Revision and phylogeny of the dung beetle genus *Zonocopris* Arrow 1932 (Coleoptera: Scarabaeidae: Scarabaeinae), a phoretic of land snails

Fernando Z. Vaz-de-Mello

Instituto de Ecología A.C., Departamento de Biodiversidad y Ecología Animal, Km 2.5 Carretera Antigua a Coatepec, 351, Congregación El Haya, 91070 Xalapa, Veracruz, Mexico. Present address: Departamento de Biologia, Universidade Federal de Lavras, Lavras, MG 37200-000, Brazil

Abstract. A revision of the Neotropical genus *Zonocopris* is presented. This genus consists of two species, *Z. gibbicollis* (Harold 1868), distributed in Bolivia, Argentina, Paraguay and Brazil and *Z. machadoi* **n. sp.**, from Paraguay and Brazil. Based on morphological data, a phylogenetic analysis of the relationships of the genus *Zonocopris* found it to be closely related to *Cryptocanthon, Paracryptocanthon* and *Bdelyrus*. Brief comments are made on the behaviour of *Zonocopris* and its association with giant land snails.

Résumé. Révision et phylogénie des scarabées du genre *Zonocopris* Arrow 1932 (Coleoptera : Scarabaeidae : Scarabaeinae), phorétiques sur des escargots terrestres. L'auteur présente une révision du genre néotropical *Zonocopris*, qui comprend deux espèces, *Z. gibbicollis* (Harold 1868), distribuée en Bolivie, en Argentine, au Paraguay et au Brésil, et *Z. machadoi* **n. sp.**, du Paraguay et du Brésil. Une analyse phylogénétique des affinités du genre *Zonocopris,* fondée sur des caractères morphologiques, a montré qu'il était étroitement apparenté aux genres *Cryptocanthon, Paracryptocanthon* et *Bdelyrus*. L'association des deux espèces de *Zonocopris* avec des gastéropodes terrestres géants, ainsi que leur comportement, sont brièvement discutés.

Keywords: Dung beetle, Gastropoda, Neotropical region, new species, phoresy.

The genus *Zonocopris* Arrow 1932 has been placed throughout its history among different Scarabaeinae tribes and subtribes. This genus is known for its poorly understood relationships with giant South American land snails (figs 1, 2).

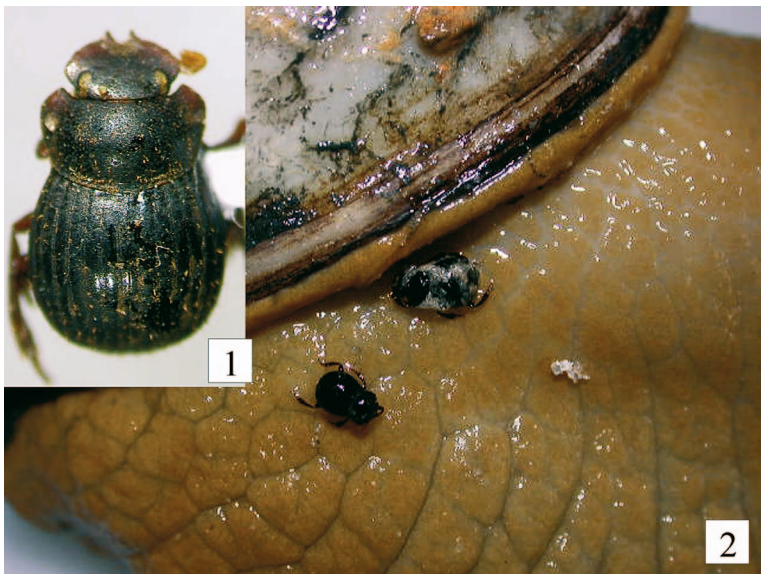
In a short note, Stein (1867) commented about a collection made in Brazil by Dr. Hensel, that included an interesting scarab, probably belonging to the genus *Onthocharis*, collected on the mantle of a living giant snail of the genus *Bulimus* Scopoli. Harold (1868) described that same scarab as *Canthon gibbicollis*, based on the same specimens, and citing Stein's note. Burmeister (1873) and Kolbe (1905) also made reference to the relationship between these scarabs and the giant land snails.

Arrow (1932) described a new scarab genus and species from Porto Alegre, Rio Grande do Sul state, Brazil, collected by P. Buck on snails then identified as *Bulimus (Strophocheilus) oblongus* Müller. He mentions that P. Buck had found up to twelve specimens on the same snail. He also listed examined specimens from Paraguay in the same paper, and called the new species *Zonocopris bucki*, characterizing it by the conspicuous mesosternal foveae, similar to those found in some species of the genus *Synapsis* Bates, and by its overall similarity with an Indian species, *Panelus setosus* Arrow.

Gillet (1933) transferred *Canthon gibbicollis* to his new monotypic genus *Plesiocanthon*. Paulian (1938, 1939) did not include *Plesiocanthon* or *Zonocopris* in his key to the American Canthonina, mentioning (1939, p. 23) that "*Le genre* Canthon *a été récemment morcelé par divers auteurs, ici je lui conserve son ancienne extension…*" [The genus *Canthon* has been recently fragmented by various authors. Herein, I consider it in its former extension...]. He did mention *Plesiocanthon gibbicollis* in the introduction on Canthonina biology. However, the original descriptions of *Zonocopris* or *Plesiocanthon* are not cited in his bibliography, nor is *Plesiocanthon* cited among the synonyms of *Canthon*.

In his key, Balthasar (1939), considered *Plesiocanthon* as a synonym of *Canthon* Hoffmannsegg, but commented (p. 189) "*Ich habe diese Art noch vorläufig im Rahmen der Gattung belassen, da ich eher geneigt bin, in ihr eine Untergattung zu erblicken*" [I left this species provisionally in this genus, as I am rather inclined to consider it as a subgenus)]. Later, in his description of the genus *Cryptocanthon* Balthasar 1942, he related it to *Zonocopris*.

E-mail: vazdemello@gmail.com, scarab@insecta.ufv.br
Accepté le 15 février 2007



Figures 1–2
Zonocopris gibbicollis. **1**, habitus; **2**, two specimens on *Megalobulimus* sp. mantle.

Blackwelder (1944) included in his catalogue *Zonocopris bucki* and *Canthon gibbicollis* (as *gibbicolle*), without mentioning *Plesiocanthon*.

