooth edge; there is an invagination toward the anterior region behind the cephalic horn, this edge then gets compressed toward the anterior angles. The anterior angle is curved. In the side view, the anterior region of the pronotum is vertical to the dorsal region, straight in the central region and curved toward the lateral zones. There are two short and curved tubercles on the central dorsal region of pronotum; from these tubercles two protuberances like humps continue toward the lateral zones, giving an appearance of an excavation in the anterior area of the pronotum. Behind and between both tubercles, there is an elongated and deep fovea that does not reach the posterior region of the pronotum. Both lateral foveae are big, deep and rounded. Hypomere with shagreened surface and dense setigerous punctures on the lateral edges with erect, long brown setae which can be seen from the dorsal view and less dense in the central region were separated by twice their diameter. In the central region the surface under the femur is smooth and brilliant with the same puncture pattern. Shagreened prosternum mid-region with corrugated surface and prolonged from its medium region until covering the antero-medial zone of mesosternum. From the posterior edge of the prosternum many yellow setae emerge directed toward the mesosternum. Elytra with strong striae, the first four of which formed by a slope with a shagreened surface, narrow in the anterior zone and becoming broader toward the middle zone before being compressed again in the final area of the elytra; the fifth to seventh striae bicarinate with uniform width through their complete length. Interstriae convex and elevated with shagreened surface and small punctures separated by three times their diameter; some of them having transverse wrinkles giving a corrugated appearance. Mesosternum strongly narrowed medially, on which there is a brilliant and smooth process that prevents the meso-metasternal suture from being seen. There is a shagreened surface toward the sides with dense setigerous punctures and yellow setae. Mesepisternum has the same surface as the lateral edges of mesosternum. Meso-metasternal suture is erased in central area by a mesosternum process, lateral margins evident and brilliant. Metasternum with shagreened, shiny central area without setae; strong carina from 1/3 of metasternum to the back ending in a deep fovea. Side edges of the anterior area shagreened with dense setigerous punctures, posterior area shagreened with large setigerous punctures. Metepisternum equal to mesepisternum.

**Abdomen:** Sternites shagreened with some punctures in the middle region in the 5th and 6th sternites. All sternites with dense ocellated punctures on lateral edges. 6th sternite very narrowed medially. Pygidium shagreened with elongated punctures and separated by one time their length, incomplete margin in the middle inferior region.



**Fig. 8.** Distribution maps of the “buqueti” species group.

**Male genital organ:** Side view of aedeagus with sub-quadrangular phallobase, basal zone with a medium bulge on both sides, apex with a constriction of approximately 115°. Parameres sub-triangular with a thin at the inferior base, which continues with an invagination toward the middle zone; thin and blunt apex with flat surface setae (Fig. 7B); dorsally symmetric with enlarged base and becoming thinner toward apical zone where ending with a blunt tip; from this view, setae can be seen too. Internal region with a convex and soft invagination toward the middle of each paramere (Fig. 7C). In the ventral view parameres are thin at the basal zone with an acute prolongation described in the lateral view: blunt and flat apex where setae can be seen. Between parameres and inserted from the apical to basal zone by membrane, there are two lamellated and overlapped processes, that of the left paramere over that of the right paramere in a characteristic way running from the apical zone to beyond two-thirds of the parameres (Fig. 7D). Internal sac tubular with raspules on the basal two-thirds; in the center one big, sub-quadrangular, brown color copulatrix lamellae, with two tubular and darker lateral prolongations, entire surface covered by bristles which become longer toward the lateral margins (Fig. 7E). Apical zone with three accessory lamellae, one long and central with undefined form, in the central area more sclerotized surrounded by semi-quitinized membrane (Fig. 7F). Left lateral lamella has “C” form, with an enlarged and less sclerotized superior margin, irregular borders, inferior zone thinner and sclerotized with defined borders (Fig. 7G). Right lateral lamella has “N” form, enlarged, sclerotized, right margin wider than the left, with a semi-quitinized membrane (Fig. 7H).

**Female:** Length 21.5–28 mm; width 12–16.5 mm. It differs from males due to exhibiting a four-pointed cephalic process on front; both central tips higher, lateral tips conical and smaller (Fig. 7I). Central tubercles of the pronotum are softer (Fig. 7J). 6th abdominal sclerite not shortened medially.

