European Journal of Taxonomy 1080: 1–65
https://doi.org/10.5852/ejt.2026.1080.3310

europeanjournaloftaxonomy.eu
ISSN 2118-9773
2026 · Bordin B.R. *et al.*

Received: 18 July 2025 • *Accepted: 6 May 2026* • *Published: 23 July 2026*

Topic editor: Tony Robillard • *Section editor: Maxwell Barclay* • *Desk editor: Pepe Fernández*

Monograph

urn:lsid:zoobank.org:pub:AD6AE2E8-601F-41F1-8784-615EE845505C

Taxonomic revision of the *Phanaeus chalcomelas* species group and a description of the new *Phanaeus achilles* species group (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini)

Bruna Ribeiro BORDIN [1,*], Jorge ARIAS-BURITICÁ [2], María Eduarda MALDANER [3] & Fernando Z. VAZ-DE-MELLO [4]

[1]Universidade Federal de Mato Grosso, Instituto de Biociências, Programa de Pós Graduação em Zoologia. Av. Fernando Corrêa da Costa, 2367, Boa Esperança, 78060–900 - Cuiabá, MT, Brazil.
[2]Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade (PPGECB), Universidade Federal de Mato Grosso (UFMT), Cuiabá 78060-900, Brazil.
[3,4]Coleção Entomológica de Mato Grosso Eurides Furtado - CEMT. Universidade Federal de Mato Grosso, Instituto de Biociências, Departamento de Biologia e Zoologia. Av. Fernando Corrêa da Costa, 2367, Boa Esperança, 78060–900 - Cuiabá, MT, Brazil.

[*]Corresponding author: bruna.r.bordin@gmail.com
[2]Email: joaariasbu@gmail.com
[3]Email: maldanerme@gmail.com
[4]Email: vazdemello@gmail.com

Abstract. The *Phanaeus chalcomelas* species group includes coprophagous and necrophagous South American scarab beetles (Coleoptera: Scarabaeidae) that are widely distributed in the Amazon Basin and along the eastern slopes of the Andes. The group is characterized by the distinctly punctuated elytral striae and the black rugosities on the pronotum. It is composed of five species: *Phanaeus chalcomelas* (Perty, 1830); *P. cambeforti* Arnaud, 1982; *P. meleagris* Blanchard, 1845; *P. lecourti* Arnaud, 2000 and *P. achilles* Boheman, 1858. The *P .chalcomelas* group was revised based on the external morphology and the morphology of the medial endophallite, which are illustrated for the first time. We provide a new diagnosis of the *P. chalcomelas* group, along with updated geographical distribution maps and diagnosis of previously described species. The *P. chalcomelas* species group now comprises seven species: two new species described herein, one revalidated, and four previously described: *P. cambeforti*, *P. chalcomelas*, *P. lecourti*, *P. meleagris*, *P. minos* Erichson, 1847 stat. rev., *P. divisor* sp. nov., and *P. mariocupelloi* sp. nov. Based on morphological evidence and previous molecular studies, we propose the new *Phanaeus achilles* species group to include: *P. achilles*, *P. arnaudorum* sp. nov., and the subfossil species *P. violetae* Zunino, 2013.

Keywords. Biodiversity, dung beetles, neotropical distribution, new species.

Bordin B.R., Arias-Buriticá J., Maldaner M.E. & Vaz-de-Mello F.Z. 2026. Taxonomic revision of the *Phanaeus chalcomelas* species group and a description of the new *Phanaeus achilles* species group (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *European Journal of Taxonomy* 1080: 1–65.
https://doi.org/10.5852/ejt.2026.1080.3310

Introduction

The *Phanaeus chalcomelas* species group comprises coprophagous and necrophagous South American scarab beetles (Coleoptera: Scarabaeidae). To date they are diagnosed by elytral striae distinctly punctate and the pronotum with black rugosities, giving an appearance of the irregularly maculated pronotal surface (Edmonds 1994). This species group is widely distributed in the Amazon and along the eastern slopes of the Andean, with one species, *P. achilles* Boheman, 1858, restricted to dry forests and shrublands in southwestern Ecuador and northwestern Peru (Edmonds 1994; Edmonds & Zídek 2012; Vaz-de-Mello *et al.* 2013; Chamorro *et al.* 2019). Five species are currently recognized in the group: *Phanaeus chalcomelas* (Perty, 1830); *P. cambeforti* Arnaud, 1982; *P. meleagris* Blanchard, 1845; *P. lecourti* Arnaud, 2000; *P. achilles* (Edmonds & Zídek 2012).

Like the other *Phanaeus* MacLeay, 1819 species groups, the *P. chalcomelas* group was defined by Edmonds (1972). He classified the species of *Phanaeus* into two groups: the *P. splendidulus* group, containing five species complexes (*palaeno*, *endymion*, *chalcomelas*, *splendidulus*, and *bispinus*), and the *P. vindex* group, with two complexes (*vindex* and *mexicanus*). The *chalcomelas* complex was composed of *P. chalcomelas* and *P. meleagris*, grouped based on the large punctures on the elytral striae and black roughness on the pronotal surface (Edmonds 1972). The species *P. achilles* was placed in the *vindex* group within the *mexicanus* species complex due to its resemblance to *Phanaeus wagneri* Harold, 1863, *Phanaeus lunaris* Taschenberg, 1870, and *Phanaeus mexicanus* Harold, 1863 (Edmonds 1972).

Edmonds (1994) revised the genus *Phanaeus* and updated the previous terminology by considering the *splendidulus* group as part of the subgenus *Notiophanaeus* Edmonds, 1994, and the *vindex* group within the subgenus *Phanaeus* s. str. Additionally, Edmonds (1994) replaced the term "species complex" (1972) for "species group". Species groups with smooth-punctate pronotal sculpture were allocated to *Notiophanaeus*, while species with a rugose pronotum were assigned to the subgenus *Phanaeus* s. str. (Edmonds 1994). According to the author, the species of the *P. chalcomelas* group do not have smooth pronotal sculpture like the other species of *Notiophanaeus*, nor as rugose as seen in *Phanaeus* s. str., representing an intermediate group between the two subgenera (Edmonds 1994). The author also added *Phanaeus cambeforti* and *P. achilles* to the *P. chalcomelas* group, despite *P. achilles* differing morphologically (except for the punctures on the elytral striae and black elevations on the pronotum) and ecologically from other species in the *P. chalcomelas* group (Edmonds 1994).

Edmonds (1994) also designated the lectotype of *Phanaeus minos* Erichson, 1847, which is a synonym of *P. meleagris* as established by Harold (1870). He restated the synonymy and ascribed a wide morphological variability to *P. meleagris*, including three "morphological types". The first type (a) is associated with the *P. meleagris* lectotype, characterized by black elytra and a red pronotum; the second type (b) exhibits dark blue or dark green tones in the dorsal and ventral portion of the body; and the third type (c) shows elytra with brown or olive-green colors corresponding with *P. minos* (Edmonds 1994). Six years later, Arnaud (2000) described *Phanaeus lecourti* as corresponding to morphotype (b) of *P. meleagris*, according to Edmonds (1994).

In the early 21st century, a large number of subspecies were described within *Phanaeus* (Arnaud 2000, 2001, 2002). In the *P. chalcomelas* group, the subspecies *P. lecourti peruanus* Arnaud, 2000 was described to differentiate the emerald green-colored population from the blue nominate subspecies (Arnaud 2000). Although the coloration of the type of *P. achilles* that bears its name is red and the type locality is the "province of Goyas", the subspecies *Phanaeus achilles lydiae* Arnaud, 2000 was described with red dorsal coloration and also for Goyas, occurring at low altitudes (below 100 m), and *P. achilles achilles* was described in Ecuador and Peru with green coloration and occurring above 1200 m (Arnaud 2000).

Later, in 2001, Arnaud designated a neotype for *P. chalcomelas* because the type locality "Prov S. Pauli et Minarum" (now states of São Paulo and Minas Gerais [Brazil]) mentioned in Perty's description did not match the locality "Brasilia" (Brazil) written on the label of the *P. chalcomelas* type deposited in Munich (Arnaud 2001). In the same work, Arnaud also described the subspecies *P. chalcomelas grossii* Arnaud, 2001 from Bolivia, characterized by a cephalic horn with tips more acute at the upper part of the basal expansion and more black elevations on the pronotal disc than the nominate subspecies (Arnaud 2001).

Arnaud (2002) presented the geographic distribution of *P. chalcomelas chalcomelas* as French Guiana, Brazil (Pará), Colombia (Meta), and Peru (Huánuco), whereas *P. chalcomelas grossii* is only found in Bolivia (Chapare). Another subspecies recognized was *P. meleagris minos* Erichson, 1847, characterized by a greenish-brown elytral coloration and occurrence in Peru, Ecuador, Colombia, and Venezuela. Meanwhile, *P. meleagris meleagris* has black elytra and is found in Bolivia (Arnaud 2002). Therefore, in 2002, the *P. chalcomelas* group comprised nine taxa: *P. achilles*, *P. achilles lydiae*, *P. cambeforti*, *P. chalcomelas*, *P. chalcomelas grossii*, *P. lecourti*, *P. lecourti peruanus*, *P. meleagris*, and *P. meleagris minos* (Arnaud 2002).

After a decade without any taxonomic work on the *P. chalcomelas* group, Edmonds & Zídek (2012) published a new revision of the genus *Phanaeus*, where they chose to avoid the subspecies category, and the following junior subjective synonyms were proposed for the *P. chalcomelas* group: *P. meleagris minos* = *P. meleagris*, *P. lecourti peruanus* = *P. lecourti*, *P. chalcomelas grossii* = *P. chalcomelas* and *P. achilles lydiae* = *P. achilles*. According to Edmonds & Zídek (2012), the distinction between *P. chalcomelas grossii* and *P. chalcomelas chalcomelas* was based on less reliable characteristics related to horn shape variations in males, and the distinction between *P. meleagris minos*, *P. lecourti peruanus*, and *P. achilles lydiae* from their nominate subspecies was based on unreliable chromatic variation. Thus, the *P. chalcomelas* species group sensu Edmonds & Zídek (2012) includes monotypic species only: *P. achilles*, *P. cambeforti*, *P. chalcomelas*, *P. lecourti*, and *P. meleagris*. Except for the description of the subfossil species *P. violetae* Zunino, 2013 from a Coprinisphaeridae Genise, 2004 ichnofossil found in Quito (Ecuador), no other work has so far dealt with the taxonomy of the *P. chalcomelas* group.

For a long time, the taxonomy of *Phanaeus* was based on the study of external morphology and the morphology of parameres (d'Olsoufieff 1924; Edmonds 1994; Arnaud 2002; Edmonds & Zídek 2012). Recent studies have shown that the endophallites morphology is helpful for identification and description of new species (Moctezuma & Halffter 2017, 2021). For the *P. chalcomelas* group, the study of the endophallites was conducted only to *P. meleagris* and *P. meleagris minos* (sensu Arnaud 2002) by Manjarres-H. & Molano-R. (2015), who found differences in the morphology of the endophallites between the two taxa. Although the authors provided a descriptive account of the morphological differences found, no illustrations of the endophallites were provided (Manjarres-H. & Molano-R. 2015).

In addition to the employment of new methodologies in taxonomic studies of *Phanaeus*, advances in molecular phylogeny provided clarification about the relationship of groups within the genus (Price 2009; Gillett & Toussaint 2020). Although Price (2009) did not include *P. cambeforti* in her analyses, Gillett & Toussaint (2020) included all species of *P. chalcomelas* group, and both studies indicate that the *P. chalcomelas* species group as polyphyletic with the species *P. achilles*. Recently, the subgenera *Phanaeus* and *Notiophanaeus* where synonymized in order to fix the non-monophyly frequently found in morphological and molecular phylogenetic studies for both subgenera (Moctezuma 2025). In addition, the available phylogenetic hypotheses have evidenced that a number of supraspecific units included within *Phanaeus* do not conform natural groups and they need to be revised and rearranged (Price 2009; Gillett & Toussaint 2020; Moctezuma *et al.* 2024).

In light of the aforementioned historical-taxonomic context, we aim to revise the taxonomy of the *Phanaeus chalcomelas* species group, based on external morphology and the morphology of

the endophallites. The redefinition of the *P. chalcomelas* group without *P. achilles* is presented and the formation of a new *Phanaeus* species group is proposed. We provide a new diagnosis of the *P. chalcomelas* group, along with updated geographical distribution maps, a new identification key and diagnosis of previously described species. Here, the endophallites of the species analyzed are illustrated for the first time and three new species of *Phanaeus* are described, two of the *P. chalcomelas* group, one of the new *Phanaeus achilles* species group.

Material and methods

We studied specimens deposited in the museums and collections (curators and collaborators in parenthesis):

CCBUMAG = Centro de Colecciones Biológicas, Universidad del Magdalena, Santa Marta, Colombia (Larry Jiménez)
CEMT = Coleção Entomológica de Mato Grosso Eurides Furtado, Instituto de Biociências – UFMT, Cuiabá, Brazil (Fernando Zagury Vaz-de-Mello)
CPFA = Patrick and Florent Arnaud Collection, Saintry sur Seine, France (Patrick Arnaud)
IAvH-E = Instituto de Investigación de Recursos Biológicas Alexander Von Humboldt, Villa de Leyva, Boyacá, Colombia (John César Neita and Edwin Torres)
IEXA = Colección Entomológica del Instituto de Ecología A.C., Xalapa, México (Viridiana Vega Badillo)
LOUNAZ = Museo de Zoología Universidad Nacional de Loja, Loja, Ecuador (Aura Paucar Cabrera)
MFNB = Museum für Naturkunde Berlin, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin (Joachim Willers, Bernd Jaeger, and Johannes Frisch)
MHNNKM = Museo de Historia Natural Noel Kempff Mercado, Colección entomológica, Santa Cruz de la Sierra, Bolivia (Julieta Ledezma and Marcelo Amaya)
MNHN = Muséum national d'Histoire naturelle, Paris, France (Olivier Montreuil and Antoine Mantilleri)
MUSM = Museo de Historia Natural, Universidad de San Marcos, Lima, Peru (Mabel Alvarado and Luis Figueroa)
NRMS = Swedish Museum of Natural History, Entomological Collections, Stockholm, Sweden (Niklas Apelqvist)
TAMU = Texas A&M University, College Station (John D. Oswald, Mario Cupello and Edward G. Riley)
UPTC-CE = Colección entomológica de referencia Museo de Historia Natural "Luis Gonzalo Andrade" Universidad Pedagógica y Tecnológica de Colombia, Tunja, Boyacá, Colombia (Juan Carvajal and Irina Morales)
ZSM = Zoologische Staatssammlung München, Germany (Michael Balke)

We followed the terminology used by Edmonds (1972) for morphological characters, except for "metasternum" and "black rugosities" (of the pronotum), which we opted to adopt "metaventritre" from Lawrence *et al.* (2011) and "black elevations", respectively. We chose to name some external morphological structures, such as "pair of anterior pronotal tubercles" and "carina adjacent to anteromedial pronotal margin", as they are essential for diagnosing species in the *P. chalcomelas* group. For the morphology of the male genitalia, we followed Tarasov & Génier (2015), except for "endophallites" (Génier 2019) to refer to the sclerotized structures of the endophallus. We followed the phylogenetic species concept defined by Wheeler & Platnick (2000) that describes a species as the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals.

To analyze the male genitalia, the endophalli were removed, unfolded and cleared with a 15% KOH solution for two hours at 80°C. After clearing, the endophalli were dissected and the structures were stored in 16 mm acrylic microvials (Paradox insects) filled with glycerol, which were attached to the specimens. We focused on the morphology of the medial endophallite (ME) as the main sources of characters in this research, as it has been used for other *Phanaeus* species groups (Price 2005; Moctezuma & Halffter 2017, 2021). We also focused on the additional and the superior right peripheral endophallites (AE and SRP, respectively), as these structures show clear interspecific variation (although the SRP endophallite may show intraspecific variation). In contrast, the fronto-lateral peripheral (FLP), axial (A), and subaxial endophallites (SA) were described only for *P. chalcomelas*, given their high morphological similarity across species of the *P. chalcomelas* and *achilles* groups.

Biogeographical classification follows Morrone *et al.* (2022). Locality data were taken from specimen labels. Google Earth software was used to obtain the approximate coordinates of the collection sites when this data were not available on the label, using the centers of the municipalities as reference points. Distributional maps were plotted using QGIS ver. 3.32.0 software. Pictures of the species were taken using the Leica motorized stereo microscope system model M205C with image capture system MC190 HD. The image plates were designed using PhotoScape software. Specimen length was measured including the head, whereas body width corresponds to the maximum width of the pronotum.

We have chosen to avoid the subgeneric level because, in addition the distinction between the two subgenera has been shown to be morphologically imprecise (Edmonds & Zídek 2012), the subgenera *Phanaeus* s. str. and *Notiophanaeus* have been indicated as polyphyletic by molecular studies (Price 2009; Gillett & Toussaint 2020; Moctezuma 2025).

Results

Taxonomy

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Scarabaeoidea Latreille, 1802
Family Scarabaeidae Latreille, 1802
Subfamily Scarabaeinae Latreille, 1802

Genus ***Phanaeus*** Macleay, 1819

For a comprehensive list of *Phanaeus* synonyms, along with complete references to the cited articles, see Moctezuma & Halffter 2021: 5–6.

Phanaeus chalcomelas species group

Diagnosis of the *Phanaeus chalcomelas* species group

Anteromedial margin of clypeus bidentate (Fig. 1A). Head of females with transverse carina, straight (Fig. 1A, D) or weakly trituberculate (in *P. chalcomelas* [Fig. 19G–H]). Pronotum bearing contrasted black elevations, variously and irregularly shaped and frequently partly anastomosed on disc regions (Fig. 1F), more abundant and anastomosed in females than males. Pronotal disc of major males triangularly flattened in dorsal view (Fig. 1F), with a pair of anterior tubercles (Figs 8D, 16–17). Pronotum of females with three (Fig. 1D) or four (in *P. chalcomelas* [Fig. 19G–H]) tubercles on anteromedial portion, sometimes poorly distinguishable from the irregular black elevations if not by their regular position. Posteromedial pronotal fossae present or absent (in *P. cambeforti*). Elytral striae punctate, basally impressed as distinct fossae

(Fig. 1H). Front tibiae tridentate, with faint, almost imperceptible fourth tooth. Dorsum dull, colored black, brown, green or blue, sometimes with red areas. Metallic sheen restricted to the following areas: around the eyes, pronotal margins, anterior margins of elytra, ventral portion of femora, hypomeron, and the pair of anteromedial pronotal tubercles in males. Widely distributed in the Amazon and along the Eastern slopes of Andes from Bolivia to Venezuela (Figs 20–21).

Key to species of the *Phanaeus chalcomelas* group (modified from Edmonds & Zídek 2012)

1. Anteromedial prominence ("angle") of metaventrite with regular callosity forming an arrowhead (isosceles triangle without base) pattern (Fig. 2A). Major males with cephalic horn abruptly narrowed basally to mid length (Fig. 16G–H). Pronotum of females with shallow anteromedial concavity surrounded by four tubercles, anterior tubercle large and distinct, the other three smaller (middle posterior tubercle always posterior to lateral ones) and may blend with the black elevations (Fig. 19G–H). Dorsal coloration olive green, olive brown or reddish brown. Ventral color dark green. Length 12–18 mm. Widely distributed in the Amazon (Fig. 21) ..... ***Phanaeus chalcomelas*** (Perty, 1830)

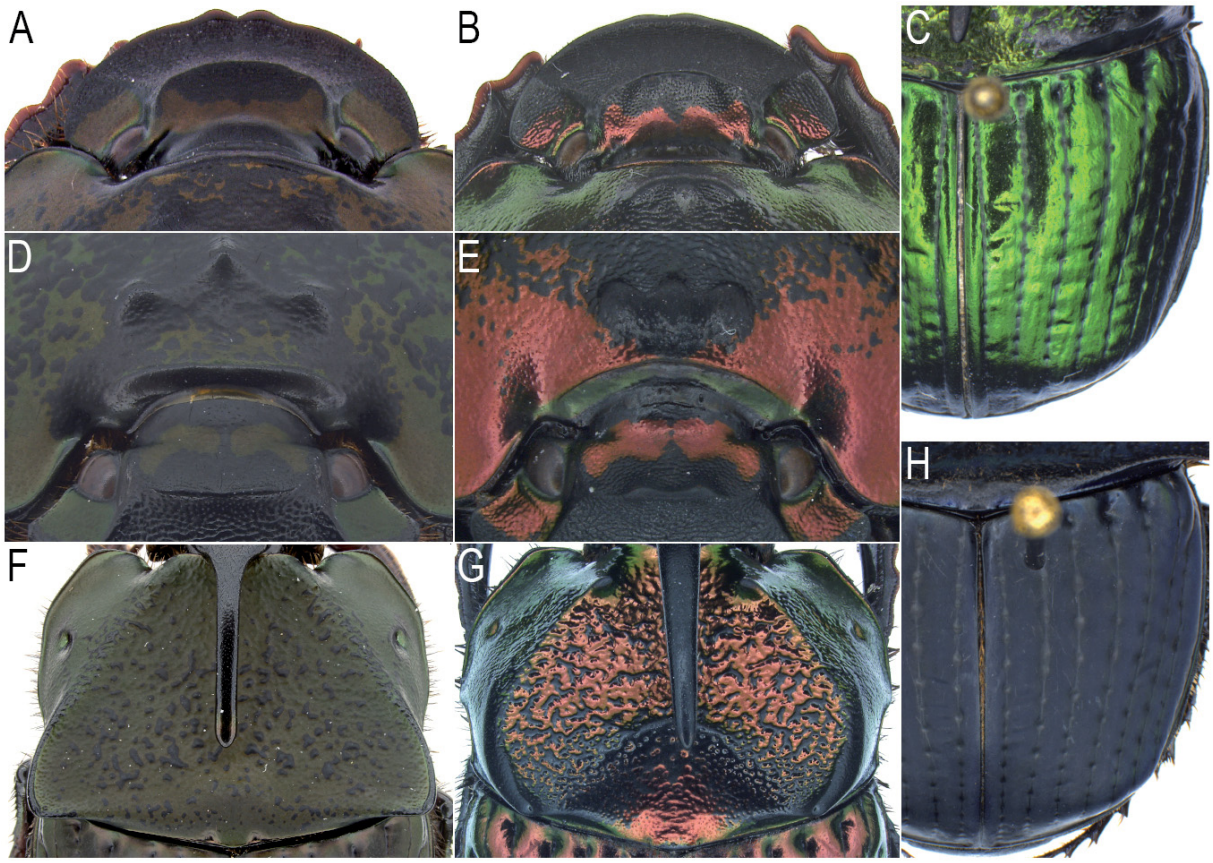

Fig. 1. External morphological differences between the *Phanaeus chalcomelas* species group and the *P. achilles* species group. **A–B**. Females head in dorsal view. **A**. *P. cambeforti* Arnaud, 1982 (CEMT). **B**. *P. achilles* Boheman, 1858 (CEMT). **C**. *P. arnaudorum* sp. nov. (CEMT), elytra in dorsal view. **D–E**. Anteromedial portion of pronotum and transverse carina of the head of females. **D**. *P. cambeforti* (CEMT). **E**. *P. achilles* (CEMT). **F–G**. Pronotal disc of major males in dorsal view. **F**. *P. chalcomelas* (Perty, 1830) (CEMT). **G**. *P. achilles* (CEMT). **H**. *P. lecourti* Arnaud, 2000 (CEMT), elytra in dorsal view.

– Anteromedial prominence of metaventrite usually without callosities, but if callose then callus not regular and far from arrowhead shaped (Fig. 2B–I). Male cephalic horn either evenly or, if basally enlarged, then gradually narrowing from enlargement to apex (Fig. 16A–F). Pronotum of females with three small tubercles arranged in a triangle, middle tubercle posterior to lateral ones (Fig. 19A–F). Color and distribution variable 2

2. Pygidium and ventral color, specifically femora and hypomeron, reddish: bright red, bronze red or red with greenish iridescence. Anteromedial prominence of metaventrite narrow and long, without trace of callosities (Fig. 2C, F, I) 3
– Ventral color not red, usually black, green, or blue. Anteromedial prominence of metaventrite wide, with or without callosities (Fig. 2D, G); distributed in the Amazon Basin. If anteromedial prominence of metaventrite long and narrow, distributed along the eastern slopes of the Andes in Peru and Bolivia 5

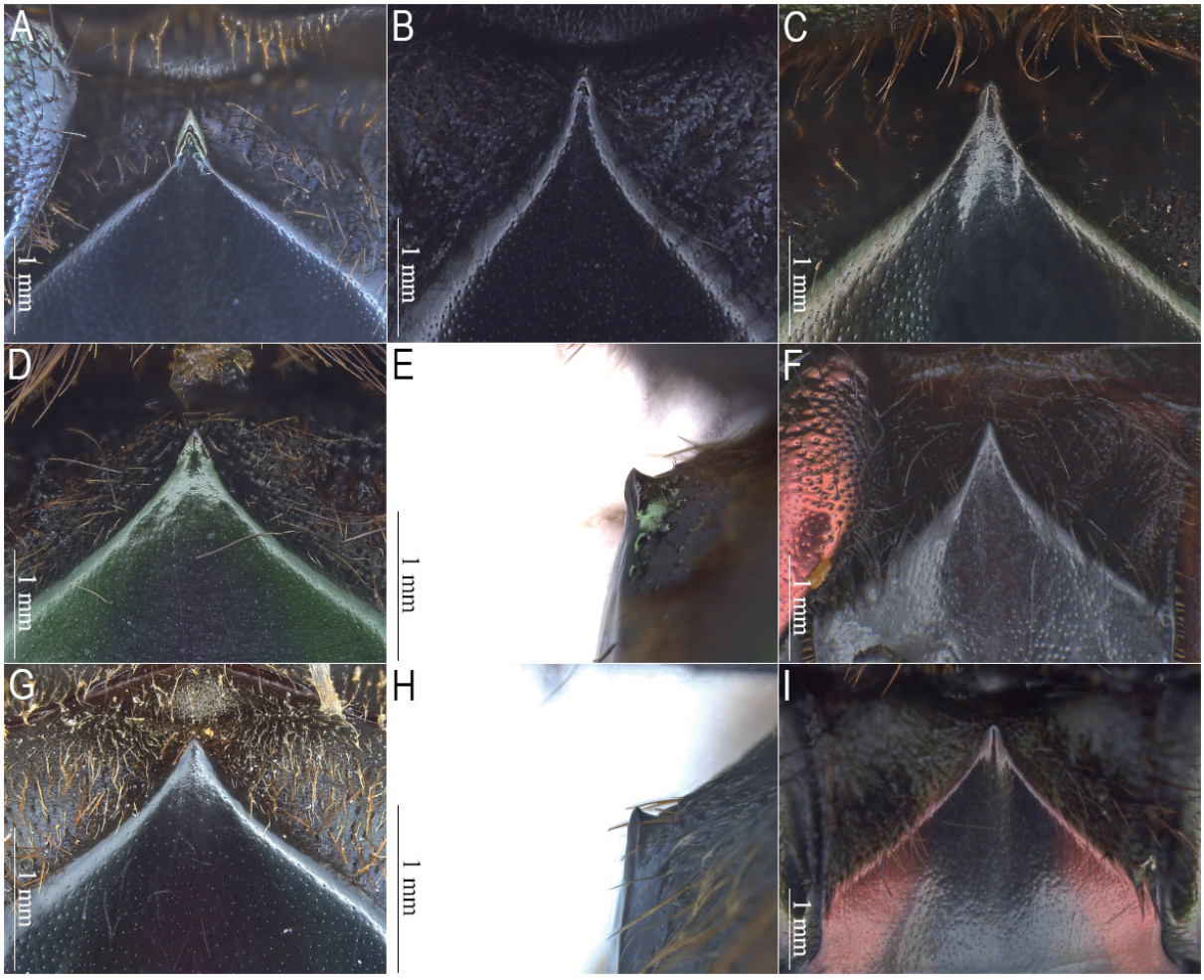

Fig. 2. Anteromedial prominence of metaventrite (*Phanaeus chalcomelas* species group). **A**. *P. chalcomelas* (Perty, 1830), from Santa Cruz de la Sierra, Bolivia (CEMT). **B**. *P. lecourti* Arnaud, 2000 (CEMT). **C**. *P. mariocupelloi* sp. nov., holotype (CEMT). **D**. *P. divisor* sp. nov., holotype (CEMT). **E**. *P. divisor* sp. nov., holotype, lateral view (CEMT). **F**. *P. meleagris* Blanchard, 1845 (CEMT). **G**. *P. cambeforti* Arnaud, 1982 (CEMT). **H**. *P. cambeforti*, lateral view (CEMT). **I**. *P. minos* Erichson, 1847 stat. rev., from Peru (CEMT).

3. Elytra completely matte black, with no other color in the interstriae (Fig. 11A–B, D). Pronotum with bright metallic red, yellow and green coloration between elevations, more visible on the sides (Figs 11A–B, D, 16D, 17D, 19D). Female carina adjacent to anteromedial pronotal margin subarcuate in frontal view, almost straight, without sinuosity in the middle (Fig. 3B). Length 16–21 mm. Bolivia and southern Peru, Yungas Province (Fig. 20) .....***Phanaeus meleagris*** Blanchard, 1845
– Elytra reddish brown, olive brown or olive green, never completely black 4

4. Elytra brown, reddish brown, or olive green in the interstriae (Fig. 12A–B, D). Each puncture of elytral striae within a black macula (Fig. 12A–B, D). Pronotum coppery brown, coppery red or rosé (Figs 12A–B, D, 16E, 17E). Female carina adjacent to anteromedial pronotal margin with sinuosity in the middle (frontal view) (Fig. 3A). Length 16–22.4 mm. Eastern slopes of the Andes from Peru to Venezuela (Fig. 20) ..... ***Phanaeus minos*** Erichson, 1847 stat. rev.
– Pronotum and elytra with uniform color, dark olive green or olive brown, without metallic red reflexes. Punctations of elytral striae without black maculae (Fig. 10A–B). Length 12.3–20 mm. Brazil, southwest of Mato Grosso state (Fig. 20) .....***Phanaeus mariocupelloi*** sp. nov.

5. Dorsal and ventral color similar, weakly lustrous, dark blue or green with faded sheen (Fig. 9). Cephalic horn of major males expanded laterally at the base and gradually narrowed towards the apex (Fig. 16A). Parameres slightly swollen apically (Fig. 13E). Length 19–24 mm. Bolivia and Peru (Fig. 20), Yungas Province .....***Phanaeus lecourti*** Arnaud, 2000
– Different dorsal and ventral colors. Dorsum olive green or olive brown, venter dark to bright green. Cephalic horn of major males without lateral expansion at the base, triangularly shaped in front view and tapering from base to apex. Parameres not swollen apically (Fig. 13A, C) 6

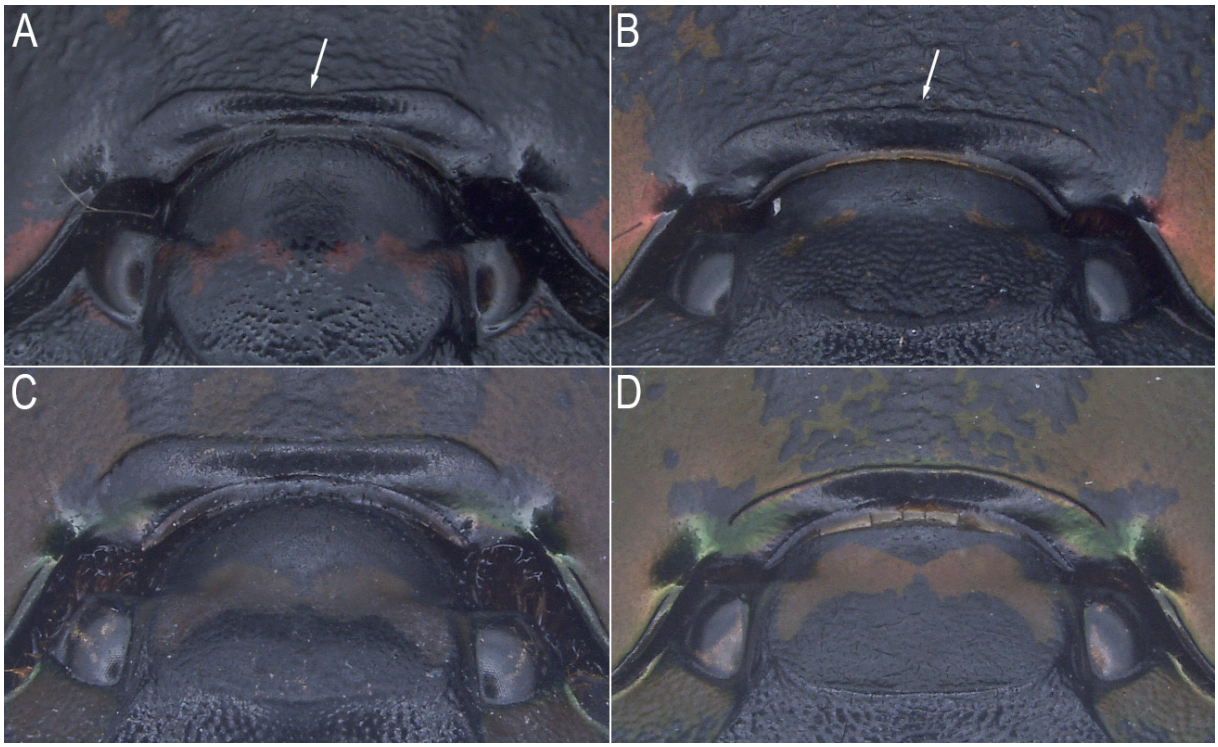

Fig. 3. Carina adjacent to anteromedial pronotal margin of females (frontal view). **A**. *Phanaeus minos* Erichson, 1847 stat. rev. (CEMT). **B**. *P. meleagris* Blanchard, 1845 (CEMT). **A–B**. Arrows indicate middle of carina. **C**. *P. cambeforti* Arnaud, 1982 (CEMT). **D**. *P. divisor* sp. nov., paratype (CEMT).

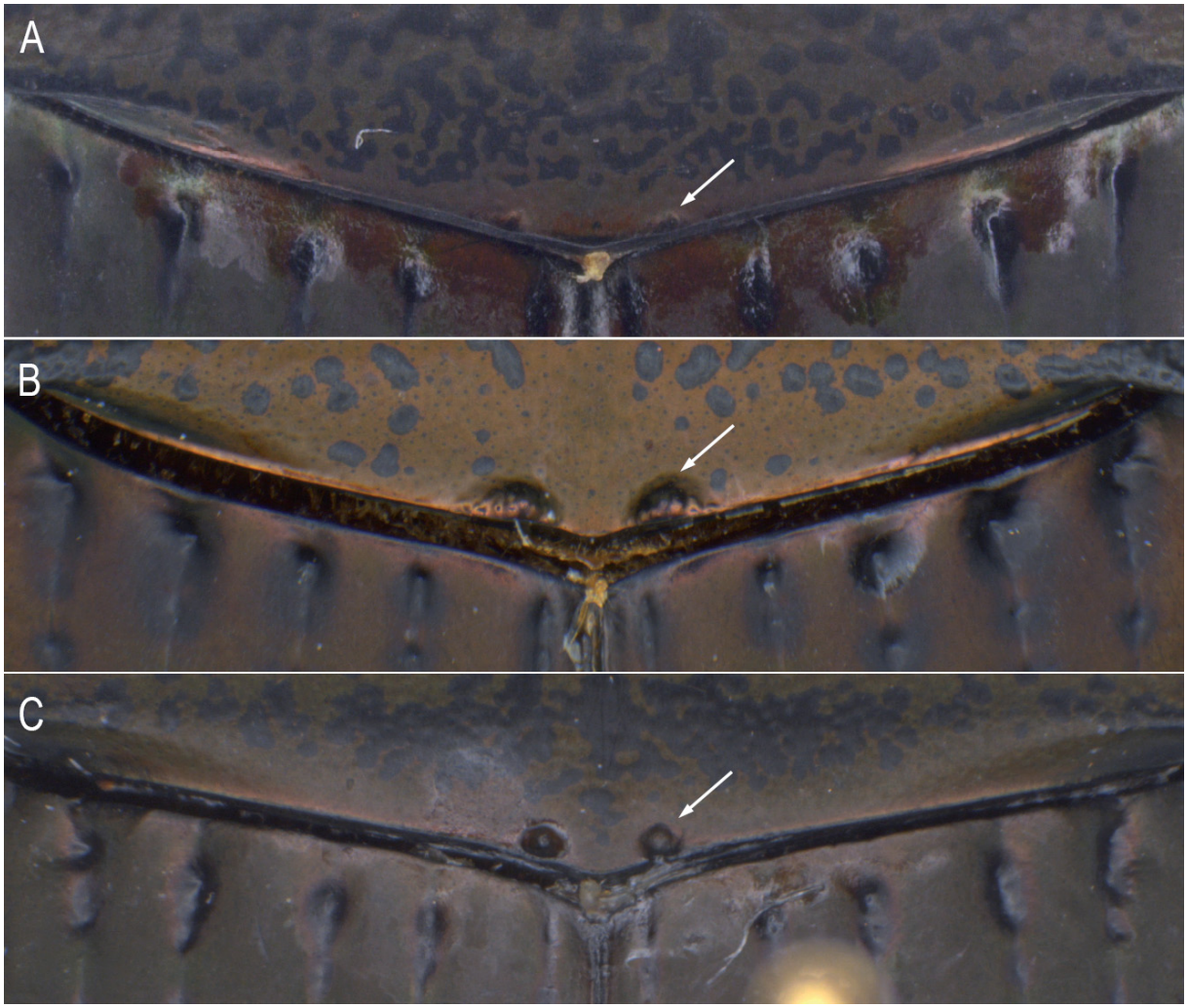

Fig. 4. Posteromedial pronotal fossae of males. **A**. *Phanaeus cambeforti* Arnaud, 1982 (CEMT). **B**. *P. divisor* sp. nov., holotype (CEMT). C. *P. mariocupelloi* sp. nov., holotype (CEMT).

