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Revision of the South American genera *Andinocopris* new genus and *Homocopris* Burmeister, 1846 (Coleoptera: Scarabaeidae: Scarabaeinae: Homocoprini new tribe)

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Abstract. Although initially described as a subgenus of *Copris* Geoffroy, 1762, *Homocopris* had long been treated as a junior synonym of *Dichotomius* Hope, 1838 (Martínez 1951) until it was reclassified as a distinct genus (Vaz-de-Mello *et al.* 2010). Herein, we revisit the taxonomy of *Homocopris*. In doing so: we describe two new species previously considered to represent the Brazilian population of *Homocopris torulosus* (Eschscholtz, 1822); revalidate *Pinotus punctatissimus* from synonymy under *Homocopris torulosus* and place it in *Homocopris* as had previously been done only informally (González *et al.* 2015; Rebolledo *et al.* 2017); recognize two new synonymies; and describe a new genus, *Andinocopris* gen. nov., which includes two former members of *Homocopris*. Presently, *Homocopris* includes four species: *H. torulosus*, *H. punctatissimus* (Curtis, 1845) comb. nov., *H. grossiorum* sp. nov. and *H. williami* sp. nov. *Andinocopris* includes *A. achamas* (Harold, 1867) gen. et comb. nov. and *A. buckleyi* (Waterhouse, 1891) gen. et comb. nov. *Pinotus simulator* Luederwaldt, 1936 is here considered a new junior synonym of *Andinocopris buckleyi*. An identification key to members of both genera is provided as well as images of diagnostic characters for all species. Finally, we discuss the placement of *Andinocopris* and *Homocopris* within Scarabaeinae and propose a new tribe, Homocoprini tribe nov., to include both genera.

Keywords. Dung beetles, Neotropical, systematics.

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Introduction

Homocopris Burmeister, 1846 is a South American dung beetle genus that was initially established as a subgenus of *Copris* Geoffroy, 1762 to accommodate a single Chilean species, *C. torulosus* Eschscholtz, 1822. Burmeister made no mention of the similar *C. punctatissimus* Curtis, 1845 in his

subgenus description. This is likely because he was unaware of the species, which had been described just a year earlier and would eventually be synonymized with *C. torulosus* by Solier (1851). Harold (1869a) synonymized the subgenus *Homocopris* with *Pinotus* Erichson, 1847, and Martínez (1951) later recognized the priority of *Dichotomius* Hope, 1838 over *Pinotus*, thereby designating *Homocopris* as a junior synonym of *Dichotomius*. Vaz-de-Mello *et al.* (2010) revalidated and elevated *Homocopris* to the rank of a distinct genus based on several distinguishing characters: a keel-like ventral clypeal process; a supplemental lateral pronotal carina located above the pronotum-hypomeron carina; a flattened, apically truncated metatibial spur; and a medial lamella-copulatrix-like endophallite. Vaz-de-Mello *et al.* (2010) included three species in *Homocopris*: *H. achamas* (Harold, 1867), *H. buckleyi* (Waterhouse, 1891) and *H. torulosus*. However, there are three other species that share the diagnostic characters of *Homocopris* outlined above. These species are *Copris punctatissimus*, *Pinotus simulator* Luederwaldt, 1936 and *P. dahli* Landin, 1955. *Copris punctatissimus* has even been referred to as "*H. punctatissimus*" by some authors in recent years (i.e., González *et al.* 2015; Rebolledo *et al.* 2017) despite the fact that the species has yet to be formally transferred from *Copris* to *Homocopris* and revalidated. As for *D. dahli* and *D. simulator*, the species are only represented in literature by their original descriptions, and the type material of both species is limited to a few specimens.

Homocopris in its former sense is generally associated with high-elevation cloud forest and occurs in three widely separated regions across South America. *Homocopris achamas* and *H. buckleyi* occur in the northern Andes, with *H. achamas* occupying Colombia and northern Ecuador, and *H. buckleyi* occupying southern Ecuador and northern Peru. *Homocopris* then reappears along the Andean Mountain range in southern Chile, where it is represented by *H. torulosus*. It is worth noting that *D. punctatissimus* and *D. dahli* both occur in this portion of the putative range of *H. torulosus*. The other portion is, strikingly, associated with the Serra da Mantiqueira, Serra do Mar, and Serra Geral Mountain ranges in southeastern and southern Brazil. Given the total absence of *H. torulosus* throughout Paraguay, Uruguay and virtually all of Argentina, it seems unlikely that gene flow is ongoing between the Chilean and Brazilian populations.

Considering the disparate populations of *H. torulosus* and the lack of literature addressing the taxonomy of *D. punctatissimus*, *D. dahli* and *D. simulator*, we consider a revision of *Homocopris* to be necessary despite its relatively recent re-classification. After an examination of morphological and geographic variation within and between each species in question, we propose that: (1) the supposed Brazilian population of *H. torulosus* in fact represents two new species, which we describe as *H. grossiorum* sp. nov. and *H. williami* sp. nov. (2) *Copris punctatissimus* is a valid species and should be transferred from *Dichotomius* to *Homocopris*, as it shares several seemingly synapomorphic characters with the type species of *Homocopris*, *H. torulosus*. (3) *Dichotomius dahli* and *D. simulator* represent synonyms of *H. torulosus* and *H. buckleyi*, respectively. (4) *Homocopris achamas* and *H. buckleyi* be transferred from *Homocopris* to a new genus, *Andinocopris* gen. nov., as the two species exhibit unique characters that are not observed in *H. torulosus*, nor any other New World scarabaeines. In its new sense, *Homocopris* includes four species: *H. torulosus*, *H. punctatissimus* comb. nov., *H. grossiorum* and *H. williami*. Finally, *Andinocopris* is proposed as a new genus for *A. achamas* gen. et comb. nov. and *A. buckleyi* gen. et comb. nov.

Material and methods

Specimens were examined with a Wild M-5 stereo microscope under a white light-emitting diode ring lamp. Aedeagi of types and selected individuals were dissected, cleaned in a solution of 20% potassium hydroxide and glued to a card paper point. The endophallus was extracted from the phallobase and non-chitinous tissue cleaned in 20% potassium hydroxide then cut open to set each of the endophallite flat to ease comparison and compare diagnostic features associated with the endophallites. Sacs and endophallites were embedded in water and alcohol-soluble dimethylhydantoin formaldehyde resin (DMHF) on a piece of white card. We illustrated the frontolateral peripheral endophallite (abbreviated

FLP in the text) for each species as its shape is diagnostic and easily comparable between species. To examine the hindwing venation and internal characters, certain specimens representing each species were disarticulated. Hindwings were mounted in DMHF on white card and pressed with glass coverslips. Sectioned body parts were stored in vials of 70% ethanol.

Specimen metadata was compiled and input into the World Scarab Database (WSD) powered by Mantis ver. 2.9 (Naskrecki 2021). Geographic data were exported from this database and used to generate specimen distribution maps in SimpleMappr (Shorthouse 2010). Images of the specimens were captured using the digital multi-focus system of a Leica Z16 APO A microscope and DFC 495 camera or a Leica Z16 APO microscope and DMC 5400 camera. Images were stacked with LAS software ver. 4.9 and 4.13.

The text of the labels of name-bearing types is recorded verbatim, each label text is set between double quotation marks (“”), using square brackets ([]) to distinguish data that has been interpreted from a label and vertical lines (|) separate each text line. This information is followed by a description of the media for each label; if no indications are given, the label is printed on white card paper. Coordinates in square bracket ([]) are inferred. The methods and format used here are detailed in Génier & Moretto (2017). The terminology for wing venation follows Kukalova-Peck & Lawrence (2004) and abbreviations used here are plotted on Fig. 64:

AA = anal anterior vein
AP = anal posterior vein
CU = cubital vein
J = jugal vein
RA = radial anterior vein
RP = radial posterior vein

This revision is based on an examination of 861 specimens borrowed from the museums and private collections listed below. Curators and individuals who assisted in providing material are gratefully acknowledged. Initialisms used in the text were taken from Evenhuis (2007) or were generated ad hoc if missing there.

