

<http://dx.doi.org/10.11646/zootaxa.3869.4.7>  
<http://zoobank.org/urn:lsid:zoobank.org:pub:7446EA9F-1C54-47AB-ABF1-0A82B1E59687>

## Revalidation of the Brazilian Atlantic Forest dung beetle species *Coprophanaeus (Metallophanaeus) machadoi* (Pereira & d'Andretta, 1955) (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini) based on morphological and distributional evidence

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### Abstract

*Coprophanaeus machadoi*, species described based on a single male from Minas Gerais, was recently synonymized with *C. saphirinus* (Sturm, 1826). In this work, based on examination of more than 500 specimens from Brazilian Atlantic Forest, we introduce new evidence supporting the validity of *C. machadoi*, including differences in male pronotal ornamentation, in the form of the parameres, and in distribution. We also describe for the first time the female of *C. machadoi* and discuss the intraspecific color variation of *C. saphirinus*.

**Key words:** Phanaeina, *Coprophanaeus saphirinus*, scarab beetle, cryptic species, endangered species, synonymy

### Introduction

As here interpreted, *Coprophanaeus* d'Olsoufieff, 1924 comprises 43 valid species in three subgenera, *Coprophanaeus* s. str., *Megaphanaeus* d'Olsoufieff, 1924, and *Metallophanaeus* d'Olsoufieff, 1924. Despite the extensive review of the genus by Edmonds & Zidek (2010), who recognized 38 species, as well as subsequent contributions by Kohlmann & Solís (2012) and Cupello & Vaz-de-Mello (2013), taxonomic problems still persist. Some of these questions involve the definition of supraspecific taxa, including subgenera and species groups (especially the confusing relationship of *Metallophanaeus* with the other subgenera), but others concern species delimitation and, in fact, this latter problem is related to described names based on only few specimens. Nonetheless, with a larger number of specimens, some synonyms or doubts about the validity of certain species were clarified: Kohlmann & Solís (2012), in addition to describing a new species from Panama (*C. gephyra* Kohlmann & Solís, 2012), concluded in a study based on more than 1000 specimens that *C. kohlmanni* Arnaud, 2000 and *C. uhleri* Malý & Pokorný, 2008, synonymized with, respectively, *C. morenoi* Arnaud, 1982 and *C. chiriquensis* (d'Olsoufieff, 1924) by Edmonds & Zidek, are valid species and distinguishable by both morphological and distributional data. After them, Cupello & Vaz-de-Mello (2013), with five new specimens in addition to the holotype, showed that *C. terrali* Arnaud, 2002 is a valid species restricted to the high lands of the Juruena-Xingu interfluvium, in Central Brazil, and not a synonym of *C. dardanus* (MacLeay, 1819). In the present work, we introduce new evidence that demonstrates the validity of another species, *Coprophanaeus (Metallophanaeus) machadoi* (Pereira & d'Andretta, 1955), from southeastern Brazil.

*Coprophanaeus machadoi* was described as *Phanaeus (Metallophanaeus) machadoi* by Pereira & d'Andretta (1955) based in a single male from Açucena, eastern Minas Gerais, Brazil. They considered this species a close

relative of *C. (M.) saphirinus* (Sturm, 1823) (cited as *Phanaeus saphirinus*), differentiated by a longitudinal carina on the anterior portion of male pronotum, punctate elytral interstriae and conspicuous elytral striae. In its turn, *C. saphirinus* lacks the pronotal carina and has smooth elytral interstriae and effaced striae. Vaz-de-Mello (2000), following the classification proposed by Edmonds (1972), was the first to place *C. machadoi* in *Coprophanaeus*, and Arnaud (2002) included this species in the saphirinus species group of the subgenus *Metallophanaeus*, along with *C. saphirinus*, *C. horus* (Waterhouse, 1891), and *C. punctatus* (d'Olsoufieff, 1924).

Edmonds & Zidek (2010) proposed the synonymy between *C. machadoi* and *C. saphirinus* because they lacked sufficient evidence to recognize it as a distinct species. They regarded the characteristics utilized by Pereira & d'Andretta, being derived from only one specimen, as insufficient to justify the recognition of *C. machadoi* as a distinct species.

With access to a large number of specimens of both species from a wide geographical area, we present here new characters (and discard others pointed out earlier) that delimit *C. machadoi* as a valid species and distinct from *C. saphirinus*. We also discuss its intraspecific variation and biogeography and describe for the first time the aedeagus (genital capsule) and the female external morphology. With this revalidation of *C. machadoi*, the genus *Coprophanaeus* comprises 43 valid species. However, additional species await description, including some that will be described in an upcoming revision of the subgenus *Metallophanaeus* by Fernando Z. Vaz-de-Mello and Patrick Arnaud.

## Material and Methods

Specimens cited in this work are deposited in the following collections (curators or contacts in parenthesis):

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

BMNH—The Natural History Museum, London, United Kingdom (Max Barclay and Malcolm Kerley);

DZUP—Coleção Entomológica Padre Jesus Santiago Moure, Departamento Zoologia, Universidade Federal do Paraná, Curitiba, Brazil (Lucia Massutti de Almeida);

FIOC—Coleção Entomológica do Instituto Oswaldo Cruz, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil (Márcio Felix and Ayr Bello);

ISNB—Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (Alain Drumont);

MNHN—Muséum National d'Histoire Naturelle, Paris, France (Antoine Mantilleri and Olivier Montreuil);

MNRJ—Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (Miguel A. Monné, Marcela L. Monné, and Mario Cupello);

MZSP—Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Sonia Casari and Carlos Campaner);

OUMNH—Hope Entomological Collection, Oxford University Museum of Natural History, Oxford, United Kingdom (Darren Mann);

PFAC—Collection Patrick and Florent Arnaud, Saintry sur Seine, France (Patrick Arnaud);

ZSMC—Zoologische Staatssammlung München, Munich, Germany (Michael Balke).

In the “material examined” section, data for each specimen are listed as follows: collecting locality, date of collection, collector—sex (collection). For *Coprophanaeus saphirinus*, red specimens, the rarest color and cause of some taxonomic discussion (i.e., on the validity of *Coprophanaeus chabillaci* (Thomson, 1857)), are referred with the statement “red form” after the name of the collection.

Description and terminology follow the same pattern of Edmonds & Zidek (2010) to permit an easy comparison with the information published by them. For the measurements, on the other hand, as they were of particular importance in this work, we give more detailed information: total length (TL) and greatest width of pronotum (PW), and, for each variable, we specify, in millimeters, average (AV), range (maximum (MX), to minimum (MN)), and standard deviation (SD).

Geographical distribution discussed here is based mainly on label information gathered by us. After observing and delimiting a general distribution pattern, we also included data published by d'Olsoufieff (1924: Cruz Alta, Rio Grande do Sul), Silva & Di Mare (2012: Silveira Martins, Rio Grande do Sul), Silva *et al.* (2013: Santa Maria, Rio

Grande do Sul), and especially Edmonds & Zidek (2010: all other reports) that could be reliably associated with each of the species; these literature reports are marked in italics in the geographic distribution sections. The compilation of this geographical information is presented in two ways: the first based on the biogeographic regionalization of the Neotropical region as defined by Morrone (2014), and the second based on the national political divisions.

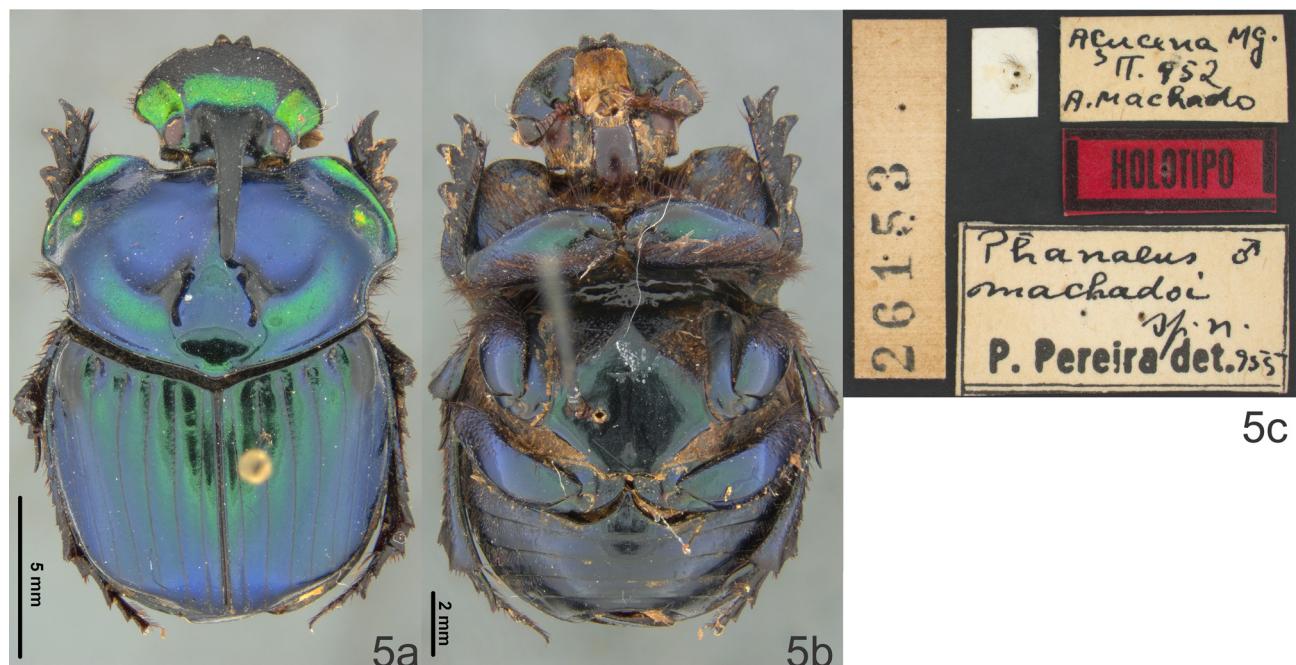


**FIGURES 1–4.** *Coprophanaeus (M.) machadoi* (Pereira & d'Andretta, 1955). 1–2) Male habitus. 3–4) Female habitus.

**Placement of *Coprophanaeus (Metallophanaeus) machadoi* (Pereira & d'Andretta, 1955) in Edmonds & Zidek's (2010) key to species of the saphirinus group:**

1. Posteromedian angle of pronotum not produced, basal fossae small, incorporated into mesial ends of basal groove. Pronotum distinctly punctured posteromedially. Paraocular areas (genae) of both sexes completely punctate, usually densely and coarsely so. Male pronotum lacking round concavities. Elytral striae carinulate, distinctly punctured (x5) ..... *Coprophanaeus (Metallophanaeus) punctatus* (Olsoufieff, 1924).
- Posteromedian angle of pronotum slightly produced posteriorly, very smooth, effacing basal fossae and mesial ends of basal

- pronotal groove. Pronotum smooth posteromedially. Male paraocular areas (genae) almost completely smooth; female paraocular area broadly rugose. Male pronotum with round concavities beneath posteromedian projections. Elytral striae simple (very rarely carinulate), very fine ..... 2
2. Anterior margin of pronotum of large males with long midlongitudinal filiform prolongation, sometimes raised in sharp and acute ridge; prolongation followed by midlongitudinal well-marked carina (Figs. 6–9) (in minor specimens, prolongation triangular, short or absent, carina sometimes absent). Parameres, in lateral view, weakly concave; posterior flap of apical process only slightly elevated (Fig. 12). Dorsal coloration blue and green (Figs. 1–5). Brazilian Atlantic Forest in eastern Minas Gerais, Espírito Santo and Rio de Janeiro (except Serra da Mantiqueira Mountains) ..... *Coprophanaeus (Metallophanaeus) machadoi* (Pereira & d'Andretta, 1955).
- Anterior margin of pronotum of large males with short triangular prolongation or rounded; pronotum smooth, midlongitudinal carina absent (Figs. 10–11). Parameres, in lateral view, strongly concave; posterior flap of apical process strongly elevated and curved (Fig. 13). Dorsal coloration blue, green, and red (Figs. 15–23). Brazilian Atlantic Forest in Serra da Mantiqueira Mountains, southern Brazil (including São Paulo), Paraguay, and Argentina ..... *Coprophanaeus (Metallophanaeus) saphirinus* (Sturm, 1826).



