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lancifer

0129

A taxonomic review of the neotropical genus *Coprophanæus*
Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae)

W. D. Edmonds

J. Zidek

Date of Issue: July 2, 2010

ensifer

bellicosus

bonariensis



Coprophanæus bonariensis (Gory)

W. D. Edmonds and J. Zidek

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Abstract. The Neotropical genus *Coprophanaeus* Olsoufieff (1924), as classified here, comprises 38 species distributed among three subgenera (*Megaphanaeus* Olsoufieff, *Metallophanaeus* Olsoufieff, and *Coprophanaeus* s. str.) and eight species groups. Keys presented help to identify supraspecific and species taxa, all of which are illustrated and diagnosed. **Lectotypes** are designated for *Phanaeus ignecinctus* Felsche and *Phanaeus ohausi* Felsche. *Coprophanaeus corythus* (Harold), formerly regarded as a subspecies of *C. telamon* (Erichson), assumes **species status**. *Coprophanaeus magnoi* Arnaud, described as a subspecies of *C. milon* (Blanchard), is raised to **species status**. New taxonomic interpretations result in 10 **new subjective synonymies** (junior synonym listed first): *Phanaeus machadoi* Pereira and d'Andretta = *Coprophanaeus saphirinus* (Perty); *Phanaeus costatus* Olsoufieff = *Coprophanaeus cyanescens* (Olsoufieff); *Phanaeus worontzowi* Pessôa and Lane = *Coprophanaeus cyanescens* (Olsoufieff); *Coprophanaeus kohlmanni* Arnaud = *Coprophanaeus morenoi* Arnaud; *Coprophanaeus pluto nogueirai* Arnaud = *Coprophanaeus pluto* (Harold); *Coprophanaeus edmondsi* Arnaud = *Coprophanaeus conocephalus* (Olsoufieff); *Coprophanaeus uhleri* Malý and Pokorný = *Coprophanaeus chiriquensis* (Olsoufieff); *Coprophanaeus henryi* Malý and Pokorný = *Coprophanaeus gilli* Arnaud; *Phanaeus perseus* Harold = *Coprophanaeus corythus* (Harold); *Coprophanaeus telamon nevinsoni* Arnaud and Gámez = *Coprophanaeus corythus*; and *Coprophanaeus florenti* Arnaud = *Coprophanaeus ohausi* (Felsche). The status of the following names remains unresolved: *Phanaeus strandi* Balthasar; *Coprophanaeus rigoutorum* Arnaud; *C. terrali* Arnaud; *C. lichyi* Arnaud; *C. lecromi* Arnaud; *C. larseni* Arnaud; and *C. vazdemeloi* Arnaud.

Introduction

The purpose of this paper is to review the taxonomy of the New World dung beetle genus *Coprophanaeus* Olsoufieff (1924), as defined by Edmonds (1972). This genus comprises at least 38 species distributed among three subgenera. *Coprophanaeus* is a member of the phanaeine assemblage as defined by Edmonds (1972), Arnaud (2002c), and Philips et al. (2004), and now generally referred to as the tribe Phanaeini. MacLeay (1819), in the original description of *Phanaeus*, subdivided his genus into several groups. His “Typus 1” was the first iteration of the group that was to become the genus *Coprophanaeus*, which he characterized as follows: “*Typus 1. Clypeus antice bidentatus. Thorax margine postico vix acuminato, punctis duobus impressis. Pectus haud longius quam latius, canaliculatum, antice carinatum. Tibiae extus quadridentatae dentibus subacutis.*” In Typus 1 he included the following species of *Phanaeus*: *P. bellicosus* (Olivier), *P. jasius* (Olivier), *P. dardanus* MacLeay, *P. abas* MacLeay, and *P. acrisius* MacLeay. MacLeay’s scheme was later adopted by Latreille (1825).

In his landmark study of the phanaeine dung beetles, Olsoufieff (1924) divided the genus *Phanaeus* into five subgenera. The first work to employ Olsoufieff’s classification on a comprehensive scale was Blackwelder (1944), who raised all of Olsoufieff’s subgenera to generic rank. Later, Edmonds (1972) combined three of Olsoufieff’s taxa, *Coprophanaeus*, *Metallophanaeus* and *Megaphanaeus*, into the single genus *Coprophanaeus*. Olsoufieff himself suggested the close relationship among these three groups in his key to the subgenera of *Phanaeus*, wherein they satisfy alternative 1, “Clypeus avec trois incisions, formant deux lobes aigus dirigés en avant ...” Indeed, the very striking clypeal dentition is but one of several features cited by Edmonds as key characters defining the genus (see the generic diagnosis below).

Arnaud's (2002c) review of the genus follows Edmonds' subgeneric classification, except for the placement of *C. bellicosus* (see Comments for *C. bellicosus*).

As used here, *Megaphanaeus* is exactly in the sense of Olsoufieff (1924), Blackwelder (1944) and Edmonds (1972), a subgeneric group of four common species remarkable for their large size. In *Metallophanaeus* Olsoufieff included but two species; Edmonds (1972) transferred into it a second species group originally placed in *Coprophanaeus s. str.*, and here we add several others distributed between the two groups. The nominate subgenus originally embraced 21 species, many of which Blackwelder (1944) erroneously transferred to *Phanaeus*. The subgenus *Coprophanaeus s. str.* is here enlarged and restructured and the arrangement proposed by Edmonds (1972), which was based on too few species, is largely abandoned. Arnaud's (2002c) organization of this subgenus is different from that proposed here. Following is a list of those 77 available (or potentially available) names here assigned to *Coprophanaeus* and their present status [brackets enclose text page reference to name]:

- abas* MacLeay - valid name [p. 50]
- acrisius* MacLeay - valid name [p. 44]
- ajax* Sturm - junior subjective synonym of *C. ensifer* [p. 20]
- alvarengai* Pereira and d'Andretta - junior subjective synonym of *C. pertyi* [p. 33]
- argentinus* Martínez - junior subjective synonym of *C. bonariensis* [p. 19]
- arrowi* Olsoufieff - junior subjective synonym of *C. dardanus* [p. 80]
- bellicosus* Olivier - valid name [p. 14]
- bitias* Harold - junior subjective synonym of *C. dardanus* [p. 80]
- bonariensis* Gory - valid name [p. 19]
- boucardi* Nevinson - valid name [p. 65]
- callegarii* Arnaud - valid name [p. 97]
- camargoi* Pessôa - junior subjective synonym of *C. acrisius* [p. 44]
- caroliae* Edmonds - valid name [p. 102]
- cerberus* Harold - valid name [p. 47]
- chabrilacci* Thompson - junior subjective synonym of *C. saphirinus* [p. 29]
- chiriquensis* Olsoufieff - valid name [p. 71]
- christophorowi* Olsoufieff - valid name [p. 85]
- conocephalus* Olsoufieff - valid name [p. 69]
- corythus* Harold - valid name [p. 93]
- costatus* Olsoufieff - junior subjective synonym of *C. cyanescens* [p. 54]
- cyanescens* Olsoufieff - valid name [p. 54]
- dardanus* MacLeay - valid name [p. 80]
- degallieri* Arnaud - valid name [p. 87]
- ducalis* Castelnau - junior subjective synonym of *C. ensifer* [p. 20]
- edmondsi* Arnaud - junior subjective synonym of *C. conocephalus* [p. 69]
- ensifer* Germar - valid name [p. 20]
- florenti* Arnaud - junior subjective synonym of *C. ohausi* [p. 104]
- gamezi* Arnaud - valid name [p. 52]
- gilli* Arnaud - valid name [p. 73]
- henryi* Malý and Pokorný - junior subjective synonym of *C. gilli* [p. 73]
- heros* Castelnau - junior subjective synonym of *C. lancifer* [p. 16]
- horus* Waterhouse - valid name [p. 25]
- ignecinctus* Felsche - valid name [p. 89]
- jasion* Felsche - junior subjective synonym of *C. dardanus* [p. 80]
- jasius* Olivier - valid name [p. 48]
- kohlmanni* Arnaud - junior subjective synonym of *C. morenoi* [p. 60]
- lancifer* Linné - valid name [p. 16]
- larseni* Arnaud - uncertain status (see Comments under *C. suredai*) [p. 104]
- lecromi* Arnaud - uncertain status (see Comments under *C. caroliae*) [p. 102]
- lichyi* Arnaud - uncertain status (see Comments under *C. ohausi*) [p. 104]
- machadoi* Pereira and d'Andretta - junior subjective synonym of *C. saphirinus* [p. 29]

- magnoi* Arnaud - valid name [p. 82]
miles Castelnau - junior subjective synonym of *C. lancifer* [p. 16]
milon Blanchard - valid name [p. 84]
morenoi Arnaud - valid name [p. 60]
morio LeConte - junior subjective synonym of *C. pluto* [p. 68]
nevinsoni Arnaud and Gámez - junior subjective synonym of *C. corythus* [p. 93]
nogueirai Arnaud - junior subjective synonym of *C. pluto* [p. 68]
obscurus Olsoufieff - junior subjective synonym of *C. milon* [p. 84]
ohausi Felsche - valid name [p. 104]
parvulus Olsoufieff - valid name [p. 89]
pecki Howden and Young - valid name [p. 60]
perseus Harold - junior subjective synonym of *C. corythus* [p. 93]
pertyi Olsoufieff - valid name [p. 33]
pressoai Pereira - valid name [p. 36]
pluto Harold - valid name [p. 68]
punctatus Olsoufieff - valid name [p. 31]
rex Balthasar - junior subjective synonym of *C. abas* [p. 50]
rigoutorum Arnaud - uncertain status (see Comments under *C. cyanescens*) [p. 56]
roubali Balthasar - junior subjective synonym of *C. conocephalus* [p. 69]
saphirinus Sturm - valid name [p. 29]
satelles Lichtenstein – junior subjective synonym of *C. lancifer* [p. 16]
satyrus Castelnau - junior subjective synonym of *C. jasius* [p. 48]
septentrionalis Pessôa - junior subjective synonym of *C. lancifer* [p. 16]
sericeus Felsche - junior subjective synonym of *C. horus* [p. 25]
solisi Arnaud - valid name [p. 64]
spitzi Pessôa - valid name [p. 44]
strandii Balthasar - uncertain status (See Comments under *C. caroliae*) [p. 102]
surenai Arnaud - valid name [p. 102]
sylvanus Castelnau - junior subjective synonym of *C. bellicosus* [p. 14]
telamon Erichson - valid name [p. 91]
terrali Arnaud - uncertain status (see Comments under *C. dardanus*) [p. 82]
thalassinus Perty - valid name [p. 36]
uhleri Malý and Pokorný - junior subjective synonym of *C. chiriquensis* [p. 71]
vazdemeloi Arnaud - uncertain status (see Comments under *Metallophanaeus*) [p. 23]
vicinus Martínez - junior subjective synonym of *C. bonariensis* [p. 19]
worontzowi Pessôa and Lane - junior subjective synonym of *C. cyanescens* [p. 54]

Following is an outline of the classification proposed here for the 38 valid species recognized in this study and listed above:

Genus *Coprophanaeus* Olsoufieff, 1924 (*sensu* Edmonds 1972)

Subgenus *Megaphanaeus* Olsoufieff, 1924

bellicosus species group

C. bellicosus (Olivier, 1789)

lancifer species group

C. lancifer (Linné, 1767)

C. ensifer (Germar, 1821)

C. bonariensis (Gory, 1844)

Subgenus *Metallophanaeus* Olsoufieff, 1924

saphirinus species group

- C. saphirinus* (Sturm, 1826)
- C. horus* (Waterhouse, 1891)
- C. punctatus* (Olsoufieff, 1924)

thalassinus species group

- C. thalassinus* (Perty, 1830)
- C. pertyi* (Olsoufieff, 1924)
- C. pessoai* (Pereira, 1949)

Subgenus *Coprophanaeus s. str.*

jasius species group

- C. jasius* (Olivier, 1789)
- C. abas* (MacLeay, 1819)
- C. acrisius* (MacLeay, 1819)
- C. cerberus* (Harold, 1869)
- C. cyanescens* (Olsoufieff, 1924)
- C. spitzi* (Pessôa, 1934)
- C. gamezi* Arnaud, 2002

pluto species group

- C. pluto* (Harold, 1863)
- C. boucardi* (Nevinson, 1891)
- C. conocephalus* (Olsoufieff, 1924)
- C. chiriquensis* (Olsoufieff, 1924)
- C. pecki* Howden and Young, 1981
- C. morenoi* Arnaud, 1982
- C. solisi* Arnaud, 1997
- C. gilli* Arnaud, 1997

dardanus species group

- C. dardanus* (MacLeay, 1819)
- C. milon* (Blanchard, 1843)
- C. telamon* (Erichson, 1847)
- C. corythus* (Harold, 1863)
- C. ignecinctus* (Felsche, 1909)
- C. parvulus* (Olsoufieff, 1924)
- C. christophorowi* (Olsoufieff, 1924)
- C. degallieri* Arnaud, 1997
- C. magnoi* Arnaud, 2002

ohausi species group

- C. ohausi* (Felsche, 1911)
- C. suredai* Arnaud, 1996
- C. callegarii* Arnaud, 2002
- C. caroliae* Edmonds, 2008

The global distribution of the genus covers roughly the northern two-thirds of South America and Mesoamerica, embracing most of the Neotropical region of Morrone (2001). *Megaphanaeus* and *Metallophanaeus* (Fig. 28 and 62, respectively) are endemic to South America east of the cordilleras. *Coprophanaeus s. str.*, while mostly South American (Fig. 113, 237-238, 291), has penetrated Mesoamerica

at least twice: an earlier event giving rise to the endemic pluto group (Fig. 172), and a later event establishing *C. corythus* (Harold) of the telamon group (Fig. 238, inset). The general distribution patterns within the genus are ones often repeated in other phanaeine groups (Edmonds 1994 and 2000; Edmonds and Zidek 2004). Geographic parallelism is especially marked between *Oxysternon* Castelnau and South American *Coprophanaeus*, illustrated in part by the following distributional pairings (species of *Oxysternon* in parentheses): *C. christophorowi* (*O. durantoni* Arnaud); *C. parvulus* (*O. festivum* [Linné]); *C. degallieri* (*O. macleayi* Nevinson); *C. lancifer* (*O. silenus* Castelnau); *C. punctatus* (*O. pteroderum* Nevinson); and *C. magnoi* (*O. palaemon* Castelnau). Parallelisms between *Coprophanaeus* and other phanaeine genera include the following: the ohausi species group (*Phanaeus meleagris* Blanchard and *Phanaeus haroldi* Kirsch); *C. gamezi* (*Sulcophanaeus leander* [Waterhouse]); *C. lancifer* (*Sulcophanaeus faunus* [Fabricius]); the pluto species group (*Sulcophanaeus auricollis* species group; *Phanaeus endymion* species group). Analysis of the historical significance of these and other parallelisms is beyond the scope of this paper and will be treated in a future work. Like other phanaeine groups, *Coprophanaeus* species tend to fall into rather loosely defined ecogeographic assemblages across subgeneric and species group lines that define in a general way what species groupings are likely to exist sympatrically in a broad sense. The following assemblages are clearly recognizable: Amazonian subregion - *C. lancifer*, *C. jasius*, *C. parvulus*, *C. degallieri* and *C. dardanus*; Paranaian subregion - *C. dardanus*, *C. punctatus*, *C. saphirinus*, *C. cerberus* and *C. bellicosus*; Cerrado province - *C. ensifer*, *C. cyanescens*, *C. magnoi* and *C. spitzii*; Caatinga province - *C. pertyi*, *C. acrisius* and *C. ensifer*; Chaco province - *C. bonariensis*, *C. pessoai*, *C. milon* and *C. cyanescens*; Yungas + Napo provinces: *C. ignecinctus*, ohausi species group and *C. telamon*; Venezuelan Llanos province - *C. gamezi*, *C. abas* and *C. telamon*. The Mesoamerican subregion is home only to the pluto species group.

Collection data overwhelmingly indicate that *Coprophanaeus* species are preferentially necrophagous with a strong preference for forest (and other closed) habitats. Except for *Metallophanaeus*, which are diurnal, flight activity of those relatively few carefully observed species is almost always crepuscular, sometimes bimodal (dawn and dusk) and usually of short (< one hour) duration (Gámez et al. 2006; Feer and Pincebourde 2005; Théry et al. 2008). The strong development of clypeal and protibial dentition characteristic of the genus has been interpreted as adaptations for cutting up carrion, a more resistant food than excrement (Edmonds 1972; Halffter and Edmonds 1981). However, most species will also utilize excrement, especially that of carnivores and meat-eating omnivores such as humans. Only very rarely will *Coprophanaeus* accept herbivore dung or other food sources such as millipedes. There is scant literature on their behavior and development of the genus; these works will be treated below under the appropriate taxon heading. However, members of the genus figure in a number of the growing body of recent works on the ecology and diversity of Neotropical dung beetle communities, among which are the following: Amézquita et al. 1999; Arellano and Halffter 2003; Arellano et al. 2008; Celi et al. 2004; Estrada et al. 1993; Favila 2005; Feer 2000; Feer and Pincebourde 2005; Forsyth et al. 1998; Halffter et al. 1992; Hamel-Leigue et al. 2006, 2009; Klein 1989; Louzada and Lopes 1997; Luzzatto et al. 1994; Medina et al. 2001; Monteresino et al. 1996; Pardo-Locarno 1997; Vaz-de-Mello 1999; and Vulinec 2002.

Methods

This study is based on examination of approximately 5700 specimens, the vast majority of which were graciously provided by the institutional and private collections cited in the Acknowledgements. Species and supraspecific diagnoses employ the terminology used by Edmonds (1972 and elsewhere). As in other phanaeines, color and secondary sexual characters (especially of males) are subject to much variation; in many cases, reliable identifications depend upon examination of well-developed ("major") males. Assessment of color is best accomplished under low magnification (x5-10) using a full-spectrum ("natural") light source such as halogen. Perceived color varies with optical perspective and descriptions here assume a line of sight more-or-less perpendicular to the surface under examination. Specified body lengths include the head; these measurements are approximate and intended only for comparing relative size. For purposes of comparing the lengths of the frons and clypeus (as viewed dorsally), the length of the frons is measured from the posterior margin of eyes to the cephalic carina/horn; that of clypeus from the cephalic carina/horn to the base of the notch separating the median clypeal teeth (see Fig. 171). In the case of males (and females of *Megaphanaeus*), taxon diagnoses emphasize maximum ("major") development.

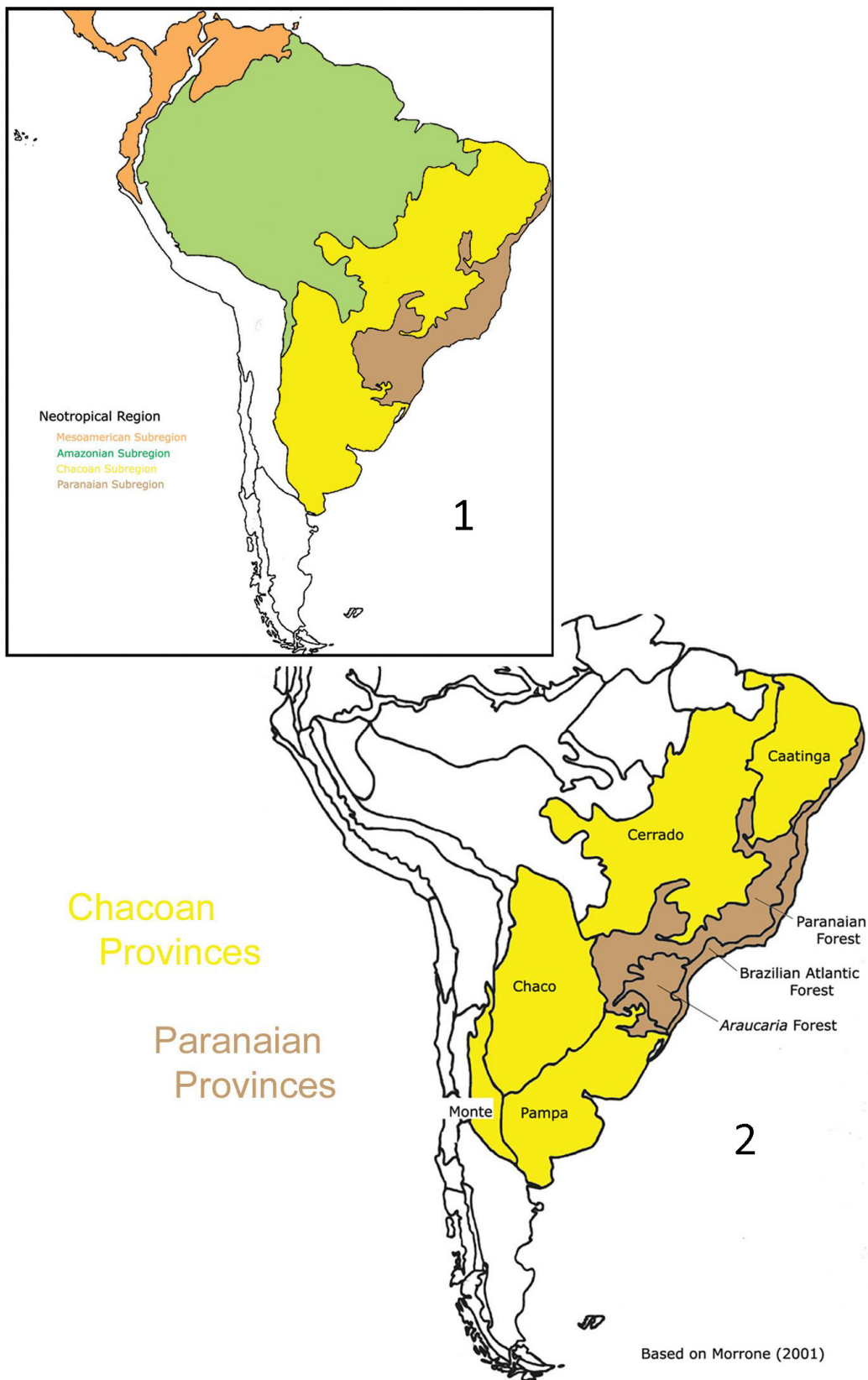


Figure 1-2. Neotropical Region distributional units (based on Morrone 2001). 1) Subregions. 2) Provinces of the Chacoan and Paranaian subregions.

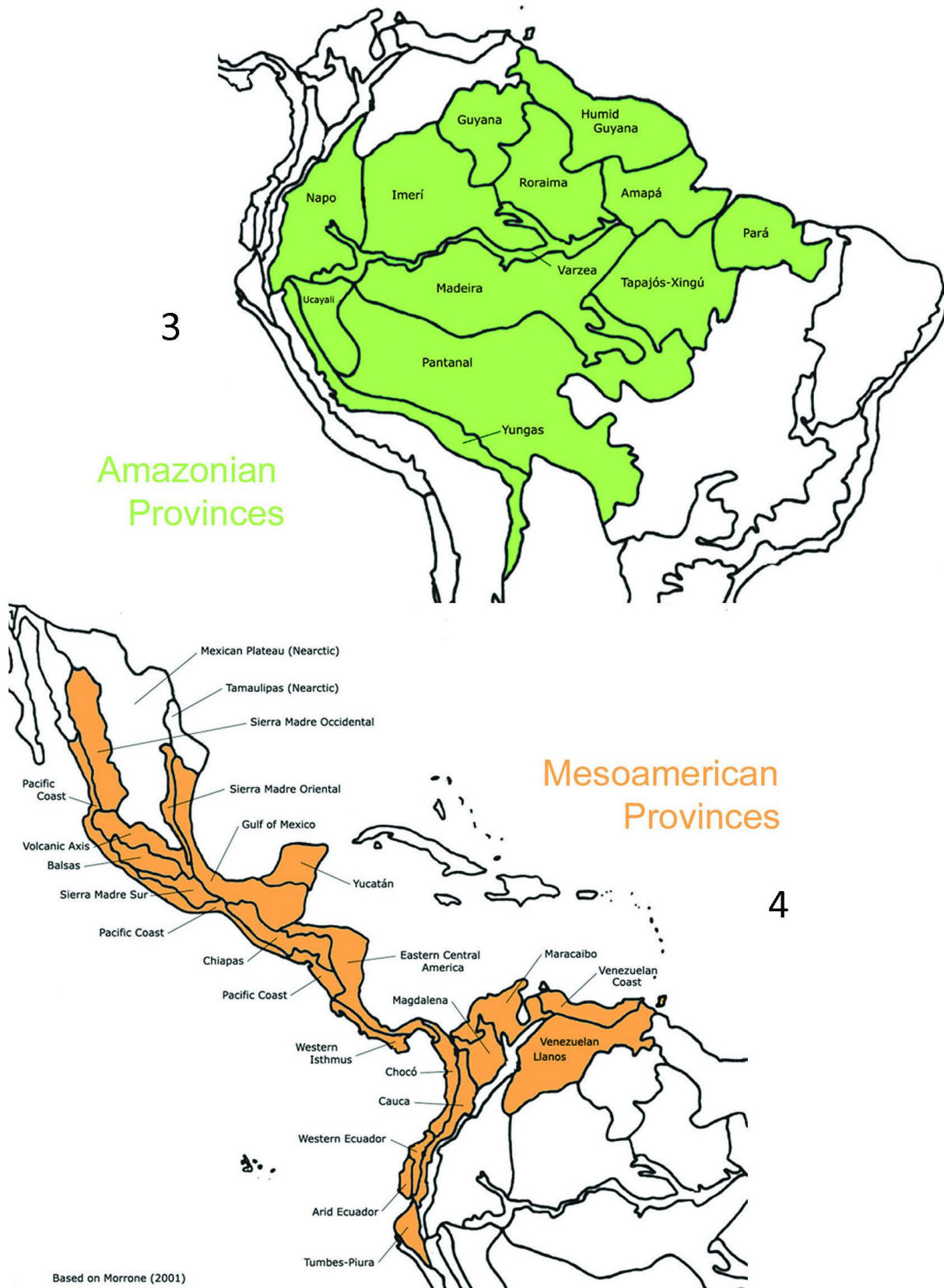


Figure 3-4. Neotropical Region distributional units (based on Morrone 2001). 3) Provinces of the Amazonian subregion. 4) Provinces of the Mesoamerican subregion.

Collection localities were gleaned mainly from specimens seen by us. They are arranged alphabetically by country followed by first-order political subdivisions (state, department, province or equivalent). Altitudes are expressed in meters. Ecuador's Orellana Province was created in 1999 from eastern Napo Province; since most data antedate its creation, the two provinces are here considered a single administrative unit referred to as Napo-Orellana. Wherever possible, we have used Google Earth (<http://earth.google.com/>) as our geographic reference base. Our reference base for classifying general regional distributions is Morrone (2001; Fig. 1-2) with the modification that our designation of Mesoamerica is roughly equivalent to Morrone's Caribeña subregion of the Neotropical minus the islands of the Caribbean (provinces of Bahamas, Cuba, Caiman Islands, Jamaica, Hispaniola, Puerto Rico and Lesser Antilles) and the Galapagos. The distribution maps (e.g. Fig. 28) represent our current hypotheses about species geographic distribution based on the collection data presented in the species treatments; they are not intended to be static representations of range. On the contrary, the margins of the shaded areas should be regarded as tenuous. But we do regard them as reliable enough for generalizations about distribution. In those cases where reliable distribution data are limited to one or very few points (e.g. *C. punctatus*), we use symbols to mark the approximate location of known collection sites.

The location of primary types (holotypes, lectotypes and neotypes), where known, is indicated by name of museum/collection and city. In the case of previously designated lectotypes and neotypes, the designation reference is specified. Lectotypes designated here bear our printed labels on white paper bordered in red. Instances where we have examined types are indicated "examined" (= specimen in hand), or "examined by photo." A weakness of this study is the fact that we were unable to examine a significant number of primary types, and this fact has made it impossible to achieve a degree of thoroughness we regard as necessary for a formal taxonomic revision (hence the use of "review" in the title rather than "revision"). Their whereabouts are simply unknown in some cases and, if formal types ever existed, they have been "missing" for many years. These cases are mainly of species described long ago, whose identity has been firmly established by usage over an extended period of time. Other cases refer to overdue loans absent from host collections that could not be retrieved during the course of our study. In these cases, we have had to rely on secondary types or customary usage in order to make taxonomic decisions about valid names and species limits. Yet other cases refer to types that are in private hands and were not made available to us. In these latter cases, most of which refer to ill-defined species often based on only one or two specimens, we have been prevented from assessing the validity of several putative taxa, which are necessarily omitted from formal consideration here and deemed of uncertain status; *viz*: *Coprophanaeus rigoutorum* Arnaud (2002a); *C. terrali* Arnaud (2002a); *C. lichyi* Arnaud (2002a); *C. lecromi* Arnaud (2002a); *C. larseni* Arnaud (2002a); and *C. vazdemeloi* Arnaud (2002a).

Genus *Coprophanaeus* Olsoufieff, 1924

Coprophanaeus Olsoufieff, 1924: 22 (as subgenus of *Phanaeus*)

Type Species: *Scarabaeus jasius* Olivier (cited as *Phanaeus jasius*), by original designation.

Diagnosis. (based on Edmonds 1972, *q.v.*) Clypeus deeply, narrowly emarginated medially, bearing two prominent, acute median teeth united on lower side by U-shaped ridge; clypeal margin lateral to teeth often angulate. Eyes usually large (except *Metallophanaeus*), width of upper portion exceeding one-fourth of interocular distance, width of lower portion exceeding twice that of oculoangular space. Circumnotal carina entire or broken behind eyes, but pronotal margin never excised to receive parietal lobes of head. Pronotum, at least anterolaterally, granulorugose, rugosities often coalescing into transverse ridging or scale-like sculpturing. Protibiae very strongly, acutely quadridentate. Protarsi absent in male, absent in female except some *Megaphanaeus*. Color most often dark, somber, with limited metallic highlights, seldom wholly metallic. Sexual dimorphism usually pronounced, but in different ways among subgenera and species groups (see below).

Comments. Members of this genus are easily distinguished from other Phanaeini by the combination of strong dentition of the tibiae and clypeus. The only other phanaeines likely to be confused with certain *Coprophanaeus* are those few robust species of *Dendropaemon* Perty, which, among other differences,

possess only two or three meso- and metatarsal segments. Olsoufieff's choice of the name for this group recognized "... leur ressemblance avec les veritable *Copris*."

As in most phanaeine groups, the taxonomy of *Coprophanæus* is male-dominated. Nevertheless, the variation in the form and degree of sexual dimorphism in the genus is striking and much more complicated than in any other phanaeine group. The particulars of each case are treated in the appropriate taxonomic section below, but several cases suggest some interesting possibilities concerning the evolution of sexual dimorphism in this genus. In *C. bellicosus*, unlike other *Megaphanaeus* species, the male and female are quite different, especially in the form of the head. The male bears a long, tapering horn, whereas the female bears a trituberculate carina with enlarged central tubercle, similar to the saphirinus group of *Metallophanæus*. Several other features suggest that *C. bellicosus* is an annectant between the two subgenera. Arnaud (2002c), also struck by the uniqueness of this species, removed *C. bellicosus* from *Megaphanaeus* and placed it in *Coprophanæus s. str.* (see Comments under *C. bellicosus*). Rowland and Emlen (2009) have provided new insights on the relationship between male horn polymorphism and reproductive strategy as exhibited primarily by the phanaeine dung beetles.

Key to subgenera of *Coprophanæus* Olsoufieff

(Modified from Edmonds 1972)

1. Posterior surface of each protibial tooth with dense, oblique clump of short setae (Fig. 5, arrow). Striae conspicuous, always carinulate, with straight or sinuous margins (Fig. 13-16). Protarsi present in female (except *C. bonariensis*). Posterior margin of hind wing lacking distinct basal notch (as in Fig. 10). Sexual dimorphism not pronounced; male and female (except *C. bellicosus*) with long, thick, tapering head horn and massive, saddle-shaped pronotal prominence projecting forward above broad concavity. Occipital areas each with angulate prominence (Fig. 11, asterisk); paraocular areas ("genae") carinate lateral to upper eye. Large to very large, length 30-50+ mm. Dorsum weakly shining metallic green or blue, or dull, dark violet. South America east of the Andes ***Megaphanaeus* Olsoufieff**
- Posterior surface of each protibial tooth with single oblique row of setae at base (Fig. 6). Striae conspicuous or not; rarely carinulate. Protarsi absent in female. Base of hind wing notched or not. Sexual dimorphism pronounced; configuration of male and female head and pronotal shape usually very distinct. Occipital areas more-or-less flattened, lacking angular prominences (Fig. 12, asterisk); paraocular areas (genae) carinate or not lateral to upper eye. Small to medium-sized, length 15-35 mm. Color and distribution variable **2**
- 2(1). Hind wing not notched basally (Fig. 10). Width of lower portion of eye less than twice (usually about equal) that of adjacent oculo-gular space. Beading of anterior portion of circumnotal carina entire, not effaced behind eyes (as in Fig. 7). Male with long, evenly tapering cylindrical head horn or shorter cylindrical horn with expanded base; female with trituberculate carina. Color often bright, metallic, occasionally dark. South America east of Andes and south of Amazonia to northern Argentina ***Metallophanæus* Olsoufieff**
- Hind wing distinctly notched basally, vein V_2 usually hooked apically (Fig. 9). Lower portion of eye large, bulging, width more than twice that of adjacent oculo-gular space. Beading of anterior margin of circumnotal carina effaced behind eye (Fig. 8) (entire in the jasius group, Fig. 7). Male head with horn or trituberculate carina; horn, if present, never a long, cylindrical, tapering protuberance. Female head with trituberculate carina. Color usually dark, somber; metallic reflections, if any, usually restricted to margins of pronotum; only seldom with metallic color conspicuous to unaided eye. Northern Argentina to northern Mexico (and extreme southern Texas) ***Coprophanæus s. str.***

Subgenus *Megaphanaeus* Olsoufieff, 1924

Megaphanaeus Olsoufieff, 1924: 23.

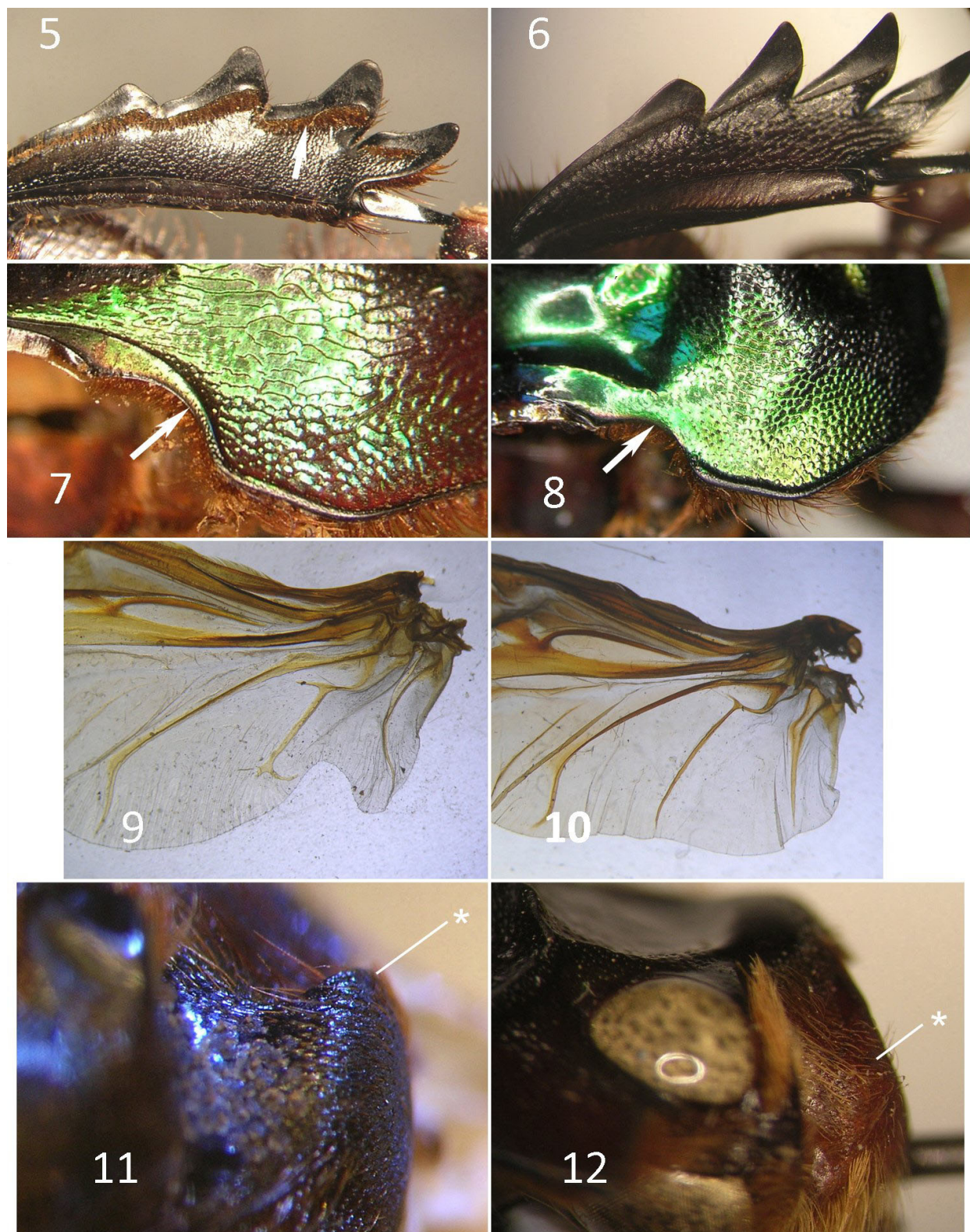


Figure 5-12. Characters of *Coprophanaeus*. **5)** Ventral view of front left tibia of *C. ensifer* (arrow marks elongate tuft of setae). **6)** Same, *C. dardanus*. **7)** Left anterolateral pronotal margin of *C. spitzi* (arrow indicates unbroken circumnotal carina). **8)** Same, *C. magnoi* (arrow indicates broken circumnotal carina). **9)** Base of left hind wing of *C. cerberus*. **10)** Same, *C. horus*. **11)** Lateral view left occipital lobe of *C. ensifer* (asterisk marks swelling). **12)** Same, *C. spitzi* (asterisk marks flat area).

Type Species: *Scarabaeus lancifer* Linné, original designation.

Diagnosis. *General* – Width of lower portion of eye about twice that of oculo-gular space. Paraocular areas (genae) distinctly carinate lateral to eyes. Occipital areas of parietals with angulate prominence (Fig. 11, asterisk). Circumnotal ridge entire, not effaced behind eyes (as in Fig. 7). Pronotum completely sculptured, lacking smooth areas (except *C. bellicosus*); anterior surfaces transversely ridged, posterior surfaces granulorugose, becoming strongly granulate posteromedially (except *C. bellicosus*); basal fossae small, punctiform. Pronotum with thick, rounded ridge (Fig. 37, arrow) on each side extending ventrally from base of median prominence (reaching lateral fossa in *C. bellicosus*, Fig. 32, arrow). Striae (Fig. 13-16) conspicuous, always carinulate, carinulae straight or undulate. Hind wing not notched basally (as in Fig. 10). Posterior surface of each protibial tooth with basal, elongate, brush-like clump of densely packed, short setae (Fig. 5, arrow). Abdominal sterna clearly punctate along entire width; puncturing finer and sparser medially. Sexual dimorphism usually subtle, female secondary sexual features male-like.

Male – Head bearing massive, posteriorly curved horn. Pronotum deeply concave; concavity transverse, posterior (dorsal) margin developed as massive prominence of varying shape. Parameres with dorsally directed apical, sometimes attenuated processes either rounded or acute in profile.

Female – Protarsi present (except *C. bonariensis*). Head bearing massive, posteriorly curved horn like that of male (except *C. bellicosus*). Pronotum transversely concave; posterior (dorsal) margin of concavity developed as massive, saddle-shaped prominence usually broader than equivalent prominence in male (except *C. bellicosus*).

Distribution. South America east of the Andes from the Amazon basin to northern Argentina comprising the Amazonian, Chacoan and Paranaian subregions of the Neotropical region.

Comments. *Megaphanaeus* is used here exactly as conceived by Olsoufieff and followed by Blackwelder (1944) and Edmonds (1972). It includes the largest known phanaeines, *C. ensifer* and *C. lancifer*, some individuals of which can exceed 50 mm in length. The other two included species, *C. bellicosus* and *C. bonariensis*, are also large but can be equaled or exceeded in size by certain *Sulcophanaeus*, *Diabroctis* Gistel and members of the jasius species group of *Coprophanaeus s. str.* All four species are very well known and the absence of known types for three of the four is not a barrier to consistent use of the species names. Martínez's (1944) review of the subgenus included six species, two of which Martínez and Pereira (1967) later synonymized. Our phylogenetic view of the subgenus has the species pair *C. ensifer*–*C. bonariensis* more closely related to *C. lancifer* than to *C. bellicosus*. The latter species is a taxonomic isolate that we place in a monobasic species group in apposition to the lancifer species group. Arnaud (2002c) moved *C. bellicosus* to *Coprophanaeus s. str.* (see Comments below under *C. bellicosus*).

The similar development and expression of secondary sexual features of the head and pronotum between the sexes is unique among “armed” phanaeines. The usual situation in *Megaphanaeus* might be called “male dominant”, because the female (except of *C. bellicosus*) has acquired a decidedly masculine form: a massive head horn and broad and massive saddle-shaped pronotal prominence. Large individuals clearly differ in details of pronotal shape, but medium-sized and small individuals are virtually identical. In two species, *C. lancifer* and *C. ensifer*, the female has retained protarsi, but in *C. bonariensis*, which lacks protarsi in both sexes, sexing these individuals requires dissection. In contrast, the females of *C. bellicosus* are easily recognizable by the tridentate cephalic process and presence of protarsi. Where present, female protarsi are very susceptible to loss, leaving only a very small empty socket at the base of the tibial spur. Determining sex in this subgenus using presence or absence of female protarsi therefore requires careful examination.

The distribution of *Megaphanaeus* occupies much of the South American portion of the Neotropical region. The exclusive Amazonian representative is *C. lancifer*. *Coprophanaeus bellicosus* inhabits the Atlantic coastal forests (Paranaian subregion) of Brazil, while the *C. ensifer*–*C. bonariensis* pair splits the wide, xeric central swath of the continent (Chacoan subregion) from the cerrados to the Chaco thorn forests. The ranges of three of the four species (all but *C. bellicosus*) converge to within very short distances in the biodiversity hotspot, Parque Nacional Noel Kempff Mercado in northeastern Bolivia; but as far as we know, no two are ecologically sympatric (collected together in the same habitat).

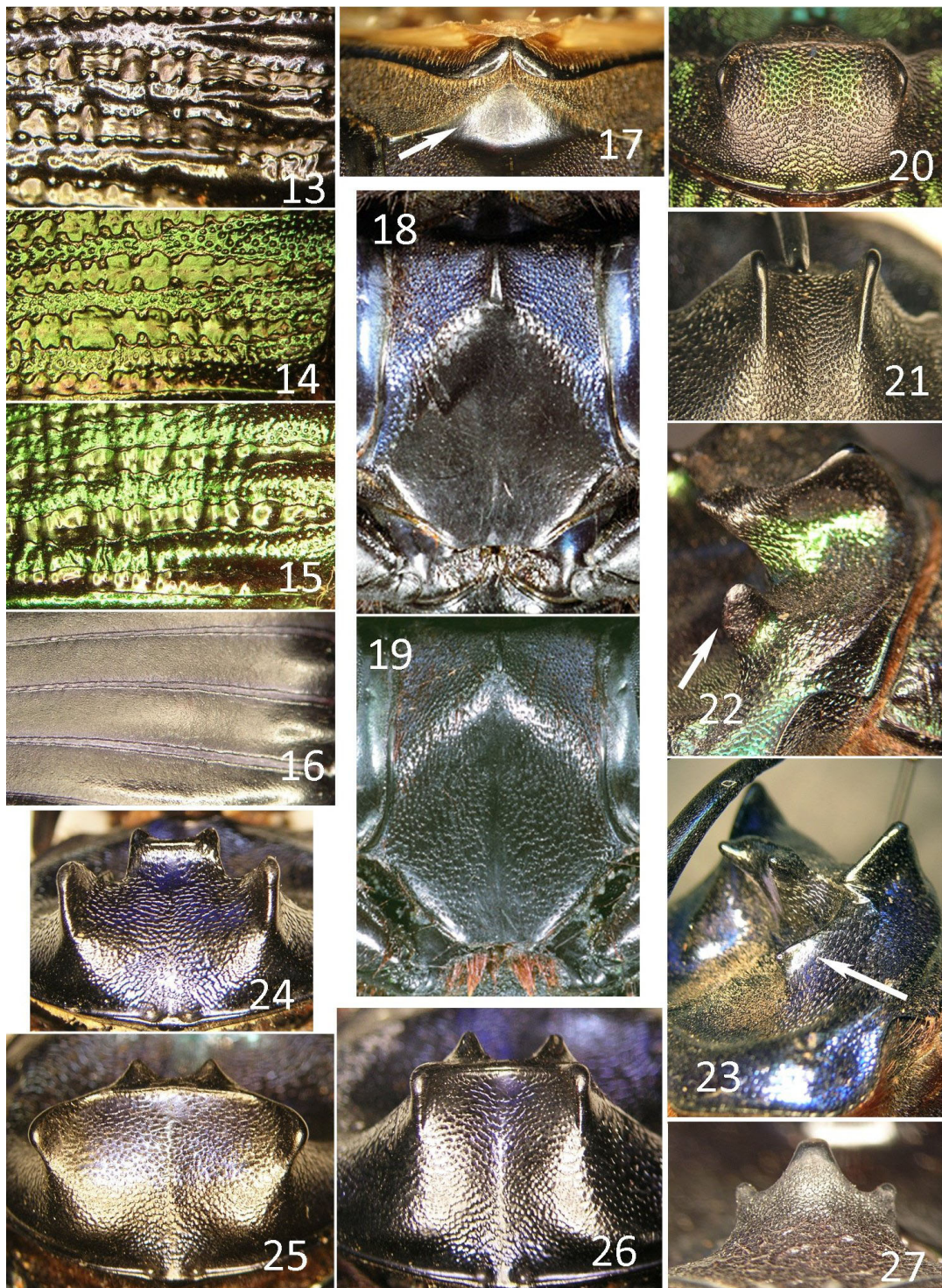


Figure 13-27. Characters of the *Coprophanaeus* subgenus *Megaphanaeus*. **13)** Elytral surface of *C. lancifer*. **14)** Same, *C. ensifer*. **15)** Same, *C. bonariensis*. **16)** Same, *C. bellicosus*. **17)** Mesosternum and anterior portion of metasternum of *C. lancifer* (arrow indicates smooth area of metasternum). **18)** Metasternum of *C. lancifer*. **19)** Same, *C. ensifer*. **20)** Dorsal view of posteromedian pronotal prominence of female *C. ensifer* (broad form). **21)** Same (narrow form). **22)** Partial lateral view of pronotum male *C. ensifer* (arrow indicates lateral spine). **23)** Same, *C. lancifer* (arrow indicates vertical ridge). **24)** Dorsal view of posteromedian pronotal prominence of male *C. lancifer*. **25)** Same, female (broad form). **26)** Same (narrow form). **27)** Anterior view of cephalic process of female *C. bellicosus*.

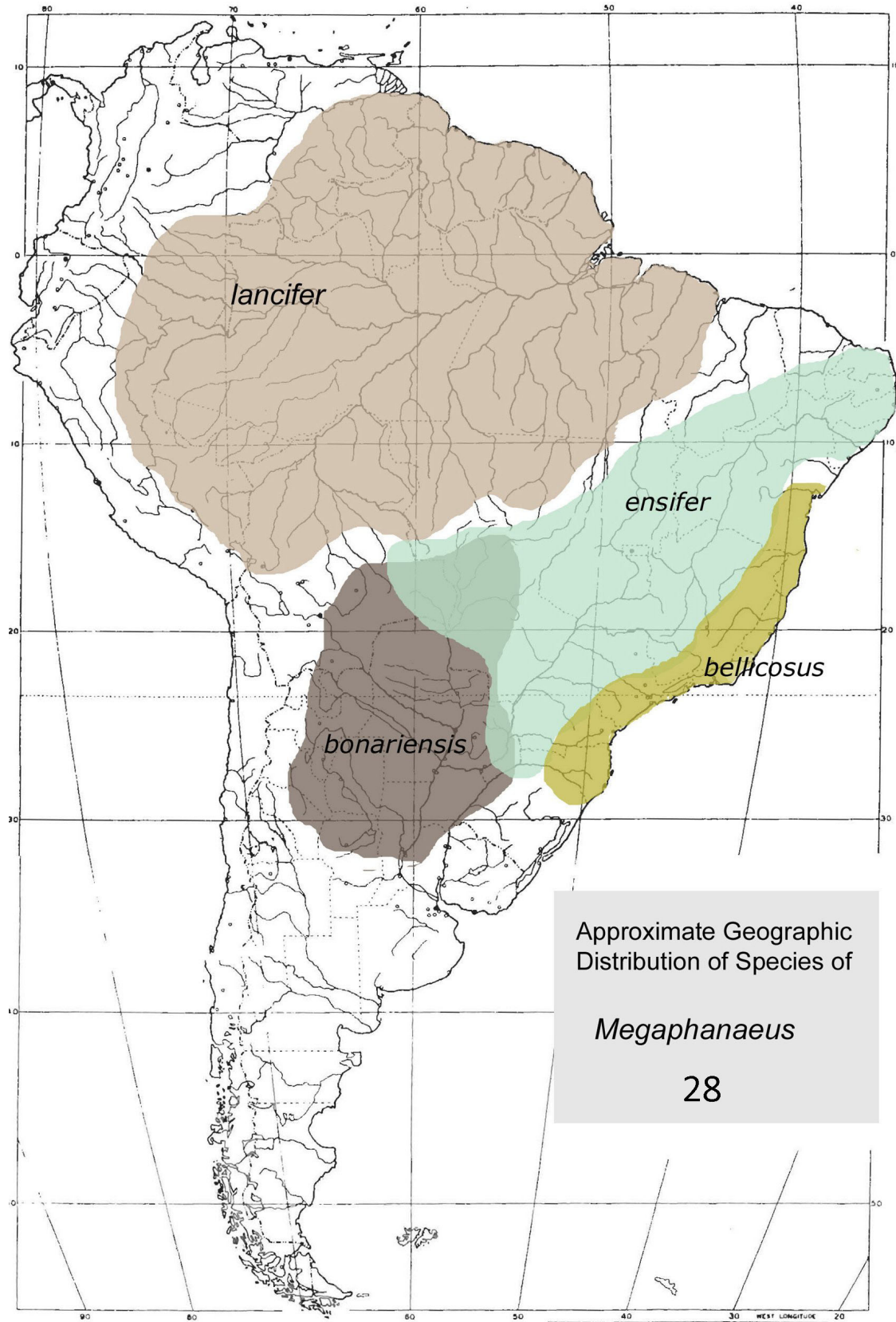


Figure 28. Approximate geographic distribution of *Coprophanæus* (*Megaphanaeus*) species.

Besides the characters mentioned in the key, there are differences among the parameres of these species that were first pointed out by Lane and Carmargo-Andrade (1935). These are not treated in the species diagnoses below but are illustrated.

Key to species of *Megaphanaeus*

1. Elytral striae (Fig. 16) narrow, smooth, sides straight, converging apically. Interstriae 1-4 smooth, devoid of coarse sculpturing (x5); interstriae 5-7 microrugose (x25), more strongly so laterally. Female cephalic process (Fig. 27) tridentate, middle tubercle strongly elevated. Atlantic coast forests of Brazil). **bellicosus species group**
 ***Coproghanaeus (Megaphanaeus) bellicosus* (Olivier)**
- Elytral striae widened, margins (especially of striae 2-4) undulate to some degree. Interstriae coarsely sculptured (x5). Female cephalic process a cylindrical horn (similar to that of male) **lancifer species group** **2**
- 2(1). Elytral interstriae (Fig. 13) at most only indistinctly granulate, usually granulorugose; granulation, if distinct, confined to apical one-third of interstriae 2-6. Basal two-thirds of elytral striae 2-4 moderately undulate, width at widest points about twice that of narrowest points; strial margins at narrow points often bearing low, rounded tubercle. Metasternal shield (Fig. 18) smooth to weakly punctate; triangular, anteromedian area of metasternum (Fig. 17, arrow) (usually hidden by retracted posterior margin of pronotum) smooth and shiny medially. Color usually dark metallic blue. Widely distributed in Amazonia (Fig. 28)
 ***Coproghanaeus (Megaphanaeus) lancifer* (Linné)**
- Elytral interstriae completely covered by large, round granules. Striae variable. Metasternal shield (Fig. 19) completely punctatorugose; triangular anteromedian portion of metasternum (usually hidden by retracted posterior margin of pronotum) finely granulate, at least laterally. Color usually green, yellowish green, rarely bluish green. Distribution variable, but never Amazonian **3**
- 3(2). Margins of elytral striae 2-4 only gently undulate (Fig. 15), strial width at narrowings at least three-fourths of that at widest points; carinulae simple, seldom tuberculate. Triangular anteromedian portion of metasternum finely granulate laterally, smooth and shiny medially. Female lacking protarsi. Smaller beetles, length 25-35 mm. Xeric forests of eastern Bolivia, Paraguay and Argentina (Fig. 28)
 ***Coproghanaeus (Megaphanaeus) bonariensis* (Gory)**
- Margins of elytral striae (Fig. 14) strongly undulate, strial width at narrowest points no more than one-half (often much less than one-half) of that at widest points; narrowings produced by apically tuberculate, finger-like projections of margins. Triangular anteromedian portion of metasternum completely finely granulate, or nearly so. Female with protarsi. Large beetles, length 30-55 mm. Dry forests of central Brazil, Bolivia, Paraguay and Argentina (Fig. 28)
 ***Coproghanaeus (Megaphanaeus) ensifer* (Germar)**

***Coproghanaeus (Megaphanaeus) bellicosus* (Olivier, 1789)**

Fig. 16, 27-34

Scarabaeus bellicosus Olivier, 1789: 109

Phanaeus sylvanus Castelnau, 1840: 80 (syn. by Nevinson 1892: 2)

Megaphanaeus bellicosus (Olivier) (recomb. by Blackwelder 1944: 209)

Coproghanaeus bellicosus (Olivier) (recomb. by Edmonds 1972: 841)

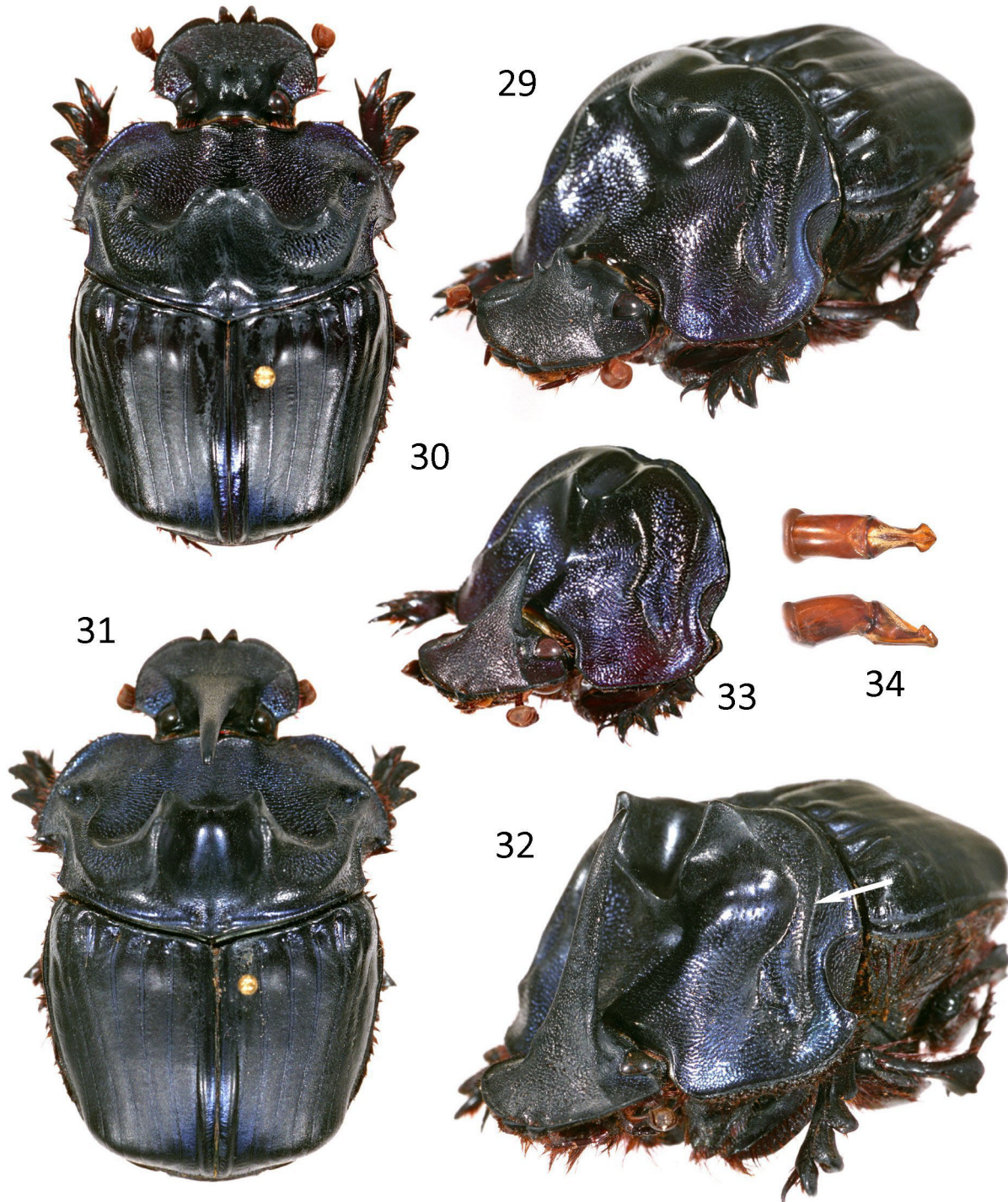


Figure 29-34. *Coprophanaeus bellicosus*. 29-30) Female habitus. 31-33) Male habitus (arrow in 32 indicates posterolateral ridge). 34) Aedeagus (lateral view below; dorsal view above).