6. Tip of anteromedial prominence of metaventrite convex (in lateral view), usually with irregular and small calluses or carinulae (Fig. 2D–E). Well-defined posteromedial pronotal fossae with punctures inside (Figs 4B, 8A–B). Carina adjacent to anteromedial pronotal margin of females regularly arched in frontal view (Fig. 3D). Length 15.4–18.5 mm. Brazil, Acre state, Serra do Divisor National Park (Fig. 20) .....***Phanaeus divisor*** sp. nov.
– Tip of anteromedial prominence of metaventrite flat (in lateral view) (Fig. 2G–H). Posteromedial fossae of pronotum absent or shallow and unpunctate (Figs 4A, 5A–B). Carina adjacent to anteromedial pronotal margin of females straight in frontal view (Fig. 3C). Length 11–18.7 mm Widely distributed in the Amazon (Fig. 20) ..... ***Phanaeus cambeforti*** Arnaud, 1982

Phanaeus cambeforti Arnaud, 1982
Figs 1A, D, 2G–H, 3C, 4A, 5, 13A, 14A, D, G, J, 16C, 17C, 18C, 19C

Phanaeus cambeforti Arnaud, 1982b: 122.

Phanaeus cambeforti – Vítolo 2000: 597. — Medina *et al.* 2001: 140. — Vulinec *et al.* 2003: 353–354, 356. — Feer & Pincebourde 2005: 23–24, 30. — Monaghan *et al.* 2007: 9, 17. — Price & May

2009: 215–216, 236. — Carvajal *et al.* 2011: 320. — Larsen 2011: 99; 2013: 97. — Santos-Heredia *et al.* 2011: 403. — Noriega 2012: 4. — Korasaki *et al.* 2012: 427–428. — Feer & Boissier 2015: 169. — Ratcliffe *et al.* 2015: 197. — Lizardo *et al.* 2022: 548, 553, 560. — Moctezuma *et al.* 2024: 5. — Moctezuma 2025: 4.

Phanaeus (*Notiophanaeus*) *cambeforti* – Edmonds 1994: 28, 31. — Vaz-de-Mello 2000: 194. — Arnaud 2002: 86–87. — Vítolo 2004: 285, 304, 306. — Price 2007: 13–14, 17. — Hamel-Leigue *et al.* 2009: 47, 50, 65, 74, 92. — Edmonds & Zídek 2012: 3, 5, 10, 37, 41. — Krajcik 2012: 204. — Figueroa *et al.* 2014: 127, 131, 134, 136. — Pacheco & Vaz-de-Mello 2015: 3, 6, 7. — Boilly *et al.* 2016: 90, 93, 96. — Chamorro *et al.* 2018: 98; 2019: 214, 215, 309. — Hielkema & Hielkema 2019: 105–106. — Gillett & Toussaint 2020: 673.

Diagnosis

Dorsal color ranging from olive green to reddish brown. Ventral color dark green or black with green sheen (Fig. 5C). Pronotal disc with faint punctation (× 40 magnification), absent in some specimens (Fig. 5A–B, D). Posteromedial fossae of pronotum absent or shallow in a few large specimens, mainly in females (Fig. 4A). Pronotum, in frontal view, with the transverse carina just posterior and adjacent to the anterior medial margin appearing straight (Figs 3C, 16C, 19C). Pronotum of males with few black elevations, these rarely anastomosed (Fig. 5A). Width of the pronotal disc in major males rarely exceeds the greatest width of elytra. Tip of anteromedial prominence of the metaventrite flat in lateral view (Fig. 2H). Length 11–18.7 mm. Pygidium mostly brown (Fig. 18C), rarely green. Endophallites: ME in dorsal view, elongate and blade-like, with a broad, rounded basal portion tapering gradually into a narrow, curved apex; left margin slightly concave, right margin nearly straight; left margin with a small fold near basal portion, not very pronounced compared to the other species of the group with a similar structure (Fig. 14D). AE with a straight base, not sharp; right margin (dorsal view) almost straight, with a small tooth-like projection in the middle, more visible in lateral view (Fig. 14G). SRP circular, as long as wide (Fig. 14J).

Type material

Holotype

FRENCH GUIANA • ♂; "Saül; Guyane française, IV-1977, M. DURANTON leg."; MNHN (Arnaud 1982b: 122: fig. 6.

Paratypes

FRENCH GUIANA • 1 ♂, 1 ♀ (examined from photographs provided in Arnaud 2002: 87).

Non-type material examined (193 ♂♂, 203 ♀♀)

BOLIVIA – **La Paz** • 3 ♂♂, 2 ♀♀; Iturralde, Rio Nuanu; 12°33′23″ S, 67°43′44″ W; 21–23 Sep. 2002; W. Aliaga leg.; MHNNKM • 2 ♂♂, 4 ♀♀; same data as for preceding; 12°33′9″ S, 67°42′32″ W; 22–24 Sep. 2002; MHNNKM. – **Pando** • 1 ♂, 2 ♀♀; Nicolás Suárez, Rutina; 25 May 2009; O. Terrán *et al.* leg.; MHNNKM • 1 ♂; same data as for preceding; Sep. 1998; MHNNKM.

BRAZIL – **Acre** • 3 ♂♂, 5 ♀♀; Bujari, FES Antimary; 09º25′41″ S, 68º17′7″ W; 15 Mar. 2017; B.S. Bitencourt leg.; pitfall human dung; CEMT • 1 ♀; Mâncio Lima; 7°28′58″ S, 72°54′11″ W; 5 Dec. 2018; Luiz H.M.B. leg.; CEMT • 1 ♂; Mâncio Lima, Parque Nacional da Serra do Divisor; 7°24′58″ S, 73°37′56″ W; 10–14 Dec. 2019; R.A. Azevedo leg.; flight interception trap; CEMT • 1 ♂, 1 ♀; same data as for preceding; 7°26′46″ S, 73°39′28″ W; 7–11 Dec. 2019; CEMT • 1 ♂; same data as for preceding; 7°26′46″ S, 73°39′27″ W; pitfall human dung; CEMT • 2 ♂♂, 3 ♀♀; same data as for preceding; 7°27′04″ S, 73°38′57″ W; 6–14 Dec. 2019; flight interception trap; CEMT • 1 ♂; same data as for preceding; pitfall human dung; CEMT • 1 ♀; same data as for preceding; 7°28′59″ S,

72°54′11″ W; CEMT • 2 ♂♂, 3 ♀♀; Rio Branco, Fazenda Catuaba; Feb. 1997; F.Z. Vaz-de-Mello leg.; pitfall human dung; CEMT • 1 ♂, 1 ♀; Senador Guiomard; 10°04′ S, 67°37′ W; 14 Apr. 2017; B.S. Bitencourt; pitfall human dung; CEMT • 1 ♂, same data as for preceding; 20 Apr. 2018; CEMT. – **Amapá** • 1 ♂, 2 ♀♀; Serra do Navio, Cava Urucum-Amapari; 0°53′06″ N, 51°52′53″ W; Dec. 2000; R. Ribon leg.; CEMT. – **Amazonas** • 4 ♂♂, 3 ♀♀; Barcelos, Parque Nacional do Jaú; 2°00′24″ S, 61°33′1″ W; 10–14 Nov. 2021; R.A. Azevedo leg.; flight interception trap; CEMT • 2 ♀♀; same data as for preceding; 2°00′26″ S, 61°32′49″ W; 14–16 Nov. 2021; pitfall human dung; CEMT • 1 ♂, same data as for preceding; 2°00′25″ S, 61°32′55″ W; CEMT • 2 ♀♀; same data as for preceding; 2°00′23″ S, 61°32′01″ W; CEMT • 2 ♂♂, 4 ♀♀; same data as for preceding; 2°00′22″ S, 61°32′03″ W; CEMT • 2 ♀♀; same data as for preceding; 2°00′21″ S, 61°32′06″ W; CEMT • 1 ♂, same data as for preceding; 2°00′20″ S, 61°33′10″ W; CEMT • 2 ♂♂; same data as for preceding; 2°00′19″ S, 61°33′13″ W; CEMT • 2 ♂♂, 1 ♀; same data as for preceding; 2°00′18″ S, 61°33′16″ W; CEMT • 2 ♂♂, 2 ♀♀; same data as for preceding; 1°50′54″ S, 61°34′01″ W; CEMT • 3 ♀♀; same data as for preceding; 1°50′35″ S, 61°34′07″ W; flight interception trap; CEMT • 1 ♀; same data as for preceding; 2°02′55″ S, 61°32′52″ W; 13–17 Nov. 2021; CEMT • 1 ♀; Careiro, BR-319; 4°07′58″ S, 60°44′09″ W; 2 Dec. 2015; D. Pires leg.; pitfall human dung; CEMT • 1 ♀; same data as for preceding; 4°08′28″ S, 60°43′57″ W; CEMT • 1 ♀; same data as for preceding; 4°08′58″ S, 60°43′44″ W; CEMT • 1 ♀; same data as for preceding; 4°09′10″ S, 60°43′08″ W; 3 Dec. 2015; CEMT • 1 ♂, 1 ♀; same data as for preceding; 4°09′28″ S, 60°43′32″ W; 2 Dec. 2015; CEMT • 1 ♂; Presidente Figueiredo; Oct.–Nov. 1996; E. Anderson leg.; CEMT • 1 ♂, 1 ♀; Silves, Fazenda Saracá; 2°50′45″ S, 58°35′07″ W; 5–12 May 2019; R.S. Moura leg.; CEMT. – **Rondônia** • 1 ♂; Cacaulândia, Fazenda Rancho Grande; Nov. 1996; K. Vulinec leg.; CEMT • 1 ♀; same data as for preceding; Feb. 1997; V.Z. Vaz-de-Mello leg.; CEMT • 1 ♀; same data as for preceding; Feb. 1998; CEMT • 1 ♂; Guajará-Mirim, Sítio Coletti; 10°19′47″ S, 64°45′12″ W; elev. 170 m; 28 Jan. 2010; pitfall human dung; F. Coletti leg.; CEMT • 1 ♀; same data as for preceding; carcass; CEMT • 1 ♀; Porto Velho, Abunã; 9°38′09″ S, 65°32′47″ W; 13–15 Jan. 2011; J.C.F. Falcão leg.; pitfall human dung; CEMT • 3 ♂♂, 2 ♀♀; Porto Velho, ESEC Cuniã; 8°04′08″ S, 63°28′06″ W; 11–15 Aug. 2012; M.A.P.A. Silveira leg.; pitfall human dung; CEMT • 4 ♀♀; same data as for preceding; 8°04′11″ S, 63°28′34″ W; elev. 83 m; 10–12 Nov. 2013; CEMT.

COLOMBIA – **Amazonas** • 1 ♀; Leticia, Estación Biológica El Zafire; 4°00′21″ S, 69°53′55″ W; elev. 150 m; 2–4 Dec. 2007; L. Franco and S. Flórez; pitfall human dung; IAvH-E. – **Caquetá** • 1 ♂, 2 ♀♀; Puerto Solano, PNN Serranía de Chiribiquete, Puerto Abeja; 0°04′27″ N, 72°27′0.5″ W; elev. 200 m; Jul. 1999; M. Álvares and G. Mejía; IAvH-E • 1 ♂; Puerto Solano, PNN Serrania de Chiribiquete, Río Cunãre; 0°20′ N, 72°37′50″ W; elev. 250 m; 2–4 Nov. 2000; M. Ospina and E. González leg.; flight interception trap; UPTC-CE • 2 ♀♀; same data as for preceding; 0°31′44″ N, 72°37′50″ W; 22–24 Nov. 2000; UPTC-CE • 3 ♀♀; same data as for preceding; 0°30′ N, 72°37′50″ W; 2–4 Nov. 2000; pitfall human dung; IAvH-E • 3 ♀♀; same data as for preceding; 0°32′4″ N, 72°37′57.5″ W; 19–21 Nov. 2000; IAvH-E • 1 ♀; same data as for preceding; 15 Nov. 2000; flight interception trap; IAvH-E • 1 ♂; Puerto Solano, PNN Serranía de Chiribiquete, Río Cuñare - Amú; 0°12′34.5″ N, 72°24′55.1″ W; elev. 250 m; 14 Feb. 2001; E. González and M. Ospina leg.; flight interception trap; IAvH-E • 1 ♂; same data as for preceding; 15–17 Feb. 2001; pitfall human dung; IAvH-E • 1 ♀; same data as for preceding; 0°12′42.8″ N, 72°25′3.2″ W; 21 Feb. 2001; IAvH-E • 1 ♂; same data as for preceding; 0°12′47.8″ N, 72°25′25.4″ W; 1–3 Mar. 2001; IAvH-E • 1 ♀; same data as for preceding; 0°13′3.4″ N, 72°25′22.7″ W; 7–9 Mar. 2001; IAvH-E • 2 ♀♀; Puerto Solano, PNN Serranía de Chiribiquete, Río Mesay; 0°15′38″ N, 72°55′24″ W; elev. 250 m; 24 Jan. 2000; F. Quevedo leg.; pitfall human dung; IAvH-E • 1 ♀; same data as for preceding; 0°14′24″ N, 72°56′2″ W; 25 Jan. 2000; IAvH-E • 1 ♂, 1 ♀; same data as for preceding; 0°14′54″ N, 72°56′5″ W; 28 Jan. 2000; IAvH-E • 1 ♂; same data as for preceding; 0°14′32″ N, 72°56′15″ W; 4 Feb. 2000; IAvH-E • 1 ♂, 1 ♀; Puerto Solano, PNN Serranía de Chiribiquete, Río Sararamano; 0°10′47″ N, 72°37′24″ W; elev. 250 m; 4 Apr. 2000; E. González leg.; flight interception trap; IAvH-E • 1 ♂, 1 ♀; same data as for preceding; 0°09′26″ N, 72°37′45″ W; 11 Apr. 2000; pitfall human dung; IAvH-E • 1 ♂; same data as for preceding; 0°08′26″ N, 72°37′45″ W; 11 Nov. 2000; flight

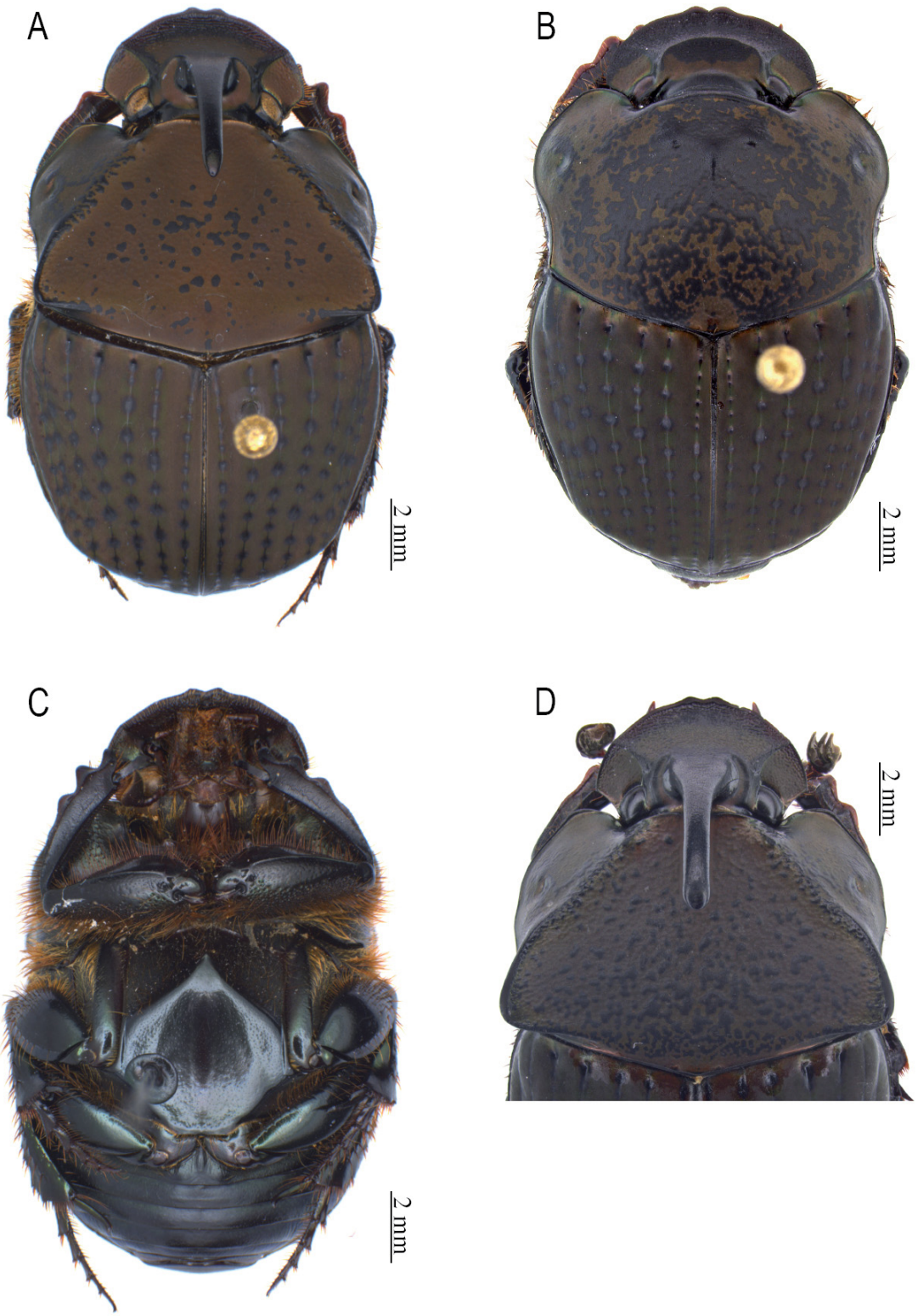

Fig. 5. *Phanaeus cambeforti* Arnaud, 1982. **A**. Male from Amapá, Brazil (CEMT), dorsal view. **B**. Female from Villavicencio, Colombia (CEMT), dorsal view. **C**. Male from Amapá, ventral view (CEMT). **D**. Head and pronotum of major male from Padmi, Ecuador (CEMT), dorsal view.

interception trap; UPTC-CE. – **Cundinamarca** • 1 ♀; Medina, alto del Río Gazaunta; 4°35′ N, 73°23′ W; elev. 550 m; Mar. 1997; F. Escobar leg.; pitfall trap; UPTC-CE • 1 ♂; same data as for preceding; IAvH-E • 4 ♀♀; Medina, Miralindo; 4°35′33″ N, 73°27′17″ W; elev. 550 m; Feb.–Mar. 1997; F. Escobar leg.; pitfall human dung; IAvH-E. – **Guaviare** • 1 ♀; Cerro Cocuy and Cerro Moyano; 2°10′02″ N, 71°10′54″ W; elev. 200 m; 30–31 Jan. 1996; F. Escobar leg.; pitfall human dung; CEMT • 1 ♂; same data as for preceding; IAvH-E • 2 ♂♂, 4 ♀♀; same data as for preceding; 2°10′35″ N, 71°15′58″ W; elev. 300 m; Feb. 1996; IAvH-E. – **Meta** • 1 ♀; Villavicencio, El Carmen; 4°08′38″ N, 73°39′57″ W; elev. 748 m; 23 Apr. 2019; D.C. Martínez leg.; carcass; CEMT • 1 ♂, 1 ♀; Villavicencio, Bosque Bavaria; 4°09′ S, 73°38′ W; elev. 550 m; J. Noriega leg.; pitfall human dung; CEMT • 3 ♂♂; Villavicencio; 29 Feb.–5 Mar. 1972; S. Peck and J. Peck leg.; TAMU • 1 ♀; 30 km Villavicencio; 1–4 Mar. 1972; S. Peck and J. Peck leg.; dung; TAMU • 1 ♀; 16 km of Villavicencio; 2–4 Mar. 1972; S. Peck leg.; dung; TAMU • 1 ♀; 500 m of Villavicencio; 29 Feb.–5 Mar. 1972; Peck and J. Peck leg.; bait traps; TAMU. – **Putumayo** • 1 ♀; Puerto Leguizamo; 00°04′20″ S, 74°59′19″ W; 17 Feb. 2008; L. Jiménez leg.; CCBUMAG.

ECUADOR – **Orellana** • 1 ♀; Francisco de Orellana; 4 May 2000; A. Dávalos leg.; pitfall carcass; CEMT. – **Napo** • 1 ♂, 2 ♀♀; Estación Científica Yasuni Puce, Río Tiputini; 0°40′ S, 76°24′ W; Jul. 1999; A. Trischechkin leg.; flight interception trap; CEMT. – **Zamora-Chinchipe** • 120 ♂♂, 88 ♀♀; Padmi, Estación Experimental El Padmi UNL, BN Ladera; 3°43′58″ S, 78°37′09″ W; elev. 897–970 m; Dec. 2021–Jan. 2022; J. Jiménez leg.; pitfall human dung; LOUNAZ • 2 ♂♂, 1 ♀; same data as for preceding; CEMT.

FRENCH GUIANA – **Cayenne** • 1 ♀; Régina, Réserve Naturelle Nationale des Nouragues; 1996; CEMT • 1 ♀; same data as for preceding; 10 Apr. 1997; CEMT • 1 ♂; same data as for preceding; 31 Mar. 2002; F. Feer leg.; CEMT • 1 ♀; same data as for preceding; 21 Mar. 2003; CEMT. – **Saint- Laurent-du-Maroni** • 1 ♀; Bas Maroni; TAMU.

PERU – **Junín** • 1 ♂, 1 ♀; Satipo, Río Venado; elev. 1137 m; May 2005; A. Santibáñez leg.; TAMU. – **Lima** • 1 ♀; 11 Oct. 1970 (data error); CEMT. – **Loreto** • 1 ♂, 1 ♀; Río Pucacuro; 2°05′55″ S, 75°40′39″ W; elev. 208 m; 26 Nov. 2007; C. Moreno leg.; pitfall human dung; CEMT. – **Madre de Dios** • 1 ♂, 1 ♀; CICRA Field Station, 12°33′07″ S, 70°06′34″ W; elev. 295 m; 7–9 Jun. 2011; Chaboo team leg.; flight interception trap; MUSM • 2 ♂♂, 1 ♀; Pantiacolla Lodge, Alto Madre de Dios River; 12°39′10″ S, 71°15′28″ W; elev. 500 m; 23–26 Oct. 2000; R. Brooks leg.; flight interception trap; CEMT • 1 ♂, 2 ♀♀; PNN Manu, Estación Biológica Pantiacolla; 12°38′48″ S, 71°14′36″ W; 2010; S. Pérez leg.; UPTC-CE. – **San Martín** • 2 ♂♂, 2 ♀♀; Juanjuí; 7 Aug. 2005; P. Melendes leg.; TAMU. – **Ucayali** • 1 ♀; Padre Abad, Boquerón del Padre Abad; elev. 500–550 m; 16 Sep. 1962; J. Schunke L. leg.; carcass; TAMU.

Type locality

French Guiana, Saül.

Distribution

Widely distributed in the Amazon, from the slopes of the Colombian Andes southwards to Bolivia and northeast wards all the way to French Guiana (Fig. 20) between 80 to 438 m a.s.l.

Taxonomic discussion

The smallest species within the *P. chalcomelas* species group, specifically the males. Major males are very rare and seem never to show strongly developed secondary sex characteristics as males of the other species in the group. We observed that the width of the pronotal disc in males exceeded the width of the elytra only in a population collected in Ecuador (Estación Experimental El Padmi Universidad Nacional de Loja, Loja) (Fig. 5D).

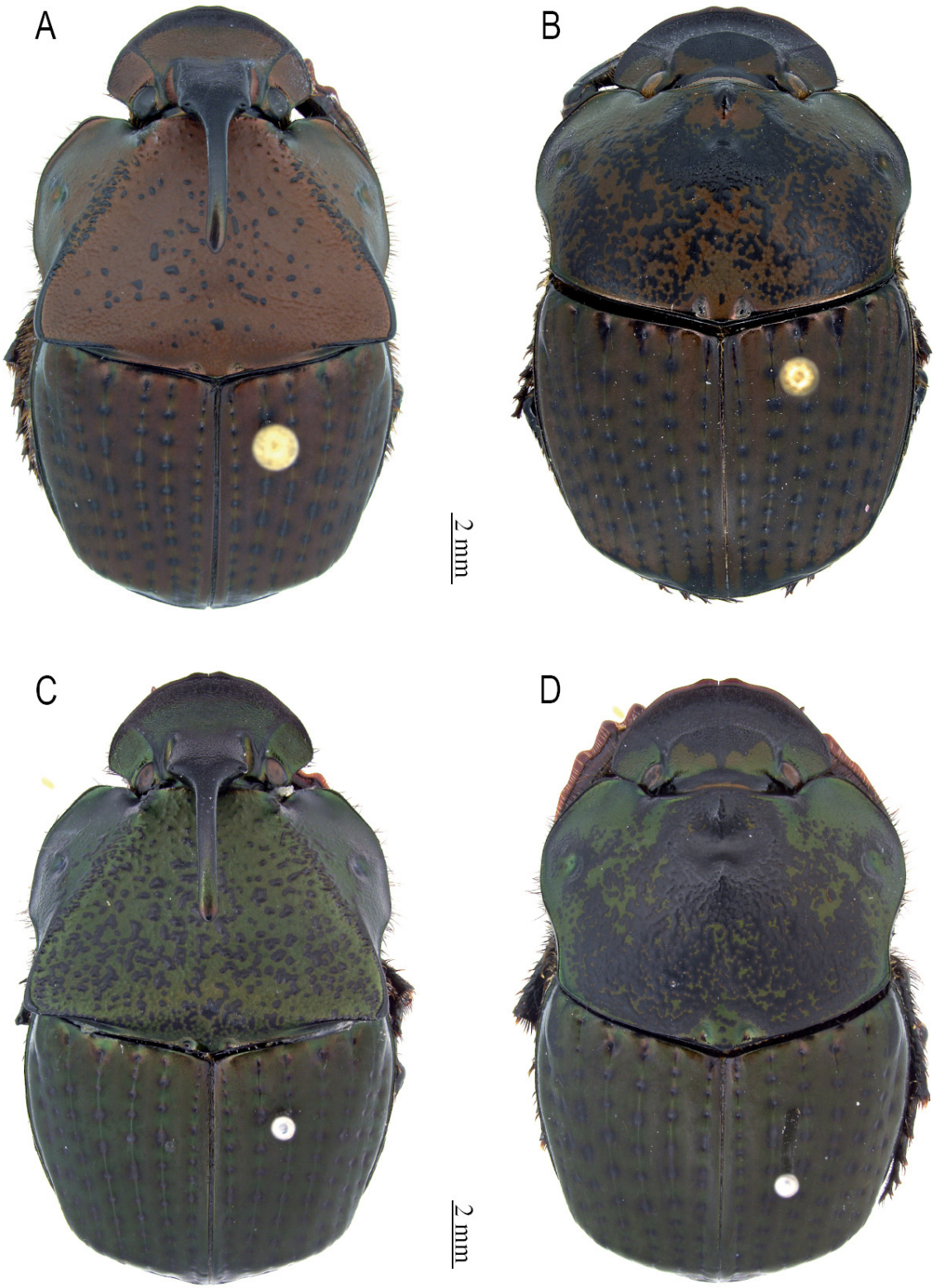

Fig. 6. *Phanaeus chalcomelas* (Perty, 1830), dorsal view. **A–B**. From Amazonas State, Brazil (CEMT). **C–D**. From Santa Cruz de la Sierra, Bolivia (CEMT). A, C = males; B, D = females.

Phanaeus chalcomelas (Perty, 1830)
Figs 1F, 2A, 6–7, 16G–H, 17G–H, 18G–H, 19G–H, 28A

Onitis chalcomelas Perty, 1830: 40.

Phanaeus chalcomelas – Harold 1859: 198; 1869: 1017. — Nevinson 1892: 2. — Gillet 1911b: 82. — d'Olsoufieff 1924: 40, 98, 135, 152. — Blackwelder 1944: 209. — Vulcano & Pereira 1967: 574. — Edmonds 1972: 832. — Vítolo 2000: 597–598. — Medina *et al.* 2001: 140. — Vulinec *et al.* 2003: 353–354. — Feer & Pincebourde 2005: 23–24, 30. — Hamel-Leigue *et al.* 2006: 6, 17. — Cabral-de-Mello *et al.* 2008: 1244, 1247, 1249. — Price & May 2009: 215–216, 236. — Larsen 2011: 99; 2013: 97. — Korasaki *et al.* 2012: 427–428. — Noriega 2012: 4. — Cupello & Vaz-de-Mello 2013: 445, 451. — Feer & Boissier 2015: 169. — Ratcliffe *et al.* 2015: 197. — Lozano de la Rosa *et al.* 2024: 223. — Lizardo *et al.* 2022: 548, 553, 557, 560. — Moctezuma *et al.* 2024: 5. — Moctezuma 2025: 4.

Phanaeus (*Phanaeus*) *chalcomelas* – Pessôa 1934: 305, 312.

Phanaeus (*Notiophanaeus*) *chalcomelas* – Edmonds 1994: 27–28, 100. — Vaz-de-Mello 2000: 194. — Arnaud 2001: 5; 2002: 84–85. — Vítolo 2004: 285, 305–306. — Price 2007: 2–3, 13–14; 2009: 139, 143–144, 146. — Hamel-Leigue *et al.* 2009: 50, 65, 74, 92. — Vaz-de-Mello *et al.* 2011: 84, 89, 96, 99. — Edmonds & Zídek 2012: 3, 5, 10–11, 37, 39. — Krajcik 2012: 204. — Figueroa *et al.* 2014: 127, 131, 134. — Pacheco & Vaz-de-Mello 2015: 3, 6–7. — Boilly *et al.* 2016: 90, 93, 96. — Chamorro *et al.* 2018: 98; 2019: 215–216, 309. — Hielkema & Hielkema 2019: 106. — Gillett & Toussaint 2020: 671, 673, 676.

Phanaeus (*Notiophanaeus*) *chalcomelas grossii* – Arnaud 2001: 5–6; 2002: 84–85. — Hamel-Leigue *et al.* 2009: 65. — Krajcik 2012: 204. — Edmonds & Zídek 2012: 4–5, 8, 11 (as synonym of *P. chalcomelas*).

Onitis chalcomelas – Cupello & Vaz-de-Mello 2013: 445 (as basionym of *P. chalcomelas*). — Cupello *et al.* 2022: 981 (as basionym of *P. chalcomelas*). — Lozano de la Rosa *et al.* 2024: 223 (as basionym of *P. chalcomelas*).

Diagnosis

Dorsum olive green, olive brown or reddish brown (Fig. 6). Ventral color dark green. Anteromedial prominence of metaventrite with regular callosity forming arrowhead pattern (Fig. 2A). Major males with cephalic horn abruptly narrowed basally to mid length (Fig. 16G–H). Pronotum of females with a shallow anteromedial concavity surrounded by four tubercles, anterior tubercle large and distinct, the other three smaller (middle posterior tubercle always posterior to lateral ones) and may blend with the black elevations (Figs 6B, D, 19G–H). Aedeagus: parameres gradually narrowing apically, exhibiting a conical shape (Fig. 7A). Phallobase without sulcus or incisions (Fig. 7B). Endophallus with six endophallites (Fig. 7C–E). Endophallites: A+SA joined by a basal membrane (Fig. 7C–E). Axial endophallite V-shaped, with one branch apically expanded and rounded, and the other narrow and unexpanded; subaxial endophallite broad. FLP narrow and curved, like an arch (Fig. 7C). AE with sharp base and straight apical margin (Fig. 7H). SRP vertically elongated, much larger than other species of *P. chalcomelas* group (Fig. 7I). ME bears three main projections, roughly resembling a Y-shape with asymmetrical and smoothly angled arms (dorsal view); small, slightly more than half a millimeter (Fig. 7F–G).

Type material

Holotype of *Phanaeus chalcomelas* (studied from photographs)

BRAZIL • ♀; Perty, 1830: 40; ZSM. The Amazon rainforest, somewhere visited by Spix and Martius along the Amazon River, the Japura, the lower Madeira, or the Rio Negro (see Papavero 1971 for a map with these places indicated) (see discussion below)

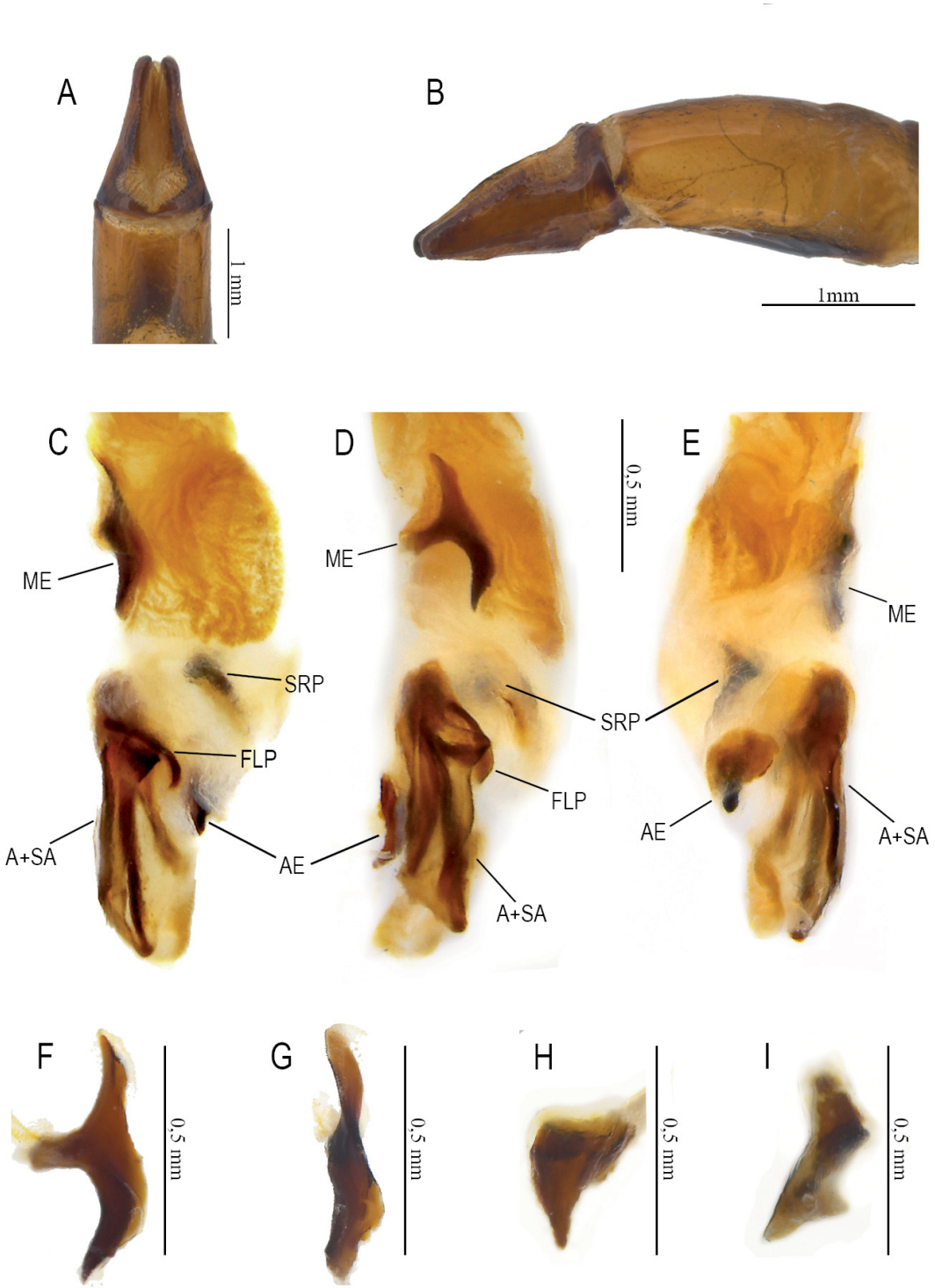

Fig. 7. Male genitalia of *Phanaeus chalcomelas* (Perty, 1830) (CEMT). **A–B**. Aedeagus. **A**. Dorsal view. **B**. Lateral view. **C–E**. Endophalli. **C**. Lateral view. **D**. Dorsal view. **E**. Ventral view. **F–G**. Medial endophallite (ME). **F**. Dorsal view. **G**. Lateral view. **H**. Additional endophallite (AE), ventral view. **I**. Superior right peripheral endophallite (SRP), ventral view. Abbreviations: A = axial endophallite; AE = additional endophallite; FLP = fronto-lateral peripheral endophallite; ME = medial endophallite; SA = subaxial endophallite; SRP = superior right peripheral endophallite.

Paratypes of *Phanaeus chalcomelas grossii*

BOLIVIA – **Chapare** • 1 ♂, 1 ♀; (examined from photographs provided in Arnaud 2002: 84). – **Cochabamba** • 1 ♂; "67.5 km E. Villa Tunari, Est. Biol. Valle Sajta, Univ. San Simon 300 m, 17°06′19″ S 64°46′57″ W; 7–9.II.1999, F. Génier, lowland rain for., ex. dung tp. 3, 99-045"; MHNNKM.