Pereira (1946) synonymized Harold's and Arrow's specific names, and, consequently, *Plesiocanthon* and *Zonocopris* (the latter being valid), adding as a synonym *Diciphycus* Burmeister *in litt.* The capture of individuals of *Zonocopris gibbicollis* (Harold) on live snails was once again cited in that paper, and he added to its distribution the provinces of Salta and Misiones in Argentina and the states of Mato Grosso do Sul (then part of the Mato Grosso) and Goiás in Brazil. Martínez (1947) published an *addenda* and *corrigenda* to Blackwelder's (1944) catalogue, including the synonymies proposed by Pereira (1946).

Pereira & Martínez (1956) also commented on the relationship between *Zonocopris* and snails, but did not include the genus in their key to the genera of American Canthonini, nor did they make comments about its tribal or subtribal placement. Martínez (1959) included this genus among the Ateuchini (=Dichotomiina), citing *Zonocopris gibbicollis* from Misiones, Salta, Jujuy (Argentina), Bolivia, Paraguay and Brazil. There are no comments about the reasons for including the genus among the Ateuchini, and once again its presumed "symbiosis" with snails of the genera *Helix* Linnaeus and *Strophocheilus* Spix is mentioned, adding that the scarab apparently feeds on feces and not mucus as mentioned in earlier literature.

Balthasar (1963) cited *Zonocopris* in his listing of Canthonina genera, and its phoresy on *Bulimus haematostoma* Scopoli and *Strophocheilus* sp. Vulcano & Pereira (1964) did not include it in their catalogue of the Canthonina of the Western Hemisphere. Halffter & Matthews (1966) included it among the Dichotomiina, probably following Martínez (1959), but without comments on its placement.

Halffter & Martínez (1977) finally included *Zonocopris* among the Canthonina, associating it with the "Menthophilina" that Matthews (1974) considered for the Australian fauna.

Bacchus (1978) reported eight syntypes of *Zonocopris bucki*, two in the British Museum collection, collected by Pio Buck in 1931, and six at the Museu de Zoologia da Universidade de São Paulo, all from Porto Alegre, Rio Grande do Sul, Brazil. He mentions that the exact syntype number was unknown, but that in the original description, Arrow noted that "*...there were many examples and 12 specimens were found inside one snail shell*" (sic). He did not mention any syntype specimens from Paraguay.

Halffter & Edmonds (1982), Martínez (1987) and Hanski & Cambefort (1991) included this genus among the Canthonina, and Cambefort (1991a, b) and Gill (1991) commented again on its relationship with snails.

The aim of this study is three-fold: to review the species in the genus *Zonocopris*, to explore its phylogenetic relationships with other scarab genera, and to present some new data on its behaviour.

Material and methods

The specimens examined belong to the following collections (curators in parenthesis):

CMNC, Canadian Museum of Nature, Ottawa, Canada (François Génier);
IBSP, Adolph Hempel Entomological Collection, Instituto Biológico, São Paulo, Brazil (Sergio Ide);
GVHC, Gonzalo and Violeta Halffter private collection, Coatepec, Mexico;
FMNH, Field Museum of Natural History, Chicago, USA (Alfred Newton);
FVMC, Fernando Z. Vaz-de-Mello private collection, Lavras, Brazil;
MNKC, Museo Noel Kempf, Santa Cruz de la Sierra, Bolivia (Julieta Ledezma);
MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (Sonia Casari and Carlos Campaner);
USNM, United States National Museum, Washington, USA (Nancy Adams).

I examined and dissected the specimens under a stereomicroscope and photographed them using a digital Nikkon Coolpix 4500. I conducted the phylogenetic analyses using NoNa (Goloboff, 1993), with Fitch parsimony and equally weighted characters. None of the morphological characters contained codification difficulties. I also included genera that present a general similarity to *Zonocopris*, genera representative of the tribes to which *Zonocopris* has been historically assigned to, and two unrelated scarab genera as outgroups. I inferred clade support by the Bremer index (decay index), with up to ten extra steps (about 50% of the coded characters), and applying a Bootstrap of the original matrix resampling it to a ten-fold matrix.

I conducted behavioural observations from October 2002 to February 2004, using three *Zonocopris gibbicollis* males and four females, collected in Diamantino municipality (Mato Grosso state, Brazil), as well as two giant unidentified snails from the same site. I maintained the specimens in a terrarium at the Zoology Laboratory, Biology Department, Universidade Federal de Lavras, Minas Gerais state, Brazil.

Results and Discussion

The genus *Zonocopris* Arrow 1932

Synonymy

Dicyphicus Burmeister *i. litt.*, Pereira 1946: 294 (considered as a synonym of *Zonocopris*).

Zonocopris Arrow 1932: 223; Blackwelder 1944: 203; Pereira 1946: 293; Martínez 1947: 113; Martínez 1959: 61; Balthasar 1963: 57, 257; Halffter & Matthews 1966: 257; Halffter & Martínez 1977: 34, 44, 51, 59; Halffter & Edmonds 1982: 139; Martínez 1987: 59; Hanski & Cambefort 1991: 473; Vaz-de-Mello 2000: 186, 195.

Plesiocanthon Gillet 1933, Paulian 1938: 227, Balthasar 1939: 189 (considered as synonym of *Canthon*), Pereira 1946: 293 (considered as synonym of *Zonocopris*).

Diagnosis. This genus is readily distinguishable from all other Scarabaeinae genera by the combination of two characters: the presence of a conspicuous round fovea at each side of the mesosternum, and the presence of a supraunguicular spine in the last tarsomere of all legs.

Description. Body: small-sized species (2.5–5.0 mm), color black, except for reddish-brown mouthparts, tibiae and tarsi, and grey antennal clubs. General body form ovoid, but pronotum and elytra each separately rounded and convex, separated by a conspicuous humeral constriction (fig 1). Head: clypeus anteriorly with two large acute teeth, separated by a U-shaped emargination that exposes posteriorly the spiniform ventral clypeal process, which is visible from above. Head dorsally flat, without any traces of tubercles or carinnae. Eyes big (width of the dorsal interocular area seven to nine times greater than one eye dorsal width), ovoid, and narrowed posteriorly. Prothorax strongly convex, disc almost transverse, separated from the posterior margin by a wide transverse depression extending to the lateral borders and anterior angles. Anterior pronotal angles flat and expanded laterally, lateral foveae inconspicuous and incorporated to the anterior-lateral flat region. Posterior margin bordered by a transverse row of umbilicated setigerous puntures bearing scale-like setae. Elytra with wide and deep striae, composed by anastomosed punctures. Striae wider and deeper on apex, where interstriae bear short erect setae that are also present on the sides. Humeri narrowed, calli absent. Pseudoepipleuron wide, bearing a carina, extending from the elytral base to the apex of the second elytral stria. Disc separated from pseudoepipleuron by a conspicuous lateral carina exterior to the seventh elytral stria, that extents from the base almost to the apex of the sixth elytral stria. Hind wings normally developed. Legs: trochanters with an acute anterior angle. Fore femurs ovoid, with a distinct, rounded basal anterior trochantofemoral pit. Protibiae subtriangular, flat, with three external teeth, the apical one much more prominent than the others, apical internal angle straight. Protibial spur short, a bit longer than the first two tarsomeres together. Length of protarsi equal to two thirds of the apical tibial width; last tarsomere with a large, straight and conical supraunguicular spine and short falciform claws. Mesotibiae strongly widened at base, subconical. Metatibiae subconical, with a strong ventro-apical longitudinal carina, bearing a conspicuous row of red to yellow setae. Meso- and metatibial spurs short, conical. Length of first tarsomere subequal to the second one in the middle legs, and slightly shorter than the second one on the hind legs. Last tarsomeres similar in all legs. Venter: mesosternum as long as one third of its width, with a conspicous round pit on each side of the disc. Each mesosternal pit covered by long thick setae. Metasternum barely convex, without discrimen, laterally covered by large, rough punctures and short setae. Abdomen short, ventrites covered by umbilicated punctures. Pygidium transverse and strongly convex, with a deep basal sulcus, and apical border effaced. Parameres shorter than two thirds of the fallobase in length, apically narrowed, flattened and with apex truncated.