Type. *S. bellicosus* – holotype male, Hunterian Museum, University of Glasgow (examined by photo); *P. sylvanus* – unknown to us.

Diagnosis. *General* – Pronotum (Fig. 30-31) punctate posteromedially, not granulate. Posterolateral pronotal ridge long, extending to lateral pronotal fossa (Fig. 32, arrow). Metasternal shield largely smooth

(as in Fig. 18); anterior portion of metasternum smooth. Elytral striae (Fig. 16) narrow, sides carinulate, straight, converging apically; interstriae 1-4 smooth, 5-7 finely rugose. Dorsal color black or dark brown, sometimes dark blue or bluish violet. Length 28-38 mm.

Male (Fig. 31-33) – Pronotal concavity broad, shallow, lacking lateral protuberances. Dorsal prominence with narrow, median, scoop-shaped element. Apical process of parameres rounded in profile.

Female (Fig. 29-30) – Cephalic process tridentate, middle tubercle much larger than laterals. Pronotal prominence a transverse, weakly bitumid, narrow process near posterior margin; pronotal concavity very broad, shallow, similar to that of male. Protarsi present.

Specimens examined – 150.

Distribution. Atlantic coast forests of Brazil (Paranaian subregion) (Fig. 28).

Collection Records. BRAZIL: **Bahia** – Entre Rios (Jan); Encruzilhada (Dec). **Espirito Santo** – Sooretama (Jun, Nov); Tijuco Prêto (Dec); Fazenda Lagoa do Macuco [Município Linhares], 19°03'50"S 39°58'43"W (Jan); Timbuhy. **Minas Gerais** – Viçosa [Mata do Paraíso], 20°48'18"S 42°51'20"W, 750 m (Feb, Nov). **Rio Grande do Sul** – São Alberto (Jan). **Rio de Janeiro** – Nova Friburgo (Jan, Oct); 17 km E Nova Friburgo, 22°23'04"S 42°33'30"W, 750 m (Jan). **Santa Catarina** – Joinville (Nov-Dec); Tijuca Forest (Jan). **São Paulo** – São João dos Campos (Feb); Nova Cantareira (Apr); 50 km SE Mogi das Cruzes [Serra do Mar Biological Station "Boraceia"], 800-900 m (Apr); Tremembé (Dec).

Comments. Arnaud (2002c) transferred this species to the subgenus *Coprophanaeus s. str.* stating only that, while it was isolated from other members of that subgenus, it could not "... en aucune manière, si ce n'est sa taille, être associé au groupe *lancifer*." We disagree and maintain its placement in *Megaphanaeus* because of the suite of characters it shares with *C. lancifer*, *C. ensifer* and *C. bonariensis* (see key to subgenera). But we do agree that it is a taxonomic isolate within the subgenus with, in our view, a closer affinity with the saphirinus group of *Metallophanaeus* than with any constituent of *Coprophanaeus s. str.* In this context, the affinity is suggested by secondary sexual characteristics of both sexes and the texture of the elytra. Interestingly, Nevinson (1892) in his "Suggested order of the species, and the groups into which they more-or-less naturally fall," proposed *C. bellicosus* as an isolated annectant between the *lancifer* and saphirinus groups. To Martínez (1944) the females of *C. bellicosus* "... se asemejan a ciertos [two male symbols] del subgenero *Coprophanaeus* del grupo *jasius*."

Coprophanaeus bellicosus is a denizen of the Atlantic coast forests of Brazil, and its range, along with that of *C. cerberus*, has undoubtedly contracted in recent decades because of widespread agriculturization and urbanization of Brazil's eastern seaboard.

***Coprophanaeus (Megaphanaeus) lancifer* (Linné, 1767)**

Fig. 13, 17-18, 23-26, 28, 35-39

Scarabaeus lancifer Linné, 1767: 544

Scarabaeus satelles Lichtenstein, 1796: 5 (syn. by Nevinson 1892: 5)

Phanaeus heros Castelnau, 1840: 80 (syn. by Nevinson 1892: 5)

Phanaeus miles Castelnau, 1840: 80 (syn. by Nevinson 1892: 5)

Phanaeus septentrionalis Pessôa, 1934: 291 (syn. by Martínez and Pereira 1967: 60)

Megaphanaeus lancifer (L.) (recomb. by Blackwelder 1944: 209)

Coprophanaeus lancifer (L.) (recomb. by Edmonds 1972: 841)

Type. *S. lancifer* – unknown to us; *P. heros* – unknown to us; *P. miles* – unknown to us; *S. satelles* – unknown to us; *P. septentrionalis* – holotype female, Museu de Zoologia, Universidade de São Paulo, São Paulo.

Diagnosis. General – Pronotum (Fig. 25-26, 35, 38) strongly granulate posteromedially. Posterolateral pronotal ridge (Fig. 37, arrow) short, not extending to lateral pronotal fossa. Metasternal shield (Fig. 18) smooth centrally, punctate peripherally; anterior portion of metasternum completely smooth, shiny medially, finely granulate laterally. Basal two-thirds of elytral striae 2-4 moderately undulate, width at

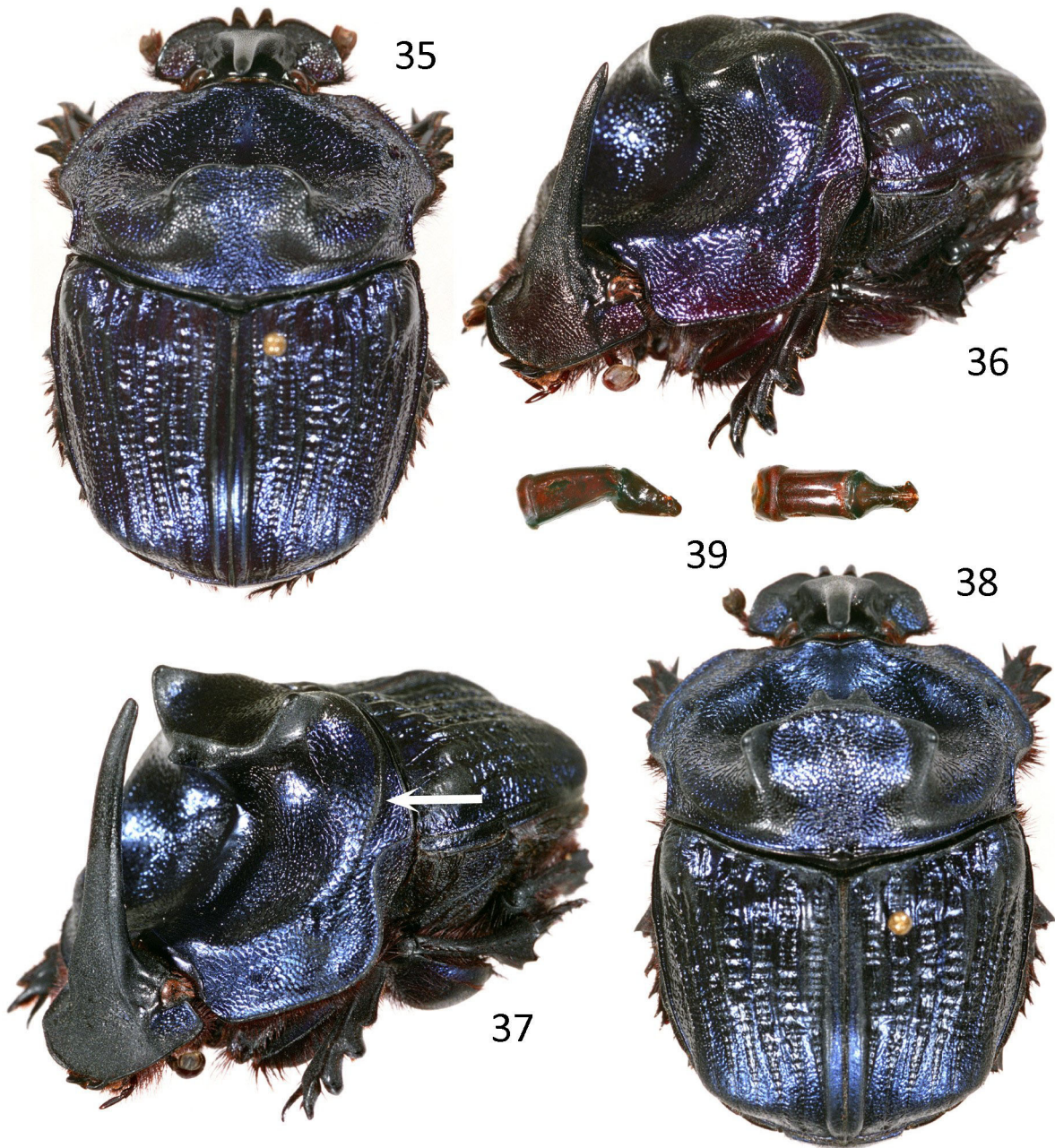


Figure 35-39. *Coprophanaeus lancifer*. 35-36) Female habitus. 37-38) Male habitus (arrow in 37 indicates posterolateral pronotal ridge). 39) Aedeagus (lateral view on left; dorsal view on right).

widest points about one-half of that at narrowings; carinulate margins usually tuberculate at narrowings (Fig. 13). Interstriae granulorugose, granulation, if distinct, confined to apical one-third of interstriae 2-6. Dorsal color usually dark blue, rarely green or bluish green. Length 28-50 mm.

Male (Fig. 23-24, 37-39) – Pronotal concavity flanked on each side beneath central prominence by sharp, oblique carina (Fig. 23, arrow). Dorsal prominence wide, width of saddle usually much greater than length. Apical process of parameres acute in profile.

Female (Fig. 25-26, 35-36) – Protarsi present. Pronotal concavity lacking oblique carinae.

Specimens examined – 351.

Distribution. Amazonian subregion of the Neotropical region (Fig. 28).

Collection Records. **BOLIVIA:** **Beni** – Magdalena (Apr). **Pando** – Cobija [Reserva San Sebastian Tahuamanu], 11°24'27"S 69°01'04"W (Dec); Guayaramerin (Dec); near Guayaramerin, 11°50'S 65°22'W, 120 m (Feb, Dec); 2 km E Fortaleza, 9°47'S 65°30'W, 120 m; Río Negro, 9°52'S 65°42'W, 120 m (Feb); 20 km SW Villa Bella, 10°22'S 65°22'W, 120 m (Feb); Tahuamanu, 11°24'27"S 69°01'04"W, 280 m; Malecón, 11°57'S 68°48'W, 190 m; Florida, 12°18'S 68°40'W, 190 m (Nov); Río Negro, 9°52'S 65°42'W, 120 m (Feb); near Bella Vista, 10°22'S 65°22'W, 120 m; Santa Rosa, 12°00'S 68°52'W, 180 m (Oct). **BRAZIL:** **Amazonas** – 30 km N Manaus [Reserva Forestal Ducke] (Mar- May, Aug); Manaus (Jan, Mar-Apr, Jul, Dec); 60 km N Manaus [Fazenda Esteio] (Jun); Manacapuru (Mar); São Paulo de Olivença (May, Jul, Dec); Tefé (Aug). **Mato Grosso** – Rosário Oeste (Jul); Nobres (Jan, Jul). **Pará** – Belém [Água Preta] (Jan-Feb); Tucuruí; Obidos (Mar-May, Jul, Nov-Dec); Santarém (Jan, May); Taperinha; Monte Dourado [Apui], 00°46'S 52°35.5'W (Jan); Monte Dourado [Tingilingi], 00°57'S 52°45.5'W (Apr). **Rondônia** – 9 km NE Cacaúlândia (Feb, Nov) **GUYANA:** **East Berbice-Corentyne** – Bartica (May). **Upper Demerara-Berbice** – Ituni (Jul). **PERU:** **Madre de Dios** – Río Madre de Dios, 12°34'10.0" S 70°06'01.4"W, 290 m (Apr); Río Tambopata, 12°38'59"S 69°06'24"W, 230 m (Sep); Río Palma Real Grande, 12°32'20"S 68°51'40"W, 220 m; 30 km SW Puerto Maldonado [Río Tambopata Reserve], 12°50'S 69°20'W, 290 m. **SURINAME:** **Commewijne** – Akintosoela, CELOS Camp, 39 km SE Suriname river bridge, road to Redi Dodi, 40 m, 5°16'17"N 54°55'15"W (Jul). **Sipaliwini** – Lely Plateau, 46°13'N 54°44'18"W, 650 m (Oct); Oelemarie, ~ 3°6'0"N 54°32'00"W (Feb, Aug, Oct); Palumeu, ~3°21'30.3"N 55°26'38.2"W (Jun); Kwamalasumutu (Jul). **VENEZUELA:** **Amazonas** – Río Mavaca camp, 2°02'N 65°06'W. **Bolívar** – Las Trincheras [Río Cauca] (Aug); Puerto Cabello (Río Cauca] (Aug).

Comments. This is a common species occurring sometimes in large numbers throughout much of the Amazon basin. Among all *Coprophanaeus* species, *C. lancifer* is the best choice as indicator species of Amazonia and is an important component of many local dung beetle communities (see, for example, Gardner et al. 2008, and Quintero and Halffter 2009). We have seen no specimens from eastern Ecuador and Colombia, but its absence there is unlikely. The color of this species is usually a consistent dark metallic blue; Trond Larsen has collected bright green examples in southeastern Peru. Besides the commonly used baits of dung and carrion, this species is also attracted to decomposing millipedes (Conrad Gillett, pers. comm.)

Théry et al. (2008) interpreted the crepuscular flight activity of this species as a mechanism that improves visual communication among conspecifics. At mid-range (> 0.5 m) in the low-intensity dusk lighting, the dark blue, metallic (structural) body coloration is seen at higher contrast against ambient background and active individuals become more visible to each other; at shorter range (< 0.5 m), enhancement of contrast between the black head horn and metallic pronotum probably functions in species recognition.

Except for the presence of protarsi, medium-sized and small females closely resemble equal-sized males. Pessôa's (1934) description of *C. septentrionalis* was based on five females; Lane and Camargo-Andrade (1935) re-examined the type series and found that it included one male. The pronotal prominence of large females (Fig. 25-26) is subject to considerable variation in width, but not as extreme as in *C. ensifer* (q.v.).

This species is the first *Coprophanaeus* depicted in print, as far as we know. Voet's (1766) illustrations (pl. 23, fig. 1-2 and 38) are unmistakably of *C. lancifer*. His fig. 1 and 2 are cited by Linné (1767) in his description of *Scarabaeus lancifer* and can be regarded as at least part of the type series. Voet's fig. 38 is of interest because, as Olsoufieff (1924) pointed out, it depicts the body of a male *C. lancifer* "... mais avec une tête (?) d'un autre Scarabaéide." In the text caption Voet stated that [specimen 38] "Forgan haec femina est No. 1 vel 2" ["Could be the female of either N. 1 or 2"]. Herbst's (1789) illustration (pl. VIII, fig. 6, under the name *Hamadrias*) is a copy of Voet's "hybrid;" but his pl. XV, fig. 1 depicts a male *C. lancifer* placed correctly under the name "*Scarab[aeus] lancifer*."

***Coprophanaeus (Megaphanaeus) bonariensis* (Gory, 1844)**

Fig. 15, 28, 40-44

Phanaeus bonariensis Gory, 1844: 79*Megaphanaeus bonariensis* (Gory) (recomb. by Blackwelder 1944: 209)*Phanaeus vicinus* Martínez, 1944: 187 (syn. by Martínez and Pereira 1967: 61)*Phanaeus vicinus argentinus* Martínez, 1944: 187 (syn. by Martínez and Pereira 1967: 61)*Coprophanaeus bonariensis* (Gory) (recomb. by Edmonds 1972: 841)

Type. *P. bonariensis* – unknown to us; *P. vicinus* s. str. holotype male, Museo Argentino de Ciencias Naturales “Bernadino Rivadavia,” Buenos Aires; *P. vicinus argentinus*, holotype male, Museo Argentino de Ciencias Naturales “Bernadino Rivadavia,” Buenos Aires.

Diagnosis. *General* – Pronotum strongly granulate posteromedially. Posterolateral pronotal ridge (Fig. 40, cf. Fig. 37) short, not extending to lateral pronotal fossa. Metasternal shield completely coarsely punctured (as in Fig. 19); anterior portion of metasternum finely granulate laterally, smooth medially. Carinulate margins of striae 2-4 gently undulate such that width of stria at narrowings is at least three-fourths of that at widest points (Fig. 15); carinulae simple, rarely tuberculate. Interstriae completely covered by large, round granules. Dorsal color usually shade of green or yellowish green. Length 21-35 mm.

Male (Fig. 42-44) – Pronotal concavity with dorsally inclined spiniform process on each side below prominence (Fig. 43). Dorsal prominence narrow, scoop-shaped, width of saddle less than length (Fig. 42). Apical process of parameres acute in profile.

Female (Fig. 40-41) – Pronotal concavity lacking lateral spines. Protarsi lacking.

Specimens examined – 222.

Distribution. Cerrado and Chaco provinces of Chacoan subregion (Fig. 28).

Collection Records. **ARGENTINA:** **Catamarca** – Catamarca (Feb). **Chaco** – Miraflores (Apr). **Córdoba** – San Javier, Las Rosas (Jan); Quilino (Dec). **Corrientes** – Bella Vista (Feb); Ituzaingo (Jan, Nov); Ituzaingo [Alto Paraná] (Sep). **Formosa** – Gran Guardia (Jan). **Jujuy** – 6 km W Yuto (Feb); El Quemado (Apr). **Misiones** – Ayolas (Oct). **Santiago del Estero** – Termas de Río Hondo (Dec); Santiago del Estero (Feb); Río Salado; Campo Gallo (Mar). **Tucuman** – Trancas (Jan); Benjamin Araoz (Mar); Gobernador Garmendia (Jan). **BOLIVIA:** **Beni** – Magdalena (Feb). **Santa Cruz** – San Matias, 16°34'S 59°09'W; Santa Cruz de la Sierra; Ichila, 400 m; Charagua, 20°14'11"S 63°13'52"W, 960 m (Apr); Urubigua, 20°14'11"S 63°13'52"W; Buena Vista (Jan); La Peña (Nov); Cabezas (Jan); Santiago de Chiquitos, 18°20'S 59°36'W (Feb); Santa Elena El Pantanal, 17°57'53"S 59°01'33"W (Apr); 1.6 km ESE Santiago de Chiquitos, 18°20.103'S 59°35.007'W, 622 m (Nov); 20 km NE Santiago de Chiquitos (Tucavaca River), 18°14.590'S 59°27.907'W, 215 m (Nov). **Tarija** – between Caiza and Creveaux, 21°50'19"S 63°24'58"W, 490 m (Jan). **BRAZIL:** **Mato Grosso** – 5 km S Cuiabá [Várzea Grande] (Dec); Rosario Oeste (Feb). **PARAGUAY:** **Boquerón** – Estación La Patria [trans-Chaco highway] (Mar, Dec); Nueva Asunción, 20°48'S 61°55'W; Mariscal Estigarribia (Feb, May). **Central** – Aregua (Dec); Altos; Colonia Nueva Italia (Feb); Asunción (Nov); Puerto Villeta (Jan). **Concepción** – Horqueta (Nov). **Cordillera** – Altos (Apr); Compañía Narajo (Nov). **Misiones** – Ayolas (Oct); **Paraguari** – Sapucay (Jan-Apr, Oct-Dec). **Presidente Hays** – Laguna Capitán (Jan).

Comments. This species largely replaces *C. ensifer* in the chiquitano, cerrado and chacoan habitats of eastern Bolivia and surrounding portions of Argentina, Paraguay and Brazil.

We here correct the record concerning female protarsi in *C. bonariensis*; contrary to Edmonds (1972), they are absent in this species. Consequently, medium-sized females and smaller males are virtually indistinguishable externally.

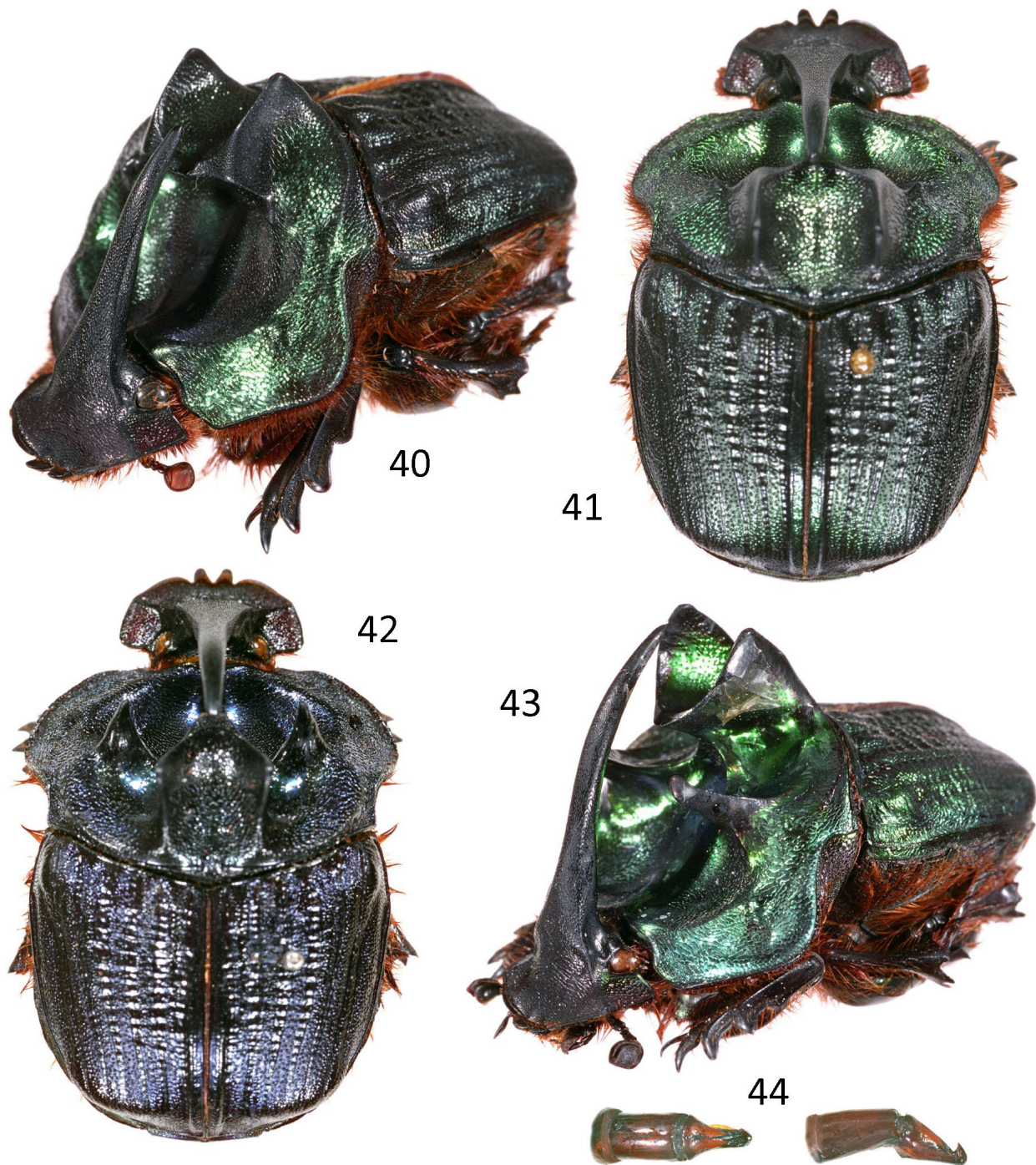


Figure 40-44. *Coprophanaeus bonariensis*. 40-41) Female habitus. 42-43) Male habitus. 44) Aedeagus (dorsal view on left; lateral view on right).

***Coprophanaeus (Megaphanaeus) ensifer* (Germar, 1821)**

Fig. 5, 11, 14, 19-22, 28, 45-49

Copris ensifer Germar, 1821: 147

Phanaeus ajax Sturm, 1826: 125 (syn. by Nevinson 1892: 3)

Phanaeus ducalis Castelnau, 1840 : 79 (syn. by Nevinson 1892: 5)

Megaphanaeus ensifer (Germar) (recomb. by Blackwelder 1944: 209)

Coprophanaeus ensifer (Germar) (recomb. by Edmonds 1972: 841)

Type. *C. ensifer* – unknown to us; *P. ajax* – unknown to us; *P. ducalis* – unknown to us.

Diagnosis. *General* – Pronotum strongly granulate posteromedially (Fig. 20-21, 46-47). Posterolateral pronotal ridge short, not extending to lateral pronotal fossa (Fig. 45, cf. Fig. 37). Metasternal shield completely, coarsely punctured (Fig. 19); anterior portion of metasternum completely finely granulate. Carinulate margins of striae 2-4 strongly undulate such that width of stria at narrowings is no more than one-half (usually much less) of that at widest points; carinulate margins strongly tuberculate at narrowings (Fig. 14). Interstriae completely covered by large, round granules. Dorsal color usually shade of green or bluish green, rarely blue. Length 30-56 mm.

Male (Fig. 22, 47-49) – Pronotal concavity with dorsally inclined spiniform process on each side below prominence (Fig. 22). Dorsal prominence wide, width of saddle much greater than length. Apical process of parameres rounded in profile.

Female (Fig. 20-21, 45-46) – Pronotal concavity lacking spiniform processes. Protarsi present.

Specimens examined – 133.

Distribution. Caatinga and Cerrado provinces of Chacoan subregion (Fig. 28).

Collection Records. **ARGENTINA:** Misiones – Loreto. **BOLIVIA:** Santa Cruz – Parque Nacional Noel Kempff Mercado [Los Fierros], 14°33'28"S 60°55'51"W and 15°15'6.3"S 61°14'41"W (Jan-Feb); Caparú, 14°50'S 61°10'W; Las Conchas, 17°34'S 59°28'W; La Guardia, 17°53'S 63°20'W; Basilio, 18°07'S 63°12'W; Estancia Perforación, 19°45'S 62°00'W; 20 km SW Perseverancia, 14°44'S 62°47'W, 230 m. **BRAZIL:** Alagoas – Maceio (Jul). Bahia – Encruzilhada (Dec). Distrito Federal – Brasilia, 600 m (Nov-Dec). Goiás – Bananeiras (Jan). Mato Grosso – Rio Verde (Nov); Fazenda São João, 14°14'10"S 56°08'11"W, 400 m (Jan); Arinos (Nov). Mato Grosso do Sul – Piraputanga (Mar); Selvíria (Jan). Minas Gerais – Lagoa Santa; Machacalis (Dec); Uberlândia (Dec). Paraíba – Mamanguape [Rebio Guaribas], 6°41'S 35°10'W; João Pessoa [Mata do Buraquinho] (May). Pernambuco – Recife [campus Universidade Federal de Pernambuco] (Aug). São Paulo – Assis (Dec); Descalvado (Mar); Colina (May); Itirapina (Feb); Ilha Solteira (Feb); São José do Rio Preto (Dec); Riberão Preto (Feb); Bálsamo (Nov); Rio Claro (Feb-Mar); Araraquara (Oct); Urupês (Nov); Planalto (Apr); Limeira (Feb); São José dos Campos (Oct-Nov); Rio Preto (Dec); Franca (Nov); Mogi Guaçu [Fazenda Campininas] (Jan); Campinas (Nov-Dec). PARAGUAY: Alto Paraná – Limoy (Sep-Oct). Anambay – Cerro Cora Feb, Dec). Caaguazú – Caaguazú (Nov-Dec). Concepción – Cororó (Nov). Guairá – Villarrica (Dec); Independencia; Melgarejo (Sep). Kanindeyu – Carapa (Apr).

Comments. Endres et al. (2005) studied the phenology of *C. ensifer* in Paraíba (Brazil) and found that adult abundance and activity are greatest during the April–September rainy season and that beetles showed no preference for carrion type used to bait traps. Otronen (1988) provided observations and interpretations on horn variation and combat in this species in both sexes. Fighting in *C. ensifer* occurs both intra- and intersexually. Males fight males to defend or gain resources and to win females; females fight females and males to defend their burrows.

This species varies in color. The usual tone is dark metallic green, often with contrasting bluish reflections. Pessôa (1934) reported rare metallic blue individuals from Lussanvira, São Paulo, and bluish-green individuals from Mato Grosso. A very dark bluish-green form occurs in the gallery forests of northern Mato Grosso (Querencia, Diamantino, Trivelato), where the species has evidently invaded a decidedly Amazonian habitat; the male of this form has a small median tooth between larger lateral ones born apically on the median projection of the pronotal prominence (Fernando Vaz-de-Mello, pers. comm.).

The female pronotal prominence takes two forms. The summit of the more frequent one is broadly saddle-shaped (Fig. 20). In the less frequent condition the sides of the median saddle are closely appressed, producing a fluted salience (Fig. 21). Both forms occur together in the region of Brasilia.

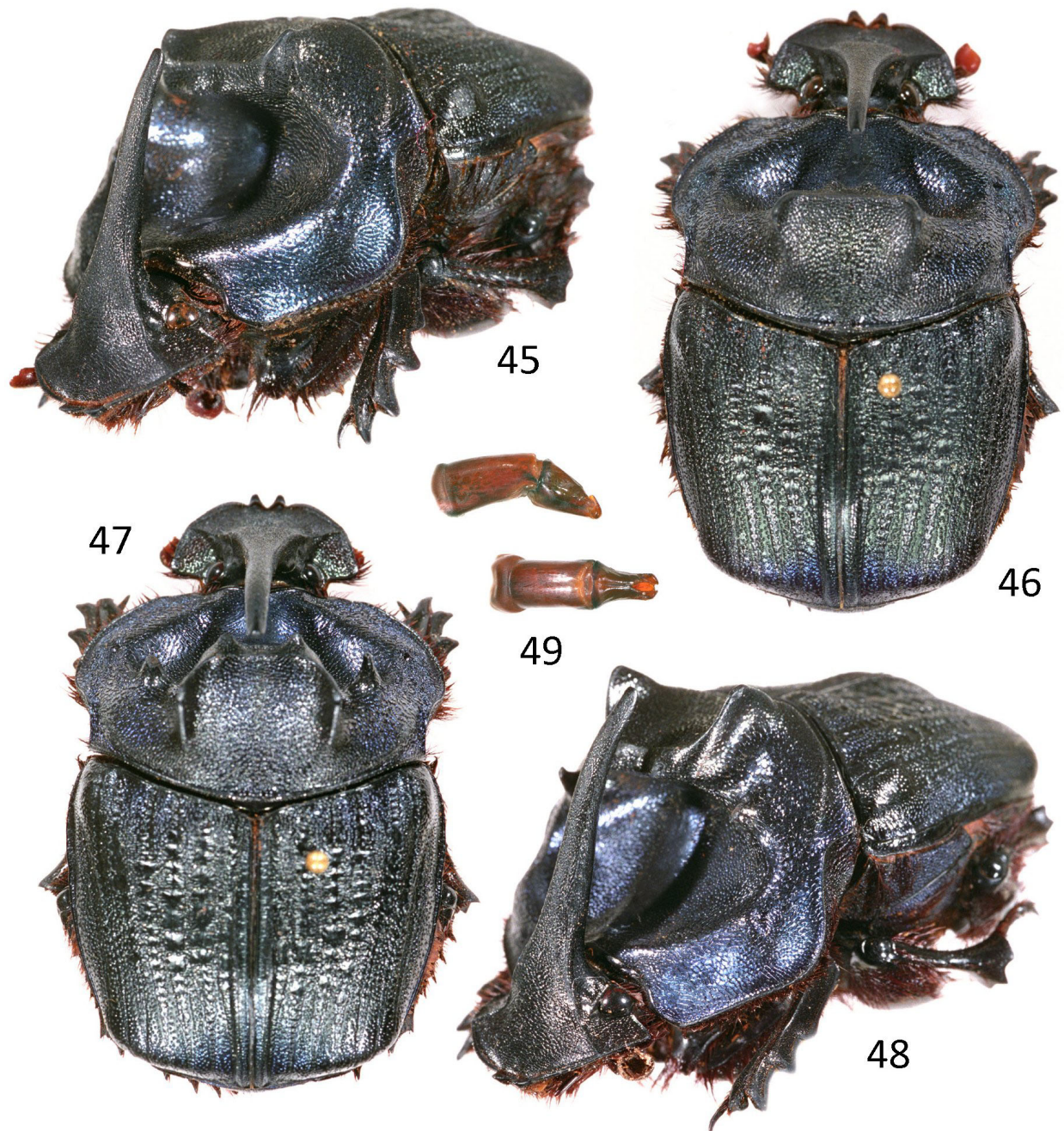


Figure 45-49. *Coprophanaeus ensifer*. 45-46) Female habitus. 47-48) Male habitus. 49) Aedeagus (lateral view above; dorsal view below).

Subgenus *Metallophanaeus* Olsoufieff, 1924

Metallophanaeus Olsoufieff, 1924: 23.

Type Species: *Phanaeus saphirinus* Sturm, original designation.

Diagnosis. General – Lower portion of eye small, width no more, and usually less, than twice that of oculogular space. Paraocular areas (genae) carinate or not lateral to eyes. Occipital areas of parietals more-or-less flattened, lacking angulate prominence (as in Fig. 12). Circumnotal ridge entire, not effaced behind eyes (as in Fig. 8). Pronotal sculpturing variable, usually granulorugose anterolaterally, punctate

to some degree posteromedially; basal fossae variable. Pronotum lacking posterolateral ridge. Striae fine, simple or carinulate, anterior ends of 1-4 impressed to some degree. Hind wing not notched basally (Fig. 10). Posterior surface of protibial tooth with single basal row of long setae (as in Fig. 6). Abdominal sterna usually smooth medially. Sexual dimorphism marked.

Male – Head bearing posteriorly curved horn. Pronotum variable, flattened or transversely concave anteromedially. Parameres variable.

Female – Protarsi absent. Pronotum variable, usually with transverse process near anterior margin.

Distribution. Eastern Brazil (east of Amazonia) southward to northeastern Argentina.

Comments. This subgenus brings together eight mostly colorful species distributed between two different species groups recognized by Edmonds (1972) and Arnaud (2002c). Only six of the eight are treated in the key and species accounts (see below). As far as we know, all *Metallophanaeus* species are diurnal and copronecrophagous. The subgenus as here constituted is undoubtedly paraphyletic. Affinities to *Megaphanaeus* (mainly via *C. bellicosus*, *q.v.*) are clearly suggested in the saphirinus group by, in particular, similarity in male secondary sexual characters (form of head and pronotum and apically hooked parameres). Affinities to the jasius group of *Coprophanaeus s. str.* are equally demonstrable in the thalassinus group by male and female secondary sexual characters (male head horn and pronotal shape; swollen tips of parameres; pronotal ridge and oval concavity in female). A cogent argument can be made to isolate the two species groups of *Metallophanaeus* into separate subgenera. Indeed, Olsoufieff included only *C. saphirinus* and *C. horus* in this subgenus, which he defined mainly on the basis of the male pronotum; *C. pertyi*, *C. punctatus* (of which Olsoufieff had no male) and *C. thalassinus* he placed in *Coprophanaeus s. str.* We have combined the two groups here mainly because both lack (by symplesiomorphy, we presume) the notching of the hind wing (a synapomorphy) characteristic of the nominate subgenus. Our preference now is to maintain the current, probably artificial, inclusion of both groups in *Metallophanaeus*; any decision otherwise should await a more formal phylogenetic analysis of the entire *Coprophanaeus* lineage, including *Dendropaemon*.

The salient differences between the two species groups recognized here reside in secondary sexual characters and in the shape of the anterior portion of the metasternum. Regarding the latter, the thalassinus group exhibits a tendency for the anterior metasternal angle (viewed in profile) to be enhanced to some degree – either squared or obviously prolonged anteriorly in contrast to the evenly curved profile seen in the saphirinus group. Accentuation of the anterior metasternal angle of the thalassinus group (supposedly most developed in *C. vazdemeloi*) correlates with a tendency for the profemora to be swollen posteriorly, and for the swollen posterior surface to be divided longitudinally into a flat, glabrous area and a rounded setose area behind it. Sexual dimorphism is striking but expressed differently in the two groups. In the saphirinus group, as in *Phanaeus*, *Sulcophanaeus* and *Oxysternon*, the male possesses a long, gradually tapering, cylindrical head horn and prominent posteromedian pronotal salience; the female, a trituberculate cephalic carina and a convex pronotum with subtle relief and (usually) a transverse crest near the anterior margin. In the thalassinus group, the male head horn is proportionately shorter with a distinctly swollen base and the pronotum bears a transverse ridge; the female has a trituberculate cephalic carina and the pronotum bears a strong anteromedian crest followed by an oval concavity (as in many species of *Coprophanaeus s. str.*). Protarsi are absent in both sexes of all *Metallophanaeus* species.

We are not able to treat formally in this review two undoubtedly valid species belonging to the thalassinus group. One is *C. vazdemeloi* Arnaud (2002a), known from the holotype male and one paratype female (BRAZIL: Piauí – São Raimundo Nonato, Parque Nacional Serra de Capivara [Jan]) housed in the private collection of Patrick Arnaud. We have been unable to examine these specimens, which are reported to be unique among the thalassinus group for the very strong prolongation of the anteromedian angle of the metasternum. Since we have no way to reliably assess other characters of this species and to formally compare it with other members of the species group, we are obliged to exclude it from formal consideration at this time. We refer the reader to the original description and to the photographs and comments in Arnaud (2002c).

The key and species treatments below also do not consider an eighth species from the Chapada do Parecis (northern Mato Grosso, Brazil) assignable to the thalassinus group and currently under study by Fernando Vaz-de-Mello and Patrick Arnaud. It will key out below to *C. thalassinus*, from which it differs

by the following combination of characters: new species – a) posteromedian portion of pronotum granulorugose; b) paraocular areas flat; c) abdominal sterna distinctly punctured medially; d) elytra golden with green reflections basally and along elytral suture; pronotal disk bluish green, sides and head golden; antennal club golden; e) from Mato Grosso; f) all elytral interstriae more-or-less evenly convex; first interstria not more strongly raised than others. *Coprophanaeus thalassinus* differs from the new species as follows: a) posteromedian portion of pronotum with punctures grading to fine ridges to scale-like granules around basal fossae; b) posterior portion of paraocular areas convex; c) abdominal sterna smooth medially at least along midline; d) dorsum metallic green and dark blue; antennal club black; e) from Bahia; f) elytral interstriae weakly convex except first; first more strongly raised and shinier than others.

Key to species of *Metallophanaeus*

1. Anterior metasternal profile (viewed laterally, Fig. 59) evenly and broadly rounded; angle usually with distinct beading visible ventrally as V- or I-shaped cap. Ventral surface of protibia lateral to longitudinal carina (Fig. 50) usually completely, evenly punctate–punctatorugose (weakly so in *C. punctatus*). Pronotum of large male with pair of small, closely set, apically convergent processes near posterior margin, separated by strong concavity (Fig. 63, 69, 78); disk below processes with deep, round concavity on each side (except *C. punctatus*). Female pronotum lacking deep, rounded anteromedian concavity (e.g. Fig. 67-68). Basal pronotal fossae variable. Male cephalic horn evenly tapering from base to apex, base not prominent (Fig. 69). Parameres with lobate, laterally directed apical processes (e.g. Fig. 66). **saphirinus species group .. 2**
- Anterior metasternal profile (viewed laterally, Fig. 57-58) squared or prolonged anteroventrally to some degree and seldom beaded. Ventral surface of protibia lateral to longitudinal carina mostly smooth, usually with single or double row of shallow, confluent punctures paralleling longitudinal carina (Fig. 50, arrow). Pronotum of large male with deep anteromedian concavity whose summit is marked by transverse crease-like ridge (lobate medially in *C. pertyi*, Fig. 80-81). Female pronotum with deep, rounded anteromedian concavity that bears strongly raised, trituberculate, quadrate process adjacent to anterior margin (e.g. Fig. 84). Basal pronotal fossae distinct, round or oblong (Fig. 52-53). Male cephalic horn a slender, cylindrical process arising from a thickened base (Fig. 80). Tips of parameres swollen as thickened lateral flanges (Fig. 89). **thalassinus species group 4**
- 2(1). Female pronotum (Fig. 67-68) lacking rounded crest adjacent to anterior margin; disk bearing transverse ridge followed by midlongitudinal depression extending to posterior margin. Posterior portion of paraocular areas (genae) strongly, transversely raised in front of eyes (swelling sometimes ridge-like, Fig. 60), coarsely punctured in front of swelling. Basal pronotal fossae present, rounded. Elytral interstriae usually distinctly convex, first, second and/or fourth often more strongly so. Pygidium (Fig. 56) with broad, shallow basal sulcus, distinctly shagreened in contrast to smooth pygidial surface. Apical processes of parameres (viewed laterally) angulate. Dorsum (Fig. 63-68) shiny green with strong yellow reflections, strongest on head and pronotum ***Coprophanaeus (Metallophanaeus) horus (Waterhouse)***
- Female pronotum (Fig. 73, 76) with small trituberculate crest adjacent to anterior margin; crest followed by weak concavity flanked posteriorly by pair of rounded tumosities. Paraocular areas (genae) at most only weakly convex, sculpturing variable. Basal pronotal fossae variable. Elytral interstriae flat. Pygidium usually lacking any indication of distinct basal groove. Apical processes of parameres rounded. Dorsal coloration variable **3**
- 3(2). Posteromedian angle of pronotum slightly produced posteriorly, very smooth, effacing basal fossae and mesial ends of basal pronotal groove. Pronotum smooth posteromedially. Paraocular areas mostly smooth, highly shining. Male pronotum with round concavities beneath posteromedian projections. Elytral striae simple, very fine (x5) ***Coprophanaeus (Metallophanaeus) saphirinus (Sturm)***

- Posteromedian angle of pronotum not produced, basal fossae small, incorporated into mesial ends of basal groove. Pronotum distinctly punctured posteromedially. Paraocular areas completely punctured, usually densely and coarsely so. Male pronotum lacking round concavities. Elytral striae (Fig. 54) carinulate, distinctly punctured (x5)
 *Coprophanaeus (Metallophanaeus) punctatus* (Olsoufieff)
- 4(1). Transverse pronotal ridge of male lobate medially (Fig. 81). Posteromedian portion of pronotum smoother and shinier than remainder of disk, simply punctate, less strongly and densely so near basal fossae. Apical angle of metasternum (viewed laterally, Fig. 57) salient, rounded, laterally compressed, beading at most faintly indicated. Cephalic carina of female simple, scarcely elevated, at most only weakly trituberculate. Paraocular areas (genae) nearly flat, strongly, densely punctate, with short carina lateral to eyes. Pygidium lacking basal groove. Tips of parameres only slightly swollen laterally, lacking distinct flanges. Elytra dull black; pronotum, head, pygidium and venter with strong bluish-green metallic reflections. NE Brazil
 *Coprophanaeus (Metallophanaeus) pertyi* Olsoufieff
- Transverse pronotal ridge of male straight or weakly curved, not lobate (Fig. 85, 92). Posteromedian portion of pronotum (Fig. 52-53) not obviously smoother than surrounding surface, densely, evenly punctate or punctatorugose. Metasternal angle (Fig. 58) squared or acutely salient. Cephalic carina of female with prominent, conical median tubercle. Paraocular areas swollen to some degree, strongly rugose, carina lateral to eye at most only vaguely indicated, usually obliterated by rugosity. Pygidium with broad, shallow basal groove. Tips of parameres with distinct lateral flanges (Fig. 89). Elytra colored, not black 5
- 5(4). Posteromedian portion of pronotum (Fig. 53) strongly, densely punctate, lacking distinct granules or ridges (sculpturing stronger in females). Anterior end of metasternum acutely angled, sometimes almost conical. Inner two-thirds of paraocular areas (genae) strongly swollen (Fig. 61). Base of pronotum with distinct groove in front of beaded margin; groove opens into elongate basal fossae (Fig. 53). Elytral interstriae flat, irregularly transversely wrinkled. Tips of parameres with strongly developed rounded, flat flanges (Fig. 53)
 *Coprophanaeus (Metallophanaeus) pessoai* (Pereira)
- Posteromedian portion of pronotum (Fig. 52), at least near fossae, granulate or granulorugose. Anterior angle of metasternum squared (Fig. 58), not distinctly salient. Paraocular areas (genae) weakly swollen. Pronotum lacking distinct basal groove (Fig. 52); basal fossae distinct, oval. Elytral interstriae smooth, weakly convex, first strongly raised and shiny. Tips of parameres have rounded flanges with slightly upturned margins (Fig. 94)
 *Coprophanaeus (Metallophanaeus) thalassinus* (Perty)

***Coprophanaeus (Metallophanaeus) horus* (Waterhouse, 1891)**

Fig. 10, 56, 60, 62-68

Phanaeus horus Waterhouse, 1891: 129

Phanaeus sericeus Felsche, 1901: 152 (syn. by Martínez and Pereira 1960: 80)

Metallophanaeus horus (Waterhouse) (recomb. by Blackwelder 1944: 209)

Coprophanaeus horus (Waterhouse) (recomb. by Edmonds 1972: 842)

Type. *P. horus* – holotype male, The Natural History Museum, London (examined); *P. sericeus* – unknown to us.

Diagnosis. *General* – Posterior portion of paraocular areas (Fig. 60) strongly transversely raised in front of eyes (swelling sometimes ridge-like), coarsely punctured in front of swelling. Pronotum smooth posteromedially, otherwise weakly granulorugose; posterior angle normal, basal fossae large, conspicuous, incorporated into inner ends of sulcus paralleling posterior margin. Anteromedian angle of metasternum (seen in profile, as in Fig. 59) rounded, not salient; angle capped with elongate thickening (bead).

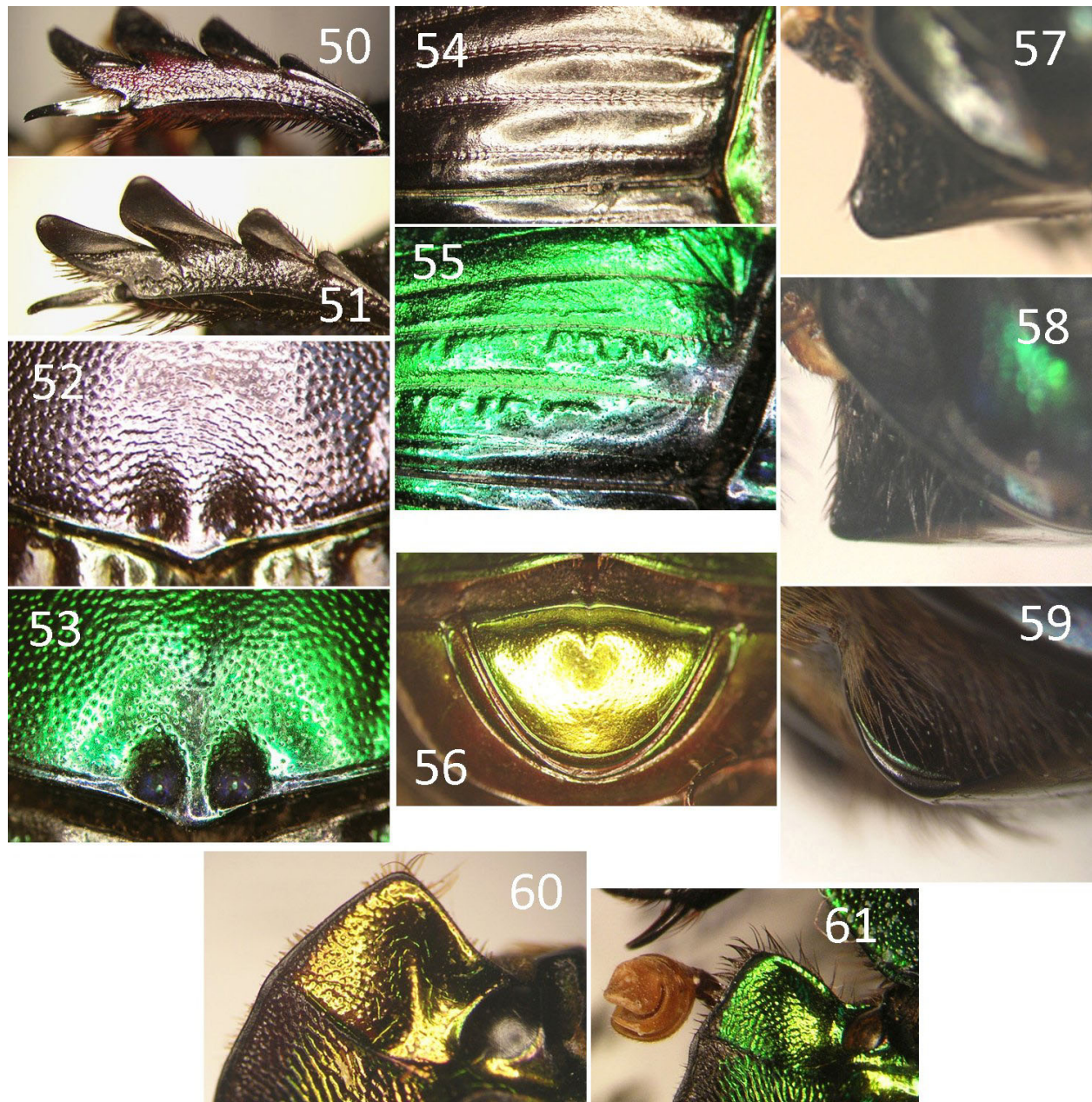


Figure 50-61. Characters of the *Coprophanaeus* subgenus *Metallophanaeus*. **50)** Ventral view of left protibia of *C. saphirinus*. **51)** Same, *C. pertyi*. **52)** Dorsal view of posterior portion of pronotum of *C. thalassinus*. **53)** Same, *C. pessoai*. **54)** Dorsal view of left elytron of *C. punctatus*. **55)** Same, *C. pessoai*. **56)** Posterior view of pygidium of *C. horus*. **57)** Lateral view of metasternal angle of *C. pertyi*. **58)** Same, *C. pessoai*. **59)** Same, *C. saphirinus*. **60)** Dorsal view of right side of head of *C. horus*. **61)** Same, *C. pessoai*.

Striae (x5) simple, weakly impressed; bases of striae 1-4 impressed, not distinctly fossate. Elytral interstria usually distinctly convex, first, second and/or fourth often more strongly so. Ventral surface of protibia lateral to longitudinal carina paralleling inner margin entirely punctatorugose. Pygidium (Fig. 56) with broad basal groove. Length 15-22 mm. Color green or yellowish green with strong golden highlights.

Male (Fig. 63-65) – Head with evenly tapering long horn whose base is not abruptly swollen. Pronotum with pair of closely set, apically convergent processes near posterior margin, separated by strong concavity; disk anterior to processes with pair of conspicuous round concavities. Pronotal disk punctate posteromedially, otherwise granulorugose. Apical processes of parameres angulate.

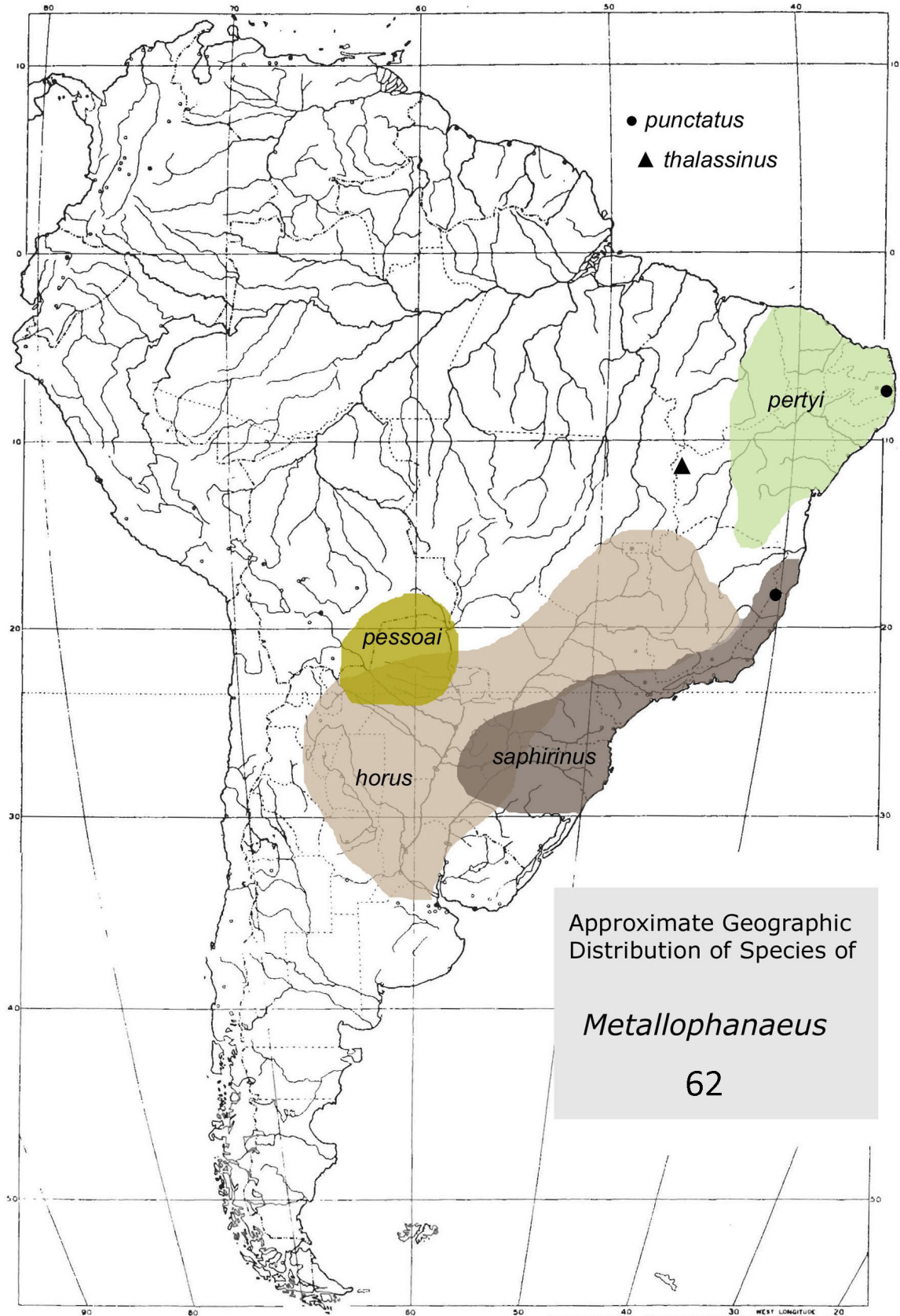


Figure 62. Approximate geographic distribution of *Coprophanaeus* (*Metallophanaeus*) species.