Non-type material examined (447 ♂♂, 568 ♀♀)

BOLIVIA – **Cochabamba** • 1 ♂; PN Carrasco, Río Sajta; Feb. 1993; L. Peña leg.; CEMT • 1 ♀; same data as for preceding; Feb. 1994; CEMT • 1 ♂, 1 ♀; PN Carrasco, Valle Sajta; 17°06′19″ S, 64°46′57″ W; elev. 300 m; 9–13 Feb. 1994; F. Genier leg.; MHNNKM • 3 ♂♂, 3 ♀♀; Palmar; 26 Dec. 2009; T. Vidaurre leg.; MHNNKM • 1 ♂, 2 ♀♀; Chapare, Villa Tunari; 26–29 Oct. 2004; J. Ledezma and I. García leg.; MHNNKM • 2 ♂♂; same data as for preceding; Feb. 1984; P. Arnaud leg.; CEMT. – **La Paz** • 21 ♂♂, 12 ♀♀; Iturralde, Río Nuanu; 21–23 Sep. 2002; W. Aliaga leg.; MHNNKM. – **Santa Cruz** • 1 ♂; Andrés Ibáñez, Espejillos; 27 Apr. 2007; M. Amaya leg.; MHNNKM • 3 ♂♂, 1 ♀; Andrés Ibáñez, Jardín Botánico; 17°46′ S, 63°03′ W; elev. 398 m; 30 Apr. 2006; T. Vidaurre *et al.* leg.; MHNNKM • 14 ♂♂, 9 ♀♀; same data as for preceding; 16–19 Jul. 2006; MHNNKM • 3 ♂♂, 3 ♀♀; Santa Cruz de la Sierra, Jardín Botánico; 17°45′51″ S, 63°39′30″ W; 10 Nov. 2006; Scarabnet exped. leg.; CEMT • 1 ♂; same data as for preceding; 17°47′02″ S, 63°03′47″ W; elev. 400 m; 7–8 Nov. 2006; W.D. Edmonds leg.; pitfall human dung; TAMU • 2 ♀♀; Caballero, Karawasi; 22 Nov. 1998; MHNNKM • 2 ♂♂, 2 ♀♀; Santa Cruz de la Sierra, 4–6 km SSE of Buena Vista, F&F Hotel; elev. 420–450 m; 2–12 Feb. 2000; J.E. Wappes leg.; pitfall dung/carrion; TAMU • 1 ♂, 2 ♀♀; Ichilo, Buena Vista; elev. 400 m; F. Steinbach leg.; TAMU • 10 ♂♂, 7 ♀♀; Ichilo, Buena Vista; 12–13 Feb. 2010; T. Vidaurre leg.; MHNNKM • 1 ♂, 1 ♀; same data as for preceding; 2–9 Nov. 2004; P.H. Sullivan leg.; MHNNKM • 2 ♂♂, 3 ♀♀; same data as for preceding; 2–12 Feb. 2000; J.E. Wappes leg.; MHNNKM • 2 ♂♂, 2 ♀♀; same data as for preceding; 2–13 Feb. 2000; M.C. Thomas leg.; MHNNKM • 1 ♀; same data as for preceding; 23–25 Apr. 1997; S. Amezquita leg.; MHNNKM • 1 ♂, 1 ♀; same data as for preceding; 27–30 Nov. 1997; S. Amezquita leg.; MHNNKM • 2 ♂♂, 3 ♀♀; Ichilo, Campamento Mataracú; 11–17 Oct. 1997; MHNNKM • 2 ♀♀; same data as for preceding; Oct. 1997; RAP-97 exped. leg.; MHNNKM • 2 ♂♂, 2 ♀♀; same data as for preceding; 17–20 Sep. 1997; S. Aysama leg.; MHNNKM • 1 ♂, 1 ♀; same data as for preceding; 3 Mar. 1997; J. Ledezma leg.; MHNNKM • 1 ♂; Ichilo, Caranda; 6–7 Nov. 2004; F. Aguanta leg.; MHNNKM • 1 ♂, 1 ♀; Ichilo, Chore; 17°01′ S, 64°11′ W; elev. 253 m; 9–10 May 1997; F. Copa leg.; MHNNKM • 4 ♂♂, 8 ♀♀; Ichilo, Yapacani (BEEM); 8–12 Aug. 2006; I. García *et al.* leg.; MHNNKM • 1 ♂; Ñuflo de Chavez, San Javier; 29 Nov. 1995; I. García leg.; MHNNKM • 2 ♂♂; San Ignacio de Velasco, Las Gamas; 24–27 Feb. 1997; I. García leg.; MHNNKM • 1 ♂, 1 ♀; same data as for preceding; 21 Nov. 1997; MHNNKM • 3 ♂♂, 3 ♀♀; San Ignacio de Velasco, Los Fierros; 25 Jan. 1997; S. Spector *et al.* leg.; MHNNKM • 1 ♂; San Ignacio de Velasco, RPPN Caparú, 14°48′ S, 61°10′ W; elev. 150 m; 13 Dec. 2005; C. Hamel leg.; MHNNKM • 1 ♂; San Ignacio de Velasco, RPPN Caparú, Lagunitas; 20 Feb. 2007; A. Alcoba and M. Saldias leg.; MHNNKM • 1 ♂, 1 ♀; same data as for preceding; 11 Jan. 2008; R. Palomino leg.; MHNNKM • 1 ♂, 1 ♀; same data as for preceding; 16 Mar. 2008; MHNNKM • 1 ♂; San Ignacio de Velasco, San Miguel; 26 Jan. 2009; T. Vidaurre leg.; MHNNKM • 1 ♀; P.N. Noel Kempf Mercado; 13°54′59″ S, 60°48′51″ W; elev. 500 m; 17–20 Nov. 1999; S. Spector and A. Ayzama leg.; CEMT.

BRAZIL – **Acre** • 3 ♂♂, 4 ♀♀; Mâncio Lima, Parque Nacional da Serra do Divisor; 7°27′4″ S, 73°38′57″ W; 6–8 Dec. 2019; R.A. Azevedo leg.; pitfall human dung; CEMT • 1 ♂, 1 ♀; same data as for preceding; 2–14 Dec. 2019; flight interception trap; CEMT • 5 ♂♂, 6 ♀♀; same data as for preceding; 7°24′58″ S, 73°37′56″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 7°26′46″ S, 73°39′27″ W; 7–9 Dec. 2019; pitfall human dung; CEMT • 5 ♂♂, 8 ♀♀; same data as for preceding; 7°24′59″ S, 73°37′56″ W; 6–8 Dec. 2019; pitfall human dung; CEMT • 1 ♀; Manoel Urbano, Parque Estadual Chandless; 9°22′26″ S, 69°55′20″ W; 11 Jul. 2013; T.F. Brito leg.; CEMT • 5 ♂♂, 1 ♀; Rio Branco, Fazenda Catuaba; Feb. 1997; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♂, 2 ♀♀; Senador Guiomard; 10°04′ S,

67°37′ W; 14–20 Apr. 2017; B.S. Bitencourt leg.; pitfall human dung; CEMT • 1 ♀; Senador Guiomard, Reserva Catuaba; 10°4′27″ S, 67°36′14″ W; 16–21 Jul. 2019; Casagrande leg.; CEMT • 1 ♂; Xapuri, Reserva Chico Mendes; 10°14′ S, 68°42′ W; 19 Oct. 2008; J. Silveira leg.; pitfall human dung; CEMT • 1 ♀; same data as for preceding; 10°15′ S, 68°42′ W; CEMT • 1 ♂; same data as for preceding; 10°31′ S, 68°42′ W; CEMT. – **Amapá** • 1 ♂, 1 ♀; Serra do Navio, Cava Urucum - Amapari; 0°53′6″ N, 51°52′53″ W; Sep. 2000; R. Ribon leg.; CEMT. – **Amazonas** • 1 ♂; Benjamin Constant, Rio Javari; Jan. 1961.; CEMT • 1 ♂, 1 ♀; Benjamin Constant, Guanabara II; 10 Mar. 2004; P.H. Silva leg.; CEMT • 3 ♀♀; Borba, BR–319, km 220; 4°24′3″ S, 60°56′10″ W; 29 Dec. 2015; D. Pires leg.; pitfall human dung; CEMT • 1 ♂; same data as for preceding; 4°24′6″ S, 60°55′22″ W; 30 Dec. 2015; CEMT • 1 ♀; same data as for preceding; 4°22′55″ S, 60°57′19″ W; 29 Dec. 2015; CEMT • 1 ♂; Carauari, Reserva de Desenvolvimento Sustentável de Uacari; 5°46′06″ S, 67°42′40″ W; Jul. 2009; Nicols *et al.* leg.; CEMT • 1 ♀; Careiro, BR–319; 4°8′9″ S, 60°43′31″ W; 3 Dec. 2015; D. Pires leg.; pitfall human dung; CEMT • 3 ♀♀; same data as for preceding; 4°7′39″ S, 60°43′43″ W; CEMT • 6 ♂♂, 3 ♀♀; same data as for preceding; 4°8′40″ S, 60°43′20″ W; CEMT • 3 ♀♀; same data as for preceding; 4°7′58″ S, 60°43′9″ W; 2 Dec. 2015; CEMT • 1 ♂, 6 ♀♀; same data as for preceding; 4°8′58″ S, 60°43′44″ W; CEMT • 1 ♀; same data as for preceding; 3°21′46″ S, 59°51′10″ W; 9 Dec. 2015; CEMT • 2 ♀♀; same data as for preceding; 4°8′28″ S, 60°43′57″ W; 2 Dec. 2015; CEMT • 1 ♀; same data as for preceding; 4°9′28″ S, 60°43′32″ W; CEMT • 2 ♀♀; Coari, Lago Uauaçu; 4°12′59″ S, 62°27′10″ W; elev. 66 m; Jan.–Sep. 2018; J.B.R. Alencar leg.; pitfall human dung; CEMT • 1 ♀; same data as for preceding; 4°13′7″ S, 62°27′9″ W; elev. 63 m; CEMT • 1 ♀; same data as for preceding; 4°15′45″ S, 62°16′2″ W; elev. 55 m; 29 Oct. 2018; CEMT • 1 ♀; Itapiranga, Fazenda Itapiranga; 2°39′56″ S, 58°40′23″ W; 3 May 2019; R.S. Moura leg.; CEMT • 1 ♂, 2 ♀♀; Manaus, Reserva Florestal Adolpho Ducke; 18 Jul. 1978; B.C. Ratcliffe leg.; CEMT • 1 ♂, 1 ♀; same data as for preceding; 25 Oct.–22 Nov. 1977; CEMT • 1 ♀; same data as for preceding; 8 Nov. 1978; CEMT • 4 ♂♂, 5 ♀♀; Manicoré, Reserva Extrativista Lago Capanã Grande, BR 319, km 45; 5°54′33″ S, 62°23′56″ W; 30 Oct.–1 Nov. 2019; R.A. Azevedo leg.; pitfall human dung; CEMT • 2 ♀♀; same data as for preceding; 5°1′5″ S, 62°29′25″ W; 31 Oct.–2 Nov. 2019; CEMT • 1 ♂, 3 ♀♀; same data as for preceding; 5°58′24″ S, 62°27′38″ W; CEMT • 4 ♂♂, 4 ♀♀; same data as for preceding; 5°54′33″ S, 62°23′56″ W; 22–26 Oct. 2019; flight interception trap; CEMT • 6 ♀♀; same data as for preceding; 26–30 Oct. 2019; CEMT • 2 ♂♂, 3 ♀♀; same data as for preceding; 5°58′24″ S, 62°27′38″ W; 23–27 Oct. 2019; CEMT • 3 ♀♀; same data as for preceding; 6°1′5″ S, 62°29′25″ W; CEMT • 2 ♂♂, 3 ♀♀; same data as for preceding; 27–31 Oct. 2019; CEMT • 1 ♂; same data as for preceding; 31 Oct.–4 Nov. 2019; CEMT • 2 ♂♂, 1 ♀; Manicoré, BR 319, km 350; 5°12′56″ S, 61°50′22″ W; 30 Jul.–2 Aug. 2007; H. Gasca leg.; CEMT • 1 ♂, 5 ♀♀; Presidente Figueiredo; Nov. 1997; E. Andresen leg.; CEMT • 1 ♀; same data as for preceding; Oct.–Nov. 1996; CEMT • 1 ♂; same data as for preceding; *Alouatta* dung; CEMT • 1 ♂; Silves; 2°53′53″ S, 58°54′10″ W; 4–11 May 2019; R.S. Moura leg.; CEMT. – **Mato Grosso** • 2 ♂♂; Alta Floresta; May 2008; E. Berenguer leg.; pitfall human dung; CEMT • 2 ♂♂, 2 ♀♀; same data as for preceding; 9°56′52″ S, 56°3′2″ W; CEMT • 2 ♂♂, 4 ♀♀; same data as for preceding; 9°41′24″ S, 55°56′28″ W; Jun. 2008; CEMT • 1 ♀; same data as for preceding; 9°58′46″ S, 56°5′31″ W; CEMT • 2 ♀♀; same data as for preceding; 9°52′53″ S, 56°6′13″ W; CEMT • 2 ♀♀; same data as for preceding; 9°53′40″ S, 56°16′34″ W; CEMT • 4 ♂♂, 8 ♀♀; same data as for preceding; 9°49′44″ S, 56°19′51″ W; CEMT • 4 ♀♀; Alta Floresta, Ceplac; 24 May 2009; V. Gonçalves leg.; CEMT • 1 ♂, 1 ♀; Alta Floresta, Parque Estadual do Cristalino; 9°35′50″ S, 55°53′40″ W; 11–15 Nov. 2019; R.A. Azevedo leg.; flight interception trap; CEMT • 1 ♂, 5 ♀♀; same data as for preceding; 9°40′59″ S, 55°54′58″ W; 12–16 Nov. 2019; CEMT • 1 ♂, 3 ♀♀; same data as for preceding; 20–24 Nov. 2019; CEMT • 1 ♀; same data as for preceding; 16–20 Nov. 2019; CEMT • 2 ♂♂; same data as for preceding; 9°35′50″ S, 55°53′40″ W; 15–17 Nov. 2019; CEMT • 2 ♀♀; same data as for preceding; pitfall human dung; CEMT • 3 ♀♀; same data as for preceding; 9°32′45″ S, 55°54′56″ W; CEMT • 3 ♀♀; same data as for preceding; 9°40′59″ S, 55°53′40″ W; CEMT • 2 ♂♂, 1 ♀; Araputanga, Fazenda Bandeirantes; 15°23′26″ S, 58°24′48″ W; elev. 296 m; 18–20 Jan. 2013; R.J Silva leg.; pitfall human dung; CEMT • 1 ♂, 2 ♀♀; same data as for preceding; 15°23′6″ S, 58°26′2″ W; elev. 308 m; 19–21 Jan. 2013; CEMT • 2 ♂♂; same

data as for preceding; 15°23′4″ S, 58°26′ W; elev. 296 m; 21–23 Jan. 2013; CEMT • 1 ♂, 2 ♀♀; Aripuanã, Fazenda Águas Claras; 10°12′9″ S, 52°34′26″ W; elev. 275 m; 9–11 Oct. 2018; R.J Silva leg.; flight interception trap; CEMT • 1 ♀; Aripuanã, Serra do Expedito; 10°4′22″ S, 59°30′41″ W; 25 Jan. 2017; T. Semedo leg.; CEMT • 1 ♂; Brasnorte, Fazenda Estrela do Sul; 12°27′30″ S, 58°6′29″ W; elev. 336 m; 30 Jan.–1 Feb. 2018; U.F. Santos leg.; pitfall human dung; CEMT • 1 ♀; same data as for preceding; Fazenda Agriter; 13°2′37″ S, 57°52′55″ W; elev. 434 m; CEMT • 1 ♀; Carlinda; 13 May 2008; C.R. Menezes leg.; CEMT • 1 ♀; Carlinda; 14 Oct. 2008; I.B. Banheza leg.; CEMT • 1 ♂; Carlinda; 15 Oct. 2008; B.R. Krause leg.; CEMT • 1 ♂; Carlinda; 16 Oct. 2008; I.B. Banheza leg.; CEMT • 1 ♀; same data as for preceding; L.A. Aguiar leg.; CEMT • 3 ♂♂, 10 ♀♀; Carlinda; 21–23 Oct. 2008; K. Segatto *et al.* leg.; CEMT • 1 ♂; Carlinda; 12 Oct. 2009; J.S. Costa leg.; CEMT • 1 ♀; Claudia, Fazenda Continental; 11°25′41″ S, 55°18′54″ W; 20 Oct. 2011; M.F. Souza leg.; pitfall human dung; CEMT • 1 ♀; Cotriguaçu, Fazenda São Nicolau; 9°50′24″ S, 58°15′10″ W; elev. 250 m; 5 Oct. 2009; F.Z. Vaz-de-Mello leg.; pitfall human dung; CEMT • 7 ♂♂, 10 ♀♀; same data as for preceding; 8–12 Oct. 2009; CEMT • 1 ♀; same data as for preceding; 9°51′18″ S, 58°13′20″ W; elev. 200 m; Oct. 2009; CEMT • 1 ♂, 6 ♀♀; same data as for preceding; 9°50′19″ S, 58°15′3″ W; 8 Oct. 2009; CEMT • 2 ♀♀; same data as for preceding; pitfall cow dung; CEMT • 7 ♂♂, 2 ♀♀; same data as for preceding; 9°51′36″ S, 58°12′53″ W; Oct. 2009; pitfall human dung; CEMT • 3 ♂♂, 3 ♀♀; same data as for preceding; 9°50′53″ S, 58°14′36″ W; 11 Dec. 2009; CEMT • 4 ♂♂; same data as for preceding; 9°50′24″ S, 58°15′10″ W; elev. 250 m; 13 Dec. 2009; CEMT • 1 ♂, 2 ♀♀; same data as for preceding; 9°50′19″ S, 58°15′3″ W; Dec. 2009; horse dung; CEMT • 6 ♂♂, 9 ♀♀; same data as for preceding; 11–13 Dec. 2009; pitfall human dung; CEMT • 1 ♀; same data as for preceding; 9°49′9″ S, 58°15′47″ W; 8–10 Dec. 2009; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°51′36″ S, 58°12′53″ W; 11–13 Dec. 2009; CEMT • 1 ♀; same data as for preceding; 9°49′9″ S, 58°15′30″ W; 24–31 Oct. 2014; M. Karam-Gemael leg.; CEMT • 2 ♀♀; same data as for preceding; 9°50′19″ S, 58°15′15″ W; 30 Oct. 2017; F.Z. Vaz-de-Mello leg.; matinha do Fernando; flight interception trap; CEMT • 3 ♂♂, 5 ♀♀; same data as for preceding; 3 Nov. 2017; CEMT • 3 ♂♂, 2 ♀♀; same data as for preceding; 9°49′17″ S, 58°15′32″ W; PPBio 1; 1–3 Nov. 2017; CEMT • 1 ♀; same data as for preceding; 9°52′31″ S, 58°16′21″ W; 2 Nov. 2017; R. Stofel leg.; trail of garrote; CEMT • 8 ♂♂, 4 ♀♀; same data as for preceding; 9°51′ S, 58°14′ W; 4–6 Nov. 2017; J.P. Santos leg.; pitfall human dung; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°50′15″ S, 58°15′14″ W; 23–29 Oct. 2018; V. Costa-Silva leg.; CEMT • 2 ♀♀; same data as for preceding; 9°50′05″ S, 58°16′04″ W; 18–20 Oct. 2021; J. Mariano *et al.* leg.; pitfall human dung; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°50′07″ S, 58°16′ W; CEMT • 2 ♀♀; same data as for preceding; 9°50′10″ S, 58°16′ W; CEMT • 3 ♂♂, 2 ♀♀; same data as for preceding; 9°50′47″ S, 58°14′09″ W; 19–21 Oct. 2021; CEMT • 1 ♂, 3 ♀♀; same data as for preceding; 9°50′49″ S, 58°14′04″ W; CEMT • 3 ♀♀; same data as for preceding; 9°52′08″ S, 58°15′19″ W; CEMT • 4 ♀♀; same data as for preceding; 9°51′25″ S, 58°15′16″ W; 27–29 Oct. 2021; CEMT • 6 ♂♂, 4 ♀♀; same data as for preceding; 9°50′ S, 58°15′ W; 28–30 Oct. 2021; CEMT • 7 ♂♂, 1 ♀; same data as for preceding; 9°49′12″ S, 58°15′30″ W; CEMT • 3 ♂♂, 2 ♀♀; same data as for preceding; 9°49′47″ S, 58°16′19″ W; 1–3 Nov. 2021; CEMT • 2 ♂♂, 2 ♀♀; same data as for preceding; 9°49′47″ S, 58°16′21″ W; CEMT • 4 ♂♂, 4 ♀♀; same data as for preceding; 9°49′47″ S, 58°16′22″ W; CEMT • 3 ♂♂; same data as for preceding; 9°49′47″ S, 58°16′24″ W; CEMT • 2 ♀♀; same data as for preceding; 9°49′47″ S, 58°16′26″ W; CEMT • 1 ♂, 2 ♀♀; same data as for preceding; 9°50′10″ S, 58°15′49″ W; CEMT • 1 ♂, 2 ♀♀; same data as for preceding; 9°50′11″ S, 58°15′50″ W; CEMT • 2 ♀♀; same data as for preceding; 9°51′43″ S, 58°13′10″ W; 2–4 Nov. 2021; CEMT • 1 ♂; same data as for preceding; 9°51′42″ S, 58°13′11″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°51′26″ S, 58°14′24″ W; CEMT • 1 ♂; same data as for preceding; 9°51′32″ S, 58°14′23″ W; CEMT • 1 ♂; same data as for preceding; 9°51′31″ S, 58°14′23″ W; CEMT • 1 ♀; same data as for preceding; 9°51′28″ S, 58°14′23″ W; CEMT • 2 ♂♂, 5 ♀♀; same data as for preceding; 9°49′43″ S, 58°16′30″ W; 3–5 Nov. 2021; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°49′43″ S, 58°16′32″ W; CEMT • 1 ♂, 2 ♀♀; same data as for preceding; 9°49′43″ S, 58°16′34″ W; CEMT • 3 ♀♀; same data as for preceding; 9°49′43″ S, 58°16′35″ W; CEMT • 1 ♂, same data as for preceding;

9°49′44″ S, 58°16′29″ W; CEMT • 1 ♀; same data as for preceding; 9°49′26″ S, 58°15′49″ W; 4–6 Nov. 2021; CEMT • 1 ♀; same data as for preceding; 9°49′48″ S, 58°16′11″ W; CEMT • 1 ♀; same data as for preceding; 9°49′49″ S, 58°16′09″ W; CEMT • 1 ♂, same data as for preceding; 9°49′50″ S, 58°16′06″ W; CEMT • 2 ♂♂, 1 ♀; same data as for preceding; 9°50′53″ S, 58°15′19″ W; CEMT • 7 ♂♂, 4 ♀♀; same data as for preceding; 9°50′54″ S, 58°15′21″ W; CEMT • 2 ♀♀; same data as for preceding; 9°50′55″ S, 58°15′21″ W; CEMT • 1 ♀; same data as for preceding; 9°50′56″ S, 58°15′22″ W; CEMT • 1 ♀; same data as for preceding; 9°50′58″ S, 58°15′23″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°50′55″ S, 58°14′10″ W; 5–7 Nov. 2021; CEMT • 2 ♀♀; same data as for preceding; 9°50′56″ S, 58°14′08″ W; CEMT • 3 ♂♂, 3 ♀♀; same data as for preceding; 9°51′01″ S, 58°14′10″ W; CEMT • 1 ♂, 3 ♀♀; same data as for preceding; 9°51′02″ S, 58°14′07″ W; CEMT • 3 ♂♂; same data as for preceding; 9°51′03″ S, 58°14′06″ W; CEMT • 1 ♂, 4 ♀♀; same data as for preceding; 9°49′25″ S, 58°16′17″ W; CEMT • 5 ♀♀; same data as for preceding; 9°49′26″ S, 58°16′38″ W; CEMT • 2 ♀♀; same data as for preceding; 9°49′27″ S, 58°16′38″ W; CEMT • 1 ♂; same data as for preceding; 9°49′27″ S, 58°16′14″ W; CEMT • 1 ♂; same data as for preceding; 9°49′29″ S, 58°16′39″ W; CEMT • 2 ♂♂, 6 ♀♀; same data as for preceding; 9°49′30″ S, 58°16′12″ W; CEMT • 2 ♂♂, 4 ♀♀; same data as for preceding; 9°49′30″ S, 58°16′39″ W; CEMT • 1 ♂, 3 ♀♀; same data as for preceding; 9°49′32″ S, 58°16′39″ W; CEMT • 3 ♂♂, 4 ♀♀; same data as for preceding; 9°50′56″ S, 58°14′06″ W; CEMT • 2 ♂♂, 1 ♀; same data as for preceding; 9°50′57″ S, 58°14′05″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°51′02″ S, 58°14′09″ W; CEMT • 2 ♀♀; same data as for preceding; 9°51′08″ S, 58°16′20″ W; CEMT • 1 ♀; same data as for preceding; 9°51′09″ S, 58°16′21″ W; CEMT • 1 ♀; same data as for preceding; 9°51′11″ S, 58°16′22″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°51′43″ S, 58°15′50″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°51′48″ S, 58°15′50″ W; CEMT • 1 ♀; Diamantino; Feb. 2003; E. Furtado leg.; CEMT • 1 ♂; Diamantino; 16 Mar. 2018; L.G. Nunes and E. Carvalho leg.; CEMT • 1 ♂, 1 ♀; same data as for preceding; 13°48′07″ S, 56°41′32″ W; 17 Mar. 2018; pitfall human dung; CEMT • 1 ♀; same data as for preceding; 13°48′02″ S, 56°41′08″ W; pitfall human dung; CEMT • 1 ♂; same data as for preceding; Semidouro; 13°48′51″ S, 56°41′32″ W; pitfall human dung; CEMT • 3 ♂♂, 1 ♀; Indiavaí, Faz. Alto Jaurú; 15°27′18″ S, 58°33′12″ W; elev. 231 m; 14–16 Jan. 2013; R.J. Silva leg.; pitfall human and pig dung; CEMT • 2 ♂♂, 1 ♀; Juína, Fazenda Quiles; 29 Nov. 2013; R.J. Silva leg.; carcass; CEMT • 1 ♂; Nova Maringá, Faz. Nova Fronteira; 13°15′02″ S, 57°04′45″ W; elev. 356 m; 19–21 Dec. 2017; U.F. Santos leg.; pitfall human dung; CEMT • 2 ♂♂, 1 ♀; Novo Mundo, Parque Estadual do Cristalino; 9°28′01″ S, 55°47′43″ W; May 2013; V. Magalhães leg.; pitfall; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°28′06″ S, 55°50′36″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 9°28′09″ S, 55°48′15″ W; CEMT • 1 ♂; same data as for preceding; 9°27′6″ S, 55°50′02″ W; CEMT • 1 ♂, 1 ♀; Paranaíta; 9°14′16″ S, 57°0′14″ W; Dec. 2015; M.A.L. Bragança leg.; pitfall; CEMT • 1 ♂; same data as for preceding; 9°15′39″ S, 56°48′50″ W; CEMT • 1 ♂; 9°15′56″ S, 56°58′45″ W; CEMT • 1 ♀; same data as for preceding; 9°15′40″ S, 56°48′46″ W; CEMT • 2 ♂♂; Paranaíta, Rio Teles Pires; 24 Oct. 2009; H.A.B. Faria leg.; CEMT • 3 ♂♂; São José do Rio Claro; 13°53′10″ S, 56°40′42″ W; 30 Jun. 2018; L.G. Nunes and E. Carvalho leg.; pitfall human dung; CEMT • 1 ♀; Tangará da Serra, Fazenda Curitiba; 14°22′18″ S, 57°29′24″ W; elev. 343 m; 31 Mar. 2012; R.J. Silva leg.; pitfall cow dung; CEMT • 1 ♂, 1 ♀; Tangará da Serra, Fazenda Rosa Branca; 14°34′ S, 57°45′24″ W; elev. 468 m; 18–27 Feb. 2011; R.J. Silva leg.; pitfall human and pig dung; CEMT • 1 ♂, 3 ♀♀; Tangará da Serra, Fazenda Netolândia; 14°42′18″ S, 57°54′14″ W; elev. 310 m; 14–21 Dec. 2012; R.J. Silva leg.; flight interception trap; CEMT • 1 ♂, 1 ♀; same data as for preceding; 14°41′05″ S, 57°54′08″ W; elev. 263 m; 25–27 Mar. 2012; pitfall cow dung; CEMT • 1 ♂; same data as for preceding; 14°39′56″ S, 57°54′08″ W; elev. 304 m; 20–22 Mar. 2012; CEMT • 1 ♂; same data as for preceding; 14°39′54″ S, 57°55′05″ W; elev. 330 m; 12–14 Mar. 2012; pitfall human and pig dung; CEMT. – **Pará** • 1 ♂; Almeirim, Monte Dourado, 1°1′ S, 52°44′ W; elev. 150 m; Jul. 2004; T.A. Gardner leg.; pitfall dung; CEMT • 5 ♂♂, 1 ♀; Monte Dourado, Pacanari; 0°38′ S, 52°35′ W; Mar. 2006; Gardner and Hernandez leg.; dung trap; TAMU • 1 ♂, 1 ♀; Cachimbo; Oct. 1995; Pe. Pereira leg.; TAMU • 5 ♂♂, 2 ♀♀; 9°12′21″ S, 56°57′34″ W; Dec. 2015; M.A.L. Bragança leg.; pitfall; CEMT • 1 ♂; same data as for preceding; 9°12′35″ S, 56°57′39″ W; CEMT • 1 ♀;

Jacareacanga, Rio Teles Pires; 9°15′48″ S, 56°46′42″ W; 9 Jun. 2009; M.F. Souza and M. Uehara-Prado leg.; pitfall human dung; CEMT • 1 ♂; same data as for preceding; 9°19′3″ S, 56°46′41″ W; 8 Jun. 2009; CEMT • 2 ♀♀; Novo Progresso, Fazenda Florentino; 7°8′51″ S, 55°23′38″ W; Jan. 2011; T.D. Pelissari leg.; pitfall human dung; CEMT • 1 ♀; same data as for preceding; 7°6′54″ S, 55°24′23″ W; CEMT • 1 ♂; same data as for preceding; 7°6′21″ S, 55°25′13″ W; Mar. 2011; CEMT • 1 ♀; same data as for preceding; 7°54′19″ S, 55°29′59″ W; 2 Jan. 2011; CEMT • 1 ♀; same data as for preceding; 7°53′18″ S, 55°30′26″ W; 12 Jan. 2011; CEMT • 3 ♂♂, 1 ♀; Redenção, Fazenda Marajoara; 7°50′ S, 50°16′ W; Oct. 1998; P.Y. Scheffer leg.; CEMT • 1 ♂, 1 ♀; Redenção, Pinkaiti - Aik; 7°46′ S, 51°58′ W; Oct. 1999; P.Y. Scheffer leg.; CEMT • 1 ♂, 1 ♀; Santarém, Reserva Tapajós; 2°46′ S, 55°40′ W; 25 Dec. 2008; R. Andrade leg.; pitfall human dung; CEMT • 1 ♂, 1 ♀; Tailândia, Empresa Agropalma; 9–15 Jul. 2016; F. Silva leg.; CEMT. – **Rondônia** • 1 ♂; Alto Paraíso; Jul. 2002; E. Furtado leg.; CEMT • 2 ♂♂, 1 ♀; same data as for preceding; 12–17 Aug. 2002; CEMT • 2 ♀♀; same data as for preceding; Sep. 2002; CEMT • 5 ♂♂, 2 ♀♀; same data as for preceding; W. Furtado leg.; CEMT • 1 ♂, 1 ♀; same data as for preceding; Oct. 2002; CEMT • 3 ♂♂, 2 ♀♀; same data as for preceding; Nov. 2002; CEMT • 1 ♀; same data as for preceding; 13–23 Apr. 2013; E. Furtado leg.; CEMT • 1 ♂, 1 ♀; 62 km SW of Ariquemes, Fazenda Rancho Grande; 18–29 Sep. 1996; D.G. Marqua leg.; TAMU • 1 ♀; 60 km SW of Ariquemes, Fazenda Rancho Grande; Feb. 1997; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♂, 2 ♀♀; Cacaulândia, Fazenda Rancho Grande; Feb. 1997; F.Z. Vaz-de-Mello leg.; CEMT • 1 ♀; Guajará-Mirim, Fazenda Agropecuária AJB; elev. 180 m; 15 Jan. 2010; F. Coletti leg.; carcass; CEMT • 1 ♂; Guajará-Mirim, Aristeu; 10°22′16″ S, 64°44′47″ W; elev. 220 m; 27 Jan. 2010; F. Coletti leg.; carcass; CEMT • 1 ♂; same data as for preceding; Fandinho; 10°44′57″ S, 64°19′ W; elev. 138 m; 24 Aug. 2010; cow dung; CEMT • 1 ♀; Itapuã do Oeste, FloNa Jamari; 9°11′34″ S, 63°06′34″ W; 20 Feb. 2013; J.F. Cerveira leg.; *Mazama americana* dung; CEMT • 1 ♀; same data as for preceding; 9°11′33″ S, 63°06′47″ W; CEMT • 1 ♀; same data as for preceding; 9°11′29″ S, 63°06′48″ W; CEMT • 1 ♀; same data as for preceding; 9°11′27″ S, 63°06′36″ W; *Mazama gouazoubira* dung; CEMT • 1 ♂; same data as for preceding; 9°11′32″ S, 63°06′35″ W; CEMT • 1 ♀; same data as for preceding; 9°05′39″ S, 63°08′55″ W; CEMT • 1 ♀; same data as for preceding; 9°11′24″ S, 63°06′50″ W; *Mazama nemorivaga* dung; CEMT • 2 ♀♀; Pimenta Bueno; 11°43′3.21″ S, 61°28′19.8″ W; 27–29 Jul. 2015; elev. 249 m; D.C. Castro leg.; pitfall human dung; CEMT • 1 ♂; same data as for preceding; 11°43′3.26″ S, 61°28′20.41″ W; CEMT • 2 ♂♂; same data as for preceding; 11°43′3.28″ S, 61°28′21″ W; CEMT • 1 ♂; same data as for preceding; 11°43′3.32″ S, 61°28′21.64″ W; CEMT • 2 ♀♀; same data as for preceding; 11°43′3.8″ S, 61°28′21.5″ W; CEMT • 3 ♀♀; same data as for preceding; 11°43′4.8″ S, 61°28′18.4″ W; CEMT • 1 ♂; same data as for preceding; 11°43′4.96″ S, 61°28′21.64″ W; CEMT • 1 ♀; same data as for preceding; 11°43′5.43″ S, 61°28′18.39″ W; CEMT • 1 ♂, 1 ♀; same data as for preceding; 11°43′3.17″ S, 61°28′19.2″ W; 9–11 Dec. 2015; CEMT 2 • ♀♀; same data as for preceding; 11°43′3.82″ S, 61°28′20.32″ W; CEMT • 1 ♀; same data as for preceding; 11°43′4.29″ S, 61°28′18.39″ W; CEMT • 2 ♀♀; same data as for preceding; 11°43′4.32″ S, 61°28′19.08″ W; CEMT • 1 ♀; same data as for preceding; 11°43′4.9″ S, 61°28′21.35″ W; CEMT • 1 ♂; same data as for preceding; 11°43′5.49″ S, 61°28′20.26″ W; CEMT • 1 ♀; same data as for preceding; 11°43′5.49″ S, 61°28′21.71″ W; CEMT • 1 ♀; Porto Velho, Abunã; 9°35′46″ S, 60°40′19″ W; 17–19 May 2010; L.R. Silva and F.F. Albertoni leg.; pitfall human dung; CEMT • 1 ♂; same data as for preceding; 9°36′38″ S, 65°21′33″ W; elev. 200 m; 19 Sep. 2010; J.C.F. Falcão leg.; pitfall human dung; CEMT • 1 ♀; same data as for preceding; Jirau; 9°35′48″ S, 65°21′56″ W; elev. 250 m; J.C.F. Falcão and L.R. Silva leg.; flight interception trap; CEMT • 1 ♂, 2 ♀♀; Porto Velho, EsEc Cuniã; 8°4′11″ S, 63°28′34″ W; elev. 83 m; 10–12 Nov. 2013; M.A.P.A. Silveira leg.; pitfall human dung; CEMT • 1 ♂; same data as for preceding; 13–15 Aug. 2012; C. Moreno leg.; CEMT • 1 ♂, 1 ♀; Porto Velho, Mutum Paraná; 9°35′ S, 63°03′ W; 15–17 Sep. 2010; J.C.F. Falcão and L.R. Silva leg.; pitfall human dung; CEMT • 1 ♂, 2 ♀♀; same data as for preceding; 9°35′46″ S, 63°02′27″ W; Sep. 2012; R.V. Nunes leg.; CEMT • 2 ♀♀; Porto Velho, Nova Mutum Paraná; 9°26′31″ S, 60°12′44″ W; 27–28 Feb. 2010; L.R. Silva and R.L.R. Silva leg.; pitfall human dung; CEMT.