Sexual dimorphism. Males have protibiae more strongly widened apically, and with the internal edge more curved than in females; in females protibiae are subtriangular; an internal apical tooth is present in males; male protibial spurs are also shorter than in females, and spatuliform and conical respectively. Differences of metatibiae vary according to species. Apparently there are no sexual differences in metasternal disc shape, and very few differences in the shape of the last urosternite, which is centrally narrower in males.

Distribution. Brazil, northern and northeastern Argentina, southern Bolivia and Paraguay (fig. 9).

Remarks. All specimens with capture data were collected on giant land snails of the genera *Strophocheilus* and *Megalobulimus*, in malaise-flight intercept traps, and in one case in a pitfall baited with human feces. In this last case, however, a giant land snail was also inside the trap (G. Schiffler, *pers. comm.*).

Key for the species of *Zonocopris* Arrow

1. Clypeus rounded externally to median teeth; elytral insterstriae without punctures; protibiae denticulated between teeth; male metatibiae curved internally; parameres very short, with strong hook-like external prolongations in the apico-lateral angles ..... *Z. gibbicollis* (Harold 1868)
- Clypeus bisinuated externally to median teeth; elytral insterstriae with two irregular rows of umbilicated punctures; protibiae not denticulated between teeth; male metatibia strongly medially internally widened; parameres longer, barely arqued externally in the apices ..... *Z. machadoi* **sp. nov.**

Zonocopris gibbicollis (Harold 1868)

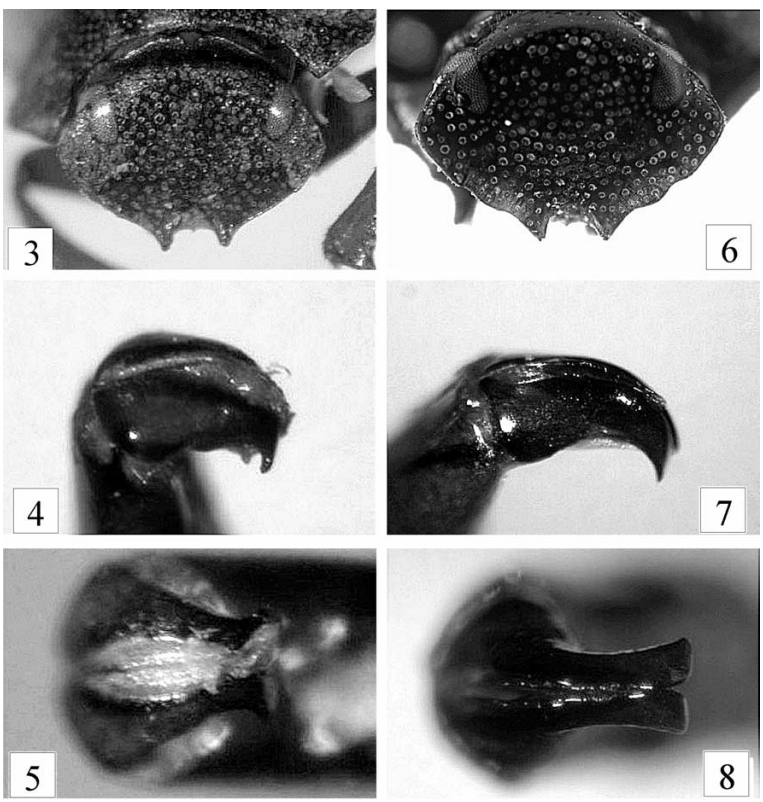
Canthon gibbicollis Harold 1868: 138; Gemminger & Harold 1869: 991; Kolbe 1905: 494; Gillet 1911: 29; Balthasar 1939: 189.
Coprobius gibbicollis (Harold 1868); Burmeister 1873: 417.
Zonocopris bucki Arrow 1932: 223; Blackwelder 1944: 203, Bacchus 1978: 100 (synonymized by Pereira 1946: 293).
Canthon gibbicolle Harold 1868; Blackwelder 1944: 199.
Dicyphicus gibbicollis (Harold 1868): Burmeister *in litt.* (Pereira 1946: 294)
Plesiocanthon gibbicollis (Harold 1868): Gillet 1933: 323, Paulian 1938: 227.
Zonocopris gibbicollis (Harold 1868): Pereira 1946: 293; Martínez 1947: 113; Martínez 1959: 61; Balthasar 1963: 57; Halffter & Matthews 1966: 22; Halffter & Martínez 1977: 59; Martínez 1987: 59; Cambefort 1991a: 32; Cambefort 1991b: 57; Gill 1991: 215; Vaz-de-Mello 2000: 195.

Type material. *Canthon gibbicollis* Harold 1868: Number of syntypes not specified, originally at the Berlin Museum (Harold 1868), but not found at the Museum für Naturkunde der Humboldt-Universität (J. Frisch *in litt.*). Possibly some syntypes have been later deposited in the Oberthür collection. However those have not been found at the Muséum National d'Histoire Naturelle (O. Montreuil *in litt.*).
Zonocopris bucki Arrow 1832: The Natural History Museum, London, specimens not examined; five specimens examined in São Paulo that appear to correspond to the original series (of six cited by Bacchus 1978), but are not labelled as types.