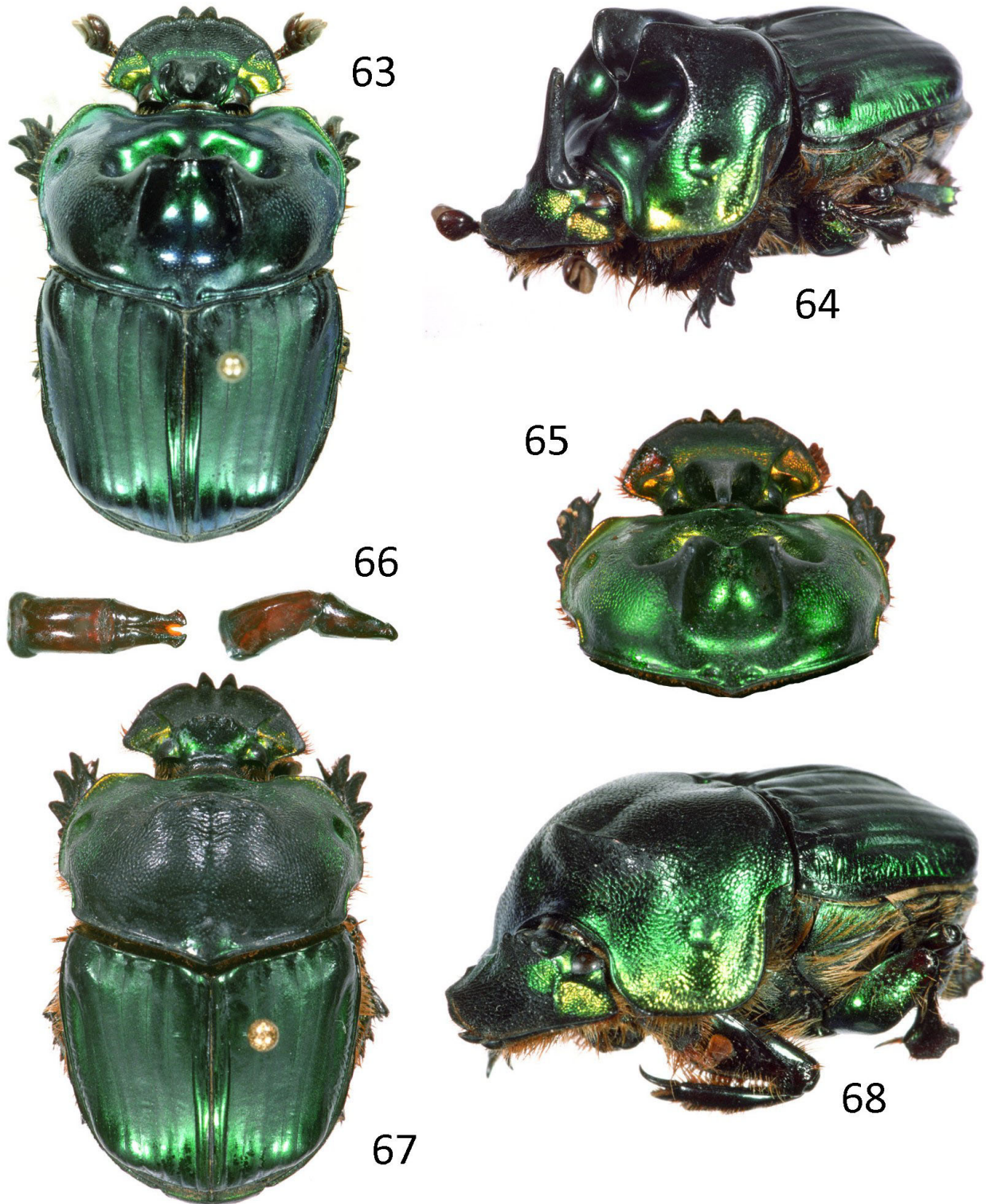


Figure 63-68. *Coprophanaeus horus*. 63-65) Male habitus. 66) Aedeagus (dorsal view on left; lateral view on right). 67-68) Female habitus.

Female (Fig. 67-68) – Pronotum with transverse, weakly margined ridge followed by midlongitudinal groove. Pronotum finely granulorugose on disk and sides, punctate posteromedially.

Specimens examined – 31.

Distribution. Chaco and Cerrado provinces (Fig. 62).

Collection Records. ARGENTINA: **Buenos Aires** – General Sarmiento (Jan); General Belgrano. **Córdoba** – Cruz Alta (Feb, Nov); Leones (Feb). **Misiones** – Loreto (Jan, Nov). **Tucuman** – Los Ralos. BRAZIL: **Distrito Federal** – Brasilia (Nov). **Minas Gerais** – 100 km SSE Lavras [Carrancas, Chapada das Perdizes] (Dec). **Paraná** – Mamborê (Feb). **Rio Grande do Sul** – Canôas (Oct); Colorado (Dec); Botucatu (Feb). PARAGUAY: **Boquerón** – Nueva Asunción (Jan, Apr, Dec). **Caaguazú** – Caaguazú (Dec). **Presidente Hays** – Laguna Capitan (Jan).

Comments. This is the only *Metallophanaeus* species whose female lacks an anteromedian transverse crest adjacent to anterior pronotal margin, a departure from “normal” female pronotal type also seen in *C. cerberus* (q.v.)

References to *C. horus* by Pessôa (1934) and Pessôa and Lane (1941) are actually to *C. pessoai* (Pereira, 1949). Martínez (1959) reported *C. horus* to be strictly necrophagous. Felsche’s species (*Phanaeus sericeus*) was based on specimens from the southern part of the range, where individuals take on a more muted color tone than in the central Cerrado.

***Coprophanaeus (Metallophanaeus) saphirinus* (Sturm, 1826)**

Fig. 50, 59, 62, 69-74

Phanaeus saphirinus Sturm, 1826: 65

Phanaeus chabrillici Thompson, 1857: 117 (syn. by Harold 1869: 65)

Metallophanaeus saphirinus (Sturm) (recomb. by Blackwelder 1944: 209)

Phanaeus machadoi Pereira and d’Andretta, 1955: 257, **New Synonymy**

Coprophanaeus saphirinus (Sturm) (recomb. by Edmonds 1972: 841)

Type. *P. saphirinus* – holotype male, Zoologische Staatssammlung, Munich; *P. chabrillici* – unknown to us; *P. machadoi* – holotype male, Museu de Zoologia, Universidade de São Paulo, São Paulo.

Diagnosis. *General* – Paraocular areas (genae) mostly smooth, at most only weakly convex, not carinate lateral to eyes. Pronotum smooth posteromedially, otherwise weakly granulorugose; posterior angle flattened, slightly explanate, basal fossae and inner portions of sulcus paralleling posterior margin effaced. Anteromedian angle of metasternum (seen in profile, Fig. 59) rounded, not salient; angle capped with elongate thickening (bead) usually visible from below as broad V. Elytral interstriae flat; striae (x5) simple, very fine, superficial, not at all impressed (x5); bases of striae 1-4 distinctly fossate, fossae progressively larger laterally. Ventral surface of protibia lateral to longitudinal carina paralleling inner margin entirely punctatorugose (Fig. 50). Pygidium lacking basal groove. Length 12-22 mm. Color (Fig. 69-74) shining metallic blue, violet, red or rarely green.

Male (Fig. 69-71) – Head with evenly tapering long horn, base not abruptly swollen. Pronotum with pair of closely set, apically convergent processes near posterior margin, separated by strong concavity; disk anterior to processes with deep, round concavity on each side, otherwise slightly convex, rarely with pair of closely set small acute tubercles about midway to anterior margin. Pronotal sculpturing limited to weak rugosity on lateral margins; otherwise surface nearly smooth. Apical processes of parameres rounded.

Female (Fig. 73-74) – Pronotum with small, weakly trituberculate crest adjacent to anterior margin followed by weak concavity bounded posteriorly by pair of weak tumosities near middle of disk. Pronotum finely granulorugose on disk and sides, punctate posteromedially.

Specimens examined – 381.

Distribution. Paranaian subregion (Fig. 62).

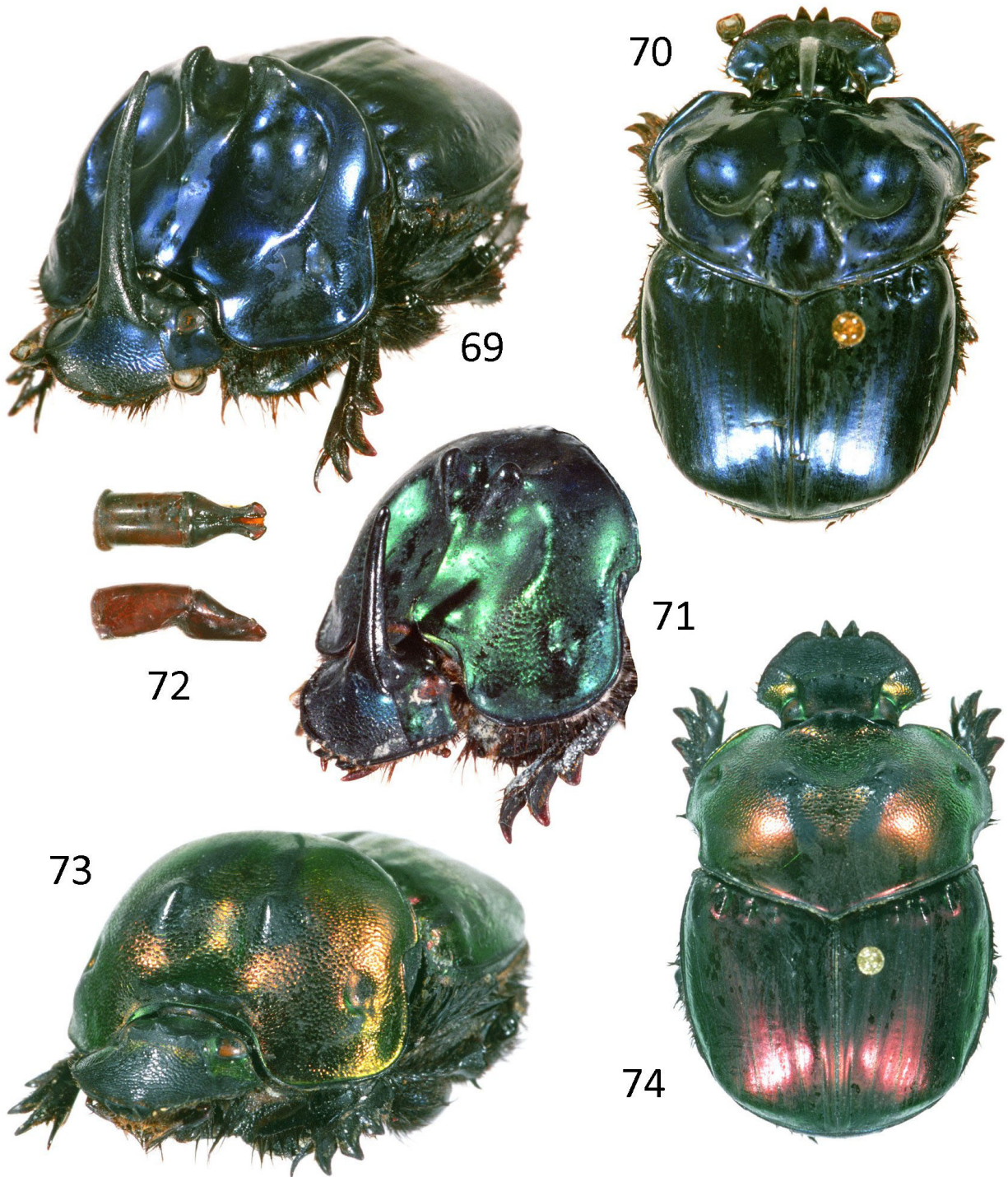


Figure 69-74. *Coprophanaeus saphirinus*. 69-71) Male habitus. 72) Aedeagus (dorsal view above; lateral view below). 73-74) Female habitus.

Collection Records. ARGENTINA: Chaco – Miraflores (Apr). Misiones – Posadas (Dec); Coñapirú (Dec); Garuhapé (Oct); Mocona (Dec); Dorado (Apr); Aristóbulo del Valle [Depto. Cainguas] (Dec); Dos de Mayo (Sep, Nov); Santa María; Parque Nacional Iguazú, 200 m (Jan-Feb, Dec); Cosapiel (Nov); Loreto (Dec). Tucumán – Tucumán (Feb). BRAZIL: Bahia – Entre Rios. Espírito Santo – Timbuhy (Dec). Minas Gerais – Virginia, 1500 m (Nov); Poços do Caldas [Morro da Ferra] (Feb). Paraná – Londrina

(Dec); Lapa (Mar); Curitiba (Feb, Apr, Oct–Dec); Bariqui (Apr). **Rio de Janeiro** – Itatiaia (Jan, Mar, Nov); Floresta da Tijuca (Oct, Dec); Ilha Grande (Apr); Petropolis (Nov–Dec); Nova Friburgo (Jan); 17 km E Nova Friburgo, 22°23'04"S 42°33'30"W, 750 m (Jan, Mar). **Rio Grande do Sul** – São Borja (Dec). **Santa Catarina** – Pinhal (Dec); Rio das Antas; Corupá (Jan, Oct–Nov); Nova Teutônia, 27°11'S 52°23'W (Sep–Nov, Jan); Rio Vermelho (Feb); São Francisco (Nov). **São Paulo** – 50 km SE Mogi das Cruzes [Serra do Mar Biological Station “Boraceia”], 800–900 m (Apr); São Bernardo (Jan); São Paulo (Mar); Cantareira (Dec); Campos do Jordão (Dec); Tremembé (Mar). **PARAGUAY: Alto Paraguay** – Bella Vista (Dec). **Caazapá** – Parque Nacional Caaguazú [San José Cristal] (Oct, Dec). **Cordillera** – Naranjo (Dec). **Guairá** – Paso Yobai (Sep); Villarrica (Nov); Colonia Independencia (Nov); Colonia Natalicio Talavera (Dec); Colonia Nueva Talavera; Yoveré [Cordillera Ybytyruzú] (Jan). **Itapúa** – Yatai [San Rafael Reserve], 26°38'13"S 55°39'50"W (Sep). **Paraguari** – Paraguari (Nov).

Comments. *Coprophanaeus saphirinus* is one of the most common species of the genus and by far the most common in the subgenus. Its range is broad; and while it prefers forest habitat, it does venture into the more open Chaco formations of northeastern Argentina. The color of this species varies more than in any other member of the genus. Dark metallic blue predominates. A red form (Fig. 71), described as *Phanaeus chabrillicci* and sometimes regarded as a subspecies, occurs sporadically in the southern part of its extensive range; and a green form (Fig. 71) occurs most commonly in populations in the coastal forests of Rio de Janeiro. The bright colors of this species are associated with diurnal activity (Medina-Hernandez 2002).

Concerning *Phanaeus chabrillicci*, we echo Harold's (1869) sentiments, “Das typische Stück [of *C. chabrillicci*] ist nichts als eine schön kupfrigrothe Varietät [of *C. saphirinus*]”, and we agree with his synonymy. This morph of *C. saphirinus* occurs widely and in populations dominated by the bluish-violet form; it is not a distinct taxon in our opinion. Fernando Vaz-de-Mello (pers. comm.) has observed that the red form tends to occur more frequently in populations at somewhat higher elevations than does the blue form, and only in the southern portion of the species range. Thomson's species was originally spelled “*chabrillicci*”, and in the literature it commonly appears so written. He named it for the collector of the type series, François Chabrillicc. Harold (1869), followed by Blackwelder (1944), emended the name to “*chabrillicci*”.

The elytral striae (more frequently the lateral ones) of this species are often micropunctate (x10), but they are never carinulate. Pereira and d'Andretta's (1955) description of *C. machadoi* was based on a single male with stronger strial and interstitial puncturing than typical *C. saphirinus* and with curious modifications of the pronotal disk. Fernando Vaz-de-Mello (pers. comm.) reports that coastal populations of this species (“*machadoi*”) in Rio de Janeiro, Espiritu Santo and some adjacent regions of Minas Gerais differ from populations in the main range of *C. saphirinus*. These populations, which include blue and green individuals, present a weak, midlongitudinal ridge on the anterior (declivitous) portion of the pronotum and stronger elytral striae that at times appear punctured (as in *C. punctatus*). Other large male variants exist; we have observed one with a pair of acute tubercles along the midline of the pronotal disk.

Pereira (1949) reported observing dimorphic males of *C. saphirinus*. Besides those bearing a tapering head horn, he described small males with a bituberculate swelling of the kind also observed in the palaeno group of *Phanaeus* and in *Oxysternon*. In none of the smallest males observed by us have we seen a bituberculate swelling; the minimum condition has been only a small bump or an obsolete tubercle.

Martínez (1959) cited *C. saphirinus* as strictly necrophagous, but it is regularly collected also from human feces.

***Coprophanaeus (Metallophanaeus) punctatus* (Olsoufieff, 1924)**

Fig. 54, 62, 75–79

Phanaeus punctatus Olsoufieff, 1924: 71

Coprophanaeus punctatus (Olsoufieff) (recomb. Edmonds 1972: 843)

Type. Lectotype female (des. by Arnaud, 1982: 116), Muséum National d'Histoire Naturelle, Paris (examined).

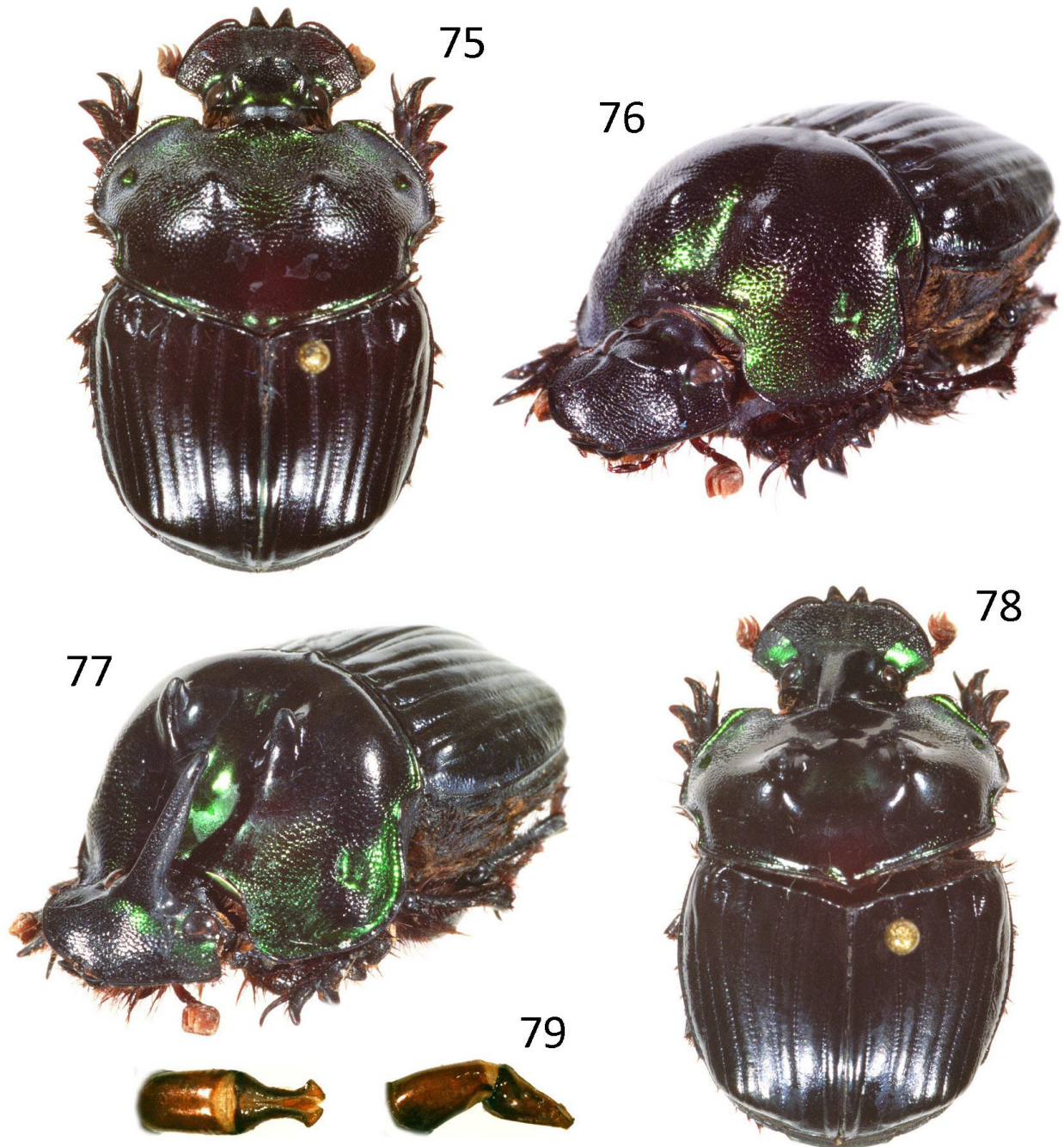


Figure 75-79. *Coprophanaeus punctatus*. 75-76) Female habitus. 77-78) Male habitus. 79) Aedeagus (dorsal view on left; lateral view on right).

Diagnosis. General—Paraocular areas (genae) completely punctured, usually coarsely and densely so, at most only weakly convex, not carinate lateral to eyes. Pronotum smooth posteromedially, otherwise weakly granulorugose; posterior angle normal, basal fossae small, incorporated into inner ends of sulcus paralleling posterior margin. Anteromedian angle of metasternum (seen in profile, as in Fig. 59) rounded, not salient; angle capped with elongate thickening (bead). Elytral interstriae (Fig. 54) weakly convex; striae (x5) weakly impressed, carinulate, appearing weakly punctate (x5; see Comments below); bases of striae 1-4 impressed, not distinctly fossate. Ventral surface of protibia lateral to longitudinal carina paralleling

inner margin entirely punctatorugose. Pygidium lacking basal groove. Length 13-17 mm. Elytra black, pronotum with green to yellowish-green areas (Fig. 75-78).

Male (Fig. 77-79) – Head with evenly tapering long horn whose base is not abruptly swollen. Pronotum with pair of closely set, apically convergent processes near posterior margin, separated by strong concavity; disk anterior to processes lacking concavities. Pronotal disk punctate posteromedially, otherwise granulorugose. Apical processes of parameres rounded.

Female (Fig. 75-76) – Pronotum with small, weakly trituberculate crest adjacent to anterior margin followed by weak concavity bounded posteriorly by pair of weak tumosities near middle of disk. Pronotum finely granulorugose on disk and sides, punctate posteromedially.

Specimens examined – 6.

Distribution. Known only from isolated localities in northern Brazilian Atlantic Forest province (Fig. 62).

Collection Records. **BRAZIL: Espiritu Santo** – Fazenda Lagoa do Macuco [Mun. Linhares], 19°03'50"S 39°58'43"W, 10 m (Jan). **Pernambuco** – Igarassú [Reserva Ecologica Charles Darwin] (Mar, May-Jul, Oct).

Comments. Olsoufieff (1924) had only three females at hand when he described this species. But he was rightly suspicious of placing it in *Coprophanaeus s. str.*, noting “L'absence des tarsi antérieurs et la forme de l'épistome les font placer ici [*Coprophanaeus s. str.*], ou les ranger au groupe du *Ph. saphirinus*, dont elles ont le caractère general. Ce n'est qu'en trouvant les [two male symbols] que l'on pourra résoudre cette question.” Arnaud (2002c) confirmed its placement in this subgenus.

Olsoufieff's name refers to apparent puncturing of the elytral striae. But strial puncturing in this species (x10) is in fact vague and virtually effaced. The illusion of obvious puncturing is produced by serial widening of the striae to produce a beaded (“moniliform”) appearance. Each wide spot of the stria encloses a flat area with a micropuncture in the middle.

Coprophanaeus punctatus is a scarce species of which we have seen, in addition to the type series and a single female from Espiritu Santo, only one recently collected series from the Reserva Ecologica Charles Darwin in Pernambuco. The only strongly developed male in the series (see Fig. 77-78) resembles that of *C. saphirinus* with the difference that the tooth-like posteromedian pronotal projections point upward rather than being inclined anteriorly.

***Coprophanaeus (Metallophanaeus) pertyi* (Olsoufieff, 1924)**

Fig. 51, 57, 62, 80-84

Phanaeus pertyi Olsoufieff, 1924: 71

Phanaeus thalassinus sensu Felsche, 1901, *nec* Perty, 1830 (syn. by Martínez and Pereira 1967: 66)

Phanaeus alvarengai Pereira and d'Andretta, 1955: 253 (syn. by Martínez and Pereira 1967: 67)

Coprophanaeus pertyi (Olsoufieff) (recomb. by Edmonds 1972: 841)

Type. *P. pertyi* – lectotype male, Zoologische Staatssammlung, Munich (des. Arnaud 2002a: 6); *P. alvarengai* – holotype male, Museo de Zoologia, Universidade de São Paulo, São Paulo.

Diagnosis. *General* – Paraocular areas (genae) nearly flat, strongly and densely punctate, with short carina lateral to eyes. Posteromedian portion of pronotum appearing smoother and shinier than remainder of disk, simply punctate, less strongly and densely so near basal fossae; posterior angle normal, basal fossae small, incorporated into inner ends of distinct sulcus paralleling posterior margin. Salient anteromedian angle of metasternum (seen in profile, Fig. 57) rounded. Striae (x5) weakly impressed, simple; bases of striae 1-4 impressed, not distinctly fossate. Elytral interstriae weakly convex. Ventral surface of protibia lateral to longitudinal carina mostly smooth, usually with single or double row of shallow, confluent punctures paralleling longitudinal carina (Fig. 51, arrow). Pygidium lacking basal



Figure 80-84. *Coprophanaeus pertyi*. 80-81) Male habitus. 82) Aedeagus (dorsal view on left; lateral view on right). 83-84) Female habitus.

groove. Length 14-20 mm. Elytra dull black; pronotum, head, pygidium and venter with strong bluish-green metallic reflections.

Male (Fig. 80-82) – Head with evenly tapering long horn, base of horn abruptly swollen. Pronotum of large male with deep anteromedian concavity at summit marked by a lobate tumosity. Tips of parameres only slightly swollen laterally, lacking distinct flanges.

Female (Fig. 83-84) – Cephalic carina simple, scarcely elevated, at most only weakly trituberculate. Pronotum with deep, oval anteromedian concavity, bearing strongly raised, trituberculate, quadrate process adjacent to anterior margin.

Specimens examined – 48.

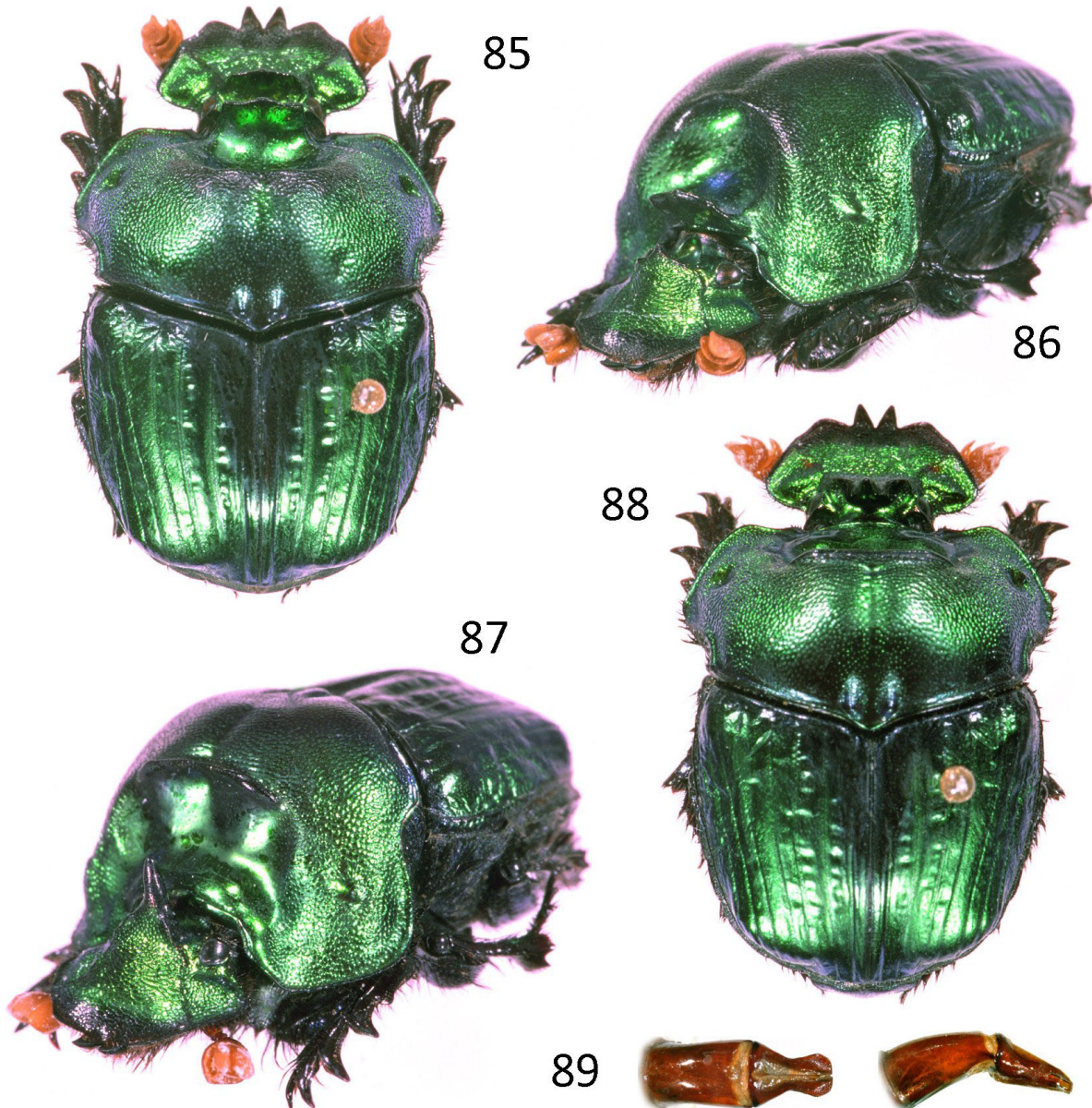


Figure 85-89. *Coprophanaeus pessoai*. 85-86) Female habitus. 87-88) Male habitus. 89) Aedeagus (dorsal view on left; lateral view on right).

Distribution. Caatinga province (Fig. 62).

Collection Records. **BRAZIL:** **Bahia** – Cruz das Almas (Apr); Maracas (Feb); Feira de Santana (Jun). **Ceará** – Maranguape, Tabatinga, 38°43'48"W; 04°00'42"S, 126 (Mar); Maranguape, Cagado, 38°45'05"W 04°01'57"S, 114 m (Apr). Maranguape, Sao Benedito, Santuario da Nossa Senhora de Penha, 38°40'48"W 03°52'29"S, 96 m (Mar); Juazeiro do Norte. **Minas Gerais** – Aguas Vermelhas (Dec). **Paraíba** – Mamanguape (Jul); Soledade (Mar); São José dos Cordeiros [Fazenda Almas], 7°28'S 36°53'W, 650 m (Feb). **Pernambuco** – Brejo Novo (Mar); Garanhuns (Mar). **Piauí** – São Raimundo Nonato [Parque Nacional Serra da Capivara] (Jan). **Rio Grande do Norte** – Canguaretama (Aug); Natal (Jun, Nov).

Comments. *Phanaeus pertyi* was proposed as a new name for the taxon Felsche (1901) erroneously regarded as *Phanaeus thalassinus* Perty (Olsoufieff 1924) (see Comments under *C. thalassinus* below).

Subsequently, Martínez and Pereira (1967) synonymized *Phanaeus alvarengai* Martínez and Pereira (1955) and *P. pertyi*. In accordance with Article 53.3 of the International Code of Zoological Nomenclature (ICZN 1999), *Phanaeus alvarengai* Martínez and Pereira is the senior primary homonym of *Phanaeus alvarengai* Arnaud (1984), currently still placed in the genus *Phanaeus* (Edmonds 1994; Arnaud 2002c). The fact that Martínez and Pereira placed their taxon in the subgenus *Coprophanaeus* of *Phanaeus* does not, in accordance with Article 57.4 of the Code (ICZN 1999), shield Arnaud's name from unavailability, and, therefore, the name *alvarengai sensu* Arnaud must be replaced. We have referred the issue to the species' author, Patrick Arnaud, for rectification.

***Coprophanaeus (Metallophanaeus) pessoai* (Pereira, 1949)**

Fig. 53, 55, 58, 85-89

Phanaeus pessoai Pereira, 1949: 226

Coprophanaeus pessoai (Pereira) (recomb. Edmonds 1972: 841)

Type. Holotype male, Museu de Zoologia, Universidade de São Paulo, São Paulo.

Diagnosis. *General* – Paraocular areas (genae) densely rugose, strongly raised in front of eye (Fig. 61), carina adjacent to eye largely obliterated by strong rugosity. Posteromedian portion of pronotum (Fig. 53) strongly and densely punctate, lacking distinct granules or ridges (sculpturing stronger in females); posterior angle normal, basal fossae small, incorporated into inner ends of distinct sulcus paralleling posterior margin. Salient anterior angle of metasternum acutely angled, sometimes almost conical (Fig. 58). Ventral surface of protibia lateral to longitudinal carina mostly smooth, usually with single or double row of shallow, confluent punctures paralleling longitudinal carina (as in Fig. 51, arrow). Striae (x5) weakly impressed, simple; bases of striae 1-4 impressed, not distinctly fossate. Elytral interstriae flat, transversely wrinkled (Fig. 55). Pygidium with broad, shallow basal groove. Length 18-21 mm. Color bright metallic green, often with golden reflections.

Male (Fig. 87-89) – Head with evenly tapering horn, base of horn abruptly swollen. Pronotum of large male with deep anteromedian concavity at summit bearing straight transverse ridge. Tips of parameres with strongly developed rounded, flat flanges.

Female (Fig. 85-86) – Cephalic carina with prominent conical median tubercle. Pronotum with deep, oval anteromedian concavity, bearing strongly raised, trituberculate, quadrate process adjacent to anterior margin.

Specimens examined – 8.

Distribution. Chaco province (Fig. 62).

Collection Records. ARGENTINA: Salta – Dist°. San Martín (Mar). BOLIVIA: Santa Cruz – Cordillera Prov., Puesto Salas (Nov); Palmar de las Islas, 19°25'S 60°32'W, 270 m (Feb). PARAGUAY: Boquerón – Guachalla [Alto Río Pilcomayo] (Oct); Filadelfia (Colonia Fernheim). Chaco – Fortín Esmeralda.

Comments. The brilliant coloration of this rare denizen of the Chaco is stunning. According to Pereira (1949), references by Pessôa (1935) and Pessôa and Lane (1941) to *C. horus* are actually to this species.

***Coprophanaeus (Metallophanaeus) thalassinus* (Perty, 1830)**

Fig. 52, 62, 90-94

Phanaeus thalassinus Perty, 1830: 40

Coprophanaeus thalassinus (Perty) (recomb. by Blackwelder 1944: 209)

Type. Holotype male, Zoologische Staatssammlung, Munich.

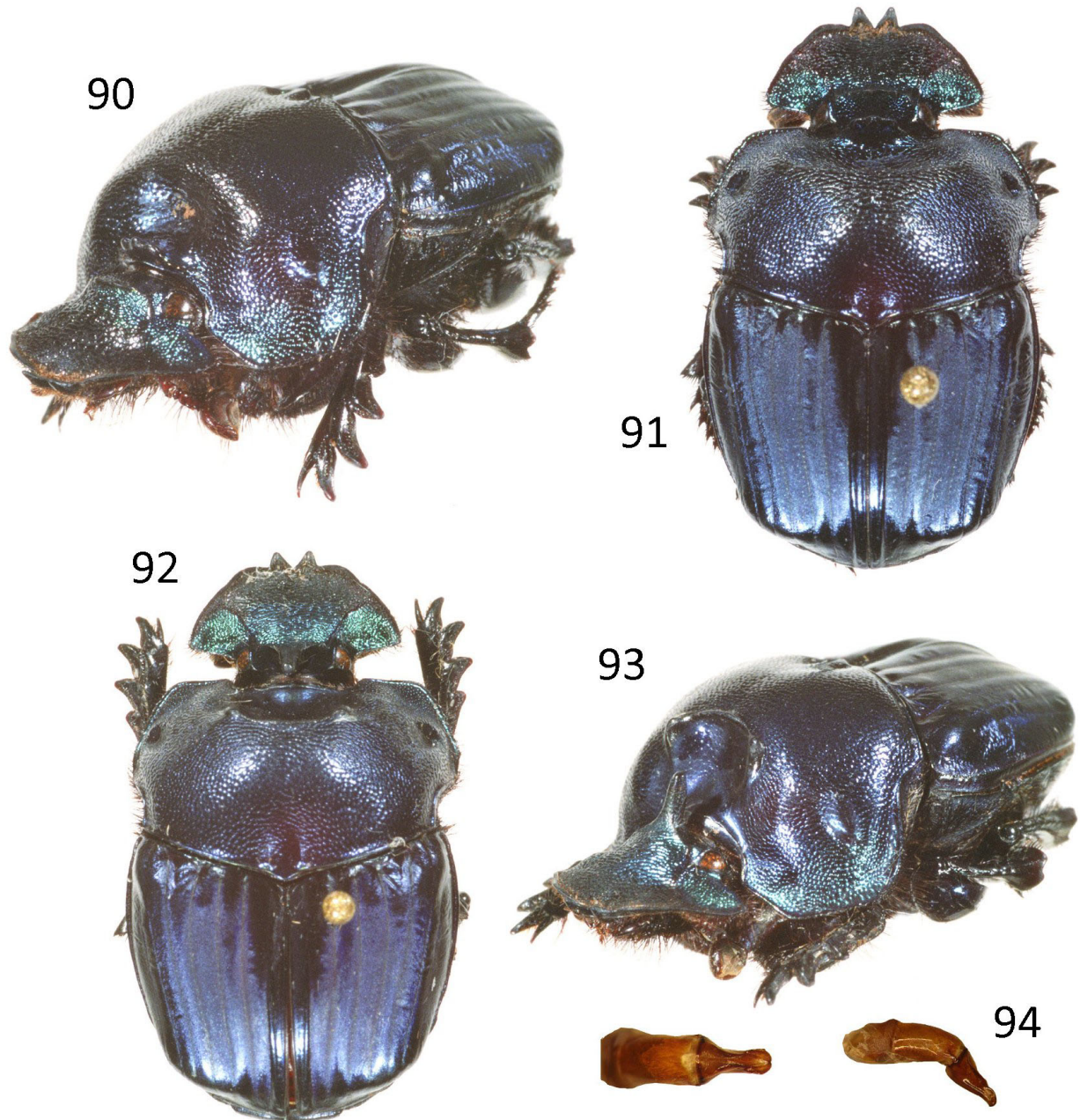


Figure 90-94. *Coprophanaeus thalassinus*. 90-91) Female habitus. 92-93) Male habitus. 94) Aedeagus (dorsal view on left; lateral view on right).

Diagnosis. General – Paraocular areas (genae) densely rugose, at most only weakly raised in front of eye; carina adjacent to eye largely obliterated by strong rugosity. Posteromedian portion of pronotum, at least near fossae, granulate or granulorugose (Fig. 52); posterior angle normal, basal fossae small; basal pronotal sulcus usually obsolete medially, not reaching basal fossae. Salient anteromedian angle of metasternum (seen in profile) quadrate, not noticeably salient. Striae (x5) weakly impressed, simple; bases of striae 1-4 impressed, not distinctly fossate. Elytral interstriae weakly convex. Ventral surface of protibia lateral to longitudinal carina mostly smooth, usually with single or double row of shallow, confluent punctures paralleling longitudinal carina (as in Fig. 51, arrow). Pygidium with broad, shallow basal groove. Length 13-19 mm. Color dark blue or green.

Male – Head with evenly tapering horn, whose base is abruptly swollen. Pronotum of large male with deep anteromedian concavity at summit bearing transverse ridge. Tips of parameres bear rounded flanges with slightly upturned margins.

Female – Cephalic carina of female with prominent conical median tubercle. Pronotum with deep, oval anteromedian concavity, bearing strongly raised, trituberculate, quadrate process adjacent to anterior margin.

Specimens examined – 7.

Distribution. Largely unknown (Fig. 62).

Collection Records. BRAZIL: Bahia – 160 km W Barrieras, 11°51'S 46°10'W, 830 m (Jan).

Comments. This is one of the two or three rarest species of the genus. We have seen only seven specimens and accept the distinct possibility that the above diagnosis may prove to be too restrictive. Martínez and Pereira (1967) provided a detailed description of the species and commentary on the prevailing confusion attending the name “*thalassinus*”. According to their analysis, Olsoufieff (1924) concluded that Felsche (1901) misidentified Perty’s species in his redescription of “*thalassinus*”, which he inadvertently based on a then undescribed species. To rectify the error, Olsoufieff redescribed Felsche’s “*thalassinus*” as *Phanaeus pertyi*, and then proceeded to invert characters of the two in the couplet of his key separating *C. thalassinus* and *C. pertyi*!

Subgenus *Coprophanaeus s. str.* Olsoufieff, 1924

Coprophanaeus Olsoufieff, 1924: 22.

Type Species: *Scarabaeus jasius* Olivier, original designation.

Diagnosis. *General* – Lower portion of eye large, width greater than twice (usually about three times or more) that of oculo-gular space. Paraocular areas (genae) not carinate lateral to eyes. Occipital areas of parietals more-or-less flattened, lacking angulate prominence (Fig. 12). Circumnotal ridge entire or broken behind eyes (Fig. 7-8). Pronotal sculpturing variable, usually granulorugose anterolaterally, punctate to some degree posteromedially; basal fossae variable. Pronotum lacking posterolateral ridge. Striae fine, simple or carinate. Posterior edge of hind wing strongly notched basally (Fig. 9). Posterior surface of each protibial tooth with single basal row of long setae (Fig. 6). Abdominal sterna usually smooth medially. Sexual dimorphism marked.

Male – Head bearing lamellate process of some sort or trituberculate carina, never a simple curved horn. Pronotum variable, flattened or transversely concave anteromedially, with strong median prominence. Parameres variable.

Female – Head with trituberculate carina, sometimes strongly raised. Protarsi absent. Pronotum variable, usually with transverse process near anterior margin followed by oval concavity.

Distribution. Neotropical region.

Comments. This subgenus embraces 29 species distributed in four species groups separated in the key below. Edmonds (1972) divided the subgenus into two species groups (*jasius* and *dardanus*); only the *jasius* group is maintained here as defined then. Our organization of this subgenus is different from that presented by Arnaud (2002c), but many of the subgroups of closely related species (Arnaud’s complexes) are the same. Keys to species appear under the treatments of each species group.

Key to species groups of *Coprophanaeus s. str.*

1. Circumnotal ridge continuous, not interrupted behind eyes (Fig. 7). Posterior margin of paraocular area straight, ending at middle of eye. Prosternal ridge with acute tubercle at anterior end (Fig.

- 112). Parameres lacking distinct apical teeth, at most with slightly swollen tips (e.g. Fig. 123). South America **jasius species group**
- Circumnotal ridge (Fig. 8) effaced behind each eye. Posterior margin of paraocular area curved, ending at posterior angle of eye. Prosternal ridge simple, not tuberculate anteriorly. Parameres with apical teeth (may be reduced) (e.g. Fig. 169-170, 217). Distribution variable **2**
- 2(1). Apical processes of parameres (Fig. 169-170) projecting laterally, not visible from side, tip of paramere not appearing at all hooked in profile (although hook-like processes often visible from above); parameres elongate, usually lacking prominent basal angle. Male and female with trituberculate cephalic carina. Mesoamerican (Fig. 172) **pluto species group**
- Apical processes of parameres (Fig. 217) elevated dorsally, tip (viewed from side) appearing acutely hooked, usually projecting above dorsal surface; parameres (viewed from side) strongly triangular, base extending well below lower margin of phallobase as heel-like protuberance. Male cephalic process variable; female bearing trituberculate cephalic carina. South America (one Mesoamerican species) **3**
- 3(2). Cephalic horn of large male more-or-less laminate, strongly raised, with apical tubercles or processes, never a trituberculate carina or raised ridge (e.g. Fig. 213, 218, 220, 227). Male head horn (and female carina) set close to eyes so that length of frons along midline usually no more than length of clypeus, often only one-half or less (cf. Fig. 171). Elytral interstriae usually flat or weakly convex, rarely narrowly raised midlongitudinally (*C. ignecinctus*, Fig. 232). South America, one species Mesoamerican (Fig. 237-238) **dardanus species group**
- Male and female with trituberculate cephalic carina, position relative to eyes variable (Fig. 287, 289). Elytral interstriae narrowly raised midlongitudinally. Eastern slopes of Andes from Bolivia to Colombia **ohausi species group**

The *jasius* species group

The *jasius* group brings together a closely knit assemblage of seven species sharing three salient, unique characters: a circumnotal ridge that is not interrupted behind eyes (Fig. 7), parameres that lack conspicuous apical projections (e.g. Fig. 118), and an acute tubercle on the anterior end of the prosternal ridge (Fig. 112). The group remains the same as that defined by Edmonds (1972) and adopted by Arnaud (2002c). In addition, the form of the male head horn (an elongate, trapezoidal base with a medial finger-like projection flanked by small denticles (Fig. 102-104) is approached elsewhere in the genus only in *C. corythus* (Harold). Many of the species included in this group, especially smaller individuals, are frequently misidentified in collections as “*jasius*”; indeed, Martínez (1959) synonymized the here valid names *C. abas*, *C. acrisius* and *C. cyanescens* with *C. jasius*. Harold’s (1869) comparison of *C. jasius* and *C. acrisius* appears to reverse the descriptions of the two species. The group is fundamentally South American, although one invasive species (*C. gamezi*) has entered Mesoamerican northern Colombia via the Lake Maracaibo depression of northwestern Venezuela. Three species (*C. jasius*, *C. abas* and *C. cerberus*) are preferentially forest-dwelling species; the remainder (*C. gamezi*, *C. cyanescens*, *C. spitzi* and *C. acrisius*) prefer more open habitats. All species have been collected from carrion and feces (especially human, very rarely herbivore).

Diagnosis. *General* – Anterior portion of circumnotal ridge entire, not broken behind eyes (Fig. 7). Posterior edge of paraocular area straight, ending at middle of eye. Front and sides of pronotum generally granularogose; disk usually at least partially punctate; basal fossae usually present. Prosternal ridge with sharp, acute tubercle at anterior end (Fig. 112). Elytral interstriae weakly convex; striae very fine. Usually dark, sombre species to unaided eye; metallic coloration inconspicuous and most obvious under magnification (x10) on anterior portion of pronotum and pygidium. Medium-sized species, length usually 20-30 mm.

Male – Apices of parameres swollen laterally, lacking teeth or other projections. Head horn consisting of trapezoidal base with apical finger-like process flanked on each side by acute tubercle (Fig. 102-104).

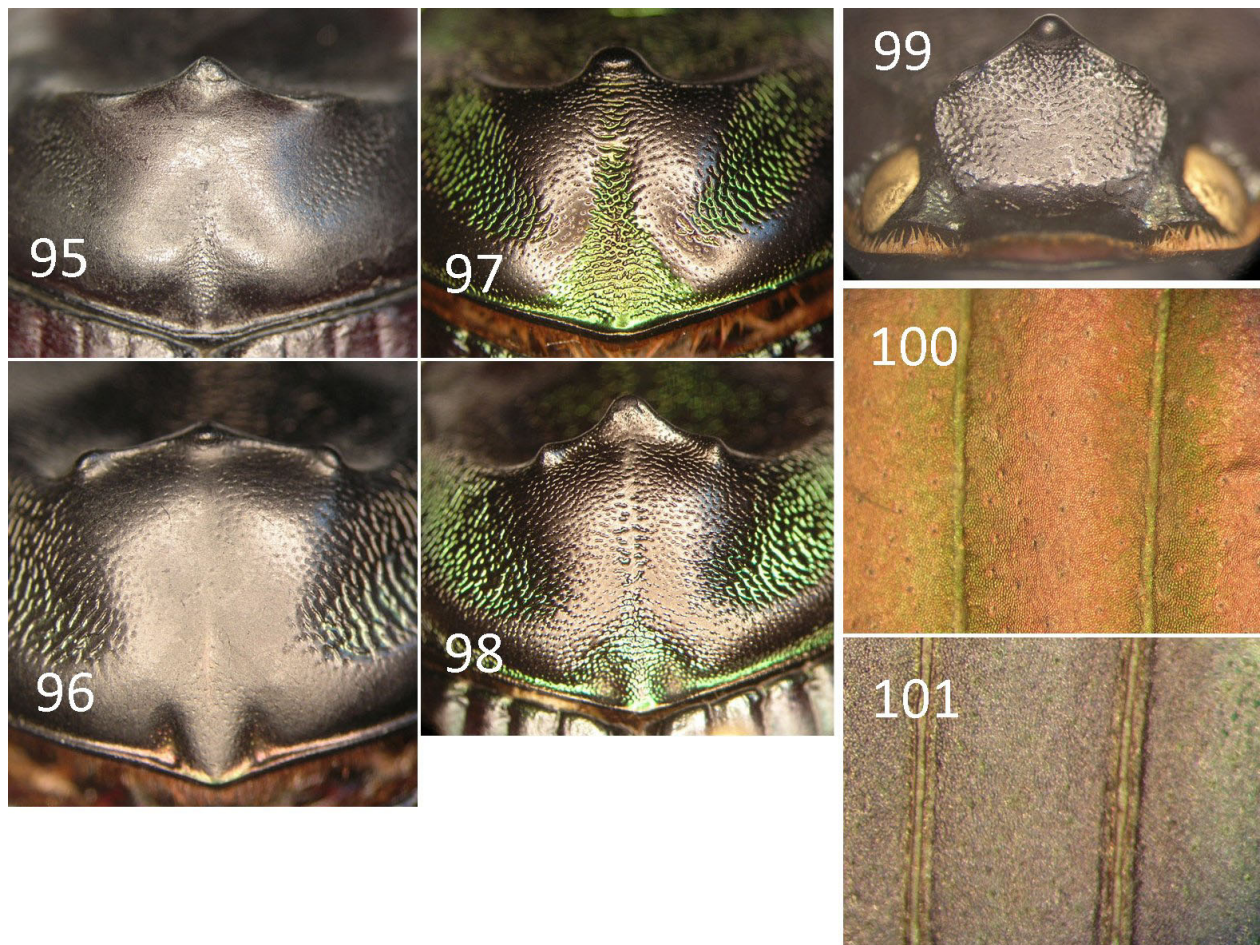


Figure 95-101. Characters of the *Coprophanaeus* (*s. str.*) *jasius* species group. **95)** Dorsal view of pronotum of male *C. cerberus*. **96)** Same, *C. jasius*. **97)** Same, *C. spitzi*. **98)** Same, *C. cyanescens*. **99)** Dorsal view of cephalic process of female *C. gamezi*. **100)** Detail of elytral surface of *C. acrisius*. **101)** Same, *C. spitzi*.

Pronotum (Fig. 95-98) with anteromedian transverse ridge, carina or other process with median tubercle or larger process often flanked by smaller tubercle on each side; surface concave below this process (in smallest individuals head horn reduced to conical tubercle and transverse pronotal process reduced to simple transverse carina near anterior margin).

Female – Head with transverse trituberculate carina usually bowed anteriorly to some degree. Pronotum (except *C. cerberus*) with oval anteromedian concavity bounded anteriorly by raised transverse crest of variable size and shape (Fig. 105-108).

Distribution. Neotropical region and Mesoamerican provinces of Venezuela (Fig. 113).

Key to species of the *jasius* group

1. Clypeal margin rounded lateral to median teeth (e.g. Fig. 114, 117), not angulate or explanate. Dorsum at least partially bright metallic green or yellowish green. Pronotum with posteromedian, more-or-less triangular, metallic green depression (Fig. 97) filled with dense, coarse granulation (x15) **2**
- Clypeal margin explanate/angulate lateral to median teeth (e.g. Fig. 124, 127). Dorsum usually mostly dark, sombre; metallic color subdued, never appearing on pronotal disk. Pronotal sculpturing variable, but not as described above **3**

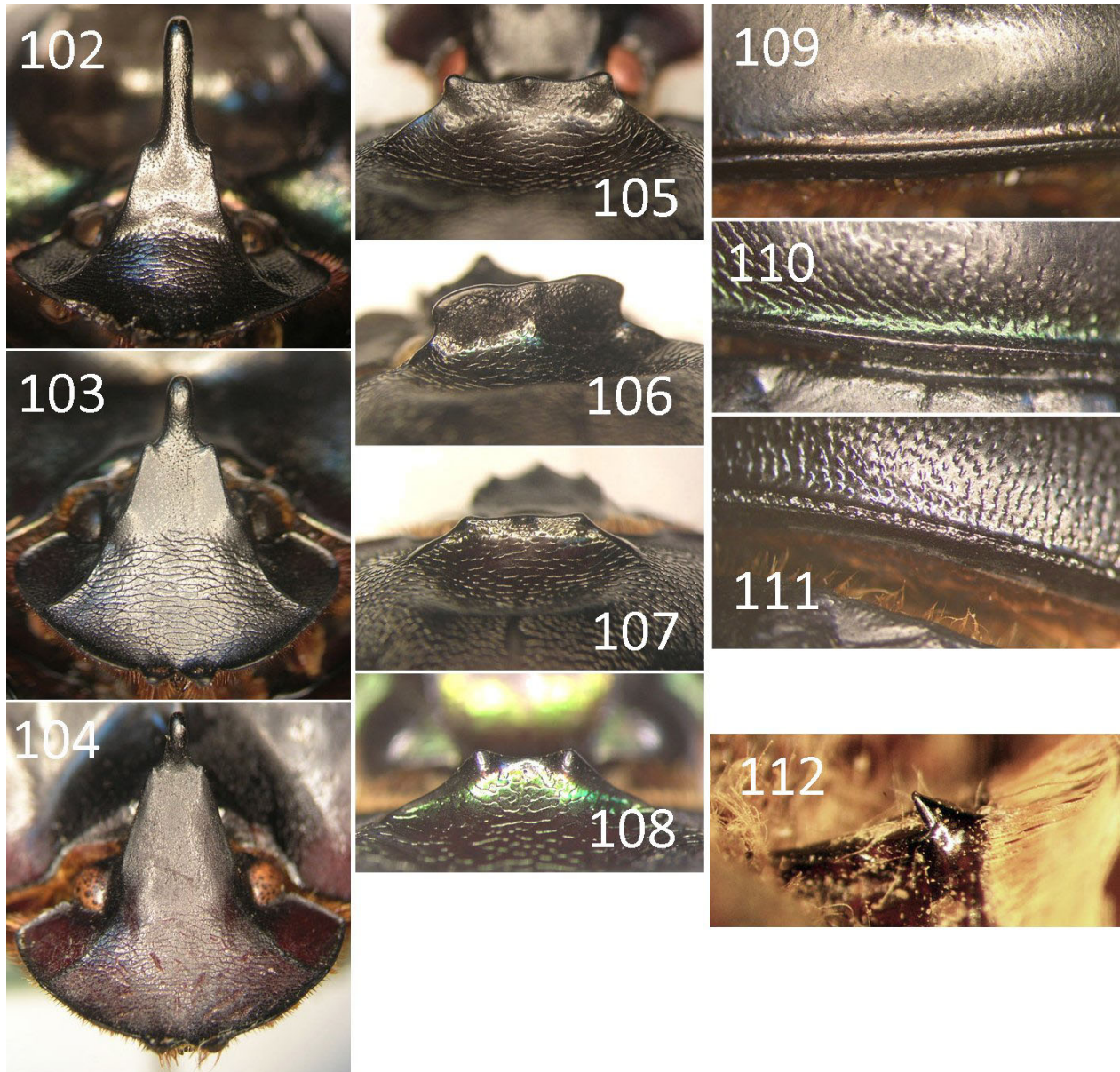


Figure 102-112. Characters of the *Coprophanaeus* (*s. str.*) *jasius* species group. **102)** Anterior view of head of male *C. abas*. **103)** Same, *C. jasius*. **104)** Same, *C. cerberus*. **105)** Pronotal crest of female *C. abas*. **106)** Same, *C. gamezi*. **107)** Same, *C. jasius*. **108)** Same, *C. spitzii*. **109)** Section of posterior pronotal margin of *C. jasius*. **110)** Same, *C. abas*. **111)** Same, *C. gamezi*. **112)** Prosternal spine of *C. spitzii*.