AMNH = American Museum of Natural History, New York, NY, USA; Lee Herman
BDGC = Bruce D. Gill personal collection, Woodlawn, Ontario, Canada
BMNH = The Natural History Museum (formerly British Museum, Natural History), London, UK; Maxwell Barclay
CAS = California Academy of Sciences, San Francisco, CA, USA; Chris Grinter
CEMT = Seção de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil; Fernando Z. Vaz-de-Mello
CMD = Michaël Dierkens personal collection, Lyon, France
CMNC = Canadian Museum of Nature, Natural Heritage Campus, Gatineau, Quebec, Canada
CNC = Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada; Pat Bouchard, Serge Laplante
CPFA = Patrick Arnaud personal collection, Saintry-sur-Seine, Essonne, France
GHCM = Gonzalo Halffter personal collection, Xalapa, Mexico
MNHN = Muséum national d’histoire naturelle, Paris, France; Olivier Montreuil, Antoine Mantilleri
MZLU = Lund University, Lund, Sweden; Roy Danielsson
MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil; Carlos Campaner
NMPC = National Museum (Natural History), Prague, Czech Republic; Jiří Hájek
PMOC = Philippe Moretto personal collection, Toulon, Var, France

For uniformity, we have used the spelling Luederwalt as opposed to Lüdewaldt throughout the text unless it was transcribed verbatim from a label.

Results

Phylum Arthropoda von Siebold, 1848
Subphylum Hexapoda Blainville, 1816
Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Scarabaeoidea Latreille, 1802
Family Scarabaeidae Latreille, 1802
Subfamily Scarabaeinae Latreille, 1802
Tribe Homocoprini trib. nov.

Genus ***Andinocopris*** gen. nov.
urn:lsid:zoobank.org:act:DB47A9F1-784F-4431-A7AA-2044987EF94D

Type species

Pinotus achamas Harold, 1867, present designation.

Differential diagnosis

Dorsal ocular width greater than one quarter of interocular distance. Lateral pronotal carina and pronotal edge joined anteriorly and posteriorly, forming closed ellipse. Pronotal armament in the form of an overhanging ridge or bifurcating projection in large individuals of both sexes. Elytral stria 8 usually absent, remnant present on apical elytral hump and connected to stria five in some individuals of *A. achamas* (Fig. 62). Meso-metasternal suture posteriorly arcuate (Fig. 60). ♂ FLP endophallite sigmoidal, abruptly narrowing and inflecting medially (Figs 31–32).

Etymology

Andinocopris is a combination of the New Latin adjective '*andinus*' and the Ancient Greek noun 'κόπρος' ('*kópros*'). The former refers to the Andes, where the genus occurs at high elevations from Colombia to Peru, and the latter refers to its association with dung.

Description

Body length 20–34 mm. Anteroventral clypeal tooth, rather small, transverse and varying from truncated to acute in frontal view. Dorsal ocular width greater than one-quarter interocular distance. Anterior pronotal edge straight (*A. achamas*) or slightly sinuous (*A. buckleyi*) medially. Anterior pronotal membrane very wide laterally, transition between membrane and anterior edge of pronotum ill-defined medially. Anteromedial pronotal surface smooth. Lateral pronotal carina and pronotal edge joined anteriorly and posteriorly, forming closed carinated ellipse. Pronotal armament in large individuals of both sexes forming overhanging ridge or bifurcating projection; ventral surface of overhanging armament uneven. Anterior apex of prosternum broadly rounded. Underside of elytron with long semi-erected setae. Elytral stria 8 usually absent, remanent present on apical elytral hump and connected to stria five in some individuals of *A. achamas*. Hindwing with AP reduced (Figs 39–40). Meso-metasternal suture posteriorly arcuate (Fig. 60). Surface of median metasternal lobe convex, some individuals with shallow and narrow longitudinal sulcus; surface setigerous anterolaterally, impunctate or finely punctate throughout. Pygidial surface finely punctate. ♂ paramere tapering slightly in lateral view; apex blunt. FLP endophallite sigmoidal, narrowing and inflecting centrally.

Distribution

Colombia, Ecuador, Peru.

Andinocopris achamas (Harold, 1867) gen. et comb. nov.
Figs 1–2, 13–14, 25, 31, 39, 46, 50, 60, 62, 65

Pinotus Achamas Harold, 1867: 99 (original description).

Pinotus Achamas — Harold 1869a: 130 (monograph); 1869b: 1009 (catalogue); 1880: 24 (distribution). — Gillet 1911: 59 (catalogue).
[*Pinotus*] *Achamas* – Heyne 1900: 62 (diagnosis, distribution).
Pinotus (*P.*) *Achamas* – Luederwaldt 1929: 634; 1936: 207 (diagnosis, comment).
Pinotus achamas – Blackwelder 1944: 206 (checklist).
Dichotomius achamas – Amat *et al.* 1997: 195 (faunistic). — Escobar 2000: 208 (faunistic). — Medina *et al.* 2001: 138 (faunistic). — Pulido *et al.* 2007: 307 (faunistic).
Homocopris achamas – Vaz-de-Mello *et al.* 2010: 192 (new combination). — Martínez & Lopera 2014: 66 (faunistic). — Moreno & Molano 2016: 68 (ecology, faunistic). — Chamorro *et al.* 2018: 96 (distribution); 2019: 158 (catalogue, faunistic). — Casas *et al.* 2021: 321 (ecology).

Differential diagnosis

Body length 22–34 mm. Dorsal ocular width greater than one quarter of interocular distance. Lateral pronotal carina and pronotal edge joined anteriorly and posteriorly, forming closed ellipse. Pronotal ridge prominently projected in large individuals of either sex. Interstriae flat, minutely punctate. Meso-metasternal suture posteriorly arcuate. Visible abdominal ventrites 1–4, 6 laterally setose; ventrite 5 setose throughout. ♂ cephalic horn emerging from anterior clypeal surface, wide and gently tapering in anterior view, appearing flattened and curved in lateral view, length never exceeding maximum clypeal width.

Name-bearing type data

Lectotype ♂ (MNHN) (Fig. 50): "Achamas | Buq." [handwritten on green paper]; "Columbia | *P.* | *Achamas* | Harold" [Harold's handwriting on white paper with red border]; "Museum Paris | ex. Coll. | R. Oberthur" [on green card]; "WORLD | SCARAB. | DATABASE | WSD00035019" [barcode label]; "LECTOTYPE ♂ | *Pinotus* | *achamas* | Harold, 1867 | des. Génier & Darling, 2018" [red card]; "*Andinocopris* | *achamas* | (Harold, 1867) | det. Génier & Darling, 2018". Present designation.

Type locality

Colombia ("Columbia").

Type material

Lectotype (present designation)
COLOMBIA • ♂ (Fig. 50); "Achamas | Buq." [handwritten on green paper]; "Columbia | *P.* | *Achamas* | Harold" [Harold's handwriting on white paper with red border]; "Museum Paris | ex. Coll. | R. Oberthur" [on green card]; "WORLD | SCARAB. | DATABASE | WSD00035019" [barcode label]; "LECTOTYPE ♂ | *Pinotus* | *achamas* | Harold, 1867 | des. Génier & Darling, 2018" [red card]; "*Andinocopris* | *achamas* | (Harold, 1867) | det. Génier & Darling, 2018"; MNHN.

Paralectotypes (5 ♂♂, 5 ♀♀)
COLOMBIA • 1 ♀; [unspecified locality]; [no date]; Lebas; MNHN • 1 ♀; Bogotá; [4°39′ N, 74°5′ W]; [no date]; von Kirsch; MNHN • 2 ♂♂, 1 ♀; same locality as for preceding; [no date]; [anonymous]; MNHN • 3 ♂♂, 2 ♀♀ (one of them alloreferent); [no date]; [anonymous]; MNHN.

Other material examined (79 ♂♂, 79 ♀♀)