Description. Body size 2.5–3.5 mm. Head (fig. 3) with clypeus rounded at each side of median teeth. Head surface covered by dense umbilicated punctures, separated by half to one puncture diameter. Dorsal interocular region as wide as seven times one eye width. Pronotum covered by umbilicated puntures, that are denser in the anterior discal declivity (where punctures are separated by about ¾ of one puncture diameter), and of greater size on the anterior angles. Posterior border with punctures less dense. Elytra with discal interstriae without punctures, each interstria with one row of small irregular and inconspicuous tubercles, visible only under good light conditions. Legs: protibiae with the internal border slightly curved in males, straight in females. Basal and medial teeth poorly developed in males, acute and conspicuous in females. Metatibiae internally curved in males, straight in females. Genitalia: Parameres short, length equal to half that of the fallobase, ventrally strongly curved, with a conspicous externally-directed apico-lateral hook (figs 4, 5).

Distribution. Northern and northeastern Argentina, southern and western Brazil (one specimen is labeled from northern Brazil), southeastern Bolivia and eastern Paraguay (fig. 9.).

Remarks. Although labelled type specimens have not been examined, little doubt remains about the synonymy proposed by Pereira (1946) for *Zonocopris bucki*, because, according to Papavero (1973), the collector of the type-series of *Canthon gibbicollis*, Hensel, lived from 1863 to 1866 in Porto Alegre, Rio Grande do Sul State, Brazil, and collected mostly there. This is exactly the type locality for Arrow's *Z. bucki.*



Figures 3–8
Zonocopris spp. **3-5,** *Z. gibbicollis*; **6-8,** *Z. machadoi*; 3, 6, head. dorsal view; 4, 7, paramera, lateral view; 5, 8, paramera, dorsal view.

Examined specimens. ARGENTINA: **Jujuy:** 6 km W Yuto, INTA, 13-14.II.1982, H.& A.Howden (5 CMNC); Calilegua Nat. Park, Aguas Negras, 500 m, 18-28.XII.1987, S.&J. Peck, forest ravine litter (6 CMNC); Calilegua Nat. Park, Estación el Cerro, 900 m, 18-28.XII.1987, S.&J. Peck, forest malaise FIT (3 CMNC); Calilegua Nat. Park, Mirador, 600 m, 18-28.XII.1987, S.&J. Peck, forest malaise FIT (15 CMNC); **Misiones:** no data, Richter (1 MZSP); Est. Exp. Loreto, A.A. Ogoblin (2 CMNC); Loreto, 16.III.1949, Rosas-Costa (6 CMNC); **Salta:** Sin localidad, I.1948, A. Martínez (3 USNM); Metán, II.1956, Pereira & Martínez (6 MZSP) ; Do. Oran *(sic)*, Tablillas, 1000 m, II.1944, A. Martínez, sobre *Helix* sp. (2 GHC, 4 MZSP); Do. Oran, El Oculto, XII.1984, H. Martínez (1 CMNC); Do. San Martín, Tablillas, II.1944, A. Martínez (3 CMNC); Do. San Martín, Tartagal, XI.1971, A. Martínez (1 CMNC); Do. San Martín, Pocitos, I.1950, A. Martínez (1 USNM); Do. San Martín, Pocitos, XI.1959, A. Martínez (1 MZSP), General Ballivian, 1931, G. L. Harrington (6 USNM); Tablillas/Tartagal, II.1944, Duret & Martínez (1 CMNC); BOLIVIA: **Santa Cruz:** Pampa Grande, 18º05'S, 64º06'W, 10.I.1996, A. Langer (2 CMNC); Florida, Pampagrande, 03.XI.1996, Fray A. Langer (1 MNKC); Andres Ibáñez, Santa Cruz de la Sierra, 18.IV.1989, Israel Vargas, encontrado entre pié y concha de un gasterópodo (4 MNKC); Roboré, 28.II-1.III.1964, C. Gans & F. Pereira (2 GHC, 11 MZSP); BRAZIL: **No Data:** (2 FMNH); USDA Intercept at Houston, TX #10687, with snails from Brazil, PHH#502, Plane N788, 29.IX.1966, O.E. Hunt (3 USNM); **Mato Grosso:** Diamantino, Alto Rio Arinos, I.2001, E. Furtado, sobre caracóis gigantes (12 FVMC); Poconé, IX.1948 (10 MZSP); **Mato Grosso do Sul:** Salôbra, 10.I.1941, F. Lane (6 MZSP); **Pará:** Canindé (Rio Gurupi), XII.1964, B. Malkin col. (1 IBSP); **Rio Grande do Sul:** (shipped from) Porto Alegre, 15.IX.1966, symbiont on *Strophocheilus oblongus musculus* from L.S. Dillon (16 FMNH); Porto Alegre, IV.1931, Pio Buck (1 MZSP, probably syntype, but not labelled); Porto Alegre, X.1931, Pio Buck (3 MZSP, probably syntypes, but not labelled); Porto Alegre, II.1933 (10 GVHC, 3 CMNC); Porto Alegre, II.1933, Pohl (2 MZSP); Porto Alegre, II.1933, Pio Buck (1 IBSP); Porto Alegre, II.1934, Pio Buck (4 MZSP); Porto Alegre, 25.IX.1966, C.P. Jaeger (22 USNM); Porto Alegre, Jardim Botânico, 30.I.2001, L. Moura & I. Heydrich, *Megalobulimus* sp. (1 FVMC); no data (1 MZSP); PARAGUAY: **Central:** A. Mburicao, 4.XI.1990, G. Arriagada (4 CMNC); A. Mburicao, 4.I.1991, G. Arriagada (3 CMNC); Asunción, 24.I.1957, C.J.D.Brown, on big land snail (2 CMNC); Asunción, 26.IX.1980, D.C. Lowrie, on snail (10 USNM); Asunción, Villa Morra (1 CMNC); San Lorenzo, Lavrelty, 3.II.1997, C Aguilar, ex. *Megalobulimus* sp. (4 CMNC); **Cordillera:** Dist. Caacupé, Cabañas, 13.VII.1981 (2 CMNC); **San Pedro:** San Bernardino, 10.VIII.1903, K. Fiebrig, am Schnecken-Schleimspur (1 FVMC).

Zonocopris machadoi sp. nov.

Zonocopris gibbicollis (Harold 1868) (*pars*): Pereira 1946: 294 (specimens cited from Goiás).