- 2(1). Pronotal carina of large male with distinct median tubercle, lacking lateral tubercles (Fig. 97). Pronotal ridge of female trapezoidal, summit bituberculate (Fig. 108). Swollen black areas flanking median rugose depression of pronotum smooth, usually only with obsolete puncturing (Fig. 97). Basal pronotal fossae obsolete (Fig. 97). Elytral striae strongly carinulate (Fig. 101). Parameres short, length barely approaching one-half that of phallobase (Fig. 118). Body length usually less than 25 mm ***Coprophanaeus* (*C.*) *spitzii* (Pessôa)**
- Pronotal carina of large male distinctly trituberculate, middle tubercle larger than lateral ones (as in Fig. 98). Pronotal ridge of female trapezoidal, summit trituberculate (as in Fig. 107). Swollen black areas flanking rugose median depression of pronotum densely punctate or entirely

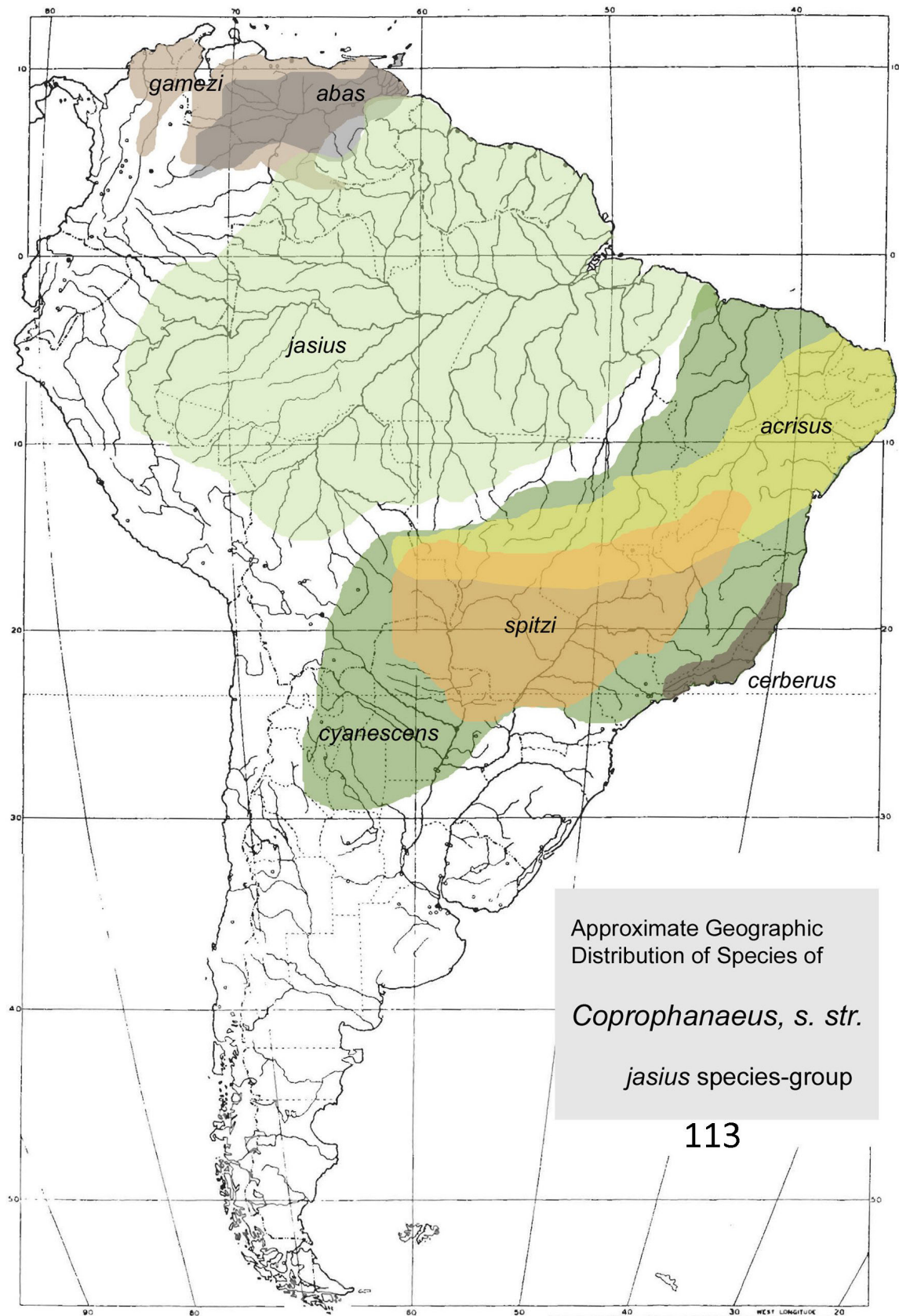


Figure 113. Approximate geographic distribution of *Coprophanaeus* (s. str.) species in the *jasius* species group.

- rugose. Basal pronotal fossae distinct. Elytral striae weakly, if at all, carinate (Fig. 100). Parameres longer, length clearly greater than one-half that of phallobase (Fig. 123). Body length usually greater than 25 mm ***Coprophanaeus (C.) acrisius* (MacLeay)**
- 3(1). Pronotal carina of large male (Fig. 95) with central tubercle only, lacking lateral tubercles. Pronotal process of female (Fig. 125) a simple transverse carina located high on disk and flanked by shallow concavities descending toward eyes; surface sharply declivitous in front of carina. Pronotum with finely rugose, elongate depression extending from middle of posterior margin to middle of disk (Fig. 95); surface slightly swollen and smooth to finely punctate posterolaterally and along sides of medial depression. Parameres short, length barely approaching one-half that of phallobase (Fig. 128). Completely black or brown, no hint of metallic color anywhere on body surface. Atlantic coast forests of Brazil ***Coprophanaeus (C.) cerberus* (Harold)**
- Pronotal carina of large male (Fig. 96, 98) clearly trituberculate (middle tubercle may be very large compared to lateral ones). Pronotal process of large female trapezoidal or quadrate (Fig. 105-106), summit usually distinctly trituberculate, set very near anterior pronotal margin and followed by oval concavity. Pronotal sculpturing variable. Color dark, often appearing black to unaided eye, but magnification (x5) under bright light always reveals metallic color (most commonly on pronotum and pygidium). Parameres longer, length clearly exceeding one-half that of phallobase **4**
- 4(3). Median area of posterior portion of pronotum (Fig. 96) more-or-less smooth, any obvious sculpturing effaced; smooth area often extends anteriorly to middle of disk and laterally some distance along posterior pronotal margin. Basal pronotal fossae with sparse punctures or microgranules (x25); adjacent area sparsely, weakly punctate **5**
- Posteromedian area of pronotum (Fig. 98) punctate to punctatorugose; sculpturing usually weaker as it radiates anteriorly from area of basal fossae. Basal pronotal fossae and surrounding area densely, finely granulate (x15) **6**
- 5(4). Male pronotal carina (Fig. 96) more-or-less straight, central tubercle only slightly larger than laterals. Base of male cephalic horn coarsely punctate (Fig. 103); maximum horn height not reaching level of pronotal carina (Fig. 131); median tubercle (viewed laterally) slightly inclined anteriorly (relative to base of horn). Female pronotal process (Fig. 107) trapezoidal, summit weakly trituberculate, width at summit less than interocular distance. Anteromedian pronotal concavity of female shallow, posterior (upper) margin simple. Sulcus in front of basal pronotal carina smooth (Fig. 109) ***Coprophanaeus (C.) jasius* (Olivier)**
- Middle tubercle of large-male pronotal process conspicuously larger than lateral ones, producing an acute projection or large, tab-like process (Fig. 137-138). Anterior surface of male cephalic horn minutely and rather sparsely punctured; median tooth elongate, reaching level of pronotal process (Fig. 137), more-or-less straight except slight posterior bend at apex. Pronotal process of large female (Fig. 105) strongly elevated, quadrate, summit strongly trituberculate, width at summit usually slightly greater than interocular distance. Anteromedian pronotal concavity of female deep, posterior (upper) margin weakly bitumose. Sulcus in front of basal pronotal carina (Fig. 110) sculptured ***Coprophanaeus (C.) abas* (MacLeay)**
- 6(4). Pronotal process of large female strongly raised, quadrate, at most only weakly tridentate (Fig. 106). Middle tubercle of female cephalic carina strongly elevated, imparting almost triangular shape to carina (Fig. 99). Width of large-male pronotal carina equal to or greater than distance separating outer margins of eyes. Basal carinate margin of pronotum densely punctate to crenulate (Fig. 111) ***Coprophanaeus (C.) gamezi* Arnaud**
- Pronotal process of large female trapezoidal, summit weakly tridentate (as in Fig. 107). Middle tubercle of female cephalic carina only slightly larger than lateral tubercles, carina only moderately raised. Width of large-male pronotal carina less than distance separating outer margins of eyes. Basal carinate margin of pronotum entire, not broken up by strong puncturing ***Coprophanaeus (C.) cyanescens* (Olsoufieff)**

***Coprophanaeus (C.) spitzi* (Pessôa, 1934)**

Fig. 7, 12, 97, 101, 108, 112-118

Phanaeus spitzi Pessôa, 1934: 303*Coprophanaeus spitzi* (Pessôa) (recomb. by Edmonds 1972: 843)**Type.** Holotype male, Museu de Zoologia, Universidade de São Paulo, São Paulo.

Diagnosis. *General* – Dorsum except for irregular black areas, head and pronotum bright metallic green or yellowish green, elytra dark green to almost black. Clypeal margin rounded, not noticeably angulate or explanate lateral to median teeth (Fig. 114, 117). Pronotum with elongate triangular depression densely packed with coarse granules extending from posterior margin to middle of disk (Fig. 97); area adjacent to depression and extending along posterior pronotal margin somewhat swollen, smooth, punctured but sometimes only weakly so. Basal pronotal fossae effaced. Elytral striae distinctly carinulate (Fig. 101), even in specimens with dark elytra. Length 18-24 mm.

Male (Fig. 97, 116-118) – Base of head horn weakly concave. Anteromedian pronotal concavity shallow, bordered posteriorly by weak transverse carina bearing rounded central tubercle; ends of transverse carina curving downward, lacking distinct tubercle.

Female (Fig. 114-115) – Cephalic carina straight, median tubercle larger than laterals. Pronotal ridge not strongly elevated, narrowly bidentate medially.

Specimens examined – 99.

Distribution. Chacoan subregion – southern Cerrado and Chaco provinces (Fig. 113).

Collection Records. **BOLIVIA:** **Beni** – Magdalena (Dec). **Santa Cruz** – Parque Nacional Noel Kempff Mercado [Los Fierros], 14°33.5'S 60°55.9'W. **BRAZIL:** **Bahia** – 150 km W Barrieras (Jan); Encruzilhada (Dec). **Distrito Federal** – Estação Forestal Cabeça do Veado, 1100 m (Oct); Brasília (Nov-Dec). **Mato Grosso** – Uirapurú [Chapada dos Parecis] (Dec). **Mato Grosso do Sul** – Selvíria (Jan, Mar, Oct). **Minas Gerais** – Cordisburgo [Fazenda Pontinha] (Dec); Turvolândia (Feb). **Paraná** – Vila Velha. **São Paulo** – Mogi Guaçu [Fazenda Campininas] (Jan); Jabaquara [Capital] (Dec); Novo Horizonte (Nov); Batatais (Mar, Dec); São Paulo [Ipiranga] (Mar); São José dos Campos (Nov). **Goiás** – Rio Verde; Vianópolis (Dec). **PARAGUAY:** **Amambay** – Cerro Corá (Feb, Dec). **Caaguazú** – Caaguazú. **Concepción** – Cororó (Nov); Concepción [Santa Morana], 23°24'S 57°26'W (Oct); Campo Zanja Morotí, 22°53'S 57°23'W (Nov). **Presidente Hayes** – Lolita (Yaragui) (Jan).

Comments. This species is the southern representative of the species pair it forms with *C. acrisius*.

***Coprophanaeus (C.) acrisius* (MacLeay, 1819)**

Fig. 100, 113, 119-123

Phanaeus jasius acrisius MacLeay, 1819: 127*Phanaeus camargoi* Pessôa, 1934: 298 (syn. by Arnaud 2002c: 30)*Coprophanaeus acrisius* (MacLeay) (recomb. by Blackwelder 1944: 209 [as synonym of *C. jasius*])

Type. *P. acrisius* – neotype male (des. by Arnaud, 2002b: 3), The Natural History Museum, London (examined); *P. camargoi* – holotype male, Museu de Zoologia, Universidade de São Paulo, São Paulo.

Diagnosis. *General* – Posterior portion of head and pronotum bright metallic green or yellowish green; elytral interstriae dull bronze, striae and margins of elytra bright green. Clypeal margin rounded (Fig. 119, 122), not noticeably angulate or explanate lateral to median teeth. Pronotum (as in Fig. 97) with elongate triangular depression densely packed with coarse granules, extending from posterior margin to middle of disk; area adjacent to depression and extending along posterior pronotal margin somewhat

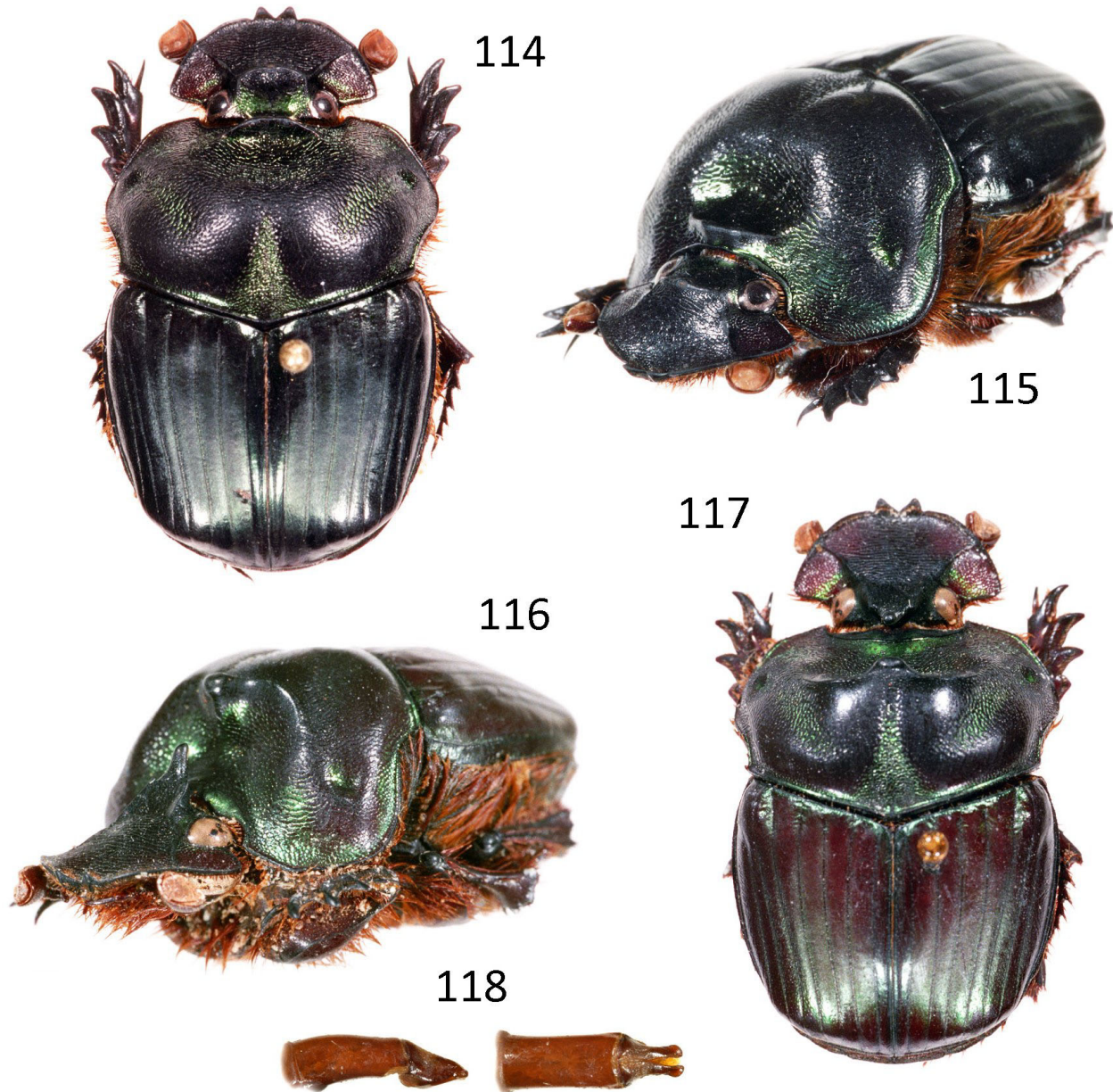


Figure 114-118. *Coprophanaeus spitzi*. 114-115) Female habitus. 116-117) Male habitus. 118) Aedeagus (lateral view on left; dorsal view on right).

swollen, densely and rather coarsely punctatorugose to granulorugose. Basal pronotal fossae distinct. Elytral striae at most only very weakly carinulate (Fig. 100). Length 22-30 mm.

Male (Fig. 121-123) – Base of head horn flat. Anteromedian pronotal concavity shallow, bordered posteriorly by distinctly tridentate transverse carina.

Female (Fig. 119-120) – Cephalic carina straight, median tubercle larger than laterals. Pronotal ridge elevated, trapezoidal, tridentate.

Specimens examined – 35.

Distribution. Chacoan subregion – northern Cerrado and Caatinga provinces (Fig. 113).

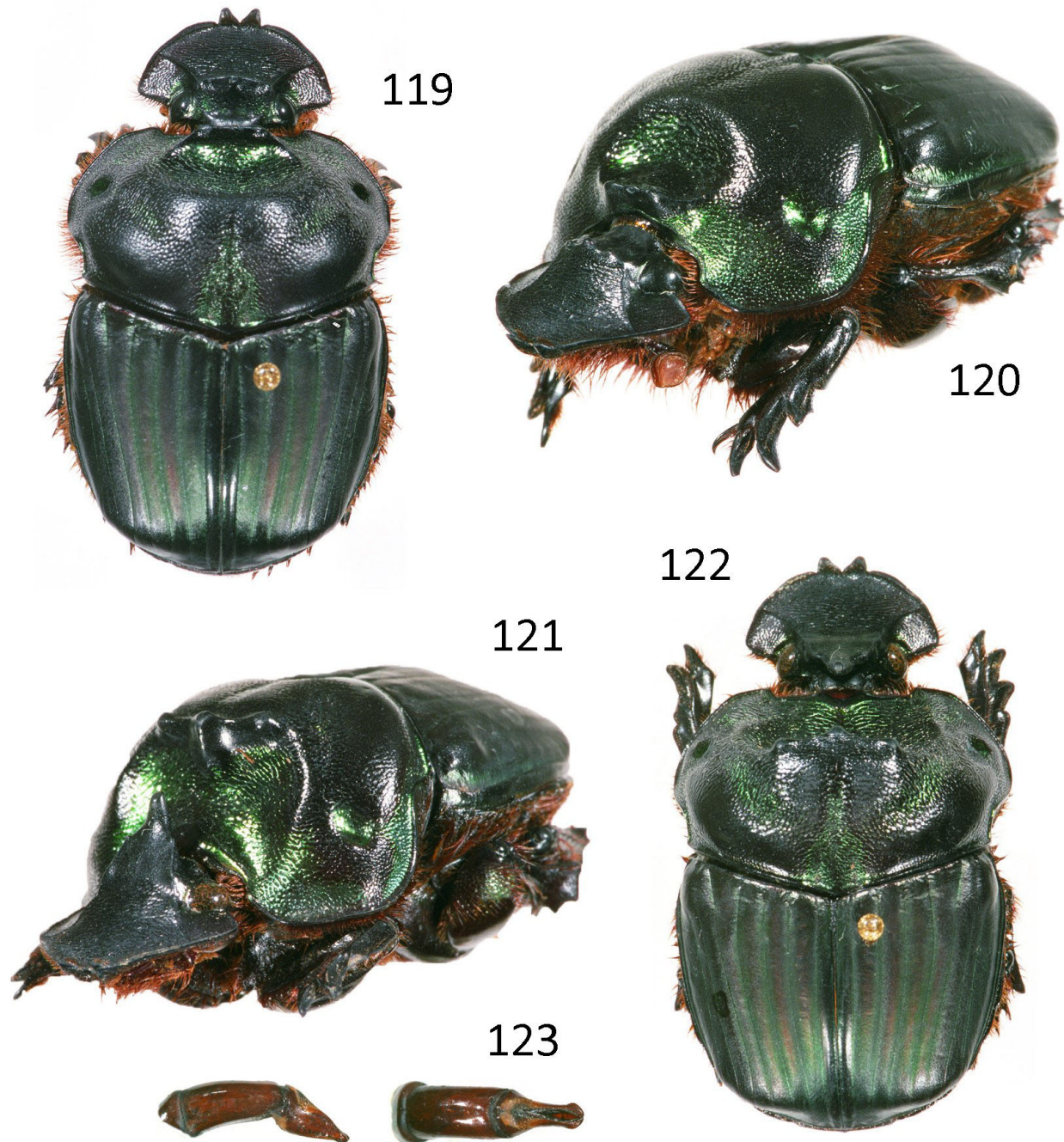


Figure 119-123. *Coprophanaeus acrisius*. 119-120) Female habitus. 121-122) Male habitus. 123) Aedeagus (lateral view on left; dorsal view on right).

Collection Records. **BOLIVIA:** Beni – Magdalena, 180 m (Dec). Santa Cruz – Parque Nacional Noel Kempff Mercado [Los Fierros], 14°33'28"S 60°55'51"W (Jan-Feb); Parque Nacional Noel Kempff Mercado [Huanchaca], 13°54'12.5"S 60°48'57.1"W (Oct). **BRASIL:** Bahia – Cruz das Almas (Apr, Jun). Maranhão – Santa Quitéria de Maranhão, Fazenda Rodiador, 42°40'46"W 03°24'50"S, 47 m (Feb, May). Mato Grosso – 14 km S Posto do Gil, 14°37'55"S 56°16'23"W, 240 m (Jan); 25 km N Posto do Gil, 14°22'29"S 56°07'28"W, 500 m (Jan); Fazenda São João, 14°23'38"S 56°08'50"W, 520 m (Jan); Serra do Tombador, 14°36'47"S 56°15'12"W, 450 m (Jan); Alto Rio Arinos, Diamantino (Dec). Paraíba – Joãozeirinho (Jun). Pernambuco – Recife [campus Universidade Federal de Recife]; Tejucupapo (Apr).

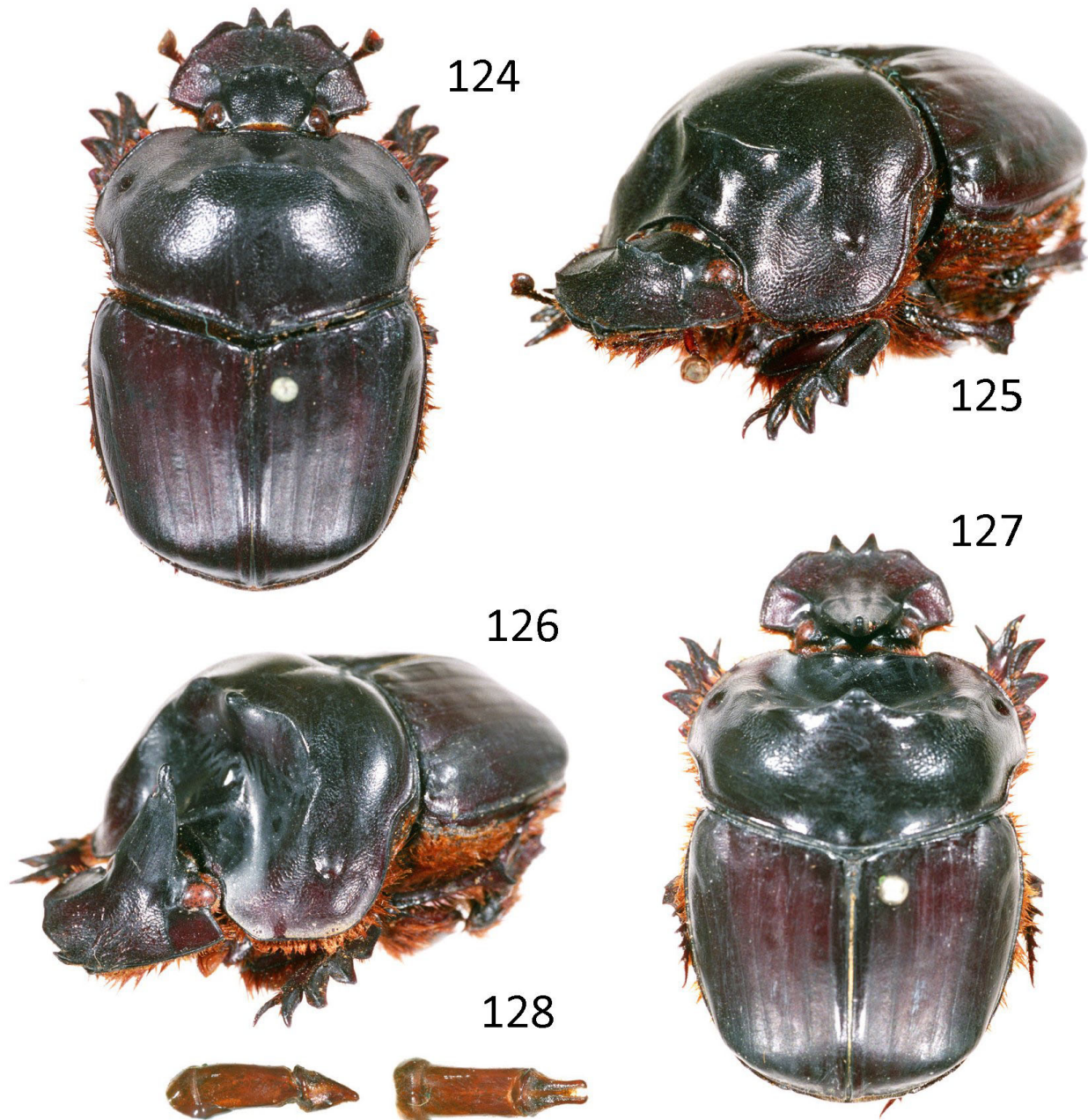


Figure 124-128. *Coprophanaeus cerberus*. 124-125) Female habitus. 126-127) Male habitus. 128) Aedeagus (lateral view on left; dorsal view on right).

Comments. *Coprophanaeus acrisius* is the northern partner of the *C. spitzi*–*C. acrisius* species pair. MacLeay proposed *C. acrisius* as variety of *C. jasius*, and we cite its original name above, in accordance with ICZN Article 45.6.4 (ICZN 1999), as *Phanaeus jasius acrisius* MacLeay. Fernando Vaz-de-Mello (pers. comm.) has also observed specimens from the coast of Maranhão.

***Coprophanaeus* (*C.*) *cerberus* (Harold, 1869)**

Fig. 9, 95, 104, 113, 124-128

Phanaeus cerberus Harold, 1869: 65

Coprophanaeus cerberus (Harold) (recomb. by Blackwelder 1944: 209)

Type. Lectotype male (des. by Arnaud, 1982:115), Muséum National d'Histoire Naturelle, Paris (examined by photo).

Diagnosis. *General* – Dorsum black or brown, lacking metallic coloration. Clypeal margin noticeably angulate or explanate lateral to median teeth (Fig. 124, 127). Pronotum weakly granulose anterolaterally, disk smooth except for elongate, anteriorly narrowed depression filled with coalesced coarse granules often mixed with punctures extending from posterior margin toward middle of disk (Fig. 95). Basal pronotal fossae effaced or only weakly indicated. Length 19-25 mm.

Male (Fig. 95, 104, 126-128) – Middle process of head horn short, length about one-fourth that of horn base. Anteromedian pronotal concavity shallow, bordered posteriorly by weak transverse carina bearing rounded central tubercle; ends of transverse carina thickened, lacking distinct tubercle.

Female (Fig. 124-125) – Cephalic carina straight, trituberculate, tubercles equal-sized and closely set, distance between lateral tubercles about one-half of interocular distance. Pronotum lacking anteromedian concavity, with simple transverse carina at upper edge of smooth, declivitous area reaching anterior margin; declivity bounded on each side by shallow depression extending toward eye.

Specimens examined – 66.

Distribution. Brazilian Atlantic Coast Forest province of Paranaian subregion (Fig. 113).

Collection Records. **BRAZIL: Espiritu Santo** – Parque Estadual Pedra Azul, 1500 m (Feb-Mar). **Minas Gerais** – Poco de Caldas (Jan, Dec); Poços do Coicos (Dec). **Rio de Janeiro** – 17 km E Nova Friburgo, 22°23'04"S 42°33'30"W, 750 m (Jan); Mury, 8 km E . Nova Friburgo, 22°21'49"S 42°33'07"W, 1150 m (Jan); Itatiaia, 700 m (Feb, Nov); Tijuca Forest (Jan). **São Paulo** – Catareira (Mar); Piauiti; 50 km SE Mogi das Cruzes, Estação Biológica Boraceia (Serra do Mar), 800-900 m (Oct, Dec); Bocaina (Apr).

Comments. Olsoufieff's (1924) erroneously synonymized *P. perseus* Harold with *C. cerberus* (see comments under *C. corythus*).

The coarse sculpturing of the posteromedian groove of the pronotum links this species with *C. spitzii* and *C. acrisius* (cf. Fig. 95 and 97). The form of the female pronotum is unique to the genus and more reminiscent of females of *Phanaeus mexicanus* group than other *Coprophanaeus*. Sculpturing of head and pronotum is weakest of species in the *jasius* group.

***Coprophanaeus (C.) jasius* (Olivier, 1789)**

Fig. 96, 103, 107, 109, 113, 129-133

Scarabaeus jasius Olivier, 1789: 109

Phanaeus satyrus Castelnau, 1840: 80 (syn. by Nevinson 1891: 1 as *P. acrisius*)

Coprophanaeus jasius (Olivier) (recomb. by Blackwelder 1944: 209)

Type. *S. jasius* – neotype male (des. by Arnaud 2002a: 7), Muséum National d'Histoire Naturelle, Paris (examined by photo); *P. satyrus* – unknown to us.

Diagnosis. *General* – Metallic coloration green to yellowish green (seldom with red reflections) confined to posterior areas of head and pronotal sides and margins. Clypeal margin (Fig. 129, 132) clearly explanate/angulate lateral to median teeth. Posteromedian portion of pronotum (Fig. 96) smooth, bearing sparse, effaced puncturing (weakest in large males). Sulcus paralleling carinate posterior margin of pronotum smooth (Fig. 109), lacking conspicuous puncturing or asperities (x25); carina entire. Posterior pronotal fossae with sparse puncturing and/or microgranules; area surrounding fossae virtually smooth. Length 18-27 mm.

Male (Fig. 96, 103, 131-133) – Tip of head horn never reaching level of prothoracic carina; anterior surface of base usually coarsely punctate; central process (viewed laterally) inclined slightly anteriorly from base, its length less than one-half that of base. Pronotal carina (Fig. 96) weakly, broadly angulate

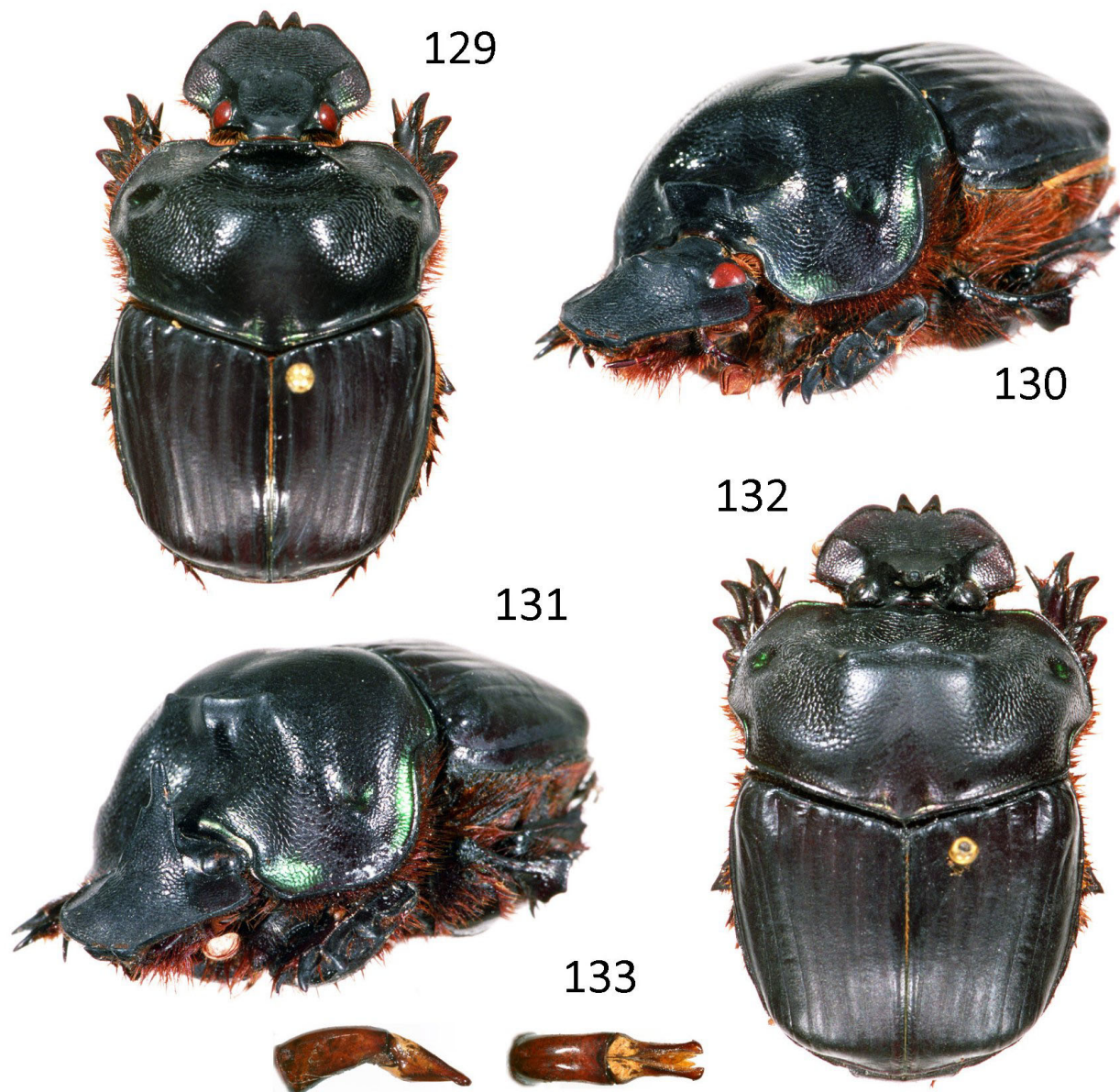


Figure 129-133. *Coprophanaeus jasius*. 129-130) Female habitus. 131-132) Male habitus. 133) Aedeagus (lateral view on left; dorsal view on right).

medially, trituberculate, medial tooth only slightly larger than laterals. Parameres long, length at least three-fourths that of phallobase.

Female (Fig. 107, 129-130) – Cephalic carina bowed or angulate medially, median tooth larger than laterals. Vertex coarsely, densely punctured. Pronotal ridge trapezoidal, summit weakly trituberculate, width at summit slightly less than interocular width. Anteromedian concavity shallow, posterior (upper) margin simple, not bitumose.

Specimens examined – 274.

Distribution. Amazonian subregion (Fig. 113).

Collection Records. **BRAZIL: Amazonas** – 26 km N Manaus [Reserva Forestal Ducke] (Oct-Dec); 60 km N. Manaus, Fazenda Esteio and Fazenda Dimona (Jan, Jun-Jul); Municipio Itacoatiara, Fazenda Aruana [AM Hwy 10, km 215] (Nov); Manacapuru (Mar). **Pará** – Belém [Agua Preta] (Jan-Feb); upper Rocana River.

Rondônia – 9 km NE Cacaulândia (Feb). **FRENCH GUIANA:** 7 km N Saul, 3 km NW Les Eaux Claires, Mt. La Fumée, 490 m, 3°39'46"N 53°13'19"W (Jun); Saül, Mt. Galbao, 3°37'18"N 53°16'42"W 740 m (Jun); Nouragues Field Station, 4°05'N 52°40'W. **GUYANA:** **Cuyuni-Mazaruni** – Bartica District (May). **Potaro-Siparuni** – Iwokrama Forest Reserve, 4°40'19"N 58°41'04"W, 100-200 m (May-June). **SURINAME:** **Sipaliwini** – Central Suriname Nature Reserve, environs of Voltzberg research station, 4°40.90'N 56°11.13'W, 100 m (Mar); Central Suriname Nature Reserve, environs of Lolopasi field station, 4°42.91'N 56°12.83'W, 80 m (Mar); Central Suriname Nature Reserve, environs of Conservation International field station approx. 50 m (Mar); Oelemarie, ~ 3°6'0"N 54°32'0"W (Aug); Palumeu, ~3°21'30.3"N 55°26'38.2"W (Jun). **VENEZUELA:** **Bolívar** – Lago Guri Islands, 7°21'S 62°52'W (Jun); Las Trincheras [Río Caura] (Aug); Puerto Cabello [Río Caura] (Aug); Jabillal [Río Caura – Orinoco] (Oct). **Delta Amacuro** – 11 km W Piacoa.

Comments. There has been much confusion attending the use of the name “*jasius*”; it has been regularly and erroneously applied to practically all members of the *jasius* group. Arnaud’s (2002a) designation of a neotype resolved much of the identity problem of this, the type species of the genus. *Coprophanaeus jasius* is an Amazonian species commonly found in the same communities as its congeners *C. parvulus*, *C. dardanus* and *C. lancifer*. It is a copronecrophagous forest dweller. Its closest known relative is *C. abas*, originally described by MacLeay as a variety of *C. jasius* and first recognized as a separate species by Arnaud (2002c). Of the members of the *jasius* group, only *C. jasius* and *C. abas* have a conspicuously smooth posteromedian portion of the pronotum.

Pereira and Martínez (1956; see also 1960) synonymized *C. cyanescens* and *C. camargoi* with *C. jasius*, but neither is now considered in the context of Olivier’s taxon. We consider *C. cyanescens* (*q.v.*) a valid species and *C. camargoi* a synonym of *C. acrisius* (*q.v.*). Arnaud (2002c) has a wider definition of *C. jasius* than our own; he cites the species from Colombia, Ecuador, Peru and Bolivia. While we have seen no specimens from any of these countries, its occurrence in Amazonian habitats in any or all of them is not out of the question and we so indicate in the distribution depicted in Fig. 113.

Arnaud (1982) pointed out that the type of *Phanaeus costatus* is in fact a “hybrid” combining the forebody of a *Coprophanaeus* with the hindbody of *Diabroctis mimas* (Linné). He identified the forebody as *C. jasius*, which he synonymized with *C. costatus*. C.P.D.T. Gillett (pers. comm.) has kindly informed us that the forebody is of *C. cyanescens*, requiring that the synonymy be reassigned accordingly (see Comments under *C. cyanescens*).

***Coprophanaeus (C.) abas* (MacLeay, 1819)**

Fig. 102, 105, 110, 113, 135-139

Phanaeus jasius abas MacLeay, 1819: 126

Phanaeus rex Balthasar, 1939: 239 (syn. by Arnaud 1982c: 125)

Coprophanaeus abas (MacLeay) (recomb. by Blackwelder 1944: 209 [as synonym of *C. jasius*])

Type. *P. abas* – neotype male (des. by Arnaud 2002b: 3), The Natural History Museum, London (examined); *P. rex* – holotype male, National Museum, Prague (examined).

Diagnosis. *General* – Metallic color green to yellowish green and confined to posterior areas of head and pronotal sides and margins. Clypeal margin clearly explanate/angulate lateral to median teeth (Fig. 135, 138). Posteromedian portion of pronotum smooth, bearing sparse, effaced puncturing (weakest in large males). Sulcus paralleling carinate posterior margin of pronotum (Fig. 110) with obvious sculpturing (x25); carina entire. Posterior pronotal fossae with sparse puncturing and/or microgranules. Length 20-29 mm.

Male (Fig. 102, 137-139) – Head horn long, tip reaching level of summit of pronotum; anterior surface of horn base usually only weakly punctured; central process (viewed laterally) inclined slightly posteriorly from base, its length at least twice that of base. Pronotal process strongly produced medially as lobate tooth, itself sometimes weakly bilobed, flanked on each side by small, acute tooth (process reduced to strongly angulate transverse carina in smallest individuals). Parameres long, length at least three-fourths that of phallobase.

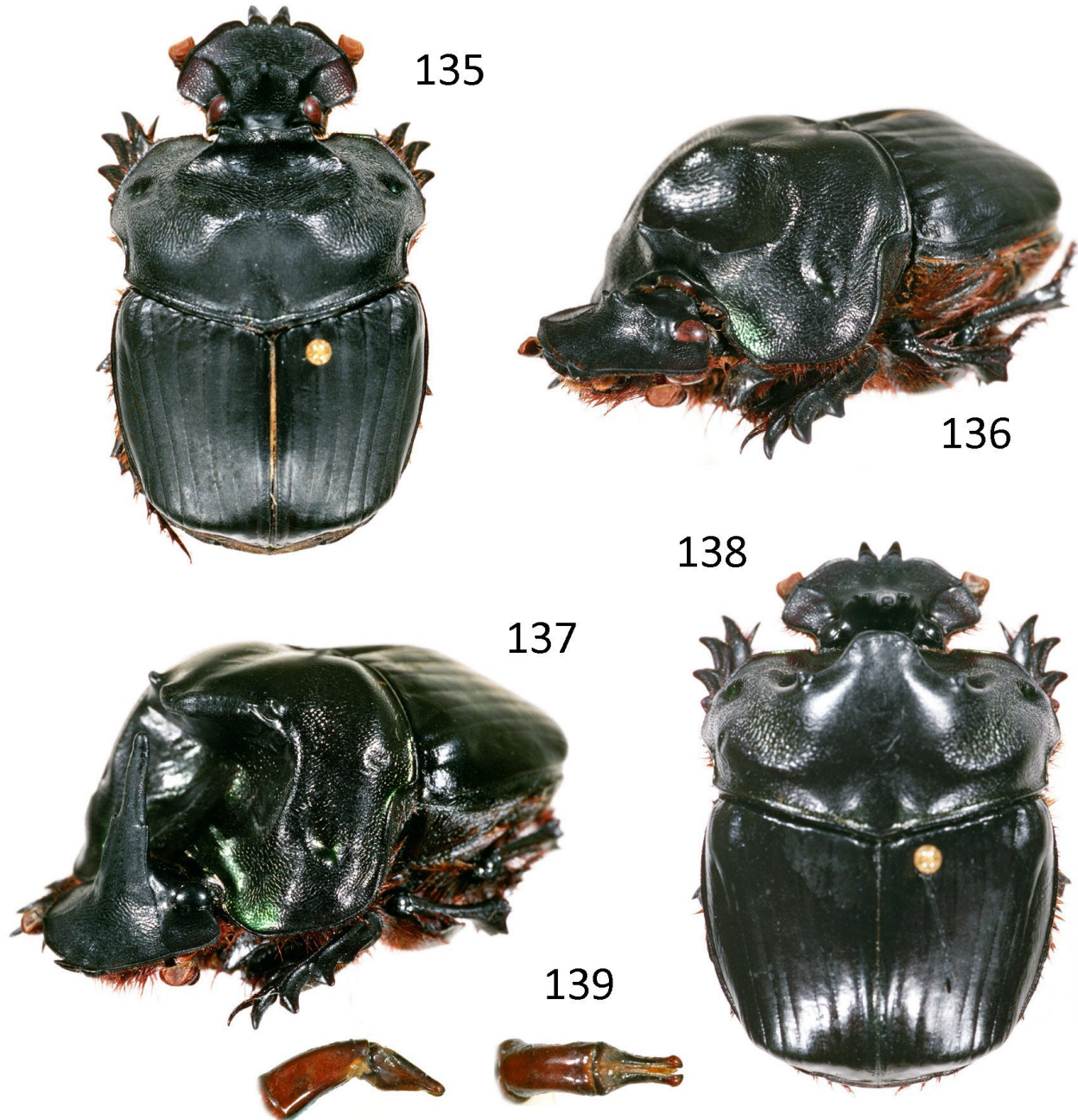


Figure 135-139. *Coprophanaeus abas*. 135-136) Female habitus. 137-138) Male habitus. 139) Aedeagus (lateral view on left; dorsal view on right).

Female (Fig. 105, 135-136) – Cephalic carina bowed or angulate medially, median tooth larger than laterals. Vertex moderately punctured. Pronotal ridge (Fig. 105) strongly elevated, quadrate, summit strongly trituberculate, width at summit slightly more than interocular width. Anteromedian pronotal concavity oval, deep, posterior (upper) margin clearly bitumose (except in smallest individuals).

Specimens examined – 57.

Distribution. Mesoamerica – Venezuelan Llanos province and adjacent Amazonia (Fig. 113).

Collection Records. **COLOMBIA:** **Guaviaré** – San José [Finca Esmeralda], 2°33'N 72°38'W, 240 m (Oct). **Caquetá** – Puerto Solario, PNN La Serranía de Chiribiquete, 0°12'47.8"N 72°25'25.4"W, 250 m

(Feb-Mar). **TRINIDAD – TOBAGO:** 11 km SE Arima [Arena Forest Reserve], 80 m (Jun-Jul); 13 km S Arima, 2 km N Talparo, 50 m (Jun-Jul). **VENEZUELA: Amazonas** – Gavilán (May). **Araugua** – 20 km NW Maracay [Rancho Grande], 1000 m (Jun). **Barinas** – Barinitas [Mpio. Libertador, Quebrada Miraflores], 650 m (Aug). **Bolívar** – Lago Guri Islands, 7°21'N 62°52'W (Jun); Río Caura, Las Trincheras (Aug); 85 km S El Dorado (Aug); 33 km S El Dorado, 220 m (Aug); Sipao [110 km E Caicara del Orinoco] (Jun-Aug); 26 km N Guasipati (Jun-Jul); Canaima [220 km SSE Cd. Bolívar] (Aug); Caura River, Jabillal, Orinoco, 200 m (Aug).

Comments. This species, along with *C. acrisius*, was proposed by MacLeay (1819) as a variety of *C. jasius* (*q.v.*); in accordance with Article 45.6.4 (ICZN 1999), its original name is *Phanaeus jasius abas* MacLeay. In smaller individuals the large median pronotal tab is replaced by a central tubercle and the overall appearance becomes more similar to *C. jasius*. We do not understand well the distribution of this species, which may later become clearer as more material is collected. Our information suggests that it occurs in the Venezuelan Llanos province (?mainly along gallery forests of the Orinoco basin) and adjacent Amazonian provinces. The general area, especially in the Venezuelan state of Bolívar, is also home to *C. jasius* and eastern populations of *C. gamezi*; but we do not know if they are ecologically sympatric in the region.

***Coprophanaeus (C.) gamezi* Arnaud, 2002**

Fig. 99, 106, 111, 113, 140-144

Coprophanaeus gamezi Arnaud, 2002a: 8

Type. Holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France (examined by photo).

Diagnosis. *General* – Metallic coloration dark green, blue or yellowish green, confined to posterior areas of head and pronotal sides and margins; elytra black or tinged with highlights of same tone as pronotum. Clypeal margin clearly explanate/angulate lateral to median teeth (Fig. 140, 143). Posteromedian portion of pronotum granulate, granules often coalescing as transverse, squamose ridging. Sulcus paralleling carinate posterior margin of pronotum (Fig. 111) distinctly sculptured (x25); carina usually broken up by dense puncturing, often crenulate. Posterior pronotal fossae and surrounding area densely, finely granulate. Length 18-28 mm.

Male (Fig. 142-144) – Tip of head horn almost reaching level of prothoracic carina; anterior surface of base usually punctate; length of central process equal to that of base. Pronotal prominence with strongly developed rounded, tab-like projection, itself often weakly bitumose; median process flanked on each side by small, acute tubercle. Length of parameres about one-half that of phallobase.

Female (Fig. 99, 106, 140-141) – Cephalic carina bowed anteriorly, trituberculate, median tooth raised, much larger than lateral tubercles (Fig. 99). Vertex coarsely, densely punctured. Pronotal ridge quadrate, summit scarcely trituberculate, if at all (Fig. 106). Anteromedian concavity shallow, posterior (upper) margin simple, not bitumose.

Specimens examined – 201.

Distribution. Mesoamerica – Maracaibo, Venezuelan Coast and Venezuelan Llanos provinces and adjacent Amazonia (Fig. 113).

Collection Records. **BRAZIL: Roraima** – Serra da Moça (Jul). **COLOMBIA: Bolívar** – Mompox, 9°14'N 74°25'W (Jun); Zambrano, Hacienda Monterrey, 9°37'48"N 74°54'44"W, 135 m (Feb). **Boyacá** – El Mortiño (Aug). **Cundinamarca** – Tocaima (Mar). **Magdalena** – Onaca, 770 m (Dec); Bonda (Jun). **GUYANA: Rupununi** – Parara Ranch, 3°37.3'N 59°44.2'W (Apr). **Vichada** – Municipio Cumaribo, PNN El Tuparro, 5°21'03"N 67°52'15"W, 135 m (Feb); Puerto Correrio (Nov). **VENEZUELA: Amazonas** – Puerto Ayacucho (May); 32 km S Puerto Ayacucho [Cataniapo River] (May). **Aragua** – Maracay, 450 m

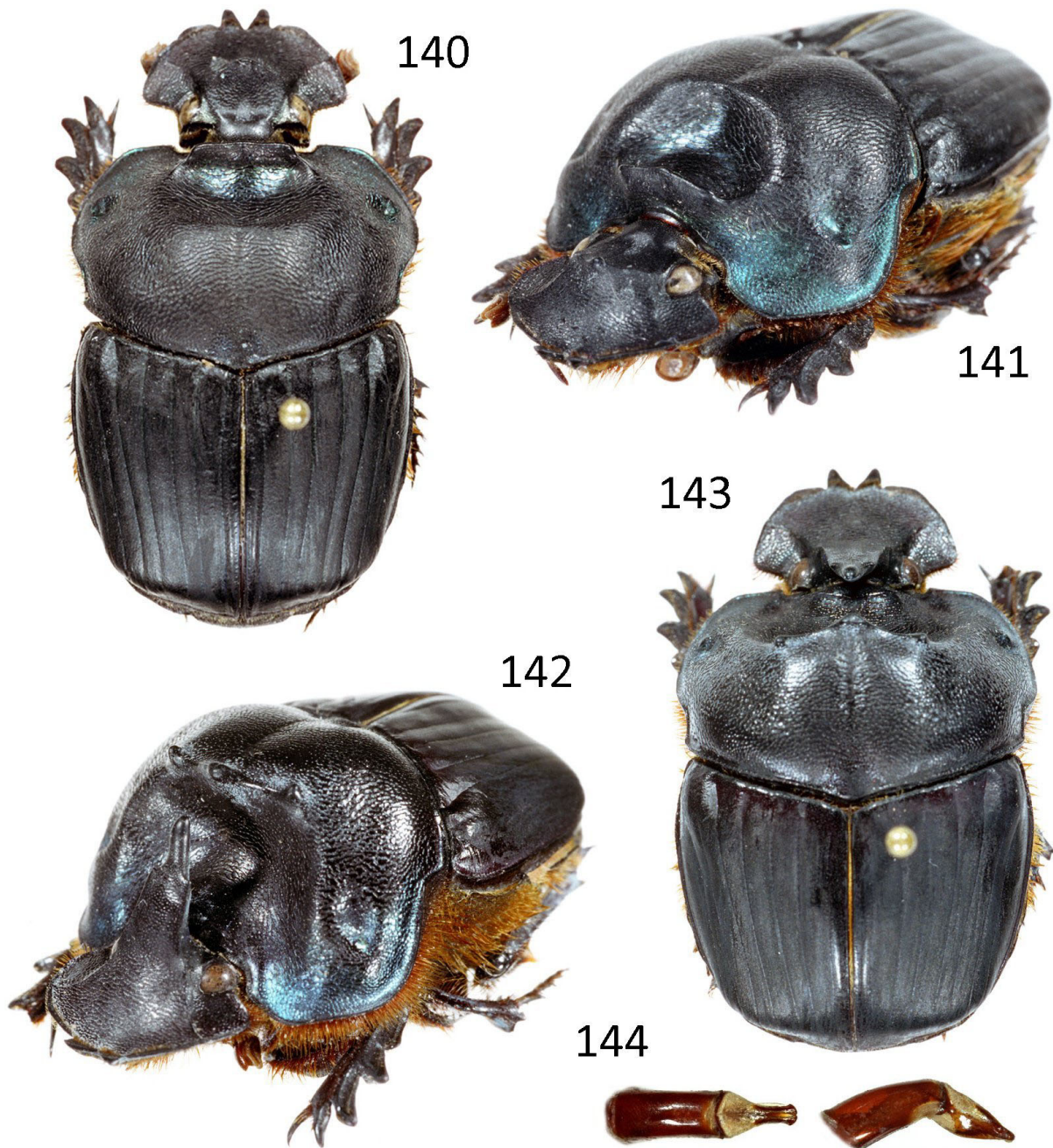


Figure 140-144. *Coprophanaeus gamezi*. 140-141) Female habitus. 142-143) Male habitus. 144) Aedeagus (dorsal view on left; lateral view on right).

(Nov). **Barinas** – Maravillas (Sep); Saboneta [Mpio. Alberto Torrealba], 200 m (Jun). **Bolívar** – 48 km ESE Cd. Bolívar [Rancho Santa Rita], 7°55'N 63°10'W (Jul); Suapuré River (Jul); Sipao, 110 km E Caicara del Orinoco (Jun, Aug); 70 km W. Caicara del Orinoco; 70 km W Cd. Bolívar, Puente Cocuizas (Jun-Aug); 35 km SW Puerto Ordaz (Jul-Aug); Guri (Jul); Caura River, Jabillal, Orinoco, 200 m (Aug); El Dorado [Minas de Payapal] (May). **Carabobo** – San Esteban [near Puerto Cabello] (Dec); Saman Mocho, Flor Amarillo (Feb, Jul). **Delta Amacuro** – 11 km W Piacoa (Jul). **Guárico** – Tucupido (Jul) **Mérida** – Mpio. Padre Noguera, Sector Cuenca del Río Capara, 7°50'32"N 71°30'34"W, 280 m (Apr). **Sucre** – Cumanacoa

(Dec). **Zulia** – Santa Ana [Mpio. Colón Hacienda], 8°54'30"N 71°52'17"W, 175 m (Aug); El Caracolí [Mpio. Colón], 70 m (May); Mpio. Colón, Sector Bancada de Limones, Finca El Recreo (Apr).

Comments. This species most closely resembles *C. cyanescens* (*q.v.*) from which it differs, among other characters, by the coarse sculpturing of the posterior margin of the pronotum (Fig. 111) and female pronotal ridge (Fig. 99). Gámez (2004) and Gámez and Acconcia (2009) studied this species in the Maracaibo district of Mérida, where it prefers open habitats and readily invades induced pasture lands, and presented detailed information on its activity.

***Coprophanaeus* (*C.*) *cyanescens* (Olsoufieff, 1924)**

Fig. 98, 113, 145-150

Phanaeus cyanescens Olsoufieff, 1924: 65

Phanaeus costatus Olsoufieff, 1924: 66 **New Synonymy**

Coprophanaeus cyanescens (Olsoufieff) (recomb. by Blackwelder 1944: 209)

Phanaeus worontzowi Pessôa and Lane, 1937: 325 **New Synonymy**

Type. *P. cyanescens* – lectotype male (des. by Arnaud 1982a: 116), Muséum National d'Histoire Naturelle, Paris (examined by photo); *P. costatus* – holotype, hybrid specimen (examined; see Comments), The Natural History Museum, London; *P. worontzowi* – holotype male, Museu de Zoologia, Universidade de São Paulo, São Paulo.