COLOMBIA • 24 ♂♂, 23 ♀♀; [unspecified locality]; [no date]; [anonymous]; MNHN • 3 ♂♂, 1 ♀; [unspecified locality]; [no date]; Hogue; MNHN • 4 ♂♂, 7 ♀♀; [unspecified locality]; [no date]; Felipe Ovalle Q.; AMNH • 1 ♂; same collection data as for preceding; CMNC. – **Boyacá** • 1 ♂, 1 ♀; Iguaque, Villa de Leiva; [5°40′ N, 73°28′ W]; 2800 m; 17 Jun. 1996; V. Malý; BDGC • 1 ♀; Muzo; [5°32′ N, 74°6′ W]; [no date]; [anonymous]; CPFA. – **Cauca** • 1 ♀; 11 mi E of Silvia; [2°40′30″ N, 76°18′00″ W]; 3048 m; 15 Jul. 1970; H. & A. Howden; CMNC • 1 ♂; 12 km E of Silvia; [2°36′50″ N, 76°17′20″ W]; 3048 m; 15 Jul. 1970; J.M. Campbell; CNC • 1 ♀; 12 mi E of Silvia; [2°41′ N, 76°17′ W]; 3353 m; 16 Jul. 1970; H. and A. Howden; CNC • 1 ♀; 15 mi E of Silvia; [2°41′ N, 76°15′ W]; 3962 m; 16 Jul. 1970; H. and A. Howden; CMNC • 1 ♀; 16 km E of Silvia; [2°35′30″ N, 76°16′0″ W]; 2743 m; 22 Feb. 1970; H. Howden; CMNC • 2 ♂♂, 3 ♀♀; Popayán; [2°26′ N, 76°37′ W]; 1899; Abbé Gaujon; MNHN • 1 ♂, 1 ♀; Termales de San Juan de Pilimbalá, Parque Nacional Natural Puracé; [2°20′25″ N, 76°18′48″ W]; 3 Apr. 1972; Bordón; CMD • 1 ♂, 2 ♀♀; same locality as for preceding; 4 Jun. 1972; Bordón; BDGC. – **Cundinamarca** • 1 ♂; El Colegio; [4°34′51″ N, 74°26′33″ W]; 25 Mar. 1976; F. Chalumeau; CMNC • 1 ♂; same collection data as for preceding; MNHN • 1 ♀; El Tabuzo, Subachoque; [4°56′ N, 74°10′ W]; 2700 m; 15 Apr. 1995; A. Lopera; BDGC • 2 ♀♀; Fusagasugá; [4°21′ N, 74°22′ W]; [no date]; [anonymous]; CPFA • 1 ♂, 2 ♀♀; same collection data as for preceding; MNHN • 1 ♂; Girardot; [4°25′ N, 74°45′ W]; 29 Oct. 1969; A. Pouliquen; MNHN • 1 ♂; La Aguadita; [4°23′ N, 74°19′30″ W]; 1524 m; 7 Jul. 1970; H. and A. Howden; CMNC • 1 ♂; La Mesa; [4°37′45″ N, 74°27′40″ W]; [no date]; [anonymous]; MNHN • 1 ♀; Salto del Tequendama; [4°36′22″ N, 74°21′1″ W]; 27 Feb.–6 Mar. 1972; S. and J. Peck; forest, dung trap; CMNC • 3 ♂♂, 2 ♀♀; Sopó; [4°53′30″ N, 73°57′30″ W]; 2800 m; Sep. 1972; Martínez; CMNC • 1 ♂; Tequendama; [4°34′30″ N, 74°17′30″ W]; 2438 m; 6 Jul. 1970; H. and A. Howden; CMNC. – **Distrito Capital** • 3 ♂♂, 2 ♀♀; 12 mi S of Bogotá; [4°23′20″ N, 74°8′34″ W]; 3048 m; 28 Feb.–6 Mar. 1972; S. and J. Peck; *Eucalyptus* plantation, dung trap; CMNC • 3 ♂♂; same collection data as for preceding; CNC • 2 ♂♂, 3 ♀♀; above Bogotá; [4°39′ N, 74°5′ W]; 3048 m; 1877; O. Thieme; MNHN • 1 ♂; Bogotá; [4°39′ N, 74°5′ W]; 1877; O. Thieme; MNHN • 1 ♀; same locality as for preceding; 1914; E. Pehlke S.; NMPC • 2 ♂♂, 2 ♀♀; same locality as for preceding; [no date]; [anonymous]; CNC • 3 ♂♂, 1 ♀; same locality as for preceding; [no date]; [anonymous]; CPFA • 9 ♂♂, 10 ♀♀; same locality as for preceding; [no date]; [anonymous]; MNHN • 1 ♂; same locality as for preceding; [no date]; [anonymous]; NMPC • 1 ♀; same locality as for preceding; 1 Apr. 1928; T. Hallinan; AMNH • 1 ♂; Bogotá; [4°39′ N, 74°5′ W]; 2865 m; 10 Oct. 1937; T. Hallinan; AMNH. – **Huila** • 1 ♀; Volcán Puracé; [2°15′ N, 76°21′ W]; 3400 m; 20 Nov. 1971; Bordón; CMNC. – **Meta** • 2 ♀♀; Villavicencio; [4°9′38″ N, 73°39′43″ W]; [no date]; [anonymous]; CPFA • 1 ♂; same locality as for preceding; 1–26 May 1945; L. Richter; AMNH. – **Norte de Santander** • 1 ♂; 12 km S of Pamplona; [7°18′ N, 72°36′ W]; 3000 m; 9–13 May 1974; S. Peck; dung trap; CMNC • 1 ♀; same locality as for preceding; 9–13 May 1974, S. Peck; CNC • 1 ♂; same locality as for preceding; 9 May 1974; H. and A. Howden; CMNC • 1 ♀; 14 km SW of Pamplona; [7°25′30″ N, 72°42′0″ W]; 3500 m; 25 May 1974; H. and A. Howden; CMNC • 1 ♂, 1 ♀; Pamplona; [7°22′30″ N, 72°38′50″ W]; Apr. 1920; P. Rochereaux; MNHN • 1 ♂; Pamplona; [7°22′30″ N, 72°38′50″ W]; 2300 m; 1921; P. Rochereaux; MNHN. – **Tolima** • 1 ♂; Honda; [5°12′ N, 74°44′ W]; [no date]; [anonymous]; CPFA • 1 ♂; Ibaqué; [4°26′N, 75°14′W]; [no date]; [anonymous]; MNHN. – **Valle del Cauca** • 1 ♂; Las Cruces; [3°30′ N, 76°40′ W]; [no date]; Maquanal; MNHN • 1 ♂, 1 ♀; Santiago de Cali; [3°25′ N, 76°31′ W]; [no date]; [anonymous]; MNHN.

ECUADOR – **Carchi** • 2 ♀♀; Tulcán; [0°47′ N, 77°43′ W]; Nov. 1996; S. Pokorný; NMPC.

Description

Male lectotype (Figs 1, 13, 46)

Measurements. Body length 23.4 mm.

Figs 1–4. Dorsal habitus. **1**. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov., lectotype, ♂ (MNHN). **2**. *Andinocopris achamas*, alloreferent paralectotype, ♀ (MNHN). **3**. *Andinocopris buckleyi* (Waterhouse, 1891) gen. et comb. nov., specimen ♂ (MNHN). **4**. *Andinocopris buckleyi*, specimen ♀ (MNHN).

Head. Clypeal edge lacking teeth, slightly sinuous medially. Anteroventral clypeal tooth acute. Clypeal and genal surface rugose, clypeogenal suture well defined throughout. Posterior genal angle obtuse. Frons broad with shallow, irregular excavations. Dorsal ocular width greater than one-quarter interocular distance. Interocular surface smooth posteromedially. Cephalic horn emerging from anterior clypeal surface, wide and gently tapering in anterior view, appearing flattened and curved in lateral view, posteriorly merging with frontal surface, 6.1 mm in length (measured from horn apex to base of eye).

Prothorax. Carina along anterior pronotal edge broad medially, narrowing laterally. Anterolateral pronotal lobe smooth, sectioned posteriorly by abrupt shelf. Lateral pronotal carina and pronotal edge distinctly forking anteriorly then merging posteriorly, forming closed elongate carinated ellipse. Pronotal surface smooth anteriorly, transitioning posterolaterally into chagrined texture. Centrally raised ridge with lateral tubercles and sheer vertical anterior surface defined by uneven, rippled texture. Propleuron and prosternum broadly setose; with long (~2 mm) rufous setae. Anterior prosternal apex rounded.

Elytra (Fig. 46). Matt overall. Striae 1–6 widest anteriorly; narrowing posteriorly. Eighth stria absent on lateral declivity, exclusively appearing along posterior declivity. Ninth stria effaced along anterior quarter of elytral length. Interstriae flat, minutely punctate.

Hindwing (Fig. 39). Membrane edge between AP and AA sinuous. AP vein reduced.

Ventrites. Meso-metasternal suture posteriorly arcuate (Fig. 60). Surface of median metasternal lobe broadly smooth and convex, with lateral setigerous punctation and shallow median sulcus. Lateral metasternal lobe densely setose. Visible abdominal ventrites 1–4, 6 laterally setose; ventrite 5 setose throughout. Pygidium finely punctate.

Prothoracic legs. Anterior and posterior surfaces of profemur with dense row of long setae. Ventral profemoral surface finely punctate, lacking setae. Protibia with three distinct teeth, proximal one indistinct. Protibial forespur straight; apex slightly tapering inward.

Mesothoracic legs. Posterior surface of mesotrochanter with dense tuft of long rufous setae. Anterior and posterior surfaces of mesofemur with dense row of long rufous setae. Outer surface of mesotibia serrate. Width at mesotibial apex one-third mesotibial length.