Type material. Holotype male: BRAZIL: **Minas Gerais:** Ribeirão Vermelho, mata do Leleco (21°11'13"S, 45°04'10"W), XII.2001, G. Schiffler, pitfall fezes humanas (MZSP, ex FZVM). Paratypes: BRAZIL: **No Data** (1 CMNC); **Goiás:** Campinas (14°18'36"S, 49°09'04"W), I.1934, R. Spitz (2 MZSP, 1 IBSP); **Mato Grosso:** Chavantina *(sic)* (14°40'24"S, 52°21'11"W), 26.XII.1946, Sick (1 CMNC, 1 MZSP); **Minas Gerais:** Arcos, Mineração CSN, área Bocaina (20°16'55"S, 45°32'22"W), 28.I.2006, R.L. Ferreira (4 FVMC); Itaúna (20°04'43"S, 44°34'35"W), 15.II.2002, M. Souza-Silva, mata seca, sobre *Megalobulimus* (2 FVMC)**;** Lagoa Santa (19°37'38"S, 43°52'23"W), 28.I.1963, Papavero & Leme (1 CMNC); Ribeirão Vermelho, mata do Leleco (21°11'13"S, 45°04'10"W), XII.2001, G. Schiffler, pitfall fezes humanas (4 FVMC); Sete Lagoas (19°27'57"S, 44°14'48"W), Reinhardt, paa em *Bulimus (sic)* (1 CMNC); Vespasiano (19°41'31"S, 43°55'24"W), I.1951, A. Machado, sobre *Strophocheilus* sp. (1 FVMC); **Santa Catarina:** Nova Teutônia (27°09'49"S, 52°25'12"W), XI.1936, B. Pohl (1 MZSP); PARAGUAY: **Caazapá:** Estero Cristal (26°06'00"S 55°45'36"W), 20.IX.1999, J. Jensen (2 FVMC).

Etymology. A patronym honouring Dr. Ângelo Machado, eminent Brazilian odonatologist, conservationist and writer, who provided me with invaluable help since I became interested in scarabs. The first specimen that I examined of this new species, was collected by him in 1951, and was part of a general reference collection identified by Pereira that Ângelo presented to me as a gift when I was 12 years old.

Diagnosis. Clypeus laterally bisinuated. Elytral interstriae with two rows of umbilicated punctures.

Description. **Holotype** male. Head (fig. 6) with clypeus bisinuated each side of median teeth, forming a conspicuous rounded external lobe. Head surface covered by very dense umbilicated punctures, separated by less than half of the diameter of one puncture. Dorsal intercular area as wide as nine times one eye width. Pronotum covered by umbilicated punctures, denser in the discal anterior declivity (separated there by about one half punctures diameter) and twice as large on anterior angles. Pronotal posterior border almost without punctures in the middle, with sparse lateral punctures. Elytra: discal interstriae with two rows of umbilicated punctures, separated by less than one diameter between rows and less than a half diameter within, each row without tubercles. Legs: protibiae with internal borders conspicuously curved, and basal and medial teeth inconspicuous. Metatibiae strongly dilated at the apical half of internal borders.

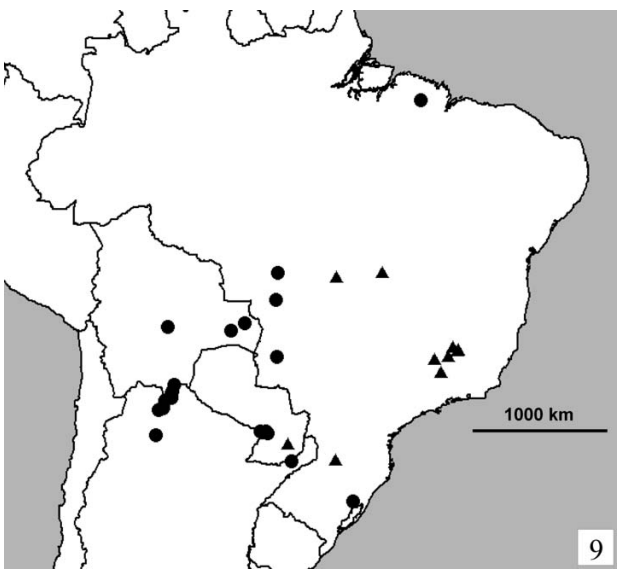
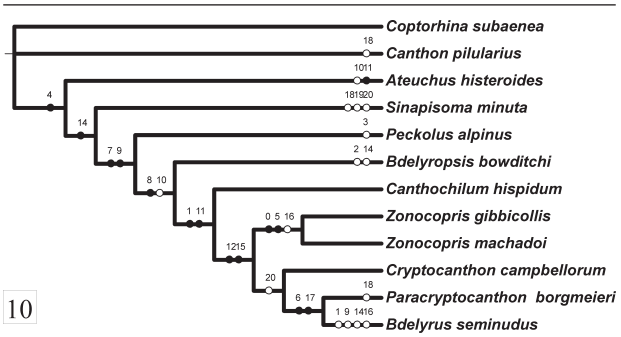
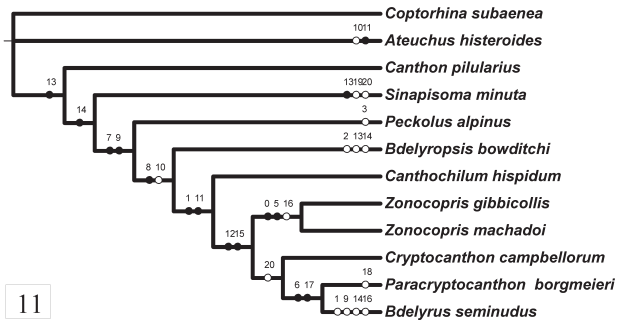


Figure 9
Zonocopris spp., distribution in South America. circles: *Z. gibbicollis*; triangles: *Z. machadoi*.





Figures 10–11
Trees 1 and 2 of five most-parsimonious trees, length = 40 , consistency index = 0.57 and retention index = 0.68.

Genitalia: Parameres (figs 7, 8) as long as 3/5 of phallobase, ventraly curved. Apico-lateral angles slightly externally directed.

Variation. Paratypes vary in size (4.0–5.0 mm) and in sexual characters. Females have anterior tibiae less curved internally, with basal and medial teeth acute and conspicuous; metatibiae almost straight.

Distribution. Brazil (Santa Catarina, Minas Gerais, Goiás and Mato Grosso) and Paraguay (Caazapá) (fig. 9).

Remarks. Specimens collected in pitfall traps were probably asociated with a giant land snail found in the same trap (see above). The locality for Mato Grosso, *Chavantina* (sic) is dubious. Although it is labeled as Mato Grosso, the right name for this locality should be *Xavantina*, and there is another locality with the same name in Santa Catarina state.