Diagnosis. *General* – Metallic coloration green or dark blue, or intermediate tones, confined to posterior areas of head and pronotal sides and margins; elytra black or tinged with highlights of same tone as pronotum. Clypeal margin clearly explanate/angulate lateral to median teeth (Fig. 45, 148). Posteromedian portion of pronotum, except around basal fossae, punctured or punctatorugose, sometimes densely so. Sulcus paralleling carinate posterior margin of pronotum weakly sculptured (x25); carina entire, sometimes weakly punctate. Posterior pronotal fossae and surrounding area densely, finely granulate. Length 19-27 mm.

Male (Fig. 147-150) – Tip of head horn almost reaching level of prothoracic carina; anterior surface of base usually punctate; length of central process equal to that of base. Pronotal prominence widely V-shaped, trituberculate, medial tooth distinctly larger than laterals, width less than distance separating outer margins of eyes. Length of parameres about one-half that of phallobase.

Female (Fig. 145-146) – Cephalic carina weakly bowed anteriorly, trituberculate, median tooth slightly larger than laterals. Vertex coarsely, densely punctured. Pronotal ridge trapezoidal, summit weakly trituberculate. Anteromedian concavity shallow, posterior (upper) margin simple, not bitumose.

Specimens examined – 416.

Distribution. Chacoan subregion (Fig. 113).

Collection Records. **ARGENTINA:** **Catamarca** – La Viña (Jan). **Chaco** – Miraflores (Apr, Sep); Chaco National Park, 100 km NW Resistencia (Dec); Puerto Bermejo. **Formosa** – Gran Guardia (Nov). **Jujuy** – El Quemado (Apr); 12 km S. Ledesma [Río Ledesma], 500 m (Dec); Calilegua National Park [Mirador; El Cortaderal; Aguas Negras], 500-900 m (Dec); 6 km W Yuto (Feb). **Misiones** – Dos de Mayo (Feb); El Dorado (Nov); Iguazú National Park, 200 m (Dec); Garuhapé (Mar). **Salta** – Tablillas, 700 m (Feb); General Martín Miguel de Güemes (Feb); Pocitos [Distrito San Martín] (Jan, Nov); El Rey Nacional Park, 890 m (Nov-Dec); Rosario de Lerma, 1325 m (Mar). **Tucuman** – Famaillá (Jan). **BOLIVIA:** **Chuquisaca** – Rosario [Lago Rocagua] (Nov). **Beni** – Rurrenbaque (Jun); Magdalena, 180 m (Dec). **Santa Cruz** – Santa Cruz Botanic Garden, 17°47'02"S 63°03'47"W, 400 m (Nov); Buena Vista (Feb-Mar); El Refugio Reserve, 14°46'S 61°02'W; Santiago (Feb); Parque Nacional Noel Kempff Mercado [El Refugio], 14°45'58"S 61°01'59"W (Jan); Reserva Municipal Tucavaca, 18°12'S 59°28'W, 150 m (Apr); RPPN Caparú, 14°50'S 61°10'W, 180 m (Dec); 1.6 km ESE Santiago de Chiquitos, 18°20.103'S 59°35.007'W, 622 m (Nov); 20 km NE Santiago de Chiquitos (Tucavaca River), 18°14.590'S 59°27.907'W, 215 m (Nov). **Tarija** –

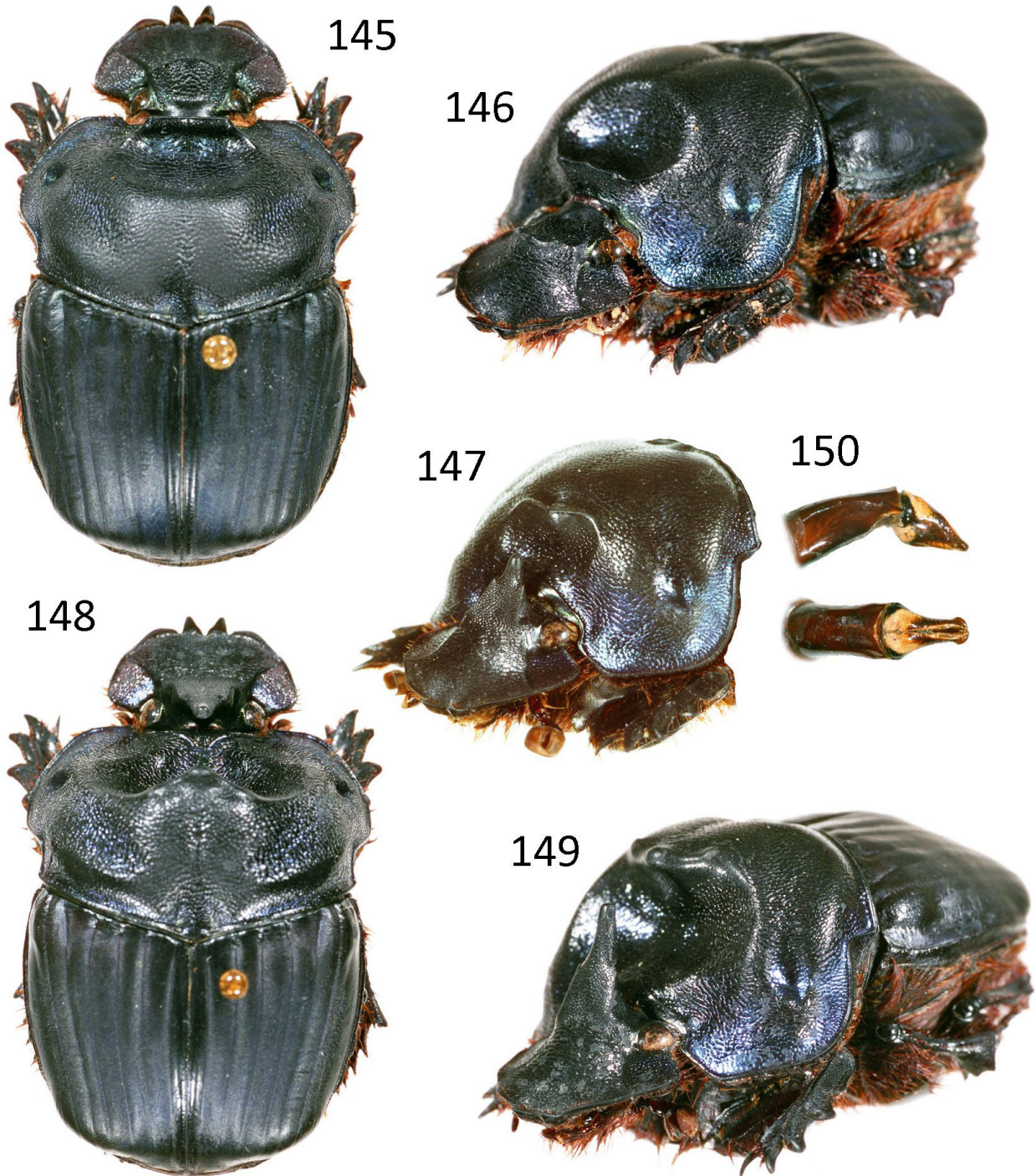


Figure 145-150. *Coprophanaeus gamezi*. 145-146) Female habitus. 147-149) Male habitus. 150) Aedeagus (lateral view above; dorsal view below).

between Caiga and Creveaux, 20°50'19"S 63°24'58"W, 490 m (Jan); between Yaguacua and Caiza, 21°50'52"S 63°36'26"W (Jan); Entre Ríos (Quebrada de Abra) (Feb); Yacuiba (May-Jun); TCO Yumao [Kaaguasu], 19°05'S 63°35'W, 500 m (Feb). **BRAZIL:** Bahia – Feira de Santana (Jun); Encruzilhada (Dec); Cruz das Almas (Apr). Ceará – Uirapuru, Serra de Baturité, 4°20'S 38°56'W (Jun); Maranguape, São Benedito, Sanc. Nossa Senhora de Penha, 38°40'48"W 03°52'29"S, 96 m (Mar). Maranguape, 3°54'S 38°42'W (Jun); Maranguape, São Benedito, Santuario da Nossa Senhora de Penha, 38°40'53"W 03°52'18"S, 160 m (Mar-

Apr); Maranguape, Tabatinga, 38°43'48"W 04°00'42"S, 126 m (Mar); Serra de Baturité, Uirapuru, 38°54'22"W 04°17'27"S, 620 m (Mar, May); Maranguape, Piraponga, 38°41'59"W 03°53'26"S, 200 m (Feb-Mar). **Distrito Federal** – 15 km N Brasília, 1250 m (Mar). **Espírito Santo** – Timbuhy (Dec); Linhares (Mar, Nov, Jan). **Maranhão** – Codó (Feb); Santa Quitéria de Maranhão, Fazenda Rodiador, 42°40'46"W 03°24'50"S, 47 m (Feb, May). **Mato Grosso** – 13.4 km S Posto do Gil, 14°37'55"S 56°16'23"W, 240 m (Jan); 20.2 km S Posto do Gil, 14°40'58"S 56°17'57"W, 240 m (Jan); Fazenda São João, 14°14'10"S 56°08'11"W, 400 m.; Vale de Solidão, 14°22'S 56°07'W (Mar). **Mato Grosso do Sul** – Paranaíba (Mar); Selvíria (Oct); Campo Grande (Oct, Dec). **Minas Gerais** – Sete Lagoas (Dec); Ipatinga (Nov); Sabará; Rio das Velhas. **Pará** – Belém (Feb). **Paraná** – Londrina [Mata Godoy] (Jan-Mar, Dec). Paraíba – Mamanguape [Rebio Guaribas], 6°41'S 35°10'W (Apr); João Pessoa [Mata do Buraquinho] (Jun); Fazenda Pacatuba (Jul). **Pernambuco** – Recife. **Rio de Janeiro** – Rio Bonito (Apr); Pocos de Caldas (Dec). **Rio Grande do Norte** – Lajes. **São Paulo** – Piracicaba (Oct); Indiana (Feb); Ilha Solteira (Mar); Campinas (Jan); Batatais (Dec); Anhembi [Fazenda Barriero Rico] (Nov). **PARAGUAY: Alto Paraguay** – Puerto Bertoni; Primavera (Nov). **Alto Paraná** – Estación Dimas (Jan-Feb). **Amambay** – Cerro Cora (Feb, Dec); Pedro Juan Caballero (Nov). **Caaguazú** – Caaguazú. **Canindeyú** – Reserva Nacional Bosque Mbaracayú [Jejuí-Mí] (Jan, Nov). **Central** – Asunción; Capiatá (Oct). **Concepción** – Concepción [Santa Morana], 23°24'S 57°26'W (Nov); Horqueta (Dec); Cororó (Nov); Campo Zanja Morotí, 22°53'S 57°23'W (Mar, Nov-Dec). **Cordillera** – Altos (Mar); Naranjo (Oct, Dec). **Guairá** – Melgarejo (Apr, Sep); Colonia Sudetia (Jan); Yaparucu (Nov); Villarrica (Oct). **Itapúa** – Encarnación; San Rafael Reserve, 26°31'24"S 55°48'18"W, 90 m (Nov). **Misiones** – Santa Rosa (Oct). **Paraguari** – Sapucay (Jan-Apr, Oct-Dec). **San Pedro** – Yatevó.

Comments. This is a widespread species that, along with *C. ensifer* and *C. bonariensis*, is an indicator of the Chacoan subregion. Metallic coloration can be blue or green, and there seems to be no geographic pattern associated with color variability. Fernando Vaz-de-Mello (pers. comm.) reports that in the Atlantic coast forest of Brazil the blue form frequents forest habitats while the green form predominates in pastures and other open habitats. Conrad Gillett (pers. comm.) reports that in Ceará it occurs commonly in Atlantic forest fragments and less commonly in caatinga; specimens from both habitats there are bluish green. Rare individuals can present a crenulate posterior pronotal margin similar to that of *C. gamezi*. We have not seen *C. rigoutorum*, but our interpretations of Arnaud's descriptions (2002a, 2002c) place it near, or perhaps in synonymy with *C. cyanescens*.

Arnaud (2002c: 36) listed *P. worontzowi* as a synonym of *C. jasius*; our interpretation of the latter results in the new synonymy of *P. worontzowi* and *C. cyanescens*. Edmonds' (1967) reference to *Phanaeus jasius* undoubtedly applies to *C. cyanescens*.

We here reassign the synonymy of *Phanaeus costatus* to *C. cyanescens*, which Arnaud (1982a) synonymized with *C. jasius* (see Comments under *C. jasius*).

The pluto species group

The pluto group brings together at least eight species comprising three subgroups as follows: a) *Coprophanaeus pecki* and *C. morenoi*; b) *C. pluto*, *C. boucardi* and *C. solisi*; and c) *C. conocephalus*, *C. chiriquensis* and *C. gilli*. All are Mesoamerican and collectively diagnosed by the presence of a trituberculate cephalic carina in both sexes (shared with the ohausi species group) and the unique form of the male parameres.

Diagnosis. General – Length of frons at least equal to that of clypeus, often much greater (especially in large males; see Fig. 171). Anterior portion of circumnotal ridge interrupted behind eyes (as in Fig. 8). Posterior edge of paraocular area abruptly curved toward posterior angle of eye. Anterior one-half of pronotum generally bearing squamose granulation, often coalescing into short, transverse ridges; remainder of pronotum punctate, puncturing becoming progressively weaker toward posterior margin (more so in larger males); basal fossae distinct (except *C. pecki* and *C. morenoi*). Prosternal ridge simple, lacking acute tubercle at anterior end. Elytral interstriae variable; striae very fine. Usually dark, sombre species to unaided eye; metallic coloration inconspicuous and most obvious under magnification (x10), restricted to anterior portion and margins of pronotum and pygidium; venter always showing reflections of same tone as dorsum. Medium-sized to large species, length usually exceeding 20 mm.

Male – Length of parameres about equal to that of phallobase; apices of parameres with laterally projecting rounded teeth never visible in profile, base scarcely if at all extending below phallobase (Fig. 169-170). Head with trituberculate carina, never horned. Pronotal prominence either cleat-shaped (e.g. Fig. 185) or bitumid (e.g. Fig. 177).

Female – Head with straight, transverse, trituberculate carina set well in front of eyes; length of frons at least equal to that of clypeus. Pronotum with rounded, bituberculate, transverse crest very near anterior margin followed by shallow depression or distinct concavity.

Distribution. Mesoamerica, from northwestern Colombia to extreme south-central United States (Fig. 172).

Key to species of the pluto group

1. Cephalic carina of larger males set far forward, length of frons more than twice that of clypeus (Fig. 171) (length of female frons usually about one and half times that of clypeus). Posterior one-half of paraocular areas smooth, at most with very faint puncturing; at least posterior one-half of frons smooth, puncturing, if any, confined to anterior one-half. Beaded anterior angle of metasternum (viewed laterally, Fig. 168) salient, presenting acute posterior angle (subject to wear). Basal pronotal fossae effaced. Pygidium with wide basal groove (Fig. 162-163). Elytral interstriae flat. Parameres (viewed dorsally) with wide, flattened subapical tooth (Fig. 178). Usually completely black, only very rarely with slight metallic coloration on anterior margin of pronotum. **pecki subgroup** 2
 - Length of frons variable. Paraocular area completely sculptured or nearly so, sculpturing becoming weaker near eye. Pronotal prominence of larger males variable. Beaded anterior metasternal angle (viewed laterally, Fig. 167) rounded. Basal pronotal fossae weak but almost always indicated, sometimes punctiform. Pygidium, interstriae, and parameres variable. Dorsum usually with restricted areas of metallic coloration 3
 - 2(1). Pronotal prominence of large male (Fig. 177) with narrow, weakly bilobed median salience, distance between lobes clearly less than interocular distance; carina demarking pronotal prominence ending on each side in oval fovea mesial to lateral fossa. Costa Rica, Panama ***Coprophanaeus (C.) pecki* Howden and Young**
 - Pronotal prominence of male, viewed dorsally, broad, width exceeding interocular distance; bimorphic, either cleat-shaped (Fig. 183, upper view) or quadrilobate (Fig. 183, lower view) with lobes linked by thick carina, middle lobes more salient than lateral lobes; prominence flanked by broad concavities descending to anterior pronotal margin. NW Ecuador to Honduras ***Coprophanaeus (C.) morenoi* Arnaud**
- 3(1). Pronotal prominence of large male broad, cleat-shaped (e.g. Fig. 185). Cephalic carina of both sexes set near head midlength, length of frons about equal to that of clypeus. Basal margin of pygidium usually distinctly grooved. Parameres (viewed dorsally) lacking distinct subapical flange or tooth. Costa Rica to extreme southern Arizona and Texas. **pluto subgroup** 4
 - Pronotum of large male with transverse bitumid prominence, either more-or-less quadrate (Fig. 202-203) or two isolated conical processes separated by punctate concavity (Fig. 154-159). Length of male frons about one and half times that of clypeus; in female length of frons and clypeus about equal. Basal margin of pygidium rarely distinctly grooved. Parameres (viewed dorsally, Fig. 207, 212) usually with acute subapical denticle (sometimes nearly effaced in *C. conocephalus*). NW South America to Mexico. **conocephalus subgroup** 6
 - 4(3). Elytral interstriae strongly convex (Fig. 165). Posterior portion of pronotum largely smooth, at most with scarcely visible, feeble puncturing never reaching posterior margin (Fig. 185). Metallic color red to reddish green. Smaller size, length not exceeding 15 mm. Costa Rica ***Coprophanaeus (C.) solisi* Arnaud**

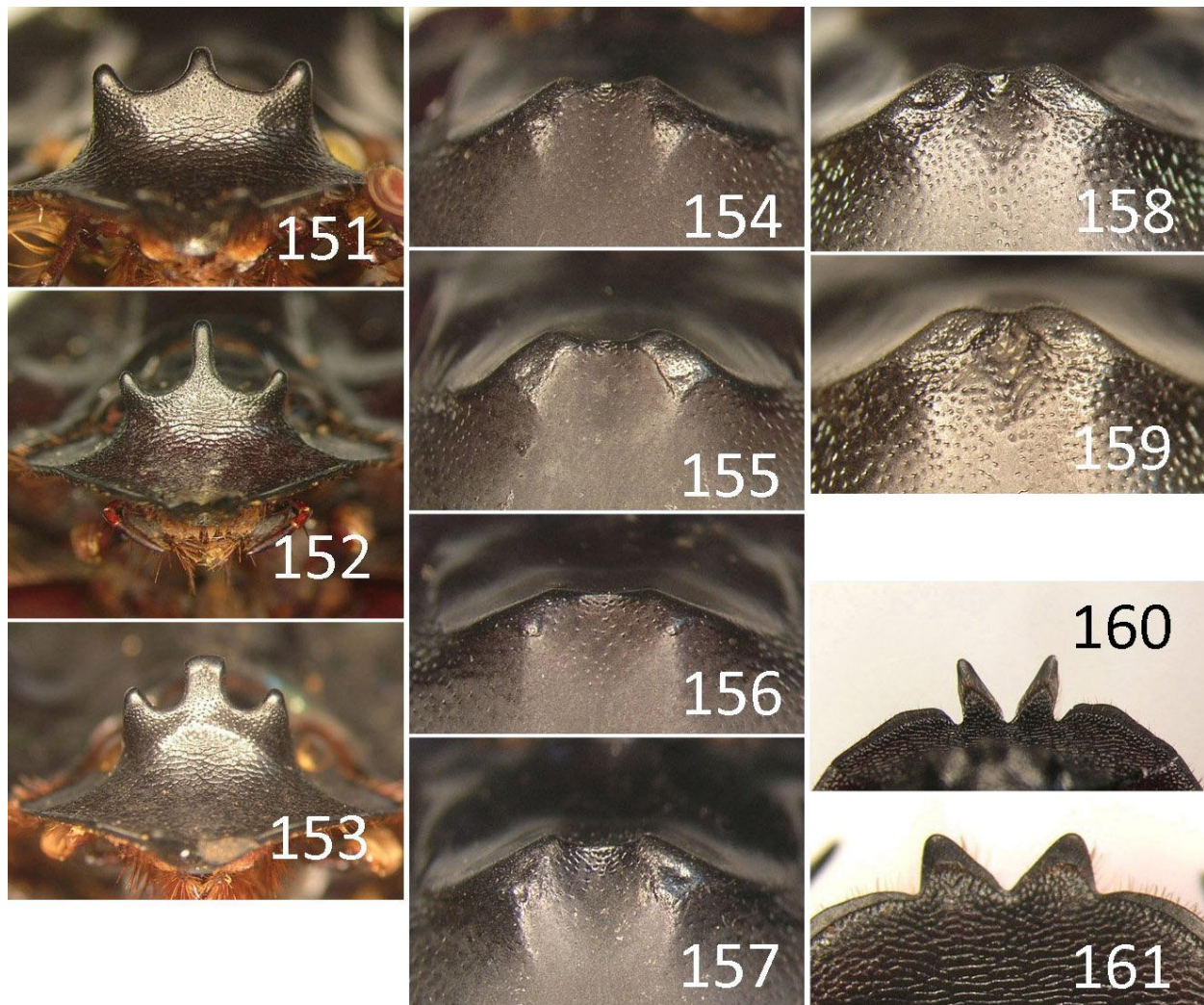


Figure 151-161. Characters of the *Coprophanaeus* (*s. str.*) *pluto* species group. **151-153)** Anterior views of male cephalic process of *C. pluto*. **154-157)** Dorsal views of male pronotal prominence of *C. chiriquensis*. **158-159)** Same, *C. gilli*. **160)** Clypeal margin of *C. boucardi*. **161)** Same, *C. pluto*.

- Elytral interstriae at most only weakly convex (Fig. 166). Posterior portion of pronotum distinctly punctured, sometimes only weakly so, puncturing reaching posterior margin. Metallic color green to yellowish green. Larger, length usually exceeding 20 mm **5**

- 5(4). Puncturing of posterior portion of pronotum strong (x10), weakly asperate, becoming less pronounced posteromedially. Median teeth (unworn) of clypeus (Fig. 160) long, narrow, length of tooth about one and half times width at base. Lateral angles of pronotal prominence of large male attenuated, overall width of prominence about same as emarginate anteromedian margin of pronotum. Width of upper portion of eye about one-third of interocular distance. Costa Rica to Mexico
 ***Coprophanaeus* (*C.*) *boucardi* (Nevinson)**

- Puncturing of posterior portion of pronotum weaker, not distinctly asperate. Median teeth of clypeus (Fig. 161) wider, length about equal to width at base. Lateral angles of large male pronotal prominence strongly produced, width of prominence greater than that of emarginate anteromedian portion of pronotal margin. Width of upper portion of eye one-fourth to one-fifth of interocular distance, only rarely approaching one-third. Honduras to United States
 ***Coprophanaeus* (*C.*) *pluto* (Harold)**

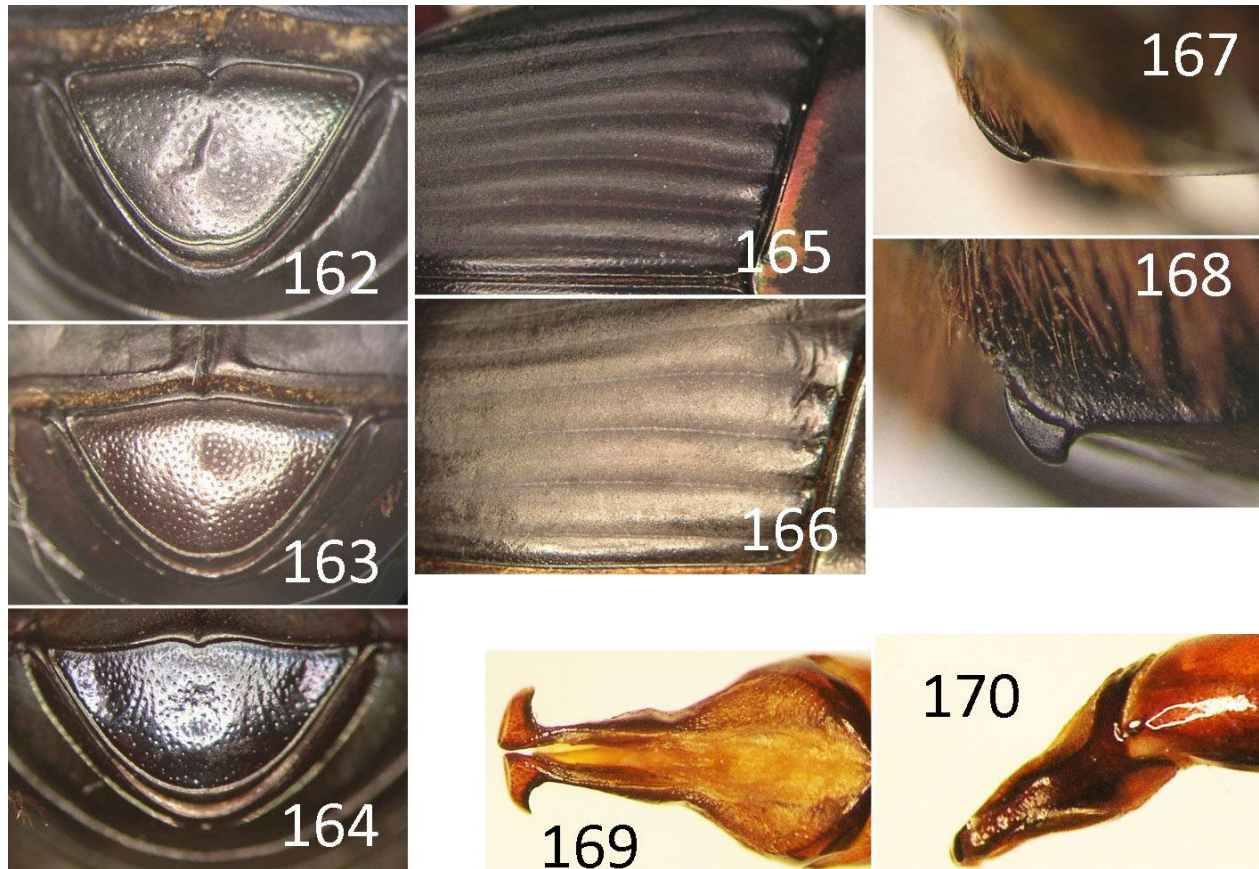


Figure 162-170. Characters of the *Coprophanaeus* (*s. str.*) pluto species group. **162-163)** Posterior view of pygidium of *C. morenoi*. **164)** Same, *C. chiriquensis*. **165)** Dorsal view left of elytron of *C. solisi*. **166)** Same, *C. pluto*. **167)** Metasternal prominence of *C. pluto*. **168)** Same, *C. pecki*. **169)** Dorsal view of parameres of *C. pluto*. **170)** Lateral view, same.

- 6(3). Male pronotum (Fig. 202) lacking distinct fovea above lateral fossa. Pronotal prominence of large male bitumid, tumescences connected by uninterrupted ridge. Teeth of female (and usually also male) cephalic carina closely set, distance between outer teeth about one-half of interocular distance. Elytral interstriae flat or weakly convex, seldom shinier midlongitudinally. Parameres at most with indistinct subapical tooth. Western Andean valleys and slopes of Colombia and Ecuador *Coprophanaeus* (*C.*) ***conocephalus*** (Olsoufieff)
- Male pronotum with distinct oval fovea above lateral fossa (Fig. 210, arrow). Male pronotal prominence bitumid or simple transverse ridge. Distance separating lateral teeth of cephalic carina clearly greater than one-half of interocular distance. Elytral interstriae distinctly convex, usually somewhat shinier midlongitudinally. Parameres with distinct subapical tooth (Fig. 207, 212). Central America 7
- 7(6). Tumescences of large male pronotal prominence widely separated, flattened, triangular (Fig. 154-157). Puncturing of posteromedian portion of pronotum effaced or nearly so, especially in males. Panama and Costa Rica *Coprophanaeus* (*C.*) ***chiriquensis*** (Olsoufieff)
- Male pronotal prominence a simple, thickened carina with small, closely set tumescences, sometimes scarcely broken medially (Fig. 158-159). Posteromedian portion of pronotum distinctly punctured, usually more strongly so in females. Honduras to southern Mexico *Coprophanaeus* (*C.*) ***gilli*** Arnaud

***Coprophanaeus* (*C.*) *pecki* Howden and Young, 1981**

Fig. 168, 172-178

Coprophanaeus pecki Howden and Young, 1981: 144

Type. Holotype male, Canadian Museum of Nature, Ottawa (examined).

Diagnosis. *General* – Completely black, no metallic coloring anywhere. Frons smooth, at most with faint puncturing behind transverse carina. Clypeal teeth normal, length about equal to width at base. Width of dorsal portion of eye about one-fourth or less of interocular distance (sometimes greater than one-fourth in large females). Posterior portion of paraocular area smooth. Postero-medial portion of pronotum smooth, devoid of distinct sculpturing; basal pronotal fossae effaced or only very faintly indicated. Anterior angle of metasternum bearing elevated cap (seen in profile, Fig. 168). Elytral interstriae flat. Pygidium with wide basal groove (as in Fig. 163). Length 22–26 mm.

Male (Fig. 175–178) – Length of frons of large male exceeding twice that of clypeus (as in Fig. 171). Pronotum with transverse carina developed medially as two closely set rounded lobes (Fig. 177); carina extending laterally to oval fovea adjacent to lateral fossa (only poorly defined in Fig. 176); declivitous surface of pronotum beneath carina smooth, devoid of sculpturing. Parameres with wide subapical tooth.

Female (Fig. 173–174) – Length of frons about one and half times that of clypeus. Transverse pronotal carina bidentate medially, followed by transverse depression with summit weakly bitumid.

Specimens examined – 28.

Distribution. Western Isthmus province of Costa Rica and Panama (Fig. 172).

Collection Records. **COSTA RICA: Puntarenas** – Osa Peninsula [Río Piro La Joya], 8°23'56"N 83°19'51"W, 350m (Aug-Sep); San Vito [Las Cruces], 1200 m (Aug-Sep); 6 km S San Vito, 1000 m (May-Jun); 15 km NE Potrero Grande [Finca Helechales] (Sep); Estación Los Patos, 200 m (Sep); Golfito [Reserva Forestal Golfo Dulce - Estación Agujas], 300 m (Apr). **PANAMA: Chiriquí** – 4km N Santa Clara [Hartmann's Finca], 1500 m (Jun-Jul); 15km NE Gualaca [Cerro Hornito], 1200 m (Jun); 10 km W Cerro Pando (May).

Comments. The distribution of *C. pecki* is sympatric with *C. solisi* in the Pacific coast rainforest of Osa Peninsula, from which it ascends into the cloud forests of the Costa Rica–Panama central range. The form of the large male pronotum with its very closely set median lobes is unique to the genus and imparts a superficial appearance quite different from that of its close relative, *C. morenoi*. The virtually identical head structure of the two species, especially the exceedingly long frons in the male as well as the other characters mentioned in the key clearly attest to their close relationship. The distributions of this species pair are separated by the Panama–Costa Rica central cordillera.

Coprophanaeus (C.) morenoi Arnaud, 1982

Fig. 162–163, 171–172, 179–184

Coprophanaeus morenoi Arnaud, 1982b: 121

Coprophanaeus kohlmanni Arnaud, 2002a: 5 **New Synonymy**

Type. *C. morenoi* – holotype male, Muséum National d'Histoire Naturelle, Paris (examined by photo); *C. kohlmanni* – holotype male, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia.

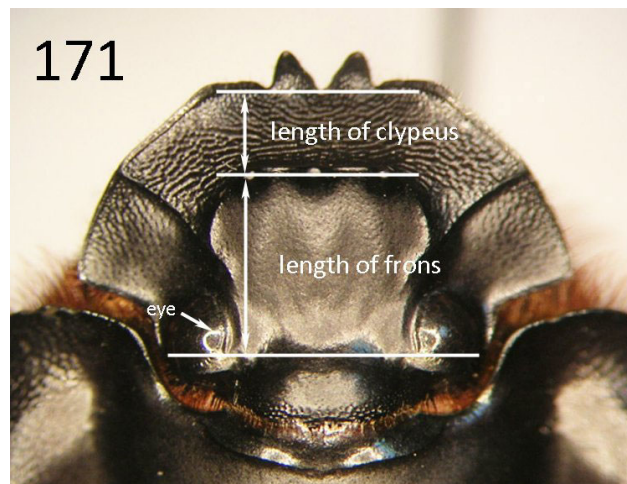


Figure 171. Characters of the *Coprophanaeus* (*s. str.*) pluto species group. Dorsal view head of male *C. morenoi* showing landmarks for measuring lengths of frons and clypeus (see Methods).

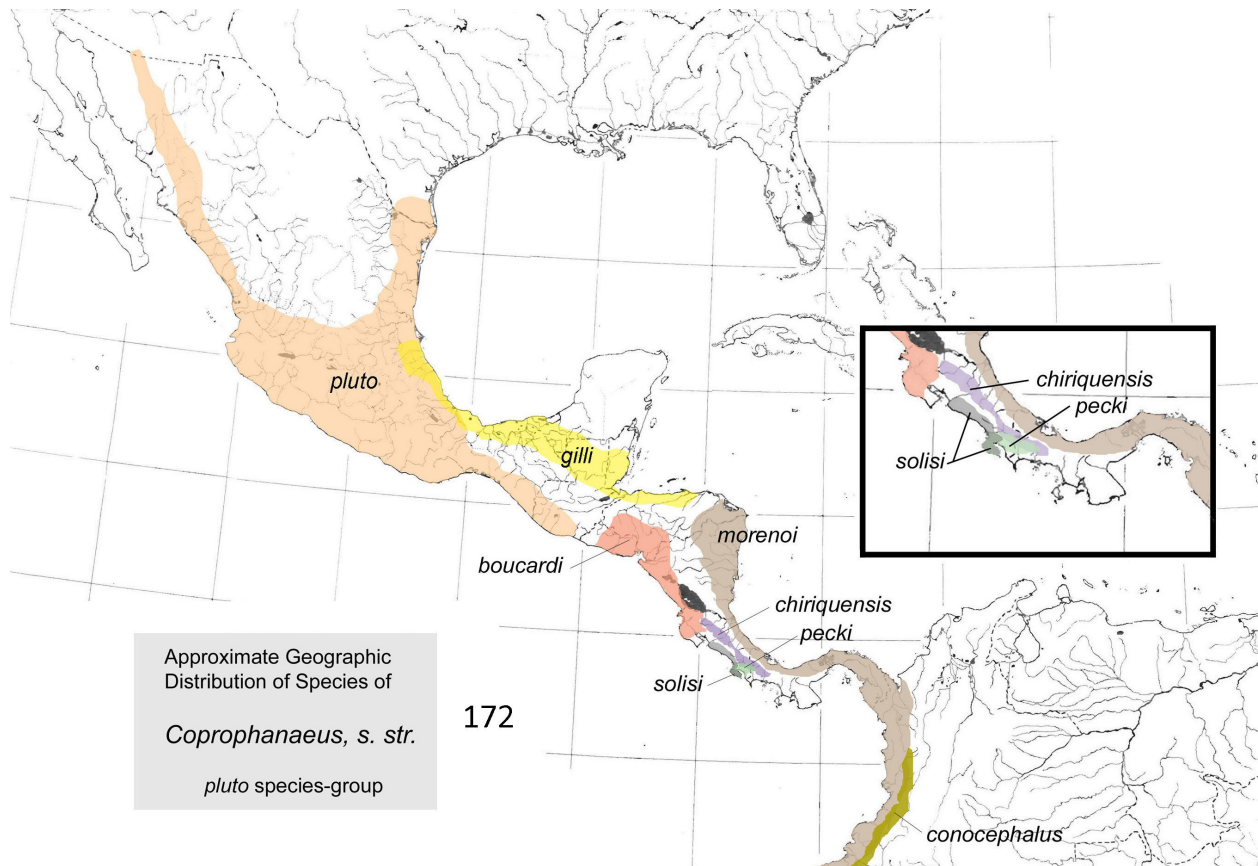


Figure 172. Approximate geographic distribution of *Coprophanaeus* (*s. str.*) species in the pluto species group.

Diagnosis. General – Completely black, only very rarely with metallic coloration along anterior pronotal margin. Clypeal teeth normal, length about equal to width at base. Width of upper portion of eye slightly greater than one-fourth of interocular distance. Frons smooth, at most with faint puncturing behind transverse carina. Posterior portion of paraocular area smooth. Posteromedian portion of pronotum smooth, devoid of distinct sculpturing; basal pronotal fossae effaced. Anterior angle of metasternum bearing elevated cap (seen in profile, as in Fig. 168). Elytral interstriae flat. Pygidium with wide basal groove (Fig. 162-163). Length 15-23 mm.

Male (Fig. 181-184) – Pronotal prominence bimorphic, either cleat-shaped (Fig. 183, upper view) or quadrilobate with lobes linked by thick carina (Fig. 183, lower view); prominence flanked by broad concavities; declivitous surface of pronotum beneath carina smooth, devoid of sculpturing. Parameres with wide subapical tooth (Fig. 184).

Female (Fig. 179-180) – Length of frons about one and one-half times that of clypeus. Transverse pronotal carina bidentate medially, followed by transverse depression summit of which weakly bitumid.

Specimens examined – 327.

Distribution. Chocó and Eastern Central American provinces (Fig. 172).

Collection Records. COLOMBIA: Chocó – Quibdó (Sep); El Amargal Biological Station, 5.6°N 77.4°W, 150-500 m (Aug); 30 km S Quibdó [Lloró], 5°30'N 76°33.5'W, 90 m (Feb); Pacurita, 5°41'N 76°40'W, 50 m (Nov); 20 km NE Quibdó [Tutumendó], 60 m (Nov). **Valle de Cauca** – 70 km E Buenaventura [Anchicaya Dam], 350 m (Jul). **COSTA RICA: Alajuela** – 3.5 km E Bijagua [Heliconias Lodge], 10°42'45.2"N 85°02'28.5"W, 730 m (May-Jun). **Heredia** – Reserva Biológica La Selva, 10°26'N 86°59'W, 75 m (Oct). **Limón** – Sector Cerro Cocori, Finca de E. Rojas, 150 m (Oct). **San José** – Estación Bijagual (north of



Figure 173-178. *Coprophanaeus pecki*. 173-174) Female habitus. 175-176) Male habitus. 177) Dorsal view of pronotal prominence of large male. 178) Aedeagus (dorsal view above; lateral view below).

Bijagualito), 600 m (Jun). **ECUADOR:** **Esmeraldas** – Borbón, 1°04'44"N 78°58'48"W, 25 m (Aug); San Miguel, 00°40'18"N 79°53'00"W (Dec); 11 km SE San Lorenzo [La Chiquita Forest Station] (Jun); Punta Venado (Nov-Dec); Yalere (Nov); Playa de Oro (Feb-Mar, Oct); La Concordia (Nov); Palma Real (Mar). **Los Ríos** – Río Palenque Research Station, 0°35'S 79°22'W, 200 m (Jan-Feb, Jun-Jul). **Pichincha** – Quevedo (Apr-May); 113 km NW Quito on Puerto Quito road, 800 m (Aug); 11 km E Tinalandia, 600 m (Jul). **NICARAGUA:** **Jinotega** – 32 km NW Jinotega [Finca El Jaguar], 13°14'28"N 86°03'16"W, 1340 m (Dec). **Matagalpa** – Selva Negra, 13°00'01"N 85°54'32"W, 1350 m (May). **Río San Juan** – 8 km S El Castillo [Refugio Bartola], 10°56.6'N 84°20.4'W, 30 m (Mar, May). **PANAMA:** **Colón** – 16 km SE Colón [Santa Rita Ridge], 270 m (Jun). **Darien** – Estación Ambiental Cana, 7°45.32'N 77°41.07'W, 600-750 m



Figure 179-184. *Coprophanaeus morenoi*. **179-180)** Female habitus. **181-182)** Male habitus. **183)** Dimorphism of male pronotal prominence (cleat-shaped form above; quadrilobate form below). **184)** Aedeagus (dorsal view on left; lateral view on right).

(Jun). **Panamá** – Capira [Cerro Campana], 8°44'N 79°57'W, 790 m (Jun, Dec); Chepo-Carti Road, 400 m (Jun-Aug); Cerro Azul, 650 m (May, Dec); 7.5-9.6 km N El Llano, 475 m (Jan); 12 km N El Llano on road to Carti, 250 m (May).

Comments. The occurrence of bimorphic major males in this species is unique to the genus and, although in different descriptive terms and under the name “*ohausi*”, it was first described by Howden and

Young (1981). The unusual form (Fig. 183, lower view) is so far known only from certain populations in the environs of El Llano (Panamá province), where it occurs with the typical cleat-shaped form (Fig. 183, upper view). Because the quadrilobate condition of the male pronotum occurs in individuals otherwise “major” in size and other respects, we consider it a developmental option to the cleat-shaped prominence in typical males rather than a step in the gradient from “major” to “minor” individuals.

The middle of basal margin of pygidium is sometimes weakly angulate and tooth-like, at least partially interrupting basal groove (Fig. 162). This was a key character in the original description that has revealed itself to be highly variable. The toothed condition is more frequent in Ecuadorian, Colombian and eastern Panamanian populations, but it becomes very rare beyond the Darien province.

For most of this study we regarded *C. kohlmanni* as a species distinct from *C. morenoi*; the primary criteria for doing so were its somewhat larger size and presumed isolated distribution. It turns out, however, that the distribution of *C. morenoi* is continuous from northwestern Ecuador through Panama along Caribbean coast into Nicaragua, and the species is subject to local variations along the way, the most striking of which is the unusual male type from western Panama. Costa Rican populations formerly assigned to *C. kohlmanni* are part of a continuum and tend to be somewhat larger than in other populations.

***Coprophanaeus (C.) solisi* Arnaud, 1997**

Fig. 165, 172, 185-188

Coprophanaeus solisi Arnaud, 1997: 6

Type. Holotype male, Canadian Museum of Nature, Ottawa (examined).

Diagnosis. *General* – Black except for red to reddish-green metallic coloring on pronotum and pygidium. Clypeal teeth normal, length about equal to width at base (Fig. 161). Length of frons about equal to that of clypeus. Width of upper portion of eye one-fourth to one-fifth of interocular distance. Frons smooth, at most with faint puncturing behind transverse carina. Paraocular area completely sculptured, sculpturing weakening closer to eye. Posteromedian portion of pronotum only weakly punctured, becoming smooth near posterior margin; basal pronotal fossae distinct. Anterior angle of metasternum with rounded cap (seen in profile, as in Fig. 167). Elytral interstriae convex (Fig. 165). Pygidium with wide basal groove. Length 13-16 mm.

Male (Fig. 185-187) – Tubercles of cephalic carina small, equal-sized. Pronotal prominence of large male cleat-shaped, width greater than that of emarginate, anteromedian portion of pronotal margin. Parameres lacking subapical tooth (Fig. 187).

Female (Fig. 188) – Transverse pronotal carina bidentate medially, followed by transverse depression with summit very weakly bitumid.

Specimens examined – 14.

Distribution. Western Isthmus province of Costa Rica (Fig. 172).

Collection Records. COSTA RICA: **Puntarenas** – Osa Peninsula [Río Piro La Joya], 8°23'56"N 83°19'51"W, 350 m (Aug-Sep); Rincón de Osa, 8°41.14'N 83°31.11'W, 150 m (Jun); Osa Peninsula [Rancho Quemado], 200m (Jul, Dec); Estación Agujas, Sendero Zamia, 300 m (Apr, Oct); Estación Quebrada Bonita [Reserva Biológica Carara], 50 m (Sep); Estación Los Patos, 200 m (Sep).

Comments. The distribution of *C. solisi* lies in the Pacific rainforest of the lower elevations of Puntarenas province of Costa Rica. This area includes the Osa Peninsula and extends northwest along the coast to the Tárcoles River, a landmark limit to Pacific coast species distributions discussed by Kohlmann and Wilkinson (2007). It is partially sympatric with *C. pecki* (*q.v.*).

***Coprophanaeus (C.) boucardi* (Nevinson, 1891)**

Fig. 160, 172, 189-194

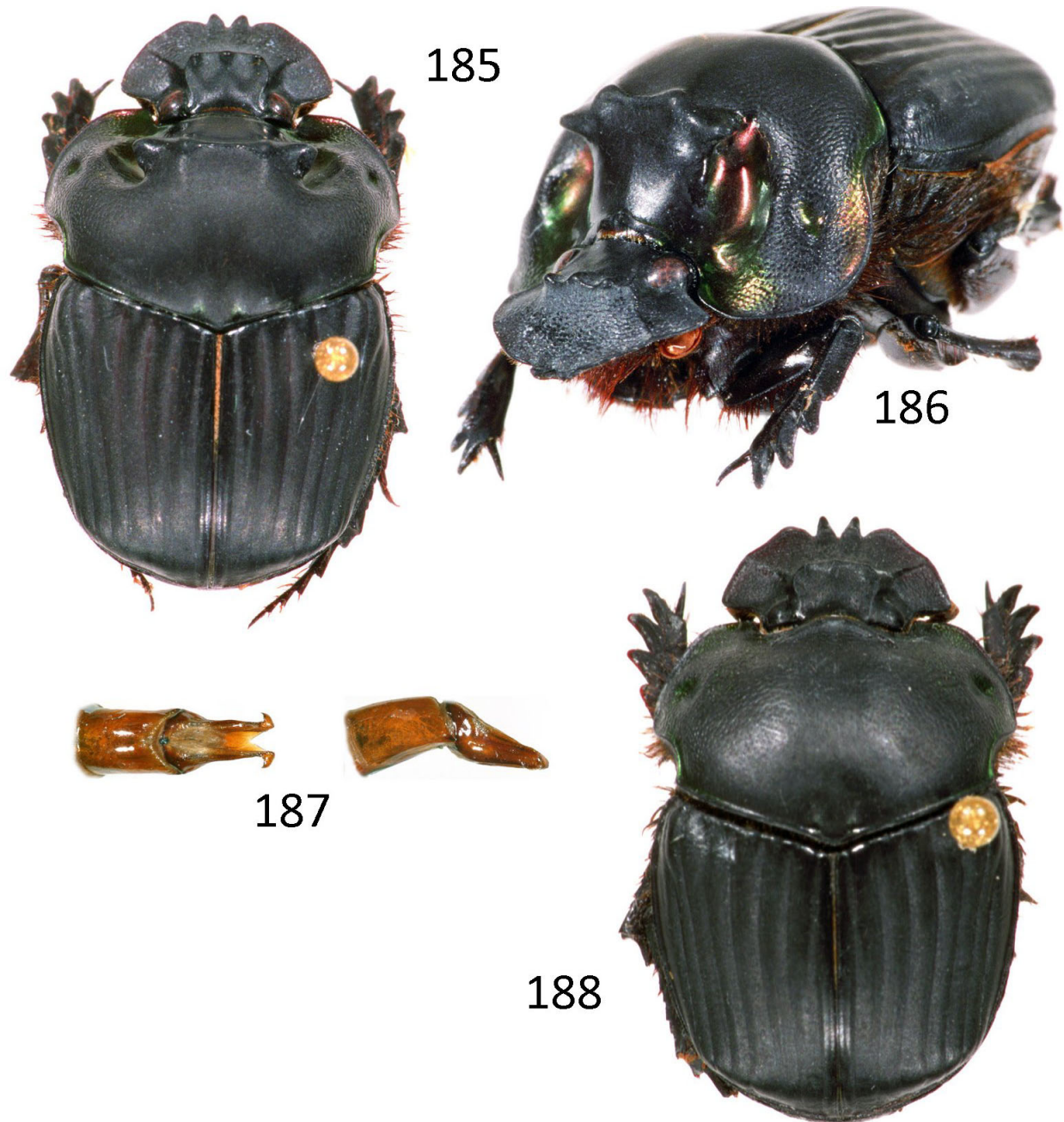


Figure 185-188. *Coprophanaeus solisi*. 185-186) Male habitus. 187) Aedeagus (dorsal view on left; lateral view on right). 188) Female habitus.

Phanaeus boucardi Nevinson, 1891: 208

Coprophanaeus boucardi (Nevinson) (recomb. by Edmonds 1972: 843)

Coprophanaeus pluto boucardi (Nevinson) (recomb. by Arnaud 2002c: 41)

Type. Lectotype male (des. by Arnaud 2002a: 9), The Natural History Museum, London (examined).

Diagnosis. *General* – Black except for green to yellowish-green metallic coloring on pronotum and pygidium. Clypeal teeth (subject to wear) elongate, length about one and half width at base (Fig. 160).

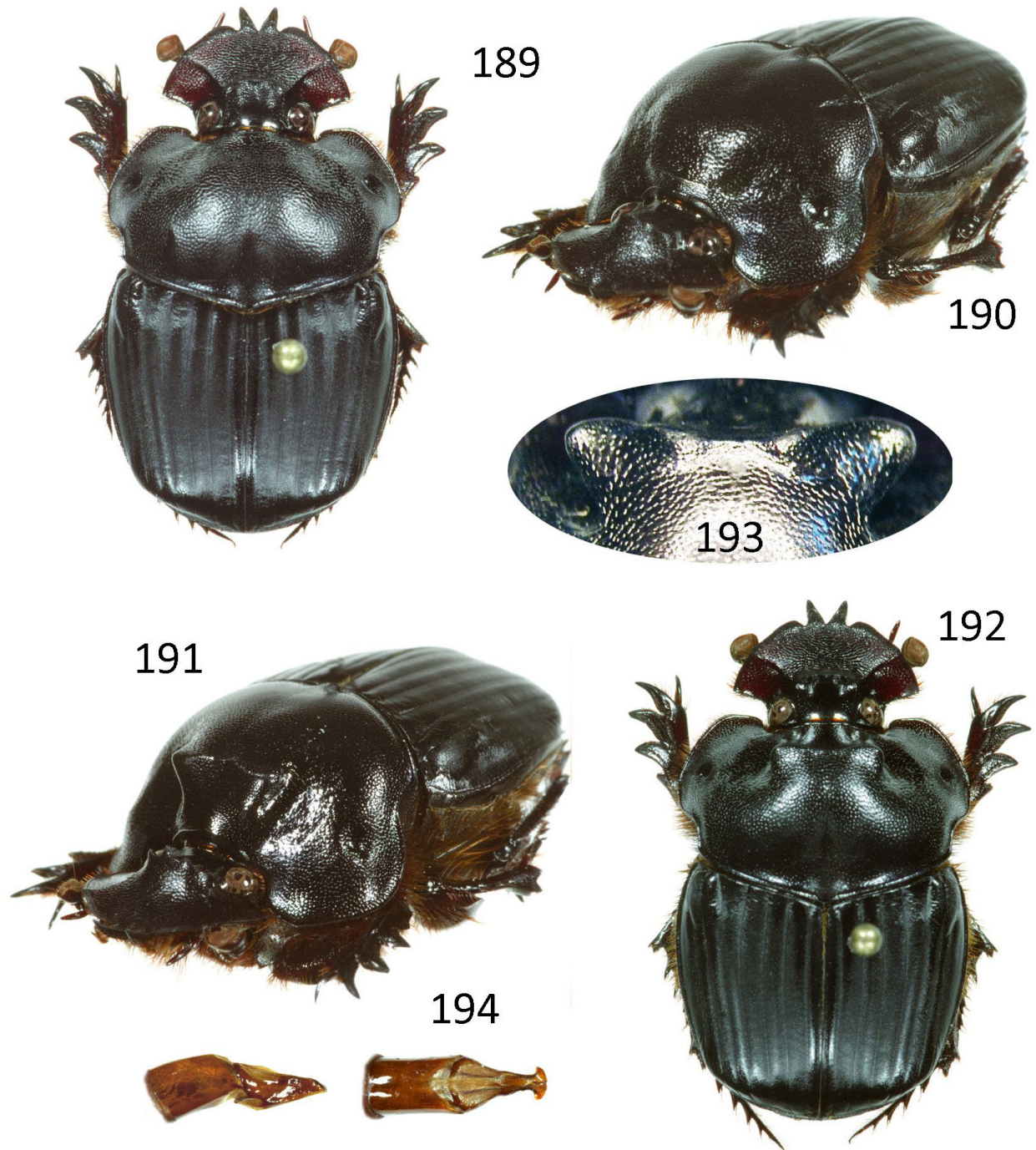


Figure 189-194. *Coprophanaeus boucardi*. 189-190) Female habitus. 191-192) Male habitus. 193) Dorsal view of pronotal prominence of large male. 194) Aedeagus (lateral view on left; dorsal view on right).

Length of frons about equal to that of clypeus. Eyes large, width of upper portion about one-third to one-fourth of interocular distance. Anterior one-half of frons punctate, smooth posteriorly. Paraocular area completely sculptured, sculpturing weakening closer to eye. Posteromedian portion of pronotum strongly punctured, punctures asperate, becoming weaker and sparser near posterior margin; basal pronotal fossae distinct. Anterior angle of metasternum with rounded cap (seen in profile, as in Fig. 167). Elytral interstriae at most only weakly convex (as in Fig. 166). Pygidium with wide basal groove (as in Fig. 163). Length 13-25 mm.

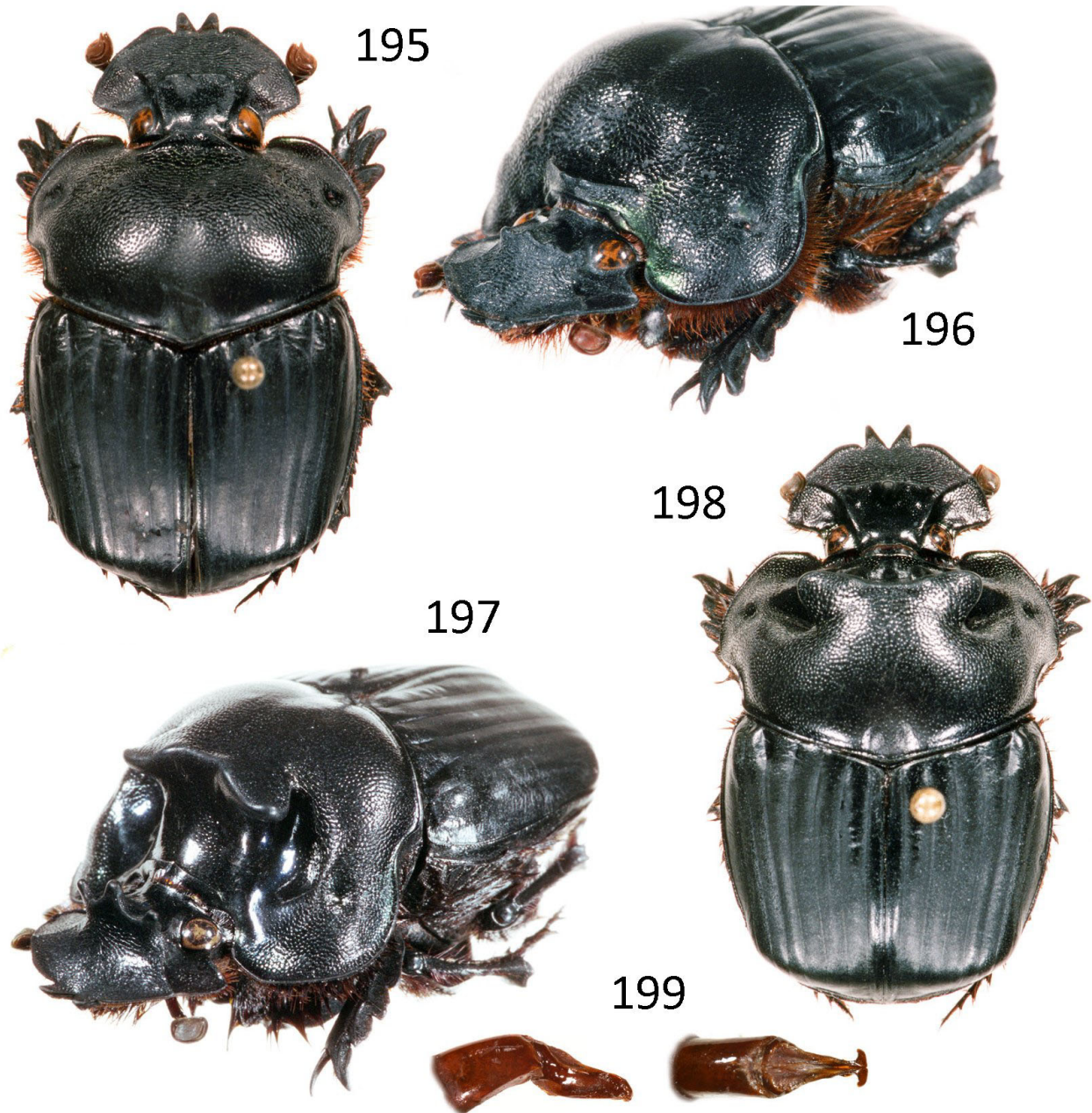


Figure 195-199. *Coprophanaeus pluto*. 195-196) Female habitus. 197-198) Male habitus. 199) Aedeagus (lateral view on left; dorsal view on right).