Metathoracic legs. Posterior surface of metatrochanter with dense tuft of long rufous setae. Anterior and posterior edges of metafemur with dense row of long rufous setae. Outer edge of metatibia serrate. Width at metatibial apex one-quarter metatibial length.

Male genitalia. Aedeagus missing from lectotype. Description of male genitalia based on a similarly developed Colombian male specimen collected from an unspecified locality by Felipe Ovalle, Q (Ac. 33501) deposited in the CMNC (specimen ID = WSD00035003). Aedeagus length: 5.5 mm. Medially and laterally paired endophallite of genital segment broad, contiguous. Paramere (Fig. 25) horizontally flattened, gently tapered, apex broad and slightly inclined. FLP endophallite (Fig. 31) sigmoidal; broad distally, narrowing and inflecting centrally.

Female alloreferent (paralectotype MNHN) (Figs 2, 14)

Similar to male lectotype with the following exceptions: body length 24.5 mm. Cephalic horn low, truncated, 3.1 mm in length. Anterolateral pronotal lobe surface feebly granulate, continuous with lateral pronotal surface. Central pronotal ridge prominently overhanging, with deep anterior excavation. Posterolateral and posterior pronotal surface uniformly granulate.

Variation

Body length 18–34 mm. Cephalic horn minute and conical in females and small males. Central pronotal ridge atrophied and slightly overhanging in poorly developed specimens of either sex. Elytra matt to glossy overall.

Distribution (Fig. 65)

High elevation (2300–3960 m) in the Colombian and northern Ecuadorian Andes.

Natural history

No data except for a single specimen collected in an unspecified type of forest and eight specimens collected in a *Eucalyptus* L'Hér. plantation, all using dung traps.

Remarks

Despite the similarities between *Andinocopris achamas* and *A. buckleyi* (i.e., genital structure), the unique armament and body size of *A. achamas* distinguishes it from both *Homocopris* and *A. buckleyi*.

Andinocopris buckleyi (Waterhouse, 1891) gen. et comb. nov.
Figs 3–4, 15–16, 26, 32, 40, 42, 51, 65

Pinotus Buckleyi Waterhouse, 1891: 359 (original description).
[*Pinotus*] *simulator* Luederwaldt, 1936: 209 (original description).

Pinotus Buckleyi – Gillet 1911: 59 (catalogue).
Pinotus (*P.*) *Buckleyi* – Luederwaldt 1929: 652 (monograph).
Pinotus (*P.*) *buckleyi* – Luederwaldt 1936: 208 (diagnosis, distribution).
Pinotus buckleyi – Blackwelder 1944: 206 (checklist).
Dichotomius simulator – Vulcano & Pereira 1967: 584 (distribution, identification key).
Homocopris buckleyi – Vaz-de-Mello *et al*. 2010: 192 (new combination). — Chamorro *et al.* 2018: 96 (distribution); 2019: 159 (catalogue, faunistic).
Dichotomius buckleyi – Saavedra *et al.* 2017: 111 (faunistic).

Differential diagnosis

Body length 15–20 mm. Dorsal ocular width greater than one quarter of interocular distance. Lateral pronotal carina and pronotal edge distinctly forking anteriorly then merging posteriorly, forming a closed carinated ellipse. Interstriae convex and impunctate. Meso-metasternal suture posteriorly arcuate. Visible abdominal ventrites laterally setose. ♂ cephalic horn emerging centrally from clypeofrontal surface, parallel-sided with horizontal apex, curved throughout, flattened apically and length up to twice the interocular distance.

Name-bearing type data

Pinotus buckleyi Waterhouse: holotype ♂ (BMNH) (Fig. 51): "Chiguin | -da | 80.14" [handwritten]; "Type" [white disc with red border]; "*Pinotus* | *Buckleyi* | (Type) Waterh." [handwritten].

Pinotus simulator Luederwaldt: holotype, by monotypy, ♂ (BMNH) (Fig. 56): "Amazon"; "Degand"; "17140" [handwritten]; "Fry Coll. | 1905-100"; "*Copr*. | *simulator*" [handwritten]; "*Pinotus* ♀ | *Buckleyi* Wat.? | illegible | Lüderw. det. 1934" [Luederwaldt's handwriting]; "HOLOTYPE" [black border on red card]; "WORLD | SCARAB. | DATABASE | WSD00001803" [barcode label]; "*Homocopris* | *buckleyi* ♂ | dét. F. Génier, 2008" [partly handwritten]; "*Pinotus* Holot | *simulator* Lued. | des. F.Vaz-de-Mello,

2011" [partly handwritten]. The number '17140 corresponds in Fry's notebooks in BMNH to 'Copris, Brazil, Upper Amazon, Degand' (M.V.L. Barclay pers. comm.).

Type locality

Pinotus buckleyi: Chiguinda, Morona-Santiago, Ecuador; *Pinotus simulator*: Amazonas.

Type material

Holotype of *Pinotus buckleyi*
ECUADOR • ♂; Morona-Santiago, Chiguinda; [3°18′ S, 78°41′ W]; [no date]; Buckley"; BMNH.

Holotype of *Pinotus simulator*
UNSPECIFIED COUNTRY • ♂; Amazon; [no date]; Degand; BMNH.

Material examined (16 ♂♂, 9 ♀♀)

ECUADOR • 1 ♂, 1 ♀; [unspecified locality]; [no date]; Buckley; BMNH • 1 ♂; same collection data as for preceding; MNHN. – **Loja** • 1 ♂, 1 ♀; Bosque Natural Huashapamba, Saraguro; [3°40′ S, 79°16′ W]; 2920 m; 10 Dec.2005; [anonymous]; CEMT • 1 ♂; Loja; [3°59′30″ S, 79°11′36″ W]; [no date]: Abbé Gaujon; CMNC • 6 ♂♂, 2 ♀♀ (one of these was used for the descriptions of both sexes); same collection data as for preceding; MNHN. – **Pastaza** • 1 ♂; Sarayacu; [1°44′ S, 77°29′ W]; 1879; Buckley; MNHN.

PERU – **La Libertad** • 1 ♀; Cumpang, above [Río] Uctubamba on trail to Ongón; [8°20′ S, 76°59′ W]; 2625 m; 16 Oct. 1979; J.L. Barkley; cloud forest; BDGC. – **Piura** • 1 ♂; Ayabaca; [4°38′ S, 79°43′ W]; 3000 m; Jan. 2016; Roja and Gonzales; CMD • 1 ♂; Provincia de Ayacaba, Bosque de Chin Chin, San Juan, Distrito de Pacaipampa; [4°59′59″ S, 79°39′29″ W]; 3055 m; 16 Apr. 2009; D. Saavedra; cloud forest, bovine dung; CEMT • 1 ♂, 1 ♀; same collection data as for preceding; PMOC • 1 ♂, 2 ♀♀; Bosque de Ramos, Comunidad Campesina de Samanga del Sector Espíndola; [4°42′4″ S, 79°27′43″ W]; 2834 m; 16 Feb. 2009; D. Saavedra; cloud forest, pitfall trap: fish; CEMT • 1 ♂, 1 ♀; same locality as for preceding; 27 May 2009; D. Saavedra; cloud forest, pitfall trap: fish; CEMT.