COLOMBIA – **Amazonas** • 1 ♂, 1 ♀; Leticia; elev. 213 m; 23 Feb.–2 Mar. 1974; S. Peck leg.; TAMU • 1 ♀; Leticia, Estación Biológica El Zafire; 4°00′21″ S, 69°53′55″ W; elev. 150 m; 2–4 Dec. 2007; L. Franco and S. Flórez leg.; pitfall human dung; IAvH-E • 3 ♂♂, 1 ♀; same data as for preceding; 3°59′15″ S, 69°54′10″ W; elev. 164 m; 9–11 Dec. 2007; IAvH-E. – **Caquetá** • 2 ♀♀; Puerto Solano, PNN Serranía de Chiribiquete, Estación Puerto Abeja; 0°04′27″ N, 72°27′0.5″ W; elev. 200 m; Jul. 1999; M. Álvarez and G. Mejía leg.; IAvH-E • 1 ♀; Puerto Solano, PNN Serranía de Chiribiquete, Río Amú; 0°12′42″ N, 72°25′3″ W; elev. 250 m; 21 Mar. 2001; M. Ospina and E. González leg.; pitfall human dung; UPTC-CE • 1 ♂, 1 ♀; Puerto Solano, PNN Serranía de Chiribiquete, Río Cuñare; 0°20′ N, 72°37′50″ W; elev. 250 m; 2–4 Nov. 2000; M. Ospina and E. González leg.; pitfall human dung; UPTC-CE • 4 ♂♂, 1 ♀; same data as for preceding; IAvH-E • 2 ♂♂, 4 ♀♀; same data as for preceding; 0°31′3″ N, 72°38′27.7″ W; 10–12 Nov. 2000; IAvH-E • 1 ♂, 1 ♀; same data as for preceding; 0°32′4″ N, 72°37′57.5″ W; 19– 21 Nov. 2000; IAvH-E • 1 ♂; same data as for preceding; Río Cuñare - Amú; 0°12′34.5″ N, 72°24′55.1″ W; 15–17 Feb. 2001; IAvH-E • 2 ♂♂, 2 ♀♀; same data as for preceding; 0°12′42.8″ N, 72°25′3.2″ W; 21 Feb. 2001; IAvH-E • 1 ♂, 1 ♀; same data as for preceding; 0°12′47.8″ N, 72°25′25.4″ W; 1–3 Mar. 2001; IAvH-E • 1 ♂, 3 ♀♀; Puerto Solano, PNN Serranía de Chiribiquete, Río Mesay; 0°15′38″ N, 72°55′24″ W; elev. 250 m; 24 Jan. 2000; F. Quevedo leg.; pitfall human dung; IAvH-E • 2 ♂♂, 1 ♀; Puerto Solano, PNN Serranía de Chiribiquete, Río Sararamano; 0°09′26″ N, 72°37′45″ W; elev. 250 m; 11 Apr. 2000; E. González leg.; pitfall human dung; UPTC-CE • 2 ♀♀; same data as for preceding; IAvH-E • 1 ♂, 2 ♀♀; same data as for preceding; flight interception trap; UPTC-CE • 2 ♀♀; same data as for preceding; 0°10′02″ N, 72°36′35″ W; 8 Apr. 2000; pitfall human dung; IAvH-E • 1 ♂, 2 ♀♀; same data as for preceding; 4 Apr. 2000; flight interception trap; IAvH-E • 1 ♂, 2 ♀♀; same data as for preceding; 0°10′47″ N, 72°37′24″ W; IAvH-E • ♀; same data as for preceding; pitfall human dung; IAvH-E • 1 ♂, 1 ♀; same data as for preceding; 6 Apr. 2000; IAvH-E • 2 ♀♀; same data as for preceding; 19 Apr. 2000; IAvH-E. – **Meta** • 10 ♂♂, 15 ♀♀; PNN Tinigua, CIEM, Río Duda; 2°40′ N, 74°10′ W; elev. 350 m; Jan. 1996; I. Jiménez leg.; pitfall human dung; IAvH-E • 3 ♂♂, 6 ♀♀; Puerto López, El Naranjal; 04°05′14″ N, 72°57′30″ W; elev. 220 m; Feb. 1997; F. Escobar leg.; IAvH-E • 1 ♂; Puerto López, Vereda Remolino; 4°11′57.8″ N, 72°33′36.5″ W; elev. 2015 m; 10 Nov. 2018; pitfall human dung; D.C. Martínez leg.; IAvH-E • 1 ♀; same data as for preceding; 4°15′10.1″ N, 72°34′10.8″ W; elev. 210 m; IAvH-E • 1 ♀; same data as for preceding; 4°12′34.5″ N, 72°34′54.9″ W; elev. 201 m; 11 Nov. 2018; IAvH-E • 1 ♂; same data as for preceding; 4°13′30.9″ N, 72°34′3.2″ W; elev. 193 m; IAvH-E • 1 ♀; same data as for preceding; 4°15′3.7″ N, 72°34′11.5″ W; elev. 207 m; IAvH-E • 1 ♂; same data as for preceding; 4°11′57.2″ N, 72°33′32.8″ W; elev. 214 m; 12 Nov. 2018; IAvH-E • 1 ♂, 2 ♀♀; San Martín, La laguna; 3°42′27.09″ N, 73°32′32.76″ W; elev. 337,4 m; I. Lina leg.; pitfall human dung; IAvH-E • 3 ♂♂, 3 ♀♀; Villavicencio; 4°03′07″ N, 74°15′57″ S; elev. 350 m; Mar. 1998; A. Camacho leg.; pitfall human dung; UPTC-CE • 1 ♂, 1 ♀; same data as for preceding; IAvH-E • 1 ♂, 3 ♀♀; same data as for preceding; 04°02′ N, 75°78′15″ W; elev. 150 m; IAvH-E • 2 ♂♂, 1 ♀; same data as for preceding; 4°02′ N, 73°15′ W; elev. 200 m; 19 Oct. 2009; D. López leg.; UPTC-CE • 1 ♂, 1 ♀; 33 km E of Villavicencio; 2–4 Mar. 1972; S. Peck and J. Peck leg.; dung trap; TAMU. – **Putumayo** • 1 ♂, 1 ♀; Puerto Leguizamo; 00°04′20″ S, 74°59′19″ W; 17 Feb. 2008; L. Jiménez leg.; CCBUMAG • 1 ♂; same data as for preceding; 00°05′03″ S, 74°59′28″ W; 20 Feb. 2008; L. Jiménez leg.; CCBUMAG • 1 ♂; Santa Rosa, headwaters Río San Miguel; 24–25 Oct. 1970; Malkin and Burchard leg.; TAMU. – **Vaupés** • 2 ♂♂, 4 ♀♀; Reserva Natural Mosiro-Itajura (Caparú); 1°04′ S, 69°31′ W, elev. 100 m; Nov. 1995; D. Forero leg.; pitfall human dung; IavH-E.

ECUADOR – **Pastaza** • 1 ♀; Ashuara, Río Macuma, 10 km from Rio Morona; 3 elev. 00 m; 7–16 Jul. 1971; B. Malkin leg.; TAMU. – **Pichincha** • 2 ♂♂, 1 ♀; Gualea; Jun. 1929; TAMU • 1 ♀; Quito; TAMU.

PERU – **Amazonas** • 1 ♀; Condorcanqui, Santa Maria de Nieva; 4°28′23″ S, 77°53′02″ W; elev. 274 m; 12–13 Oct. 2019; F. Paz leg.; MUSM. – **Cusco** • 5 ♂♂, 3 ♀♀; La Convención, Megantoni; elev. 420–442 m; 13 Mar. 2022; S. Bejar and B. Cocamareshi leg.; MUSM • 1 ♂; same data as for

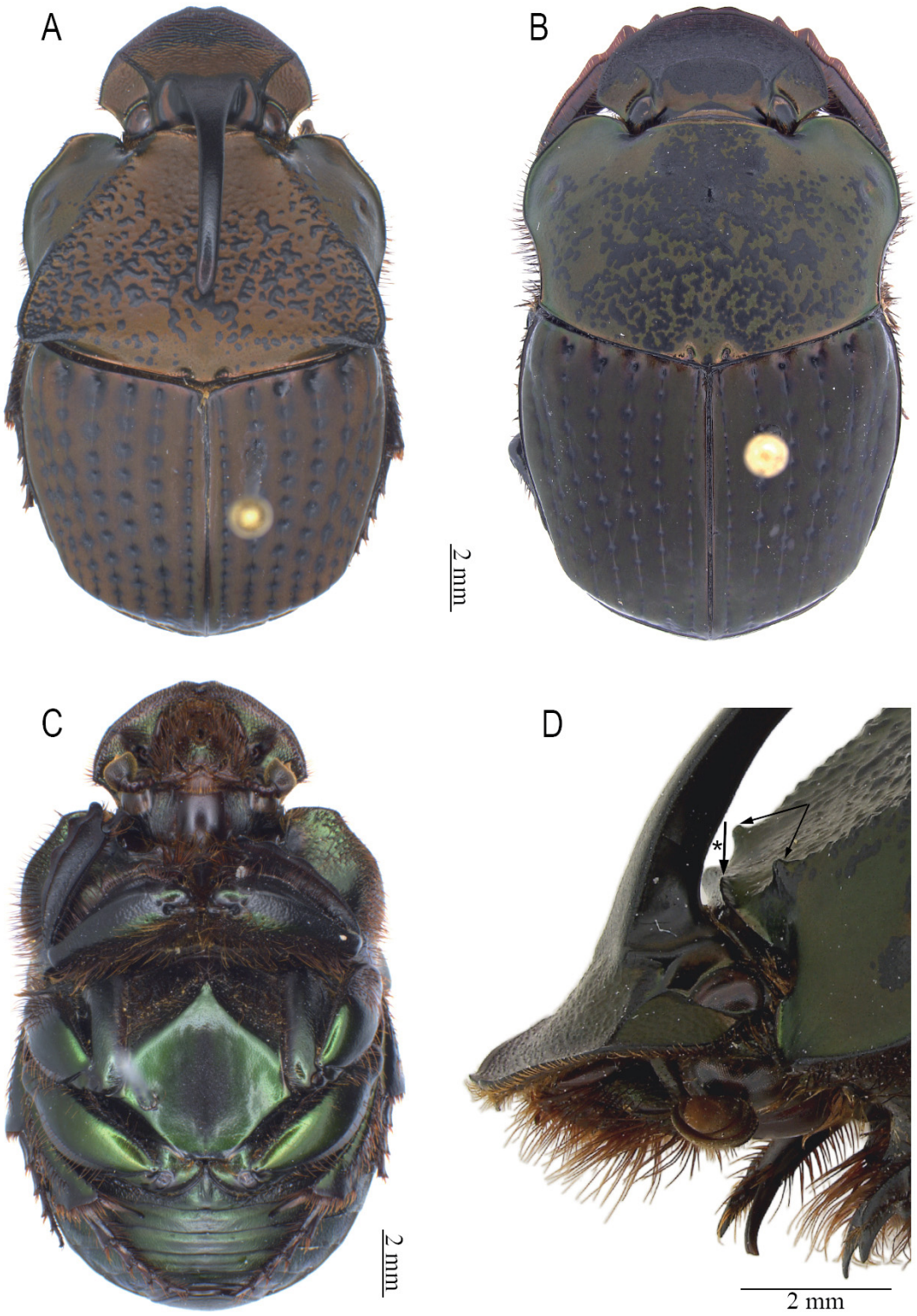

Fig. 8. *Phanaeus divisor* sp. nov. **A, C–D**. Holotype, ♂ (CEMT). **A**. Dorsal view. **B**. Paratype, ♀, dorsal view (CEMT). **C**. Ventral view. **D**. Head and anterior pronotal portion in lateral view. Arrows indicate the anteromedial pronotal tubercles; asterisk arrow indicates the carina adjacent to anteromedial pronotal margin.

preceding; 20 Jun. 2023; R. Curo leg.; MUSM. – **Huánuco** • 1 ♂; Leoncia Prado Tingo Maria, Monson Valley; 20 Nov. 1954; E.I. Schlinger and E.S. Ross leg.; TAMU. – **Loreto** • 1 ♀; Datem del Marañón; 4°59′44″ S, 76°18′25″ W; elev. 132 m; 3 Jul. 2012; C. Espinoza leg.; MUSM • 1 ♀; Loreto; 4°38′23″ S, 76°10′ W; elev. 114 m; 30 Jun. 2012; C. Espinoza leg.; MUSM • 1 ♂, 1 ♀; Río Ungumayo; elev. 137 m; 29–30 Nov. 2009; L. Sulca leg.; MUSM. – **Madre de Dios** • 5 ♂♂, 5 ♀♀; CICRA Field Station; 12°33′09″ S, 70°06′36″ W; elev. 295 m; 10–15 Jul. 2010; Chaboo team leg.; flight interception trap ; MUSM • 2 ♂♂, 2 ♀♀; same data as for preceding; 12°33′07″ S, 70°06′34″ W; 9–13 Jun. 2011; MUSM • 1 ♀; Nueva Arequipa; elev. 231 m; 23–27 Sep. 2009; C. Peña and E. Martínez leg.; MUSM • 1 ♂, 1 ♀; PN Bahuaja-Sonene; 13°11′38″ S, 70°07′58″ W; elev. 347 m; 3–19 Jun. 2013; J. Grados leg.; MUSM • 2 ♀♀; PNN Manú, Estación Biológica Pantiacolla; 12°38′48″ S, 71°14′36″ W; 2010; S. Pérez leg.; UPTC-CE • 1 ♂, 1 ♀; Reserva Comunal Amarakaeri; naciente Qda. Pinquiri; 12°55′43″ S, 70°51′41″ W; elev. 421 m; 4 Jun. 2011; M. Vilchez leg.; MUSM • 1 ♂, 1 ♀; Rio Tambopata; Collpa de Guacamayos; 13°8.5′ S, 69°36.4′ W; elev. 300 m; Oct. 1995; F. Forsyth leg.; MUSM • 1 ♀; Río Tambopata; RR.NN. Explorer's inn.; 12°50′30″ S, 69°17′31″ W; elev. 161 m; 15–18 May 2019; L. Figueroa and M. Alvarado leg.; MUSM.

Distribution

Widely distributed in the Amazon, from Colombia and Bolivia to French Guiana and northeastern Pará, in Brazil (Fig. 21). In lowlands, below 500 m a.s.l.

Phanaeus divisor sp. nov.
urn:lsid:zoobank.org:act:16D03340-F1FA-4E1D-B16F-FF9FEA86A94D
Figs 2D–E, 3D, 4B, 8, 13C, 14B, E, H, K, 16B, 17B, 18B, 19B

Diagnosis

This new species is diagnosed by the following combination of character states: venter bright green color (Fig. 8C); tip of anteromedial prominence of metaventrite convex in lateral view, usually with irregular and small calluses or carinulae (Fig. 2D–E); pronotum with deep posteromedial fossae with punctations inside (Figs 4B, 8A–B); pronotal punctures strong, clearly visible over entire pronotal surface under 20× magnification; carina adjacent to anteromedial pronotal margin of females appearing regularly arched in frontal view (Fig. 3D); major males with elongate triangular horn and well-developed, pyramidal pronotal tubercles (Fig. 8D).

Etymology

The specific epithet refers to the type locality, Serra do Divisor National Park.

Type material (9 ♂♂, 10 ♀♀)

Holotype

BRAZIL • ♂; Acre, Mâncio Lima, Parque Nacional da Serra do Divisor; 7°26′46″ S, 73°39′27″ W; 7–9 Dec. 2019; R.A. Azevedo leg.; pitfall human dung; plotAP06; CEMT.

Paratypes

BRAZIL – **Acre** • 6 ♂♂, 9 ♀♀; same data as for holotype; CEMT • 1 ♂, 1 ♀; same data as for holotype; TAMU • 1 ♂; same data as for holotype; 7°26′46″ S, 73°39′28″ W; 11–15 Dec. 2019; flight interception trap; CEMT.

Type locality

Brazil, Acre, Mâncio Lima, Serra do Divisor National Park.

Description

Major male (holotype)

Measurements. Length 18.5 mm. Width 10.3 mm.

Head. Clypeus bidentate with striated sculpture (Fig. 8A). Anterior margin of clypeus and horn black (Fig. 8A). Olive brown on paraocular area and posterior portion of clypeus (Figs 8A, 16B). Cephalic horn triangular, long, curved posteriorly over pronotum (Figs 8A, 16B, 17B). Discrete sheen around the eyes and at apex of horn (Fig. 8A).

Pronotum. Olive brown with irregularly black elevations (Fig. 8A). Punctures strong, clearly visible over entire pronotal surface under 20× magnification. Disc triangular, flattened, with two well-developed, pyramidal anterior tubercles (Fig. 8D). Carina adjacent to anteromedial pronotal margin elevated (Fig. 8D). Lateral pronotal expansion of pronotum slightly curved posteriorly in dorsal view (Fig. 8A). Posteromedial fossae semicircular with punctations inside (Figs 4B, 8A). Discrete sheen on entire pronotal margin (Fig. 8A).

Elytra. Striae punctate, basally impressed as distinct fossae; each strial puncture within a black macula (Fig. 8A). Interstriae olive brown with scabriculous surface giving opaque appearance. Anterior margin with discrete sheen (Fig. 8A).

Metaventrite. Tip of anteromedial prominence of metaventrite convex in lateral view, with irregular carinulae (Fig. 2D–E). Surface with large, deep, and dense punctures (Fig. 2D). Black color in the central portion; green color near the insertion of the mesocoxae and metacoxae (Fig. 8C).

Pygidium. Almost completely brown, except for green anterior portion (Fig. 18B). Scabriculous surface with lateral waves and a smooth medial area, with strong punctures.

Endophallites. ME in dorsal view elongate and blade-like, with a broad, rounded basal portion tapering gradually into a narrow, curved apex; left margin slightly concave, right margin arched, convex; left margin with a pronounced fold, occupying the basal half portion (Fig. 14E). AE with tapered base; right margin (dorsal view) sinuous, with a small tooth-like projection near the base, more visible in lateral view (Fig. 14H). SRP wider than long (Fig. 14K).

Variation

Dorsal color varies from reddish brown to olive green, with iridescence between green and brown in some specimens. Male sizes: length 16–18.5 mm, width 9–11.3 mm. Female sizes: length 15.4–17.6 mm, width 9.6–10.9 mm. Females: head with transversal carina (Figs 3D, 8B); pronotum with three tubercles arranged in V, two anterior rounded and one posterior elongated longitudinally (Figs 8B, 19B); carina adjacent to anteromedial pronotal margin appearing regularly arched in frontal view (Fig. 3D); posteromedial pronotal fossae triangular (Fig. 8B). Minor males: short horn or without horn; if hornless, only with a transverse carina on the head; triangular pronotal disc, but without lateral expansions and diminute pair of anterior pronotal tubercles.

Distribution

Brazil, Acre, Serra do Divisor National Park (Fig. 20). As shown for another dung beetle originally described exclusively from the Brazilian side of the Divisor Range (Arias-Buriticá *et al.* 2023, 2024), this species is also likely present on the Peruvian side and perhaps in other areas further within this country.

Taxonomic discussion

Although the external morphology and the parameres of *Phanaeus divisor* sp. nov. are similar to *P. cambeforti* (Figs 5, 8, 13A, C), differences in the external morphology and endophallites observed between the two taxa gave us the confidence to describe this new species from Serra do Divisor National Park. Externally, they can be easily distinguished by the punctations inside of posteromedial pronotal fossae in *P. divisor*, absent in *P. cambeforti*. In *P. divisor*, the anteromedial prominence of the metaventrite terminates bears a convex tip in lateral view, with distinct carinae. In contrast, *P. cambeforti* exhibits a flat tip of the anteromedial prominence of the metaventrite, without carinae. In addition, the ME and AE differ in shape and size (Fig. 14D–E, G–H).

Phanaeus lecourti Arnaud, 2000
Figs 1H, 2B, 9, 13E, 14C, F, I, L, 16A, 17A, 18A, 19A

Phanaeus lecourti Arnaud, 2000: 6.

Phanaeus lecourti peruanus – Arnaud 2000: 6.
Phanaeus (*Notiophanaeus*) *lecourti* – Arnaud 2002: 86. — Price 2007: 1, 5, 17; 2009: 139, 143–144, 146. — Edmonds & Zídek 2012: 3, 6, 10, 37, 41. — Figueroa *et al.* 2014: 127, 131, 136. — Krajcik 2012: 204. — Gillett & Toussaint 2020: 673.
Phanaeus (*Notiophanaeus*) *lecourti peruanus* – Arnaud 2002: 86–87. — Edmonds & Zídek 2012: 1, 8, 11 (as synonym of *P. lecourti*). — Krajcik 2012: 204.
Phanaeus lecourti – Price & May 2009: 216. — Lizardo *et al.* 2022: 548, 552, 554, 557, 560.
Phanaeus (*Phanaeus*) *lecourti* – Hamel-Leigue *et al.* 2009: 50, 55, 67, 74, 94.
Phanaeus (*Phanaeus*) *lecourti peruanus* – Hamel-Leigue *et al.* 2009: 67.

Diagnosis

Dorsal and ventral color similar, weakly lustrous, dark blue or green with faded sheen (Fig. 9). Triangular clypeal teeth (Fig. 9). Cephalic horn of major males expanded laterally at base and gradually narrowing towards apex (Fig. 16A). Pronotum of females with three tubercles arranged in a triangle, with the lateral tubercles longer latitudinally than the middle one, which is rounded (Figs 9B, D, 19A). Variation: length: 19–24 mm; the coloration varies from purplish blue to emerald green; pronotum and elytra may show different colors, one blue, the other green. Endophallites: ME in dorsal view strongly curved, hook-shaped, with a broad basal region and a long, narrow, apically tapering process directed anteriorly; basal and right margin together form a single, strongly convex arch; left margin with a boomerang-shaped fold, occupying the basal half (Fig. 14F). AE long, with U-shaped base; right margin (dorsal view) straight, with a small tooth-like projection in the middle, more visible in lateral view (Fig. 14I). SRP circular formed by two sclerotized parts connected by a membrane (Fig. 14L).

Type material

Holotype of *Phanaeus lecourti*
BOLIVIA • ♂; "(LA PAZ) N. Yungas, Caranavi-Carasco, 700-1200 m; 11.91; G. Lecourt leg."; CPFA.

Paratypes of *Phanaeus lecourti*
BOLIVIA • 1 ♂, 1 ♀; (examined from photographs provided in Arnaud 2002: 87).

Holotype of *Phanaeus lecourti peruanus*
PERU • ♂; "(HUA), Pucalpa, III.76; Monguillon leg."; CPFA.

Paratypes of *Phanaeus lecourti peruanus*
PERU • 1 ♂, 1♀ ; (examined from photographs provided in Arnaud 2002: 87).

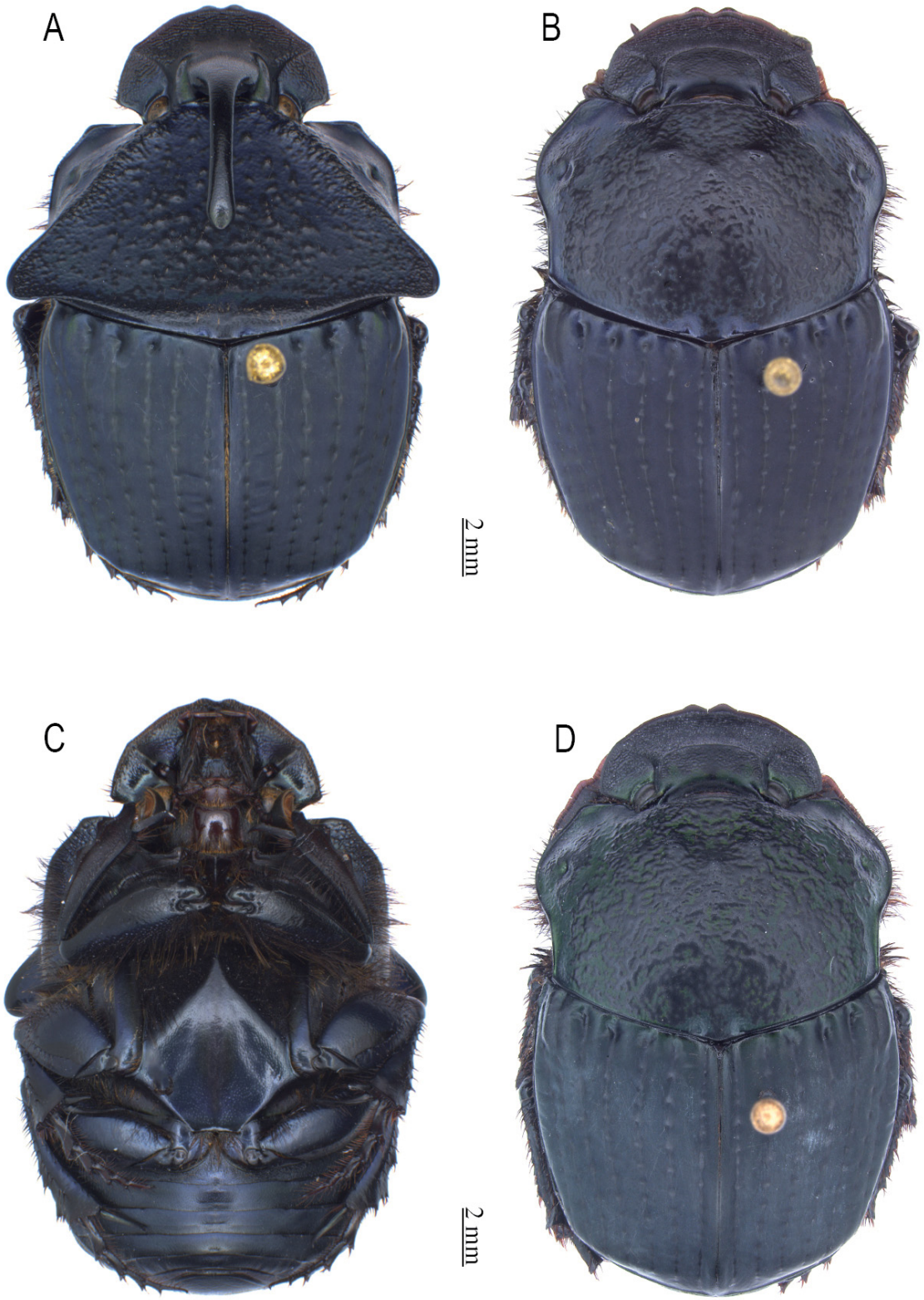

Fig. 9. *Phanaeus lecourti* Arnaud, 2000. **A–C**. Blue form. **A**. Major male from Junín (Peru), dorsal view (CEMT). **B**. Female from Cochabamba (Bolivia), dorsal view (CEMT). **C**. Major male (Junín), ventral view (CEMT). **D**. Green form ♀, from Leoncio Prado (Peru), dorsal view (CEMT).

Non-type material examined (25 ♂♂, 19 ♀♀)

BOLIVIA – **Cochabamba** • 1 ♂, 1 ♀; Huayllas; Dec. 2006; CEMT. – **La Paz** • 1 ♂; Nor Yungas, rt. Caranavi-Carrasco; P. Arnaud leg.; CEMT • 1 ♂; Nor Yungas, Cotapata; 19–30 Sep. 2000; Y. Gareca and P. Blacut leg.; MHNNKM • 1 ♀; Nor Yungas, E.B.T.; 30 May 2001; P. Coro leg.; MHNNKM.

PERU – **Ayacucho** • 2 ♂♂; Moyobamba; 13°05′14″ S, 73°30′23″ W; elev. 1918 m; 28 Feb.–1 Mar. 2022; M. Alvarado leg.; MUSM. – **Cusco** • 1 ♂; La Convención, Encharate; 12°32′40″ S, 73°8′10″ W; elev. 1600 m; 21 Aug. 2022; E. Quispe leg.; MUSM • 1 ♂, 3 ♀♀; same data as for preceding; CC. Ozanampiato; 12°39′38″ S, 73°09′18″ W; elev. 1708 m; 22–24 Jan. 2010; C. Carranza and C. Rossi leg.; MUSM • 1 ♀; same data as for preceding; 12°39′32″ S, 73°09′32″ W, elev. 1681 m; MUSM • 5 ♂♂, 4 ♀♀; same data as for preceding; CC. Santa Rosa; 12°34′15″ S, 73°05′10″ W; elev. 1693 m; 26–29 Jan. 2010; MUSM • 2 ♂♂, 1 ♀; same data as for preceding; elev. 1685 m; MUSM • 1 ♀; same data as for preceding; 12°34′10″ S, 73°05′15″ W; elev. 1693 m; 18–21 Sep. 2010; M. Alvarado and J. Peralta leg.; pitfall; MUSM • 1 ♂; same data as for preceding; 12°34′12″ S, 73°05′13″ W; elev. 1709 m; MUSM • 1 ♀; San Pedro; 13°03′15″ S, 71°32′54″ W; elev. 300 m; 19–20 Nov. 1999; T. Larsen leg.; pitfall human dung; MUSM • 1 ♂; Union, along road; 13°5′24″ S, 71°34′53″ W; elev. 1900 m; Dec. 1996; N. Quinte leg.; cloud forest; pitfall human dung; CEMT. – **Huánuco** • 1 ♀; Leoncio Prado Tingo Maria; May 2008; CEMT • 1 ♂, 1 ♀; PN Cordillera Azul; 39 km NE of Tingo Maria; elev. 1700 m; 11–14 Jan. 1983; A. Newton and M. Thayer leg.; pitfall human dung; TAMU. – **Junín** • 2 ♂♂, 1 ♀; Calabaza; elev. 2000 m; 1–20 Sep. 2004; Callegari leg.; TAMU • 2 ♂♂, 1 ♀; near Satipo; elev. >1000 m; Jul. 2004; A. Santibáñez leg.; pitfall human dung; TAMU • 2 ♂♂; Santuario Nacional Pampa Hermosa; 10°59′51″ S, 75°25′35″ W; elev. 1879 m; 30 May 2011; D. Silva leg.; TAMU • 1 ♂; Satipo; May 2005; TAMU • 1 ♂; Satipo; elev. 600 m; 3–16 Apr. 2003; A. Santibáñez leg.; TAMU • 1 ♂; Satipo, Huerto Edén; Dec. 2004; CEMT • 1 ♂; same data as for preceding; Apr. 2007; CEMT • 1 ♂; same data as for preceding; elev. 1400 m; Dec. 2007; CEMT • 1 ♀; Satipo, Puerto Ocopa; elev. 450 m; Jul. 2004; CEMT • 1 ♀; Satipo, Santos Atahualpa, Río Tambo; 12 Dec. 2007; R. Poerster leg.; CEMT • 2 ♂♂; Satipo; Nov. 2004; CEMT.

Type locality

Bolivia, La Paz.

Distribution

Yungas Province in Bolivia and Peru (Fig. 20) at elevations between 400 and 1100 m.a.s.l.

Phanaeus mariocupelloi sp. nov.
urn:lsid:zoobank.org:act:22700B47-85BB-4C1F-91B5-83D6CF3DFAA2
Figs 2C, 4C, 10, 13F, 15C, F, I, L, 16F, 17F, 18F, I, 19F

Diagnosis

This species is diagnosed by the following combination of character states: ventral color iridescent greenish red (Fig. 10C); dorsum dull, dark olive green to dark olive brown (Fig. 10A–B, D); posteromedial pronotal fossae always present (Figs 4C, 10A–B, D); pair of anterior pronotal tubercles of males small, distinguishable from the black elevations by the bright spot (Figs 10A, D, 16F); semicircular clypeal teeth in females (Fig. 10B).

Etymology

This species is dedicated to Mario Jardim Cupello in recognition of his significant contributions to the knowledge of Scarabaeidae.

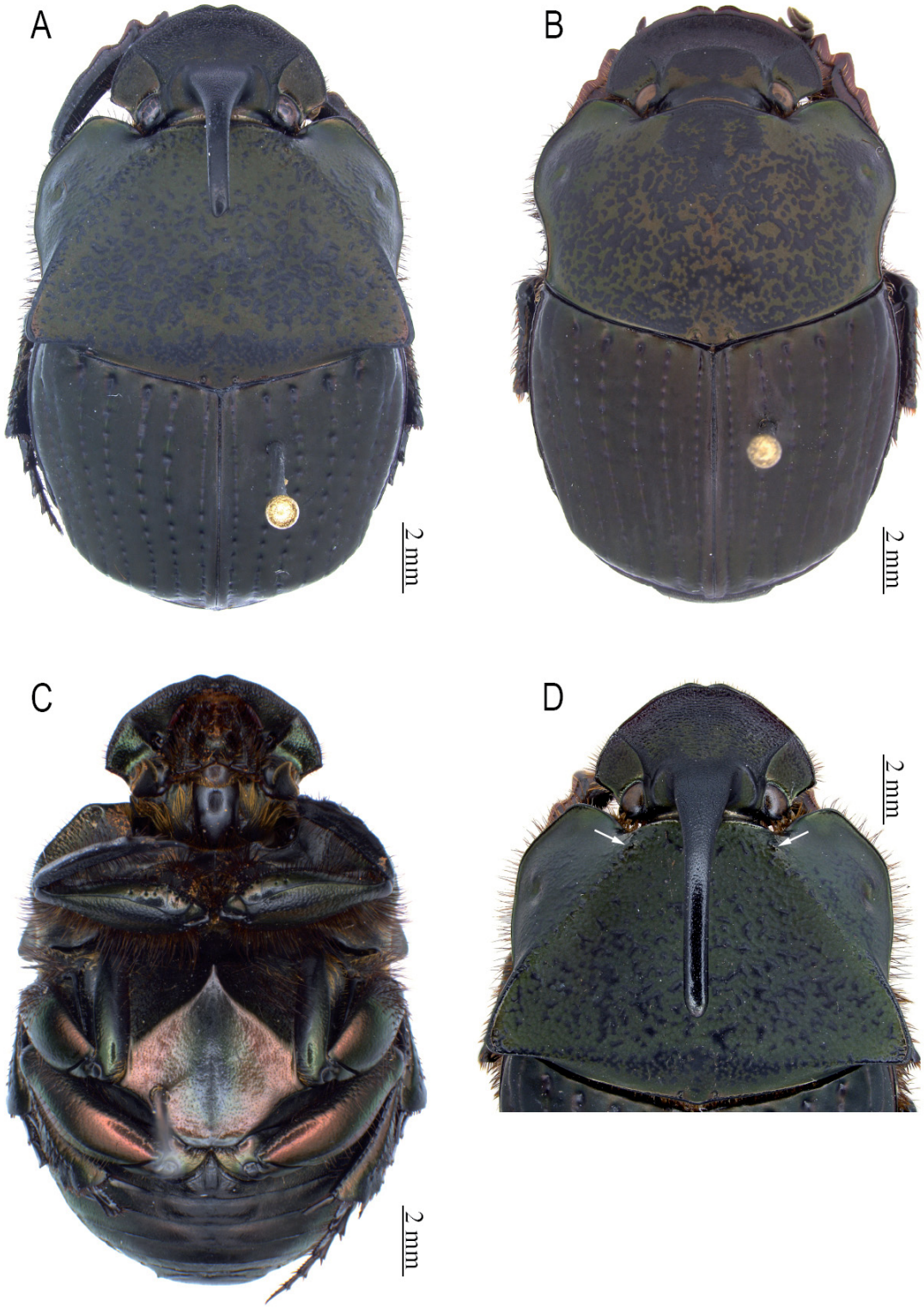

Fig. 10. *Phanaeus mariocupelloi* sp. nov. **A**. Holotype, ♂, dorsal view (CEMT). **B**. Paratype, ♀, dorsal view (CEMT). **C**. Holotype, ♂, ventral view. **D**. Paratype, ♂, head and pronotum in dorsal view. Arrows indicate the anteromedial pronotal tubercles.

Type material (13 ♂♂, 31 ♀♀)

Holotype

BRAZIL • ♂; Mato Grosso, Araputanga, Fazenda Araputanga; 15°23′15″ S, 58°24′43″ W; elev. 298 m; 7–9 Jan. 2024; F.Z. Vaz-de-Mello, M.E. Maldaner and B.R. Bordin leg.; pitfall human dung; CEMT.

Paratypes

BRAZIL – **Mato Grosso** • 6 ♂♂, 13 ♀♀; Araputanga, Fazenda Bandeirantes; 15°23′26″ S, 58°24′48″ W; elev. 296 m; 18–20 Jan. 2013; R.J. Silva leg.; pitfall human+pig dung; CEMT • 1 ♂, 2 ♀♀; same data as for preceding; TAMU • 1 ♀; same data as for preceding; 15°23′06″ S, 58°26′02″ W; elev. 308 m; 19–21 Jan. 2013; CEMT • 2 ♂♂; same data as for preceding; 15°23′04″ S, 58°26′W; elev. 296 m; 21–23 Jan. 2013; CEMT • 1 ♀; same data as for preceding; 15°22′18″ S, 58°26′23″ W; elev. 297 m; CEMT • 2 ♂♂, 8 ♀♀; Araputanga, Fazenda Sudam; 15°15′22″ S, 58°27′12″ W; elev. 352 m; 28–30 Jan. 2013; R.J. Silva leg.; pitfall human+pig dung; CEMT • 3 ♀♀; same data as for preceding; 15°15′45″ S, 58°26′23″ W; 29–31 Jan. 2013; CEMT • 2 ♂♂, 1 ♀; Indiavaí, Fazenda Alto Jaurú; 15°27′18″ S, 58°33′12″ W; elev. 231 m; 14–16 Jan. 2013; R.J. Silva leg.; pitfall human+pig dung; CEMT • 1 ♀; Mirassol d'Oeste, Fazenda Santa Helena; 15°33′34″ S, 57°58′13″ W; elev. 240 m; 25–27 Jan. 2013; R.J. Silva leg.; pitfall human+pig dung; CEMT.

Type locality

Brazil, Mato Grosso state, Araputanga.

Description

Major male (holotype)

Measurements. Length 16.8 mm. Width 10.7 mm

Head. Clypeus bidentate with striated sculpture (Fig. 10A). Anterior margin of clypeus and horn black; olive green on paraocular area and posterior portion of clypeus (Fig. 10A). Cephalic horn black, curved posteriorly over pronotum. Soft sheen around the eyes (Fig. 10A).

Pronotum. Disc flat, triangular in dorsal view; dark olive green, with irregularly black elevations over the whole surface (Fig. 10A). Pronotal punctures strong, clearly visible over entire pronotal surface with 20× magnification. Pair of anterior pronotal tubercles small, distinguishable from black rugosities by bright spot. Posteromedial fossae as entire deep circles, aligned with the first elytral striae (Figs 4C, 10A).

Elytra. Dark olive green with scabriculous surface, giving an opaque appearance (Fig. 10A). Elytral striae punctate, basally impressed as distinct fossae (Fig. 10A). Anterior margin with bronze-green sheen, lighter than the rest of the surface (Fig. 10A).

Metaventrite. Anteromedial prominence long and narrow, slightly expanded at the apex (Fig. 2C). Surface with large, deep and dense punctures. Central portion black, with a greenish-red coloration near the insertion of the mesocoxae and metacoxae, spreading to the legs (Fig. 10C).

Pygidium. Olive brown, bronze in the middle; scabriculous surface with waves on the sides and smooth in the middle, with strong punctures (Fig. 18F).

Endophallites. ME in dorsal view elongate and blade-like, with a broad, rounded basal portion tapering gradually into a narrow, curved apex; left margin with a pronounced fold, occupying the basal half portion; left margin slightly concave, with a sinuosity near apex; right margin almost straight (Fig. 15F). AE with tapered base; right margin (dorsal view) with a diagonal projection, more visible in lateral view (Fig. 15I). SRP square, with a diagonal projection (dorsal view) (Fig. 15L).

Variation

The dorsal color varies from dark olive green to dark reddish brown. The ventral color varies from redder to greener. Male sizes: length 12.3–20 mm; width 8.2–12.6 mm. Female sizes: length 15.2–19.8 mm; width 8.6–11.5 mm. Females: head with transversal carina and semi-circular clypeal teeth (Fig. 10B); pronotum with three small tubercles arranged in a triangle, middle tubercle posterior to lateral ones (Figs 10B, 19F); triangular posteromedial pronotal fossae (Fig. 10B); pygidium of big females with a black spot on the posterior portion (Fig. 18I); smaller females with uniformly colored pygidium, as males. Minor males: short horn or without horn; if hornless, only with a transverse carina on the head; triangular pronotal disc, but without lateral expansions and without a pair of anterior pronotal tubercles.

Distribution

Brazil, southwestern region of the Mato Grosso state, in remnants of the Amazon rainforest (Fig. 20).