**Commentaries:** The species is distinguished from the others of the group “buqueti” because the males have an only central horn on the front and females with four-pointed cephalic process. Pronotum with two short and curved tubercles on the central region from these tubercles two protuberances like humps continue toward the lateral edges, giving an appearance of an excavation in the anterior area of the pronotum. Behind and between both tubercles, there is an elongated and deep fovea that does not reach the posterior region of the pronotum. Black elytra with strong striae where the final part of the first to the fourth are widened. This

species is associated to low mountains of the Pampa biome, in extremely intervened areas, where natural vegetation is scarce.

**Distribution:** This species is distributed in Argentina in the Buenos Aires province, in Brazil in the Rio Grande do Sul state and in Uruguay in the Rocha department (Fig. 8).

#### *Dichotomius ribeiroi* (Pereira, 1954)\*

**Diagnosis:** Triangular head. Males with cephalic process at the front, flattened and directed backwards. Females with cephalic process with broad base, ending in two processes. Males and females with a deep and smooth excavation in the central zone of the pronotum. Head, thorax and elytra with calluses that give a corrugated appearance (for a detailed description see Arias-Buriticá and Vaz-de-Mello, 2013).

**Commentaries:** Because of the morphology of the head and pronotum, this species was included in the “buqueti” species-group, however, due to characteristics of the morphology of the male genitalia and calluses on the head, pronotum and elytra this was transferred to the “cotopaxi” species-group (Arias-Buriticá and Vaz-de-Mello, 2013).

#### Conflicts of interest

The authors declare no conflicts of interest.

#### Acknowledgments

Thanks to the curators of the entomological collections visited for their support and collaboration. To Orlando Rangel -Ch. and the “Biodiversidad y Conservación” research group (Universidad Nacional de Colombia). JAAB expresses many thanks to Mateus Souza, Ricardo Vicente and Miquéias Ferrão (UFMT) for their collaboration and hospitality and to Jhon Neita for his advice on preparing illustrations and Timothy Baker for the English revision. FZVM is supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico 304925/2010-1, 302997/2013-0, 405697/2013-9, 484035/2013-4, 202327/2013-2, 248299/2012-3, 306745/2016-0). Part of this work was granted by the Synthesys Project (<http://synthesys3.myspecies.info/>), which is financed by the European Community Research Infrastructure Action

under the FP7 (GB-TAF-3855) and L'Institut de Systématique, Evolution, Biodiversité (ISYEB, Muséum National d'Histoire Naturelle, Center National de la recherche scientifique, France. UMR 7205 CNRS/MNHN).