Description

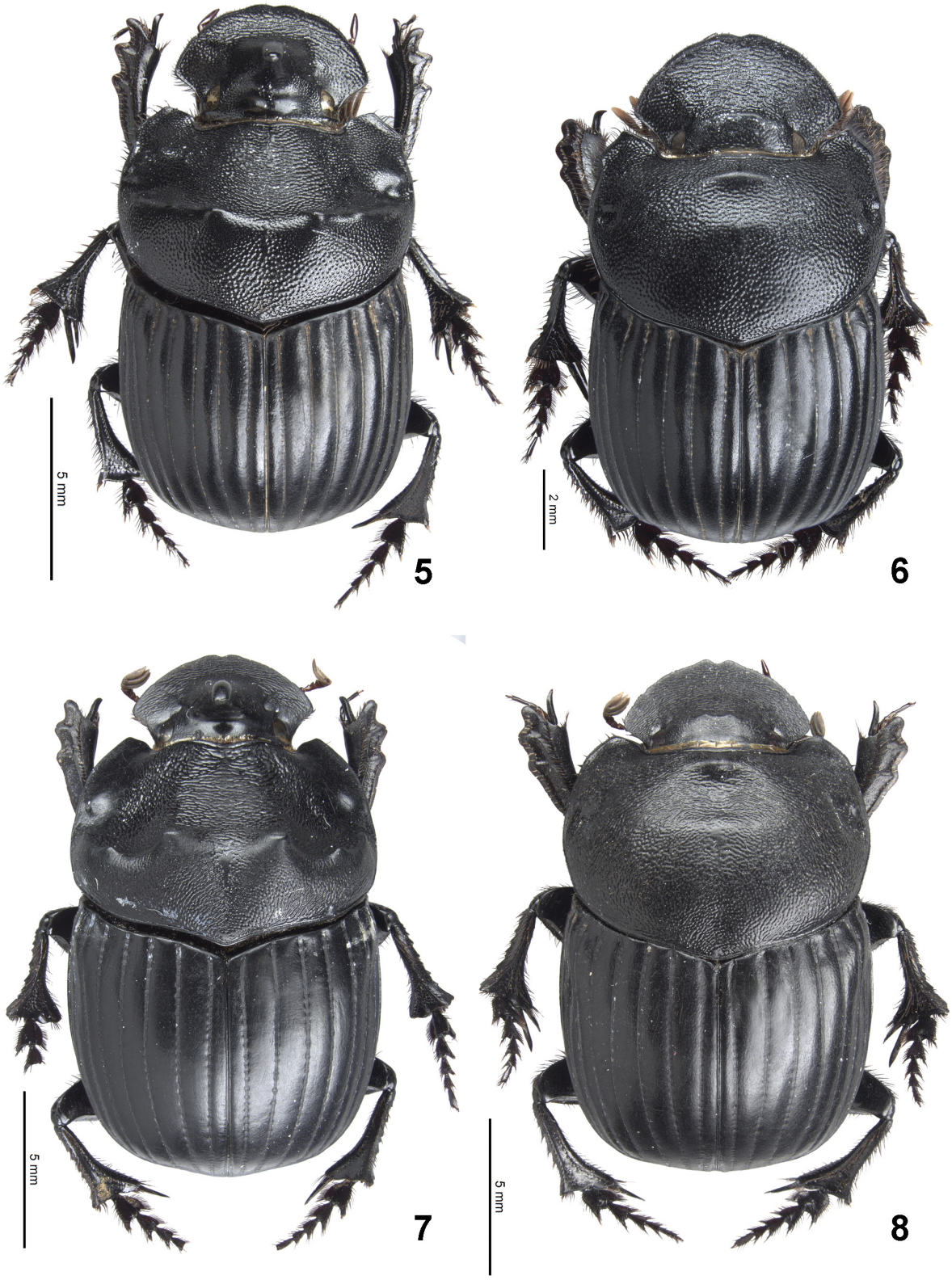
The holotype was previously studied, but is not available for a detailed description.

Male specimen (Figs 3, 15, 26, 32, 40, 42)
Measurements. Body length 16.4 mm.

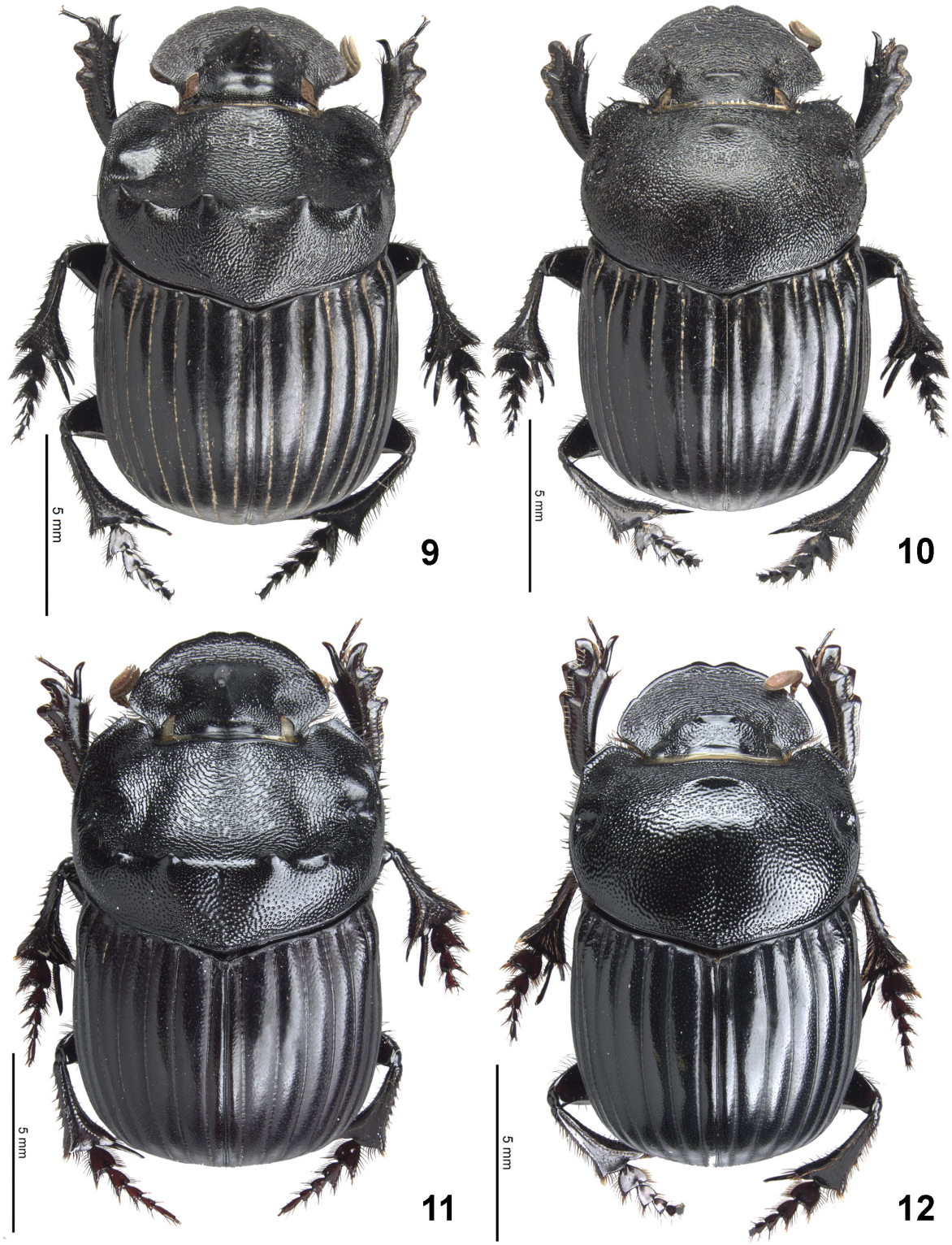
Head. Clypeal edge broadly arcuate, lacking teeth. Anteroventral clypeal tooth acute. Clypeal and genal surface rugose, clypeogenal suture ill-defined. Posterior genal angle obtuse. Frontal surface reduced, smooth. Dorsal ocular width greater than one-quarter interocular distance. Interocular surface smooth. Cephalic horn emerging centrally from clypeofrontal surface, parallel-sided with quadrate apex, curved throughout, apically flattened, 5.7 mm in length.

Prothorax. Carina along anterior pronotal edge broad medially, narrowing laterally. Anterolateral pronotal lobe smooth, sectioned posteriorly by abrupt shelf. Lateral pronotal carina and pronotal edge distinctly forking anteriorly then merging posteriorly, forming closed carinated ellipse. Pronotal surface smooth anteriorly, transitioning posterolaterally into chagrined texture. Centrally raised projection bifurcated with deeply excavated anteroventral surface defined by uneven texture. Propleuron and prosternum broadly setose; with long (~1 mm) dark setae. Anterior prosternal apex rounded.

Elytra. Glossy overall. Striae 1–6 widest anteriorly; narrowing posteriorly. Elytral stria eighth absent. Elytral striae nine absent on basal sixth. Interstriae convex, impunctate.



Figs 5–8. Dorsal habitus. **5**. *Homocopris grossiorum* Darling & Génier sp. nov., holotype, ♂ (CEMT). **6**. *Homocopris grossiorum*, allotype, ♀ (CEMT). **7**. *Homocopris punctatissimus* (Curtis, 1845), specimen ♂ (CMNC). **8**. *Homocopris punctatissimus*, specimen ♀ (NMPC).



Figs 9–12. Dorsal habitus. **9**. *Homocopris torulosus* (Eschscholtz, 1822), neotype, ♂ (CMNC). **10**. *Homocopris torulosus*, specimen ♀ (repository unknown). **11**. *Homocopris williami* Darling & Génier sp. nov., holotype, ♂ (MZSP). **12**. *Homocopris williami*, allotype, ♀ (MZSP).

Hindwing (Fig. 40). Membrane edge between AP and AA lobed. AP vein reduced.