**FIGURE 5.** Holotype of *Coprophanaeus machadoi*. 5a) Dorsal view. 5b) Ventral view. 5c) Labels.

***Coprophanaeus (Metallophanaeus) machadoi* (Pereira & d'Andretta, 1955), revalidated**  
Figs. 1–9, 12–13.

*Phanaeus (Metallophanaeus) machadoi* Pereira & d'Andretta, 1955: 257–260, figs. 14–17; Edmonds & Zidek, 2010: 29.  
*Coprophanaeus (Metallophanaeus) machadoi*: Vaz-de-Mello, 2000: 192; Arnaud, 2002: 56; Biodiversitas, 2007: 123;  
Edmonds & Zidek, 2010: 2, 31.

*Phanaeus saphirinus*: sensu Harold, 1875: 42.

*Phanaeus (Metallophanaeus) saphirinus*: sensu Edmonds, 1967: 97–104.

*Coprophanaeus (Metallophanaeus) saphirinus*: sensu Edmonds & Zidek, 2010: 30, fig. 71.

**Type specimen:** Holotype: male ("Holotipo", "Phanaeus machadoi sp. n. ♂, P. Pereira det. 955", "Açucena, Mg. 5.II.952, A. Machado", "26153"), MZSP (examined) (Figs. 5–6).

**Type locality:** Açucena, Minas Gerais, Brazil (Pereira & d'Andretta, 1955).

**Description:** *General*—Paraocular areas (genae) not carinate lateral to eyes. Pronotum smooth posteromedially, or, in minor specimens, sparsely punctured; posterior angle slightly and triangularly produced posteriorly; posterior fossae absent and sulcus paralleling posterior margin of pronotum effaced medially. Anteromedian angle of metasternum rounded, not salient; angle capped with elongate thickening usually visible from below as a broad “V”. Elytral interstriae flat; striae simple, very fine, superficial, not impressed, but, in light-colored specimens, much more clearly visible by their darker coloration (usually dark blue); bases of striae 1–4

distinctly fossate, fossae progressively larger laterally. Ventral surface of protibia, lateral to longitudinal carina paralleling inner margin, entirely punctatorugose. Pygidium lacking basal groove. Color usually shining both metallic green and blue (Figs. 1–4), but sometimes entirely light green or dark blue; never with metallic red.

**Male**—Paraocular areas mostly smooth, rugosity present at most only adjacent to outer margin (in minor specimens, rugosity sometimes more widespread, but never as females). Head with evenly tapering long horn, base not abruptly swollen. Pronotum with pair of closely set, apically slightly convergent processes near posterior margin, separated by strong concavity (in minor specimens, processes and concavity progressively reduced); disk anterior to processes with deep, round concavity on each side, or, in minor specimens, only slightly concave or completely absent. In major males, anterior margin of pronotum with long midlongitudinal filiform prolongation, sometimes raised into a sharp and acute ridge; prolongation followed by midlongitudinal well-marked carina (Figs. 6–9); anterior slope of pronotum sometimes ornamented by pair of divergent tubercles (Fig. 9). In minor specimens, filiform prolongation progressively shorter or absent, sometimes slightly triangular. Pronotal sculpturing limited to weak rugosity on lateral margins. Parameres only slightly concave laterally; apical processes rounded and with posterior flap only slightly curved (Fig. 12).

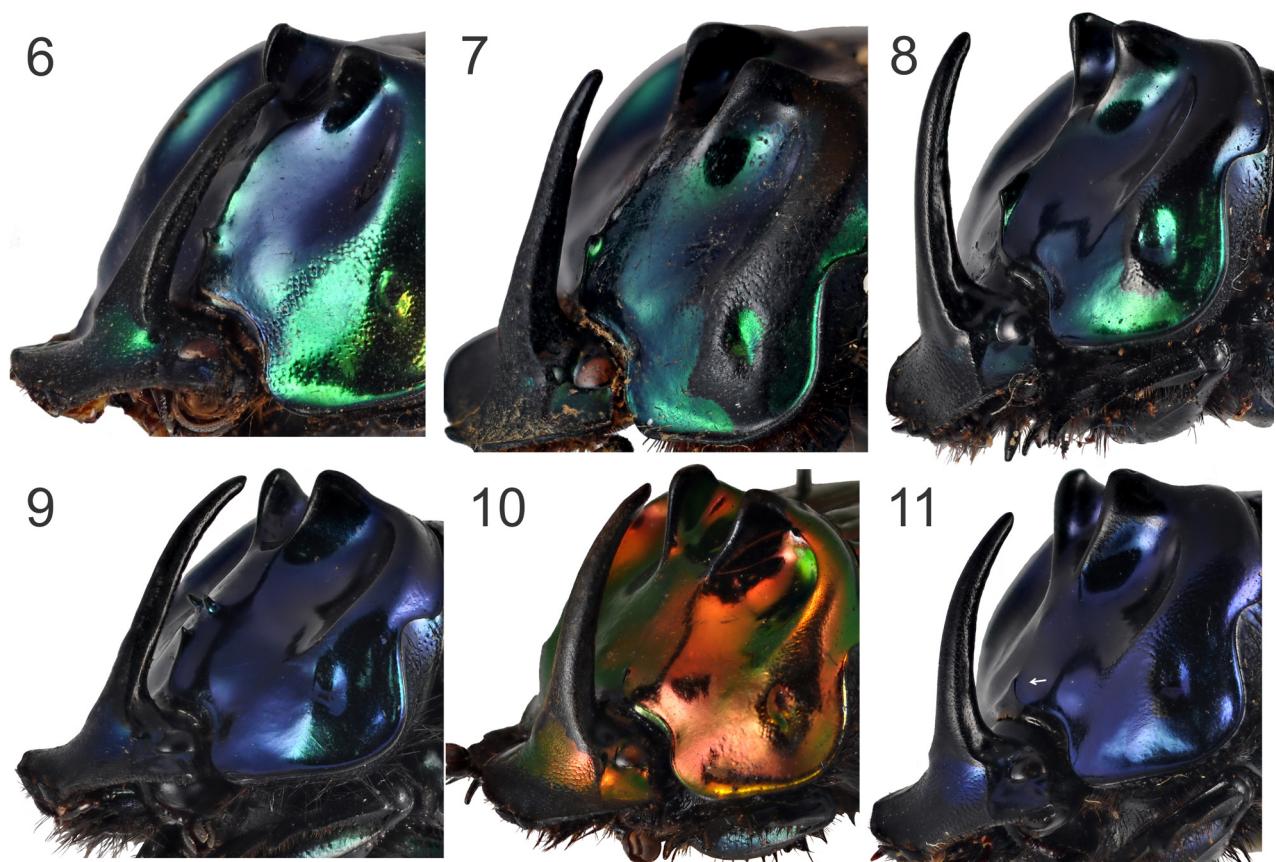
**Female**—Paraocular areas broadly rugose, smooth only near to eyes. Pronotum with small, weakly trituberculate crest adjacent to anterior margin followed by weak concavity bounded posteriorly by pair of weak tumosities near middle of disk; in minor specimens, crest and concavity reduced and tumosities absent. Pronotum finely granulorugose on disk and sides, punctate posteromedially; in minor specimens, granulorugosity progressively more widespread posteriorly.

**Measurements:** **Males (15 specimens):** TL: AV: 17.31; MX: 21; MN: 15; SD: 1.89. **PW:** AV: 10.93; MX: 13; MN: 9.3; SD: 1.25. **Females (15 specimens):** TL: 18.08; MX: 23; MN: 15; SD: 2.42. **PW:** AV: 10.97; MX: 14; MN: 9; SD: 1.74. **Total (30 specimens):** TL: AV: 17.7; SD: 2.2. **PW:** AV: 10.95; SD: 1.49.

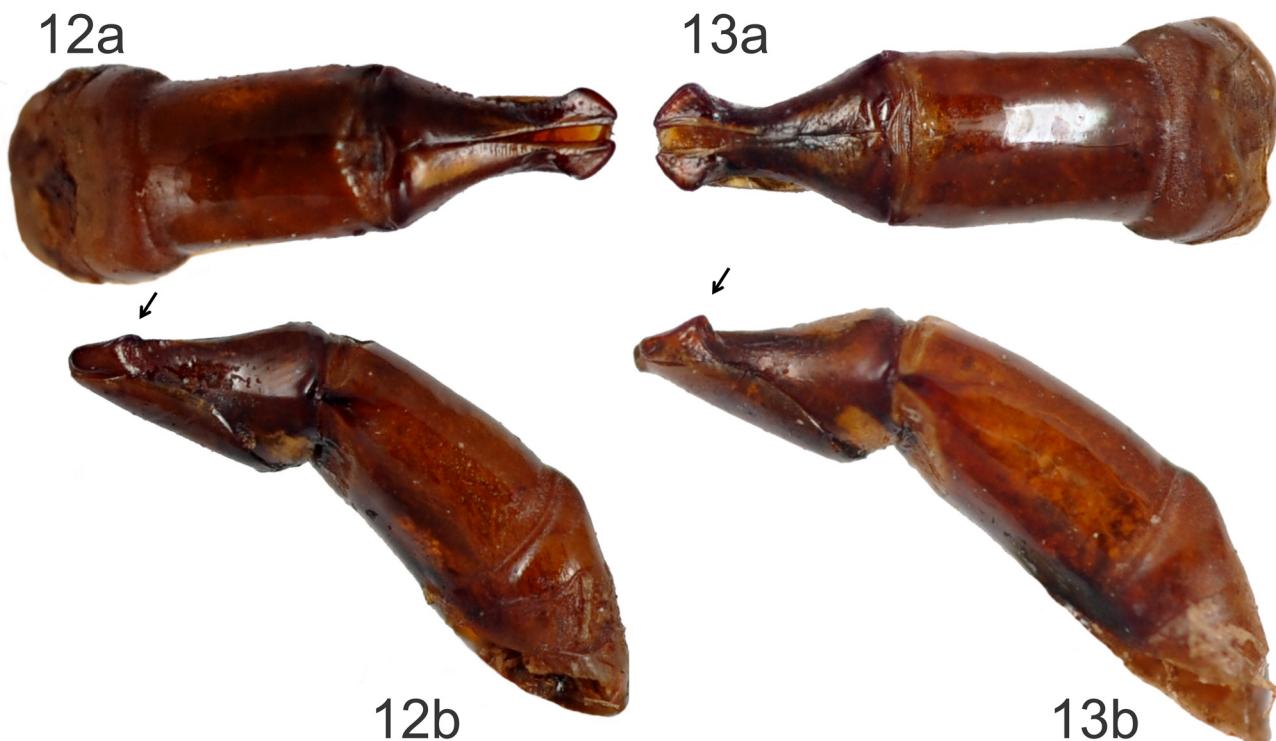
**Intraspecific variation and taxonomic discussion:** *Coprophanaeus machadoi* is a cryptic species widely confused with *C. saphirinus* and identified in collections and publications with this latter name. In most large collections we have examined (BMNH, CPFA, MNHN, MNRJ, and MZSP), including that where the holotype is deposited, no specimen (but the holotype) of *C. machadoi* was identified as such, and individuals of this species were mixed among large series of *C. saphirinus*. In addition to the type specimen, only a single male was correctly identified in a publication as *C. machadoi* (Arnaud, 2002), but even in that work, other *C. machadoi* were certainly misidentified as *C. saphirinus* since Arnaud cited Espírito Santo (Brazil) as part of the distribution range of the latter species. In fact, part of this confusion is due to the fact that the only two specimens so far correctly identified as *C. machadoi* lacked the aedeagus and, therefore, the more easily observed characteristics that differentiate the two species had not been detected until now (Pereira & d'Andretta, 1955; Arnaud, 2002; see below). Furthermore, the lack of distinction between the females of these two species contributes to the cryptic nature of *C. machadoi*. Nevertheless, two evident morphological characteristics observed by us support the validity of *C. machadoi* and, being in agreement with the distribution of the two species, make identification easier.