Taxonomic discussion

Phanaeus mariocupelloi sp. nov. is similar to *P. cambeforti*, which has not been recorded in this region. *Phanaeus cambeforti* has the posteromedial fossae of pronotum shallow or absent, while *P. mariocupelloi* always has conspicuous posteromedial pronotal fossae. Additionally, *P. cambeforti* is smaller, with fewer black elevations on the pronotum of males, and with a dark green, almost black ventral color. *Phanaeus mariocupelloi* is the only species of the *P. chalcomelas* group with red ventral color that occurs in Brazil and the only species of the group with semicircular clypeal teeth in females. Although the parameres resemble *P. cambeforti* (Fig. 13A, F), the endophallites are very different between the two species. The ME is very similar to *P. minos* (Fig. 15E–F). Despite having a distinctive dorsal projection, the SRP has a general shape similar to *P. meleagris* (Fig. 15J, L).

Phanaeus meleagris Blanchard, 1845
Figs 2F, 3B, 11, 13B, 15A, D, G, J, 16D, 17D, 18D, 19D

Phanaeus meleagris Blanchard, 1845: 176. (In livraison 80 dated as 1845 according to Bousquet (2016)).

Phanaeus meleagris – Harold 1869: 1018. — Nevinson 1892: 5. — Gillet 1911b: 84. — d'Olsoufieff 1924: 41, 99, 135, 152. — Blackwelder 1944: 210. — Vulcano & Pereira 1967: 574. — Edmonds 1972: 832. — Arnaud 1982a: 114. — Hamel-Leigue *et al.* 2006: 17. — Lizardo *et al.* 2022: 548, 554, 557, 560. — Moctezuma *et al*. 2024: 5. — Moctezuma 2025: 4.

Phanaeus (*Phanaeus*) *meleagris* – Pessôa 1934: 305, 312.

Phanaeus (*Notiophanaeus*) *meleagris* – Edmonds 1994: 28, 31, 102. — Arnaud 2002: 85–86. — Hamel-Leigue *et al.* 2009: 50, 65, 74, 93. — Carvajal *et al.* 2011: 321. — Edmonds & Zídek 2012: 3, 6, 11, 37–38, 43. — Krajcik 2012: 204 — Price 2007: 13–14, 17; 2009: 139, 143–144, 146. — Gillett & Toussaint 2020: 673.

Diagnosis

Elytra completely matte black, with no other color on striae punctation (Fig. 11A–B, D). Black ventral color, except for bright red femora with green reflections (Fig. 11C). Pronotum covered with highly anastomosed black elevations (Fig. 11A–B, D). Pronotum with bright metallic red, yellow, and green coloration between elevations, more visible on the sides (Figs 11A–B, D, 16D, 17D, 19D). Females with carina adjacent to anteromedial pronotal margin subarcuate in frontal view, almost straight, without sinuosity in the middle (Fig. 3B). Variation: length 16–21 mm. The color between the pronotal elevations can be red, yellow, and green or just red. The black elevations can almost completely cover the pronotum. Endophallites: ME in dorsal view elongate and blade-like, with a broad, rounded basal portion tapering gradually into a narrow, curved apex; left margin concave, right margin arched; left margin with a

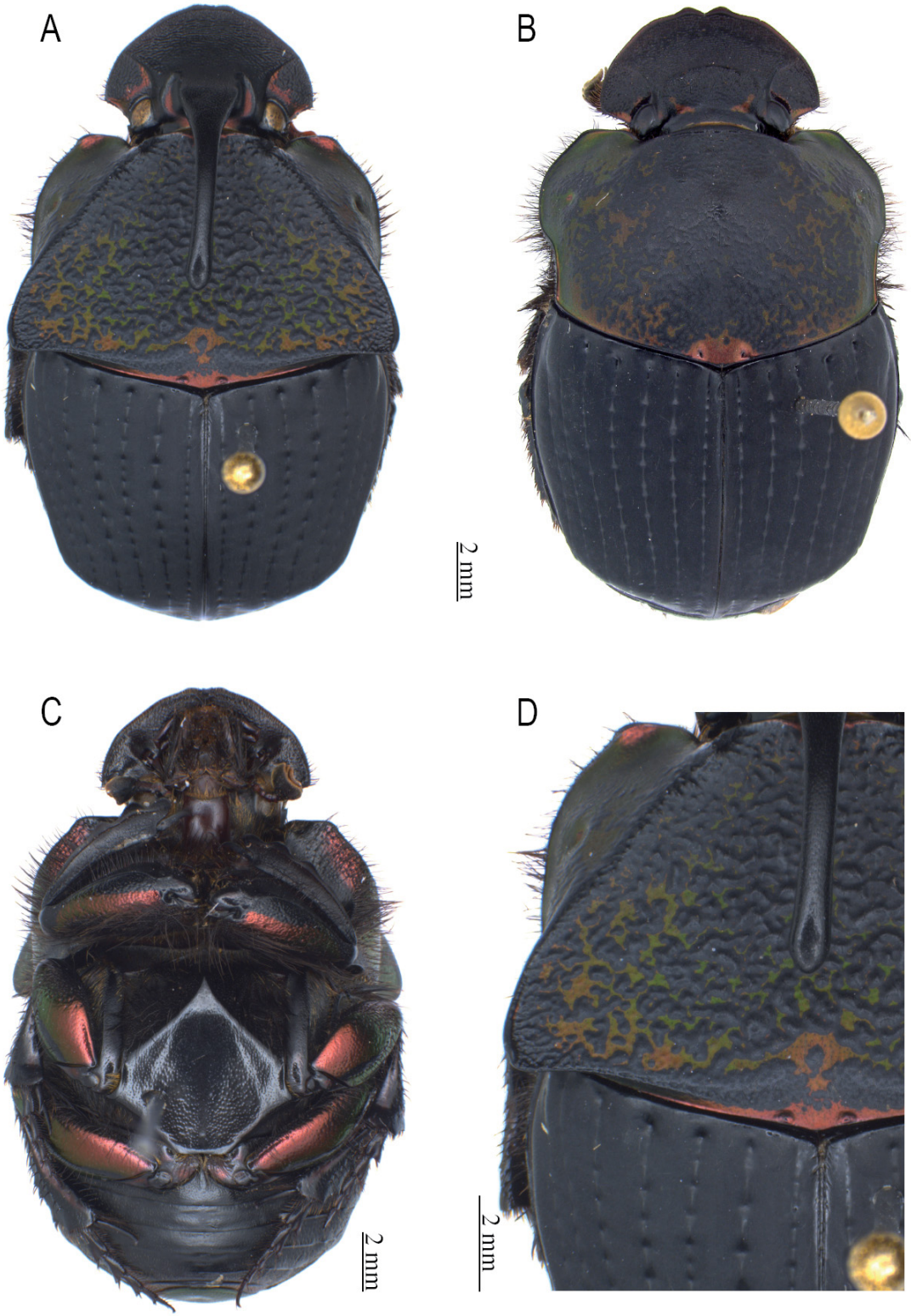

Fig. 11. *Phanaeus meleagris* Blanchard, 1845 from Santa Cruz, Bolivia (CEMT). **A**. Major male, dorsal view. **B**. Female, dorsal view. **C**. Major male, ventral view. **D**. Major male, dorsal color.

pronounced fold, occupying the basal half portion (Fig. 15D). AE with tapered base; right margin (in dorsal view) with a tooth-like projection at the middle, more visible in lateral view; left margin, in ventral view, interrupted by the projection (Fig. 15G). SRP rectangular with rounded angles (Fig. 15J).

Type material

Lectotype (studied from photographs)
BOLIVIA • ♂; "long. 18.5 mm/ *P. meleagris*, Blanch, Yungas, M. d'Orbigny /6275/1276/ M.P.C.G./."; MNHN. Designated by Arnaud (1982a: 114).

Paralectotypes (not studied)
BOLIVIA • 3 ♂♂, 3 ♀♀; MNHN.

Non-type material examined (310 ♂♂, 492 ♀♀)

BOLIVIA – Chuquisaca • 2 ♂♂, 22 ♀♀; Hernando Siles, Monteagudo; 19°43′35″ S, 63°55′03″ W, elev. 1300 m; 18–21 Apr. 2004; M. Aliaga leg.; MHNNKM • 4 ♂♂, 49 ♀♀; same data as for preceding; 19°46′15″ S, 63°53′11″ W; 9–12 Apr. 2004; MHNNKM • 1 ♀; Monteagudo, Ticucha; 19°96′15″ S, 63°53′11″ W; elev. 1300 m; M. Aliaga leg.; pitfall human dung; TAMU. – **Cochabamba** • 34 ♂♂, 35 ♀♀; Ayopaya, Altamachi; 16°02′ S, 66°40′ W; elev. 1150 m; 25–27 Sep. 2004; C. Hamel leg.; MHNNKM • 1 ♂, 1 ♀; Chapare, Cristal Mayu; 17°00′26″ S, 65°38′32″ W; Nov. 1949; TAMU • 1 ♂; Chapare, Locotal; 1100 m; Nov. 1954; Martínez leg.; ex-Gonzalo Halffter Salas; IEXA • 1 ♀; Mosetenes, Isiboro-Securé N.P.; 16°13′51″ S, 66°25′06″ W; elev. 1250 m; 1–4 Sep. 2003; A.C. Hamel leg.; pitfall human dung; TAMU • 1 ♂; same data as for preceding; 16°13′58″ S, 66°24′54″ W; TAMU • 1 ♂; same data as for preceding; 14–17 Sep. 2003; 16°14′04″ S, 66°25′06″ W; TAMU • 1 ♀; Yungas del Palmar, km 135; elev. 1600 m; Feb. 1952; Martínez leg.; TAMU. – **La Paz** • 5 ♀♀; Caranavi; Nov. 2005; P. Wagner leg.; CEMT • 2 ♀♀; same data as for preceding; Nov. 2009; CEMT • 1 ♂; Coroico; Feb. 1984; P. Arnaval leg.; CEMT • 1 ♂; Nor Yungas, Río Coroico; elev. 1200 m; Jan. 1949; Martínez leg.; ex-Gonzalo Halffter Salas; IEXA • 1 ♂; same data as for preceding; Dec. 1948; elev. 1700 m; IEXA • 1 ♀; Nor Yungas, Tunquini Biological Station; 30 May 2001; P. Coro leg.; MHNNKM. – **Santa Cruz** • 9 ♂♂, 14 ♀♀; Andrés Ibáñez, Espejillos; 27–29 Apr. 2007; M. Amaya leg.; MHNNKM • 16 ♂♂, 24 ♀♀; Andrés Ibáñez, Laguna Volcanes; Feb. 2010; T. Vidaurre leg.; MHNNKM • 4 ♀♀; Andrés Ibáñez, Potrerillos del Güendá; 17°40′21″ S; 63°27′1″ W; elev. 370 m; 15 Oct. 2010; T. Vidaurre leg.; MHNNKM • 2 ♂♂, 2 ♀♀; Bermejo, Refugio Los Volcanes; 18°06′ S, 63°36′ W; elev. 1060 m; 10 Dec. 2003; semi-deciduous forest; D.J. Mann and A.C. Hamel leg.; pitfall human dung; CEMT • 1 ♂, 1 ♀; same data as for preceding; pitfall chicken carrion; CEMT • 2 ♂♂, 2 ♀♀; same data as for preceding; 18°06′ S, 63°35′ W; elev. 1045 m; 23 Feb. 2010; T. Vidaurre leg.; pitfall human dung; CEMT • 8 ♂♂, 15 ♀♀; Cordillera, Incahuasi; 13–16 Mar. 2008; T. Vidaurre leg.; MHNNKM • 1 ♂, 1 ♀; same data as for preceding; TAMU • 9 ♂♂, 23 ♀♀; Cordillera, Parabano; 24–28 Mar. 2003; J. Ledezma *et al.* leg.; MHNNKM • 9 ♂♂, 13 ♀♀; same data as for preceding; 23–27 Mar. 2004; J.L. Aramayo, *et al.* leg.; MHNNKM • 44 ♂♂, 33 ♀♀; same data as for preceding; 28 Sep.–2 Oct. 2004; MHNNKM • 16 ♂♂, 25 ♀♀; Cordillera, R.M. Parabano; 19–30 May 2004; T. Vidaurre leg.; MHNNKM • 2 ♀♀; Cordillera, Serranía Parabado I; 13 Apr. 2002; L. Céspedes leg.; MHNNKM • 1 ♂, 1 ♀; Cordillera, Serranía Parabado II; 15–17 Apr. 2002; L. Céspedes leg.; MHNNKM • 36 ♂♂, 58 ♀♀; Cordillera, Yaguapoa; 19°53′40.7″ S, 63°40′25.3″ W; 20–21 Nov. 2007; T. Vidaurre leg.; MHNNKM • 17 ♂♂, 54 ♀♀; Cordillera, Yaguapoa; 19°51′36″ S, 63°40′35″ W; 26 Nov. 2007; T. Vidaurre leg.; MHNNKM • 2 ♂♂, 7 ♀♀; Cordillera, Yupa; 19°47′47.1″ S, 63°41′59.7″ W; 29 Nov. 2007; T. Vidaurre leg.; MHNNKM • 1 ♂; Florida, Alta Florida; elev. 1697 m; 16 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 13 ♂♂, 16 ♀♀; Florida, Bella Vista; 14–15 Nov. 2007; J. Ledezma *et al.* leg.; MHNNKM • 1 ♂, 1 ♀; Florida, Bella Vista; 25 Sep. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♂, 8 ♀♀; Florida, Buena Vista; 8 Mar. 2005; T. Vidaurre leg.; MHNNKM • 3 ♂♂, 1 ♀; Florida, Cuevas; 18 Nov. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♀; Florida, La Negra; 18 Sep. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♂, 1 ♀; Florida,

Lagunillas; 28 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 3 ♂♂, 4 ♀♀; Florida, near Samaipata; 18°8.4′ S, 63°48.1′ W; elev. 1730 m; 19 Nov. 2006; W.D. Edmonds and P. Reyes leg.; pitfall human dung; TAMU • 2 ♂♂, 6 ♀♀; same data as for preceding; 18°8.9′ S, 63°48.8′ W; elev. 1380 m; TAMU • 2 ♂♂, 2 ♀♀; Florida, Pacay; elev. 1614 m; 18 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♂; Florida, Palermo; elev. 1467 m; 18 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 3 ♂♂, 2 ♀♀; Florida, Samaipata; 18°08.4′ S; 63°48.8′ W; elev. 1380 m; 19 Nov. 2006; W.D. Edmonds leg.; MHNNKM • 1 ♀; Florida, Samaipata; 26 Nov. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♂; Ichilo, Bella Vista; 18°17′04″ S, 63°40′38″ W; 31 Dec. 2004; T. Vidaurre leg.; MHNNKM • 4 ♂♂, 5 ♀♀; same data as for preceding; 2–5 Jan. 2005; T. Vidaurre leg.; MHNNKM • 10 ♂♂, 4 ♀♀; Ichilo, Elias Meneses; 9 Nov. 2003; L. Acosta leg.; MHNNKM • 5 ♂♂, 6 ♀♀; Refugio Los Volcanes; 18°6.3′ S, 63°35.9′ W; elev. 1050 m; 21–25 Feb. 2010; W.D. Edmonds and T. Vidaurre; pitfall human dung; TAMU • 2 ♂♂, same data as for preceding; 18°06′19″ S, 63°35′49″ W; elev. 1060 m; 6 Feb. 2003; A.C. Hamel L. and S.K. Herzog leg.; TAMU • 1 ♂; same data as for preceding; 18°06′50″ S, 63°36′15″ W; elev. 1200 m; 22 Apr. 2003; TAMU • 9 ♂♂, 3 ♀♀; Vallegrande, Algodonales; 18°47′11″ S, 63°50′49″ W; 13 Apr. 2016; M. Amaya *et al.* leg.; MHNNKM • 9 ♂♂, 10 ♀♀; Vallegrande, Algodonales; 18°47′18″ S, 63°50′49″ W; 22 Oct. 2011; A. Alcoba *et al.* leg.; MHNNKM • 2 ♀♀; Vallegrande, Churcos; 5 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 4 ♂♂, 2 ♀♀; Vallegrande, Churo Citano; 18°51′30″ S, 64°49′53″ W; elev. 1761 m; 16 Apr. 2011; A. Vidaurre leg.; MHNNKM • 6 ♀♀; Vallegrande, Islas; 18°42′03″ S, 63°58′40″ W; 19 Apr. 2011; A. Alcoba leg.; MHNNKM • 2 ♂♂, 1 ♀; Vallegrande, Llorenti; 5 Oct. 2011; A. Alcoba and M. Pérez leg.; MHNNKM • 1 ♂, 1 ♀; Vallegrande, Mosquera; 18°42′43″ S, 63°42′43″ W; 5 Oct. 2011; A. Alcoba *et al.* leg.; MHNNKM • 5 ♂♂, 6 ♀♀; Vallegrande, Plan Citano; 16 May 2011; T. Vidaurre leg.; MHNNKM • 1 ♀; Vallegrande, Plan Citano; 30 Aug. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♀; Vallegrande, Postrervalle, Pampas; 18°27′12″ S, 63°42′36″ W; elev. 1234 m; 6 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 2 ♂♂, 2 ♀♀; Vallegrande, Postrervalle, Quebrada el Palo; 1 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♂; Vallegrande, Rancho Novillero; 9 Nov. 2011; T. Vidaurre leg.; MHNNKM • 1 ♂, 1 ♀; Vallegrande, Rio Villca; 18°38′39″ S, 63°47′11″ W; 6 Dec. 2011; A. Alcoba *et al.* leg.; MHNNKM • 1 ♀; same data as for preceding; 18 Sep. 2011; MHNNKM.

PERU – **Cusco** • 1 ♂; Quispicanchi Marcapata; TAMU. – **Junín** • 1 ♂; Satipo Calabaza; elev. 2000 m; 1–20 Sep. 2004; Callegari leg.; TAMU.

Type locality

Bolivia, somewhere visited by Alcide d'Orbigny in the Yungas region.

Distribution

Distributed along the eastern slopes of the Andes in southern Peru and Bolivia from 370 to 1700 m a.s.l. Yungas Province (Fig. 20).

Remarks

Differences in external morphology between *Phanaeus meleagris* and *Phanaeus minos* Erichson, 1847 stat. rev., such as the color pattern (Figs 11D, 12D) and the shape of the carina adjacent to the anteromedial pronotal margin in females (Fig. 3A–B), as well as differences in male genitalia, including narrower parameres in *P. meleagris* compared to *P. minos* (Fig. 13B, D), and distinct shapes of the endophallites (Fig. 15D–E, G–H, J–K), gave us the confidence to return *P. minos* to full species status. The geographical distribution of *P. meleagris* has also been redefined here: it occurs on the eastern slopes of the Andes in Bolivia and southern Peru, whereas *P. minos* is found in Peru, Ecuador, Colombia, and Venezuela (Fig. 20).

Phanaeus minos Erichson, 1847 stat. rev.
Figs 2I, 3A, 12, 13D, 15B, E, H, K, 16E, 17E, 18E, 19E

Phanaeus minos Erichson, 1847: 106.

Phanaeus minos – Harold 1869: 1018; 1870: 105 (as synonym of *P. meleagris*). — Nevinson 1892: 5 (as synonym of *P. meleagris*). — Gillet 1911b: 84 (as synonym of *P. meleagris*). — d'Olsoufieff 1924: 152 (as synonym of *P. meleagris*). — Pessôa 1934: 312 (as synonym of *P. meleagris*). — Blackwelder 1944: 210 (as synonym of *P. meleagris*). — Edmonds 1994: 31 (as synonym of *P. meleagris*). — Hamel-Leigue *et al.* 2009: 65 (as synonym of *P. meleagris*). — Edmonds & Zídek 2012: 3, 6, 11 (as synonym of *P. meleagris*).

Non *Phanaeus meleagris* (misidentification) – Balthasar 1941: 351; 1951: 336. — Vulcano & Pereira 1967: 574. — Medina *et al.* 2001: 140. — Ratcliffe *et al.* 2015: 197. — Vítolo 2000: 597. — Price & May 2009: 213, 216, 236.

Non *Phanaeus* (*Notiophanaeus*) *meleagris* (misidentification) – Edmonds 1994: 28–29, 31–32. — Vítolo 2004: 284, 303, 305. — Price 2009: 139, 143-144, 146 (in part). — Edmonds & Zídek 2012: 10–11, 38, 43 (in part). — Figueroa *et al.* 2014: 127, 133, 136. — Chamorro *et al.* 2018: 82, 98; 2019: 218–219, 310.

Non *Phanaeus* (*Notiophanaeus*) *meleagris minos* (misidentification) – Arnaud 2002: 85–86. — Vítolo 2004: 284. — Carvajal *et al.* 2011: 321. — Krajcik 2012: 204.

Diagnosis

Elytra brown, reddish brown (Fig 12B), or olive green in the interstriae (Fig 12A, D). Each strial puncture within a black macula (Fig 12A–B, D). Pronotum covered with highly anastomosed black elevations (Fig 12A–B, D). Elevations covering the tones of coppery brown or coppery red, which are more visible on the pronotum sides (Figs 12A–B, D, 16E, 17E, 19E). Dark coppery brown or black ventral color, except for the femora which are coppery red with green reflections (Fig 12C). Female carina adjacent to anteromedial pronotal margin with sinuosity in the middle in frontal view (Fig 3A). Variation: length 16–22.4 mm. In specimens from Peru, the metaventrite is black in the central portion and red near the insertion of the mesocoxae and metacoxae, spreading to the femora (Fig. 12C). The metaventrite is completely black in specimens from Ecuador, Colombia and Venezuela, with red coloration just on the femora. Pygidium completely coppery red in most specimens (Fig. 18E), some specimens with a black spot on the posterior portion. Endophallites: ME in dorsal view elongate and blade-like, with a broad, rounded basal portion tapering gradually into a narrow, curved apex; left margin with a pronounced fold, occupying the basal half portion; left margin slightly concave, with a sinuosity near apex; right margin almost straight (Fig. 15E). AE with wide base; in dorsal view, left margin and basal margin form a 45° angle; right margin (dorsal view) almost straight, with a sinuous projection, more visible in lateral view (Fig. 15H). SRP triangular (Fig. 15K).

Type material

Lectotype (examined from photographs)
PERU • ♂; " Mountains of Peru"; MFNB. Designated by Edmonds (1994: 31).

Paralectotypes (not studied)
PERU • 2 ♂♂, 1 ♀; " Mountains of Peru"; MFNB.

Non-type material examined (39 ♂♂, 40 ♀♀)

COLOMBIA – **Antioquia** • 1 ♀; Amalfi, Cañon del río Porce; 6°45′42.43″ N, 75°5′28.31″ W; elev. 1221 m; Sep. 2006; A. Bedoya leg.; IAvH-E. – **Arauca** • 2 ♂♂, 2 ♀♀; Tame, PNN El Cocuy; 6°30′48″ N,

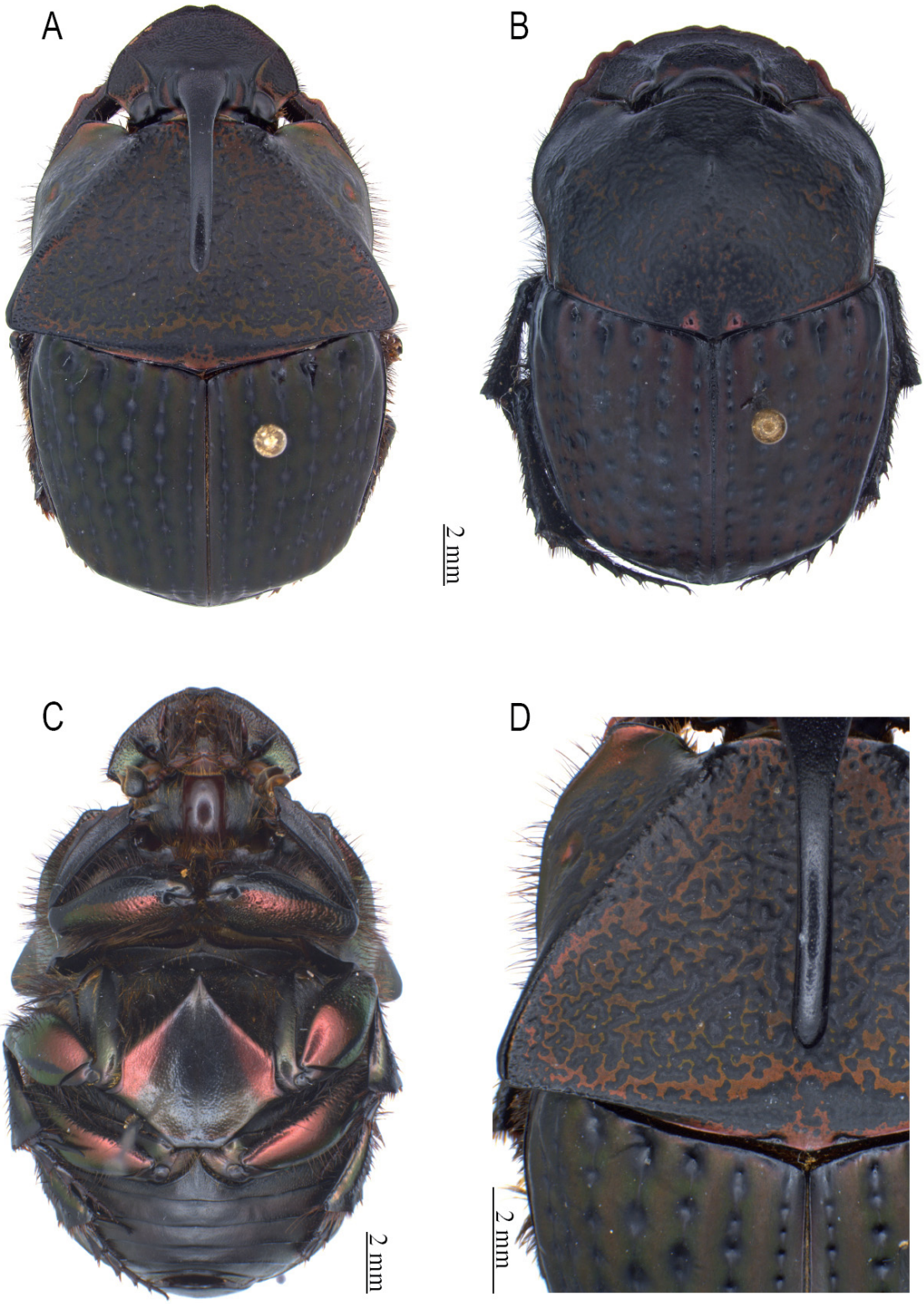

Fig. 12. *Phanaeus minos* Erichson, 1847 stat. rev. **A**. Major male from Junín (Peru), dorsal view (CEMT). **B**. Female from Tachira (Venezuela), dorsal view (CEMT). **C**. Major male from Junín, ventral view (CEMT). **D**. Major male from Junín, dorsal color (CEMT).

71°50′15″ W; elev. 1000 m; 1 Oct. 2007; F. Alvarado leg.; human dung; IAvH-E. – **Boyacá** • 2 ♂♂; Cusiana, cerca de Pajarito, Finca Guayabetal - El paisano; 5°17′ N, 72°40′ W; elev. 1300 m; May 1997; F. Escobar leg.; pitfall trap; UPTC-CE • 1 ♀; same data as for preceding; 5°17′ N, 72°41′ W; elev. 1200 m; UPTC-CE • 1 ♂; Cusiana, cerca de Pajarito; 5°23′39″ N, 72°41′17″ W; elev. 1250 m; F. Escobar leg.; pitfall trap; CEMT • 1 ♂; same data as for preceding; 5°17′ N, 72°40′ W; elev. 1300 m; 1 Jun. 1997; IAvH-E. – **Caquetá** • 2 ♂♂, 1 ♀; San Vicente del Caguán, PNN Los Picachos - Alto del Río Pato; 2°47′51″ N, 74°51′18″ W; elev. 1500 m; Nov.–Dec. 1997; pitfall trap; F. Escobar leg.; UPTC-CE • 5 ♂♂, 5 ♀♀; same data as for preceding; 2°44′ N, 74º53′ W; elev. 1300–1560 m; UPTC-CE • 1 ♂, 1 ♀; same data as for preceding; elev. 1560 m; flight interception trap; UPTC-CE • 1 ♀; same data as for preceding; 2º47′53″ N, 74º51′28″ W; elev. 1250 m; pitfall trap; UPTC-CE • 1 ♂, 1 ♀; same data as for preceding; 2º47′ N, 74º51′ W; elev. 1280 m; flight interception trap; UPTC-CE • 1 ♀; San Vicente del Caguán, camino a PNN Los Picachos; F. Escobar leg.; cow dung; UPTC-CE. – **Casanare** • 1 ♂; Salto de Candelas; elev. 1600 m; May 1997; F. Escobar leg.; trap; UPTC-CE. – **Cauca** • 1 ♀; Sn. Fortunato Bonis; TAMU. – **Cundinamarca** • 1 ♂, 1 ♀; Medina, Miralindo; 4°35′33″ N, 73°23′17″ W; elev. 1250 m; Feb.–Mar. 1997; F. Escobar leg.; pitfall human dung; CEMT • 1 ♀; same data as for preceding; elev. 1000 m; IAvH-E • 1 ♀; Medina, Vereda Periquito, finca Miramar, Campamento 2; 4°30′55″ N, 73°26′28″ W; elev. 1408 m; 14–16 Mar. 2018; pitfall human dung; M.I. Castro, J.C. Neita and E. Torres leg.; IAvH-E • 2 ♀♀; same data as for preceding; 4°30′57.7″ N, 73°26′3.1″ W; elev. 1194 m; 15–16 Mar. 2018; IAvH-E • 1 ♂; same data as for preceding; 4°30′58.4″ N, 73°26′5.9″ W; elev. 1229 m; IAvH-E • 1 ♂; same data as for preceding; 4°30′59.1″ N, 73°26′7.8″ W; elev. 1264 m; IAvH-E • 1 ♂; same data as for preceding; 4°30′56.8″ N, 73°26′11″ W; elev. 1289 m; IAvH-E • 1 ♀; same data as for preceding; 4°30′58.7″ N, 73°26′10.9″ W; elev. 1304 m; IAvH-E • 1 ♂, 1 ♀; same data as for preceding; 4°30′59.3″ N, 73°26′12.6″ W; elev. 1320 m; IAvH-E • 1 ♂, 1 ♀; same data as for preceding; 4°30′57.8″ N,

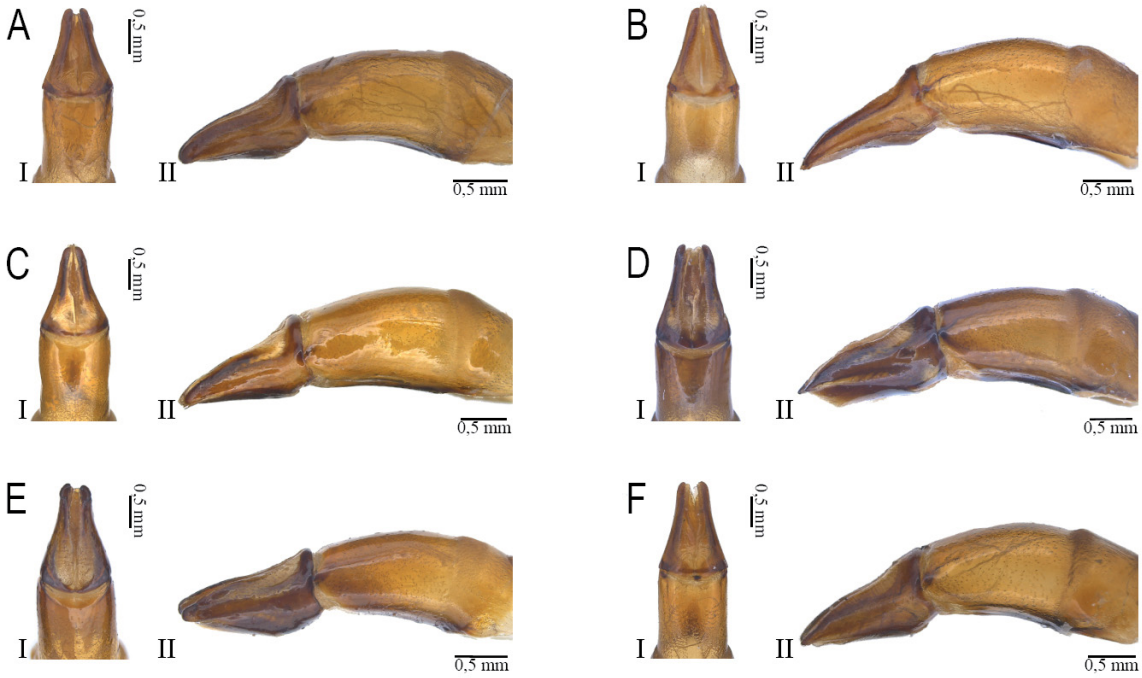

Fig. 13. Aedeagus of the *Phanaeus chalcomelas* species group. I = dorsal view; II = lateral view. **A**. *P. cambeforti* Arnaud, 1982 (CEMT). **B**. *P. meleagris* Blanchard, 1845 (CEMT). **C**. *P.* divisor sp. nov., paratype (CEMT). **D**. *P. minos* Erichson, 1847 stat. rev. (CEMT). **E**. *P, lecourti* Arnaud, 2000 (CEMT). **F**. *P. mariocupelloi* sp. nov., paratype (CEMT).

73°26′13.4″ W; elev. 1341 m; IAvH-E • 1 ♂; same data as for preceding; 4°30′58″ N, 73°26′14″ W; elev. 1346 m; IAvH-E • 1 ♀; same data as for preceding; 4°30′55″ N, 73°26′28″ W; elev. 1408 m; IAvH-E. – **Nariño** • 1 ♂; Ipiales, cuenca alta de los ríos Rumiyaco-Ranchería; elev. 1250 m; Sep. 1997; F. Escobar leg.; pitfall trap; UPTC-CE • 2 ♀♀; same data as for preceding; 0°03′ N, 77°13′ W; Oct. 1998; IAvH-E • 1 ♂; same data as for preceding; elev. 1430 m; 24. Sep. 1998; hand collecting at night ; UPTC-CE.

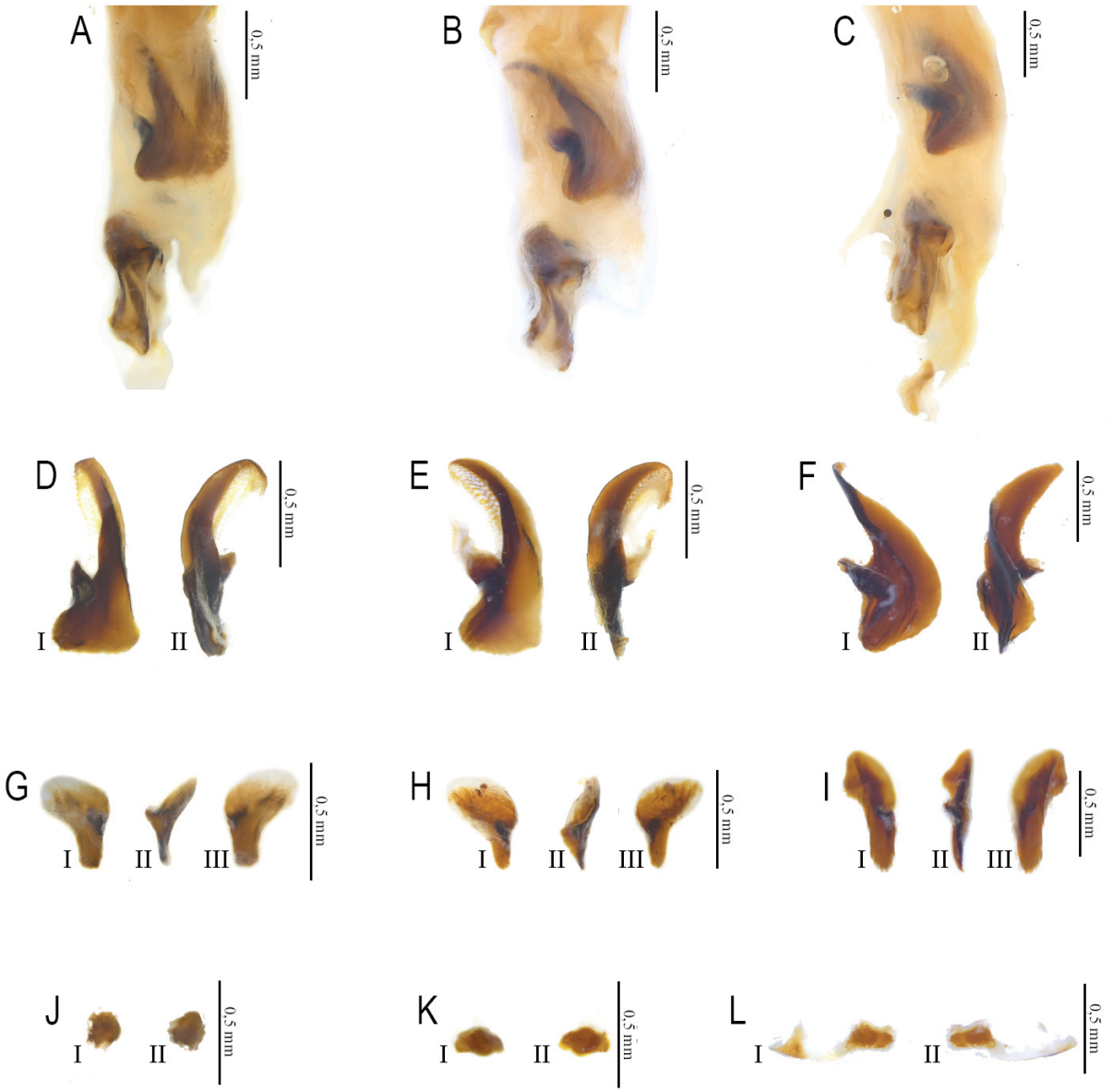

Fig. 14. Endophallus and endophallites of the *Phanaeus chalcomelas* species group. Respectively *P. cambeforti* Arnaud, 1982 (CEMT), *P. divisor* sp. nov., paratype (CEMT) and *P. lecourti* Arnaud, 2000 (CEMT). **A–C**. Endophallus in dorsal view. **D–F**. Medial endophallite (ME), dorsal (I) and lateral views (II). **G–I**. Additional endophallite (AE), dorsal (I), lateral (II) and ventral (III) views. **J–L**. Superior right peripheral endophallite (SRP), dorsal (I) and ventral views (II).