Ventrites. Meso-metasternal suture posteriorly arcuate. Surface of median metasternal lobe (Fig. 42) finely punctate and convex, with scarce setigerous punctation along mesocoxae. Lateral metasternal lobe densely setose. Visible abdominal ventrites 1–6 laterally setose. Pygidium finely punctate.

Prothoracic legs. Anterior and posterior surface of profemur with dense row of long dark setae. Ventral profemoral surface finely punctate, lacking setae. Protibia with four distinct teeth. Protibial forespur straight with apex tapering inward.

Mesothoracic legs. Posterior surface of mesotrochanter with dense tuft of long rufous setae. Anterior and posterior surface of mesofemur with dense row of long dark setae. Outer surface of mesotibia serrate. Width at mesotibial apex one-third mesotibial length.

Metathoracic legs. Posterior surface of metatrochanter with tuft of long dark setae. Anterior and posterior surface of metafemur with dense row of long dark setae. Outer surface of metatibia serrate. Width at metatibial apex one-quarter metatibial length.

Male genitalia. Aedeagus length: 3.6 mm. Medially and laterally paired sclerites of genital segment broad, ill-defined. Paramere (Fig. 26) laterally flattened, gently tapered; apex broad and slightly inclined with ventral tooth. FLP endophallite (Fig. 32) sigmoidal; broad distally, narrowing and inflecting centrally.

Female specimen (Figs 4, 16)

Similar to male with the following exceptions: body length 14.7 mm. Clypeal edge slightly sinuous medially. Clypeofrontal carina bi-tuberculate, with width equivalent to dorsal ocular width. Anterolateral pronotal lobe surface smooth, immediately transitioning to fused granulate texture posteriorly. Central pronotal ridge slightly overhanging, with lateral tubercles and shallow anterior excavation. Posterolateral and posterior pronotal surface chagrined.

Variation

Body length 15–20 mm. Clypeal teeth absent or round and indistinct. Cephalic horn acute in small males; less than 1 mm in length. Pronotal armament in small males limited to notched anterior ridge. Pronotal ridge lacking lateral tubercles in small females.

Distribution (Fig. 65)

High elevation (2625–3055 m) in the Ecuadorian and northern Peruvian Andes. The single record from "Amazon" is based on an historical specimen, the holotype of *Pinotus simulator* Luederwaldt with vague data (see Max Barclay pers. com., comment below).

Natural history

Specimens with data were collected in cloud forest using pitfall traps baited with fish and in bovine dung.

Remarks

In the original description of *Pinotus simulator*, Luederwaldt (1936) describes the type specimen as "seeming atrophied, perhaps belonging to [*P. buckleyi*]". Luederwaldt goes on to describe the cephalic and pronotal armament of the specimen as "a small quadrate hump" in place of a long cephalic horn, and a "small sinuous carina" instead of a large bifurcating pronotal projection. We suspected Luederwaldt was referring to a poorly developed male representative of *A. buckleyi*. Upon examination of photographs

of the specimen in question, we have confirmed this to be the case; the external morphology of *P. simulator* matches a typical small male of *A. buckleyi* in all respects, and the name is therefore considered a new junior synonym of *A. buckleyi*.

Genus ***Homocopris*** Burmeister, 1846

[*Copris*] (*Homocopris*) Burmeister, 1846: [3] (original description).

[*Copris*] (*Homocopris*) – Lacordaire 1855: 97 (synonymy).
Homocopris – Harold 1869b: 1009 (synonym). — Heyne 1900: 62 (synonym). — Gillet 1911: 59 (synonym). — Lucas 1920: 333 (catalogue, synonym). — Blackwelder 1944: 206 (synonym). — Martínez 1959: 80 (synonym); 1987: 64 (synonym).— Woodruff 1973: 53 (synonym). — Ratcliffe 2002: 15 (synonym). — Smith 2003: 28 (synonym). — Vaz-de-Mello *et al.* 2010: 192 (new rank); 2011: 13 (identification key). — Sarmiento-Garcés & Amat-García 2014: 25 (synonym). — Chamorro *et al.* 2018: 77 (identification key); 2019: 158 (catalogue, faunistic).

Type species

Copris torulosus Eschscholtz, 1822, by original monotypy.

Differential diagnosis

Dorsal ocular width subequal to one-sixth interocular distance. Lateral pronotal carina anteriorly joined with pronotal edge only anteriorly. Eighth elytral stria always absent. Meso-metasternal suture straight (Fig. 61). Posteromedial surface of metasternum deeply impressed. ♂ pronotal armament forming bilaterally paired tubercles along an inclined ridge in large individuals. FLP endophallite elongate and curved or reduced and rounded.

Description

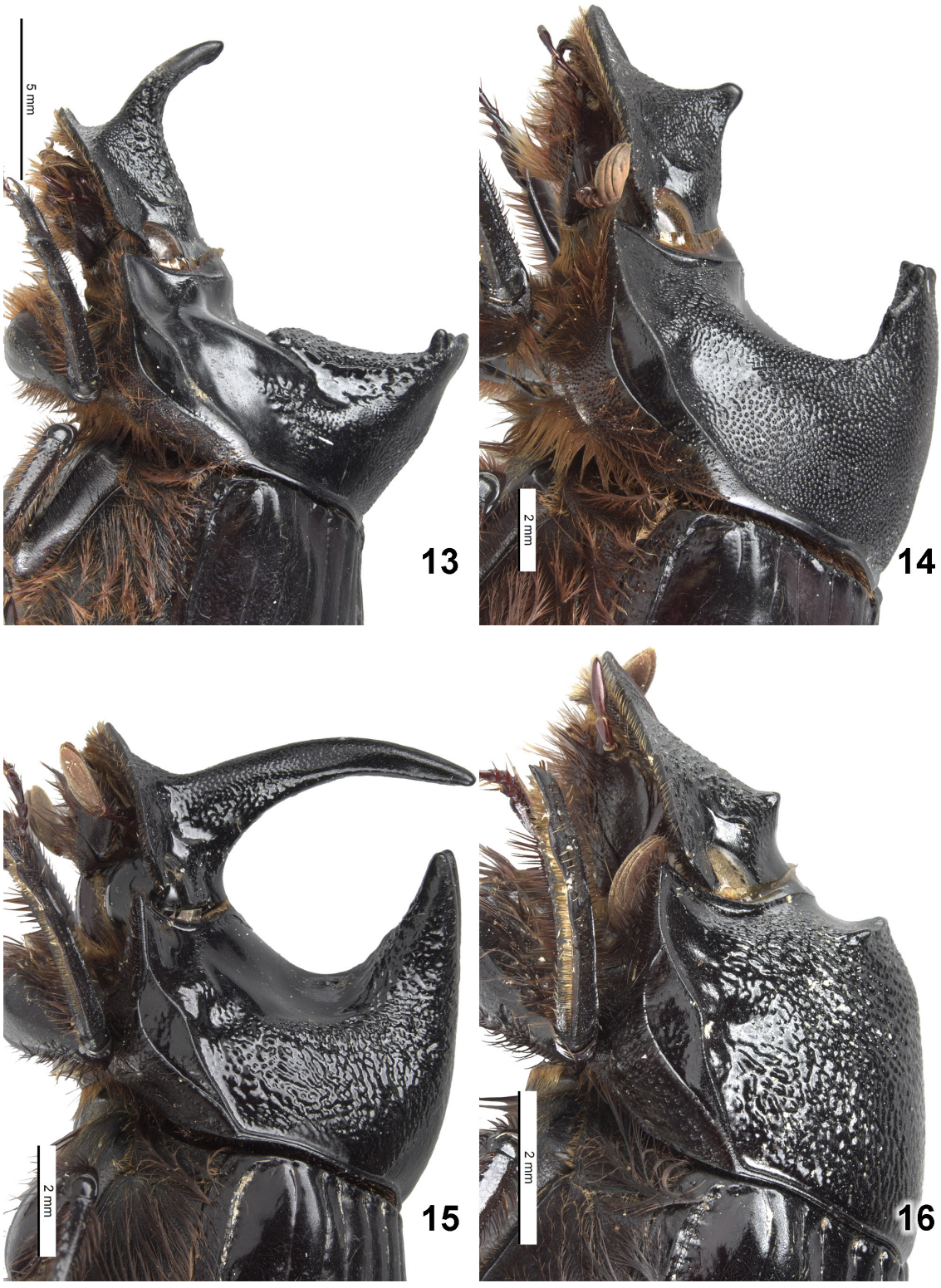
Body length 12–22 mm. Anteroventral clypeal tooth rather broad. Dorsal ocular width subequal to one-sixth interocular distance. Anterior pronotal membrane rather wide, transition between membrane and anterior edge of pronotum well-defined throughout. Anterior pronotal edge sinuous medially. Anteromedial pronotal surface chagrined or rugose. Lateral pronotal carina and pronotal edge distinct anteriorly only. Anterior apex of prosternum acutely tipped. Underside of elytron with long semi-erected setae. Eighth elytral stria always absent. Hindwing AP entire, converging with J. Meso-metasternal suture straight. Surface of median metasternal lobe lacking setae, deeply impressed, with uneven texture. Pygidial surface coarsely punctate. ♂ pronotal armament forming bilaterally paired tubercles along inclined ridge in large individuals. Paramere in one of two forms: (1) sharply tapered and acutely tipped, with length equivalent to or greater than 2 mm, or (2) gently tapered and apically rounded, with length never exceeding 2 mm. FLP endophallite elongate and curved or reduced and rounded.