Pereira & d'Andretta (1955) used the presence of a midlongitudinal carina on the anterior slope of male pronotum of *C. machadoi* to distinguish it from *C. saphirinus* (Fig. 6–9). Males *C. saphirinus*, in general, have no trace of this carina; only in a few specimens there is a very faint longitudinal line marked on the anterior slope of pronotum. In many small males of the *C. machadoi*, however, the carina may be completely absent and, without locality data, it is more difficult to distinguish them from *C. saphirinus*. In *C. machadoi*, anterior to and continuous with this carina, there is a midlongitudinal and filiform prolongation of the anterior pronotal margin that is elevated as a sharp and acute ridge in major specimens (Fig. 6–9). Minor specimens have this prolongation progressively shorter and triangular, being absent in smaller individuals. In *C. saphirinus*, regardless of the size of the male, the prolongation may be short and triangular or absent (Fig. 10–11). In this latter case, the anterior margin is simply rounded.

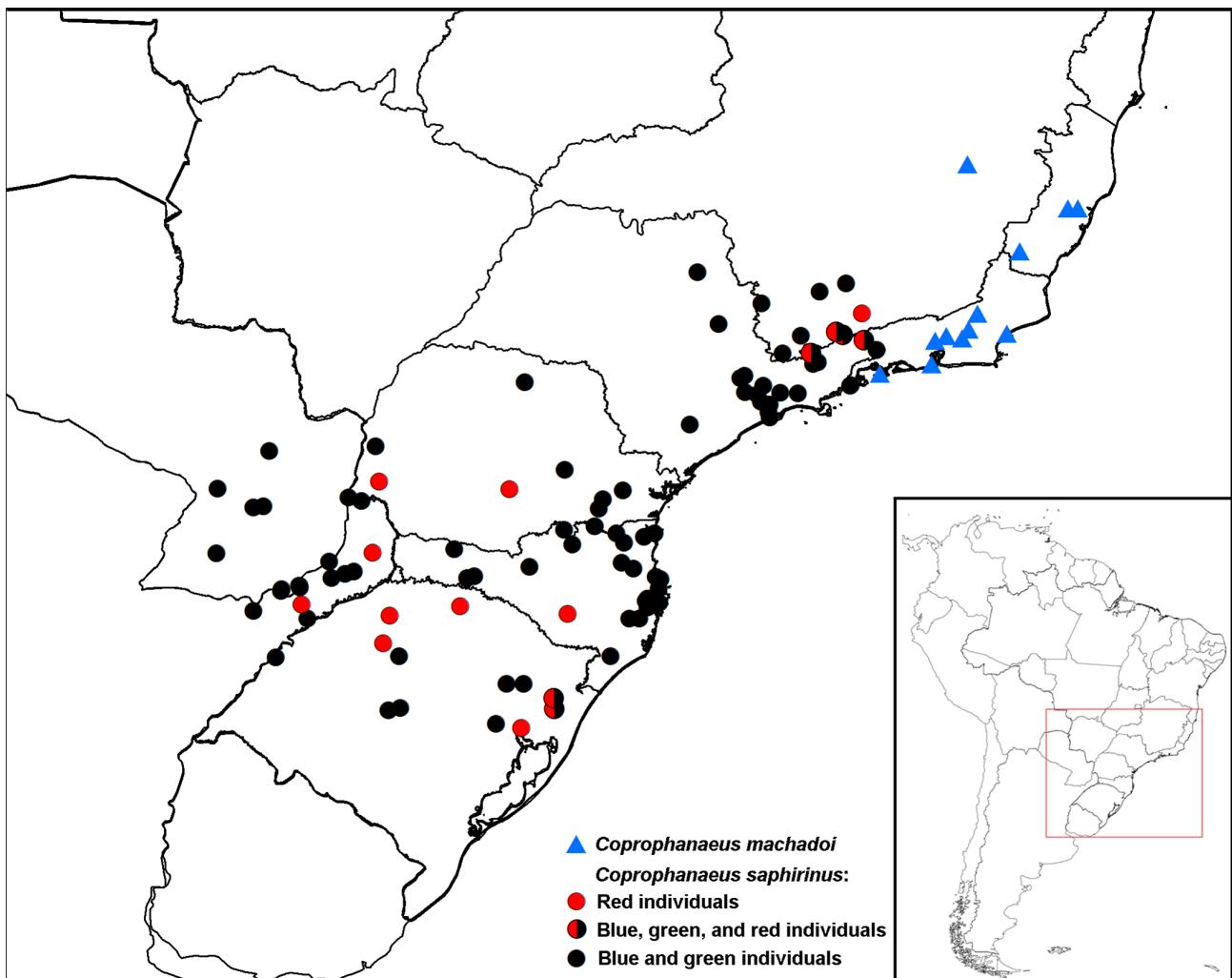
In one specimen of *C. machadoi* observed by us, the midlongitudinal carina is accompanied by a pair of divergent tubercles (Fig. 9). However, the presence of this feature does not appear to be unique to this species, since we observed two large males of *C. saphirinus*, one from Virgínia (Minas Gerais) and other from Santa Catarina, that have a pair of small elevations in the anterior slope of pronotum that we believe to be a very worn pair of tubercles. Edmonds & Zidek (2010) also observed a pair of tubercles in a specimen identified as *C. saphirinus*, but since they did not provide the origin of this individual, it is impossible to know if it really was a *C. saphirinus* or a *C. machadoi*.



**FIGURES 6–11. Male head and pronotum.** 6–9) *Coprophanaeus machadoi*. 10–11) *C. saphirinus*. White arrow indicates the midlongitudinal prolongation of the anterior margin of pronotum, which is triangular and flat in *C. saphirinus* and long, filiform, and sometimes raised in a sharp ridge in *C. machadoi*.



**FIGURE 12–13. Aedeagi.** 12) *Coprophanaeus machadoi*: 12a) Dorsal view. 12b) Lateral view. 13) *C. saphirinus*: 13a) Dorsal view. 13b) Lateral view. Arrow indicates the posterior flap of the apical process, which is just slightly elevated in *C. machadoi* and is strongly elevated and curved in *C. saphirinus*.



**FIGURE 14. Distribution map of *Coprophanaeus machadoi* and *C. saphirinus*.** *Coprophanaeus machadoi* is distributed in eastern Minas Gerais, Espírito Santo, and Rio de Janeiro, while *C. saphirinus* is present from the Serra da Mantiqueira, in the border of Minas Gerais, Rio de Janeiro and São Paulo, to southern Brazil, Paraguay and Misiones (Argentina). Both species are restricted to the Brazilian Atlantic Forest in Paraná Dominion of the Chacoan subregion.

The second distinguishing and most easily observable characteristic of *C. machadoi* is the shape of the parameres: in *C. machadoi*, the parameres are only slightly concave laterally and the posterior flap of the apical process is only slightly elevated (Fig. 12), while in *C. saphirinus* the lateral curvature is much more profound and the posterior flap of the apical process is strongly elevated and curved (Fig. 13). Indeed, this is the feature that more reliably differentiates males of both species, regardless of their size.

Pereira & d'Andretta (1955) stated that *C. machadoi* differed from *C. saphirinus* mainly by differences of elytral sculpture, with the striae being more strongly marked and the interstriae more distinctly punctured in *C. machadoi* than in *C. saphirinus*. Edmonds & Zidek (2010) considered this characteristic and the midlongitudinal carina as individual variations of the *C. machadoi* holotype within the intraspecific variation of *C. saphirinus* and thus established the synonymy between these two names. Despite that the elytral striae of the holotype of *C. machadoi* are really unusually marked (in fact, they are carinulate in a similar manner to those of *C. punctatus*), we agree that this is a peculiar individual variation and that the most common condition in *C. machadoi* is similar to that of *C. saphirinus*, i.e. with very fine and superficial striae and smooth interstriae. The midlongitudinal pronotal carina and the filiform prolongation of the anterior pronotal margin, on the other hand, are consistently correlated with the structure of the parameres and together these three characteristics support the distinction between *C. machadoi* and *C. saphirinus*.

Trends in size and degree of development also support the validity of *C. machadoi*. Although the total length (TL) and pronotal width (PW) averages are slightly larger in *C. saphirinus* than in *C. machadoi* (TL= 17.7 and

PW= 10.95, in *C. machadoi*; and TL= 19.02 and PW= 12.09, in *C. saphirinus*), the most notable difference is that males of *C. machadoi* are never as large nor have cephalic and pronotal ornamentation as developed as the largest males of *C. saphirinus* (TL MX= 21 and PW MX= 13, for *C. machadoi* males; and TL MX= 23 and PW MX= 19, for *C. saphirinus* males). The cephalic horn, for example, is strongly curved backwards in some major males of *C. saphirinus* (Figs. 11, 15), while it is generally straight or at most only slightly curved apically in larger *C. machadoi* (Figs. 6–9). Size differences are repeated in females (TL MX= 23 and PW MX= 14, in *C. machadoi*; TL MX= 24 and PW MX= 19, in *C. saphirinus*).

The coloration pattern also has tendencies that differ between the two species. Firstly, a red form has not been observed in *C. machadoi*, while it is found in *C. saphirinus* (see the discussion of *C. saphirinus*). In *C. machadoi*, there are both blue and green specimens, some being predominantly light green, while others are dark blue; nonetheless, the most frequent color is dark green. In contrast, in *C. saphirinus*, dark blue is the most common color, while light green specimens are less frequent. Thus, although it is impossible to differentiate individuals of the two species by color (except red), the relative predominance of blue or green is distinct between *C. machadoi* and *C. saphirinus*. Additionally, based on the examined specimens of *C. machadoi*, it appears that the green color is predominant at lower altitudes, while blue individuals are more common in higher altitudes, but this trend needs confirmation using more specimens.

Finally, biogeography supports the morphological observations. *Coprophanaeus machadoi* is present from eastern Minas Gerais and Espírito Santo to southern Rio de Janeiro, where it is limited by the Serra da Bocaina mountains, on the border between the states of Rio de Janeiro and São Paulo; south of Serra dos Órgãos (i.e., the northern portion of the Serra do Mar mountains), *C. machadoi* has been collected only in coastal areas (Rio de Janeiro and Ilha Grande) and is apparently absent in the Vale do Paraíba region in the state of Rio de Janeiro (Fig. 14). In its turn, *C. saphirinus* is distributed in the Serra da Mantiqueira and in the southern portion of the Serra do Mar (i.e., excluding the Serra dos Órgãos and including the portions localized in São Paulo to Santa Catarina states) south to southern Brazil, Argentina, and Paraguay. Therefore, despite both species being restricted to the Paraná dominion of the Chacoan subregion, apparently they are never found in sympatry.