## References

- Arias-Buriticá, J., Vaz-de-Mello, F., 2012. Redescripción de *Dichotomius camposeabri* y *D. nemoricola* (Coleoptera: Scarabaeidae: Scarabaeinae), con apuntes sobre su posición sistemática. *Rev. Mex. Biodivers.* 83, 387–395.
- Arias-Buriticá, J., Vaz-de-Mello, F., 2013. *Dichotomius ribeiroi* (Pereira, 1954) (Coleoptera: Scarabaeidae: Scarabaeinae): redescripción y anotaciones taxonómicas de la especie. *Caldasia* 35 (1), 209–217.
- Arrow, G., 1913. Some new species of Lamellicorn Beetles from Brazil. *Ann. Mag. Nat. Hist.* 8 (11), 456–466.
- Felsche, C., 1901. Beschreibungen coprophager Scarabaeiden. *Dtsche. Entomol. Z.* 135–155.
- Felsche, C., 1911. Coprophage Scarabaeiden (Col.). *Dtsche. Entomol. Z.* 133–141.
- Génier, F., 2000. *Dichotomius comarapensis* sp. nov., une nouvelle espèce bolivienne de scarabée brachyptère (Coleoptera: Scarabaeidae: Scarabaeinae). *Faberries* 25 (2–3), 25–31.
- Harold, E., 1867. Neuer Coprophagen. Coleopterologische Hefte, 94–100.
- Harold, E., 1869. 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.
- Hijmans, R., Guarino, L., Bussink, C., Mathur, P., 2012. DIVA GIS Version 7.5: Sistema de Información Geográfica para el Análisis de Datos de Distribución de Especies. <http://www.diva-gis.org>.
- Kohlmann, B., 2003. Tribu Coprini. In: Morón, M.A. (Ed.), *Atlas de los escarabajos de México, Coleoptera Lamellicornia, v. II, Familias Scarabaeidae, Trogidae, Passalidae y Lucanidae*. Arganía editorial, Barcelona, España, pp. 45–57.
- López-Guerrero, I., 2005. Los *Dichotomius* (Coleoptera: Scarabaeidae: Dichotomiini) de la fauna de México. *Bol. SEA* 36, 195–209.
- Lucas, M., 1857. Animaux nouveaux ou rares recueillis pendant l'expedition dans les parties centrales de l'Amérique du Sud de Rio de Janeiro à Lima, et de Lima à Para; exécutée par ordre du Government français pendant les années 1843 à 1847, sous la direction du Comite François de Castelnau. (Entomologie).
- Luederwaldt, H., 1925. Neue *Pinotus* arten. *Bol. Mus. Nal.* 2 (1), 67–69.
- Luederwaldt, H., 1929. As espécies brasileiras do gênero *Pinotus* (Coleoptera: Lamellicornidae: Coprini) com algumas considerações também sobre outras espécies. *Rev. Mus. Paul.* 16, 603–775.
- Maldaner, M., Nunes, R., Vaz-de-Mello, F., 2015. Taxonomic revision of the *Dichotomius speciosus* (Waterhouse, 1891) species group (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 3986 (5), 549–560.
- Martínez, A., 1951. Notas Coleopterológicas V: La invalidez del nombre genérico *Pinotus* Erichson y dos nuevas sinonimias. *Ann. Soc. Cient. Argent.*, 138–142.
- Martínez, A., 1974. Una nueva especie de *Dichotomius* s. str. (Coleoptera, Scarabaeidae, Coprini Ateuchina). *Physis* 33 (86), 41–45.
- Medina, C., Scholtz, C., Gill, B., 2003. Morphological variation and systematics of *Canthon* and related genera of new world Canthonini dung beetles. *Dtsche. Entomol. Z.* 50 (1), 23–68.
- Nunes, R., Carvalho, M., Vaz-de-Mello, F., 2016. Taxonomic review of the *Dichotomius* (Luederwaldtinia) *assifer* (Eschscholtz) species-group (Coleoptera: Scarabaeidae). *Zootaxa* 4078 (1), 230–244.
- Pereira, F., 1953. Notas sinonímicas (Coleoptera: Scarabaeidae). *Dusenia* 4 (5–6), 387–402.
- Pereira, F., 1954. Especies novas de Scarabaeidae Brasileiros. *Arq. Mus. Nal.* 42, 462–466.
- Valois, M., Vaz-de-Mello, F., Silva, F., 2017. Taxonomic revision of the *Dichotomius sericeus* (Harold, 1867) species group (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* 4277 (4), 503–530.
- Vaz-de-Mello, F., Louzada, J., Gavino, M., 2001. Nova espécie de *Dichotomius* Hope, 1838 (Coleoptera Scarabaeidae) do Espírito Santo, Brasil. *Rev. Bras. Entomol.* 45 (2), 99–102.
- Vaz-de-Mello, F., Edmonds, W., 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.
- Vulcano, M., Pereira, F., Martínez, A., 1976. Notas sobre Scarabaeoidea Americana (Col Lamellicornia). *Stud. Entomol.* 19 (1–4), 515–530.
- Waterhouse, Ch., 1891. XXXVII. New Scarabaeidae in the British Museum: a Fourth Contribution. *Ann. Mag. Nat. Hist.* 6 (8), 348–363.
- Zunino, M., 1978. L'armatura genital negli Onthophagini Techiche de preparazione e criteri di studio (Coleoptera Scarabaeoidea) Supplemento. *Boll. Soc. Entomol. Ital.* 90, 21–26.
- Zunino, M., 1985. Las relaciones taxonómicas de los Phanaeina (Coleoptera Scarabaeinae) y sus implicaciones biogeográficas. *Folia Entomol. Mex.* 64, 101–115.
- Zunino, M., Monteresino, E., 1990. Ideas preliminares sobre la evolución de los aparatos copuladores en Rutelinae (Coleoptera Scarabaeoidea) y la filogenia del grupo. *Rev. Soc. Entomol. Argent.* 48 (89), 3–13.