Distribution

Chilean and Argentinean Andes, and montane Atlantic Forest in southeast and south Brazil.

Remarks

The description of *Homocopris* was published by Burmeister in *Genera quaedam insectorum. Iconibus illustravit et descripsit. Volumen I. Continet tabulas XL*. This work was issued in 10 fascicules from 1838 to 1846 (Bousquet 2016). The genus *Copris* in which *Homocopris* was described as a subgenus was treated on an unnumbered page in the last fascicule published (Hefte 10). Some authors have cited the date of publication of the genus as 1838–1846 (Martínez 1959) or as 1842 (Woodruff 1973; Smith



Figs 13–16. Head and pronotum, lateral view. **13**. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov., lectotype, ♂ (MNHN). **14**. *Andinocopris achamas*, paralectotype, ♀ (MNHN). **15**. *Andinocopris buckleyi* (Waterhouse, 1891) gen. et comb. nov., specimen ♂ (MNHN). **16**. *Andinocopris buckleyi*, specimen ♀ (MNHN).

Figs 17–20. Head and pronotum, lateral view. **17**. *Homocopris grossiorum* Darling & Génier sp. nov., holotype, ♂ (CEMT). **18**. *Homocopris grossiorum*, allotype, ♀ (CEMT). **19**. *Homocopris punctatissimus* (Curtis, 1845), specimen ♂ (CMNC). **20**. *Homocopris punctatissimus*, specimen ♀ (BNPC).

Figs 21–24. Head and pronotum, lateral view. **21**. *Homocopris torulosus* (Eschscholtz, 1822), neotype, ♂ (CMNC). **22**. *Homocopris torulosus*, specimen ♀ (repository unknown). **23**. *Homocopris williami* Darling & Génier sp. nov., holotype, ♂ (MZSP). **24**. *Homocopris williami*, allotype, ♀ (MZSP).

2003; Sarmiento-Garcés & Amat-García 2014). However, all evidence supports a publication date between July and December 1846 (Bousquet 2016).

Homocopris grossiorum Darling & Génier sp. nov.
urn:lsid:zoobank.org:act:A7F14F5E-EF36-4BAA-B81F-88BDBC8FFE4F
Figs 5–6, 17–18, 27, 33, 37, 43, 48, 66

Differential diagnosis

Dorsal ocular width subequal to one-sixth interocular distance; anterior pronotal edge tends to be medially indented; posterior pronotal surface uniformly punctate; elytral interstriae punctation tends to be invisible at 10× magnification; metasternal depression divided anteriorly. ♂ pronotal ridge with a single medial pair of distinct tubercles in large individuals; paramere apex unevenly rounded, projecting dorsally; FLP endophallite reduced.

Etymology

Grossiorum is the Latin plural genitive form of Grossi. This species is named in honour of Everardo and Paschoal Grossi, two avid Brazilian collectors and accomplished entomologists.

Name-bearing type data

Holotype ♂ (CEMT) (Fig. 52): "BRASIL: Rio de Janeiro. | Itatiaia. PARNA Itatiaia. | 1700m. 22°25'5.5"S; | 44°38'6.7"W. Pitfall. | 23-26-xii-2011. | C Araújo & R Andrade"; "WORLD | SCARAB. | DATABASE | WSD00035641" [barcode label]; "HOLOTYPE ♂ | *Homocopris* | *grossiorum* | Des. Darling & Génier, 2018" [on red card with black border].

Type locality

Parque Nacional do Itatiaia, 22°25′05.5″ S, 43°38′06.7″ W, 1700 m, Itatiaia, Rio de Janeiro, Brazil.

Type material (48 ♂♂, 19 ♀♀)

Holotype

BRASIL • ♂; "Parque Nacional do Itatiaia, Itatiaia, 1700 m [22°25′5″ S, 44°38′7″ W], 20.i.2012, mata atlántica, pitfall trap: human feces, C. Araújo"; CEMT.

Allotype

BRASIL • ♀; same collection data as for holotype; CEMT.

Paratypes

BRAZIL • **Minas Gerais** • 1 ♂; Serra dos Côchos, Passa Quatro; [22°23′30″ S, 44°58′30″ W]; 1460 m; 15 Jan. 1923; J. Zikán; CEMT • 1 ♂; same locality as for preceding; 17 Feb. 1923; J. Zikán; CEMT. – **Rio de Janeiro** • 1 ♂; Itatiaia; [22°28′ S, 44°34′ W]; Jan. 1992; Celso Jr.; CEMT • 1 ♂; same locality as for preceding; Apr. 1992; C. Godinho; CEMT • 1 ♀; same locality as for preceding; Mar. 1990; [anonymous]; CEMT • 3 ♂♂, 3 ♀♀; same locality as for preceding; Jan. 1994; [anonymous]; CMD • 4 ♂♂, 3 ♀♀; same locality as for preceding; Feb. 1992; V. Allard; PMOC • 2 ♂♂; same locality as for preceding; 28 Feb. 1990; C. and D. Godinho; CEMT • 1 ♀; Itatiaia; [22°28′ S, 44°34′ W]; 1500 m; Feb. 1992; [anonymous]; PMOC • 1 ♂, 1 ♀; Macaé de Cima; [22°23′ S, 42°29′ W]; Mar. 2000; Vaz-de-Mello; CEMT • 1 ♂; same locality as for preceding; [no date]; E. and P. Grossi; CEMT • 1 ♂; same locality as for preceding; Apr. 2006; E. and P. Grossi; CEMT • 3 ♂♂; Macaé de Cima, Nova Friburgo; [22°23′ S, 42°29′ W]; 1400 m; 15 Apr. 2007; E. and P. Grossi; CEMT • 1 ♂; same locality as for preceding; Mar. 2000; Lopes-Andrade, Gumier and Vaz-de-Mello; CEMT • 1 ♀; same locality as for preceding; Mar. 2006; Vaz-de-Mello and Grossi; CEMT • 2 ♀♀; Mury, 8 km E of