Cladistic Analysis

The genera selected for sister-group prospection were *Cryptocanthon*, *Paracryptocanthon*, *Bdelyropsis*, *Bdelyrus*, *Canthochilum* and *Peckolus*, and outgroups used for rooting were *Canthon*, *Canthonella*, *Sinapisoma, Ateuchus*, and *Coptorhina*. I chose the first ones for their general resemblance with *Zonocopris* and previous conjectures of sister-group relationships (Howden 1973; Cook 1998; Cook 2002; Howden & Cook 2002; pers. obs.). On the other hand, the outgroups represent tribes in which the genus *Zonocopris* has at some time been placed or related to in literature. I included *Coptorhina* in order to give a strong root to the tree.

Twenty-one informative morphological characters were used (see tab. 1 and appendix). I conducted an exhaustive search with NoNa, using command "mswap+". It resulted in five equally parsimonious trees of length = 40 , consistency index = 0.57 and retention index = 0.68 (figs 10–15). I calculated the support of clades using the decay index (Bremmer support) (fig. 17). This index was the result of searching up to 31487 trees, from 40 to 50 steps long, that is, up to ten steps longer than the optimal ones, using the command "find" in NoNa. Bootstrap values were calculated with bootstrap matrices of 210 characters (insted of the original 21) in order to eliminate the effect of small character number decreasing bootstrap values, maintaining bootstrap as an indicator solely of character conflict. I conducted one hundred bootstrap replications, and found 119 trees, of the 1000 allowed

Table 1. Matrix used for phylogenetic analysis.

character	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2
species	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**
Coptorhina subaenea	0	0	1	0	1	0	-	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Ateuchus histeroides	0	0	1	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	1	1	1
Canthon pilularius	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Bdelyropsis bowditchi	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	1	1
Bdelyrus seminudus	0	0	1	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	1	1	0
Canthochilum hispidum	0	1	1	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	1	0	1
Cryptocanthon campbellorum	0	1	0	1	0	0	0	1	1	1	1	1	1	0	1	1	0	0	1	1	0
Paracryptocanthon borgmeieri	0	1	0	0	0	0	1	1	1	1	?	1	1	0	1	1	0	1	0	?	?
Peckolus alpinus	0	0	-	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	1
Sinapisoma minuta	0	0	1	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0
Zonocopris gibbicollis	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1
Zonocopris machadoi	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1

as maximum (fig. 16).

The monophyly of *Zonocopris* is supported by three characters, two of them which are non-homoplasic (presence of mesoesternal foveae and shape of the clypeal ventral process, dentiform and foreward directed), and the other (supraunguicular spine) that is also present in *Bdelyrus*. Wether this is a case of convergence, or a simplesiomorphy, would be the subject of a larger analysis involving more species of both *Bdelyrus* and *Cryptocanthon*. Decay index for this node is 3 and bootstrap is 100%.

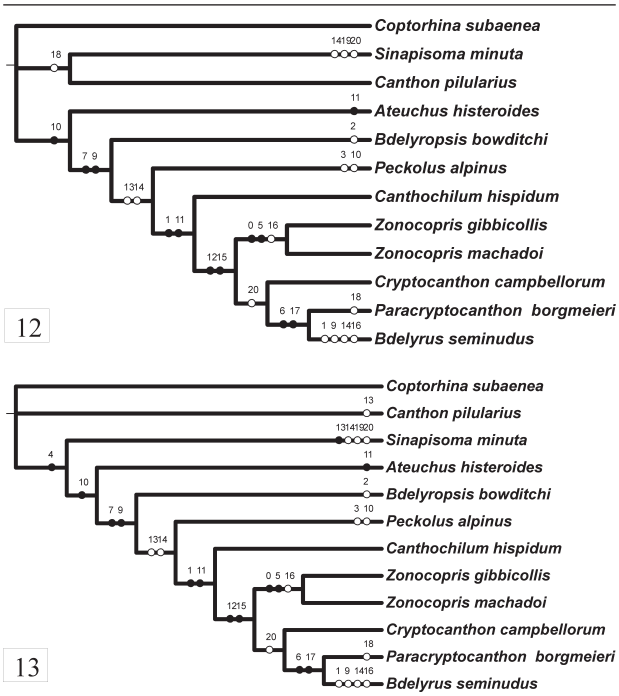
Our results show a sister group relationship between *Zonocopris* and the clade formed by *Cryptocanthon*, *Paracryptocanthon* and *Bdelyrus*. This node is supported by two characters in the metatibiae: they are uniquely ventrally apically emarginated, and with discal apical pilosity. This clade (*Zonocopris* + (*Cryptocanthon* + (*Bdelyrus* + *Paracryptocanthon*))) has a decay index of one, and a bootstrap of 94%. All these genera represent Neotropical endemics, and except for *Bdelyrus* and *Cryptocanthon* that present a few Central American species, they are all distributed in South America.

The sisterhood of *Canthochilum* to (*Zonocopris* + (*Cryptocanthon* + (*Bdelyrus* + *Paracryptocanthon*))) is supported by two non-homoplasic characters: the clypeal process located beneath the clypeal emargination and the presence of a ventro-external longitudinal metatibial setose ridge. The bootstrap value is 99%, and decay index is two. *Canthochilum* is a Greater Antillean endemic restricted to Cuba, Hispaniola and Puerto Rico.

Finally, the group of the above mentioned genera, together with *Peckolus* and *Bdelyropsis*, is well supported by two characters, the presence of elytral setae, which is non-homoplasic in relation to other species used in this analysis, but scattered over at least some species in many Scarabaeinae genera, and the unique anterior trochantofemoral pit (first described by Génier and Kohlmann, 2003), that is also present in a number of other poorly studied groups of tropical Scarabaeinae. These may represent an important clade within the Scarabaeinae, that could also include other small-sized genera, such as *Agamopus*, *Uroxys* and *Odontoloma*, as well as the group formed by *Tesserodoniella*, *Tessedoron* and *Aptenocanthon* (see Vaz-de-Mello and Halffter 2006) and many others presently ascribed to both the Ateuchini and the Canthonini.

Behavioural data for *Zonocopris gibbicollis*

During the hotter and wetter season (October to March) the observed specimens were active on the snails, rarely moving from one snail to another. The beetles were almost always walking over the mantle, and seemed to feed exclusively on mucus. They were never observed on snail feces, that were abundant in the terrarium. Many copulations were observed, and the soil in the terrarium was periodically checked for nests or larvae. However, no nests, larvae, or any new adult were ever found.