ECUADOR – **Tungurahua** • 2 ♂♂; Oriente, Abitagua; elev. 1200 m; 3 Jun. 1937; W.C. MacIntyre leg.; TAMU. – **Zamora-Chinchipe** • 1 ♂, 1 ♀; Chito, R. San Francisco; elev. 1540 m; 17 Feb. 2008; W. Chamorro and M. Amari leg.; pitfall trap; CEMT • 1 ♀; Libertad; 4°31′39″ S, 79°05′39″ W; elev. 1844 m; 28–30 Apr. 2023; M. Tapia leg.; pitfall human dung; LOUNAZ.

PERU – **Junín** • 1 ♂; Calabaza; 11º30′12″ S, 74º48′57″ W; elev. 2085 m; Nov. 2004; CEMT • 1 ♂; Calabaza; elev. 2000 m; 1–20 Sep. 2004; Callegari leg.; TAMU • 1 ♂, 2 ♀♀; ~17 km N of San Ramón;

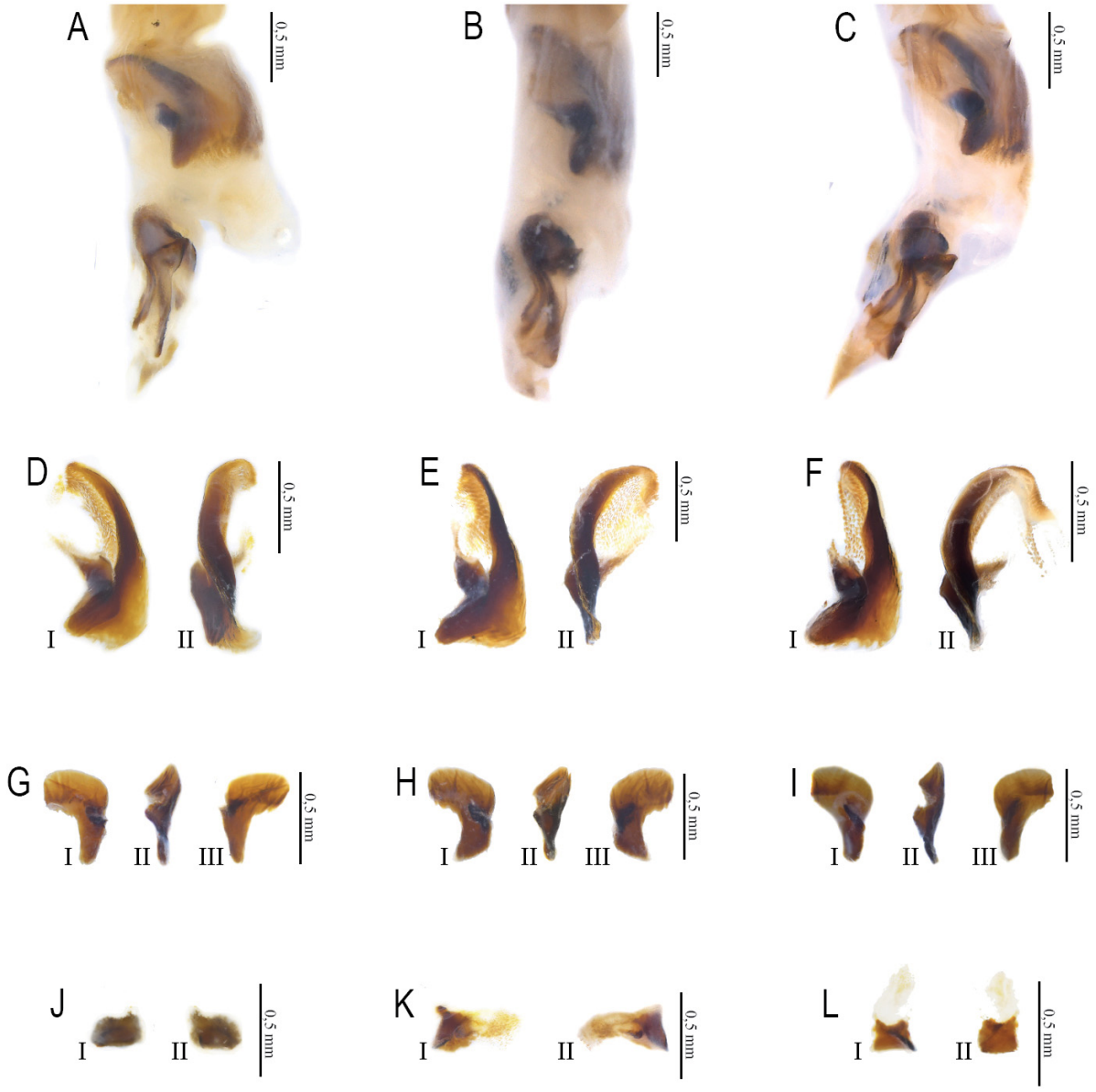

Fig. 15. Endophallus and endophallites of the *Phanaeus chalcomelas* species group. Respectively *P. meleagris* Blanchard, 1845 (CEMT), *P. minos* Erichson, 1847 stat. rev. (CEMT) and *P. mariocupelloi* sp. nov., paratype (CEMT). **A–C**. Endophallus, dorsal view. **D–F**. Medial endophallite (ME), dorsal (I) and lateral views (II). **G–I**. Additional endophallite (AE), dorsal (I), lateral (II) and ventral (III) views. **J–L**. Superior right peripheral endophallite (SRP), dorsal (I) and ventral views (II).

10°58.8′ S, 75°26.3′ W; elev. 1326 m; Mar. 2010; W.D. Edmonds and L. Figueroa leg.; human dung; TAMU • 2 ♀♀; same data as for preceding; carrion; TAMU • 1 ♂, 1 ♀; ~33 km S of San Ramón; 11°24.5′ S, 75°15.2′ W; elev. 1540 m; 6 Mar. 2010; W.D. Edmonds and L. Figueroa leg.; human dung; CEMT • 1 ♂; same data as for preceding; TAMU • 2 ♀♀; same data as for preceding; carrion; TAMU • 1 ♂, 1 ♀; Satipo; elev. 600 m; 3–16 Apr. 2003; A. Santibáñez leg.; TAMU • 1 ♂; Santuario Nacional Pampa Hermosa; 10°59′51″ S, 75°25′35″ W; elev. 1879 m; 30 May 2011; D. Silva leg.; TAMU • 1 ♂; Siete Casas, Santuario Nacional Pampa Hermosa; elev. 2220 m; 24 Oct. 2011; A. Almeyda leg.; CEMT.

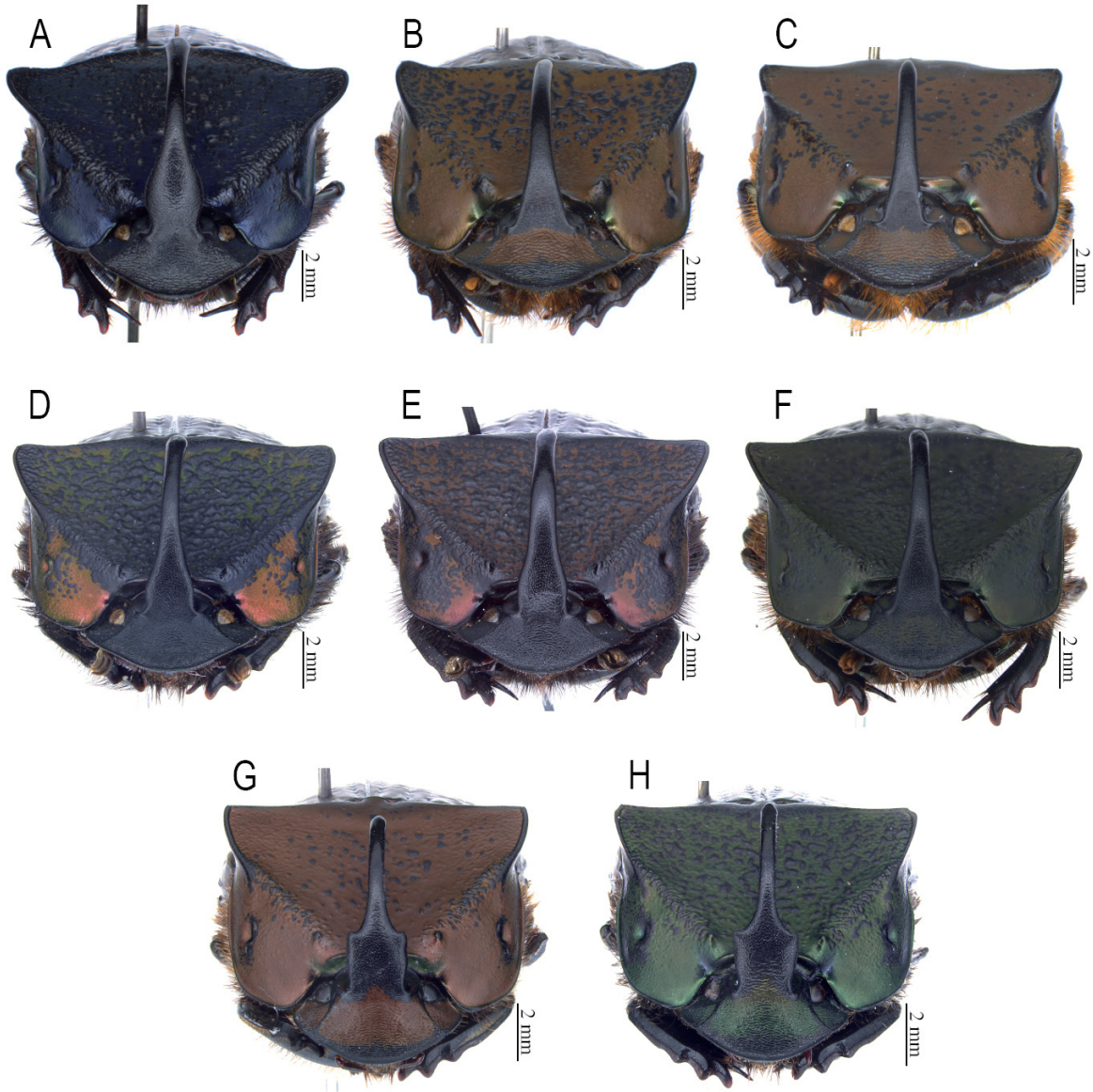

Fig. 16. Frontal view of males of the *Phanaeus chalcomelas* species group. **A**. *P. lecourti* Arnaud, 2000 (CEMT). **B**. *P. divisor* sp. nov., holotype (CEMT). **C**. *P. cambeforti* Arnaud, 1982 (CEMT). **D**. *P. meleagris* Blanchard, 1845 (CEMT). **E**. *P. minos* Erichson, 1847 stat. rev., from Ecuador (CEMT). **F**. *Phanaeus mariocupelloi* sp. nov., paratype (CEMT). **G**. *P. chalcomelas* (Perty, 1830), from Amazonas, Brazil (CEMT). **H**. *P. chalcomelas*, from Santa Cruz de la Sierra, Bolivia (CEMT).

VENEZUELA – **Táchira** • 1 ♂, 1 ♀; Vía Chorro del Indio; elev. 1345 m; Aug. 1990; J. Blanco leg.; CEMT • 1 ♂; same data as for preceding; elev. 1100 m; Jun. 1982; C.F. Romero leg.; TAMU • 2 ♀♀; km 2.5 of San Cristóbal to Chorro del Indio; elev. 1100 m; 31 Oct. 1987; D. Havranek leg.; TAMU • 1 ♂; San Cristóbal; 10–18 Aug. 1983; B. Gill leg.; TAMU • 1 ♀; San Gil, San Cristóbal; 20 May 1983; G. Borges leg.; TAMU.

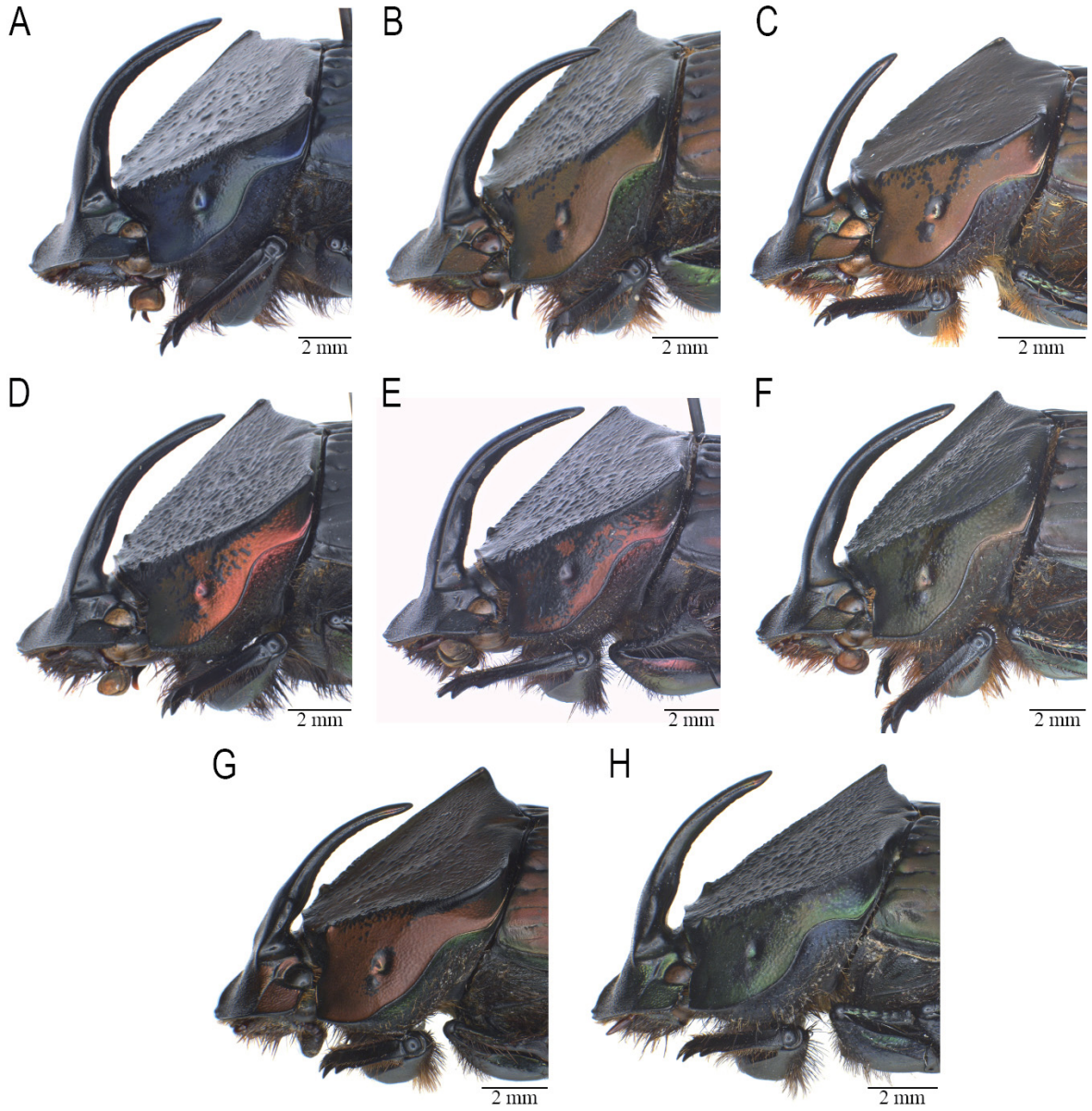

Fig. 17. Lateral view of males of the *Phanaeus chalcomelas* species group. **A**. *P. lecourti* Arnaud, 2000 (CEMT). **B**. *P. divisor* sp. nov., holotype (CEMT). **C**. *P. cambeforti* Arnaud, 1982 (CEMT). **D**. *P. meleagris* Blanchard, 1845 (CEMT). **E**. *P. minos* Erichson, 1847 stat. rev., from Ecuador (CEMT). **F**. *P. mariocupelloi* sp. nov., paratype (CEMT). **G**. *P. chalcomelas* (Perty, 1830), from Amazonas, Brazil (CEMT). **H**. *P. chalcomelas*, from Santa Cruz de la Sierra, Bolivia (CEMT).

Distribution

Along the eastern slopes of the Andes in Peru, Ecuador, Colombia and Venezuela from 600 to 2100 m a.s.l. (Fig. 20).

Remarks

Phanaeus minos was considered a synonym of *P. meleagris* by Harold (1870), Edmonds (1994) and Edmonds & Zídek (2012). However, differences in external and genital morphology were found by us. Regarding external morphology, *P. meleagris* exhibits entirely black elytra, while in *P. minos*, only the striae are black (Figs 11–12). In females, the carina adjacent to the anteromedial pronotal margin is

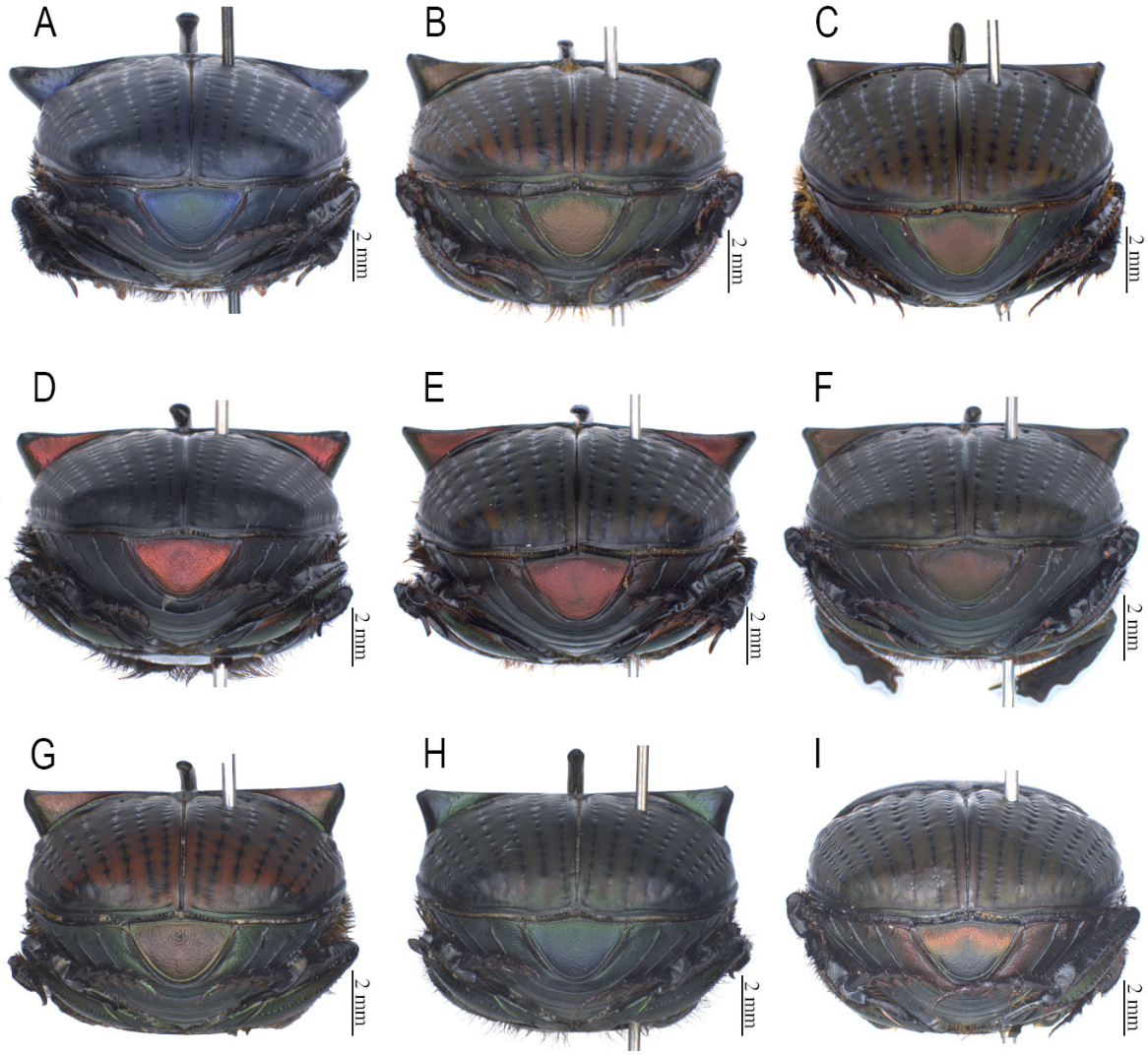

Fig. 18. A–H. Posterior view of males of the *Phanaeus chalcomelas* species group. **A**. *P. lecourti* Arnaud, 2000 (CEMT). **B**. *P. divisor* sp. nov., holotype (CEMT). **C**. *P. cambeforti* Arnaud, 1982 (CEMT). **D**. *P. meleagris* Blanchard, 1845 (CEMT). **E**. *P. minos* Erichson, 1847 stat. rev., from Peru (CEMT). **F**. *P. mariocupelloi* sp. nov., holotype (CEMT). **G**. *P. chalcomelas* (Perty, 1830), from Amazonas, Brazil (CEMT). **H**. *P. chalcomelas*, from Santa Cruz de la Sierra, Bolivia (CEMT). **I**. *Phanaeus mariocupelloi* sp. nov., paratype, ♀, posterior view (CEMT).

sinuous medially in *P. minos* (frontal view), whereas it is nearly straight and lacks medial sinuosity in *P. meleagris* (Fig. 3A–B). The cephalic horn of major males is wider and more curved in *P. minos* than in *P. meleagris* (Figs 16D–E, 17D–E). With respect to genital morphology, the parameres are narrower in *P. meleagris* than in *P. minos* in lateral view (Fig. 13B, D), and the medial, superior right peripheral, and additional endophallites exhibit distinct shapes —differences in the additional endophallite were also previously noted by Manjarres-H. & Molano-R. (2015) (Fig. 15D–E, G–H, J–K).

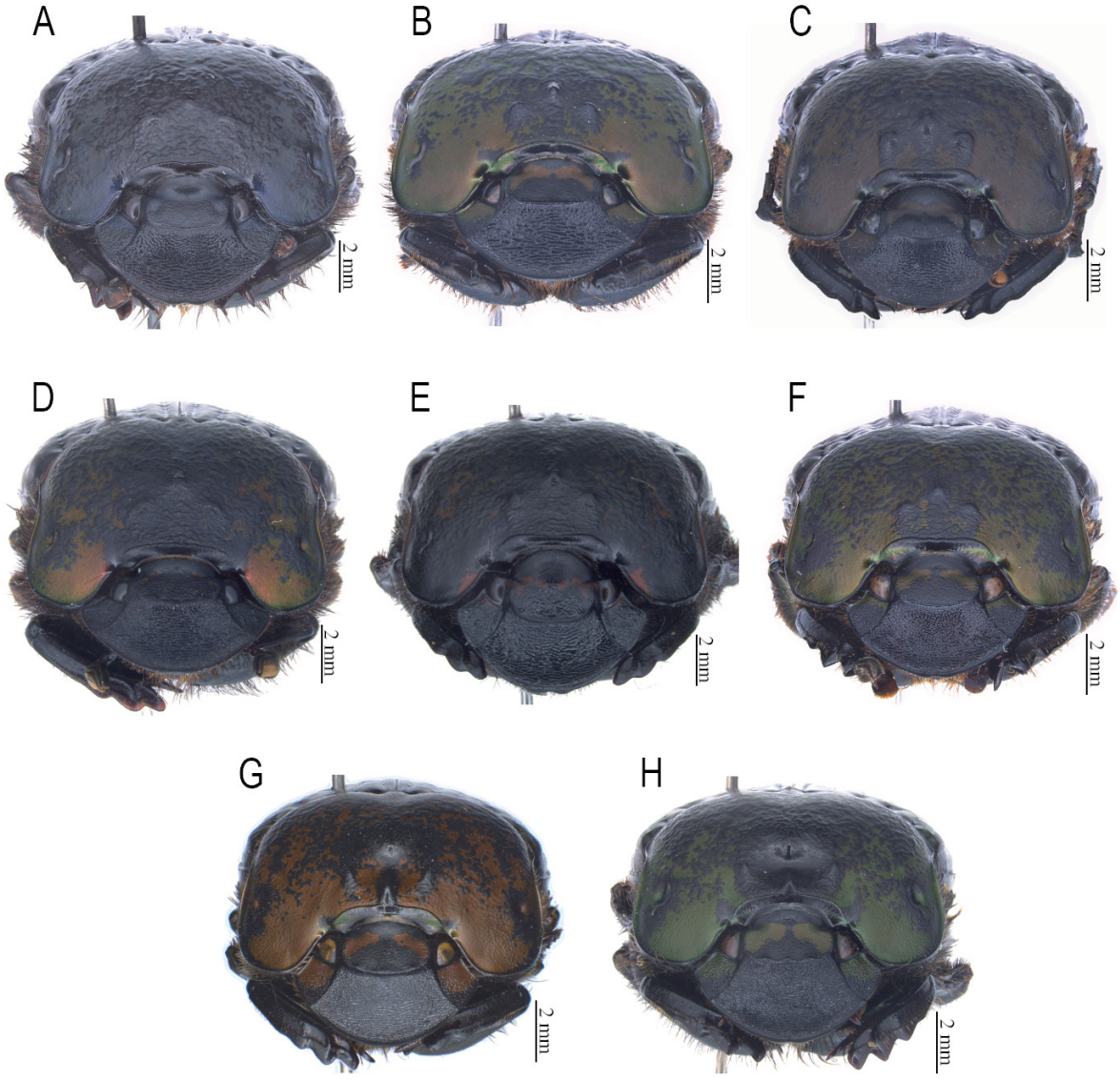

Fig. 19. Frontal view of females of the *Phanaeus chalcomelas* species group. **A**. *P. lecourti* Arnaud, 2000 (CEMT). **B**. *P. divisor* sp. nov., paratype (CEMT). **C**. *P. cambeforti* Arnaud, 1982 (CEMT). **D**. *P. meleagris* Blanchard, 1845 (CEMT). **E**. *P. minos* Erichson, 1847 stat. rev., from Venezuela (CEMT). F. *P. mariocupelloi* sp. nov., paratype (CEMT). **G**. *P. chalcomelas* (Perty, 1830), from Amazonas, Brazil (CEMT). **H**. *P. chalcomelas*, from Santa Cruz de la Sierra, Bolivia (CEMT).

Phanaeus achilles species group

Diagnosis of the *Phanaeus achilles* species group

Anteromedial margin of clypeus weakly bidentate (Fig. 1B). Head of females with transverse carina with two elevations in the middle, giving a bituberculate appearance in frontal view (Fig. 1E). Pronotum bearing contrasted black elevations, variously and irregularly shaped (Fig. 1G). Pronotum of females with more elevations and those more anastomosed than in males (Fig. 22). Pronotum of females with

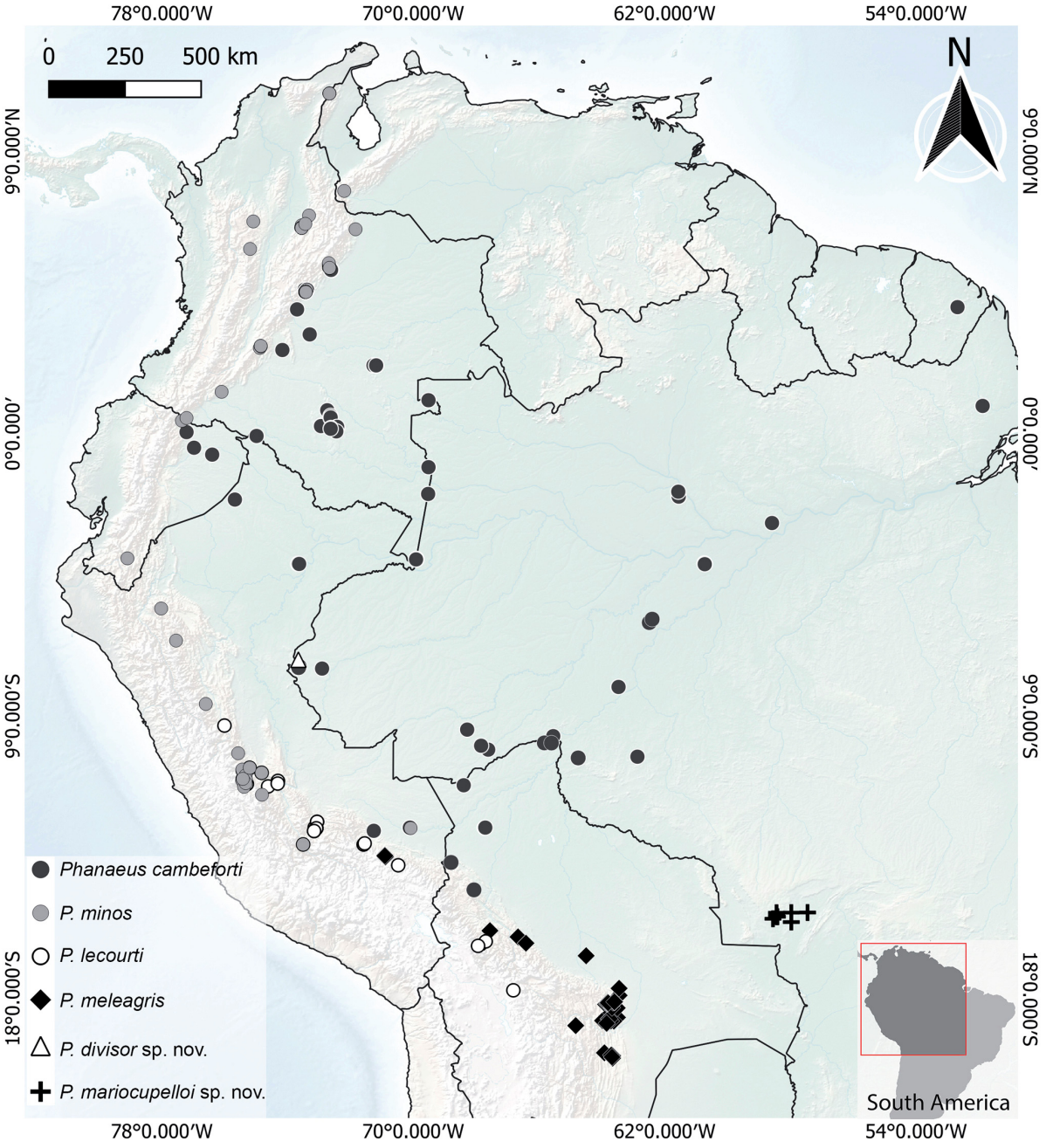

Fig. 20. Geographic distribution of the *Phanaeus cambeforti* Arnaud, 1982; *P. minos* Erichson, 1847 stat. rev.; *P. lecourti* Arnaud, 2000; *P. meleagris* Blanchard, 1845; *P. divisor* sp. nov and *P. mariocupelloi* sp. nov.

anterior W-shaped carina (Fig. 1E). Anteromedial pronotal portion of males with two longitudinal curved carinae, each forming a large posterior tubercle (Figs 23A–B, 25). Pronotal disc of major males with posterior angles expanded upwards and backwards, the apices of which are curved towards center of pronotum (Figs 23A–B, 25A–B). Posteromedial pronotal fossae present (Fig. 22). Elytral striae punctate, basally impressed as distinct fossae (Fig. 1C). Front tibiae tridentate, with faint, almost imperceptible fourth tooth. Dorsum completely shiny metallic (except for black elevations), red, red with greenish iridescence, green, or bronze green. Occurrence in dry forests and shrublands in southwestern Ecuador and northwestern Peru (Fig. 27).

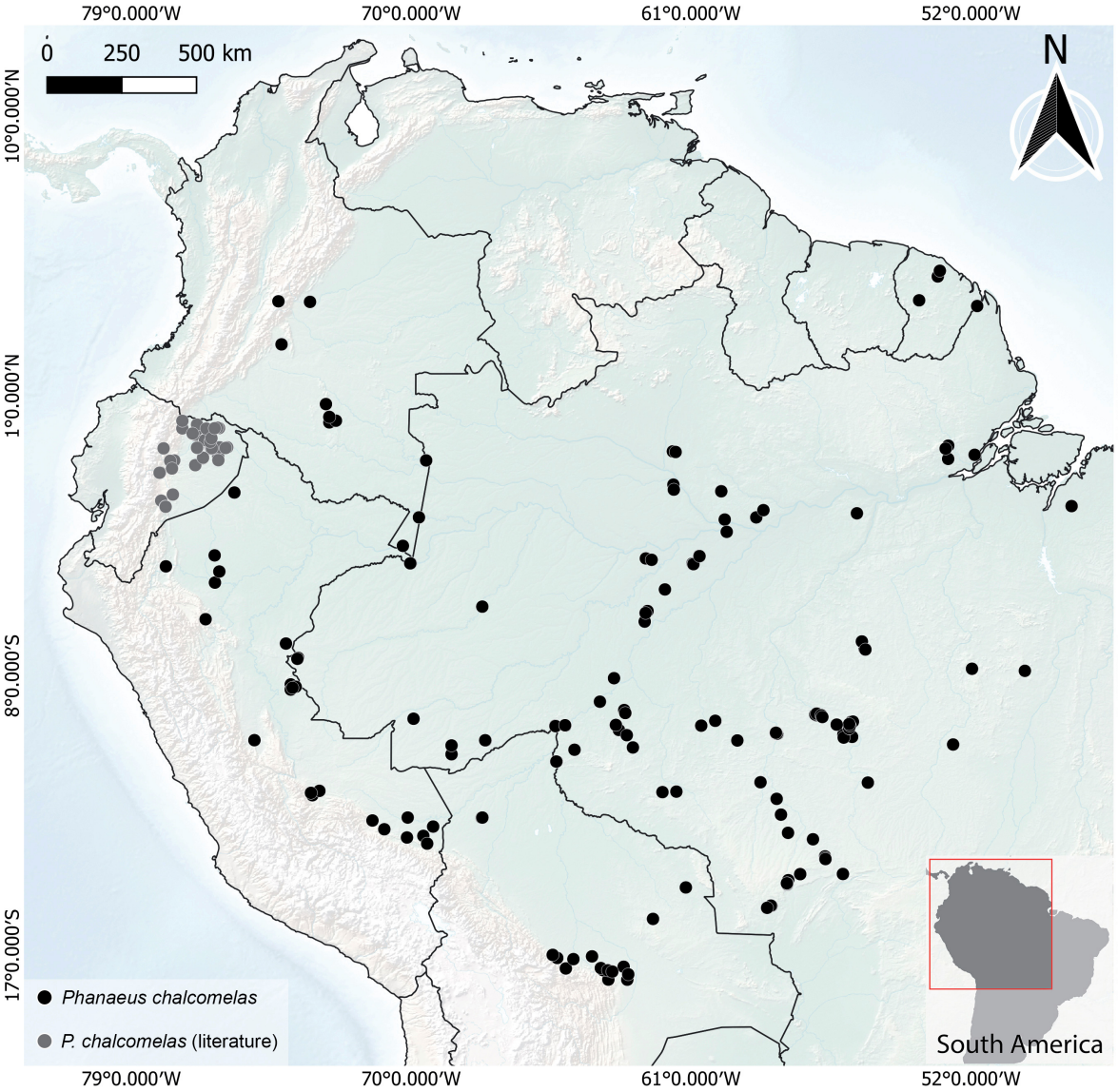

Fig. 21. Geographic distribution of *Phanaeus chalcomelas* (Perty, 1830). Black circles represent the coordinates from analyzed material. Gray circles sensu Chamorro *et al.* (2019).

Key to species of the *Phanaeus achilles* group

1. Dorsum red or red with green reflections (Fig. 22A–B). Pronotal tubercles of major males sub-quadrate with apices curved towards center of pronotum (Fig. 24A, C). Medial endophallite as Fig. 26C. Dry forests and shrublands of southwestern Ecuador (Fig. 27) at low elevations (maximum 50 m a.s.l.) ..... ***Phanaeus achilles*** Boheman, 1858
– Dorsum bright green or bronze green (Fig. 22C–D). Rounded or sub-quadrate pronotal tubercles of major males, with the apices pointing upwards (Fig. 24B, D). Medial endophallite as Fig. 26D. Dry forests and mountains in extreme northwest Peru and southwestern and southern Ecuador (Fig. 27) at low to high elevations (13 to 1210 m a.s.l) ..... ***Phanaeus arnaudorum*** sp. nov.

Phanaeus achilles Boheman, 1858
Figs 1B, E, G, 22A–B, 23A, C, E, 24A, C, 25A, 26A, C, E, G, 29A

Phanaeus achilles Boheman, 1858: 42.
Phanaeus foveolatus Harold, 1880: 152.

Phanaeus achilles – Harold 1869: 1016. — Nevinson 1892: 1. — Gillet 1911a: 319; 1911b: 81. — d'Olsoufieff 1924: 40, 97, 151 (in part). — Blackwelder 1944: 209. — Vulcano & Pereira 1967: 574 (in part). — Edmonds 1972: 834, 874. — Streit 2008: 9. — Lizardo *et al.* 2022: 548, 553, 557. — Moctezuma *et al.* 2024: 5. — Moctezuma 2025: 4.

Phanaeus foveolatus – Nevinson 1892: 4. — Gillet 1911a: 319 (as synonym of *P. achilles*); 1911b: 81 (as synonym of *P. achilles*). — Blackwelder 1944: 209 (as synonym of *P. achilles*). — Edmonds 1994: 30 (as synonym of *P. achilles*). — Arnaud 2002: 88 (as synonym of *P. achilles*). — Figueroa *et al.* 2014: 136 (as synonym of *P. achilles*). — Chamorro *et al.* 2019: 212 (as synonym of *P. achilles*).

Phanaeus (*Notiophanaeus*) *achilles* – Edmonds 1994: 1, 7, 25–26, 28 (in part). — Arnaud 2002: 88 (in part). — Vaz-de-Mello *et al.* 2013: 1–2. — Edmonds & Zídek 2012: 1, 7–8, 10–11, 37–38, 40. — Chamorro *et al.* 2018: 97 (in part); 2019: 211–212 (in part).

Phanaeus (*Notiophanaeus*) *achilles lydiae* – Arnaud 2000: 8; 2002: 88. — Carvajal *et al.* 2011: 320–321. — Krajcik 2012: 204. — Edmonds & Zídek 2012: 1, 8, 11 (as synonym of *P. achilles*). — Chamorro *et al.* 2019: 212 (as synonym of *P. achilles*).