Male (Fig. 191-194) – Tubercles of cephalic carina acute, equal-sized, somewhat elongate. Pronotal prominence of large male (Fig. 193) cleat-shaped, lateral angles reduced such that width is less than that of emarginate, anteromedian portion of pronotal margin. Parameres lacking subapical tooth (Fig. 194).

Female (Fig. 189-190) – Transverse pronotal carina bidentate medially, followed by transverse depression with summit weakly bitumid.

Specimens examined – 48.

Distribution. Extreme southern portion of the Pacific Coast province (Fig. 172).

Collection Records. COSTA RICA: Guanacaste – Liberia (Aug); 34 km N Liberia (Hacienda Poco Sol) (May-Jul); Rincón de la Vieja National Park, 775 m (Jun); Estación Santa Rosa [Parque Nacional

Santa Rosa], 10°50'23.0"N 85°37'07.0"W, 290 m (Jun-Jul); . **San José** – Santo Domingo (Aug). **EL SALVADOR: San Salvador** – San Salvador (Jul); Santa Tecla (Nueva San Salvador), 900 m (Sep); Lago Ilopango (Aug). **HONDURAS: Cortés** – Parque Nacional Cerro Azul-Meambar, 14°52.4'N 87°54.7'W, 800 m (May). **Francisco Morazán** – El Zamorano [Escuela Agrícola Panamericana], 800 m (Jul); Tatumbla, 1400 m (Oct). **Olancho** – 14 km N La Unión [Parque Nacional La Muralla], 1500 m (Aug).

Comments. Pereira (1953) regarded this species as a synonym of *C. pluto*. This very close relative of *C. pluto* is a denizen endemic to dry forests of the Pacific coast of Costa Rica, Honduras and El Salvador, where it occurs with *Phanaeus eximius* Bates and *P. demon* var. *excelsus* Bates. We have seen specimens labeled Tuxtla Gutierrez, Chiapas (530 m); while its occurrence there is a reasonable possibility, the record needs confirmation.

***Coprophanaeus (C.) pluto* (Harold, 1863)**

Fig. 151-153, 161, 166-167, 169-170, 172, 195-199

Phanaeus pluto Harold, 1863: 164

Coprophanaeus pluto (Harold) (recomb. by Edmonds 1972: 843)

Phanaeus morio LeConte, 1863: 36 (syn. by Gillet 1911: 85)

Coprophanaeus pluto nogueirai Arnaud, 2002b: 2 **New Synonymy**

Type. *P. pluto* – lectotype male (des. by Arnaud 1982a: 115), Muséum National d'Histoire Naturelle, Paris (examined by photo; see Comments); *P. morio* – holotype male, Museum of Comparative Zoology, Harvard University, Cambridge (examined by photo). *C. nogueirai* – holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France.

Diagnosis. *General* – Black except for green to yellowish-green metallic coloring on pronotum and pygidium. Clypeal teeth normal, length about equal to width at base (Fig. 161). Length of frons about equal to that of clypeus. Eyes normal, width of upper portion one-fourth to one-fifth of interocular distance. Frons smooth, at most with faint puncturing behind transverse carina. Paraocular area completely sculptured, sculpturing weakening closer to eye. Posteromedian portion of pronotum distinctly punctured, punctures reaching posterior margin; basal pronotal fossae distinct. Anterior angle of metasternum with rounded cap (seen in profile, Fig. 167). Elytral interstriae at most only weakly convex (Fig. 166). Pygidium with wide basal groove. Length 14-25 mm.

Male (Fig. 151-153, 169-170, 197-199) – Lateral tubercles of cephalic carina small, acute; middle tubercle variable: a) same size and shape as laterals (Fig. 151), b) elongate, about twice as high as laterals (Fig. 152), or c) lengthened, broadened and truncate or weakly emarginate apically (Fig. 153). Pronotal prominence of large male cleat-shaped (Fig. 197-198), width greater than that of emarginate anteromedian portion of pronotal margin. Parameres lacking subapical tooth (Fig. 169, 199).

Female – Transverse pronotal carina bidentate medially, followed by transverse depression with summit weakly bitumid.

Specimens examined – 377.

Distribution. All Mesoamerican provinces of Mexico (Fig. 172).

Collection Records. **GUATEMALA: Suchitepéquez** – Variedades, 300 m. **MEXICO: Aguascalientes** – Aguascalientes (Sep). **Chiapas** – 19 km N Mapastepec, 550 m (Aug); Tapachula; Rosario Izapa (May). **Colima** – Manzanillo (Aug); Plantanarilla, 1200 m (Jul); 1 km S El Limón, 870 m (Jul). **Guerrero** – 7 km N Taxco (Jun); 45 km NE Ixtapa (Aug). **Hidalgo** – Laguna Azteca (Sep). **Jalisco** – El Tuito, 600 m (Jul); Guadalajara (Jul); Estación Biológica Chamela; Sierra de Manantlán, La Calera, 760 m (Oct); Sierra de Quila, Tecolotlán, 1580 m (Jul); Toanya, 950 m (Jul); Sierra de Manantlán, El Tigre, 700 m (Jul); Ejutla (la Estancia), 960 m (Oct); Autlán, 875 m (Jun); Puerto Los Mazos, 1350 m (Jul); Mezquitlán, 1000 m (Jul); El Parotal, 456 m (Sep); Zenzontla, 1000 m (Jun); ~ 5 km WNW Talpa de Allende, 20°23.893'N 104°51.980'W, 1263 m (Jul). **Mexico** – Valle de Bravo (Sep); 10 km SW Valle de Bravo (Jun). **Michoacan** – road between La Huacana and Ario de Rosales (Jul). **Morelos** – Cuernavaca; Tlaltizapan (Jul); Acamilpa

(Jul). **Nayarit** – Tepic (Jul); Mesa de Nayar (Jul); Jesus María. **Nuevo Leon** – El Diente (Oct). **Oaxaca** – near Monte Albán, 17°03'34.0"N 96°45'53.4"W, 1690 m (Jul). **Queretaro** – 2 km S Valle Verde, 21.501°N 99.177°W, 1300 m (Aug). **Sinaloa** – 13 km E Villa Unión, 100 m (Jul). **San Luis Potosí** – 6.5 km E Cd.Maiz (Aug); 80 km NNW Cd. Valles (El Salto) (Jul). **Sonora** – 29 km NW Yécora, 28°23'34.7"N 109°05'30.8"W, 1350 m (Jul); 32 km NW Yécora, 28°24'03.6"N 109°06'24.4"W, 1190 m (Jul); Alamos, 400 m (Sep); 75 km W Yécora, 28°29'09"N 109°21'32"W, 935 m (Aug); 140 km W Yécora, 28°36'12"N 109°48'06"W, 550 m (Aug). **Tamaulipas** – 75 km E Cd. Victoria [Villa de Casas] (Jul); Gómez Farías [Estación Biológica Los Cedros], 350 m (Jul); 4.5 km W Gómez Farías [Altas Cimas], 900 m (Jul); Villa Aldama (Aug); Villa Allende, 90 m (Aug). **Veracruz** – Palma Sola (Jun); 11 km W Palma Sola, 19°46'N 96°25'W, 120 m (Aug-Sep); Río Playa; Córdoba (Jul); Actopan (Aug); Cerro Sonpaso, 690 m (Aug); Apazapan, 19°19'18"N 96°42'39"W, 280 m (Aug); 14 km WSW Papantla [Plan de Hidalgo] (May); Alto Lucero, 690 m (Sep). **UNITED STATES: Arizona** – Santa Cruz Co., Nogales (Sep). **Texas** – Cameron Co. - Sabal Palm Grove Sanctuary (Oct); 12.5 km N junction hwy. 106 and FM 2925; Laguna Atascosa National Wildlife Refuge (Nov); Harlingen (Nov). Hidalgo Co. – Edinburg.

Comments. The male cephalic carina of *C. pluto* is trimorphic. In the “major” state (Fig. 153) the middle tubercle is greatly thickened, much higher than the laterals, and apically truncate or weakly excised. This form is characteristic of very large males along the Gulf coast of Veracruz, Tamaulipas and into southern Texas, where it occurs along with the “minor” form. In the “minor” state (Fig. 151) the three tubercles are equal-sized. The minor state (described as the subspecies “*nogueirai*” by Arnaud 2002b; see below) is found in Gulf Coast populations and is the only known condition in populations along the Pacific coast. In the third state (Fig. 152), occurring infrequently in isolated populations in southern Mexico, the middle tubercle is acute and about twice the length of the laterals.

This is the only species of the genus known to reach the United States, where it has been collected in extreme southern Texas and Arizona. Riley and Wolfe (2003) reported *C. pluto* from Cameron, Starr and Willacy counties, which, along with Hidalgo County, comprise the southern tip of Texas. Certain individuals from southern Texas exhibit the dark blue metallic color seen also in *C. gilli*, which they can resemble at first glance. Robinson (1948) reported *C. pluto* from Arizona.

We regard the lectotype in the Paris museum as the primary type of this species on the assumption that Harold's many phanaeinae types remained there in the nineteenth century in the wake of the dispute between the Paris and London museums. However, there is a specimen in the London museum labeled as holotype; in this case none of the labels is attributable to Harold himself. Both specimens are, to our eyes, assignable to *C. pluto*.

Arnaud (2002b) based *C. pluto nogueirai* (original name “*nogueraei*” emended to “*nogueirai*” by Zidek 2005) on the structure of the “minor” male cephalic carina. For much of this study we were inclined to recognize Arnaud's taxon as valid. As far as we know, large males of “*nogueirai*” from southern Mexico and the Pacific coast always have an acute middle tubercle; that is, they are always “minor.” We have found, however, that Gulf coast populations often also include, along with “major” males, individuals identical to *C. nogueirai*. Our conclusion is that the only defining character of *C. p. nogueirai* – a male cephalic carina with three acute, usually equal-sized tubercles (Fig. 151) – is an expression of the normal intrapopulation variation of the male of *C. pluto* that has become fixed in southern and western populations of the species. The case of “*nogueirai*” poses interesting questions about male variation and the genetic status of species “*en statu nascendi*” that would be well worth an intensive population genetics study.

***Coprophanaeus (C.) conocephalus* (Olsoufieff, 1924)**

Fig. 172, 200-204

Phanaeus conocephalus Olsoufieff, 1924: 72

Coprophanaeus conocephalus (Olsoufieff) (recomb. by Blackwelder 1944: 209)

Phanaeus roubali Balthasar, 1939: 241 (syn. by Arnaud 1997: 7)

Coprophanaeus edmondsi Arnaud, 1997: 5 **New Synonymy**

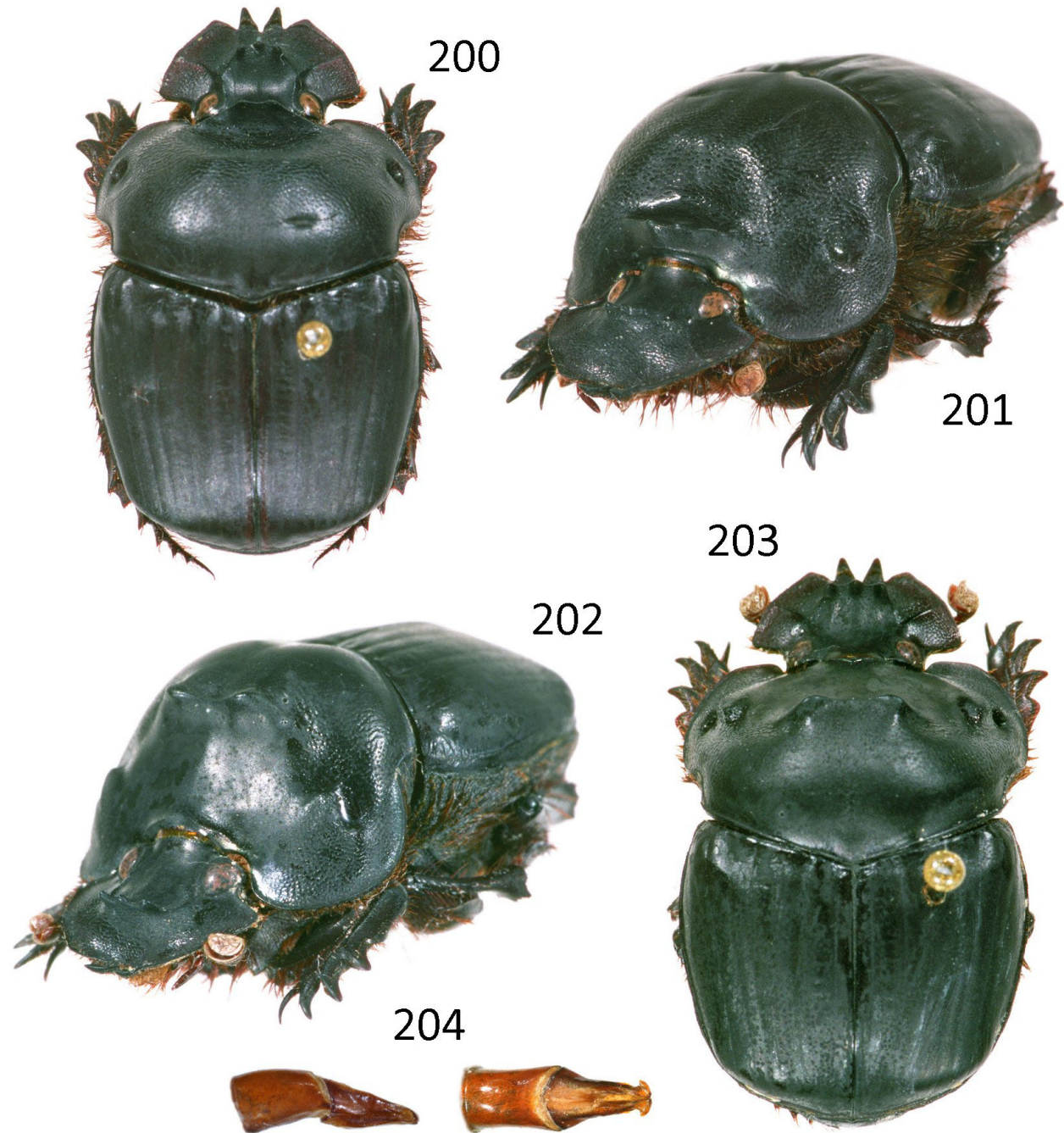


Figure 200-204. *Coprophanaeus conocephalus*. 200-201) Female habitus. 202-203) Male habitus. 204) Aedeagus (lateral view on left; dorsal view on right).

Type. *P. conocephalus* – holotype female, Muséum National d'Histoire Naturelle, Paris (examined by photo); *P. roubali* – holotype, National Museum, Prague (examined); *C. edmondsi* – holotype male, Canadian Museum of Nature, Ottawa (examined).

Diagnosis. *General* – Black except for dark blue metallic coloring on pronotum and pygidium. Clypeal teeth normal, length about equal to width at base. Eyes normal, width of upper portion one-fourth to one-fifth of interocular distance. Frons smooth, at most with faint puncturing behind transverse carina (stronger puncturing in female). Paraocular area completely sculptured, sculpturing weakening closer to

eye. Posterior portion of pronotum virtually smooth, if puncturing visible (x10) then minute and sparse; basal pronotal fossae distinct. Anterior angle of metasternum with rounded cap (seen in profile, as in Fig. 167). Elytral interstriae at most only weakly convex, seldom shinier midlongitudinally. Pygidium usually lacking distinct basal groove, rarely with narrow basal groove. Length 15-20 mm.

Male (Fig. 202-204) – Length of frons about one and half times that of clypeus. Teeth of cephalic carina closely set, distance between lateral teeth usually about one-half that of interocular distance. Pronotum lacking distinct fovea above lateral fossa; sometimes with prominent tubercle in front of lateral fossa (Fig. 202). Pronotal prominence of large male narrow, bitumid, tumescences connected by ridge. Parameres at most with indistinct subapical tooth.

Female (Fig. 200-201) – Teeth of cephalic carina closely set, distance between lateral teeth about one-half or less of interocular distance. Lengths of frons and clypeus about equal. Transverse pronotal carina bidentate medially, followed by very weak depression.

Specimens examined – 17.

Distribution. Cauca province (Fig. 172).

Collection Records. **COLOMBIA:** Nariño – Río Ñambi, 1°17'N 78°15'W, 1350 m (May). **Valle de Cauca** – Morro Frio, 1800 m (Mar); Q. Cristalina, AM Calima (Jul) **ECUADOR:** Cañar – Javin, 850-1400 m (Feb). **Carchi**, Parroquia El Goaltal, Hacienda San Francisco, 1200 m (Sep). **Guayas** – Balzar (Feb). **Pichincha** – Chiriboga, 1500 m (Feb); Chiriboga Road, 9.8 km NE Hwy. 30, 00°13'14"S 78°53'20"W, 1300 m (Mar).

Comments. There is no good reason in our opinion to maintain *C. edmondsi* as a distinct taxon in view of its close morphological and geographical relationship with *C. conocephalus*. The distribution of this species appears to parallel that of *C. morenoi* in Colombia and Ecuador at higher elevations (> 1000 m) along the western slopes of the cordillera (Note: The Ecuadorian portion of the range is not depicted in Fig. 172.) Along with *C. chiriquensis* and *C. gilli*, it forms a cluster differing from the pluto subgroup by its bitumid, rather than cleat-shaped, pronotal prominence.

***Coprophanaeus (C.) chiriquensis* (Olsoufieff, 1924)**

Fig. 154-157, 164, 172, 205-209

Phanaeus chiriquensis Olsoufieff, 1924: 73

Coprophanaeus chiriquensis (Olsoufieff) (recomb. by Blackwelder 1944: 209)

Coprophanaeus uhleri Malý and Pokorný, 2008: 6 **New Synonymy**

Type. *P. chiriquensis* – female lectotype (des. by Arnaud, 1982: 116), Muséum National d'Histoire Naturelle, Paris (examined by photo); *C. uhleri* – holotype male, National Museum, Prague (examined).

Diagnosis. *General* – Black except for dark blue metallic coloring on pronotum and pygidium. Clypeal teeth normal, length about equal to width at base. Eyes normal, width of upper portion one-fourth to one-fifth of interocular distance. Frons with weak, sparse puncturing behind transverse carina. Paraocular area completely sculptured, sculpturing weakening closer to eye. Posterior portion of pronotum usually smooth, at most with very weak, sparse puncturing; basal pronotal fossae distinct. Anterior angle of metasternum with rounded cap (seen in profile, as in Fig. 167). Elytral interstriae distinctly convex, usually shinier midlongitudinally (Fig. 205, 208). Pygidium usually lacking basal groove, rarely narrow groove present. Length 15-20 mm.

Male (Fig. 154-157, 205-207) – Length of frons about one and half times that of clypeus. Teeth of cephalic carina closely set, distance between lateral teeth usually about one-half that of interocular distance. Pronotum with large, oval fovea mesial to lateral fossa (as in Fig. 210, arrow). Pronotal prominence of large male bitumid (Fig. 154-157); tumescences widely separated, usually connected by ridge, each with flattened, triangular area on dorsal surface. Parameres with acute subapical tooth (Fig. 207, 212).



Figure 205-212. *Coprophanaeus* spp. 205-209) *C. chiriquensis*. 205-206) Male habitus. 207) Aedeagus (lateral view on left; dorsal view on right). 208-209) Female habitus. 210-212) *C. gilli*. 210-211) Male habitus. 212) Aedeagus (dorsal view above; lateral view below).

Female (Fig. 208-209) – Distance between lateral teeth of cephalic carina clearly greater than one-half of interocular distance. Lengths of frons and clypeus about equal. Transverse pronotal carina bidentate medially, followed by transverse depression.

Specimens examined – 130.

Distribution. Central cordillera of Costa Rica between Eastern Central America and Western Isthmus provinces (Fig. 172).

Collection Records. **COSTA RICA:** **Alajuela** – 3.5 km E Bijagua [Heliconas Lodge], 10°42'45.2"N 85°02'28.5"W (May-Jun); Parque Nacional Guanacaste [Estación San Ramón], 620 m (Jun); Reserva Biológica Alberto Brenes, Río San Lorencito, 850 m (Jun). **Cartago** – Río Grande de Orosi, 1150-1600 m (Dec); 19.3 km NE San José, 1010 m (May). **Guanacaste** – 9 km S Santa Cecilia [Estación Pitilla], 700 m (Jun-Jul); Tierras Morenas, 700 m (Mar); Rincón de la Vieja National Park, 775 m (Jun). **Heredia** – 16 km SSE La Virgen, 10°16'N 84°05'W, 1100 m (Mar). **Puntarenas** – San Vito [OTS Las Cruces Field Station], 1200 m (May-Jul); 6 km S San Vito, 1000 m (Apr-May); Monteverde, 1400m (May-Aug); 1 km NE Sitio Portones [Zona Protectora Las Tablas], 1530m (May); 1 km SW Cerro Biolley, Buenos Aires [Estación Altamira], 9°01'58"N 83°00'39"W, 1300-1450 m (Feb, Mar, Jul, Nov); 1.4 km NE La Tigra [Avenida El Pizote], 1300 m (Jul); Estación La Casona, Monte Verde, 10°18.5'N 84°47.8'W, 1520 m (Jun). **PANAMA:** **Chiriquí** – 4km N Santa Clara [Hartmann's Finca], 8°51'N 82°46'W, 1500 m (Jun-Aug); La Fortuna Dam, 1000m (Jul); 15km NE Gualaca [Cerro Hornito], 1200 m (Jul-Sep); 33.1 km S Chiriquí Grande, 800 m (Dec); Boquete (Jun). **Veraguas** – 8 km W Santa Fe [Cerro Tute], 8°30'26"N 81°06'49"W, 900 m.

Comments. *Coprophanaeus uhleri* is based on smaller specimens that fit well within the observed variation of *C. chiriquensis*. Pereira and Martínez (1956; see also 1960) erroneously synonymized this species with *C. corythus*. The posterior portion of the pronotum (as well as the frons) is smooth and usually devoid of any distinct punctures; rare individuals (usually large females) can show distinct, sparse puncturing (x10) (see *C. gilli*). *Coprophanaeus chiriquensis* has been collected along with *C. pecki* in the Chiriquí region of Panama; but otherwise its distribution follows the cloud forests of the central Costa Rican cordillera that separates the Western Isthmus province from Eastern Central America province.

Coprophanaeus (C.) gilli Arnaud, 1997

Fig. 158-159, 172, 210-212

Coprophanaeus gilli Arnaud, 1997: 4

Coprophanaeus henryi Malý and Pokorný, 2008: 2 **New Synonymy**

Type. *C. gilli* – holotype male, Canadian Museum of Nature, Ottawa (examined); *C. henryi* – holotype male, National Museum, Prague (examined).

Diagnosis. *General* – Black except for dark blue metallic coloring on pronotum and pygidium (rarely also on elytra). Clypeal teeth normal, length about equal to width at base. Eyes normal, width of upper portion one-fourth to one-fifth of interocular distance. Frons weakly to moderately strongly punctured behind transverse carina. Paraocular area completely sculptured, sculpturing weakening closer to eye. Postero-medial portion of pronotum distinctly punctured, punctures progressively weaker and sparser approaching posterior margin; basal pronotal fossae distinct. Anterior angle of metasternum with rounded cap (seen in profile, as in Fig. 167). Elytral interstriae distinctly convex, usually shinier midlongitudinally (as in Fig. 205, 208). Pygidium usually lacking basal groove, rarely narrow groove present. Length 15-26 mm.

Male (Fig. 158-159, 210-212) – Length of frons about one and half times that of clypeus. Teeth of cephalic carina closely set, distance between lateral teeth usually about one-half that of interocular distance. Pronotum with oval fovea above lateral fossa (Fig. 210, arrow). Pronotal prominence of large male

thickened transverse carina with pair of closely set median tumescences, sometimes scarcely broken medially. Parameres with acute subapical tooth (Fig. 212, upper view).

Female – Distance between lateral teeth of cephalic carina clearly greater than one-half of interocular distance. Lengths of frons and clypeus about equal. Transverse pronotal carina bidentate medially, followed by transverse depression.

Specimens examined – 102.

Distribution. Gulf of Mexico and Eastern Central America provinces (Fig. 172).

Collection Records. **BELIZE:** Toledo – Chiquibul National Park (Doyle's Delight), 16 29'23"N 89 02'45"W, 950 m (Aug). **HONDURAS:** Cortes – Parque Nacional Cusuco, Santo Tomás, 700-800 m (Aug). Olancho – Parque Nacional La Muralla, 1800 m (Jun). **GUATEMALA:** Alta Verapaz – Finca Seacté Cobán (Apr). Izabal – 8 km N Las Escobas [Cerro San Gil], 800 m (Jun). Zacapa – 3 km S La Unión, 1400 m (Jun). **MEXICO:** Chiapas – 10.5 km W El Bosque, 1480 m (Aug); Santa Rosa (Aug); Bonampak, 16°44'N 91°05'W, 300 m (Sep). Hidalgo – Tlanchinol (Jun, Aug); Otongo, 1120 m (Jul). Oaxaca – Huautla de Jiménez (Nov); Los Metates (Sep). Puebla – Calapan 19°55'45.92"S 97°23'07.65"W, 1250 m (Jul). Veracruz – 33 km NE Catemaco, 160 m (Jul); Cuautlapan (Aug-Sep); Pipiapan [Parque de la Fauna y Flora Silvestre Tropical], 600 m (Nov); Dos Amates [Catemaco] (Jul, Sep); Sontecomapan [Estación Biológica Tropical "Los Tuxtles"], 400 m (Jun, Oct); Ruiz Cortinas [Mpio. San Andrés Tuxtla], 1020 m (Apr). Cerro El Gallo [Mpio. Catemaco], 810 m (Apr); Guadalupe Victoria [Mpio. Tatahuicapan], 750 m (Jun); San Martín Pajapan [Mpio. Mecayapan], 720 m (Feb); Cuautlapan [Cerro Chicahuaxtla] (Aug); Ruiz Cortines (Apr).

Comments. This species is very closely related to *C. chiriquensis*, and, given the long history of intense collecting in Mexico and Central America, it is surprising that it went undiscovered until the late twentieth century. It differs from *C. chiriquensis* in geographic distribution, the shape of prominence of male pronotum, a somewhat larger average size, and usually in distinct (x10) puncturing of the frons and posterior portion of the pronotum. *Coprophanaeus henryi* is based on smaller specimens that fit well within the variation of *C. gilli*.

Among the best data we have on the local ecology of this species are those provided by Matthias Rös (pers. comm.). Careful sampling in the sierras of northern Puebla has revealed a rather broad habitat, from well conserved mesophilous forest to secondary growth, acahual (scrub), coffee plots and other highly disturbed areas between 1000 and 1300 m. Sharing this ecological spectrum there with *C. gilli* is another neotropical immigrant, *C. corythus*.

The dardanus species group

The dardanus group brings together at least nine species comprising three subgroups: a) *Coprophanaeus dardanus* [monobasic]; b) *C. milon* and *C. magnoi*; and c) *C. telamon*, *C. ignecinctus*, *C. corythus*, *C. parvulus*, *C. degallieri* and *C. christophorowi*. All except the Mesoamerican *C. corythus* are South American species. Of the *Coprophanaeus s. str.* species groups recognized here this one is the most tenuous, and it may later benefit from being split into at least two separate species groups.

Diagnosis. *General* – Frons short, length usually much less than that of clypeus. Anterior portion of circumnotal ridge interrupted behind eyes (Fig. 8). Posterior edge of paraocular area abruptly curved toward posterior angle of eye. Anterior one-half of pronotum generally bearing squamose granulation, often coalescing into short, transverse ridges; remainder of pronotum punctate, puncturing becoming progressively weaker toward posterior margin (more so in larger males); basal fossae distinct (except *C. christophorowi* and *C. parvulus*). Prosternal ridge simple, lacking acute tubercle at anterior end. Elytral interstriae variable; striae very fine. Usually dark, sombre species to unaided eye; metallic coloration inconspicuous (except in *magnoi*) and most obvious under magnification (x10), restricted to anterior portion and margins of pronotum and pygidium; venter always showing reflections of same tone as dorsum. Small to medium-sized species, length usually 12-25 mm.

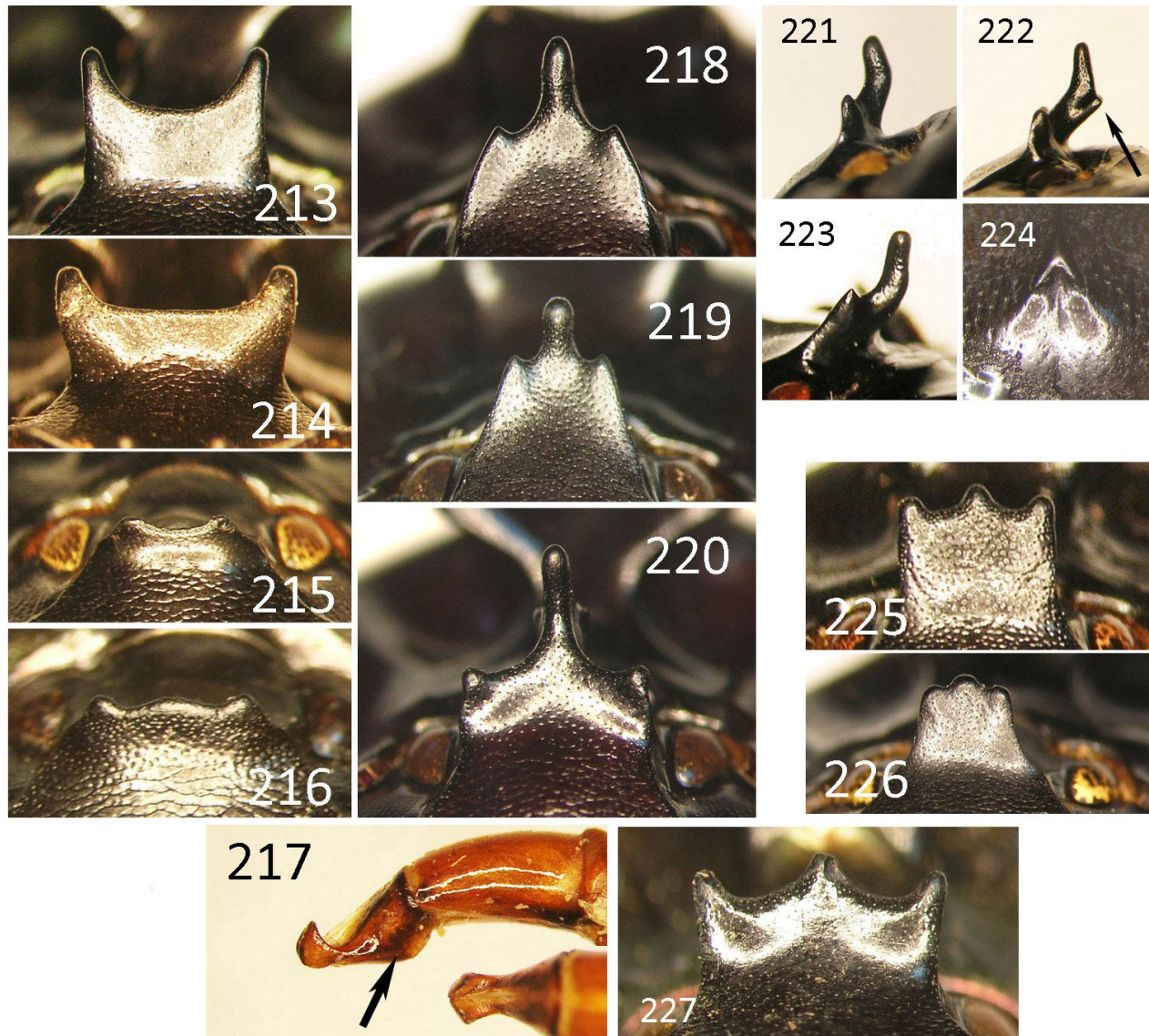


Figure 213-227. Characters of the *Coprophanaeus* (*s. str.*) *dardanus* species group. **213-214)** *C. dardanus*, anterior view of cephalic process of large male. **215)** Same, small male. **216)** Same, female. **217)** *C. telamon*, aedeagus (lateral view above; dorsal view below). **218-219)** *C. corythus*, anterior view of male cephalic process. **220)** *C. telamon*, same. **221-222)** *C. telamon*, lateral view of male cephalic process (arrow in 222 indicates posterior tubercle). **223)** *C. corythus*, lateral view of male cephalic carina. **224)** *C. degallieri*, metasternal shield. **225-226)** *C. milon*, anterior view of male cephalic process. **227)** *C. magnoi*, same.

Male – Apices of parameres (Fig. 217) with distinct, dorsally projecting, acute teeth visible in profile (attenuated in *C. parvulus* and *C. degallieri*); base extending below phallobase as heel-like prominence (Fig. 217, arrow). Head horned (horn reduced in *C. parvulus*, *C. degallieri* and *C. christophorowi*); base of horn transverse, placed just in front of eyes; apex bearing three tubercles (two in *C. dardanus*), central one sometimes drawn out as finger-like process (Fig. 218-220). Pronotal prominence often cleat-shaped, sometimes reduced to pair of rounded bumps.

Female – Head with transverse trituberculate carina set close to eyes, usually gently bowed anteriorly; frons usually clearly shorter than clypeus. Pronotum with low, rounded, transverse crest very near anterior margin followed by shallow depression or distinct concavity.

Distribution. All of Neotropical region (only one species, *C. corythus*, in Mesoamerican subregion).

Key to species of the dardanus group

1. Cephalic horn of large male (Fig. 218-223; reduced in *christophorowi*) usually strongly inclined posteriorly; anterior surface of horn base flat to concave, apex of horn with central finger-like process flanked on each side by acute tubercle. **telamon subgroup** 4
- Cephalic horn of large male (Fig. 213-215, 225-226) erect or slightly inclined anteriorly, trituberculate or very widely bituberculate 2
- 2(1). Clypeal margin usually strongly angulate adjacent to median teeth (as in Fig. 235). Male cephalic process with strongly produced, horn-like lateral angles separated by deep curve in apical margin (Fig. 213-214); female process a carina with small denticle at each end separated by broad elevation (Fig. 216). Pronotal prominence of large male cleat-shaped, produced laterally into acute lobes (Fig. 242). Pronotal disk smooth midlongitudinally. Length of clypeus about equal to that of frons. **dardanus subgroup** ***Coprophanaeus (C.) dardanus (MacLeay)***
- Clypeal margin rounded, at most only very weakly angulate lateral to median teeth (Fig. 236). Male cephalic process tridentate apically (Fig. 225-226); female process a trituberculate carina. Male pronotal prominence bilobate, lobes directed forward (Fig. 247). Pronotal disk with midlongitudinal sulcus widening posteriorly into triangular depression. Length of clypeus greater than that of frons. **milon subgroup** 3
- 3(2). Some portion of pronotum and sometimes also elytra metallic green (Fig. 244-247). Elytral striae carinulate (Fig. 234). Male pronotal prominence bilobate, lobes directed anteriorly (Fig. 247). Chaco and Cerrado provinces ***Coprophanaeus (C.) magnoi Arnaud***
- Dorsum dark, weakly shiny blue. Elytral striae (Fig. 233) rarely distinctly carinulate. Male pronotal prominence cleat-shaped, lobes acute, directed anterolaterally (Fig. 252). Chaco, Pampa and Monte provinces ***Coprophanaeus (C.) milon (Blanchard)***
- 4(1). Posterior surface of protibiae with row of coarse, confluent punctures paralleling longitudinal carina (Fig. 230, arrow), otherwise weakly sculptured. Cap of anterior angle of metasternum (viewed ventrally, Fig. 224) V-shaped (weakly so in *C. christophorowi*). Male head horn reduced, base very short. Male pronotum with transverse carina or pair of rounded tumosities, never bearing strong bilobate prominence 5
- Posterior surface of protibia completely granulorugose (Fig. 231). Cap of anterior metasternal angle simple, not bifurcated (except *ignecinctus*). Head horn of large male well developed, base as long or longer than central process (Fig. 218-223). Male pronotum with large bilobate prominence (e.g., Fig. 267) 7
- 5(4). Male pronotal prominence with simple transverse carina flanked by elongate concavities (Fig. 256-257). Apical processes of parameres strongly developed, hook-like (Fig. 258). Basal pronotal fossae lacking. Cap of anterior metasternal angle only weakly bifurcated. Humid Guyana province ***Coprophanaeus (C.) christophorowi (Olsoufieff)***
- Male pronotum with pair of blister-like tumosities separated by elongate concavity (Fig. 261, 264). Apical processes of parameres reduced, tooth-like (Fig. 263, 266). Basal pronotal fossae present or absent. Cap of anterior metasternal angle deeply bifurcate, V-shaped. Distribution variable 6
- 6(5). Apical processes of parameres attenuated, tips scarcely visible in profile and not appressed dorsally (Fig. 263). Anterior surface of metasternum (Fig. 228) densely, coarsely punctured, punctures extending to anterior margin of metasternal disk. Basal pronotal fossae small but distinct ***Coprophanaeus (C.) degallieri Arnaud***
- Apical processes of parameres not attenuated, tooth-like, tips clearly visible in profile and pressed together dorsally (Fig. 266). Anterior surface of metasternum (Fig. 229) glabrous above and along anterior margin of metasternal disk, puncturing fine, rather sparse and confined to

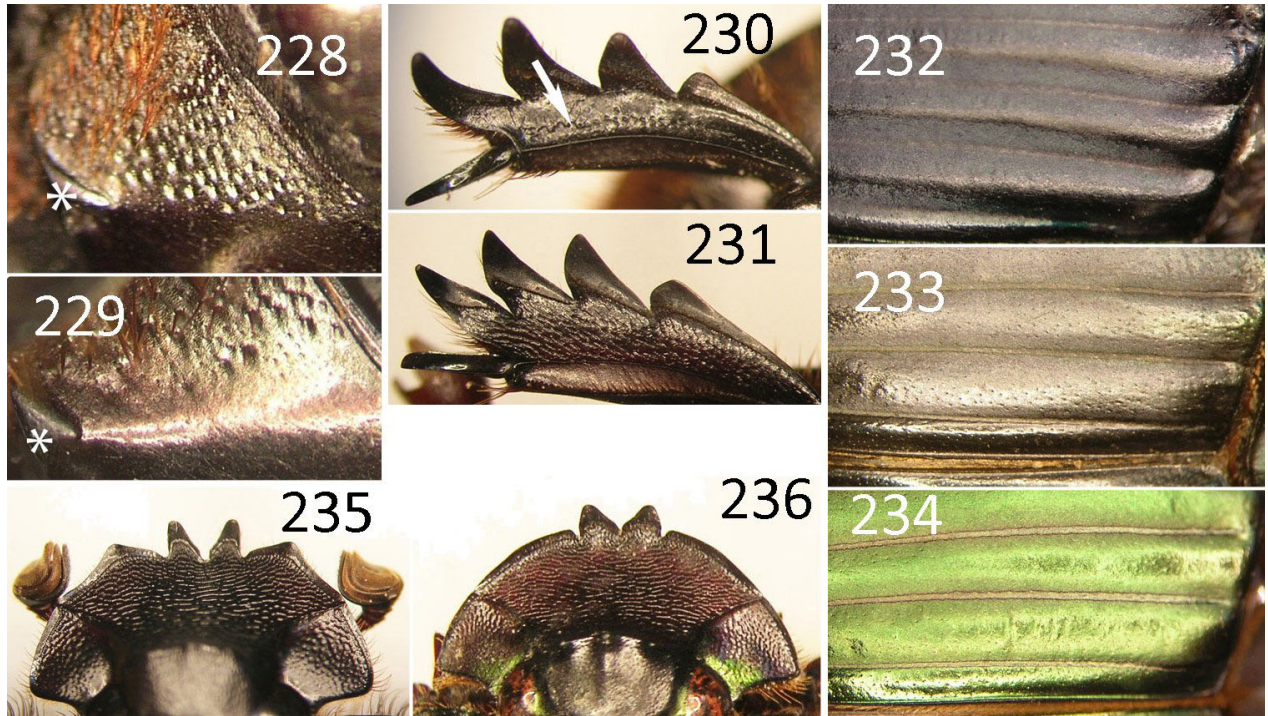


Figure 228-236. Characters of the *Coprophanaeus* (*s. str.*) *dardanus* species group. **228)** Oblique lateral view of metasternum (asterisk marks capped anterior angle of shield), *C. degallieri*. **229)** Same, *C. parvulus*. **230)** Ventral view of left protibia of *C. degallieri* (arrow marks row of coarse punctures). **231)** Same, *C. telamon*. **232)** Dorsal view surface of left elytron of *C. ignecinctus*. **233)** Same, *C. milon*. **234)** Same, *C. magnoi*. **235)** Dorsal view of head of female *C. ignecinctus*. **236)** Same, *C. magnoi*.

- upper portion of anterior surface. Basal pronotal fossae effaced
 ***Coprophanaeus (C.) parvulus* (Olsoufieff)**
- 7(4). Black except for conspicuous metallic red to greenish-red color around pronotal margin, on pygidium, sixth sternum and lower surfaces of meso- and metafemora; color easily seen with unaided eye (Fig. 267-272). Elytral interstriae 2-5 raised medially along length (Fig. 232). Sides of basal portion of male head horn convergent to weakly divergent; middle apical projection (viewed laterally) strongly and angularly bent posteriorly (as in Fig. 221). Cap of anterior metasternal angle deeply bifurcate, V-shaped; anterior surface of metasternum completely densely punctured ***Coprophanaeus (C.) ignecinctus* (Felsche)**
- Appearing black to the unaided eye; metallic green to yellowish-green color, if at all visible (x10), usually confined to anterolateral portions of pronotum. Striae flat or weakly, evenly convex, not raised midlongitudinally. Male head horn variable. Cap of anterior metasternal angle simple, not bifurcate; anterior surface of metasternum smooth adjacent to anterior margin of disk. **8**
- 8(7). Base of male head horn (viewed anteriorly, Fig. 220) usually more-or-less quadrate, sides more-or-less parallel or slightly divergent, lateral angles tuberculate; central process as long or longer than base, usually strongly and angularly bent posteriorly (Fig. 221-222), angle itself often conspicuously bituberculate (Fig. 220; 222, arrow); central process (viewed laterally) strongly inclined posteriorly, tip usually lying well posterior to line connecting lateral tubercles (Fig. 222). Pronotal process of large male flanked by deep, oval concavities, with prominent, usually acute lateral expansions such that entire process resembles nautical cleat (Fig. 273-274). Broad region east of cordillera from Bolivia to Venezuela
 ***Coprophanaeus (C.) telamon* (Erichson)**

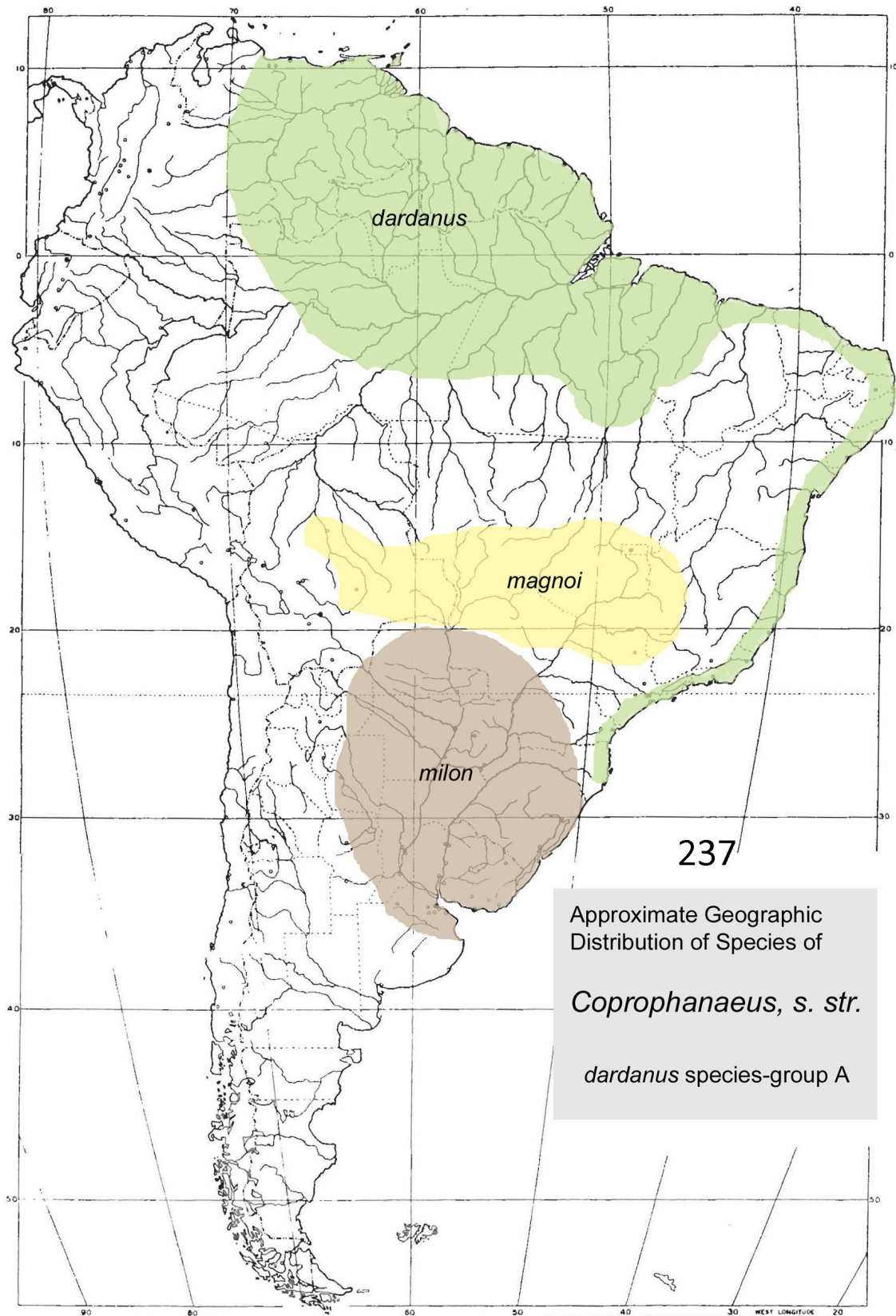


Figure 237. Approximate geographic distribution of *Coprophanaeus* (*s. str.*) species in the *dardanus* species-group A.

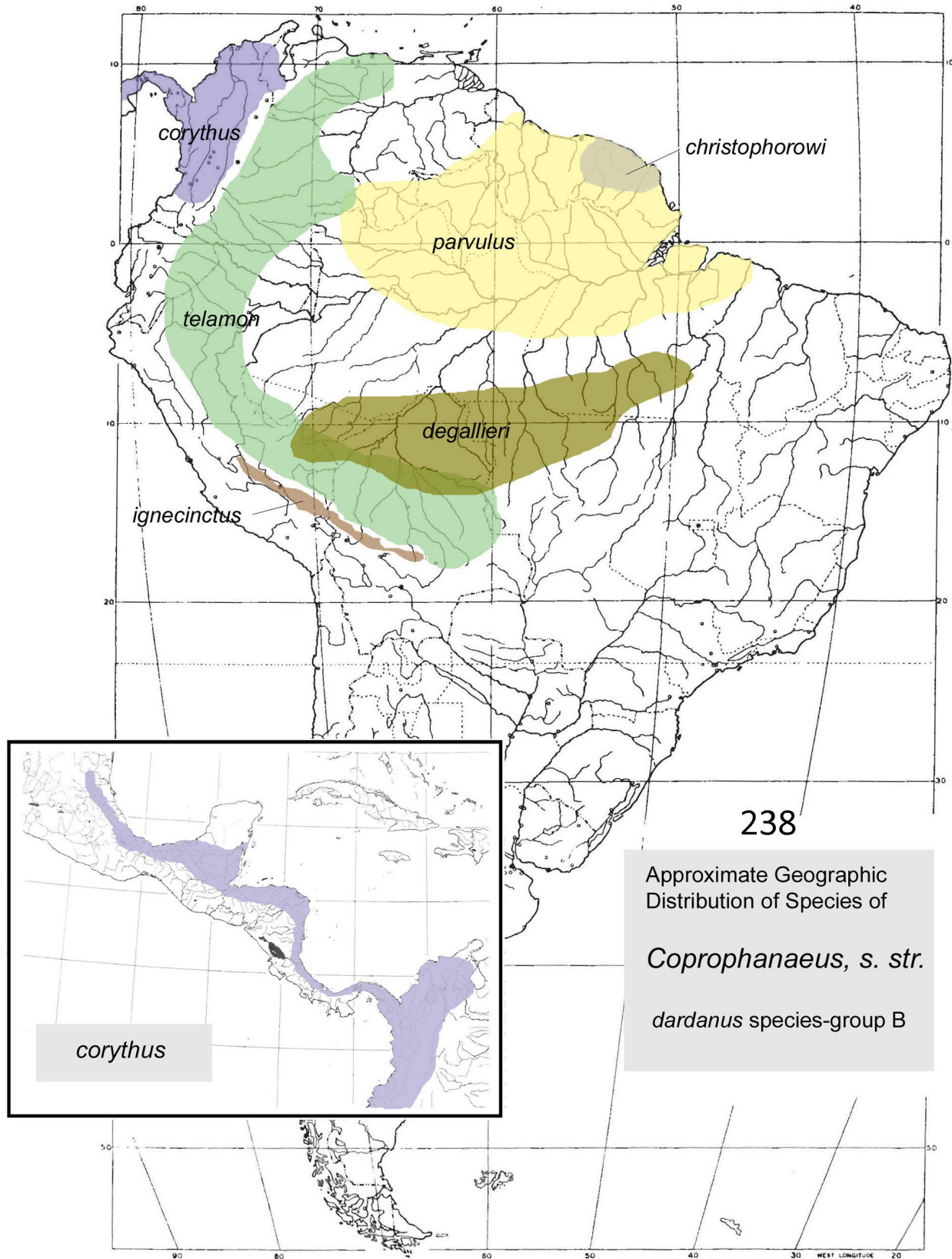


Figure 238. Approximate geographic distribution of *Coprophanaeus* (s. str.) species in the dardanus species group B.

- Base of male head horn trapezoidal, sides converging apically (Fig. 218-219); central process shorter than base, bowed posteriorly but never tuberculate, tip lying above line connecting lateral tubercles (Fig. 223). Pronotal process of large male (Fig. 275-276) a biangulate tumosity, never strongly developed laterally, never cleat-shaped or flanked by shallow concavities. Mesoamerican subregion from northwestern Venezuela to Mexico
 *Coprophanaeus (C.) corythus* (Harold)

***Coprophanaeus (C.) dardanus* (MacLeay, 1819)**

Fig. 6, 213-216, 237, 239-243

Phanaeus dardanus MacLeay, 1819: 126

Phanaeus bitias Harold, 1863: 163 (syn. by Nevinson 1892: 3)

Phanaeus jasion Felsche, 1901: 153 (syn. by Pessôa 1934: 300)

Phanaeus arrowi Olsoufieff, 1924: 68 (syn. by Arnaud 2002c: 32)

Coprophanaeus dardanus (MacLeay) (recomb. by Edmonds 1972: 843)

Type. *P. dardanus* – unknown to us (see Comments); *P. bitias* – unknown to us; *P. jasion* – holotype male, Staatliches Museum für Tierkunde, Dresden; *P. arrowi* – lectotype male (des. by Arnaud 1982: 116), Muséum National d'Histoire Naturelle, Paris (examined by photo).

Diagnosis. *General* – Dorsum dark, sombre, metallic reflections restricted to pronotum and head (Fig. 239-242). Clypeal margin distinctly angulate adjacent to median teeth. Length of clypeus about equal to that of frons. Pronotal disk lacking midlongitudinal sulcus, posterior portion smooth to very weakly punctured. Cap of anterior metasternal angle usually simple, sometimes slightly forked; anterior surface of metasternum smooth above anterior margin of disk. Elytral striae not distinctly carinate. Length 14-29 mm.

Male – Head horn (Fig. 213-215) erect, plate-like, gently curved posteriorly; width approaching interocular distance, sides parallel to slightly divergent; apex bidentate, teeth elongate, widely separated by deep, rounded emargination. Pronotal prominence (Fig. 241-242) cleat-like, strongly bilobate, lobes directed anterolaterally and flanked by deep, oval concavities, lateral margin of each concavity with weak tumosity above lateral fossa; width of prominence slightly greater than distance between outer margins of eyes. Apical processes of parameres strong, hook-like.

Female – Cephalic carina (Fig. 216) widely bidentate, apical margin between teeth widely raised, weakly angulate. Transverse crest of pronotum rounded, distinctly bidentate medially, followed by weak depression with feebly bitumose summit.

Specimens examined – 535.

Distribution. Northern Amazonian subregion and coastal Brazil (Fig. 237).