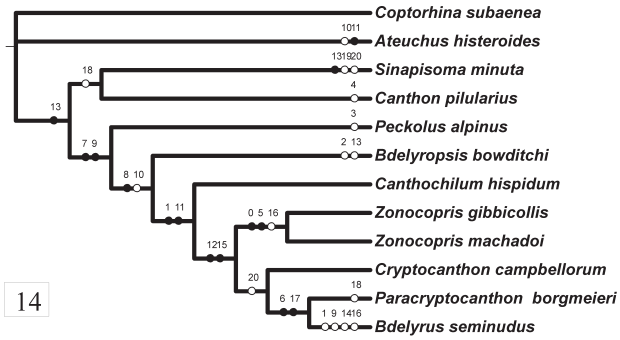


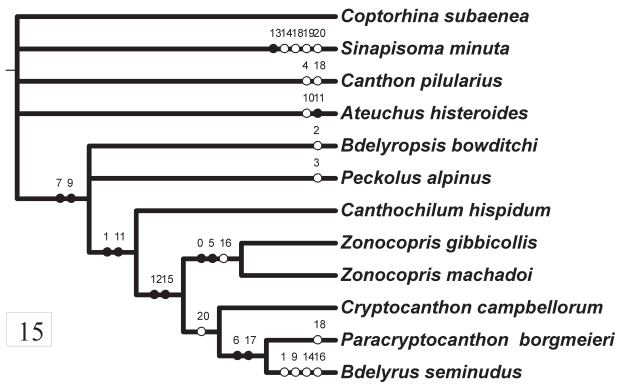
Figures 12–13
Trees 3 and 4 of five most-parsimonious trees, length = 40 , consistency index = 0.57 and retention index = 0.68.

In the dryer and colder season (April to August), the snails buried themselves in the soil, withdrew inside their shells, without forming an operculum, but producing small amounts of mucus. During that time, the beetles remained over the exposed part of the mantle, apparently less active. There was no sign of nesting or oviposition, although large quantities of both faeces and mucus were available from each estivating snail.

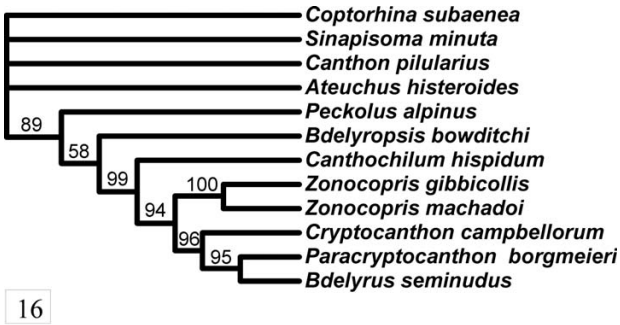
The possibility that *Zonocopris gibbicollis* larvae feed on dead snails, was not examined. However, in that case, an extremely long adult stage could be expected because of the snails longevity and the apparently unharmfullness of the relationship with the beetles for the snail.

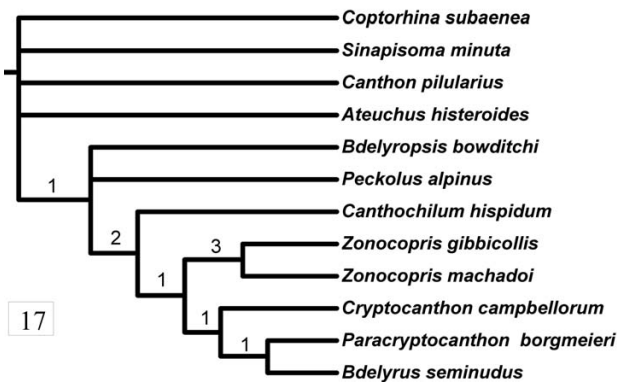
Acknowledgements. This work is part of the author's Ph.D. thesis in Systematics, at the Instituto de Ecología A. C., Xalapa, Mexico, thanks to a Capes grant (BEX 1208020). I thank Gonzalo Halffter, Juan José Morrone, Mario Zunino, Alejandro Espinosa de los Monteros and Esther Quintero for reading the manuscript and making valuable comments. François Génier was partly responsible for an enthousiastic discussion on the subject. Gustavo Schiffler, Ângelo Machado, Rodrigo Lopes Ferreira, Eurides Furtado and the curators cited in the Methods section provided me with important specimens. Júlio Louzada, Renato Gregorin and Léa Schurter helped me maintain the *Zonocopris* terrarium in Lavras and provided me a place for





Figures 14–15
14, tree 5 of five most-parsimonious trees, length = 40 , consistency index = 0.57 and retention index = 0.68; **15**, strict consensus of five most parsimoniuos trees.





Figures 16-17.
16, majority consensus resulted from 119 trees found by modified Bootstrap (see text), bootstrap values shown for each clade; **17**, Bremer support (decay index) values found for clades of strict consensus tree.

it. Joe Kirkbride, Denis Keith and Johannes Frisch indicated and provided important literature. Efraín de Luna provoked an interesting discussion of a first analysis of phylogenetic data presented here, and Esther Quintero (again) and Daniel Curoe revised the English manuscript.

References

Arrow G.J. 1932. New species of lamellicorn beetles (subfam. Coprinae) from South America. *Stylops* **1**: 223-226.

Bacchus M.E. 1978. A catalogue of the type-specimens of the Scarabaeinae (Scarabaeidae) and the smaller lamellicorn families (Coleoptera) described by G.J. Arrow. *Bulletin of the British Museum of Natural History. (Ent.)* **37**(3): 97-115.

Balthasar V. 1939. Eine Vorstudie zur Monographie der Gattung *Canthon* Hfsg. *Folia Zoologica et Hydrobiologica* **9**: 179-238.

Balthasar V. 1942. Neue Scarabaeiden aus Süd-Amerika. *Časopis Československé Společnosti Entomologické* **29**: 36-44.

Balthasar V. 1963. *Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region*. Band 1. Verlag der Tschechoslowakischen Akademie der Wissenschaften, Praha.

Blackwelder R.E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, part 2, Scarabaeoidea. *United States National Museum Bulletin* **185**: 189-265.

Burmeister H.C.C. 1873. Lamellicornia Argentina. *Stettiner Entomologische Zeitung* **34**: 403-417

Cambefort Y. 1991a. From Saprophagy to Coprophagy, p. 22-35 *in*: **Hanski I., Cambefort Y. (eds.)** *Dung Beetle Ecology.* Princeton University Press.

Cambefort Y. 1991b. Biogeography and Evolution, p. 51-67 *in*: **Hanski I., Cambefort Y. (eds.)** *Dung Beetle Ecology.* Princeton University Press.

Cook J. 1998. A revision of the Neotropical genus *Bdelyrus* Harold (Coleoptera: Scarabaeidae). *The Canadian Entomologist* **130**: 631-689.