Diagnosis

Dorsum completely shiny metallic red or red with greenish iridescence (Figs 22A–B, 23 A, C, E). Venter dark green except for black central portion of metaventrite. Pronotum bearing contrasted black elevations, variously and irregularly shaped (Figs 1G, 22A–B, 23A, E, 24A). Anteromedial pronotal region of males with two longitudinal curved carinae, each forming a large posterior sub-quadrate tubercle (Figs 23A, 24A, C). Pronotum of females with anterior W-shaped carina (Figs 1E, 23E). Elytral striae punctate, basally impressed as distinct fossae (Fig. 22A–B). Length 15– 22.5 mm. Endophallites: ME with a large tab, given triangular appearance in dorsal and ventral view; margins of tab sinuous with a lateral rounded C-shaped angle in ventral view (Fig. 26C). AE in dorsal view, triangular, with a concave left margin and convex right margin; left margin with lateral projection near the apex (Fig. 26E). SRP almost horizontal guttiform, with rounded left margin and sharp right margin (dorsal view) (Fig. 26G).

Type material

Lectotype of *Phanaeus achilles* (here designated)
ECUADOR • ♂; "Puna/ Kinb./ Riksmuseum Stockholm/ 6056 E92+/ 50 84"; NRMS.

Paralectotype of *Phanaeus achilles*
ECUADOR • 1 ♂; "Puna/ Kinb./ *Phanaeus* Mac'Leay/ *achilles* Boh./ Riksmuseum Stockholm/ 51 84"; NRMS.

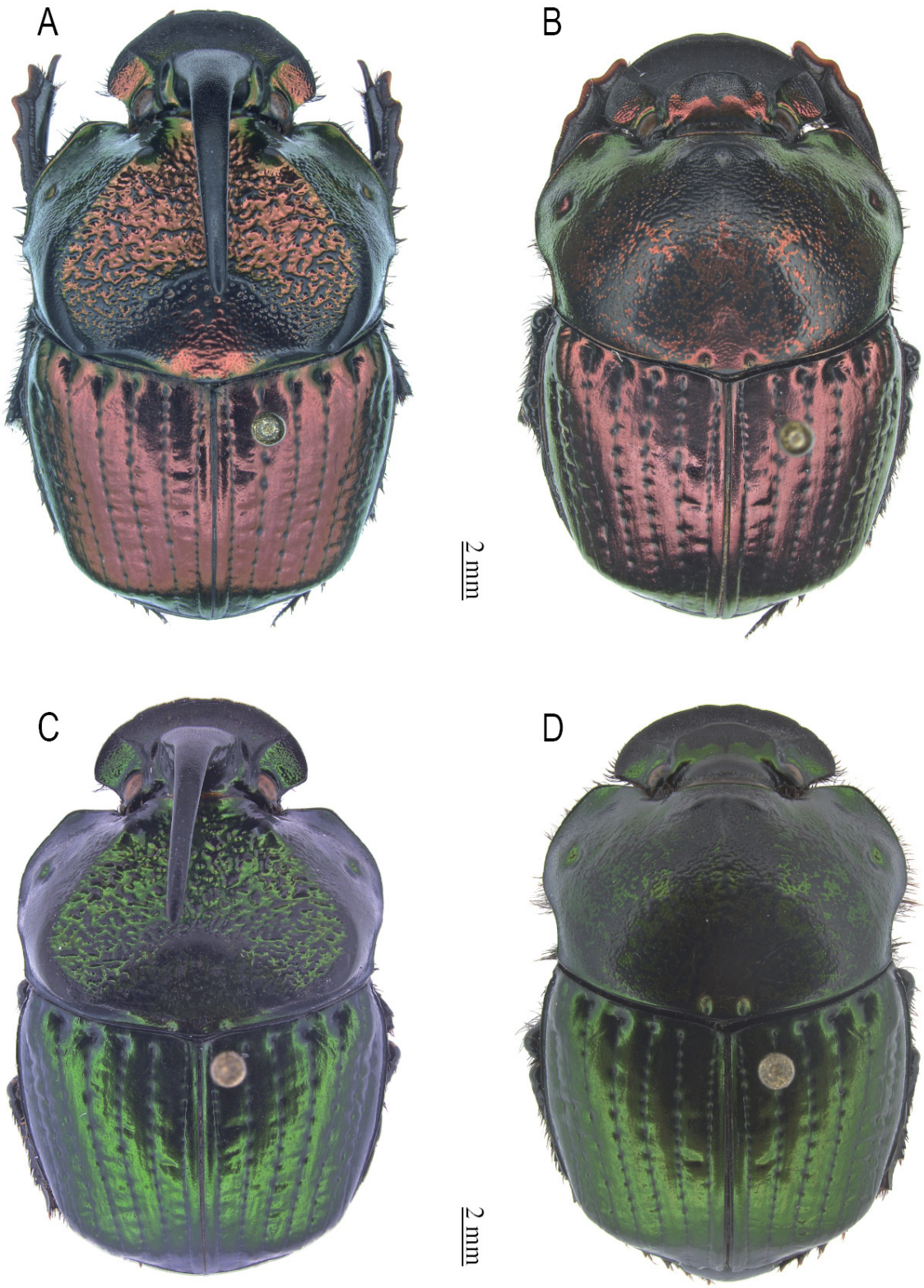

Fig. 22. *Phanaeus achilles* species group in dorsal view. **A–B**. *P. achilles* Boheman, 1858 (CEMT). **A**. Major male. **B**. Female. **C–D**. *P. arnaudorum* sp. nov. **C**. Holotype, major male (CEMT). **D**. Paratype, female (CEMT).

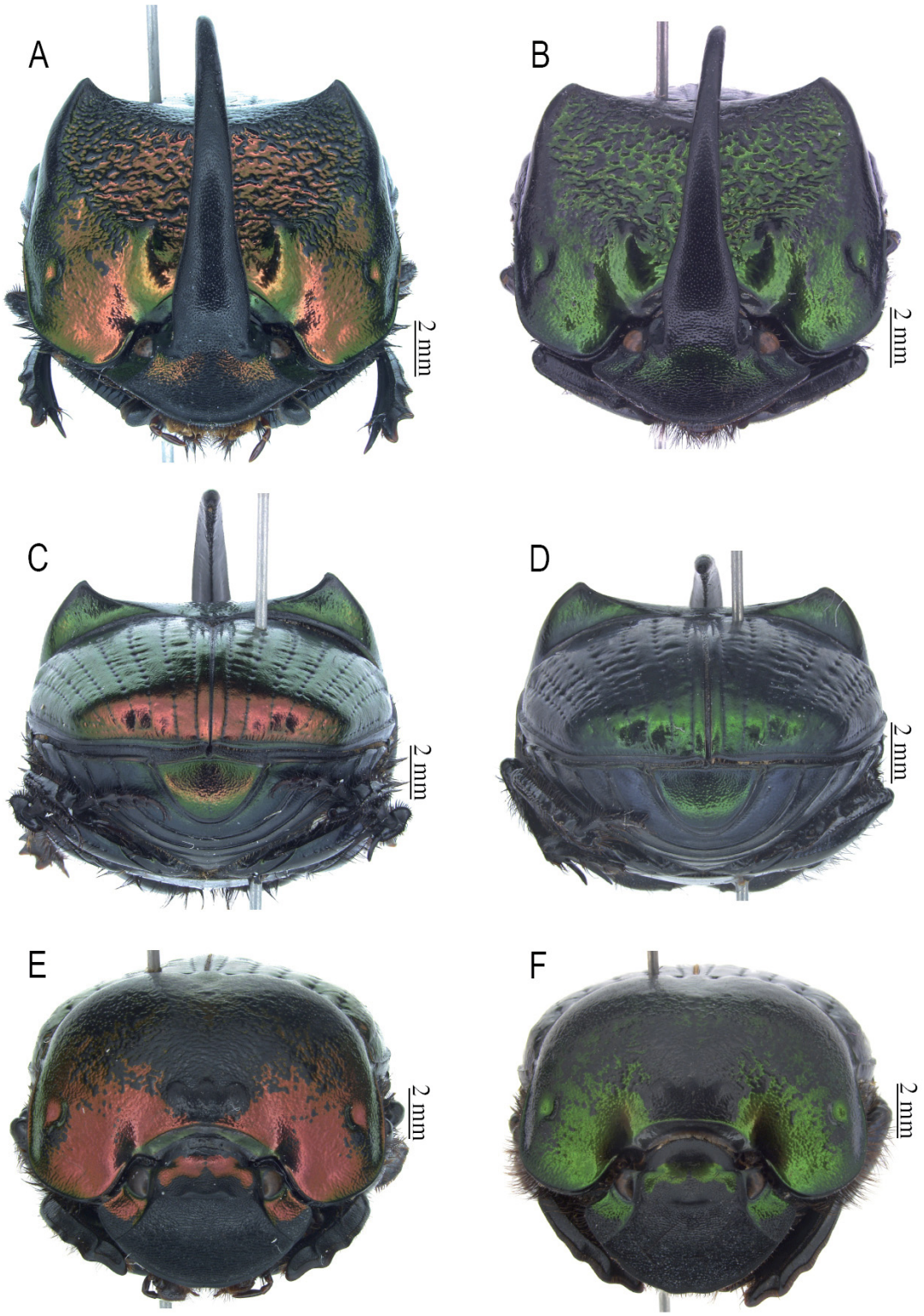

Fig. 23. *Phanaeus achilles* species group. **A**. *P. achilles* Boheman, 1858 ♂ (CEMT), frontal view. **B**. *P. arnaudorum* sp. nov., holotype, ♂ (CEMT), frontal view. **C**. *P. achilles* Boheman, 1858 ♂ (CEMT), posterior view. **D**. *P. arnaudorum* sp. nov., holotype, ♂ (CEMT), posterior view. **E**. *P. achilles* Boheman, 1858 ♀ (CEMT), frontal view. **F**. *P. arnaudorum* sp. nov., paratype, ♀ (CEMT), frontal view.

Holotype of *Phanaeus achilles lydiae*
ECUADOR • ♂; "Guayas, Los Ceibos Guayaquil; 28 Nov. 1987"; CPFA.

Paratypes of *Phanaeus achilles lydiae* (25 ♂♂, 32 ♀♀)
ECUADOR – **Guayaquil** • 1 ♀; same data as for holotype; CPFA • 3 ♂♂, 3 ♀♀; Gua. env. Cerecita. Rte Salinas; Feb. 1990; CPFA • 20 ♂♂, 26 ♀♀ same data as for preceding, 5–10 Mar. 1988; CPFA • 2 ♂♂, 2 ♀♀; Guayaquil, Los Ceibos; 29 Feb. 1988; L. Arnaud and P. Arnaud leg.; CEMT.

Holotype of *Phanaeus foveolatus* (studied from photographs)
ECUADOR • ♂; "Guayaquil: Reist./ 38678/ 1405/ foveolatus Harold."; GMFNB.

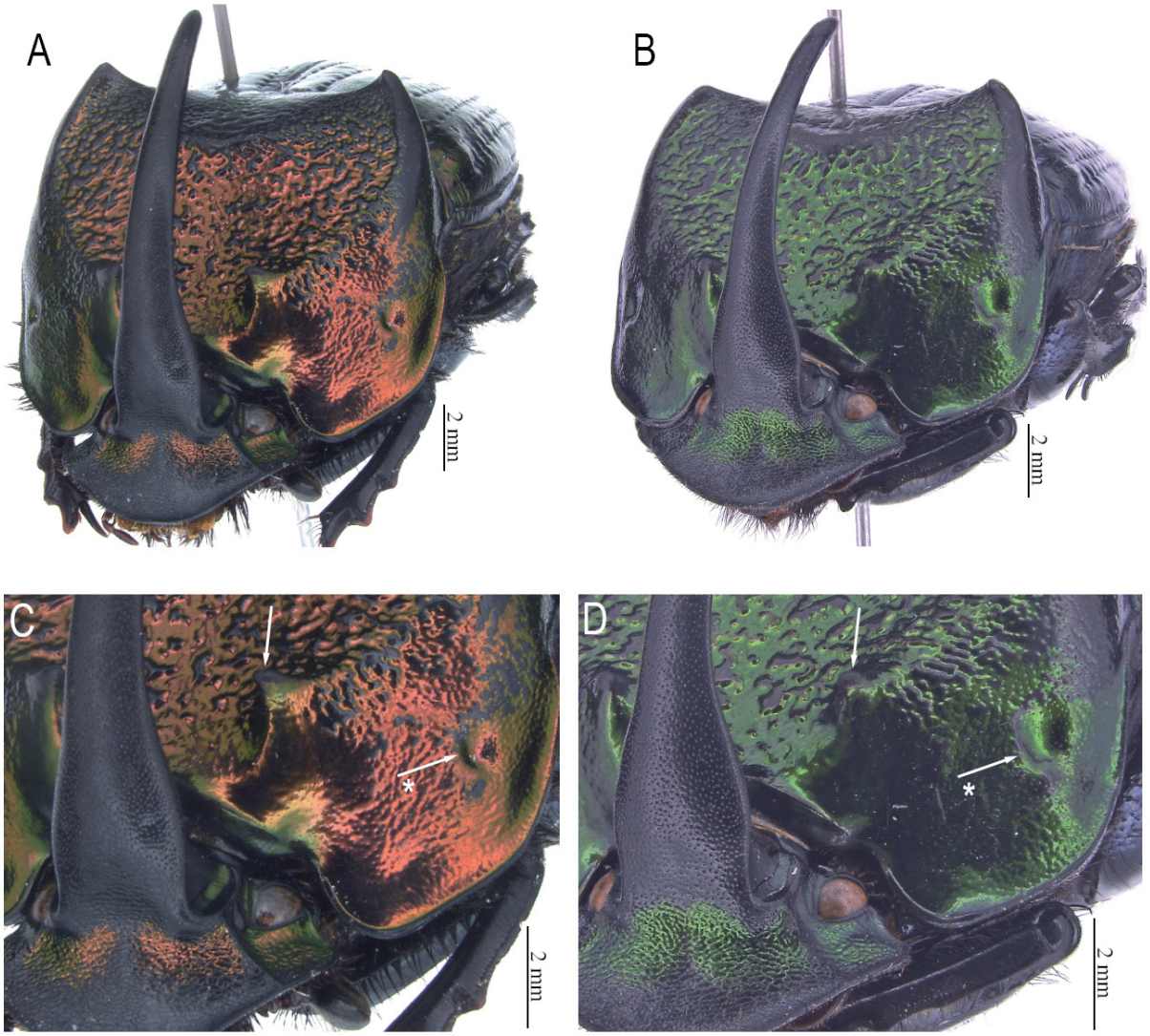

Fig. 24. Major males of *Phanaeus achilles* species group in fronto-lateral view. **A, C**. *P. achilles* Boheman, 1858 (CEMT). **B, D**. *P. arnaudorum* sp. nov., holotype (CEMT). Arrows indicate the anteromedial pronotal tubercles, larger in *P. achilles*; asterisk arrows indicate the anterolateral pronotal fossae, larger in *P. arnaudorum*.

Non-type material examined (4 ♂♂, 2 ♀♀)

ECUADOR • 1 ♀; L.W. Saylor leg.; ex-Gonzalo Halffter Salas; IEXA. – **Guayas** • 1 ♂; 40 km SW of Guayaquil; elev. 50 m; 21–22 Feb. 1981; B.D. Gill leg.; TAMU. – **Manabí** • 1 ♂, El Aromo, La Fabril; 16 May 2010; W. Chamorro leg; feces; CEMT • 1 ♂; Machalilla; 1°28′18″S, 80°45′48″W; elev. 30 m; 17 Mar. 1999; C. Rivadeneira leg.; CEMT • 1 ♂, 1 ♀; vicinity of Montecristi; 01°02′22″ S, 80°40′33″ W; 8–9 Feb. 2003; B.D. Streit leg.; pitfall human dung; TAMU.

Type locality

Ecuador, Guayas, Isla Puná.

Distribution

Dry forests and shrublands of southwestern Ecuador, from 0 to 50 m a.s.l. (Fig. 27).

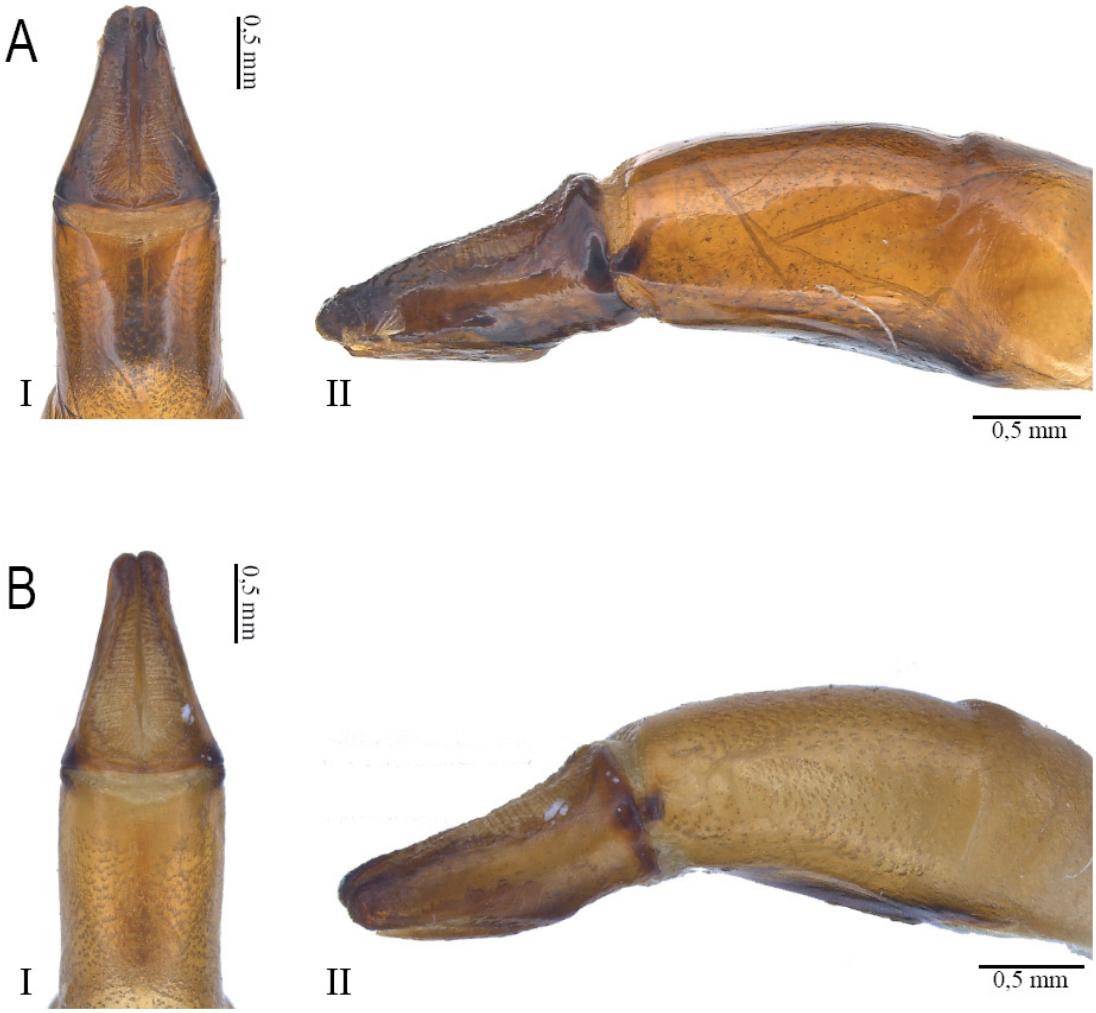

Fig. 25. Aedeagus of the *Phanaeus achilles* species group. **A**. *P. achilles* Boheman, 1858 (CEMT). **B**. *P. arnaudorum* sp. nov., paratype (CEMT), dorsal (I) and lateral (II) views.

Phanaeus arnaudorum sp. nov.
urn:lsid:zoobank.org:act:FEF361C8-1CE1-419D-B62B-FB8E76F26E11
Figs 1C, 22C–D, 23B, D, F, 24B, D, 25B, 26B, D, F, H

Non *Phanaeus achilles* (error) – d'Olsoufieff 1924: 40, 97 (in part). — Vulcano & Pereira 1967: 574 (in part). — Ratcliffe *et al.* 2015: 197. — Streit 2008: 8.
Non *Phanaeus* (*Notiophanaeus*) *achilles* (error) – Edmonds 1994: 1, 7, 25–26, 28 (in part). — Arnaud 2002: 88. — Edmonds & Zídek 2012: 1, 7–8, 10–11, 37–38, 40 (in part). — Vaz-de-Mello *et al.* 2013

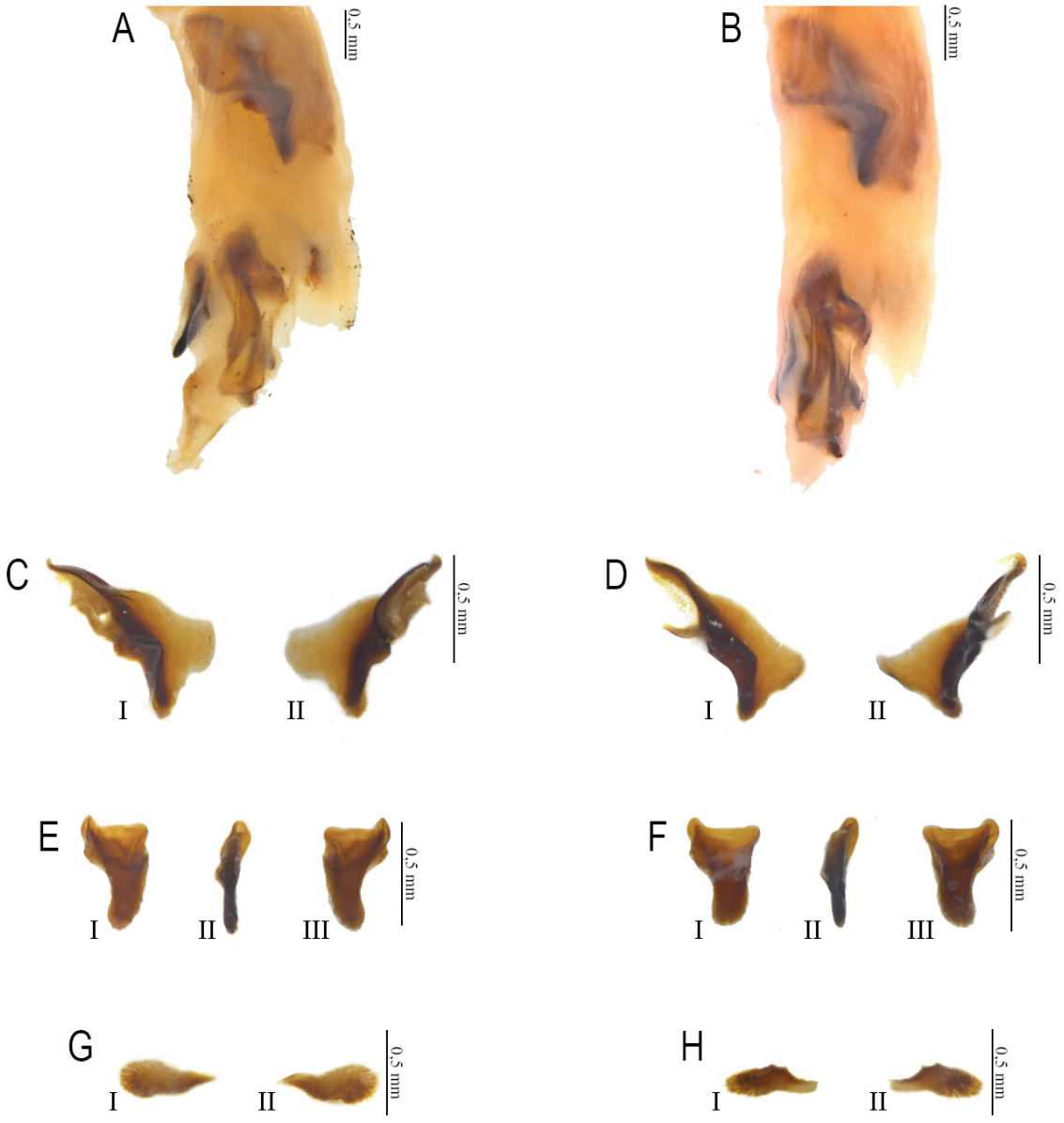

Fig. 26. Endophallus and endophallites of the *Phanaeus achilles* species group. Respectively *P. achilles* Boheman, 1858 (CEMT) and *P. arnaudorum* sp. nov., paratype (CEMT). **A–B**. Endophallus in dorsal view. **C–D**. Medial endophallite (ME), dorsal (I) and ventral (II) views. **E–F**. Additional endophallite (AE), dorsal (I), lateral (II) and ventral (III) views. **G–H**. Superior right peripheral endophallite (SRP), dorsal (I) and ventral (II) views.

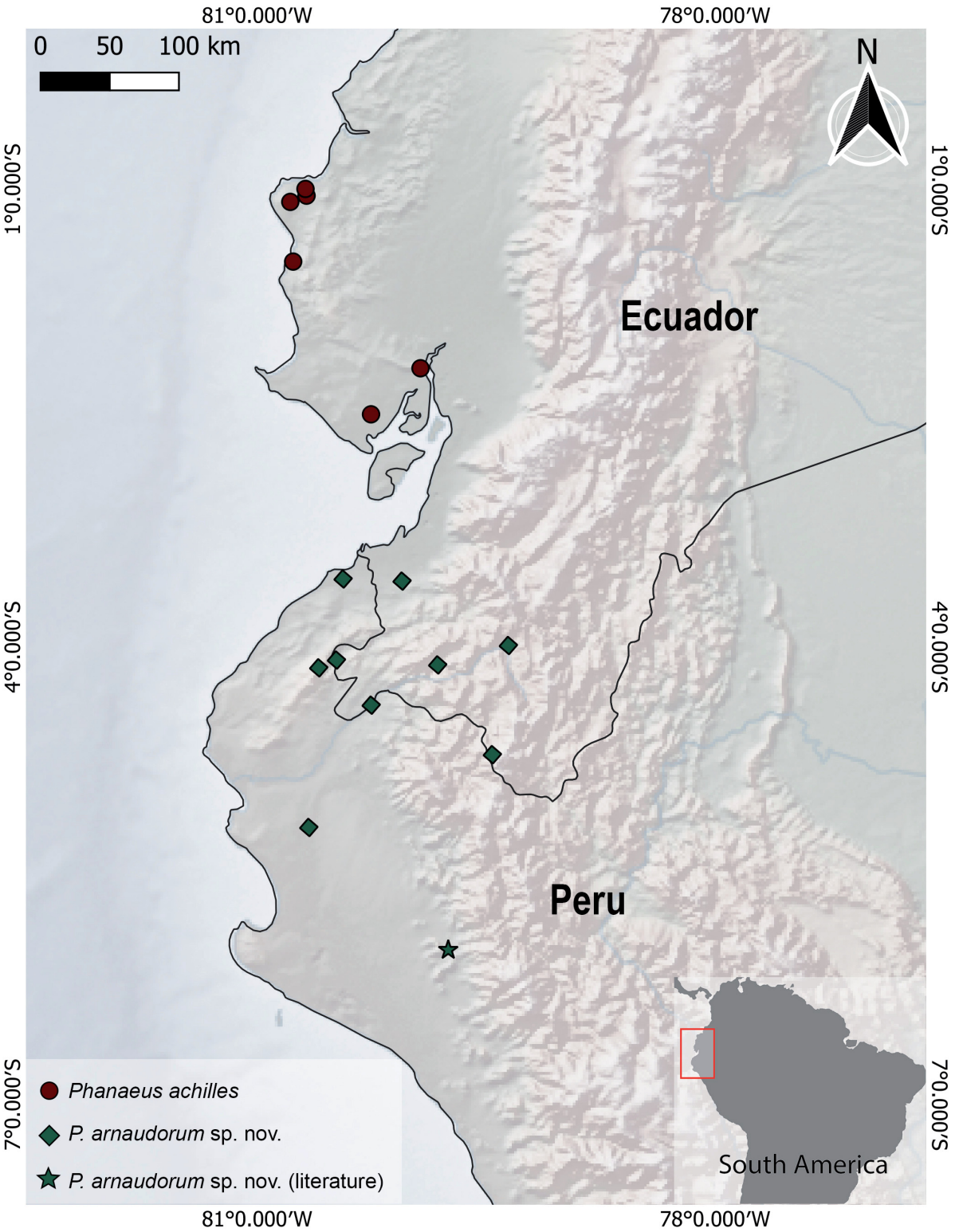

Fig. 27. Geographic distribution of *Phanaeus achilles* Boheman, 1858 and *P. arnaudorum* sp. nov. The star is sensu Figueroa *et al.* (2014).

1–2 (in part). — Figueroa *et al.* 2014: 125, 127, 131, 136. — Chamorro *et al.* 2018: 97 (in part); 2019: 211–212 (in part).

Non *Phanaeus* (*Notiophanaeus*) *achilles achilles* (error) – Arnaud 2002: 88. — Carvajal *et al.* 2011: 320–321. — Krajcik 2012: 204. — Chamorro *et al.* 2019: 212.

Diagnosis

This species is diagnosed by the following combination of characters: Anteromedial margin of clypeus weakly bidentate (Fig. 22C–D); major males with long cephalic horn curved over the pronotum (Figs 22C, 23B, 24B); pronotum bearing contrasted black elevations, variously and irregularly shaped (Figs 22C–D, 23B, F, 24B); anteromedial pronotal region of major males with two longitudinal curved carinae, each forming a pronotal tubercle, with the apices pointing upwards (Figs 23B, 24B, D); pronotum of females with anterior W-shaped carina (Fig. 23F); elytral striae punctate, basally impressed as distinct fossae (Fig. 22C–D); dorsum completely shiny metallic, green or bronze green (Figs 22C–D, 23B, D, F); black ventral color, or black with green reflections on the ventral portion of femora.

Etymology

The specific epithet is dedicated to Alain (in memoriam), Patrick, Lydie (in memoriam), Florent and Audrey Arnaud and their descendants, in honor of their contributions to Scarabaeinae collections and taxonomy, and strong friendship to one of us for so many years.

Type material (59 ♂♂, 39 ♀♀)

Holotype

ECUADOR • ♂; El Oro, Arenillas; 3°34′24″ S, 80°08′36″ W; elev. 13 m; 15 Jun. 2012; D. Marín leg.; pitfall dung; CEMT.

Paratypes

ECUADOR – **El Oro** • 29 ♂♂, 15 ♀♀; same data as for holotype; CEMT • 2 ♂♂, 1 ♀; same data as for holotype; MGCB • 5 ♂♂, 2 ♀♀; same data as for holotype; CPFA • 1 ♂, 1 ♀; 3 km S of Arenillas; elev. 50 m; 26 May 2002; Curoe leg.; CEMT. – **Loja** • 1 ♂; Catamayo; 16 Oct. 2005; F. Ohs leg.; TAMU • 1 ♂; Cazaderos; TAMU • 1 ♀; Cantón Zapotillo, Ceiba Chica; 17 Mar. 2018; T. Atocha leg.; LOUNAZ • 1 ♀; Guachanamá, Sabanilla; 4°06′58″ S, 79°48′59.4″ W; elev. 800 m; 8 Mar. 2021; W. Chamorro leg.; pitfall hum dung; LOUNAZ • 11 ♂♂, 15 ♀♀; Loja, ex Abbé Gaujon; MNHN • 1 ♂; Loja; ac: 22623; L.W. Saylor leg.; ex-Gonzalo Halffter Salas; IEXA.

PERU – **Pasco** • 3 ♂♂, 2 ♀♀; Oxapampa; elev. 1800 m; ex Le Moult; CPFA. – **Piura** • 1 ♀; Ayabaca, C.C. Samanga, Sector Espíndola; 4°42′16″ S, 79°27′30″ W; elev. 2847 m; 16 Feb. 2009; D. Saavedra leg.; CEMT. – **Tumbes** • 3 ♂♂; Canovitas; PN Cerros de Amotape; Feb. 1995; CPFA • 1 ♂; Tumbes; 16 May 2007; D. Ramírez leg.; CEMT.

Type locality

Ecuador, El Oro, Arenillas.

Description

Major male (holotype)

Measurements. Length 20 mm. Width 12.4 mm.

Head. Anteromedial margin of clypeus weakly bidentate with striated sculpture (Fig. 22C). Cephalic horn black, long, curved posteriorly over the pronotum, occupying central third of total width of head

(Figs 22C, 23B, 24B). Bright green on paraocular area and posterior portion of clypeus (Fig. 22C). Paraocular ridge distinct, extending along the entire lateral margin of eyes (Fig. 22C).

Pronotum. Bright green, with irregularly black elevations over the whole disc (Fig. 22C). Anteromedial region with two longitudinal curved carinae, each forming a posterior tubercle (Figs 23B, 24B, D). Posterior angles expanded upwards and backwards, the apices of which are curved towards center of pronotum (Fig. 23B). Posteromedial fossae rounded (Fig. 22C). Pronotal punctures strong, more visible on anterior and lateral portions (10× magnification).

Elytra. Bright green, striae punctate, basally impressed as distinct fossae (Fig. 22C). Interstriae with punctures (10× magnification) evenly spaced over the entire surface (Fig. 1C).

Metaventrite. Completely black with strong punctures (10× magnification). Tip of anteromedial prominence triangular.

Pygidium. Bright green with strong punctures over the whole surface (Fig. 23D).

Endophallites. ME with a large tab, given triangular appearance in dorsal and ventral view; margins of tab almost straight with a lateral acute angle (Fig. 26D). AE, in dorsal view, triangular, with concave lateral margins; left margin with lateral projection near the apex (Fig. 26F). SRP with rounded left margin and tapered left portion (dorsal view) (Fig. 26H).

Variation

Male sizes: length 14–22 mm; width 9–12 mm. Female sizes: length 17–22 mm; width 9.8–12 mm. Females: head with a transversal carina. Middle of the cephalic carina with two elevations, giving a bituberculate appearance in frontal view (Fig. 23F); anterior carina of pronotum W-shaped in frontal view (Fig. 23F); oval posteromedial pronotal fossae (Fig. 22D).

Distribution

Dry forests and mountains in extreme northwest of Peru and the southwest of Ecuador, from 13 to 1210 m a.s.l. (Fig. 27).

Taxonomic discussion

The external morphology and the parameres of *P. achilles* and *P. arnaudorum* sp. nov. are very similar (Figs 22, 25). However, in addition to the difference in coloration — *P. achilles* being currant red with green sheen, and *P. arnaudorum* being green or bronze green — these species also differ in the shape of the medial and additional endophallites (Fig. 26C–F). Furthermore, the anterolateral pronotal fossae are larger in major males of *P. arnaudorum* compared to *P. achilles* and the pronotal tubercles of major males are smaller in *P. arnaudorum* than in *P. achilles* (Fig. 24C–D).

Discussion

The *Phanaeus chalcomelas* species group

This is the most comprehensive revision of the *P. chalcomelas* group to date, and based on the new diagnoses herein introduced, it now includes seven species: *P. cambeforti*, *P. chalcomelas*, *P. lecourti*, *P. meleagris*, *P. minos* stat. rev., *P. divisor* sp. nov. and *P. mariocupelloi* sp. nov. Although *P. minos* was considered a synonym of *P. meleagris* by Harold (1870), Edmonds (1994) and Edmonds & Zídek (2012), and a subspecies of *P. meleagris* by Arnaud (2002), the external morphology and medial endophallite, as well as the clear geographical delimitation between the two species, gave us enough evidence to revalidate *P. minos*. The situation was different for *P. lecourti peruanus*, which remains as a junior

synonym of *P. lecourti* as we found no evident variation in the external morphology and the medial endophallite across the range of the species. Therefore, we agree with Edmonds & Zídek (2012) in considering *P. lecourti peruanus* Arnaud, 2000 as a junior synonym of *P. lecourti* Arnaud, 2000.

There is much to discuss regarding the designation of the *P. chalcomelas* neotype (Arnaud 2001). First, Edmonds (1994) reported uncertainty about whether the specimen (♀) from Munich was indeed the holotype of the species due to the label attached to the specimen bearing the inscription "*Phanaeus chalcomelas*" (Fig. 28B), since the species was described in the genus *Onitis* Fabricius, 1798, not in *Phanaeus*, and because the handwriting does not correspond to the sample of Perty's handwriting analyzed by Edmonds (1994) in Horn & Kahle (1937). Furthermore, Arnaud (2001) argued for the necessity of designating a neotype because the label with "Brasilia" (Brazil) on the specimen from the Munich Museum did not correspond to the type locality mentioned by Perty, "Prov. S. Pauli et Minarum" (now the states of São Paulo and Minas Gerais [Brazil]) in the species description. Once the described type locality does not correspond to the distribution of *P. chalcomelas*, Arnaud (2001) emphasized the need to designate a neotype from a known population and therefore chose a male specimen collected in the state of Pará (Brazil).