**Geographic distribution: Chacoan subregion:** Paraná dominion: Atlantic and Paraná Forest provinces.

**BRAZIL:** Minas Gerais: Açucena. Espírito Santo: Alegre, Fundão (Timbuí), Santa Teresa. Rio de Janeiro: Angra dos Reis (Ilha Grande), Cachoeiras de Macacu, Cantagalo, Macaé, Nova Friburgo, Petrópolis, Rio de Janeiro (Parque Nacional da Tijuca), Teresópolis (Parque Nacional da Serra dos Órgãos).

**Comments:** Giving the cited locations, Harold's (1875) report of *Phanaeus saphirinus* for Cantagalo (Rio de Janeiro) and the description of the larva of this species by Edmonds (1967) (reared from a female collected in Nova Friburgo, Rio de Janeiro) probably refer to misidentified *C. machadoi*.

**Bionomics:** Edmonds (1967) noted that the female of *C. machadoi* (cited as *Phanaeus saphirinus*) was able to build two brood balls even without the assistance of a male; he also observed that the duration of the development from egg to pupa lasted about 90 days. The female was collected using human excrement as bait.

There are collection records of *C. machadoi* for all months from October to April, suggesting that adults of this species are active only in the months of spring and summer, when the temperature is higher and there is more rain.

**Conservation status:** *Coprophanaeus machadoi* is regarded as a critically endangered species in the state of Minas Gerais and is included in its official list of protected species (Minas Gerais, 2010; Biodiversitas, 2007). Nonetheless this species is not present on the Brazilian Red List of endangered species (Machado *et al.*, 2008) nor is it considered in the IUCN Red List (IUCN, 2013). Although *C. machadoi* is certainly present in at least two Brazilian National Parks, Parque Nacional da Tijuca and Parque Nacional da Serra dos Órgãos, both in the state of Rio de Janeiro, this species is probably negatively impacted by the continuous deforestation and fragmentation of the Brazilian Atlantic Forest (an impact that was vividly exposed by Ribeiro *et al.* (2009)), especially because it is well demonstrated that *Coprophanaeus* species have a strong preference for forest habitats and, in many cases, are restricted to this environment (Edmonds, 1972; Edmonds & Zidek, 2010).

**Material examined:** 73 males and 53 females. **NO DATA**—1 male (CEMT), 9 males (MNHN), 19 males and 12 females (BMNH), and 14 males and 12 females (OUMNH). **BRAZIL:** no more data—8 males (MNHN) and 2 males (BMNH). **ESPÍRITO SANTO:** no more data—1 male and 2 females (MNHN); Alegre, Fazenda Jerusalém, 03.XI.1912, J. F. Zikán col.—1 female (FIOC); Santa Teresa, II.1991, O. Roppa col.—3 females (MNRJ). **MINAS GERAIS:** Rio José Pedro, without date, J. F. Zikán col.—1 male (CEMT); **RIO DE JANEIRO:** without date and collector—5 males and 5 females (MNHN) and 3 males and 1 female (MNRJ); Angra dos Reis, Ilha Grande,

IV.1992, Theotonio col.—1 male and 1 female (CEMT); Cachoeiras de Macacu, Boca do Mato, I-II.2000, N. Tangerini col.—1 male (MNRJ); Cantagalo (Cantagal), without date and collector—3 males and 1 female (MNHN); Macaé, Serra de Macaé, XI.1909, Garbe col.—2 males and 1 female (MZSP); Nova Friburgo, II.1998, P. Grossi col.—1 male and 1 female (CEMT); Nova Friburgo, Macaé de Cima (Haut Macahe), without date and collector—2 females (MNHN); Nova Friburgo, Macaé de Cima, 1,500 m., III.2000, Lopes-Andrade, Gumier & Vaz-de-Mello cols.—1 male (CEMT); Nova Friburgo, Macaé de Cima, XII.2000, P. & E. Grossi cols.—1 male and 1 female (CEMT); Nova Friburgo, Muri, XII.1976, Gred & Guimarães cols.—1 female (MZSP); Nova Friburgo, Muri, XII.1980, Gred & Guimarães cols.—1 male (MZSP); Petrópolis, II.1939, J. C. N. Penido col.—1 male (FIOC); Petrópolis, II.1957, H. Clark col.—1 male (BMNH); Petrópolis, Alto Mosele, La Vallon, 01.II-08.III.1957, Dzley col.—1 female (MNRJ); Petrópolis, Independência, without date, Mario Rosa col.—1 male (MNRJ); Rio de Janeiro, Floresta da Tijuca, 20.XII.1966, Celso Jr. col.—1 female (CEMT); Rio de Janeiro, Floresta da Tijuca, XI.1983, C. Godinho col.—1 male (CPFA); Rio de Janeiro, Floresta da Tijuca, Represa Rio Grande, X.1962, M. Alvarenga col.—1 female (MZSP); Rio de Janeiro, Sumaré, XI.1994, Celso Godinho col.—1 female (CEMT) and 1 male (CPFA); Serra dos Órgãos, XII.1940, Parko col.—1 male (MNRJ); Teresópolis, XII.1939, Freitas col.—1 male (MNRJ); Teresópolis, VIII.1940, without collector—1 male (CPFA); Teresópolis, 14.I.1993, A. Belo col.—1 male and 3 females (CEMT); Teresópolis, Parque Nacional da Serra dos Órgãos, 26.I.1957, D. Zajciw col.—1 female (MNRJ); Teresópolis, Parque Nacional da Serra dos Órgãos, 25.X.1960, D. Zajciw col.—1 female (MNRJ). **URUGUAY (surely mislabeled):** Montevideo, without date and collector—1 male (BMNH).

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

Figs. 10–11, 13–23.

*Copris saphirina* Sturm, 1826: 65, 125, tab. II, fig. 15a, b.

*Phanaeus sapphirinus*: Dejean, 1833: 140; Dejean, 1836: 155; Nevinson, 1892: 7, 10; Gillet, 1911: 86.

*Phanaeus saphirinus*: Klug, 1841: 210; Sturm, 1843: 106; Harold, 1869a: 1019; Harold, 1869b: 65; Harold, 1875: 42 (misidentification of *C. machadoi*); Waterhouse, 1891: 129; Ohaus, 1909: 28–29; Kolbe, 1909: 529; Bruch, 1911: 190; d’Olsoufieff, 1924: 9, 15; Arnaud, 2002: 55; Almeida & Mise, 2009: 238; Edmonds & Zidek, 2010: 29.

*Phaenaeus [sic] saphirinus*: Moura et al., 1997: 271–272.

*Phanaeus (Metallophanaeus) saphirinus*: d’Olsoufieff, 1924: 22, 28, 63, 72, 74, 136, 144, pl. IV, fig. 15; Pessoa, 1934: 284–285, 293, fig. 8a,b; Pessoa & Lane, 1941: 478; Pereira, 1949: 218–222, fig. 1; Pereira & d’Andretta, 1955: 260; Martínez, 1959: 102; Halffter & Matthews, 1966: 30, 132; Edmonds, 1967: 97–104 (probably in reference to *C. machadoi*; see above).

*Metallophanaeus sapphirinus*: Blackwelder, 1944: 209.

*Phanaeus (Metallophanaeus) saphyrinus [sic]*: Redtenbacher, 1868: 56; Lange, 1947: 313.

*Coprophanaeus (Metallophanaeus) saphirinus*: Edmonds, 1972: 842–843, 874; Edmonds & Halffter, 1978: 322; Halffter & Edmonds, 1982: 89; Vaz-de-Mello, 2000: 192; Arnaud, 2002: 55; Cáceres & Monteiro-Filho, 2006: 1198–1201; Almeida & Mise, 2009: 232, 238, fig. 34; Hernández & Vaz-de-Mello, 2009: 608, 611; Edmonds & Zidek, 2010: 2–5, 22–24, 29–31, 33; Hernández et al., 2011: 5, 7–8; Silva et al., 2011: 334, 339, 342; Vaz-de-Mello et al., 2011: 54, fig. 55; Silva & Di Mare, 2012: 199–200, 202; Silva et al., 2012: 433–434, 438; Culot et al., 2013: 85, 87; Korasaki et al., 2013: 396; Silva et al., 2013: 685; Silva & Bogoni, 2014: 340–341.

*Coprophanaeus (Metallophanaeus) saphirinus saphirinus*: Arnaud, 2002: 55.

*Phanaeus chabriillacii* Thomson, 1857: 117.

*Phanaeus chabriillacii*: Harold, 1869a: 1017; Harold, 1869b: 65; Edmonds & Zidek, 2010: 29–28.

*Phanaeus saphirinus* var. *chabriillacii*: Gillet, 191: 86.

*Phanaeus (Metallophanaeus) saphirinus* var. *chabriillacii*: d’Olsoufieff, 1924: 28, 75, 144; Pessoa, 1934: 293; Pessoa & Lane, 1941: 478.

*Metallophanaeus sapphirinus* [sic] var. *chabriillacii*: Blackwelder, 1944: 209.

*Phanaeus (Metallophanaeus) saphirinus chabriillacii*: Pereira, 1949: 222; Pereira & d’Andretta, 1955: 260.

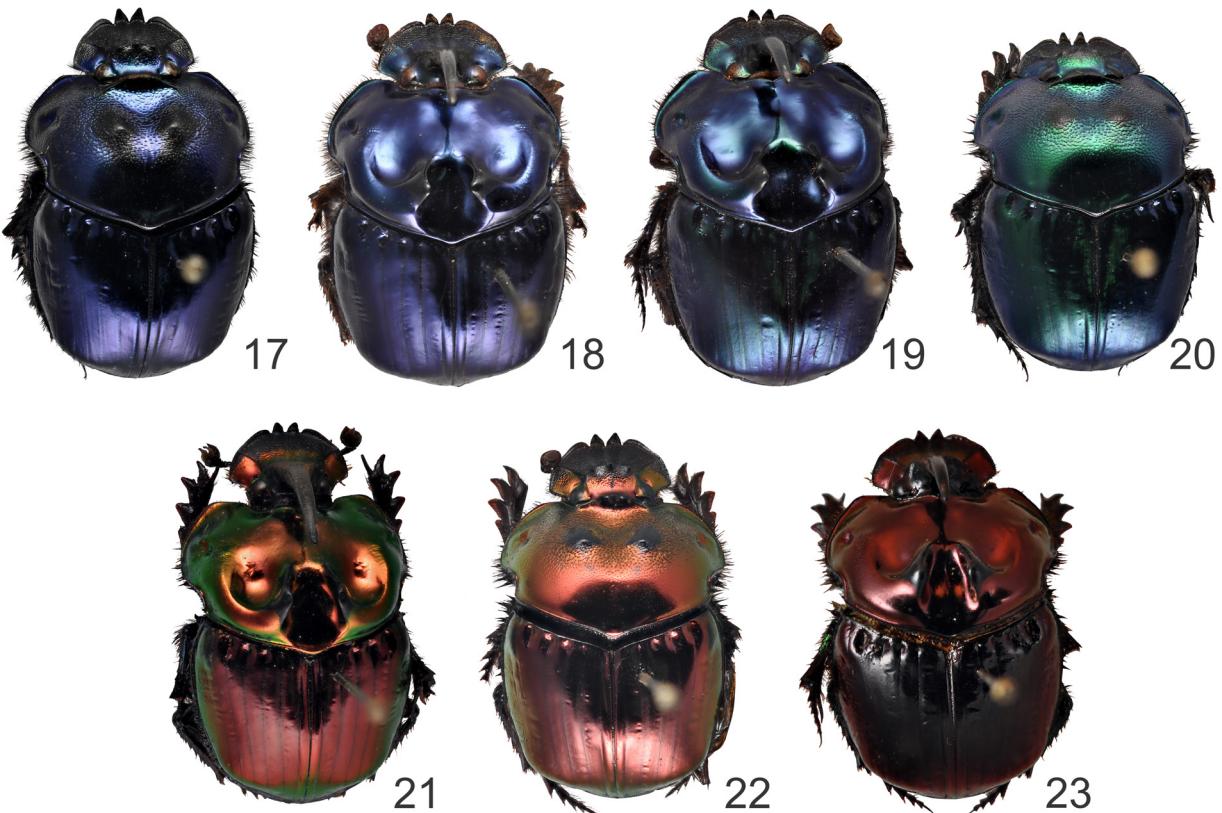
*Coprophanaeus (Metallophanaeus) saphirinus* var. *chabriillacii*: Vaz-de-Mello, 2000: 192.