Cook J. 2002. A revision of the Neotropical genus *Cryptocanthon* Balthasar (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopterists Society Monographs* **1**: 1-96.

Génier F., Kohlmann B. 2003. Revision of the Neotropical dung beetle genera *Scatimus* Erichson and *Scatrichus* gen. nov. (Coleoptera: Scarabaeidae: Scarabaeinae). *Fabreries* **28**(2): 57-111.

Gill B.D. 1991. Dung beetles in tropical American forests, p. 211-219 *in*: **Hanski I., Cambefort Y. (eds.)** *Dung Beetle Ecology.* Princeton University Press.

Gillet J. J. E. 1933. Lamellicornes Coprophages (Coléopt.) *Bulletin et Annales de la Société Entomologique de Belgique* **72**(11-12): 323-332

Goloboff P. 1993. *Nona ver. 2.0*. Software y documentación.

Halffter G., Martínez A. 1977. Revisión monográfica de los Canthonina americanos. IV Parte. Clave para géneros y subgéneros. *Folia Entomológica Mexicana* **38**: 29-107.

Halffter G., Edmonds W.D. 1982. *The nesting behavior of dung beetles (Scarabaeinae): an ecological and evolutive approach.* Instituto de Ecología, A.C., México.

Halffter G., Matthews E. 1966. The natural history of dung beetles of the subfamily Scarabaeinae. *Folia Entomológica Mexicana* **12-14**: 1-312.

Hanski I., Cambefort Y. 1991. *Dung Beetle Ecology*. Princeton University Press.

Harold E. von. 1868. Monographie der Gattung *Canthon*. *Berliner Entomologische Zeitschrift* **12**: 1-144.

Howden H.F. 1973. Revision of the New World genus *Cryptocanthon* Balthasar (Coleoptera: Scarabaeidae). *Canadian Journal of Zoology* **51**: 39-48.

Howden H.F., Cook J. 2002. *Paracryptocanthon*, a new canthonine genus from Brazil (Coleoptera: Scarabaeidae: Scarabaeinae). *The Coleopterists Bulletin* **56**: 585-588.

Kolbe H.J. 1905. Über die Lebensweise und die geographische Verbreitung der coprophagen Lamellicornien. *Zoologische Jahrbücher, Supplement* **8**: 475-594.

Martínez A. 1947. Addenda y corrigenda al trabajo de Blackwelder "Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America" (Scarabaeidae, Coprinae). *Arthropoda* **1**: 109-114.

Martínez A. 1959. Catalogo de los Scarabaeidae argentinos (Coleoptera). *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* **5**: 1-123.

Martínez A. 1987. La entomofauna de Scarabaeinae de la provincia de Salta (Col. Scarabaeoidea). *Anales de la Sociedad Científica Argentina* **1987**: 45-69.

Matthews, E.G. 1974. A revision of the Scarabaeine dung beetles of Australia. II. Tribe Scarabaeini. *Australian Journal of Zoology Supplementary Series* **24:** 1-211.

Papavero N. 1973. *Essays on the history of Neotropical dipterology*, vol. II. Museu de Zoologia, Universidade de Sao Paulo.

Paulian R. 1938. Contribution à l'étude des Canthonides américains (Coleopt. Lamellic.). *Annales de la Société Entomologique de France* **107**: 213-295.

Paulian R. 1939. Contribution à l'étude des Canthonides américains (Coleopt. Lamellic.) (suite et fin). *Annales de la Société Entomologique de France* **108**: 1-40.

Pereira F.S. 1946. Escarabeideos Americanos, p. 289-294 *in*: **Sociedade Brasileira de Entomologia (ed.).** *Livro de Homenagem a Romualdo Ferreira d'Almeida*. São Paulo, Imprensa Oficial do Estado.

Pereira F.S., Martínez A. 1956. Os gêneros de Canthonini Americanos. *Revista Brasileira de Entomologia* **6**: 91-192.

Stein F. 1867. Ueber die Eigenthümlichkeiten einiger brasilianischer Käferarten. *Berliner entomologische Zeitschrift* **11**: 211-212.

Vaz-de-Mello F.Z. 2000. Estado de conhecimento dos Scarabaeidae do Brasil. p. 183-195 *in*: **Martín-Piera F., Morrone J.J., Melic A. (ed.)** *Hacia un proyecto CYTED para el inventário y estimación de la diversidad en Iberoamérica: PRIBES 2000*. Zaragoa, SEA.

Vaz-de-Mello F.Z., Halffter G. 2006. A new dung beetle genus with two new species from Chile (Coleoptera: Scarabaeidae: Scarabaeinae). *Zootaxa* **1193**: 59-68.

Vulcano M.A., Pereira F.S. 1964. Catalogue of the Canthonini inhabiting the Western Hemisphere. *Entomologische Arbeiten aus der Museum Georg Frey* **15**: 570-685.

Appendix

Character list

0. Ventral clypeal process: 0. rounded or directed downward; 1. dentiform and foreward directed.

1. Ventral clypeal process: 0. located posteriorly; 1. located beneath clypeal emargination.

2. Dorsal ocular area: 0. not narrowed posteriorly; 1. narrowed posteriorly.

3. Labial basipalpomere: 0. cylindrical; 1. flattened.

4. Hypomeron anteriorly: 0. distinctly excavated; 1. not excavated.

5. Mesosternal lateral foveae: 0. absent; 1. present.

6. Pseudoepipleura: 0. without longitudinal carinae; 1. with longitudinal carina(e).

7. Seta on elytra: 0. absent; 1. present.

8. Elytral lateral carina just external to 7th stria: 0. absent; 1. present.

9. Anterior trochantofemoral pit: 0. absent; 1. present.

10. Apical internal pretibial angle in males: 0. simple; 1. toothed.

11. Ventro-external longitudinal metatibial setose ridge: 0. absent; 1. present; 2. setose only, without ridge.

12. Metatibial apex ventrally: 0. simple; 1. emarginated.

13. Metatibial basitarsomere: 0. shorter or subequal to next tarsomere; 1. longer than next tarsomere but less than twice; 2. more than twice the length of the next tarsomere.

14. Medium and hind tibia: 0. apically expanded (both internal and external borders divergent); 1. not expanded apically.

15. Metatibial ventro-external disc: 0. posteriorly glabrous; 1. covered with setae.

16. Supraunguicular spine: 0. absent; 1. present.

17. Pygidium position: 0. vertical; 1. horizontal.

18. Basal pygidial sulcus: 0. absent; 1. present.

19. Size of paramera in relation to phallobase: 0. smaller than 1/2; 1. larger than 1/2.

20. Parameral axis in relation to phallobase: 0. distinctly angled; 1. not angled.