Collection Records. **BRAZIL:** **Amapá** – Serra do Navio [Cava Urucum-Amapari], 00°53'06"N 51°52'53"W (Jan, Sep). **Amazonas** – 60 km N Manaus [Fazenda Esteio] **Bahia** – Porto Seguro (Jan). **Ceará** – Maranguape, Piraponga, 38°41'59"W 03°53'26"S, 200 m; Baturite, Uirapuru, 38°54'22"W 04°17'27"S, 620 m (Mar). **Goiás** – Jaraguá. **Pará** – Redenção, 7°46'S 51°58'W (Oct); Belém (Jan-Mar); Alidos (Mar); Monte Dourado, 0°42'S 52°38'W, 100 m (Mar-Apr); 45 km E Canindé (Dec). **Paraíba** – João Pessoa [Mata do Buraquinho] (Aug); Aréia [Mata do Pau Ferro], 6°58'S 35°42'W (Apr). **Paraná** – Londrina (Apr). **Pernambuco** – Cabo [Reserva Ecologica Gurjaú] (May, Oct). **Rio de Janeiro** – Itatiaia, 700 m (Oct, Dec); Rio de Janeiro [Parque Lage] (Feb); Botafogo (Mar, Nov); Floresta da Tijuca (Dec); Petropolis (Sep, Dec). **Roraima** – Caracaraí (Jul). **Santa Catarina** – Corupá (Oct-Nov); Joinville (Apr, Jun). **COLOMBIA:** **Guaviaré** – San José [Finca La Esmeralda], 2°33'N 72°38'W, 240 m (Oct). **FRENCH GUIANA:** 8.4 km SSE Roura, 4°40'41"N 52°13'25"W, 200 m (May-Jun); 7 km N Saül [Les Eaux Claires], 3°39'46"N 53°13'19"W (May-Jun); Wanaboo [Marowijne River], 4°43'35"N 54°26'36"W, 40 m (Jun); 9.7 km NW – 4.3 km SE Patawa [Kaw Mountain], 4°32'40.1"N 52°09'08.1"W (Dec); Mana, 5°39.2'N 53°49.9'W (Jul); 100

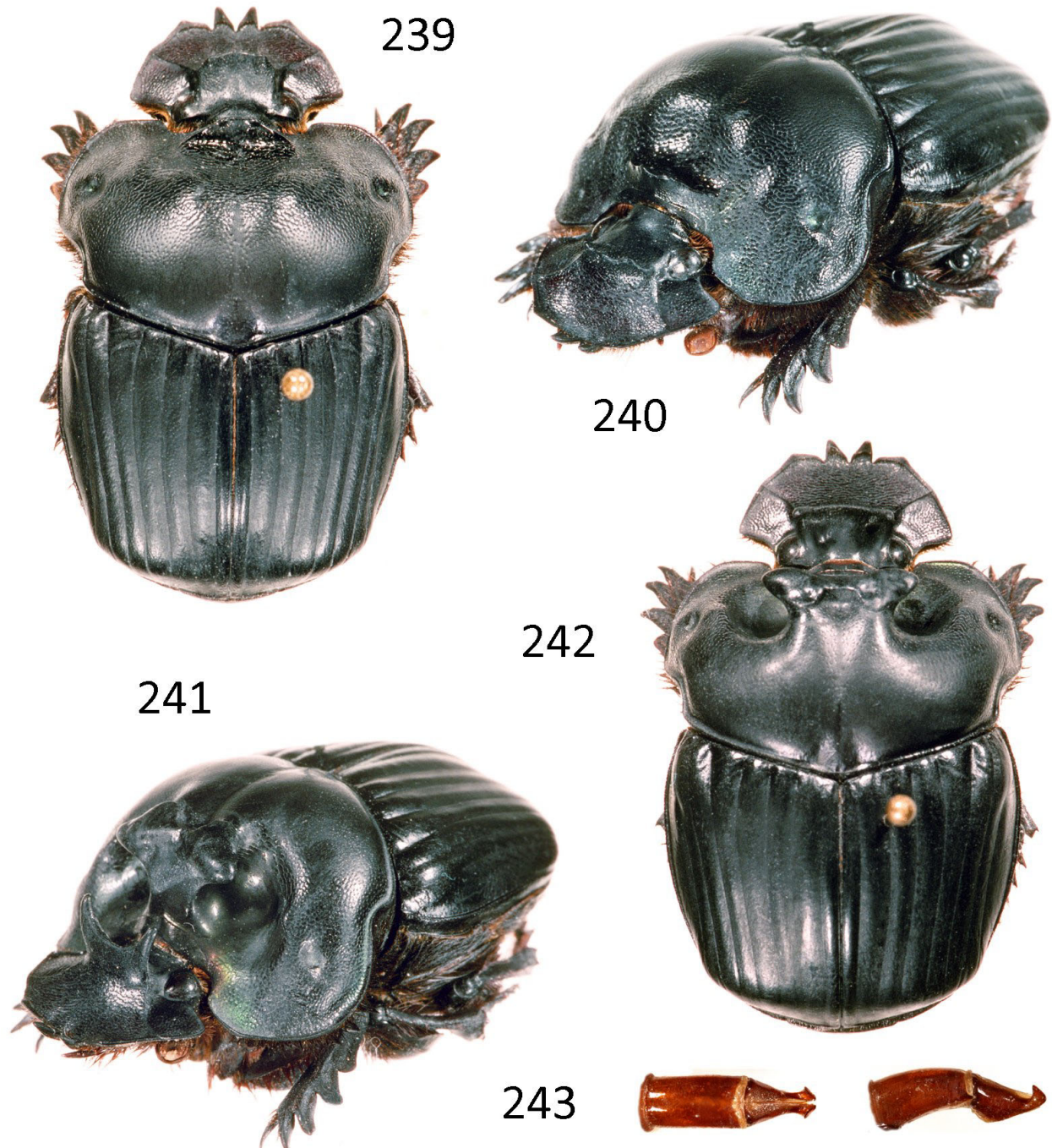


Figure 239-243. *Coprophanaeus dardanus*. 239-240) Female habitus. 241-242) Male habitus. 243) Aedeagus (dorsal view on left; lateral view on right).

km S Cayenne [Nouragues Research Station], 4°05'N 52°40'W. **GUYANA: Mazaruni-Potaro** – Takutu Mts., 6°15'N 59°05'W (Dec). **Potaro-Siparuni** – Iwokrama Forest Reserve, 4°40'19"N 58°41'04"W, 100-200 m (Jun). **SURINAME: Brokopondo** – Stoneiland, ~ approx. 4°59'N 55°09'W, 30 m (Apr-May); Rosebel gold mining area, ~ 5° 07' N; 55° 17' W (May). **Para** – ~ 20 km SSE Joden Savanne, 5°16'17"N 54°55'15"W, 40 m (Jun-Jul). **Paramaribo** – Pallisadenweg (Jul). **Sipaliwini** – Central Suriname Nature Reserve, environs of Voltzberg research station, 4°40.90"N 56°11.13" W, 100 m (Mar); Central Suriname Nature Reserve, environs of Lolopasi field station, 4°42.91'N 56°12.83'W, 80 m (Mar); Central Suriname

Nature Reserve, environs of Conservation International field station, 50 m (Mar); Central Suriname Nature Reserve, Raleighvallen, Fungu Island (= Foengoe Island), ~4°33'30"N 56°12'21"W (Jul); Bakhuis mountains, ~4°27'13"N 56°57'39"W (Nov); Palumeu, ~3°20'46.3"N 55°26'30.8"W (Jun). **Wanica** – Lelydorp (Feb); Zanderij, Hannover (Jun). **TRINIDAD-TOBAGO**: Port-of-Spain [Capuro Valley]; 16 km N Arima, 650 m (Jun); 8 km N Arima, 260 m; Maracas Valley, 600 m; 11 km SE Arima [Arena Forest Reserve], 80 m (Jun). **VENEZUELA**: **Amazonas** – Puerto Ayacucho (May); El Infierno (Jun); Atabapo (Jun); Camani (Jun-Jul). **Aragua** – Maracay [Rancho Grande] (Jun). **Bolívar** – 50 km SE El Manteco [Río El Supamo] (Dec); Paují, 1100 m; 10 km E San Francisco Yuruani, 1300 m (Jul); 20 km S Luepa, 1500 m (Jul); 10 km E Kavanayen, 1500 m (Jun); 22 km SE El Dorado (Jul); 10 km S El Dorado, 200 m (Jul-Aug); 100 km S El Dorado, 350 m (Jul-Aug); 6 km S San Isidro (Jun-Jul); Parupa, 1500 m (Jun-Jul). **Miranda** – 33 km N Altigracia de la Montaña [Guatopo National Park, La Crucita], 400 m (Jun). **Monagas** – 27 km SW Caripe, 300 m (Jun); Caripe, 700 m (Jul).

Comments. We assume that the type, or a candidate for the lectotype of this species, will be found in the MacLeay Collection at the University of Sydney. We were unable to secure specimens from Sydney for this study. However, there is little room for doubt about the identity of *C. dardanus* even from the brief description of MacLeay (1819: 126-127): “*P. nigro-viridis, capitis cornubus duobus brevibus basi connatis, thorace antice carinâ bidentatâ instructo ... Mas. Thorax fossulâ utrinque sub carinae dentibus unidentatâ ...*” (Free translation: *Black with green, head horn with two teeth broadly connected at the base; thorax with bidentate process ... Male: Lateral concavity beneath median process with single tooth ...*). His diagnosis highlights the bidentate structure of the male head horn (Fig. 213-214), which is unique to the genus and seen otherwise in phanaeines only in *Diabroctis*. The length of the teeth varies, but usually amounts to at least the height of the base. In large individuals the upper margin of the base, between the lateral teeth, is slightly raised medially. In very small males (Fig. 215) the horn is reduced to a weakly bidentate swelling reminiscent of the small males of *Oxysternon* and certain *Phanaeus*. The cephalic carina of the female (Fig. 216), even in small individuals, is also unique and highly diagnostic. It bears a small denticle at each end, separated by a broad, rounded or slightly angulate elevation.

We regard *C. dardanus* as a fundamentally Amazonian species, but it has managed to spread southward via the Atlantic coast of Brazil into portions of the Paranaian subregion as far south as Santa Catarina as well as into the central highlands (via gallery forests?). Remarkably, as far as we can see, the vast occupation of its combined range has not resulted in any detectable geographic variation. We have not seen Arnaud's (2002a) species, *C. terrali*, which was based on a single male from Mato Grosso and considered a close ally of *C. dardanus*. The single reported specimen (holotype) is part of a private collection that was not available for study. The shape of the cephalic carina of the holotype is strikingly different from that expected for *C. dardanus*, and the possibility that the shape is a teratologic form or a distinct morph in otherwise normal populations needs to be ruled out in any assessment of its validity.

***Coprophanaeus (C.) magnoi* Arnaud, 2002**

Fig. 8, 227, 234, 236-237, 244-248

Coprophanaeus milon magnoi Arnaud, 2002b: 2

Coprophanaeus magnoi Arnaud **New Status**

Type. Holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France (examined by photo).

Diagnosis. *General* – Dorsum (Fig. 244-247) with widespread metallic green reflections. Clypeal margin at most only weakly angulate adjacent to median teeth. Length of clypeus greater than that of frons, especially in male. Pronotal disk with midlongitudinal sulcus expanding posteriorly into triangular depression embracing basal fossae (Fig. 247); sulcus and triangular depression metallic green. Cap of anterior metasternal angle usually simple, sometimes bifurcate; anterior surface of metasternum smooth above anterior margin of disk. Elytral striae distinctly carinulate (Fig. 234). Length 18-29 mm.

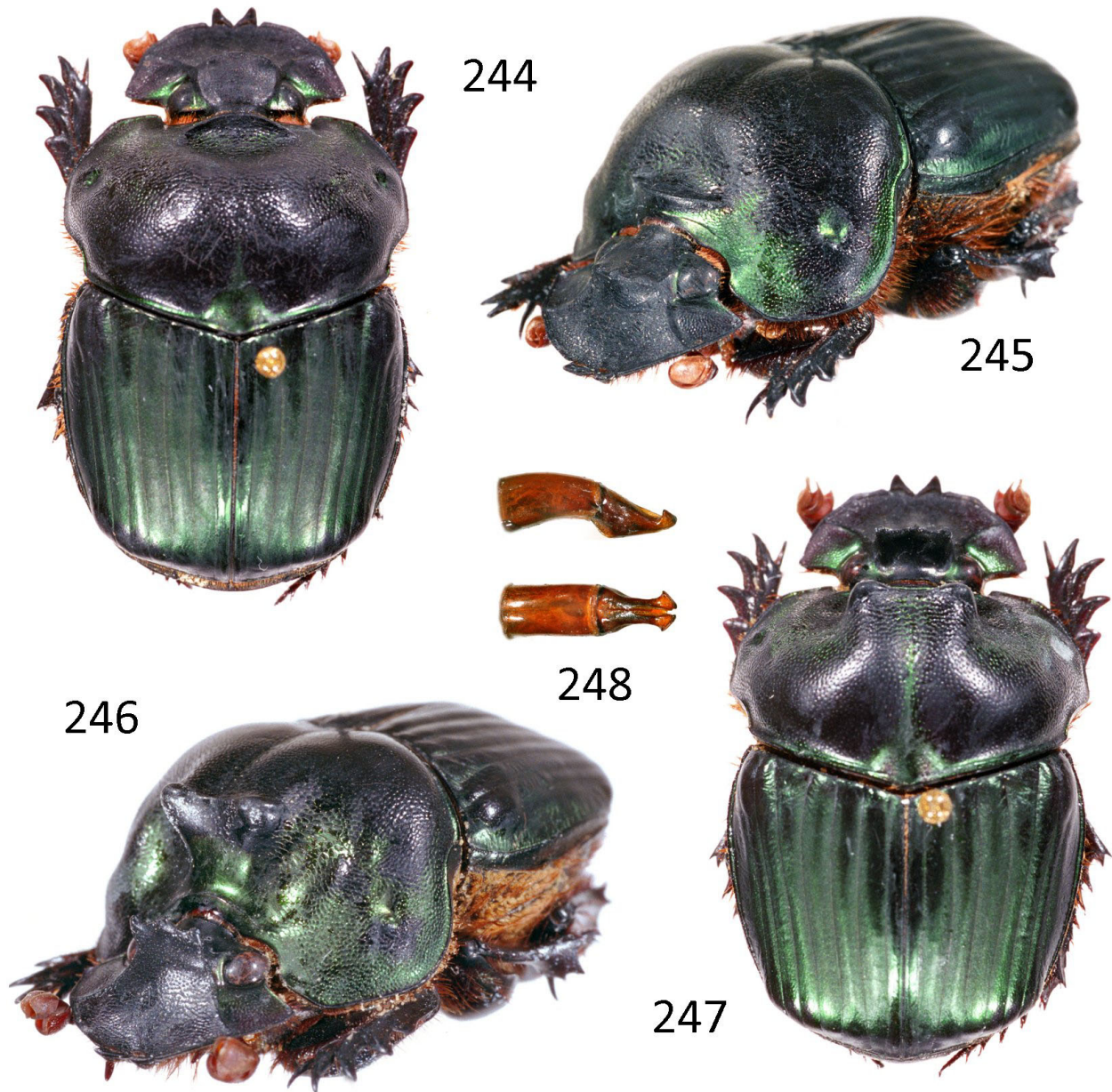


Figure 244-248. *Coprophanaeus magnoi*. 244-245) Female habitus. 246-247) Male habitus. 248) Aedeagus (dorsal view below; lateral view above).

Male – Head horn (Fig. 227) erect, plate-like, set very near eyes; width approaching interocular distance, sides more-or-less parallel; apex tridentate, emarginations separating teeth deep, rounded. Pronotal prominence (Fig. 247) strongly bilobate, lobes directed anteriorly and flanked by shallow concavities; width of prominence clearly less than distance between outer margins of eyes. Apical processes of parameres tooth-like.

Female – Transverse crest of pronotum rounded, at most only very weakly bidentate; crest followed by weak concavity with feebly bitumose summit.

Specimens examined – 62.

Distribution. Chaco and Cerrado provinces (Fig. 237).

Collection Records. **BOLIVIA:** Beni – Estación Paraparú (May); Reyes (Dec); Magdalena (Dec); Estación Biológica del Beni [Bosque El Trapiche], 14°52'10"S 66°19'58"W, 195 m; Río Ichiguita, 15°8'S 56°18'W, 155 m. **Chuquisaca** – Rosario [Lago Rocagua] (Nov). **La Paz** – Ixiamas (Dec). **Santa Cruz** – RPPN Caparú, 14°47'S 61°10'W, 180 m; General Saavedra (May); Parque Nacional Noel Kempff Mercado [Los Fierros], 14°36'53"S 60°51'01"W and 14°34'45.6"S 60°54'30.3"W, 200 m (Jan-Feb); Concepción (Jan). **BRAZIL:** **Goias** – Leopoldo de Bulhões (Dec). **Mato Grosso** – Rio Taguarassu (Nov). **Minas Gerais** – Serra do Sipo, Vao da Lagoa (Dec); Serra Caraça, 138 m (Nov); Juiz de Fora (Nov). **Paraná** – Curitiba (Feb); Vilha Velha (Feb). **São Paulo** – São Paulo (Dec); Tremembé (Mar); São Miguel (Jan); Santo Amaro.

Comments. Because of the close similarity in size and coloring, a casual assessment may confuse this species with *C. spitzzi* and *C. acrisius*. In the latter pair the pronotal sculpturing is much coarser and denser, especially posteromedially; moreover, the anterior part of the circumnotal ridge is not broken behind the eyes as it is in *C. magnoi*. Arnaud (2002b) described this taxon as a subspecies of *C. milon*. Because the distributions of the two appear to be mutually exclusive and they are consistently distinct morphologically, we have chosen to regard *C. magnoi* and *C. milon* as separate species.

Coprophanaeus (C.) milon (Blanchard, 1843)

Fig. 225-226, 233, 237, 249-253

Phanaeus milon Blanchard, 1843: 174.

Coprophanaeus milon (Blanchard) (recomb. by Edmonds 1972: 843)

Phanaeus obscurus Olsoufieff, 1924: 71 (syn. by Arnaud 1982a: 117)

Type. *P. milon* – lectotype male (des. by Arnaud 1982a: 114), Muséum National d'Histoire Naturelle, Paris (examined by photo); *P. obscurus* – holotype male, Zoologische Staatssammlung, Munich.

Diagnosis. *General* – Dorsum (Fig. 249-252) dark, sombre, metallic reflections dark blue or bluish green. Clypeal margin at most only weakly angulate adjacent to median teeth. Length of clypeus greater than that of frons, especially in male. Pronotal disk (Fig. 252) with midlongitudinal sulcus expanding posteriorly into triangular depression embracing basal fossae; sulcus and triangular depression often with metallic color. Cap of anterior metasternal angle usually simple, sometimes bifurcate; anterior surface of metasternum smooth above anterior margin of disk. Elytral striae not distinctly carinulate (Fig. 233). Length 18-25 mm.

Male – Head horn (Fig. 225-226) erect, plate-like, set very near eyes; width clearly less than interocular distance, sides convergent to divergent; apex tridentate, emarginations separating teeth shallow. Pronotal prominence (Fig. 252) strongly bilobate, lobes directed anterolaterally and flanked by deep, oval concavities; width of prominence approaching distance between outer margins of eyes. Apical processes of parameres hook-like.

Female – Transverse crest of pronotum rounded, at most only very weakly bidentate; crest followed by weak concavity, summit weakly bitumose.

Specimens examined – 138.

Distribution. Chaco and Pampa provinces (Fig. 237).

Collection Records. **ARGENTINA:** Buenos Aires – Mercedes (Mar); San Isidro (Jan); General Sarmiento San Miguel (Jan); Buenos Aires (Feb, Oct); San Fernando (Dec); Zelaya (Feb). **Chaco** – Cruce Loma Plata (Jan); Miraflores (Apr). **Córdoba** – Río Primero (Feb); Cruz Alta (Feb). **Corrientes** – Monte Caseros (Sep). **Entre Ríos** – Liebig (Dec); Pronunciamento (Feb-Mar, Oct). **Formosa** – Formosa (Nov); Gran Guardia (Oct). **Misiones** – Dos de Mayo (Feb); Puerto Iguazú (Nov). **Santiago del Estero** – Santiago del Estero (Mar). **BRAZIL:** **Mato Grosso do Sul** – Corumbá [Pantanal do Miranda] (Jan). **Paraná** – Rolândia (Nov). **Rio Grande do Sul** – Pelotas (Dec). **Santa Catarina** – São Francisco (Nov). **PARAGUAY:** **Boquerón** – Mariscal Estigarribia (Feb, May). **Presidente Hayes** – Cruce Loma Plata (Feb); Estación Yui (Dec); Laguna Capitan (Jan); Lolita (Yaragui) (Jan). **URUGUAY:** **Canelones** – Las

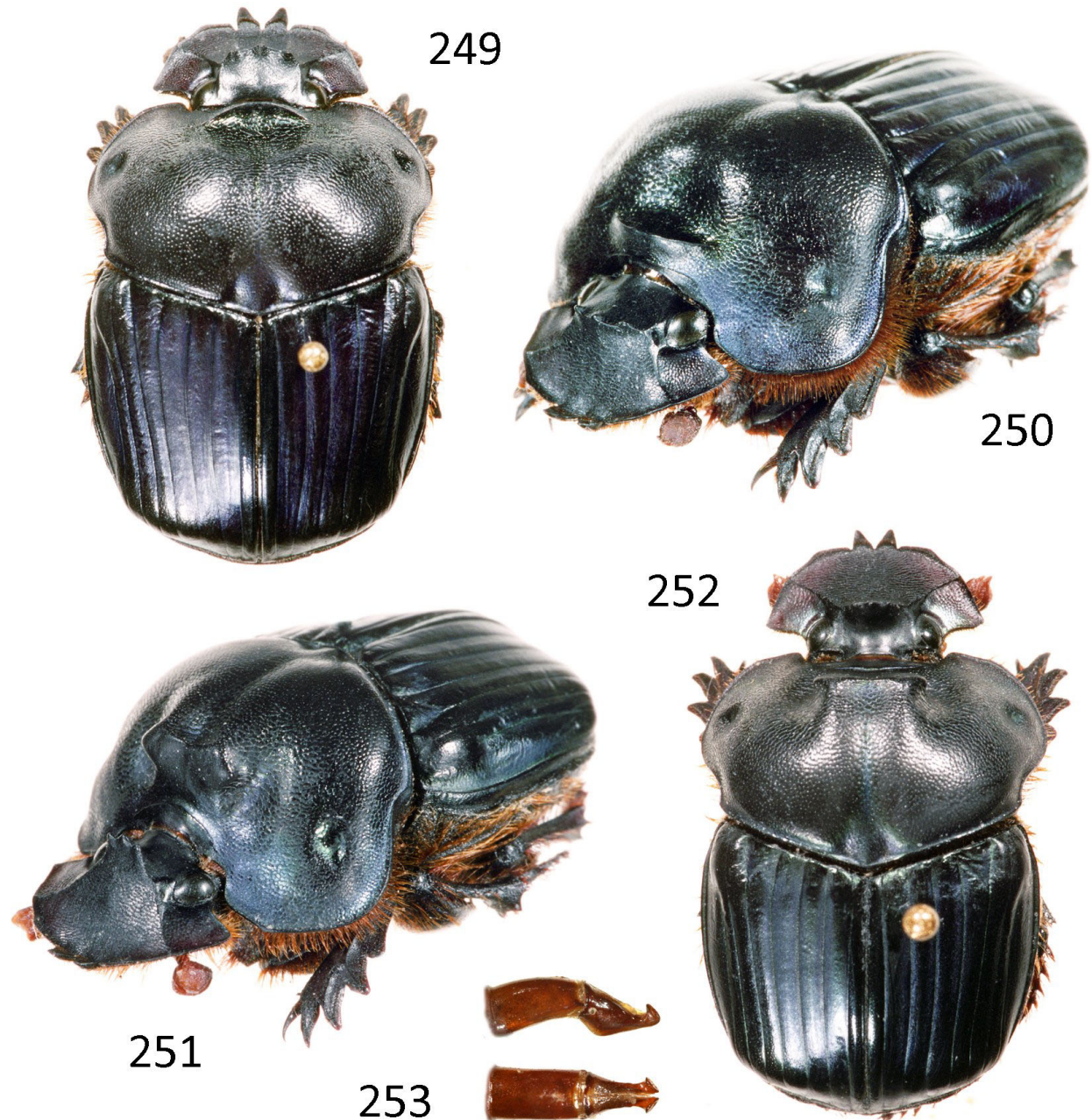


Figure 249-253. *Coprophanaeus milon*. 249-250) Female habitus. 251-252) Male habitus. 253) Aedeagus (dorsal view below; lateral view above).

Piedras (Jan); Ruta 107, km 43 Canelones-Chico (Jan). **Lavalleja** – Sierra de Minas. **Montevideo** – La Teja (Dec). **Río Negro** – Haedo (Feb).

Comments. Barattini and Sáenz (1953) described the reproductive behavior of *C. milon*. The shape of the male horn varies in this species. Usually it is parallel-sided, but in certain large individuals the sides diverge apically.

Coprophanaeus (C.) christophorowi (Olsoufieff, 1924)

Fig. 238, 254-258

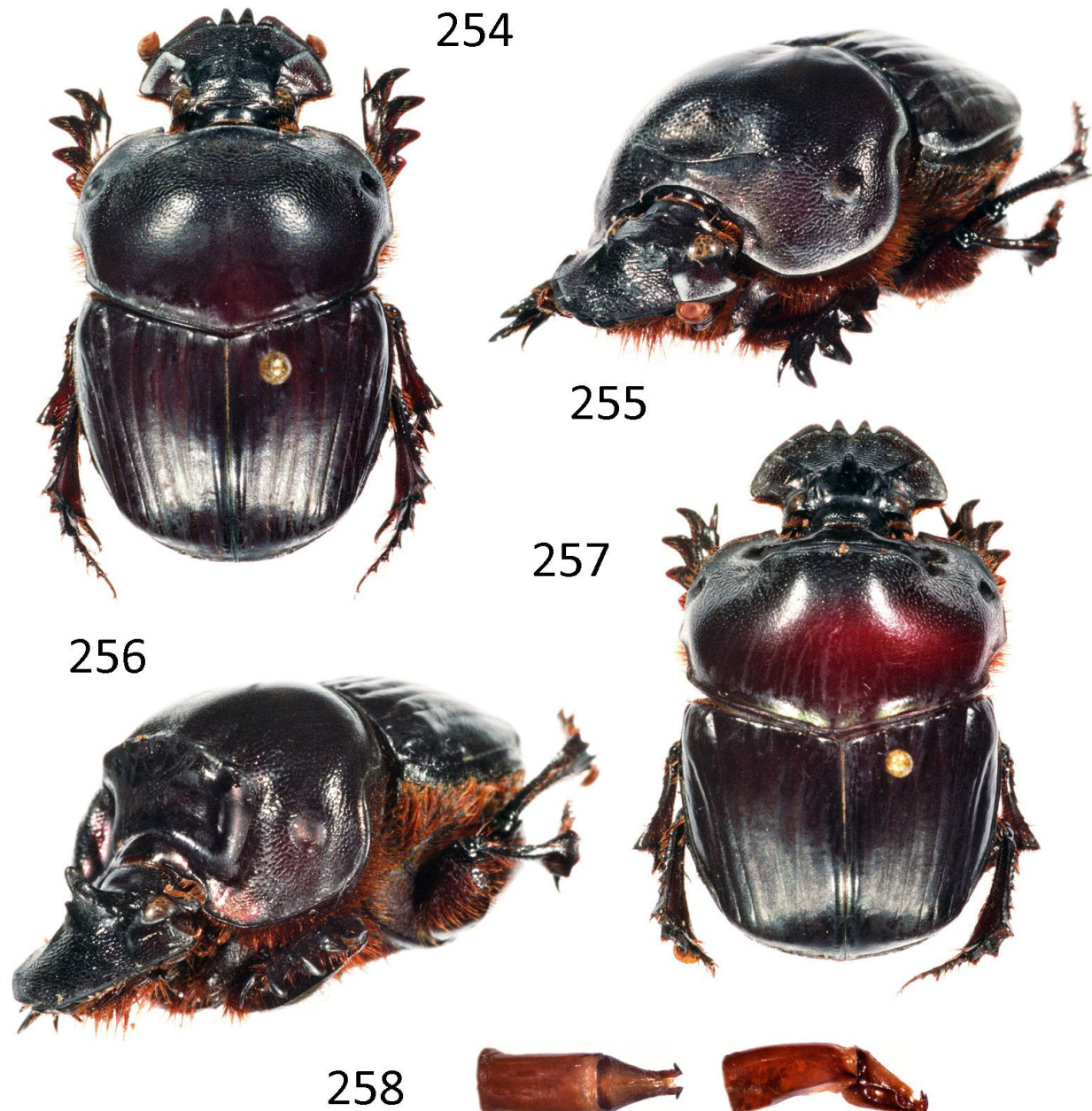


Figure 254-258. *Coprophanaeus christophorowi*. 254-255) Female habitus. 256-257) Male habitus. 258) Aedeagus (dorsal view on left; lateral view on right).

Phanaeus christophorowi Olsoufieff, 1924: 66

Coprophanaeus christophorowi (Olsoufieff) (recomb. by Blackwelder 1944: 209)

Type. Holotype male, Muséum National d'Histoire Naturelle, Paris (examined by photo).

Diagnosis. *General* – Largely weakly shining black; anterior pronotal margin with weak violet-green reflections (reddish sheen in Fig. 257 produced by teneral surface). Posterior (ventral) surface of protibia smooth except for single or double row of coarse punctures (as in Fig. 230, arrow) paralleling longitudinal carina. Cap of anterior angle of metasternum very weakly forked. Anterior surface of metasternum glabrous above anterior margin of metasternal disk, otherwise sparsely, weakly punctured. Basal pronotal fossae effaced. Length 17-23 mm.

Male – Head horn (Fig. 256) attenuated, base very short, lateral tubercles very acute. Pronotal prominence (Fig. 256-257) topped by simple transverse carina, anterior surface almost vertical, with elongate lateral concavities. Apical processes of parameres large, hook-like (Fig. 258).

Female – Cephalic carina weakly bowed anteriorly, trituberculate, middle tubercle somewhat larger than laterals; length of clypeus equal to or greater than that of frons. Pronotal ridge angulate medially, not distinctly tuberculate.

Specimens examined – 18.

Distribution. French Guiana (Fig. 238).

Collection Records. FRENCH GUIANA: Saül, Mt. Galbao, 3°37'18"N 53°16'42"W, 740 m (Jun); 7 km N Saül, 11 km NW Les Eaux Claires [Rue de Belizon Trail] 3°39'46"N 53°13'19"W, 280 m; 18.4 km SSE Roura, 4°36'38"N 53°13'25"W, 240 m (May); Nouragues Field Station, 4°05'N 52°40'W (Apr).

Comments. *Coprophanaeus christophorowi* is a taxonomic isolate within the telamon species subgroup; its highly localized distribution is similar to that of *Oxysternon durantoni* (Edmonds and Zidek 2004). The violet-green color and shape of the male pronotum are unique to the subgroup.

***Coprophanaeus (C.) degallieri* Arnaud, 1997**

Fig. 224, 228, 230, 238, 259-263

Coprophanaeus degallieri Arnaud, 1997: 8

Type. Holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France.

Diagnosis. General – Dorsum black with weak green to greenish red reflections along margin of pronotum. Posterior (ventral) surface of protibia smooth except for row of coarse punctures paralleling longitudinal carina (Fig. 230, arrow). Cap of anterior angle of metasternum deeply bifurcated, arms of cap embracing small, round fossa (Fig. 224). Anterior surface of metasternum densely, coarsely punctured, punctures extending onto metasternal disk adjacent to mesocoxae (Fig. 228). Basal pronotal fossae small, distinct. Length 13-17 mm.

Male – Head horn (Fig. 261) small, sides of base convergent, central process straight, length equal to that of base. Pronotal prominence (Fig. 261-262) a pair of rounded, blister-like tumosities separated by longitudinal depression. Apical processes of parameres tooth-like, attenuated, tips scarcely visible (viewed from side, Fig. 263), not appressed dorsally.

Female – Cephalic carina trituberculate, weakly bowed anteriorly; length of clypeus greater than that of frons. Pronotal carina only weakly raised, feebly bidentate medially.

Specimens examined – 13.

Distribution. Southern Amazonian subregion (Madeira and Tapajós-Xingu provinces) (Fig. 238).

Collection Records. BRAZIL: Acre – Rio Branco, Fazenda Catuaba (Feb). Pará – Redenção, 7°46'S 51°58'W (Nov). Rondônia – 62 km S Ariquemes [Fazenda Rancho Grande], 10°32'S 62°48'W (Nov); 9 km NE Cacaulândia (Jan, Nov). PERU: Madre de Dios – Manu [Los Amigos Field Station], 12°34'S 70°06'W, 290 m (Apr).

Comments. This species is similar in size and shape to *C. parvulus*, from which it is most easily distinguished by the completely coarsely punctate anterior metasternal surface and shape of the parameres. We have seen specimens only from widely scattered localities in the southern portion of the Amazon basin. The form of the male head horn and pronotum of this species, as well as *C. parvulus*, is like that of the smallest males of *C. telamon* and *C. corythus*.

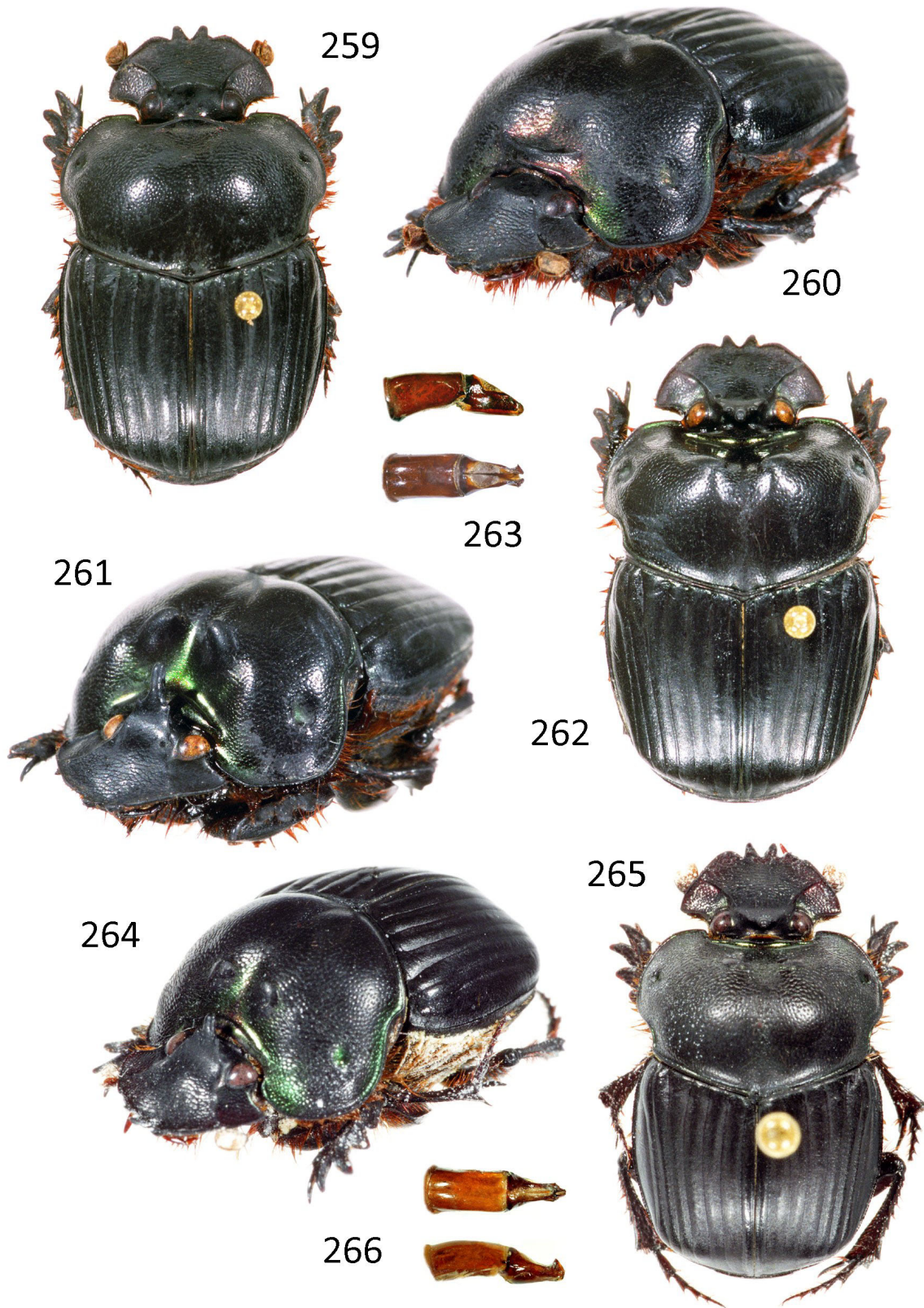


Figure 259-266. *Coprophanaeus* spp. 259-263) *C. degallieri*. 259-260) Female habitus. 261-262) Male habitus. 263) Aedeagus (dorsal view below; lateral view above). 264-266) *C. parvulus*. 264-265) Male habitus. 266) Aedeagus (dorsal view above; lateral view below).

***Coprophanaeus (C.) parvulus* (Olsoufieff, 1924)**

Fig. 229, 238, 264-266

Phanaeus parvulus Olsoufieff, 1924: 67*Coprophanaeus parvulus* (Olsoufieff) (recomb. by Blackwelder 1944: 209)

Type. Lectotype male (des. by Arnaud, 1982a: 116), Muséum National d'Histoire Naturelle, Paris (examined by photo).

Diagnosis. *General* – Dorsum black with weak green to greenish red reflections along margin of pronotum. Posterior (ventral) surface of protibia smooth except for row of coarse punctures paralleling longitudinal carina (as in Fig. 230, arrow). Cap of anterior angle of metasternum deeply bifurcated, arms of cap embracing small, round fossa. Anterior surface of metasternum glabrous above anterior margin of metasternal disk, otherwise sparsely, weakly punctured. Basal pronotal fossae effaced (Fig. 229). Length 13-17 mm.

Male – Head horn small, sides of base convergent, central process straight, length equal to that of base. Pronotal prominence (Fig. 264) a pair of rounded, blister-like tumosities separated by longitudinal depression. Apical processes of parameres tooth-like, closely appressed dorsally and clearly visible laterally (Fig. 266).

Female – Cephalic carina trituberculate, weakly bowed anteriorly; length of clypeus greater than that of frons. Pronotal carina only weakly raised, feebly bidentate medially.

Specimen examined – 104.

Distribution. Northern Amazonian subregion (Guyana, Humid Guyana, Amapá and Roraima provinces) (Fig. 238).

Collection Records. **BRAZIL: Amazonas** – Manaus (Oct); 26 km NE Manaus [Reserva Forestal Ducke] (Feb, Apr, Jul, Sep-Oct, Dec); 60 km N Manaus [Fazenda Esteio], 2°25'S 59°50'W (Jan, Jul). **Pará** – Tucurí (Dec); Monte Dourado, 1°01'S 52°44'W, 100 m. **COLOMBIA: Amazonas** – Leticia [Tarapacá] (Jul-Aug). **FRENCH GUIANA:** Crique Plomb (Sep); Belizon (May); Saül (Jul); 7 km NW Saül, Mt. La Fumée, 3°39'49"N 53°13'19"W, 490 m (Jun); 18.4 km SSE Roura, 4°36'38"N 53°13'25"W, 240 m; Nouveau Chantier; St. Jean du Maroni; Nouragues Field Station, 4°05'N 52°40'W (Mar-Apr, Oct-Nov). **SURINAME: Paramaribo** – Pallisadenweg (Jul). **Sipaliwini** – Central Suriname Nature Reserve, environs of Lolopasi field station, 4°42.91'N 56°12.83'W, 80 m (Mar); Nassau Mt., 4°48'36"N 54°31'16"W (Jun); Lely Plateau, 4°16'N 54°44'W, 640 m (Oct). **VENEZUELA: Amazonas** – El Infierno [Distr. Atures] (May, Jul). **Bolívar** – 20 km NW Guri (Jul-Aug); 8 km N Guri, 200 m (Jul-Aug); Lago Guri Lslands, 7°21'N 62°52'W, 270 m (Jun-Jul).

Comments. This is a widely distributed Amazonian species that often occurs in the same communities as *C. jasius* and *C. lancifer*. It is similar to *C. degallieri* (*q.v.*), but the distributions of the two species as now known are largely separate latitudinally similar to the case of *Oxysternon festivum* and *O. macleayi* (Edmonds and Zidek 2004). The form of the male head horn and pronotum of this species, as well as *C. degallieri*, is like that of the smallest males of *C. telamon* and *C. corythus*. After the distribution map (Fig. 238) was prepared, we had the opportunity to examine a single specimen of *C. parvulus* from northern Loreto, Peru (2°55'26"S 74°49'08"W; ~ 190 km WNW Iquitos), a considerable distance (roughly 850 km) west of the range indicated in Fig. 238. Its presence there is unsurprising, and we suspect that intervening collection sites will be identified in the future.

***Coprophanaeus (C.) ignecinctus* (Felsche, 1909)**

Fig. 232, 235, 238, 267-272

Phanaeus ignecinctus Felsche, 1909: 755*Coprophanaeus ignecinctus* (Felsche) (recomb. by Blackwelder 1944: 209)*Phanaeus telamon ignecinctus* Felsche (stat. by Pereira and Martínez 1956: 232)

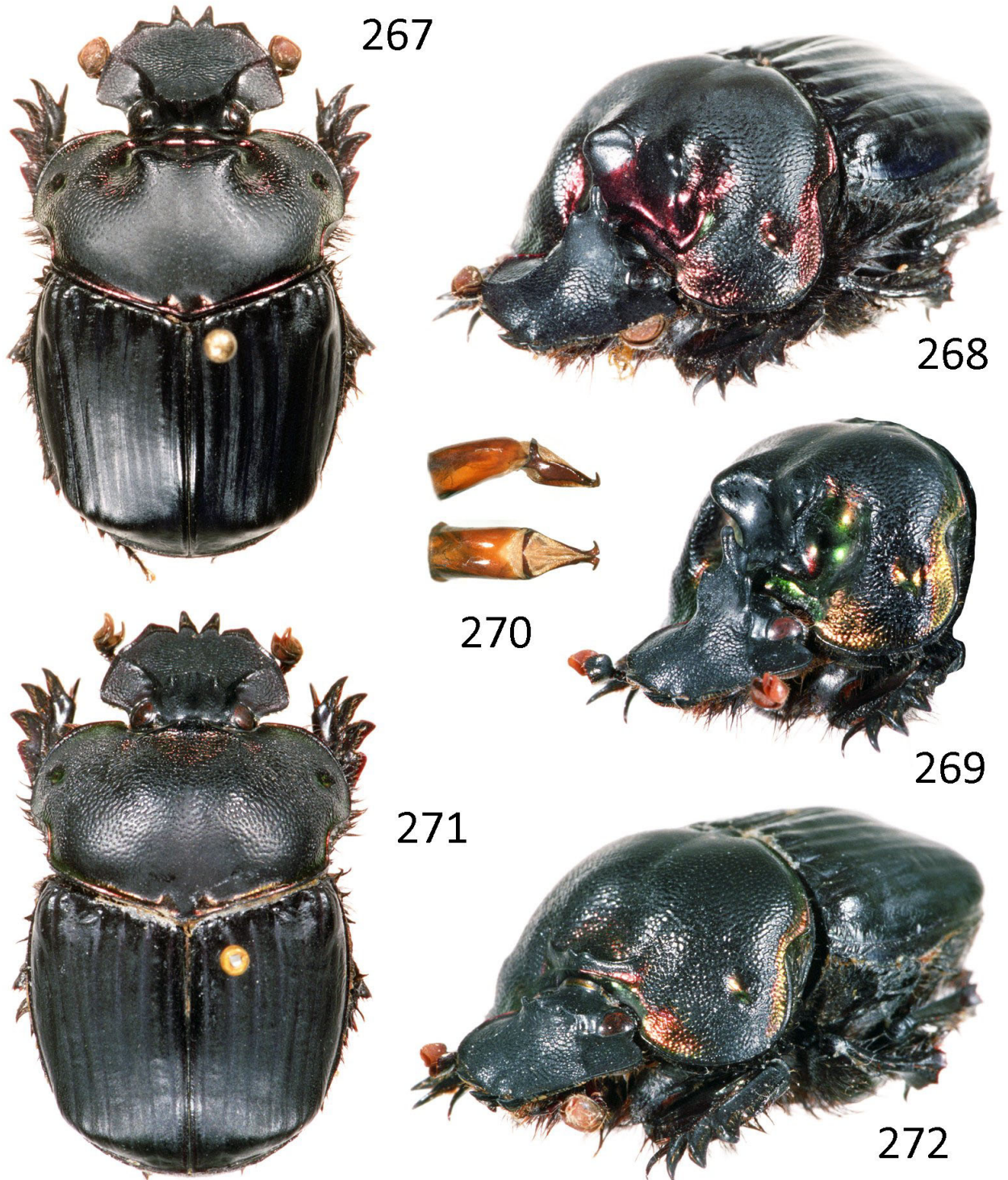


Figure 267-272. *Coprophanaeus ignecinctus*. 267-269) Male habitus. 270) Aedeagus (dorsal view below; lateral view above). 271-272) Female habitus.

Type. Lectotype male, **here designated**, Staatliches Museum für Tierkunde, Dresden.

Diagnosis. *General* – Metallic coloration (Fig. 267-271), where present, bright red (rarely with green highlights, Fig. 269). Clypeus strongly and abruptly angulate lateral to median teeth. Posterior (ventral) surface of protibia completely granulorugose (as in Fig. 231). Cap of anterior angle of metasternum deeply bifurcate. Anterior surface of metasternum completely densely punctured. Metasternal disk finely punctured, bearing compound row of larger punctures along anterior margin. Basal pronotal fossae distinct. Elytral interstriae 2-5 raised midlongitudinally (Fig. 232). Length 20-25 mm.

Male – Sides of base of head horn usually slightly convergent, rarely slightly divergent; anterior surface weakly concave, lateral angles acutely tuberculate; central process about same length as base, almost upright and angularly produced on posterior surface (as in Fig. 220). Pronotal prominence (Fig. 267-269) with rounded lateral angles, cleat-shaped, flanked by deep oval concavities; width equal to distance between outer margins of eyes.

Female – Cephalic carina trituberculate; length of clypeus greater than that of frons.

Specimen examined – 87.

Distribution. Yungas province in Bolivia and Peru (Fig. 238).

Collection Records. **BOLIVIA:** **Cochabamba** – Prov. Chaparé, 17°10.47'S 65°46.66'W, 1550 m (Feb, Nov); Yungas del Palmar, 1200 m (Jan-Feb); Limbo, 2000 m (Jan); 109 km E Cochabamba, 17°08'52"S 65°42'54"W, 1400 m (Feb); 124 km E Cochabamba [at Río Espíritu Santo], 17°03'45"S 68°38'38"W, 700 m (Feb); road from Cochabamba to Villa Tunari, 17°08'50"S 65°42'29"W, 1480 m (Feb); Cordillera Mostenes, Isiboro-Securú National Park [Laguna Carachupa], 16°13'58"S 66°24'54"W, 1310 m (Sep); Carmen Pampa, 16°37'06"S 66°28'50"W, 1820 m. **Santa Cruz** – near Bermejo [Refugio Los Volcanes], 18°06'50"S 63°36'15"W, 1080 m. **PERU:** **Cusco** – San Pedro, 13°03'15"S 71°32'54"W; Megatoni National Sanctuary, 12°11'14"S 72°28'14"W, 1350-1900 m (May); La Convención, Echarate, 12°40'14"S 73°10'21"W, 1722 m (Oct). **Junin** – Puerto Eden [Río Tambo valley], 1400 m (Mar-Apr); Calabaza, 2000 m (Sep); near Satipo, 1200 m (Dec).

Comments. Olsoufieff (1924) was unable to see specimens of Felsche's species, which he tentatively regarded as a variety of *C. telamon*. Janssens (1940) countered Olsoufieff "... cette espèce est parfaitement valable ...", but was himself countered by Pereira and Martínez (1956; see also 1960), who combined it along with *C. corythus* as a subspecies of *C. telamon*. We agree with Janssens and with Arnaud (2002c) that Felsche's taxon merits species recognition.

The form of the male horn and pronotum of *C. ignecinctus* is very similar to that of *C. telamon* (*q.v.*). The central projection of the horn is strongly bent anteriorly, and the angle of bend is angularly produced but never bituberculate.

Felsche's (1909) description of this species is brief and includes no mention of the number of specimens he had on hand. The Felsche collection holdings in Dresden include six *C. ignecinctus*, only two (a pair) of which bear labels specifying the type locality, Marcapata, Peru. These two we consider syntypes, and it is the male which we hereby designate the **lectotype**. It is a small, worn individual missing the protarsal spurs as well as the left mesotarsus and both metatarsi. It bears five labels: a) handwritten in black on white "Marcapata, Peru"; b) printed on green "Coll. C. Felsche, Kauf 20, 1918"; c) handwritten "Ph. ignecinctus [male symbol] [unintelligible]"; d) printed on white "Staatsl. Museum für Tierkunde Dresden"; and e) our lectotype designation printed on white with red margin.

***Coprophanaeus (C.) telamon* (Erichson, 1847)**

Fig. 217, 220-222, 231, 238, 273-274

Phanaeus telamon Erichson, 1847: 106

Coprophanaeus telamon (Erichson) (recomb. by Edmonds 1972: 843)

Type. Holotype male, Museum für Naturkunde der Humboldt-Universität, Berlin.

Diagnosis. *General* – Dorsum almost completely black, metallic coloration, where present, green or yellowish green. Clypeus strongly and abruptly angulate lateral to median teeth. Posterior (ventral) surface of protibia completely granulorugose (Fig. 231). Cap of anterior angle of metasternum simple, not bifurcate. Anterior surface of metasternum glabrous above anterior margin of metasternal disk, otherwise sparsely, weakly punctured. Metasternal disk finely punctured, lacking row of larger punctures along anterior margin. Basal pronotal fossae distinct. Elytral interstriae weakly and evenly convex. Length 14–26 mm (usually > 20 mm).

Male – Base of head horn parallel-sided, anterior surface strongly concave, lateral angles acutely tuberculate; central process as long or longer than base, usually strongly inclined posteriorly and angularly bent in the middle (Fig. 221–222), bend often tuberculate on each side (Fig. 222, arrow). Pronotal prominence (Fig. 274) with acute lateral angles, cleat-shaped, flanked by deep oval concavities; width equal to distance between outer margins of eyes.

Female – Cephalic carina trituberculate, weakly bowed anteriorly; length of clypeus greater than that of frons.

Specimen examined – 531.

Distribution. Western Amazonia from Bolivia to Venezuela (Pantanal, Ucayali, Napo, Venezuelan Llanos provinces) (Fig. 238).

Collection Records. **BOLIVIA:** **Beni** – Villa El Carmen, 14°38'26"S 65°01'33"W (Jul); Paraparu, 13°49'S 64°26'W, 160 m; Río Negro, 13°43'S 67°22'W, 260 m. **Cochabamba** – Parque Departamental Altamachi, 16°02'S 66°40'W, 1150 m (Sep); Laguna Carachupa (Cordillera Mostenes), 16°14'S 66°25'W, 1250 m; Sacta, 17°04'18"S 64°46'00"W and 17°06'19"S 64°46'57"W, 250 m (Dec); 67.5 km E Villa Tunari [Estación Biológica Valle Sajta], 17°06'19"S 64°46'57"W, 300 m (Feb); General Román, 450 m (Feb); Yungas del Palmar, 1200 m; Chimoré, 250 m (Jan); Río Coni, 400 m; Villa Tunari (Nov); 117 km E. Cochabamba, at Lagunitas 17°06'22"S 65°40'57"W, 1000 m (Feb); 124 km E. Cochabamba, at Río Espirito Santo, 17°03'45"S 65°38'38"W, 700 m (Feb); Río Ipiri, 16°2'S 66°40'W, 1100 m, 16°3'S 66°41'W, 700 m, 16°3'S 66°40'W, 900 m; San Antonio; Valle Sacta, 17°07'S 64°45'W, 230 m (Mar); Sacta, 17°06'19"S 64°46'57"W, 250 m (Dec); San Francisco, 280 m (Nov). **La Paz** – Parque Nacional Madidi, 13°38'S 68°44'W, 260 m (Aug); Chalalán, 14°26'S 67°55'W, 360 m; Río Cocos, 14°4'S 68°50'W, 1000 m; Serranía del Tigre, 13°35'S 68°38'W, 700 m; Alto Madidi, 13°38'S 68°44'W, 260 m; San Miguel de Huachi [Boopi Playa] (Dec); Guanay [Uyapi] (Oct). **Pando** – 2 km E Fortaleza, 120 m; Guayamerín, 11°50'S 65°22'W, 120 m (Feb); 2.5 km SW Fortaleza del Abuna, 9°47'S 65°30'W (Feb). **Santa Cruz** – Lagunita Caparú, 14°48'S 61°10'W, 180 m; Parque Nacional Noel Kempff Mercado, 13°57'43"S 60°49'45"W, 14°33.5'S 60°55.9'W and 14°31'16"S 60°22'48"W (Jan); Los Volcanes, 17°57.5'S 63°25'W, 560 m (Feb); 4.5 km S Buena Vista [Hotel Flora y Fauna], 17°29.925'S 63°39.128'W, 440 m (Dec, Feb). **BRAZIL:** **Acre** – Sector Florestal Rio Branco [PZ-UFAC] (Feb); Palmar de las Islas, 19°25'S 60°32'W, 270 m (Feb). **Mato Grosso** – Mun. Diamantino, Fazenda São João, 14°23'49"S 56°09'30"W, 480 m (Jan). **Rondônia** – Porto Velho (Mar); 62 km S Ariquemes (Fazenda Rancho Grande), 10°32'S 62°48'W, 165 m (Sep-Oct); 9 km NE Cacaúlândia (Feb); 378 km S Porto Velho [Vilha Rondônia] (Jan-Feb). **COLOMBIA:** **Amazonas** – Leticia, 200 m (Feb-Mar); Parque Nacional Amacayacu [Leticia], 70 m (Dec). Boyacá – El Mortiño (Aug). **Boyacá** – near Pajarito, 5°23'39"N 72°41'17"W, 1000 m (Jun). **Caquetá** – Puerto Solario, PNN La Serranía de Chiribiquete, 0°12'47.8"N 72°25'25.4"W, 250 m (Feb-Mar); Gigante (Feb-Apr). **Guainía** – Caño Bocón, Santa Rosa, 3°04'46"N 68°02'26"W, 100 m (Nov.). **Guaviare** – San José [Finca La Esmeralda], 2°33'N 72°38'W, 240 m (Oct); RN Nukak Maku, 2°10'35"N 71°10'58"W. **Meta** – Puerto Gaitan, 150 m (Nov); Pedro de Arimena, 250 m (Nov); Centro Agroturístico CAFAM, 4°17.6'N 72°32.8'W (Nov); San Martín, 335 m (Apr); Villavicencio (Feb-Mar, Nov); Río Duda, PNN Tinigua, 2°40'N 74°10'W, 350 m (Jan); Vista Hermosa, 3°02'44"N 73°35'42"W, 200 m (Apr) **Norte de Santander** – 3 km N Chinácota, 1000 m (May); Sur [Bucaramanga] (Nov); ~40 km SSE Toledo, PNN Tamá, 7° 07' N 72°13'W, 1450 m (Sep). **Putumayo** – Mocoa (Mar). **Vaupés** – Caparú Biological Station, Río Apoporís, 1.1°S 69.5°W, 200 m (Nov-Dec). **ECUADOR:** **Morona Santiago** – Untsuants [Cordillera de Cutucú], 2°32'57"S 77°53'23"W, 600 m. **Napo-Orellana** – Yasuní Biological Station, 00°40'S 77°24'W, 215 m (Feb, Jun-Oct); Puerto Franciso de Orellana [aka Coca] (Jun); Ávila (Jul); Dureno [Río Aguatico] (Sep); Tena, 400 m (Feb, Jul); 3.3 km E Puerto Napo (Jul); 12 km WSW Tena, 600 m (Jul); 20 km S Tena (Jul); 21 km E Puerto Napo [Jatun Sacha Biological Station], 1°03'57.6"S 77°36'59.6"W (Feb-Mar, Jul);

Lago Agrio, 200 m (Jun); Daimi (Sep); Talag Pimpilata, 750 m (Feb); Yampuna (Jan); Archidona (Sep); Tiputini Biological Station, 00°38'S 76°09'W, 220 m (Sep); Aliñahui, 24 km E Atahualpa, 1°02'56.8"S 77°36'06.5"W (Mar); 24.5 km E Ahuano, 1°00'08.0"S 77°27'13.8"W (Feb-Mar); 29 km E, 1.5 km N San Pedro de Arajuno, 00°58'48.2"S 77°25'25.2"W, 360 m (Dec); 0.6 km E Río Arajuno, 1°05'26.5"S 77°35'30.1"W, 380 m (Dec); Payamino Research Station, 00 29'36.01"S 77 17'29.15"W, 400 m (Jul-Aug). **Pastaza** – Llandia [17 km N Puyo], 1000 m (Jul); Puyo, 1°28'56"S 77°59'56"W, 940 m (Mar, Jun, Nov); 22 km SE Puyo (Jul). **Sucumbios** – Limoncocha, 250 m (Jun); 2 km N Limoncocha, 250 m (Jun). **Tungurahua** – Baños (Jan); Río Negro, 1°24'S 78°13'W. **PERU**: Quiroz, Río Paucartambo. **Cusco** – Huayllcumbre, 13°11'42.2S 70°39'27.7"W, 650 m (Jun); Megantoni National Sanctuary, 12°09'44"S 72°34'28"W, 730-900 m (Apr); Saucetambo, Cosnipata (Koshñipata) River (Mar). **Huánuco** – Tingo María, 700 m (Jul, Oct-Dec); Cuchras [Haullaga River Valley] (Jun). **Junín** – Calabaza (Sep); Satipo (Mar, May). **Loreto** – Campamento San Lorenzo, 2°18'44.85"S 75°51'46"W, 175-215 m (Jun); Pucallpa (Jul, Aug). **Madre de Dios** – Pantiacolla Lodge, 8 km NW El Mirador trail, upper Madre de Dios River, 12°39'22"S 71°13'55"W, 400 m (Oct); Cocha Cashu Biological Station, Manu National Park, 11°53'45"S 71°24'24"W, 350 m (Oct); Cocha Salvador Reserve Zone, Manu National Park, 12°00'13.5"S 71°31'36"W, 310 m; 15km NE Puerto Maldonado [Reserva Cuzco Amazónica], 200 m, 12°33'S 69°03'W (Jun); Río Tambopata, Ccolpa de Guacamayos, 13°08.5'S 69°36.4'W, 300 m (Oct); Atalaya [Hotel Amazonia, Río Madre de Dios] (Jun); Río Patuyacu [La Viuda Camp], 12°52'S 68°55'33"W, 400 m (Mar); Río Patuyacu [Oculto Camp], 12°39'00"S 65°55'33"W, 230 m (Sep); Río Madre de Dios [Los Dos Amigos camp], 12°34'10.0"S 70°06'01.4"W, 250 m (Apr). **Pasco** – Santa Rosa [Río Palcazu] (Sep); Paujil [Parque Nacional Yanachaga-Chemillén], 500 m (Sep). **San Martín** – San Jacinto (Dec); Moyobamba [Dist. Naranjos, San Agustín] (Jan, May-Jul); Mishqui-Yacu, Moyobamba, 1200 m (Jul). **VENEZUELA**: **Amazonas** – La Tuquerena Rubio (Apr). **Aragua** – Portochuelo Pass, Parque Nacional Henri Pittier, 1200 m (Jun); Estación Biológica Rancho Grande, Parque Nacional Henri Pittier, 1100 m (Feb, Jun, Aug, Dec); Cuyagua, 800 m (Oct). **Bolívar** – El Dorado [Minas de Paypal] (May); km 90 on road from El Dorado to Santa Elena (Feb). **Falcón** – Sector Cumbre de Urea-El Chorro [Mpio. Petit], 1200 m (Jul). **Mérida** – 20 km SE Azulita [La Carbonera Biological Reserve], 2300 m (Jun); Sector Cuenca del Río Capara [Mpio. Padre Noguera], 7°50'32"N 71°30'34"W. **Táchira** – Presa La Honda, 1100 m (Dec); Pregonero (Las Trampitas), 1240 m (Jul); La Fundación [Presa Las Cuevas], 600 m (Jul); San Cristóbal, 1200 m (Aug); 42 km SE San Cristóbal, 700 m; 20 km NE San Cristóbal, 1200 m (May); 10 km NE San Cristóbal (Parque Nacional Chorro del Indio), 7°43'46"N 72°12'17"W, 1300 m (May, Oct); Río Frio, 500 m (Aug); Santo Domingo, 300 m (Aug).