*Coprophanaeus (Metallophanaeus) saphirinus chabriillacii*: Arnaud, 2002: 56.

**Type specimen:** *Copris saphirina* Sturm, 1826: Holotype: male (“Brasil. B. *Copris saphirinus* Mihi.” “Type von *Copris saphirinus* Sturm”, “Coll. Sturm”, “*Metallophanaeus saphirinus* Sturm”), ZSMC (examined by photos (Fig. 15)). ***Phanaeus chabriillacii* Thomson, 1857:** Holotype: male, (“Type”, “Coll. J. Thomson”, “cf. Arch. Ent. I., 1857, p. 117”, “det. J. Thomson *Phanaeus chabriillacii* Th.”, “**Ph.** (*Metal.*) *saphirinus* var. *chabriillacii* A. Janssens rev., 1932”), ISNB (examined by photos (Fig. 16)).



**FIGURE 15.** Holotype of *Coprophanaeus saphirinus* (Sturm, 1826): 15a) Dorsal view. 15b) Ventral view. 15c) Frontal view. 15d) Lateral view. 15e) Labels. 15f) Sturm's (1826) illustration of the holotype. **16:** Holotype of *Phanaeus chabrillaci* Thomson, 1857: 16a) Labels. 16b) Dorsal view. 16c) Ventral view. 16d) Lateral view.



**FIGURES 17–23.** Color variation in *Coprophanaeus saphirinus*. 17–18) Dark blue female and male with purple reflections. 19) Blue male with greenish reflections. 20) Predominantly green female with bluish reflections. 21) Red male with greenish and yellowish reflections. 22) Predominantly red female. 23) Dark red male.

**Type locality:** *Copris saphirina*: “Aus Brasilien” (Sturm, 1826).—*Phanaeus chabriacci*: “Brésil” (Thomson, 1857).

**Measurements:** **Males (67 specimens):** TL: AV: 18.93; MX: 23; MN: 15; SD: 2.16. **PW:** AV: 12.07; MX: 15; MN: 10; SD: 1.63. **Females (66 specimens):** TL: AV: 19.11; MX: 24; MN: 14; SD: 2.42. **PW:** AV: 12.27; MX: 19; MN: 9; SD: 1.98. **Total (133 specimens):** TL: AV: 19.02; SD: 2.29. **PW:** AV: 12.09; SD: 1.62.

**Intraspecific variation and taxonomic discussion:** Edmonds & Zidek (2010) stated that *C. saphirinus* of both sexes have paraocular areas (genae) with “smooth, highly shining” tegument. However, specimens observed in this work present a different condition: males follow Edmonds & Zidek’s description and have genae mostly smooth and shining, with rugosity restricted at most only adjacent to outer margin; females, on the other hand, possess coarsely rugose genae, in the same manner as the rest of the head. Small males generally possess genae that are more rugose than large males, but never as strongly as in females.

Dorsal coloration in *C. saphirinus* is highly varied, ranging from dark metallic blue, violet and green to entirely red, yellowish and greenish red, and dark red (Figs. 17–23); ventral coloration, however, is more uniform and presents green and blue coloration and is never red (Figs. 5b, 15b, 16c–d). The most common dorsal form is predominantly blue, but specimens of all colors apparently coexist at least in the southern latitude or higher altitude populations. For example, the series collected in São Francisco de Paula (Rio Grande do Sul) is composed of blue, violet, green and red specimens. Similarly, specimens collected in Serra da Mantiqueira Mountains (localities as Itatiaia (Rio de Janeiro) and Passa Quatro and Virgínia (Minas Gerais)) since the beginning of the 20<sup>th</sup> century show that in this area all color variations coexist. Vaz-de-Mello (cited as personal communication in Arnaud (2002) and Edmonds & Zidek (2010)) hypothesized that red specimens tend to occur more frequently in higher elevations than does the blue form, but our present observations contradict this: red specimens occur in localities at sea level in southern locations (e.g., Porto Alegre, Rio Grande do Sul) as well as at high elevations above 1,500 m. (e.g., Campos do Jordão, São Paulo). In Virgínia (Minas Gerais), for instance, both blue and red specimens were collected together at 1,500 m., and our highest altitude record belongs, in fact, to a blue specimen (Campos do

Jordão, 1,700 m.). Therefore, as these forms are apparently sympatric and there is no other characteristic differentiating them, we agree with Harold's (1869b) and Edmonds & Zidek's (2010) conclusions and considered color as a matter of intraspecific variation in *C. saphirinus* and thus *Phanaeus chabrellaci* as Thomson, 1857, name proposed to distinguish red specimens in a separate taxon, its junior synonym. But it is true and noteworthy that some of the localities examined by us with a large number of collected specimens, particularly São Bento do Sul (Santa Catarina), did not present red specimens, but only blue and green ones, and that, in southeastern Brazil, no red individual has been collected at lower altitudes.

**Bionomics:** Martínez (1959) and Halffter & Mathews (1966) erroneously regarded *C. saphirinus* to be strictly coprophagous. As stated by Edmonds (1972) and Edmonds & Zidek (2010), this species also presents necrophagous habits and is found in carcasses. Silva *et al.* (2012) and Silva & Di Mare (2012), after having collected almost 600 specimens with baited pitfall traps, observed that *C. saphirinus* exhibited a special attraction to rotting chicken organs and fish and thus considered this species as preferentially necrophagous, although it was also attracted to rotting banana and to human excrement. Specimens examined by us with collecting data are those collected with human feces by Mario Cupello in Parque Nacional do Itatiaia (Rio de Janeiro), M. I. M. Hernandez in Serra do Japi (São Paulo), E. Bovy in Parque Estadual da Serra do Mar (São Paulo), and G. Viegas in Rolante (Rio Grande do Sul); with tapir dung by E. Bovy in São Miguel Arcanjo (São Paulo); in a toad carcass by J. F. Zikán in Virgínia (Minas Gerais); and with carrion by M. Rocha in Porto Belo (Santa Catarina) and François Génier & Sérgio Ide in Estação Biológica da Boracéia (São Paulo). Ohaus (1909) reported this species from cattle and mule dung, Cáceres & Monteiro-Filho (2006) observed it consuming dung of a big-eared opossum (*Didelphis aurita* Wied-Neuwied, 1826) and burying a carcass of a black-footed pygmy rice rat (*Oligoryzomys nigripes* (Olfers, 1818)), and Silva & Bogoni (2014) collected four specimens of *C. saphirinus* using rotten chicken eggs as bait.

As for *C. machadoi*, *C. saphirinus* has been recorded for all months from October to May, suggesting that adults of this species are inactive during the coldest period of the year.

**Geographic distribution:** **Chacoan subregion:** Parana dominion: Atlantic, Parana Forest, and *Araucaria* Forest provinces. **BRAZIL:** Minas Gerais: Aiuruoca, Camanducaia, Conceição dos Ouros, Ingaí (Reserva Biológica Unilavras/Boqueirão), Passa Quatro, Poço de Caldas, Varginha, Virgínia. Rio de Janeiro: Itatiaia (Parque Nacional do Itatiaia). São Paulo: Bananal (Serra da Bocaina), Barueri, Campos do Jordão, Cubatão, Jundiaí, Leme, Mogi das Cruzes, Parque Estadual da Serra do Mar (Núcleo Picinguaba, Núcleo Santa Virgínia), Parque Estadual Xixová-Japuí, Pindamonhangaba, Ribeirão Preto, Salesópolis (Estação Biológica de Boracéia), Rio Grande da Serra, São Bernardo do Campo, São Miguel Arcanjo (Parque Estadual Carlos Botelho), São Paulo, Serra da Cantareira, Serra do Japi, Tremembé. Paraná: Balsa Nova (Serra de São Luiz do Purunã), Curitiba, Foz do Iguaçu, Guarapuava, Lapa, Londrina, Marechal Cândido Rondon, Matelândia, Ponta Grossa, Rio Negro. Santa Catarina: Anitápolis, Antônio Carlos, Blumenau, Bombinhas (Área de Relevante Interesse Ecológico (ARIE) Costeira de Zimbros), Campos Novos, Canoinhas, Corupá, Florianópolis, Governador Celso Ramos, Ipumirim, Itapema, Joinville, Lages, Mafra, Monte Castelo, Nova Veneza, Porto Belo (Área de Proteção Ambiental (APA) do Araça), Rio das Antas, Santo Amaro da Imperatriz, São Bento do Sul, São Bonifácio, São Domingos, São Francisco do Sul, São Pedro de Alcântara, Seara, Timbó. Rio Grande do Sul: Barão de Cotegipe, Bento Gonçalves, Caxias do Sul, Cruz Alta, Ijuí, Porto Alegre, Rolante, Santa Maria, Santo Augusto, São Borja (Edmonds & Zidek, 2010), São Francisco de Paula, Silveira Martins, Triunfo. **PARAGUAY:** Cordillera, Guairá: Colonia Independencia, Natalicio Talavera, Paso Yobai, Villarrica. Paraguarí: Paraguarí. Caazapá: Parque Nacional Caaguazú. Itapúa. **ARGENTINA:** Misiones: Aristóbulo del Valle, Cerro Azul, Dos de Mayo, Garuhapé, Loreto, Parque Nacional Iguazu, Posadas, San Ignacio, San Pedro, San Vicente, Santa María.

We consider the reports of *C. saphirinus* for the Paraguayan department of Alto Paraguay, for the Argentinean provinces of Tucuman and Chaco (Edmonds & Zidek, 2010), and for Uruguay (d'Olsoufieff, 1924), as well as the specimen examined by us with label indicating precedence from Porto Murtinho (Mato Grosso do Sul, Brazil), as very doubtful, and therefore were excluded from the distribution presented above. The two individuals examined in the MZSP with report from Pará (Itaituba and Óbidos) are certainly mislabeled.