The same type locality problem is reported to another Amazonian species, *Gromphas aeruginosa* (Perty, 1830), whose label indicates only Brazil in the type series and the type locality in the description is São Paulo and Minas Gerais. Cupello & Vaz-de-Mello (2013) and Cupello (2024) discussed that the type series of *G. aeruginosa* and the holotype of *P. chalcomelas* were collected during the expedition of Johann Baptist von Spix and Karl Friedrich Philip von Martius through various regions of Brazil between

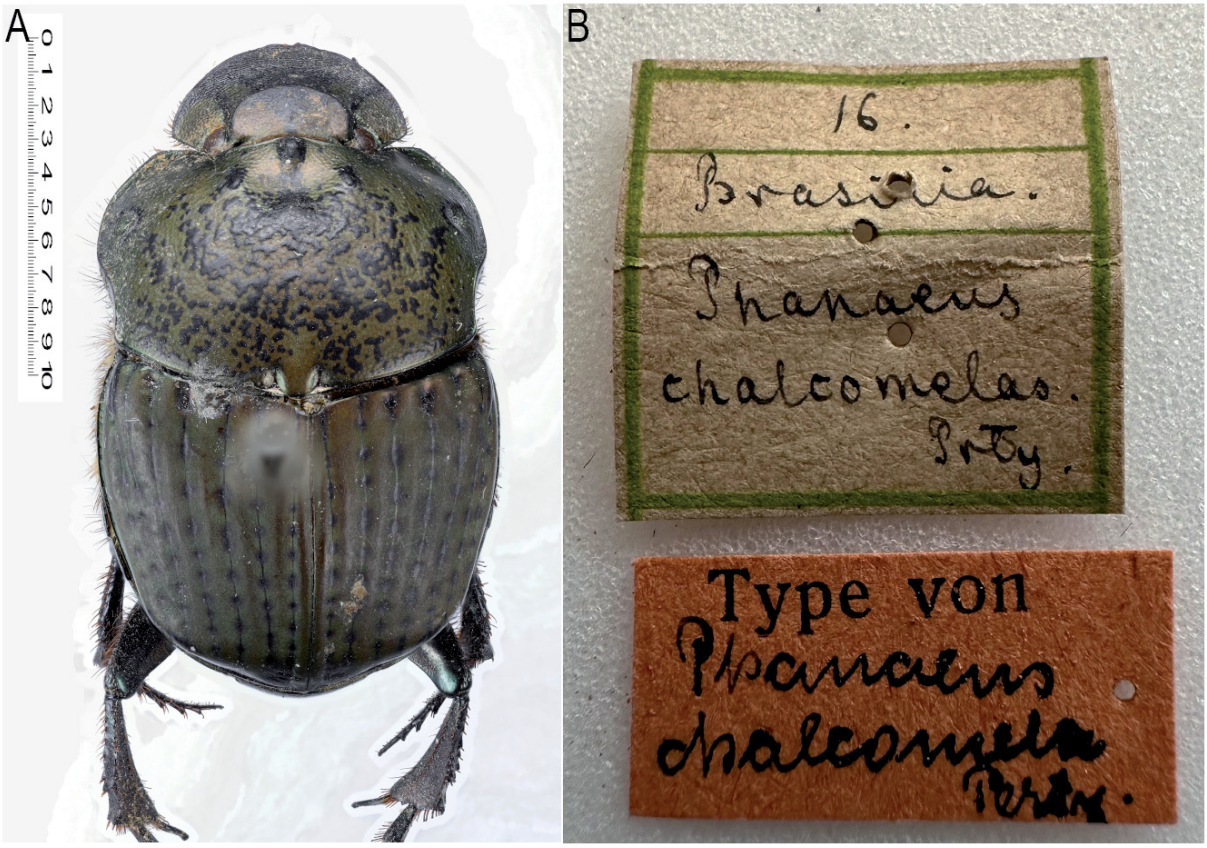

Fig. 28. A. *Phanaeus chalcomelas* (Perty, 1830), holotype, ♀ (SZM). **B**. Labels. Photographs by Dr Michael Balke.

1817 and 1820, and the material collected in the Amazon and southeastern Brazil were likely mixed, leading to Perty's mistakes regarding the locality of the specimens. Cupello & Vaz-de-Mello (2013) also provided information about the labels of the *G. aeruginosa* type series based on Scherer (1983), stating that the original labels written in pencil by Perty were removed from these specimens and replaced by other labels by later curators. For example, the label "type von *Gromphas aeruginosa* Perty" was written in the handwriting of Hans Kulzer, a former preparator at the Zoologische Staatssammlung München, and it matches the handwriting of the label "type von *Phanaeus chalcomelas* Perty" (Fig. 28B) attached to the holotype of *P. chalcomelas*. Additionally, the square label with green borders (Fig. 28B) bears the handwriting of Dr Johannes Rudolph Roth (Zoologische Staatssammlung 1843–1858) (Scherer 1983).

The questions raised by Edmonds (1994) and Arnaud (2001) are answered by the evidence presented here, and there is now no doubt regarding the validity of the holotype of *P. chalcomelas* housed in Munich. Accordingly, the designation of a neotype by Arnaud (2001) appears to have been unnecessary. Furthermore, we consider it possible to restrict the type locality (or typical population) of the species by cross-referencing the itinerary of Spix and Martius with the morphological variation documented below, which can be constrained to areas close to the Amazon River. In addition, given current knowledge, taxonomic instability does not result from the holotype being female, since females of *P. chalcomelas* are as readily diagnosable as males, based on the number and position of the anteromedial pronotal tubercles (Figs 19G–H, 28A) and the arrowhead-shaped apex of the anterior prominence of the metaventrite (Fig. 2A).

Arnaud (2001) described the subspecies *P. chalcomelas grossii* from Bolivia, characterized by a cephalic horn with tips more acute at the upper part of the basal expansion and more black elevations on the pronotal disc than the nominate subspecies. Subsequently, Arnaud (2002) indicated the geographic distribution of *P. chalcomelas chalcomelas* as French Guiana, Brazil (Pará), Colombia (Meta), and Peru (Huánuco), whereas *P. chalcomelas grossii* was reported exclusively from Bolivia (Chapare). However, *P. chalcomelas* is broadly distributed throughout the Amazon region, and the assignment of subspecies was not indicated for several other localities where the species occurs, including Ecuador, Venezuela, and multiple Brazilian states (Acre, Amapá, Amazonas, Mato Grosso, and Rondônia). One of the main objectives of our taxonomic revision of the *Phanaeus chalcomelas* species group was precisely to reassess the geographic limits of *P. chalcomelas chalcomelas* and *P. chalcomelas grossii*, and to evaluate the possibility of elevating *P. chalcomelas grossii* to species rank.

Initially, based on specimens collected from the northern and southern portions of the Amazon basin, the distinction between the two taxa appeared clear. The individuals illustrated in the plates represent these two opposite extremes of the observed variation. However, after analyzing more than a thousand specimens of *P. chalcomelas* from multiple populations across the entire distribution, we observed a continuous range of morphological variation. This variation includes the shape of the male cephalic horn, body coloration, amount of black elevations on the pronotal disc, and the morphology of the medial endophallite. These characters do not segregate into discrete, consistently diagnosable units corresponding to the previously proposed subspecies, but instead show gradual and overlapping variation among populations. Therefore, we agree with the synonymy proposed by Edmonds & Zídek (2012) between *P. chalcomelas grossii* and *P. chalcomelas*. Further studies on the phylogeography of *P. chalcomelas* may provide a better insight into the population structure of this species, as well as its historical distribution in different Amazonian regions, and could bring different taxonomic conclusions.

The *Phanaeus achilles* species group

Although *Phanaeus achilles* was assigned to the *P. chalcomelas* group, it was regarded as isolated within it because of its distinct morphology and geographic distribution (Edmonds 1994). The metallic dorsal coloration of *P. achilles* and *P. arnaudorum* sp. nov. differs from the species within the *P. chalcomelas*

group, which have opaque dorsal coloration and a metallic sheen restricted to certain portions, as around the eyes, pronotal margins, anterior margins of elytra, ventral portion of femora, and hypomeron. The shape of the pronotum of *P. achilles* and *P. arnaudorum* males is elevated and without lateral expansions in dorsal view, while that of the males of the *P. chalcomelas* group is flattened and with lateral expansions in the posterior portion giving a triangular shape in dorsal view. The females of *P. chalcomelas* group bear three (or four in *P. chalcomelas*) small tubercles on the pronotum, while those of *P. achilles* and *P. arnaudorum* have a W-shaped carina on the pronotum. While the members of the *P. chalcomelas* species group are distributed in the Amazon Basin and along the eastern slopes of the Andes, *P. achilles* and *P. arnaudorum* are restricted to dry forests and shrublands in southwestern Ecuador and northwestern Peru, on the opposite side of the Andes (Edmonds & Zídek 2012; Vaz-de-Mello *et al.* 2013; Chamorro *et al.* 2019). In addition, molecular phylogenetic studies (Price 2009; Gillett & Toussaint 2020; Moctezuma *et al.* 2024) have shown that the *chalcomelas* group is polyphyletic when including *P. achilles*. Considering these morphological, geographical and molecular evidence, we consider that *P. achilles* and *P. arnaudorum* do not belong to the *P. chalcomelas* species group. The same goes for the subfossil species *P. violetae* Zunino, 2013, which, being virtually identical to *P. achilles* and found in Quito (Ecuador), should also not belong to the *chalcomelas* group.

In the description of *P. achilles*, Boheman (1858) describes the coppery dorsal color and black ventral color ("supra cupreus, subtus niger"), a long horn for males, a short horn for females (characteristic of small males), and mentions a green-bronze coloration variety "Var. a: Supra viridi-aeneus". Although Boheman (1858) did not designate a holotype for *P. achilles* and clearly indicated the existence of more than one specimen in the description, the "holotype" of *P. achilles* (NRMS) is mentioned by Edmonds (1994) and Chamorro *et al.* (2019). Although no publications regarding the designation of the *P. achilles* lectotype were found, an analysis of the specimens described by Boheman (deposited in the NRMS) revealed that the bronze-green male specimen (Fig. 29C) bears a holotype label by Edmonds from 1983 (Fig. 29D), and the two red specimens (one large male [Fig. 29A] and one small male) have paratype labels from the same authority and year (Fig. 29B). We also observed a label marked "Type" attached to the bronze-green specimen (Fig. 29D), which probably led Edmonds to choose this specimen as the holotype of *P. achilles*. The larger red specimen also bears a lectotype label from Vaz-de-Mello (2014) (Fig. 29B), while the smaller red male and a green male have paralectotype labels with the same signature and date (Fig. 29D).

Despite the "Type" label on the bronze-green specimen, two issues arise concerning the *P. achilles* "holotype": the typical coloration of *P. achilles* described is red whereas the green coloration was described as a variation. The International Code of Zoological Nomenclature, ICZN (1999) in Article 72.4.1, defines that specimens to which the author has referred as distinct variants (e.g., by name, letter or number) are excluded from the type series. Since the green-bronze coloration was described as variety "a", the green specimen that was chosen as the holotype of *P. achilles* does not belong to the type series. Article 72.4.7 states that a mere citation of "Type" or an equivalent expression, either in a published work not establishing the nominal taxon of the species group, in an unpublished museum catalog, or on a label, does not necessarily constitute evidence that a specimen is fixed as a holotype or lectotype. Thus, the "Type" label on the green specimen alone does not serve as evidence to consider it as the holotype of *P. achilles*, especially given that its characters differ from those described for the species. Considering this, combined with the fact that Boheman (1858) did not designate a holotype for the species, and the "Type" label being attached to the specimen that is not part of the type series of *P. achilles*, we here designate the larger red specimen as the lectotype, with the smaller red specimen becoming a paralectotype.

Accepting that the "green" specimen was the holotype of *P. achilles*, Arnaud described the subspecies *P. achilles lydiae* for red specimens occurring in Guayaquil (Ecuador) at lower elevations. Later,

Edmonds & Zídek (2012) synonymized *P. achilles lydiae* with *P. achilles*, believing that the coloration difference reported by Arnaud (2000) was a chromatic variation of *P. achilles*. With the correct identity of the type material and color (red) of *P. achilles* clarified, we confirm that *Phanaeus achilles lydiae* Arnaud, 2000 is indeed a junior synonym of *Phanaeus achilles* Boheman, 1858. We also agree with the synonymy of *Phanaeus foveolatus* Harold, 1880 with *P. achilles* pointed out by Gillet (1911a), since the type locality of *P. foveolatus* is Guayaquil and the color described is red.

Regarding the subfossil species *P. violetae*, we initially considered synonymizing it under *P. achilles*, since the characteristics described by Zunino (2013) are present in *P. achilles*, and no morphological differences between *P. violetae* and *P. achilles* were reported in the description of *P. violetae*. However, an important character described by Zunino is the elevation at which *P. violetae* was found (2900 meters), significantly higher than the known range of *P. achilles* (0–50 m a.s.l.). Due to this altitudinal difference, combined with the fact that we only know the head of one female of *P. violetae*, whereas the heads of the females of close species of the genus *Phanaeus* are extremely similar (e.g., *P. achilles* and *P. arnaudorum* sp. nov.), we chose not to synonymize *P. achilles* and *P. violetae*.

Fig. 29. A–B. Lectotype of *Phanaeus achilles* Boheman, 1858 (here designated) (NRMS). **A**. Typical dorsal color. **B**. Labels. **C–D**. Green specimen wrongly cited as holotype of *Phanaeus achilles* by Edmonds (1994) (NRMS) and its labels.

Despite the morphological similarities between the *Phanaeus mexicanus* species group and *P. achilles* (also pointed out by Boheman 1858 and Edmonds 1972), such as the shape of the male horns, elytral punctures and metallic dorsal coloration, we did not include *P. achilles* and *P. arnaudorum* sp. nov. in the *P. mexicanus* group. Besides the different elytral striae, punctate in *P. achilles* and *P. arnaudorum* and simple in the *P. mexicanus* group, members of the *P. mexicanus* species group have a distinct incision on the clypeo-genal margin, which is absent in *P. achilles*, *P. arnaudorum* and *P. violetae*. In addition, the pronotum of females of the *P. mexicanus* group has a large anteromedial prominence, flanked on each side by a vertical depression that extends from the disc to the anterior margin of the pronotum (Edmonds & Zídek 2012). In contrast, the pronotum of the females of *P. arnaudorum* and *P. achilles* has only a W-shaped carina, without a large prominence or deep lateral depressions. For these reasons, we decided to create the new *Phanaeus achilles* species group to accommodate *P. achilles*, *P. arnaudorum* and *P. violetae*.

Acknowledgments

BRB receives a Scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, code 001). JAAB is supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) (166085/2020-0, 441646/2020-4 PROTAX 2021-2025). JAAB thanks the Secretaría de Educación de Boyacá (Colombia) for the work license to develop his doctoral study. MEM receives a PDJ scholarship sponsored by CNPq (152670/2024-6). FZVM is a CNPq fellow (CNPq 313397/2021-0). This work was developed with support from the Mato Grosso Research Foundation (FAPEMAT-PRO.0002206/2025), within the scope of activities conducted by researchers of the National Institute of Coleoptera (INCol/CNPq 408430/2024-9) and FAPEMAT - PROTAX (57886.805.21346.06032025), also CNPq - PROTAX (445678/2024-0). We would like to thank Subproject EECBio UFMT/Finep No 01.12.0359.00 and Subproject Peixes de Mato Grosso INCT-Peixes funded by MCTIC/CNPq No 405706/2022-7 for the photography system. We thank the researchers/curators Aura Cabrera (LOUNAZ), Bernd Jaeger (MFNB), Irina Morales (UPTC-CE), Julieta Ledezma and Marcelo Amaya (MHNNKM), Joachim Willers (MFNB), John Neita (IAvH-E), Juan Carvajal (UPTC-CE), Larry Jiménez (CCBUMAG), Letícia Vieira (UFLA), Luis Figueroa (MUSM), Mabel Alvarado (MUSM), Mario Cupello (TAMU) and Michael Balke (ZSM), for making it possible to analyze many specimens in this study. We would especially like to thank Mario Cupello, who not only sent us specimens that were analyzed by Edmonds in the 1994 revision, but also helped us unravel the problem of the type locality of *Phanaeus chalcomelas*.

References

Arias-Buriticá J.A., Bach A., Peres C.A., Haugaasen T., Hawes J. E., Azevedo R. A. & Vaz-de-Mello F.Z. 2023. A new species of *Isocopris* Pereira and Martínez, 1960 (Coleoptera: Scarabaeidae: Scarabaeinae) from the southwest Brazilian Amazon. *The Coleopterists Bulletin* 77 (4): 629–635. https://doi.org/10.1649/0010-065X-77.4.629

Arias-Buriticá J.A., Figueroa L. & Vaz-de-Mello F.Z. 2024. First record and range extension of *Isocopris rossinii* Arias-Buriticá *et al.*, 2023 (Coleoptera: Scarabaeidae: Scarabaeinae) for the Peruvian Amazon. *The Coleopterists Bulletin* 78 (4): 567–569. https://doi.org/10.1649/0010-065X-78.4.567

Arnaud P. 1982a. Liste des types de Phanaeini du Muséum national d'Histoire naturelle de Paris [Coleoptera, Scarabaeidae]. *Revue française d'Entomologie* 4: 113–118.

Arnaud P. 1982b. Description de deux nouvelles espèces de Phanaeini (Col. Scarabaeidae). *Miscellanea Entomologica* 49: 121–124.

Arnaud P. 2000. Description de nouvelles espèces de Phanaeides. (Col. Scarabaeidae). *Besoiro* 5: 6–8.

Arnaud P. 2001. Description de nouvelles espèces de Phanaeides. (Col. Scarabaeidae). *Besoiro* 6: 2–8.

Arnaud P. 2002. *Phanaeini. Dendropaemon, Tetramereia, Homalotarsus, Megatharsis, Diabroctis, Coproohanaeus, Oxysternon, Phanaeus, Sulcophanaeus*. Hillside Books, Canterbury.

Balthasar V. 1941. Scarabaeidae Laparostictae (Col.). *Beiträge zur Fauna Perus* 1: 337–358.

Balthasar V. 1951. Scarabaeidae Laparostictae (Col.). *Beiträge zur Fauna Perus* 2: 322–344.

Blackwelder R.E. 1944–1957. Checklist of the coleopterous insects of Mexico, Central American, the West Indies, and South America. Parts 1–6. *United States National Museum, Bulletin* 185: 1–1492. https://doi.org/10.5479/si.03629236.185.927

Blanchard E. 1836–1847. *Voyage dans l'Amérique méridionale (le Brésil, la République Orientale del' Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivia, la République du Pérou) exécuté pendant les Années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, par Alcide d'Orbigny. Tome sixième. 2.e Partie: Insectes*. Bertrand, Paris. https://doi.org/10.5962/bhl.title.110540

Boheman C.H. 1858. Coleoptera. Species novas descripsit. *In*: Boheman C.H. (ed.) *Kongliga Svenska Fregatten Eugenies resa omkring Jorden*. *Zoologi, I, Insecta*: 40–58. Norstedt, Stockholm. https://doi.org/10.5962/bhl.title.2467

Boilly O., Lapéze J., Dalens P.H., Giuglaris J.L. & Touroult J. 2016. Les Phanaeini de Guyane: liste commentée, clés et iconographie (Coleoptera, Scarabaeidae). *Contribution à l'étude des Coléoptères de Guyane* 10: 86–97.

Bousquet Y. 2016. Litteratura Coleopterologica (1758–1900): a guide to selected books related to the taxonomy of Coleoptera with publication dates and notes. *ZooKeys* 583: 1–776. https://doi.org/10.3897/zookeys.583.7084

Cabral-de-Mello D.C., Oliveira S.G., Ramos I.C. & Moura R.C. 2008. Karyotype differentiation patterns in species of the subfamily Scarabaeinae (Scarabaeidae, Coleoptera). *Micron* 39: 1243–1250. https://doi.org/10.1016/j.micron.2008.04.002

Carvajal V., Villamarín S. & Ortega A.M. 2011. *Escarabajos del Ecuador. Principales Géneros*. Instituto de Ciencias Biológicas. Escuela Politécnica Nacional. Serie Entomología, Nro. 1. Quito, Ecuador.

Chamorro W., Marín-Armijos D., Granda V. & Vaz-de-Mello F.Z. 2018. Listado de especies y clave de géneros y subgéneros de escarabajos estercoleros (Coleoptera: Scarabaeidae: Scarabaeinae) presentes y presuntos para Ecuador. *Revista colombiana de Entomología* 44: 72–100. https://doi.org/10.25100/socolen.v44i1.6545

Chamorro W., Marin-Armijos D. & Asenjo A. 2019. Scarabaeinae dung beetles from Ecuador: a catalog, nomenclatural acts, and distribution records. *ZooKeys* 826: 1–343. https://doi.org/10.3897/zookeys.826.26488

Cupello M. 2024. The genus *Gromphas* Dejean, 1836 (Coleoptera, Scarabaeinae): nomenclature, distribution, and conservation, including a contribution to the debate on electronic publications in zoology. *Zoosystema* 46 (2): 23–59. https://doi.org/10.5252/zoosystema2024v46a2

Cupello M. & Vaz-de-Mello F.Z. 2013. Taxonomic revision of the South American dung beetle genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini: Gromphadina). *Zootaxa* 3722 (4): 439–482. https://doi.org/10.11646/zootaxa.3722.4.2

Cupello M., Ribeiro-Costa C.S. & Vaz-de-Mello F.Z. 2022. The evolution of *Bolbites onitoides* (Coleoptera: Scarabaeidae: Phanaeini): its phylogenetic significance, geographical polychromatism and the subspecies problem. *Zoological Journal of the Linnean Society* 194 (3): 973–1034. https://doi.org/10.1093/zoolinnean/zlab090

d'Olsoufieff G. d'. 1924. Les Phanaeides (Coleoptera-Lamellicornia). Famille Scarabaeidae – Tr. Coprini. *Insecta*, *Revue illustrée d'Entomologie* 13: 4–172.

Edmonds W.D. 1972. Comparative skeletal morphology, systematics and evolution of the Phanaeine dung beetles (Coleoptera: Scarabaeidae). *The University of Kansas Science Bulletin* 49: 731–874.

Edmonds W.D. 1994. Revision of *Phanaeus* Macleay, a New World genus of Scarabaeinae dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contributions in Science, Natural History Museum of Los Angeles County* 443: 1–105. https://doi.org/10.5962/p.208079

Edmonds W.D. & Zídek J. 2012. Taxonomy of *Phanaeus* revisited: Revised keys to and comments on species of the New World dung beetle genus *Phanaeus* Macleay, 1819 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini). *Insecta Mundi* 274: 1–108.

Erichson W.F. 1847. Conspectus insectorum coleopterorum quae in Republica Peruana observata sunt. *Archiv für Naturgeschichte* 13: 67–185.
Available from https://www.biodiversitylibrary.org/page/7251438 [accessed 12 Jun. 2026].

Feer F. & Boissier O. 2015. Variations in dung beetle assemblages across a gradient of hunting in a tropical forest. *Ecological Indicators* 57: 164–170. https://doi.org/10.1016/j.ecolind.2015.04.034

Feer F. & Pincebourde S. 2005. Diel flight activity and ecological segregation within an assemblage of tropical forest dung and carrion beetles. *Journal of Tropical Ecology* 21:21–30.
https://doi.org/10.1017/S0266467404002056

Figueroa L., Edmonds W.D. & Martínez N.L. 2014. La tribu Phanaeini (Coleoptera, Scarabaeidae, Scarabaeinae) en el Perú. *Revista peruana de Biología* 21: 125–138.
https://doi.org/10.15381/rpb.v21i2.9815

Génier F. 2019. Endophallites: a proposed neologism for naming the sclerotized elements of the insect endophallus (Arthropoda: Insecta). *Annales de la Société entomologique de France (N.S.)* 55: 482–484. https://doi.org/10.1080/00379271.2019.1685907

Genise J.F. 2004. Ichnotaxonomy and ichnostratigraphy of chambered trace fossils in palaeosols attributed to coleopterans, ants and termites. *Geological Society, London, Special Publications* 228: 419–453. https://doi.org/10.1144/GSL.SP.2004.228.01.19

Gillet J.J.E. 1911a. Lamellicornes coprophages nouveaux ou peu connus d'Amérique du sud. *Annales de la Société entomologique de Belgique* 55: 315–319. https://doi.org/10.5962/bhl.part.2978

Gillet J.J.E. 1911b. *Coleopterorum Catalogus. Pars 38: Scarabaeidae: Coprinae I*. W. Junk, Berlin. Available from https://www.biodiversitylibrary.org/page/48405679 [accessed 12 Hun. 2026].

Gillett C.P.D.T. & Toussaint E.F.A. 2020. Macroevolution and shifts in the feeding biology of the New World scarab beetle tribe Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae). *Biological Journal of the Linnean Society* 130: 661–682. https://doi.org/10.1093/biolinnean/blaa058

Hamel-Leigue A., Mann D.J., Vaz-de-Mello F.Z. & Herzog S.K. 2006. Hacia un inventario de los escarabajos peloteros (Coleoptera: Scarabaeinae) de Bolivia: primera compilación de los géneros y especies registrados para el país. *Revista Boliviana de Ecología y Conservación Ambiental* 20: 1– 18.

Hamel-Leigue A., Herzog S.K., Mann D.J., Larsen T.H., Gill B.D., Edmonds W.D. & Spector S. 2009. Distribución e historia natural de escarabajos coprófagos de la tribu Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae) en Bolivia. *Kempffiana* 5: 43–95.

Harold E. 1859. Beitrage zur kenntnis einiger coprophagen lamellicornien. *Berliner Entomologische Zeitschrift* 3: 193–224. https://doi.org/10.1002/mmnd.18590030208

Harold E. 1863. Note sur les espèces mexicains du genre *Phanaeus* et descriptions de quelques espèces nouvelles de coléoptères mexicains. *Annales de la Société entomologique de France, 4e Série* 3: 161–176. Available from https://www.biodiversitylibrary.org/page/8257099 [accessed 12 Jun., 2026].

Harold E. 1869. *Catalogous Coleopterorum hucusque descriptorum synonymicus et systematicus Vol. 4*. Sumptu E.H. Gummi, Munich [Monachii]. https://doi.org/10.5962/bhl.title.9089

Harold E. 1870. Berichtigungen und Zusätze zum *Catalogus Coleopterorum synonymicus et systematicus*. *Coleopterologische Hefte* 6: 94–110. Available from https://www.biodiversitylibrary.org/page/25162493 [accessed 12 Jun. 2026].

Harold E. 1880. Einige neue Coleopteren. *Mitteilungen des Münchener Entomologischen Verein* 4: 148–171. Available from https://www.biodiversitylibrary.org/page/12660352 [accessed 12 Jun. 2026].

Hielkema A.J. & Hielkema M.A. 2019. An annotated checklist of the Scarabaeoidea (Insecta: Coleoptera of the Guianas. *Insecta Mundi* 732: 1–306.

Horn W. & Kahle I. 1936. Über entomologische sammlungen (ein beitrag zur geschichte der entomomuseologie). Teil II. *Entomologische Beihefte aus Berlin-Dahlem* 3: 161–296.

ICZN [International Commission on Zoological Nomenclature] 1999. *International Code of Zoological Nomenclature. Fourth Edition.* International Trust for Zoological Nomenclature, London. Available from https://www.iczn.org/the-code/the-code-online/ [accessed 12 Jun. 2026].

Krajcik M. 2012. Checklist of the World Scarabaeoidea. *Animma.X* Supplement 5: 1–278.

Korasaki V., Vaz-de-Mello F.Z., Braga F., Zanetti J. & Louzada J. 2012. Taxocenose de Scarabaeinae (Coleoptera: Scarabaeidae) em Benjamin Constant, AM. *Acta Amazonica* 42 (3): 423–432. https://doi.org/10.1590/S0044-59672012000300015

Larsen T.H. 2011. Dung beetles of the Kwamalasamutu region, Suriname (Coleoptera: Scarabaeidae: Scarabaeinae). *In*: O'Shea B.J., Alonso L.E. & Larsen T.H. (eds) *A Rapid Biological Assessment of the Kwamalasamutu Region, Southwestern Suriname*; 91–103. RAP Bulletin of Biological Assessment 63, Conservation Internacional, Arlington, VA. https://doi.org/10.1896/054.063.0108

Larsen T.H. 2013. Dung beetles of the Upper Palumeu River watershed (Grensgebergte and Kasikasima) of southeastern Suriname (Coleoptera: Scarabaeidae: Scarabaeinae). In: Alonso L.E. & Larsen T.H. (eds) *A Rapid Biological Assessment of the Upper Palumeu River Watershed (Grensgebergte and Kasikasima of Southeastern Suriname*: 90–101. RAP Bulletin of Biological Assessment 67, Conservation International, Arlington, VA. https://doi.org/10.1896/054.067.0113

Lawrence J.F., Ślipiński A., Seago A.E., Thayer M.K., Newton A.F. & Marvaldi A.E. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. *Bio One* 61 (1): 1–217. https://doi.org/10.3161/000345411X576725

Lizardo V., Moctezuma V. & Escobar F. 2022. Distribution, regionalization, and diversity of the dung beetle genus *Phanaeus* MacLeay (Coleoptera: Scarabaeidae) using species distribution models. *Zootaxa* 5213 (5): 546–568. https://doi.org/10.11646/zootaxa.5213.5.4

Lozano de la Rosa C., Cupello M. & Vaz-de-Mello F.Z. 2024. The dung beetles of Venezuela (Coleoptera: Scarabaeidae: Scarabaeinae): catalogue and updated distribution. *European Journal of Taxonomy* 959: 1–272. https://doi.org/10.5852/ejt.2024.959.2677

Macleay W.S. 1819. *Horae entomologicae: or Essays on the annulose Animals. Vol. I. Part I*. S. Bagster, London. https://doi.org/10.5962/bhl.title.48636

Manjarres-H. E.H. & Molano-R. F. 2015. Estudio de la variación de la genitalia masculina de las especies de la tribu Phanaeini (Scarabaeidae: Scarabaeinae) en Colombia. *Boletín Científico Centro de Museos, Museo de Historia Natural, Universidad de Caldas* 19: 245–257. https://doi.org/ 10.17151/bccm.2015.19.1.18

Medina C.A., Lopera A., Vítolo. A. & Gill B. 2001. Escarabajos coprófagos (Coleoptera: Scarabaeinae) de Colombia. *Biota Colombiana* 2: 131–144.

Moctezuma V. 2025. Taxonomic and nomenclatural issues revisited in the New World Scarabaeinae dung beetles (Coleoptera: Scarabaeoidea: Scarabaeidae). *Journal of Insect Biodiversity* 62 (2): 55–66. https://doi.org/10.12976/jib/2025.62.2.3

Moctezuma V. & Halffter G. 2017. A new species of *Phanaeus* Macleay (Coleoptera: Scarabaeidae: Scarabaeinae) from Los Chimalapas, Oaxaca, Mexico. *The Coleopterists Bulletin* 71: 47–56. https://doi.org/10.1649/0010-065X-71.1.47

Moctezuma V. & Halffter G. 2021. Taxonomic revision of the *Phanaeus endymion* species group (Coleoptera: Scarabaeidae), with the descriptions of five new species. *European Journal of Taxonomy* 747: 1–71. https://doi.org/10.5852/ejt.2021.747.1333

Moctezuma V., Monteros A.E.D.L & Halffter G. 2024. Phylogenetic analyses of the subfamily Scarabaeinae (Coleoptera: Scarabaeinae) provide new insights into the Mexican Transition Zone theory. *Zootaxa* 5415 (4): 501–528. https://doi.org/10.11646/zootaxa.5415.4.1

Monaghan M.T., Inward D.J.G,, Hunt T. & Vogler A.P. 2007. A molecular phylogenetic analysis of the Scarabaeinae (dung beetles). *Molecular Phylogenetics and Evolution* 45: 674–692. https://doi.org/10.1016/j.ympev.2007.06.009

Morrone J.J., Escalante T., Rodríguez-Tapia G., Carmona A., Arana M. & Mercado-Gómez J.D. 2022. Biogeographic regionalization of the Neotropical region: New map and shapefile. *Annals of the Brazilian Academy of Sciences* 94 (1): e20211167. https://doi.org/10.1590/0001-3765202220211167

Nevinson B.G. 1892. *Revised Synonymic List of Species in the Genera Phanaeus Macleay and Oxysternon Castelnau*. Published privately, London. https://doi.org/10.5962/bhl.title.9416

Noriega J.A. 2012. Dung beetles (Coleoptera: Scarabaeinae) attracted to *Lagothrix lagotricha* (Humboldt) and *Alouatta seniculus* (Linnaeus) (Primates: Atelidae) dung in a Colombian Amazon Forest. *Psyche* 2012: 437589. https://doi.org/10.1155/2012/437589

Pacheco T.L. & Vaz-de-Mello F.Z. 2015. Dung beetles of the tribe Phanaeini (Coleoptera: Scarabaeidade: Scarabaeinae) from Roraima state, Northern Brazil: checklist and key to species. *Biota Neotropica* 15: 1–9. https://doi.org/10.1590/1676-06032015014514

Papavero N. 1971. *Essays on the history of Neotropical dipterology, with special reference to collectors (1750–1905). Vol. I.* Museu de Zoologia, Universidade de São Paulo, São Paulo. https://doi.org/10.5962/bhl.title.101715

Pessôa S.B. 1934. Contribuição para o conhecimento das espécies brasileiras do gênero *Phanaeus*. *Annaes da Faculdade de Medicina da Universidade de São Paulo* 10: 279–314.

Perty J.A.M. 1830. De Insectorum in America Meridionali habitantium vitae genere, moribus ac distributione geographica, observationes nonnulae. *In*: Spix J. & Martius C. (eds) *Delectus animalium articulatorum, quae in itinere per Brasiliam annis MDCCCXVII–MDCCCXX jussu et auspiciis Maximiliani Josephi I. Bavariae regis augustissimi peracto collegerunt Dr. J.B. de Spix, et Dr. C.F.Ph. de Martius. Digessit, descripsit, pingenda curavit Dr. Maximilianus Perty, praefatus est edidit Carol. Frederic. Philip. de Martius, accedit dissertatio de insectorum in America Meridionali habitantum vitae genere, moribus et distributione geographica, Fasc. 1*. Frid. Fleischer, Munich [Monachii]. https://doi.org/10.5962/bhl.title.158694

Price D.L. 2005. Descriptions of the male and female genitalia of *Phanaeus* (Macleay) (Scarabaeidae: Scarabaeinae): the *vindex* species group. *The Coleopterists Bulletin* 59 (2) : 197–203. https://doi.org/10.1649/743

Price D.L. 2007. A phylogenetic analysis of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae) based on morphological data. *Insect Systematics & Evolution* 38: 1–18. https://doi.org/10.1163/187631207788784058

Price D.L. 2009. Phylogeny and biogeography of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae). *Systematic Entomology* 34: 137–150. https://doi.org/10.1111/j.1365- 3113.2008.00443.x

Price D.L. & May D.L. 2009. Behavioral ecology of *Phanaeus* dung beetles (Coleoptera: Scarabaeidae): review and new observations. *Acta Zoológica Mexicana* 25 (1): 211–238. https://doi.org/10.21829/azm.2009.251621

Ratcliffe B.C., Jameson M.L., Figueroa L., Cave R.D., Paulsen M.J., Cano E.B., Beza-Beza C., Jiménez-Ferbans L. & Reyes-Castillo P. 2015. Beetles (Coleoptera) of Peru: A survey of the families. *Journal of the Kansas Entomological Society* 88 (2): 186–207. https://doi.org/10.2317/kent-88-02-186-207.1

Santos-Heredia C., Andresen E. & Stevenson P. 2011. Secondary seed dispersal by dung beetles in an Amazonian forest fragment of Colombia: influence of dung type and edge effect. *Integrative Zoology* 6: 399–408. https://doi.org/10.1111/j.1749-4877.2011.00261.x

Scherer G. 1983. Die von J.B.v. Spix und C.F.Ph.v. Martius in Südamerika gesammelten Coleopteren. *Spixiana* 9: 295–305.

Streit B.D. 2008. Notes on four species of *Phanaeus*. *Scarabs* 31: 5–9.

Tarasov S. & Génier F. 2015. Innovative Bayesian and parsimony phylogeny of dung beetles (Coleoptera, Scarabaeidae, Scarabaeinae) enhanced by ontology-based partitioning of morphological characters. *PLoS ONE* 10: e0116671. https://doi.org/10.1371/journal.pone.0116671

Taschenberg E.L. 1870. Neue Käfer aus Columbien und Ecuador. *Zeitschrift für die Gesammten Naturwissenschaft* 35: 177–199.

Vaz-de-Mello F.Z. 2000. Estado atual de conhecimentos dos Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) do Brasil. *In*: Martín-Piera F., Morrone J.J. & Melic A. (eds) *Hacia un Proyecto CYTED para el Inventario y Estimación de la Diversidad entomológica en Iberoamérica: PrIBES-2000*. M3m: Monografías Tercer Milenio vol. 1: 183–195. Sociedad Entomológica Aragonesa (SEA), Zaragoza.

Vaz-de-Mello F.Z., Silva R.L.R., Nunes L.G.O.A. & Corrêa P.R.O.A. 2011. Os besouros rola-bosta (Insecta: Coleoptera: Scarabaeidae: Scarabaeinae) da Fazenda São Nicolau. *In*: Rodrigues D.J., Izzo T.J. & Battirola L.D (eds) *Descobrindo a Amazônia Meridional: Biodiversidade da Fazenda São Nicolau*: 76-102. Pau e Prosa Comunicação, Mato Grosso.

Vaz-de-Mello F.Z., Larsen T., Silva F., Favila M., Spector S. & Gill B. 2013. *Phanaeus achilles*. *The IUCN Red List of Threatened Species* 2013: e.T137148A43041876. https://doi.org/10.2305/IUCN.UK.2013-2.RLTS.T137148A43041876.en

Vítolo A.L. 2000. Clave para la identificación de los géneros y especies phanaeinas de Colombia. *Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales* 24 (93): 591–601.

Vítolo A.L. 2004. Escarabajos estercoleros de la tribu Phanaeini de Colombia (Coleoptera: Scarabaeoidea: Scarabaeidae). *In*: Fernández F., Andrade M.G. & Amat G.D. (eds) *Insectos de Colombia* 3: 277–318. Facultad de Ciencias, Universidad Nacional de Colombia, Bogotá.

Vulinec K., Edmonds W.D. & Mellow D.J. 2003. Biological and taxonomic notes on a rare phanaeine dung beetle, *Phanaeus alvarengai* Arnaud (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin* 57: 353–357. https://doi.org/10.1649/639

Vulcano M.A. & Pereira F.S. 1967. Sinópse dos Passalidae e Scarabaeidae s. str. da região Amazônica (Insecta, Coleoptera). *Atas do Simpósio sôbre a Biota Amazônica* 5: 533–603.

Wheeler Q.D. & Platnick N.I. 2000. The phylogenetic species concept (sensu Wheeler and Platnick). *In*: Wheeler Q.D. & Meier R. (eds) *Species Concepts and Phylogenetic Theory: A Debate*: 55– 69. Columbia University Press, New York.

Zunino M. 2013. Primer hallazgo de un escarabajo en un ichnofósil Coprinisphaeridae: *Phanaeus violetae* n. sp. (Coleoptera: Scarabaeinae) de una bola de cangahua del Ecuador. *Acta Zoológica Mexicana* 29 (1): 219–226. https://doi.org/10.21829/azm.2013.291397

Printed versions of all papers are deposited in the libraries of two of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France and Royal Museum for Central Africa, Tervuren, Belgium. The other members of the consortium are: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Meise Botanic Garden, Meise, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.