Comments. This species is widely distributed at lower elevations (<1000 m) along the eastern slopes of the Andes. Its range comes close to that of *C. corythus* in northwestern Venezuela, where the dividing line between the two is the Mérida–Zulia cordillera. While its ecological distribution is normally in mesophilic forests, it can enter more xeric habitats (Vidaurre et al. 2008).

The normal form of the male head horn is unique and closely approached only in *C. ignecinctus*. In some populations (e.g. from Bolivia's Parque Nacional Noel Kempff Mercado) the central process is cylindrical, bent forward and lacks any hint of the posterior tubercles.

***Coprophanæus (C.) corythus* (Harold, 1863)**

Fig. 218-219, 223, 238, 275-279

Phanaeus corythus Harold, 1863: 163

Phanaeus perseus Harold, 1880: 27 **New Synonymy**

Phanaeus telamon corythus Harold (stat. by Pereira and Martinez 1956 : 234)

Coprophanæus telamon corythus (Harold) (recomb. by Arnaud 2002c: 35)

Coprophanæus telamon nevinsoni Arnaud and Gámez, 2002: 10 **New Synonymy**

Coprophanæus corythus (Harold) **New Status**

Type. *P. corythus* – lectotype male (des. by Arnaud 1982a: 115), Muséum National d'Histoire Naturelle, Paris (examined by photo); *P. perseus* – lectotype male (des. by Arnaud 1982a: 115), Muséum National

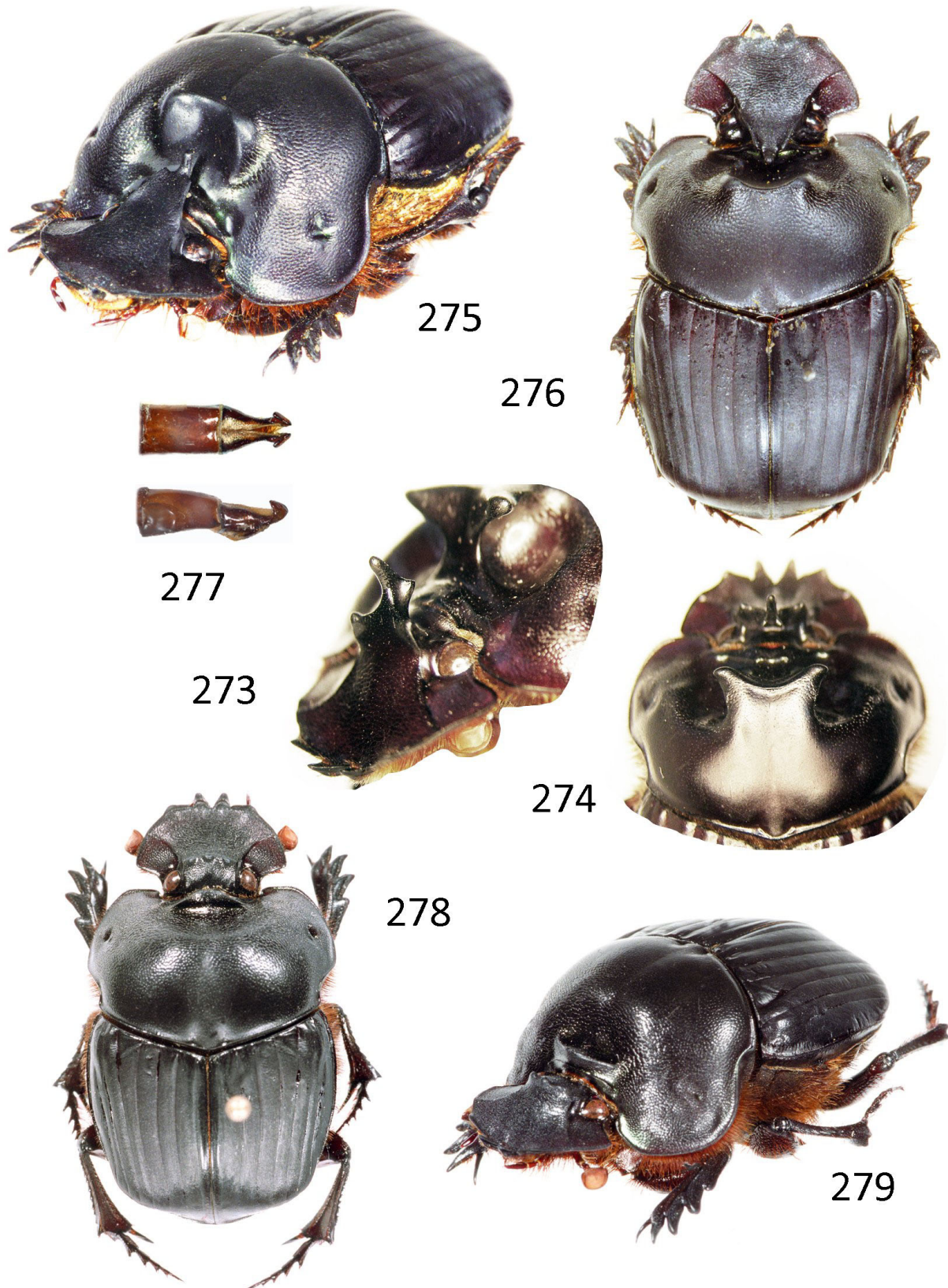


Figure 273-279. *Coprophanaeus* spp. 273-274) *C. telamon*, forebody of male. 275-279) *C. corythus*. 275-276) Male habitus. 277) Aedeagus (dorsal view above; lateral view below). 278-279) Female habitus.

d'Histoire Naturelle, Paris (examined by photo); *C. nevinsoni* -- holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France.

Diagnosis. *General* – Metallic coloration, where present, green or yellowish green. Clypeus strongly and abruptly angulate lateral to median teeth. Posterior (ventral) surface of protibia completely granulorugose (as in Fig. 231). Cap of anterior angle of metasternum simple, not bifurcate. Anterior surface of metasternum glabrous above anterior margin of metasternal disk, otherwise sparsely, weakly punctured. Metasternal disk finely punctured, lacking row of larger punctures along anterior margin. Basal pronotal fossae distinct. Elytral interstriae weakly and evenly convex. Length 16-26 mm (usually > 20 mm).

Male – Base of head horn (Fig. 218-219) with convergent sides, anterior surface at most only weakly concave, lateral angles acutely tuberculate; central process conspicuously shorter than base, at most only weakly inclined posteriorly, evenly curved posteriorly and never tuberculate or angulate on posterior surface. Pronotal prominence (Fig. 275-276) bilobate, saddle-shaped, never with acute lateral lobes, flanked by shallow concavities; width less than distance between outer margins of eyes.

Female – Cephalic carina trituberculate, weakly bowed anteriorly; length of clypeus greater than that of frons.

Specimen examined – 563.

Distribution. Middle America from Venezuela and Colombia along Caribbean coast to southeastern Mexico (Cauca, Chocó, Eastern Central America and Gulf of Mexico provinces) (Fig. 238).

Collection Records. **BELIZE:** **Cayo** – Belmopan (Jul-Aug); Chiquibul Forest Reserve [Las Cuevas Research Station], 16°44'N 88°59'W, 550 m (Jun, Aug). **Orange Walk** – Lamanai (Feb); Río Bravo Preserve (Apr). **Toledo** – Punta Gorda (Apr, Sep-Oct); Blue Creek Village (Jun). **COLOMBIA:** **Antioquia** – Amalfi, 1100 m (Mar); San Luis [Río Claro], 1440 m (Mar). **Bolívar** – SFF Los Colorados, 9°51'33"N 73°06'38"W, 300 m (Aug); Mompos (Jun). **Cesar** – Valledupar; San Alberto Indupalma (Sep). **Chocó** – Pacurita, 5°41'N 76°40'W; Tutumendó; Quibdó; El Amargal Biological Station, 5.6°N 77.4°W, 150-500 m (Aug). **Cundinamarca** – Santandercito (Jul). **Quindío** – Buenavista, 4°23'N 75°44'W, 1200 m. **Risaralda** – Pereira, 1850 m (Apr). **Santander** – Vélez (Sep); Bucaramanga (Jul). **Tolima** – Mariquita, 650 m (Sep); Ibagué (Mar); Guyabal [Armero], 250 m (Oct). **Valle de Cauca** – Buenaventura [Bajo Calima], 50 m (Apr); Palmira (Feb). **COSTA RICA:** **Cartago** – Turrialba (May). **Guanacaste** – Parque Nacional Santa Rosa, Estación Santa Rosa, 10°50'21.4"N 85°37'05.8"W, 295 m (Jun-Jul, Nov); Canas [Taboga] (Jun-Jul). **Heredia** – Puerto Viejo [Finca La Selva] (Jun). **Limón** – La Selva (Jul, Apr); Pandora [Valle Río Estrella] (Feb); La Ceiba (Jun); Sector Cerro Cocori, Finca de E. Rojas, 150 m (Jun). **Puntarenas** – Parque Nacional Manuel Antonio (Nov-Dec); Estación Sirena, Parque Nacional Corcovado, 100 m (Mar, Dec); Estación Quebrada Bonita, Estación Biológica Carara, 50 m (Mar-Apr); Osa Peninsula, Río Piro La Joya, 8°23'56"N 83°19'51"W, 350 m (Aug-Sep). **GUATEMALA:** **Petén** – Uaxactún (Dec). **Zacapa** – La Unión, 850 m (Jul); 3.5 km SE La Unión, 1500 m (Jun). **HONDURAS:** **Atlántida** – Tela [Lancetilla Botanic Gardens], 15°46'N 87°27'W (May-Jun). **Francisco Morazán** – El Zamorano; Tegucigalpa (May). **Gracias a Dios** – Krausirpi, 15°03'N 84°52'W (May). **La Paz** – La Paz (May). **MEXICO:** **Campeche** – Escarcega (Jul). **Chiapas** – San Antonio (Aug); Bonampak, 16°42'N 91°04'W (Sep); Santa Rosa (Aug); Boca de Chijul (Dec); 1.2 km and 6.2 km NE Estación Biológica Chajul, 16°07'07.1"N 90°55'51.9"W and 16°09'10.0"N 90°54'17.1"W, 200 m (May); Laguna Bélgica, 16 km NW Ocozocoautla, 970 m (Jun); Palenque, 600 m (May-Jul); Rosario Izapa (May); Selva Lacandona, Laguna Miramar (Oct). **Hidalgo** – 6.5 km SW Chapulhuacan (Jul). **Oaxaca** – Distrito Yautepec, Juquila Mixes (Sep); 10 km S. Valle Nacional, 600 m (Jul); confluencia Ríos Sarabia y Coatzacoalcos [Finca San Carlos (Mar); La Nueva Esperanza (Aug); Tuxtepec (Nov). **Puebla** – Calapan 19°55'45.92"S 97°23'07.65"W, 1250 m (Jul). **Quintana Roo** – 12 km N. Felipe Carrillo Puerto (Oct); Cedral (Mar); Tintal (Mar); X-Can (Jun-Jul, Oct); Nuevo X-Can (Oct); 68 km W Chetumal (Jul). **Veracruz** – Veracruz (Aug); Córdoba (Jul-Aug); Coatepec, 1200 m (May); Guadalupe Victoria, 750 m (Jun); Omealca (Oct); 33 km N Catemaco, 160 m (Jul-Aug); San Andrés Tuxtla (May-Jun); Fortín de la Flores, 900 m (Jun); Los Tuxtlas (Jul); Tezonapa (Sep); Palma Sola (Jun); 11 km W Palma Sola (Sep); Xalapa, 1350 m (Jul, Sep); Actopan, 240 m (Aug); Espinal, 900 m (Aug); Cerro Leon, 700 m (Nov); Sontecomapan (Estación Biológica Tropical Los Tuxtlas), 400 m (Jun, Aug, Oct). **NICARAGUA:** **Atlántico Norte** – Waslala (Dec); **Río San Juan** – 8 km SE El Castillo [Refugio Bartola], 10°56.6'N

84°20.4'W (May). **PANAMA: Colón** – 16km SE Colón, Santa Rita Ridge, 270m (Jun); 14km N junction Escobal Road and Piña Road, 20m (Jun); Gatún Island (May-Jun, Dec); Corozal (May); Barro Colorado Island (Jul). **Darién** – Río Tacarcuna, 580m (Jul); Estación Ambiental Cana, 7°45.32'N 77°41.07'W, 600-750 m (Jun). **Panama** – 11-15 km N El Llano, 350 m (May); Cerro Azul, 650 m (May); 31 km E Canita, 50 m (May); Lago Bayano, Isla Majé (Dec); Howard Air Force Base (Pacific entrance Panama Canal), 10m (Jul-Aug); Cerro Jefe, 1000 m (May); Cerro Campana, 860 m (May). **VENEZUELA: Mérida** – Finca Campo Alegre [Mpio. Zea-Mérida], 8°28'56"N 71°44'38"W, 650 m (Sep).

Comments. Pereira and Martínez (1956; see also 1960) regarded *C. corythus* (along with *C. ignecinctus* [q.v.]) as a subspecies of *C. telamon*. We here return to former usage (Gillett 1911; Olsoufieff 1924; and Blackwelder 1944, among others) and restore *C. corythus* to species rank. Pereira and Martínez (1956) erroneously synonymized *C. chiriquensis* with *C. corythus*.

Coprophanaeus corythus is a common denizen of forest–pasture mosaic habitats of Chiapas (Arellano et al. 2008; Navarrete and Halffter 2008), more common in continuous forest than pastures. The phenology and daily activity of this species (cited as *C. telamon nevinsoni*) in the Maracaibo depression of extreme western Mérida, Venezuela, was reported by Gámez et al. (2006). There it occurs in both relic forest patches and open cultivated areas, with highest frequency in forest habitat; it is collected all year with greatest abundance during rainfall peaks in April–May and October–November.

The large male head horn is most variable in the South American populations of this species, where it can be intermediate between the shape in typical *C. corythus* and that of certain *C. telamon* (cf. Fig. 218-219, 275-276). Certain of these intermediates, which we regard as intraspecific variants, were named *C. telamon nevinsoni* by Arnaud and Gámez (2002). There seems to be no solid basis at present to maintain the taxonomic distinction.

Olsoufieff (1924) erroneously synonymized *Phanaeus perseus* Harold with *Phanaeus cerberus* Harold. Olsoufieff, who examined Harold's type, correctly pointed out that Harold did not notice that his specimen was damaged, "... l'auteur n'a pas fait attention que l'épistome était presque symétriquement grignoté (cassé) des deux côtés des lobes aigus, ce qui faisant illusion de 4 dents séparées"; but he mistakenly associated it with *C. cerberus*, the female of which is quite different. The holotype agrees fully with Harold's description, including the misplaced reference to the broken clypeus, "... das Kopfschild vorn mit 4 Zähnen ... die seitlichen ... zwischen diesen [die mittleren] und dem stumpfwinkeligen vorderen Wangeneck eine ziemlich tiefe Ausbuchtung." And it was the apparently strongly quadridentate clypeus that prompted him to recognize it as a new species, "... so habe ich doch in Anbetracht der höchst eigenthümlichen Zahnung des Clypeus kein Bedenken getragen, dieselbe als neu zu beschreiben." Ironically, he unconsciously corrected his own error, declaring "Sieht man von der verschiedenen Kopfbildung ab, so stimmt das Weibchen in allem übrigen vollkommen mit dem des Corythus überein." Harold's type is a female *C. corythus* with a broken clypeus.

The ohausi species group

Of the four species groups of *Coprophanaeus s. str.* recognized here, the ohausi group is the least understood and in greatest need of further scrutiny. As here defined, it embraces at least four uncommon South American species (*C. ohausi*, *C. caroliae*, *C. suredai* and *C. callegarii*) occupying the foothill corridor along the eastern side of the Andes from Bolivia to Colombia. This group shares with the pluto group a close similarity between the cephalic structure of males and females (both with a transverse, trituberculate carina); and with the dardanus group the strongly elevated, acute apical teeth of the parameres. The most widely distributed and variable species of the group is *C. ohausi*. We have been unable to place several putative taxa which, if valid species, are very likely assignable to this group: *Coprophanaeus lichyi* Arnaud, *C. lecromi* Arnaud, *C. larseni* Arnaud and *C. strandi* Balthasar.

Diagnosis. General – Frons of variable length relative to clypeus. Anterior portion of circumnotal ridge interrupted behind eyes. Posterior edge of paraocular area abruptly curved toward posterior angle of eye. Anterior one-half of pronotum generally bearing squamose granulation, often coalescing into short, transverse ridges; remainder of pronotum punctate, puncturing becoming progressively weaker toward posterior margin (more so in larger males); basal fossae present. Prosternal ridge simple, lacking acute tu-

bercle at anterior end. Elytral interstriae distinctly raised midlongitudinally; striae very fine. Usually dark, sombre species to unaided eye; metallic coloration inconspicuous and most obvious under magnification (x10), restricted to anterior portion and margins of pronotum and pygidium; venter always showing reflections of same tone as dorsum. Medium-sized species, length usually 15-25 mm.

Male – Apices of parameres with distinct, dorsally projecting teeth visible in profile (strongly elevated in *C. ohausi* and *C. callegarii*, attenuated in *C. caroliae* and *C. suredai*). Head with trituberculate transverse carina; tubercles equal-sized and closely set – distance between lateral teeth not exceeding three-fourths of interocular width. Pronotum with anteromedian transverse ridge, carina or other process flanked by elongate depression on each side.

Female – Head with transverse trituberculate carina configured as in male. Pronotum with low, oval, transverse crest very near anterior margin followed by indistinct depression.

Distribution. Extreme western Amazon basin along foothills to about 1200 m from Bolivia to eastern Colombia.

Key to species of the ohausi group

1. Frons short, length at most equal to that of clypeus (Fig. 287). Anterior (declivitous) face of metasternum with setigerous punctures concentrated medially. Apical processes of parameres (Fig. 296) conspicuous, strongly elevated, acute teeth. Smaller size, length seldom exceeding 15 mm ***Coprophanaeus (C.) callegarii* Arnaud**
- Frons longer, length usually at least one and half that of clypeus (Fig. 289). Anterior (declivitous) face of metasternum with setigerous punctures widely distributed over most of surface. Apical processes of parameres variable. Larger beetles, length usually greater than 15 mm, often approaching 20 mm **2**
- 2(1). Pronotal prominence of large male (Fig. 299-300) with a pair of blunt, isolated conical bumps separated by small concavity; pronotum with deep, oval fovea above lateral fossa. Apical processes of parameres small, attenuated (viewed from side, Fig. 301). Dorsum black with narrow metallic red band around pronotal margin; lower surfaces of femora and at least base of pygidium with metallic red coloration. Yungas of Bolivia ***Coprophanaeus (C.) caroliae* Edmonds**
- Pronotal prominence of large male a broad salience with cusps, ridges and angles, never a pair of isolated conical bumps. Other characters variable **3**
- 3(2). Pronotal process of large male (Fig. 290) more-or-less trapezoidal, with well-defined triangular lateral angles. Apical processes of parameres small, attenuated (Fig. 305) ***Coprophanaeus (C.) suredai* Arnaud**
- Pronotal process of large male variable, but always more-or-less bitumid, with transverse carina or thickening of variable shape connecting tumescences (Fig. 280-286). Apical processes of parameres long, slender, parameres appearing strongly hooked in profile (Fig. 313) ***Coprophanaeus (C.) ohausi* (Felsche)**

***Coprophanaeus (C.) callegarii* Arnaud, 2002**

Fig. 287-288, 291-296

Coprophanaeus callegarii Arnaud, 2002a: 4

Type. Holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France.

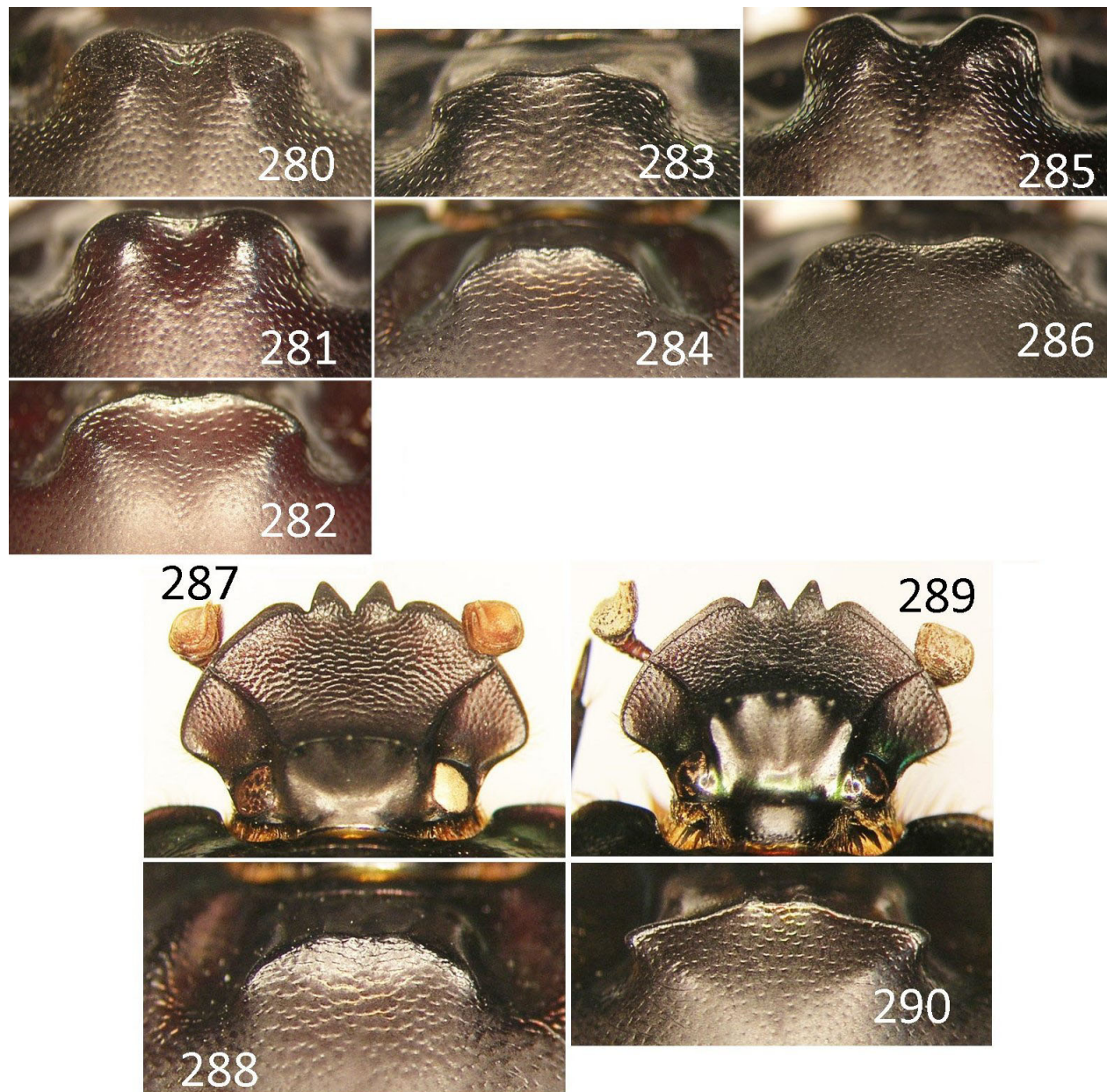


Figure 280-290. Characters of the *Coprophanaeus* (*s. str.*) *ohausi* species group. **280-284)** Dorsal views of male pronotal prominence variation in population from Satipo, Junin (Peru). **285)** Dorsal view of pronotal prominence of male from eastern Ecuador. **286)** Dorsal view of pronotal prominence like that of lectotype male. **287)** *C. callegarii*, dorsal view of male head. **288)** Same, dorsal view male of pronotal prominence. **289)** *C. suredai*, dorsal view of male head. **290)** Same, dorsal view of male pronotal prominence.

Diagnosis. General – Dorsum largely black, metallic color (red, green or coppery green) restricted to posterior portion of head and anterior portion and margin of pronotum and pygidium; venter with subdued violet reflections. Frons short, length less than that of clypeus. Anterior (declivitous) face of metasternum with setigerous punctures concentrated medially. Length 11-15 mm.

Male – Apical processes of parameres strongly elevated, clearly visible in profile. Pronotal prominence arcuate, lacking well-defined tubercles or angles, narrow, width less than distance between outer margins of eyes (in small males prominence reduced to arcuate ridge very near anterior margin).

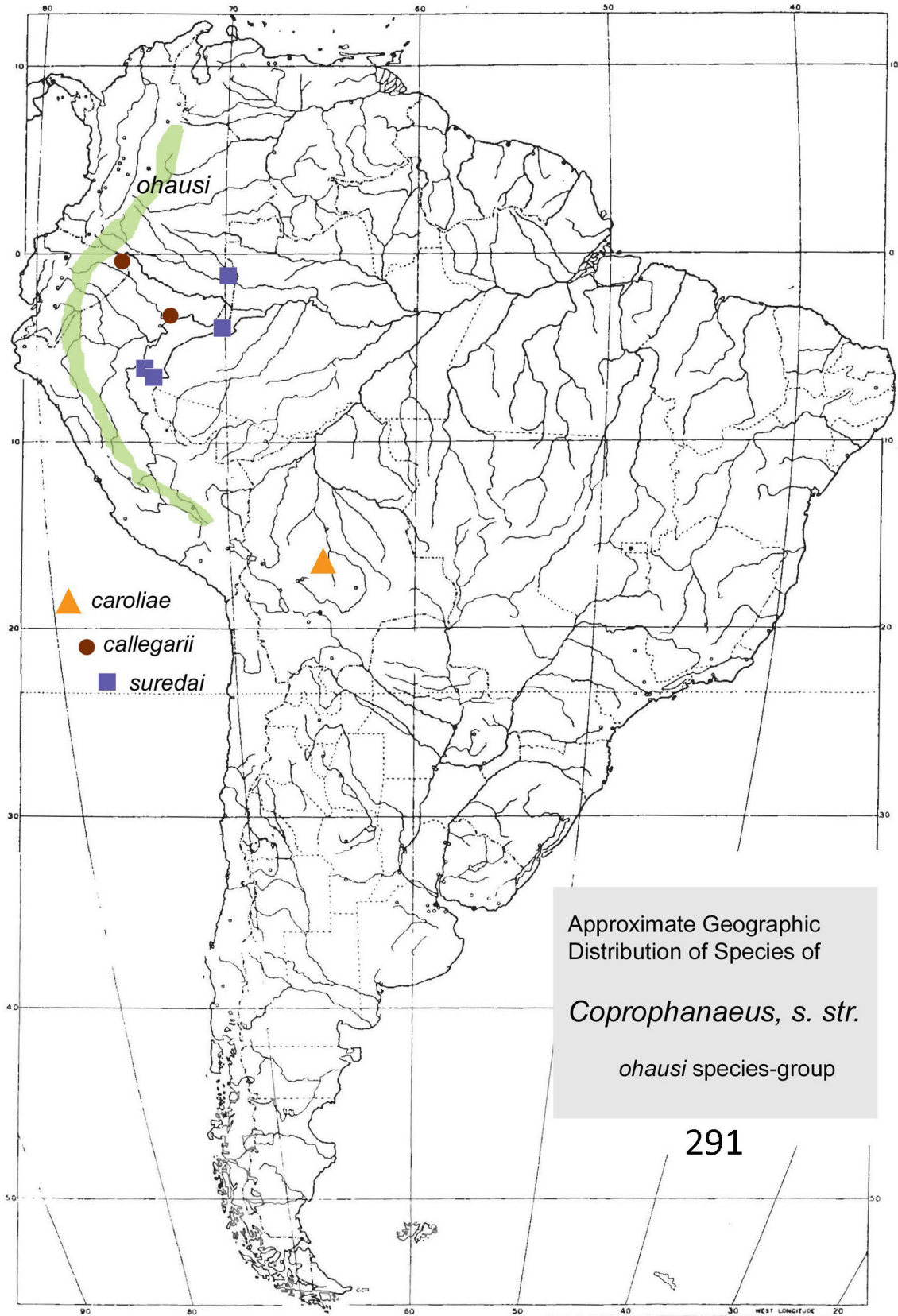


Figure 291. Approximate geographic distribution of *Coprophanaeus* (s. str.) species in the *ohausi* species group.

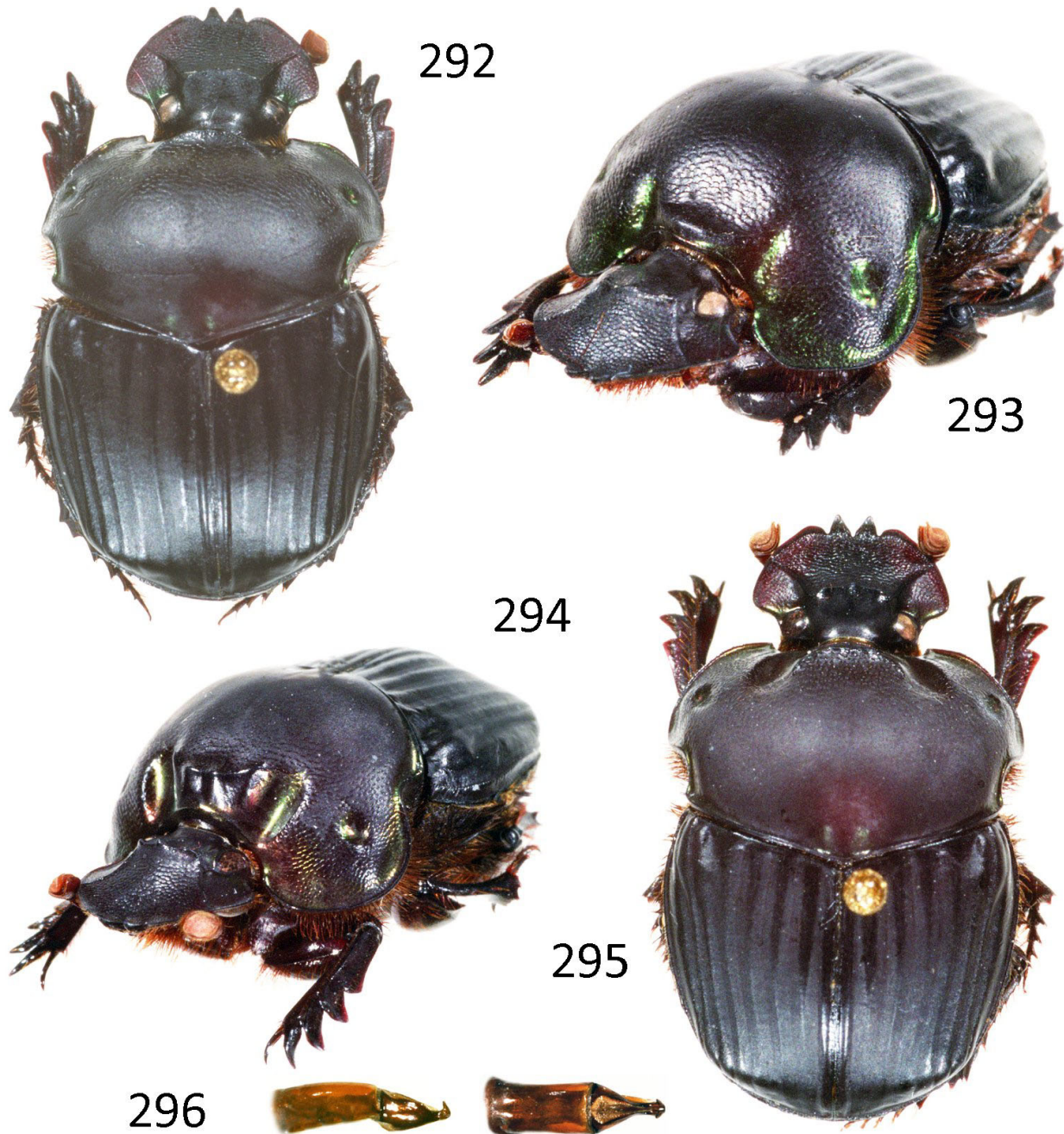


Figure 292-296. *Coprophanaeus callegarii*. 292-293) Female habitus. 294-295) Male habitus. 296) Aedeagus (lateral view on left, dorsal view on right).

Female – Pronotal carina very near anterior pronotal margin, only weakly raised, lacking distinct median tubercles.

Specimen examined – 34.

Distribution. Upper Amazon River basin of Napo province.

Collection Records. PERU: Loreto – Iquitos (Feb) (see Comments below).

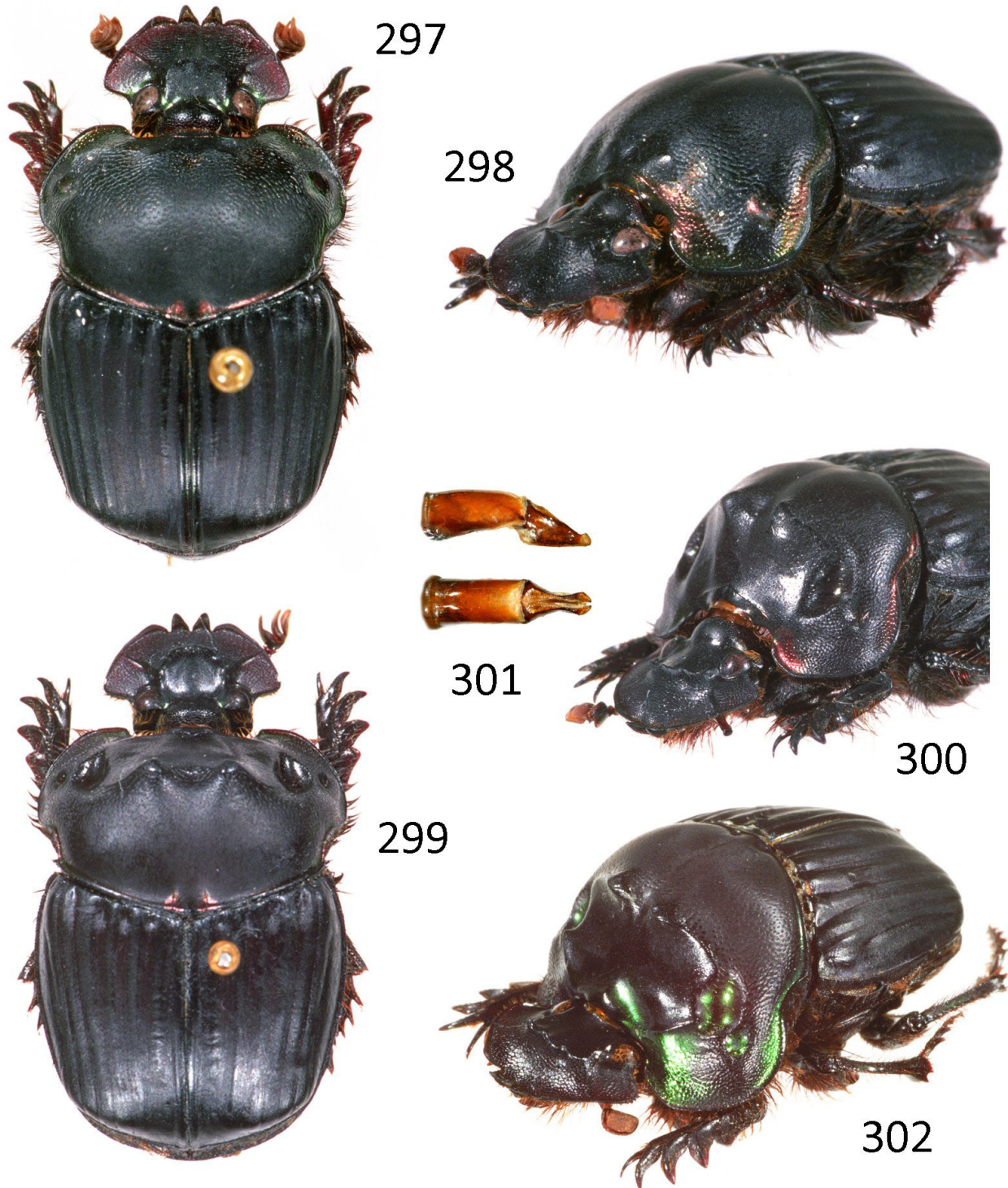


Figure 297-302. *Coprophanaeus* spp. **297-301)** *C. caroliae*. **297-298)** Female habitus. **299-300)** Male habitus. **301)** Aedeagus (lateral view above, dorsal view below). **302)** *C. strandi*, holotype male habitus.

Comments. Thanks to Darren Mann (Oxford University Museum of Natural History) we examined and assigned to this species a long series from the type locality (Iquitos). A paratype male was cited by Arnaud (2002a) as from “Brasil: Para, S. Paulo de Olivença ...”. We regard the state record (Pará) as erroneous; São Paulo de Olivença lies in the state of Amazonas about 450 km downriver from Iquitos. Arnaud’s

description was based on two males, neither regarded as well developed: “Ce critère [description of male pronotum] est à prendre avec prudence car l’examen de peu de spécimens ne permet pas de juger si les exemplaires sont de forme majeure.” Our series of 34 specimens includes 15 males, none of which is more robustly developed than the holotype pictured by Arnaud (2002c). Since we have examined neither the holotype nor the paratype, our identification of this series as *C. callegarii* must be regarded as provisional.

***Coprophanaeus (C.) caroliae* Edmonds, 2008**

Fig. 291, 297-301

Coprophanaeus caroliae Edmonds, 2008: 43

Type. Holotype male, Colección Boliviana de Fauna, La Paz (examined; on loan to Museo de Historia Natural Noel Kempff Mercado, Santa Cruz).

Diagnosis. *General* – Dorsum largely black, red metallic color restricted to posterior portion of head and anterior portion and margin of pronotum and pygidium; venter with scattered reflections of same tone as dorsum. Frons long, length at least one and half times that of clypeus. Anterior (declivitous) face of metasternum with setigerous punctures widely distributed over most of surface. Length 17-22 mm.

Male – Apical processes of parameres attenuated, tips barely visible in profile. Pronotal prominence of larger individuals consisting of two conical bumps separated by small concavity.

Female – Pronotal carina a distinctly raised, medially bidentate crest followed by very weak depression.

Specimen examined – 23.

Distribution. Yungas province in Bolivia.

Collection Records. **BOLIVIA: Cochabamba** -- Cordillera Mosestenes, Isiboro-Securé National Park, 16 14'10"S 66 24'46"W, 1350 m (Sep).

Comments. *Coprophanaeus caroliae* is known only from the low yungas of Cordillera Mosestenes, whose dung beetle community received close scrutiny from Hamel-Leigue et al. (2008). This species is similar to *C. strandi* (Balthasar, 1939) and apparently also to *C. lecromi* Arnaud, 2002a, and it may later be judged a synonym of either or both. These two species were based on single male specimens. We have examined the holotype and only known specimen of Balthasar's species deposited at the National Museum of Natural History in Prague, which we illustrate here for the record (Fig. 302). But we have not seen that of *C. lecromi*, which is housed in the private collection of its describer. Until more specimens (including females) and information on *C. strandi* and *C. lecromi* become available, a thorough comparison and analysis of the three taxa will not be possible (see Edmonds 2008, for further observations).

***Coprophanaeus (C.) suredai* Arnaud, 1996**

Fig. 289-291, 303-307

Coprophanaeus suredai Arnaud, 1996: 6

Type. Holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France.

Diagnosis. *General* – Dorsum (Fig. 303-307) mostly black, golden or red coloration with green highlights present on head and anterior portion and margins of pronotum; venter with metallic highlights of same tone as dorsum. Anterior (declivitous) face of metasternum with setigerous punctures widely distributed over most of surface. Length 12-14 mm.

Male – Pronotal prominence (Fig. 290) more-or-less trapezoidal, with acute lateral angles. Apical processes of parameres attenuated, scarcely visible in profile (Fig. 305).

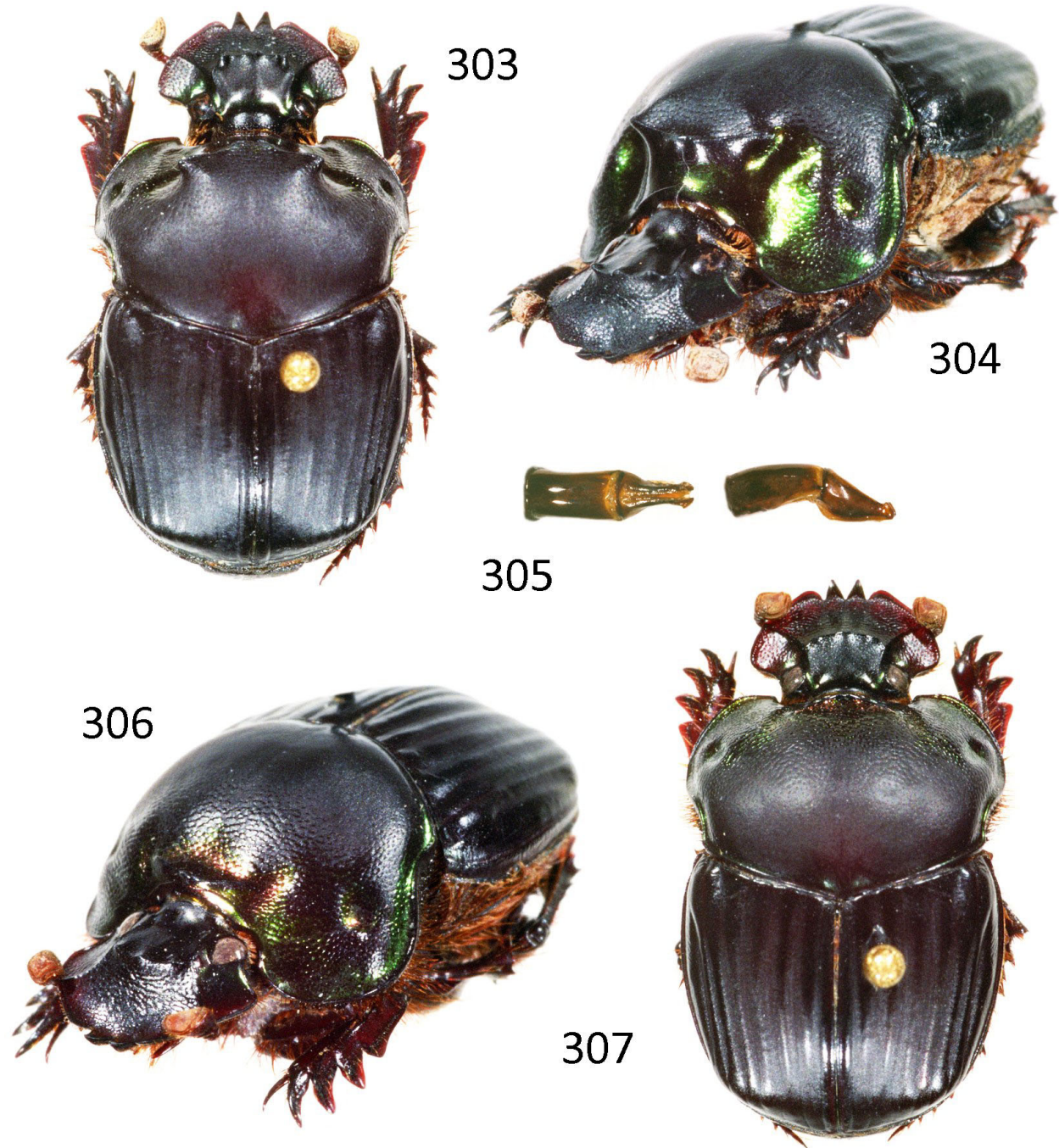


Figure 303-307. *Coprophanaeus suredai*. **303-304)** Male habitus. **305)** Aedeagus (lateral view on right, dorsal view on left). **306-307)** Female habitus.

Female – Pronotal ridge curved, very slightly bidentate medially.

Specimen examined – 9.

Distribution. Eastern Napo province.

Collection Records. **COLOMBIA:** Amazonas – Leticia (Feb). Vaupés – Río Apaporis (Caparú Biological Station), 1.1 S 69.5 W, 200 m (Nov-Dec). **PERU:** Loreto – Quebrada Ubuya, 74°01'24"W 6°57'19"S, 202 m (Mar); Quebrada Punga, 74°00'59"W 6°27'40"S, 145 m (Feb).

Comments. Arnaud (2002a, 2002c) places *C. larseni* near *C. suredai*. Among the few specimens of *C. suredai* that we have seen are the Leticia paratypes in the Canadian Museum of Nature. The original description was based on 10 specimens from western Amazonia, including Lago Agrio (Ecuador) and “Peru”. The Canadian Museum also has two female specimens which resemble *C. suredai*, from Brazil: Amazonas – Estirão do Ecuador, Rio Javari (Feb); and Bolivia: Pando – 11°50’S 65°22’W (Feb). We could not locate Estirão do Ecuador, but it presumably lies along the Brazil–Peru border (formed by the Rio Javari) near Tabatinga (Brazil) and Leticia. The coordinates specified for the latter lie in the northern extremity of the department of El Beni (near but not in Pando), about 1000 km SSE of Leticia. Hamel et al. (2009) cite this species from 2 km E Fortaleza (Pando) and Guayaramerin (Beni) in Bolivia.

***Coprophanaeus (C.) ohausi* (Felsche, 1911)**

Fig. 280-286, 291, 308-313

Phanaeus ohausi Felsche, 1911: 138

Coprophanaeus ohausi (Felsche) (recomb. by Blackwelder 1944: 209)

Coprophanaeus florenti Arnaud, 2002a: 5 **New Synonymy**

Type. *P. ohausi* – lectotype male, **here designated**, Staatliches Museum für Tierkunde, Dresden (examined); *C. florenti* – holotype male, private collection of Patrick Arnaud, Saintry sur Seine, France.

Diagnosis. *General* – Dorsum largely black, metallic color (dark green or blue), if any, usually restricted to posterior portion of head and anterior portion and margin of pronotum and pygidium; sometimes present on elytra; venter with scattered reflections of same tone as dorsum. Frons long, length at least one and half times that of clypeus, often longer. Anterior (declivitous) face of metasternum with setigerous punctures widely distributed over most of surface. Length 16-21 mm.

Male – Apical processes of parameres strongly elevated, clearly visible in profile. Pronotal prominence of larger individuals variable, usually distinctly bitumid, lobes rounded and usually finely carinate anteriorly (in small males prominence reduced to transverse carina above anterior margin).

Female – Pronotal ridge distinctly raised, medially bidentate and followed by very weak depression.

Specimen examined – 68.

Distribution. Yungas and western Napo provinces.

Collection Records. **COLOMBIA:** **Casanare** – Aguazul, 375 m (Nov). **Meta** – Puerto Gaitan, 400 m (Oct). **Santander** – Veléz, 2400 m (Sep). **ECUADOR:** **El Oro** – Piñas, 3 42’S 79 42’W (Mar). **Morona-Santiago** – Ángel Rouby (Cordillera Cutucú), 2°21.6’S 78°4.0’W (Feb); Cordillera Cutucú, 2 32’57”S 77 53’23”W. **Napo-Orellana** – Loreto road, 7.9 km E Narupa junction, 00 43’06.9”S 77 45’44.0”W, 1380 m (Mar); Río Hollin, 00 41.702’S 77 43.842’W, 1068 m (Dec); Aliñahui (Feb); Puerto Napo (Apr); Yasuní National Park, Yasuní Research Station, 00°38’S 76°36’W, 215 m; Limoncocha, 250m (Jun); Puerto Francisco de Orellana (“Coca”) (May); km 11.1 road Sarayacu to Loreto, 1200 m (Jul). **Pastaza** – 22 km SE Puyo, 900 m (Jul); 17km N Puyo [Llandia], 1000 m (Jul). **Tungurahua** – 6 km and 8 km E Río Negro, 1400 m (Jul). **Zamora-Chinchipe** – Bombuscaro (Parque Nacional Podocarpus), 1146 m, 4°06’09”S 78°57’46”W (May). **PERU:** **Junin** – Satipo, 1100 m (Mar). **San Martín** – Moyobamba (Jan); Alto Nieva (Aug).

Comments. Of the species comprising this group, *C. ohausi* exhibits the greatest variation in form of the well-developed male prothorax. The median prominence is bitumid, but its swellings are connected by a transverse carina that varies in shape. Figures 280-284 illustrate this variation in a single population from Satipo, Peru. In well-developed individuals of both sexes the frons widens anteriorly and produces the false impression that the transverse carina is markedly narrower than in other species. Howden and Young’s (1981) reference to *C. ohausi* is in fact to *C. morenoi* Arnaud (Howden and Gill 1987). The description of *C. lichyi* Arnaud suggests that it is closely related to, or perhaps synonymous with *C. ohausi*.

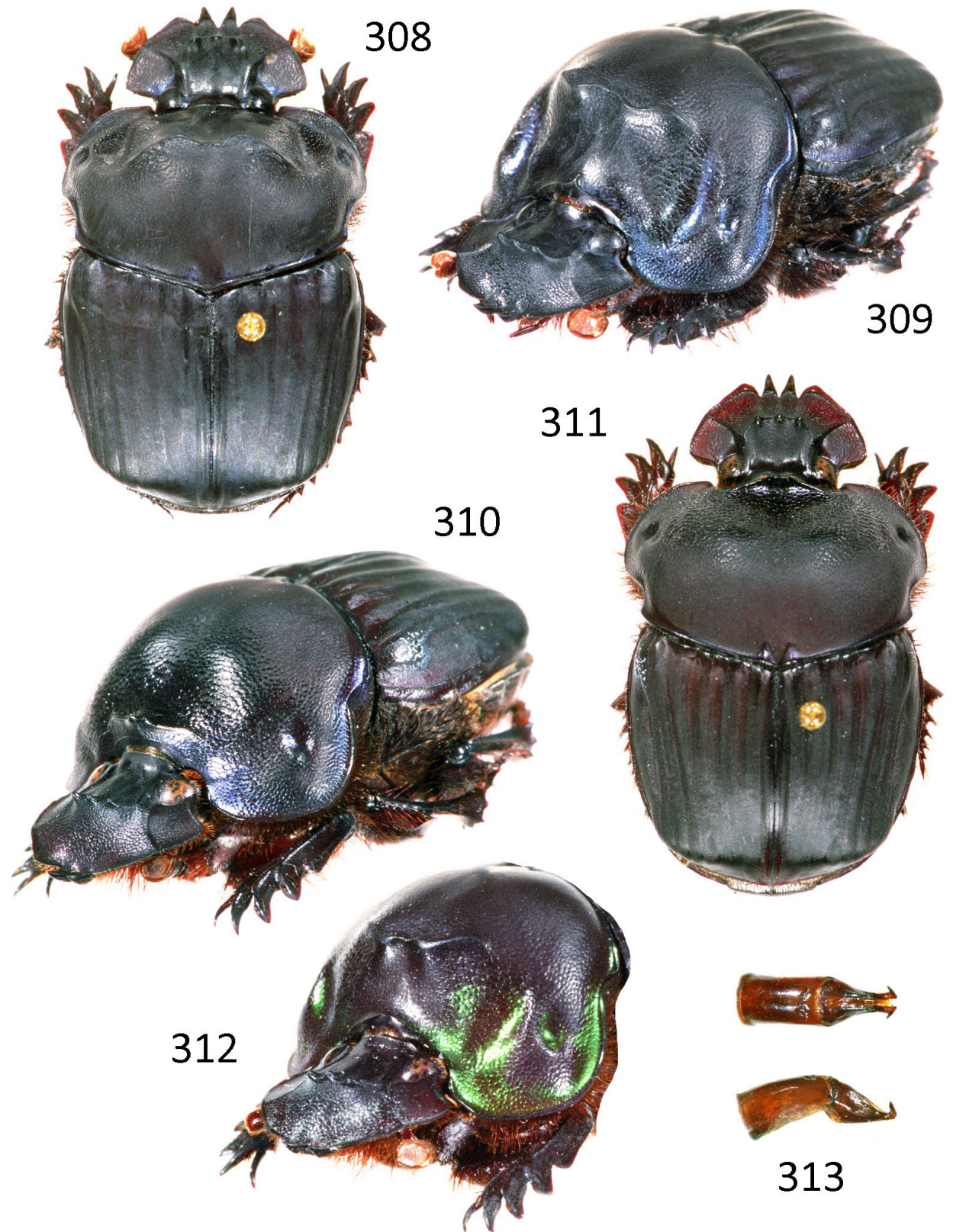


Figure 308-313. *Coprophanaeus ohausi*. 308-309) Male habitus. 310-311) Female habitus. 312) Male forebody, green phase. 313) Aedeagus (lateral view below, dorsal view above).

The type material of *C. florenti* was not available to us for study. Our point of reference for synonymizing this name with *C. ohausi* is a large series of *C. florenti* in the Canadian Museum of Nature collection identified by Arnaud. The color and male pronotal structure cited by Arnaud in his description, as well as that in the aforementioned series, fit well within the range of variation of *C. ohausi* as here defined.

The Staatliches Museum für Tierkunde collection in Dresden includes three specimens that we regard as the type series of this species. Two are labeled “Macas” [Ecuador] and the third “Teremotillo”. Felsche’s original description of *Phanaeus ohausi* cites two Ecuadorian localities for the material at hand: Teremotillo and Jivaria. Felsche stated that Ohaus gave him the specimen from Teremotillo – “... das andere, das er mir gütigst überlassen, bei Teremotillo; ...”. We exclude the Macas specimens from the type series, leaving the Teremotillo specimen as putative type. We hereby designate this specimen the **lectotype**. We assume that the Jivaria specimen seen by Felsche is lost or elsewhere. The lectotype is a large male with dark blue dorsal metallic coloration (including on the elytra), somewhat worn and dirty, and missing the left mesotarsus and the right metatarsus. It bears nine labels: a) [white rectangle] “Ecuad. Ostcordill./Teremotillo/F. Ohs. 14.12.05”; b) [green rectangle] “Col. C. Felsche/Kauf 20, 1918”; c) [green square] “1910/4”; d) [folded white] “Ohausi” handwritten in red ink; e) [oblong white] “Ph. ohausi/ {illegible}” handwritten in black ink; f) [red] “Typus” printed, “ohausi Felsche” handwritten; g) white “Staatsl. Museum für/Tierkunde”; h) our lectotype label printed on white with red border.

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