**Material examined:** 252 males and 198 females. **NO DATA**—3 males (MNHN), 1 male and 1 female (MNRJ; female of the red form), 1 male (BMNH), and 1 male (OUMNH). **ARGENTINA:** MISIONES: Alto Paraná, Puerto Aguirre, 1933-34, K. J. Hayward col.—1 female (BMNH); Arroyo Cuñápirú, 02.III.1996, without collector—1 male and 1 female (CEMT; male of the red form); “Papiri”, 22.III.1991, without collector—2 males

(CEMT; red form); Parque Nacional Iguazu, XII.2004 without collector—1 female (CPFA, red form); Posadas, 22.XI.1995, without collector—1 male (CEMT); Puerto Azul (=Cerro Azul?), 10.XI.2002, R. Foerster col.—2 males and 2 females (CPFA, all red form); San Ignacio, Tijucuare, without date and collector—1 female (MNHN); San Pedro, XI.2012, P. Wagner col.—2 females (CEMT; red form); San Vicente, Salto La Golondrina, 500 m., 27°7'19"S 54°30'43"W, XI.2006, E. Abadie col.—1 male (CEMT; red form). **BRAZIL**: no more data—2 males and 1 female (MNHN; female of the red form) and 4 males and 1 female (CPFA, 2 males and female of red form). **PARÁ [mislabeling]**: Itaituba, Santarenzinho, Rio Tapajós, III.1961, Dirings col.—1 male (MZSP); Óbidos, XII.1931, B. Pohl col.—1 male and 1 female (MZSP). **MATO GROSSO DO SUL [mislabeling?]**: Porto Murtinho, XII.1929, Spitz col.—1 female (MZSP). **MINAS GERAIS**: Aiuruoca, VI.2009, P. H. Bernardo col.—1 female (CEMT; red form); Aiuruoca, Parque Estadual da Serra do Papagaio, 1,700m, X.1993, A. Machado col.—1 male (CEMT; red form); Camanducaia, Monte Verde, 13.XI.1970, J. Halik col.—1 female (MZSP); Conceição dos Ouros, I.2003, G. P. Almeida col.—2 males (CEMT); Fazenda dos Campos, 20.XII.1920, J. F. Zikán col.—1 female (FIOC); Ingáí, Reserva Biológica Unilavras/Boqueirão, II.2003, Fernando Z. Vaz-de-Mello col.—1 female (CEMT); Passa Quatro, without date, J. F. Zikán col.—1 male (FIOC); Passa Quatro, 1915, Jaeger col.—1 female (MNRJ; red form); Passa Quatro, 02.XII.1915, Zikán col.—3 males (MNRJ); Passa Quatro, 915 m., 14.XII.1922, J. F. Zikán col.—1 male (FIOC); Passa Quatro, Fazenda dos Campos, XI.1917, J. F. Zikán col.—1 male and 1 female (MNRJ); Passa Quatro, Faz. dos Campos, 17.XII.1918, J. F. Zikán col.—1 male (MNRJ); Passa Quatro, Faz. dos Campos, 01.XI.1920, J. F. Zikán col.—1 female (MNRJ); Passa Quatro, Faz. dos Campos, 09.XI.1920, J. F. Zikán col.—1 male (MNRJ; red form); Varginha, without date, Zoroastro col.—1 female (FIOC); Virgínia, 1,500 m., 08.X.1918, J. F. Zikán col.—1 female (FIOC); Virgínia, 1,500 m., 1920, J. Zikán col.—1 female (FIOC); Virgínia, 1,500 m., 06.I.1922, J. F. Zikán col.—1 female (FIOC); Virgínia, Fazenda dos Campos, 1,500 m., 25.X.1915, J. F. Zikán col.—1 male (FIOC; in a toad carcass); Virgínia, Faz. dos Campos, 1,500 m., 15.XII.1915, J. F. Zikán col.—1 male (FIOC); Virgínia, Faz. dos Campos, 1,500 m., 07-23.XI.1917, J. Zikán col.—1 male (MNRJ) and 1 female (FIOC); Virgínia, Faz. dos Campos, 1,500 m., 25.I.1919, J. Zikán col.—1 male (MNRJ); Virgínia, Faz. dos Campos, 1,500 m., 22.X.1920, J. F. Zikán col.—1 female (FIOC); Virgínia, Faz. dos Campos, 1,500 m., 16.XI.1920, J. F. Zikán col.—1 male (DZUP; red form); 1 male (FIOC; red form), 2 males and 1 female (MNRJ), and 1 male (MZSP; red form); Virgínia, Faz. dos Campos, 1,500 m., 25-30.XI.1920, J. F. Zikán col.—2 males and 2 females (FIOC); Virgínia, Faz. dos Campos, 1,500 m., 28.XI.1921, J. F. Zikán col.—1 male (FIOC; red form); Virgínia, Faz. dos Campos, 1,500 m., 08.XII.1921, J. F. Zikán col.—1 male (CEMT; red form); Virgínia, Faz. dos Campos, 1,500 m., 08.XI.1926, J. F. Zikán col.—1 female (FIOC). **PARANÁ**: Balsa Nova, Serra de São Luiz de Purunã, Fazenda Monjolo, 1,116 m., 25°45'S 49°70'W, I.2007, P. Lowenberg Neto col.—3 males and 1 female (CEMT); Curitiba, without date and collector—1 female (MNHN); Curitiba, XII.1940, Claretiano col.—1 male (MZSP); Curitiba, Barigui, II.1941, Claretiano col.—1 female (MZSP); Curitiba, XI.1963, R. R. Teixeira col.—2 females (DZUP); Curitiba, 900 m., 12.XII.1968, Dep. Zoo. col.—1 male (DZUP); Foz do Iguaçu, XI.1984, A. Soares col.—1 male (CEMT); Guarapuava, XI.1960, I. Schneider col.—1 female (MNRJ; red form); Marechal Cândido Rondon, Porto Artaza, without date and collector—1 male (MZSP); Matelândia, XI.1961, A. Maller col.—1 male (MZSP; red form); Matelândia, I.1962, A. Maller col.—1 female (MNRJ; red form) and 1 male and 1 female (MZSP; red form); Ponta Grossa, XII.1942, without collector—1 male and 1 female (DZUP); Rio Negro, Tijuco Preto, 810m, 26°45'S 39°45'53"W, V.2012, Randy Marcolino col.—1 male and 1 female (CEMT). **RIO DE JANEIRO**: Itatiaia, 08.II.1991, Celso Jr. col.—1 male (CEMT; red form); Itatiaia, XI.1991, Celso Godinho col.—2 females (CEMT); Itatiaia, 08.XI.1991, Celso Jr. col.—1 male (CPFA); Itatiaia, II.1992, Celso Godinho col.—1 male (CEMT); Itatiaia, IV.1992, Celso Godinho col.—2 females (CEMT; one of the red form); Itatiaia, 02.XI.1992, Celso Jr. col.—1 male and 2 females (CPFA, all red form); Itatiaia, III.1993, Celso Godinho col.—4 males (CEMT); Itatiaia, III.1995, Celso Godinho Jr.—1 female (CEMT; red form); Itatiaia, 850 m., 18.III.1934, J. F. Zikán col.—1 female (FIOC; red form); Itatiaia, Parque Nacional do Itatiaia, Casa do Pesquisador, 810 m., 22-25.II.2013, Mario Cupello col.—1 male and 2 females (MNRJ). **RIO GRANDE DO SUL**: no more data—3 males and 2 females (MNHN) and 2 females (BMNH); Barão de Cotegipe, 31.XII.1965, F. Giacomet col.—1 male (DZUP); Bento Gonçalves, IX.2001, C. Arioli col.—4 males (CEMT); Caxias do Sul, XI.1926, without collector—2 females (MNRJ); Ijuí, 19.IX.2012, J. Lima col.—1 male (CEMT; red form); Porto Alegre, without date and collector—1 male (MNRJ; red form); Rolante, 29°27'43"S 56°09'12"W, 19-22.X.2010, G. Viegas col.—3 males and 1 female (CEMT; one male of the red form); Santo Augusto, X.1958, O. Roppa col.—3 males and 1 female (MNRJ; red form); Santo Augusto, X.1966, without collector—2 males (CPFA, red form); São Francisco

de Paula, 29°29'16"S 50°10'60"W, 20.II-19.III.2002, R. Ott col.—3 males and 3 females (CEMT); São Francisco de Paula, 13-14.I.2008, L. Audino col.—3 males and 3 females (CEMT; one female of the red form); São Francisco de Paula, 10-13.XII.2009, Paschoal C. Grossi col.—1 male and 1 female (CEMT); Triunfo, 17.IX-17.X.1993, without collector—1 male and 1 female (CEMT). SANTA CATARINA: no more data—2 males and 1 female (MNHN), 1 female (MNRJ), 1 male and 2 females (CPFA), and 2 males and 2 females (BMNH); without date, Friedenreich col.—1 male (MNRJ); Anitápolis, I.1928, B. Pohl col.—2 females (MZSP); Anitápolis, 27°54'S 49°07'W, 28.I.2013, T. R. O. Simões col.—1 male and 1 female (CEMT); Antônio Carlos, 27°25'S 48°51'W, 19.XII.2012, J. A. Bogoni col.—1 male and 1 female (CEMT); Blumenau, XII.1924, Luederwaldt col.—1 male (MZSP); Bombinhas, ARIE Costeira de Zimbros, 27°S 48°W, 14.X.2011, C. C. Oliveira col.—1 female (CEMT); Campos Novos, 27°23'S 51°12'W, II.2010, M. I. M. Hernández & G. Viegas cols.—2 males (CEMT); Canoinhas, Pinhal, XII.1951, A. Maller col.—2 females (MNRJ); Corupá, X (without year), Anton Maller col.—3 males (MNRJ); Corupá, XI (without year), Anton Maller col.—2 females (MNRJ); Corupá (Hansa Humboldt), X.1942, collector illegible—1 male (MZSP); Corupá, III.1952, A. Maller col.—2 males and 1 female (MNRJ); Corupá, XI.1952, A. Maller col.—1 male (MNRJ); Corupá, III.1953, A. Maller col.—1 female (MNRJ); Corupá, XII.1996, without collector—3 males and 1 female (CPFA); Corupá, II.1954, A. Maller col.—1 female (DZUP); Corupá, II.1992 without collector—4 males and 2 females (CPFA); Florianópolis, 27°31'S 48°30'W, 09-10.I.2013, P. G. Silva col.—1 male and 1 female (CEMT); Florianópolis, 27°42'S 48°31'W, 01.II.2013, P. G. Silva col.—1 male and 1 female (CEMT); Florianópolis, Lagoa do Peri, 27°43'S 48°32'W, IX.2007, P. Condé & M. Hernández cols.—1 male (CEMT); Florianópolis, Lagoa do Peri, X.2007, P. Condé & M. Hernández cols.—4 males and 1 female (CEMT); Florianópolis, Lagoa do Peri, XI.2007, P. Condé & M. Hernández cols.—1 male (CEMT); Florianópolis, Lagoa do Peri, 27°49'S 45°92'W, I.2009, P. Condé & M. Hernández cols.—1 female (CEMT); Florianópolis, Vila Harmonia, XII.1914, Luederwaldt col.—1 female (MZSP); Governador Celso Ramos, 27°23'S 48°33'W, 27.I.2012, P. G. Silva col.—1 male and 1 female (CEMT); Governador Celso Ramos, 27°25'S 48°34'W, 24.I.2013, P. G. Silva col.—1 male and 1 female (CEMT); Ipumirim, 27°02'S 52°10'W, 25.XII.2012, J. A. Bogoni col.—2 males (CEMT); Itapema, 27°03'S 48°36'W, 17.I.2013, P. G. Silva col.—1 male and 1 female (CEMT); Joinville, without date, Dirings col.—2 females (MZSP); Joinville, 1919, Schmith col.—2 males and 1 female (MNRJ); Joinville, Rio Bracinho, without date, Dirings col.—3 males and 2 females (MZSP); Lages, without date and collector—1 male (MNHN; red form); Mafra, IV.1976, P. Arnaud col.—3 males (CPFA); Monte Castelo, 815m, 26°39'S 50°18'W, 24.XII.2012, A. L. Brandi col.—1 female (CEMT); Monte Castelo, 881m, 26°43'S 50°19'W, 07.I.2013, A. L. Brandi col.—2 males and 1 female (CEMT); Nova Veneza, 28°33'S 49°35'W, 20.III.2013, J. A. Bogoni col.—1 male and 1 female (CEMT); Porto Belo, APA do Araça, 27°S 48°W, 15.II.2011, M. Rocha col.—1 male (CEMT); Rio Vermelho, I.2003, without collector—2 males (CPFA); Rio Vermelho, II.1995, without collector—1 male (CPFA); Santo Amaro da Imperatriz, 27°44'S 48°48'W, XI.2009, C. B. Marcon & M. I. M. Hernández cols.—3 males and 1 female (CEMT); São Bento do Sul, without date, Dirings col.—1 male and 1 female (MZSP); São Bento do Sul, 1921, collector illegible—1 male (MNRJ); São Bento do Sul, I.1952, without collector—1 male (MNRJ); São Bento do Sul, IV.1949, Dirings col.—1 male (MZSP); São Bento do Sul, I.1950, Dirings col.—1 male (MZSP); São Bento do Sul, III.1952, without collector—1 male (MNRJ); São Bento do Sul, Rio Natal, III.1957, Dirings col.—1 male and 1 female (MZSP); São Bento do Sul, Rio Vermelho, without date, Dirings col.—21 males and 16 females (MZSP); São Bento do Sul, Rio Vermelho, XII.1948, Dirings col.—2 males (MZSP); São Bento do Sul, Rio Vermelho, III.1949, Dirings col.—4 males (MZSP); São Bento do Sul, Rio Vermelho, XI.1949, Dirings col.—1 male (MZSP); São Bento do Sul, Rio Vermelho, II.1957, A. Maller col.—1 male (MNRJ); São Bento do Sul, Rio Vermelho, I.1962, Dirings col.—1 male (MZSP); São Bento do Sul, Rio Vermelho, 850 m., IV.1974, Rank col.—1 male (DZUP); São Bento do Sul, Rio Vermelho, 850 m., V.1974, Rank col.—2 females (DZUP); São Bonifácio, 27°53'S 48°51'W, 15.XII.2012, J. A. Bogoni col.—1 male and 1 female (CEMT); São Domingos, 26°26'S 52°34'W, 28.XII.2011, A. Bugoni col.—1 male and 1 female (CEMT); São Pedro de Alcântara, 27°37'S 48°53'W, 27.II.2013, J. A. Bogoni col.—1 female (CEMT); Seara, Nova Teutônia ("Hansa"), without date, J. Clermont col.—1 male and 2 females (CPFA); Seara, Nova Teutônia ("Hansa Humboldt"), without date and collector—5 males and 1 female (MNHN); Seara, Nova Teutônia, I.1934, B. Pohl col.—1 male and 1 female (MZSP); Seara, Nova Teutônia, X.1934, B. Pohl col.—1 male (MZSP); Seara, Nova Teutônia, I.1935, B. Pohl col.—1 male (MZSP); Seara, Nova Teutônia, 31.X.1940, F. Plauman col.—1 female (MNRJ); Seara, Nova Teutônia, XII.1944, Dirings col.—1 female (MZSP); Seara, Nova Teutônia, VIII.1948, Dirings col.—2 females (MZSP); Seara, Nova Teutônia, III.1949, Dirings col.—1 female (MZSP); Seara, Nova Teutônia, 04.XI.1950, F.

Plauman col.—1 female (MNRJ); Seara, Nova Teutônia, X.1951, F. Plauman col.—1 male and 1 female (MNRJ); Seara, Nova Teutônia, XII.1964, F. Plaumann col.—1 male (MZSP); Seara, Nova Teutônia, X.1965, F. Plaumann col.—1 male (MZSP); Seara, Nova Teutônia, 27°11'S 52°23'W, II.1980, Fritz Plaumann col.—1 male (DZUP); Timbó, IV.1956, Dirings col.—1 female (MZSP); Timbó, X.1961, Dirings col.—1 male (MZSP). SÃO PAULO: no more data—1 male and 1 female (BMNH); Bananal, Serra da Bocaina, I.1937, D. Mendes col.—1 female (MNRJ); Barueri, 16-23.II.1955, K. Lenko col.—2 males (DZUP); Barueri, 28.II.1956, K. Lenko col.—1 male (DZUP); Barueri, 04.II.1968, K. Lenko col.—1 female (MZSP); Campos do Jordão, without date and collector—1 female (MZSP); Campos do Jordão, 20.XI.1952, P. Pereira col.—1 female (MZSP; red form); Campos do Jordão, XII.1955, J. Lane col.—1 male (MZSP); Campos do Jordão, 09.V.1964, H. Ebert col.—1 female (FIOC); Campos do Jordão, I.2004, G. P. Almeida Neto col.—8 females (CEMT); Campos do Jordão, 1,600 m., 25.IV.1955, E. C. Freire col.—1 male (MNRJ; red form); Campos do Jordão, 1,600 m., 29.IV.1955, E. C. Freire col.—1 female (MNRJ); Campos do Jordão, 1,700 m., 24.I.1966, H. Ebert col.—1 male (FIOC); Cubatão, XI.2004, A. A. da Silva col.—1 male (MZSP); Cubatão, 14-19.II.2005, A. A. da Silva col.—2 males (MZSP); Estação Biológica da Boracéia, 800-900m., 28-30.IV.1997, F. Génier & S. Ide cols.—1 female (MZSP); Jundiaí, without date and collector—1 male (MZSP); Leme, 1930, Riditer col.—1 female (MZSP); Mogi das Cruzes, 1932, Elisa & Vianna cols.—1 female (MZSP); Parque Estadual da Serra do Mar, Núcleo Caraguatatuba, 23°35'27"S 45°25'19"W, 13.I.2012, E. Bovy col.—1 male (CEMT); Parque Estadual da Serra do Mar, Núcleo Picinguaba, 23°20'11"S 44°50'03"W, 14.I.2012, E. Bovy col.—4 males and 13 females (CEMT); Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, Sede Vargem Grande, 23°26'33"S 45°14'19"W, 17.I.2012, E. Bovy col.—17 males and 15 females (CEMT); Parque Estadual Xixová-Japuí, 28.X-17.XI.1999, “Grupo” col.—1 female (CEMT); Parque Estadual Xixová-Japuí, 21.II.2000, “Grupo” col.—1 male; Pindamonhangaba, Eugênio Lefevre, 21.II.1963, Exp. Dep. Zoo. col.—1 male (MZSP); Ribeirão Preto, 1906, without collector—1 female (MZSP); Rio Grande da Serra, II.1963, without collector—1 male (MZSP); Salesópolis, Estação Biológica da Boracéia, 21.I.1966, Reichardt col.—1 female (MZSP); Salesópolis, Est. Biol. Boracéia, 01-28.XI.2001, S. A. Casari & I. B. Francini cols.—1 male (MZSP); São Bernardo do Campo, X.1933, without collector—1 male (MNRJ); São Miguel Arcanjo, Parque Estadual Carlos Botelho, 762 m., 24°04'01"S 47°59'40"W, 25.XI.2011, E. Bovy col.—1 male (CEMT); São Paulo, without date and collector—1 male (MZSP); São Paulo, Ipiranga, 1901, Lima col.—1 female (MZSP); São Paulo, Ipiranga, 1902, without collector—1 male (MZSP); São Paulo, Jabaquara, 08.I.1934, without collector—1 male (MNRJ); São Paulo, Santana, 04.XII.1965, J. Halik col.—1 male and 1 female (MZSP); São Paulo, Santo Amaro, 1933, without collector—1 male (MNRJ); Serra da Bocaina, IV.1924, Luederwaldt & R. Spitz cols.—2 males and 1 female (MZSP); Serra da Bocaina, 27.X.1963, H. S. Lopes col.—1 female (FIOC); Serra da Cantareira, IV.1931, R. Spitz col.—1 female (MZSP); Serra da Cantareira, I.1966, J. Halik col.—1 male and 1 female (MZSP); Serra do Japi, 1,050m., 23°14'S 46°56'W, 1998, M. I. M. Hernández col.—1 male (CEMT).

## Acknowledgments

We are very grateful to W. D. Edmonds (Marfa, Texas, U.S.A.), Miguel A. Monné and Juan Pablo Botero (MNRJ), and one anonymous reviewer for their kind and careful review of the manuscript. We are also grateful to all curators, collection managers, and collaborators cited in the Material and Methods section. Our sincere thanks also go to Sonia Casari, Carlos Campaner, and Ana Maria Vasques for the great assistance while the first author was at the MZSP and for the loan of *Coprophanaeus machadoi* holotype; to Darren Mann (OUMNH), Malcolm Kerley and Max Barclay (BMNH), and Antoine Mantilleri and Olivier Montreuil (MNHN) for their kind hospitality to the first author in his visits to the museums; and to Allan Carelli (MNRJ), Thaynara Pacheco and Luis Gabriel Nunes (CEMT) for the help with the morphological analysis. The MZSP staff was responsible for the photographs of *C. machadoi* holotype and we are very thankful to Guilherme Ide and Carlos Lamas (MZSP) for permission to publish these images. The photographs of *C. saphirinus* holotype were kindly made available to us by Katja Neven (ZSMC), while those of *Phanaeus chabriacci* holotype were by Alain Drumont (ISNB) and Stéphane Hanot (Musée Royal de l'Afrique Centrale, Tervuren, Belgium), and we are indebted to them. MC is supported through scholarship offered by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and FZVM received grants from CNPq (304925/2010-1, 302997/2013-0, 405697/2013-9, 484035/2013-4, 202327/2013-2) and from the Synthesys Project (<http://synthesys3.myspecies.info/>) which is financed by the European Community Research Infrastructure Action under the FP7 (BE-TAF-3985 and GB-TAF-3855).

## References

- Almeida, L.M. & Mise, K.M. (2009) Diagnosis and key of the main families and species of South American Coleoptera of forensic importance. *Revista Brasileira de Entomologia*, 53, 227–244.  
<http://dx.doi.org/10.1590/s0085-56262009000200006>
- Arnaud, P. (2002) *Phanaeini. Les coléoptères du monde. Vol. 28.* Hillside Books, Canterbury, 151 pp.
- Biodiversitas (2007) *Revisão das listas das espécies da flora e da fauna ameaçadas de extinção do estado de Minas Gerais. Relatório Final, Volume 3(Resultados: lista vermelha da fauna de Minas Gerais).* Fundação Biodiversitas, Belo Horizonte, 142 pp.
- Blackwelder, R.E. (1944) Checklist of the coleopterous insects of Mexico, Central America, West Indies and South America. Part 2. *United States National Museum Bulletin*, 185, 189–341.  
<http://dx.doi.org/10.5479/si.03629236.185.2>
- Bruch, C. (1911) Catálogo sistemático de los coleópteros de la República Argentina. Pars IV. Familias Lucanidae, Scarabaeidae (Coprini-Cetonini), Passalidae. *Revista del Museo de La Plata*, XVII (IV), 181–225.
- Cáceres, N.C. & Monteiro-Filho, E.L.A. (2006) The action of post-dispersal beetles (Coleoptera: Scarabaeidae) and ants (Hymenoptera: Formicidae) on scats of *Didelphis spp.* (Mammalia: Didelphidae). *Revista de Biología Tropical*, 54 (4), 1197–1203.  
<http://dx.doi.org/10.15517/rbt.v54i4.14102>
- Culot, L., Bovy, E., Vaz-de-Mello, F.Z., Guevara, R. & Galetti, M. (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. *Biological Conservation*, 163, 79–89.  
<http://dx.doi.org/10.1016/j.biocon.2013.04.004>
- Cupello, M. & Vaz-de-Mello, F.Z. (2013) New evidence for the validity of *Coprophanaeus (C.) terrali* Arnaud, 2002 (Coleoptera: Scarabaeidae: Scarabaeinae: Phanaeini), a dung beetle from Brazil. *Zootaxa*, 3717 (3), 359–368.  
<http://dx.doi.org/10.11646/zootaxa.3717.3.5>
- Dejean, P.F.M.A. (1833–1936) *Catalogue des Coléoptères de la collection de M. le Comte Dejean.* Méquignon-Marvis Père et Fils, Paris, 443 pp.
- Dejean, P.F.M.A. (1836–1837) *Catalogue des Coléoptères de la collection de M. le Comte de Dejean. Troisième Édition, revue, corrigée et augmentée.* Méquignon-Marvis Père et Fils, Paris, V–XIV, 503 pp.
- Edmonds, W.D. (1967) The immature stages of *Phanaeus (Coprophanaeus) jasius* Oliver (sic) and *Phanaeus (Metallophanaeus) saphirinus* Sturm (Coleoptera: Scarabaeidae). *The Coleopterists Bulletin*, 21 (4), 97–105.
- Edmonds, W.D. (1972) Comparative skeletal morphology, systematics and evolution of the Phanaeine dung beetles (Coleoptera: Scarabaeidae). *The University of Kansas Science Bulletin*, 49, 731–874.
- Edmonds, W.D. & Halffter, G. (1978) Taxonomic review of immature dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Systematic Entomology*, 3, 307–331.  
<http://dx.doi.org/10.1111/j.1365-3113.1978.tb00002.x>
- Edmonds, W.D. & Zidek, J. (2010) A taxonomic review of the Neotropical genus *Coprophanaeus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). *Insecta Mundi*, 129, 1–111.
- Gillet, J.J.E. (1911) *Coleopterorum Catalogus. Pars 38: Scarabaeidae: Coprinae I.* W. Junk, Berlim, 100 pp.
- Halffter, G. & Edmonds, W.D. (1982) *The nesting behavior of dung beetles (Scarabaeinae). An ecological and evolutive approach.* Instituto de Ecología, Mexico City, 176 pp.
- Halffter, G. & Matthews, E.G. (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). *Folia Entomológica Mexicana*, 12–14, 1–312.
- Harold, E. (1869a) *Catalogus coleopterorum. Hucusque descriptorum, synonymicus et systematicus. Tom. IV. Scarabaeidae.* Sumptu E.H. Gummi, Munich, pp. 979–1346.
- Harold, E. (1869b) Ueber coprophage lamellicornien mit besonderer Berücksichtigung der Parises Sammlungen. *Coleopterologische Hefte*, 5, 46–70.
- Harold, E. (1875) Verzeichniss der von Dr. Teuscher in Cantagallo gesammelten coprophagen Lamellicornien. *Coleopterologische Hefte*, 13, 57–72.
- Hernández, M.I.M., Monteiro, L.R. & Favila, M.E. (2011) The role of body size and shape in understanding competitive interactions within a community of Neotropical dung beetles. *Journal of Insect Science*, 11, 1–14.  
<http://dx.doi.org/10.1673/031.011.0113>
- Hernández, M.I.M. & Vaz-de-Mello, F.Z. (2009) Seasonal and spatial species richness variation of dung beetle (Coleoptera, Scarabaeidae s. str.) in the Atlantic Forest of southeastern Brazil. *Revista Brasileira de Entomologia*, 53 (4), 607–613.  
<http://dx.doi.org/10.1590/s0085-56262009000400010>
- IUCN—International Union for Conservation of Nature (2013) The IUCN Red List of Threatened Species. Version 2013.2. Available from: <http://www.iucnredlist.org/> (Accessed 21 March 2014)
- Klug, J.C.F. (1841) “Juni. Gesammtisitzung der Akademie: Unzulänglichkeit der bestehenden MacLeayschen Eintheilung, eine neue Zusammenstellung der Arten der Insectengattung *Phanaeus* Mac-Leay, zunächst nach den in der Königlichen Sammlung vorhandenen Exemplaren und auf Grund der beobachteten sehr mannigfachen”. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königl. Preufs. Akademie der Wissenschaften zu Berlin*, 209–211.
- Kohlmann, B. & Solís, A. (2012) New species and revalidations of scarab beetles (Coleoptera: Geotrupidae: Athyreini and Coleoptera: Scarabaeidae: Scarabaeinae) from Costa Rica and Panama. *Zootaxa*, 3193, 28–52.
- Kolbe, H.J. (1905) Über die Lebensweise und die geographische Verbreitung der coprophagen Lamellicornier. *Zoologischen Jahrbüchern Supplement*, 8, 475–594.

- Korasaki, V., Lopes, J., Brown, G.G. & Louzada, J. (2013) Using dung beetles to evaluate the effects of urbanization on Atlantic Forest biodiversity. *Insecta Science*, 20 (3), 393–406.  
<http://dx.doi.org/10.1111/j.1744-7917.2012.01509.x>
- Lange, R.B. (1947) Ensaio da zoogeografia dos Scarabaeidae do Paraná com algumas notas eto-ecológicas. *Arquivos do Museu Paranaense*, 6, 305–315.
- Machado, A.B.M., Drummond, G.M. & Paglia, A.P. (Org.) (2008) *Livro vermelho da fauna brasileira ameaçada de extinção*. Ministério do Meio Ambiente, Brasília & Fundação Biodiversitas, Belo Horizonte, 1420 pp. [2 vols]
- Martínez, A. (1959) Catalogo de los Scarabaeidae Argentinos. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"*, *Ciencias Zoológicas*, 5, 1–126.
- Minas Gerais (2010) Deliberação normativa COPAM nº 147, de 30 de abril de 2010. Aprova a lista de espécies ameaçadas de extinção da fauna do estado de Minas Gerais. *Diário do Executivo do Estado de Minas Gerais*, Belo Horizonte, 04 May 2010. Available from: <http://www.siam.mg.gov.br/sla/download.pdf?idNorma=13192> (accessed 21 March 2014)
- Morrone, J.J. (2014) Biogeographical regionalisation of the Neotropical region. *Zootaxa*, 3782 (1), 1–110.  
<http://dx.doi.org/10.11646/zootaxa.3782.1.1>
- Moura, M.O., Carvalho, C.J.B. & Monteiro-Filho, E.L.A. (1997) A preliminary analysis of insects of medico-legal importance in Curitiba, State of Paraná. *Memórias do Instituto Oswaldo Cruz*, 92 (2), 269–274.  
<http://dx.doi.org/10.1590/s0074-02761997000200023>
- Nevinson, B.G. (1892) *Revised synonymic list of species in the genera Phanaeus MacLeay and Oxysternon Castelnau*. Private published, London, 10 pp.
- Ohaus, F. (1909) Bericht über eine entomologische studienreise in Südamerika. *Entomologische Zeitung*, 70, 3–139.
- d’Olsoufieff, G. (1924) Les Phanaeides (Coleoptera – Lamellicornia), famille Scarabaeidae – tr. Coprini. *Insecta*, 13, 4–201.
- Pereira, F.S. (1949) O subgênero *Metallophanaeus* (Coleopt. – Scarabaeidae). *Arquivos do Museu Paranaense*, 7, 217–230.
- Pereira, F.S. & d’Andretta, M.A.V. (1955) Novos escarabeídeos e novas sinonímias (Col. Scarabaeidae). *Papéis Avulsos do Departamento de Zoologia*, 12, 247–264.
- Pessoa, S.B. (1934) Contribuição para o conhecimento das espécies brasileiras do gênero *Phanaeus* (Col. Scarabaeidae). *Annaes da Faculdade de Medicina de São Paulo*, 10, 279–314.
- Pessoa, S.B. & Lane, F. (1941) Coleópteros necrófagos de interesse médico-legal: ensaio monográfico sobre a família Scarabaeidae de S. Paulo e regiões vizinhas. *Arquivos de Zoologia do Estado de São Paulo*, 2, 389–504.
- Redtenbacher, L. (1868) *Reise des österreichischen Fregatte Novara und die Erde in den Jahren 1857, 1858, 1859, unter der befehlen des Commodore B. von Wüllerstorff-Urbair. Zoologischer Theil, Zweiter Band. I. Abtheilung A. Coleopteren*. Vienna (Wien), I-IV, 249 pp. [5 pls]
- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J. & Hirota, M.M. (2009) The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications of conservation. *Biological Conservation*, 142 (6), 1141–1153.  
<http://dx.doi.org/10.1016/j.biocon.2009.02.021>
- Silva, P.G. & Bogoni, J.A. (2014) Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) attracted to rotten eggs in the Atlantic Forest in subtropical southern Brazil. *The Coleopterists Bulletin*, 68 (2), 339–342.  
<http://dx.doi.org/10.1649/0010-065x-68.2.339>
- Silva, P.G. da & Di Mare, R.A. (2012) Escarabeíneos copro-necrófagos (Coleoptera, Scarabaeidae, Scarabaeinae) de fragmentos de Mata Atlântica em Silveira Martins, Rio Grande do Sul, Brasil. *Iheringia, Série Zoológica*, 102 (2), 197–205.  
<http://dx.doi.org/10.1590/s0073-47212012000200012>
- Silva, P.G. da, Vaz-de-Mello, F.Z. & Di Mare, R.A. (2011) Guia de identificação das espécies de Scarabaeinae (Coleoptera: Scarabaeidae) do município de Santa Maria, Rio Grande do Sul, Brasil. *Biota Neotropical*, 11 (4), 329–345.  
<http://dx.doi.org/10.1590/s1676-06032011000400027>
- Silva, P.G. da, Vaz-de-Mello, F.Z. & Di Mare, R.A. (2012) Attractiveness of different bait to the Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in extreme southern Brazil. *Zoological Studies*, 61 (4), 429–441.
- Silva, P.G. da, Vaz-de-Mello, F.Z. & Di Mare, R.A. (2013) Diversity and seasonality of Scarabaeinae (Coleoptera: Scarabaeidae) in forest fragments in Santa Maria, Rio Grande do Sul, Brazil. *Anais da Academia Brasileira de Ciências*, 85 (2), 679–697.  
<http://dx.doi.org/10.1590/s0001-37652013005000033>
- Sturm, J. (1826) *Catalog meiner Insecten-Sammlung. Erster Theil, Käfer*. Private published, Nuremberg, IV–VIII, 207 pp. [pl. I–IV]
- Sturm, J. (1843) *Catalog der Käfer-Sammlung*. Private published, Nuremberg, III–XII, 386 pp. pl. [I–VI]
- Thomson, J. (1857) Description de trente-trois espèces de coléoptères. *Archives Entomologiques*, 1, 109–127.
- Vaz-de-Mello, F.Z. (2000) Estado atual de conhecimentos dos Scarabaeidae s. str. (Coleoptera: Scarabaeoidea) do Brasil. In: Martín-Piera, F., Morrone, J.J. & Melic, A. (Eds.), *Hacia un proyecto CYTED para el inventario y estimación de la diversidad entomológica en Iberoamérica: PRIBES-2000*. Vol. 1. m3m: Monografías Tercer Milenio, Sociedad Entomológica Aragonesa (SEA), Zaragoza, pp. 183–195.
- Vaz-de-Mello, F.Z., Edmonds, E.D., Ocampo, F.C. & Schoolmeesters, P. (2011) A multilingual key to the genera and subgenera of the subfamily Scarabaeinae of the New World (Coleoptera: Scarabaeidae). *Zootaxa*, 2854, 1–73.
- Waterhouse, C.O. (1891) Descriptions of two new Scarabaeidae of the genus *Phanaeus*. *The Annals and Magazine of Natural History, including Zoology, Botany and Geology*, 6 (7), 128–129.  
<http://dx.doi.org/10.1080/00222939109460584>