Nova Friburgo; [22°21′49″ S, 42°33′7″ W]; 1150 m; 22 Jan. 2000; F. Génier & S. Ide 2000-12; quasi-primary mountain Atlantic Forest, dung trap; CMNC • 1 ♂; same locality as for preceding; 22 Jan. 2000; F. Génier and S. Ide 2000-13; quasi-primary mountain Atlantic Forest, dung trap; CMNC • 1 ♂; same locality as for preceding; 22 Jan. 2000; F. Génier and S. Ide 2000-14; quasi-primary mountain Atlantic Forest, carrion trap; CMNC • 1 ♂; Parque Nacional da Serra dos Órgãos, Teresópolis; [22°27′.43″ S, 43°0′53.24″ W]; 1550 m; 16–18 Dec. 2014; C. Araújo and R. Andrade; pitfall trap; CEMT • 3 ♂♂, 1 ♀; Parque Nacional da Serra dos Órgãos, Teresópolis; [22°27′8.1″ S, 43°0′51.98″ W]; 1650 m; 16–18 Dec. 2014; C. Araújo and R. Andrade; pitfall trap; CEMT • 1 ♂; Parque Nacional da Serra dos Órgãos, Teresópolis; [22°27′11.56″ S, 43°0′56.41″ W]; 1680 m; 28–30 Jan. 2014; C. Araújo and R. Andrade; pitfall trap; CEMT • 3 ♂♂, 2 ♀♀; Parque Nacional da Serra dos Órgãos, Teresópolis; [22°27′19.3″ S, 43°1′3.79″ W]; 1750 m; 16–18 Dec. 2014; C. Araújo and R. Andrade; pitfall trap; CEMT • 1 ♂; Parque Nacional do Itatiaia; [22°28′ S, 44°34′ W]; 4 Jan. 1991; [anonymous]; CEMT • 2 ♂♂; Parque Nacional do Itatiaia, Itatiaia; [22°25′17″ S, 44°37′59″ W]; 1600 m; 4. Jan. 1991; E. and P. Grossi; CEMT • 2 ♂♂, 1 ♀; same locality as for preceding; 23–26 Dec. 2011; C. Araújo and R. Andrade; pitfall trap; CEMT • 1 ♂; same locality as for preceding; 20 Jan. 2012; C. Araújo; mata atlántica, pitfall trap: human feces; CEMT • 1 ♂; Parque Nacional do Itatiaia, Itatiaia; [22°25′20″ S, 44°38′9″ W]; 1650 m; 20 Jan. 2012; C. Araújo; mata atlántica, pitfall trap: human feces; CEMT • 1 ♂; same collection data as for holotype; CEMT • 1 ♂; same locality as for holotype; 20 Jan. 2012; C. Araújo; mata atlántica, pitfall trap: human feces; CEMT • 2 ♂♂; Parque Nacional do Itatiaia, Itatiaia; [22°25′1.1″ S, 44°38′35.5″ W]; 1850 m; 23–26 Dec. 2011; C. Araújo and R. Andrade; pitfall trap; CEMT • 1 ♂; Parque Nacional do Itatiaia, Itatiaia; [22°24′47.2″ S, 44°38′23.5″ W]; 1900 m; 23–26 Dec. 2011; C. Araújo and R. Andrade; pitfall trap; CEMT • 1 ♀ (paratype of *Pinotus torulosus* var. *Minor* Luederwaldt); Rio de Janeiro; BMNH. – **São Paulo** • 1 ♂; Campos do Jordão; [22°44′ S, 45°35′ W]; 20 Feb. 1999; E.A. Pereira; CEMT • 1 ♂, 2 ♀♀; Campos do Jordão; [22°44′ S, 45°35′ W]; 1850 m; Jan. 2005; G.P. Almeida; CEMT • 1 ♂; Horto Florestal de Campos do Jordão; [22°41′24″ S, 45°28′48″ W]; 27 Dec. 1998; G.P. Almeida; CEMT • 2 ♂♂; [NO DATA]; [no date], [anonymous]"; MNHN.

Description

Male holotype (Figs 5, 17, 27, 33, 37, 43, 48)

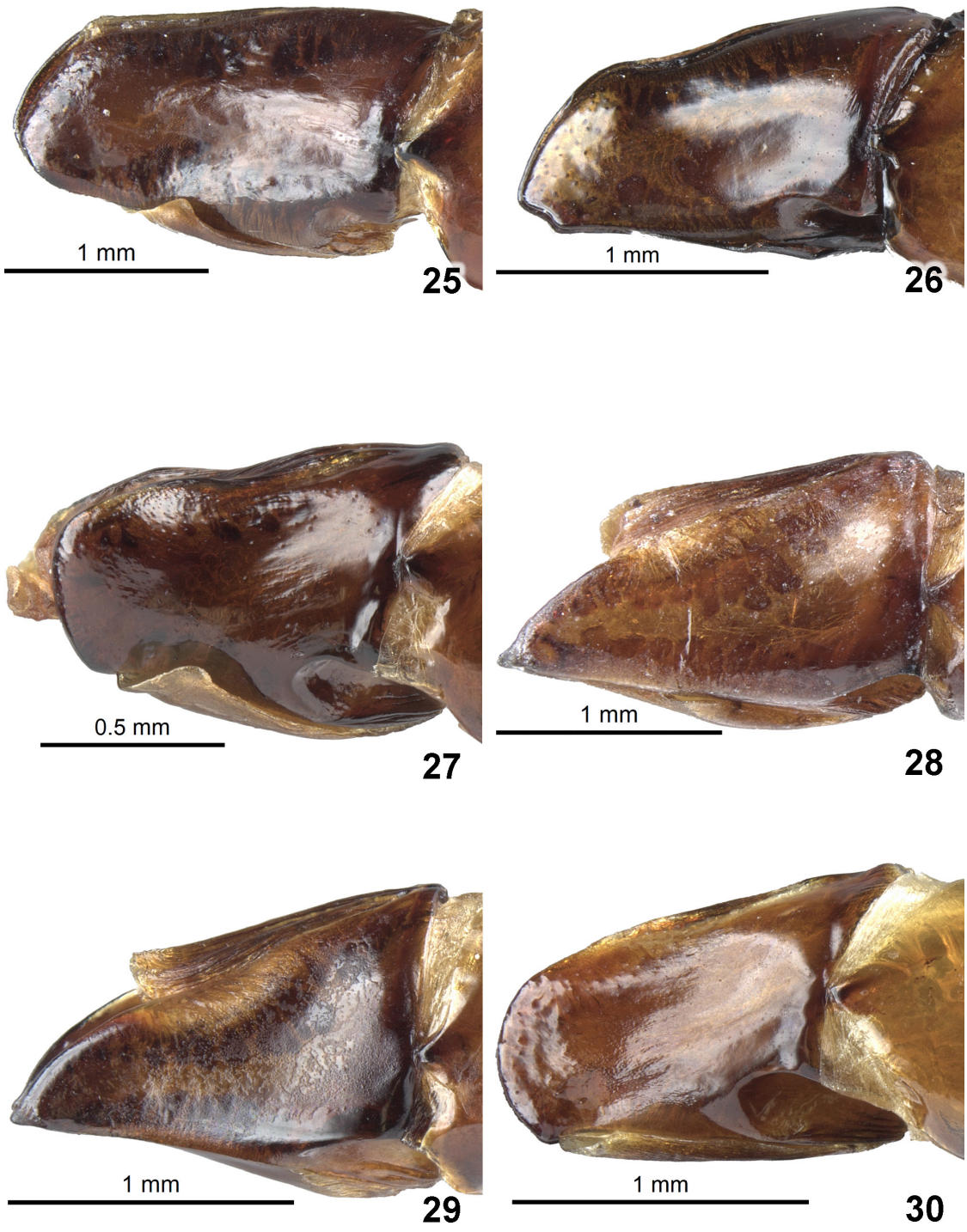
Measurements. Body length 14.4 mm.

Head. Clypeus bidentate with broad, rounded teeth. Anteroventral clypeal process broad. Clypeal and genal surface rugose, clypeogenal suture demarcated by shallow notch. Posterior genal angle obtuse. Frontal surface reduced, smooth. Dorsal ocular width subequal to one-sixth interocular distance. Interocular surface medially smooth. Cephalic horn emerging centrally from clypeofrontal surface, tapering apically, gently curved, 3.6 mm in length.

Prothorax. Anterior pronotal edge medially indented. Lateral pronotal edge angular on anterior fourth in dorsal view. Anterior pronotal declivity surface (Fig. 48) with fine transverse rugosities. Centrally paired tubercles along transverse pronotal ridge distinct, lateral pair indistinct. Posterior pronotal surface uniformly punctate. Prosternal apex acutely tipped.

Elytra. Glossy overall. Striae 1–6 widest anteriorly; narrowing posteriorly. Third and fourth striae posteriorly joined. Eighth stria absent throughout. Ninth stria effaced along anterior quarter of elytral length. Interstriae convex, minutely punctate.

Hindwing. Membrane edge between AP and AA sinuous. AP vein entire, converging with J.



Figs 25–30. Paramere, lateral view. **25**. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov., specimen ♂ (CMNC). **26**. *Andinocopris buckleyi* (Waterhouse, 1891) gen. et comb. nov., specimen ♂ (MNHN). **27**. *Homocopris grossiorum* Darling & Génier sp. nov., holotype, ♂ (CEMT). **28**. *Homocopris punctatissimus* (Curtis, 1845), specimen ♂ (CMNC). **29**. *Homocopris torulosus* (Eschscholtz, 1822), neotype, ♂ (CMNC). **30**. *Homocopris williami* Darling & Génier sp. nov., holotype, ♂ (MZSP).

Ventrites. Meso-metasternal suture straight. Surface of median metasternal lobe (Fig. 43) with uneven texture and deep, anteriorly divided impression. Lateral metasternal lobe densely setose. Fifth abdominal ventrite with sparse medial punctation. Pygidium coarsely punctate.

Prothoracic legs. Anterior and posterior surface of profemur with dense row of long dark setae. Ventral profemoral surface finely punctate, sparsely setose. Protibia with three distinct teeth. Protibial forespur apically tapered, curving inward.

Mesothoracic legs. Posterior surface of mesotrochanter with tuft of long dark setae. Anterior and posterior surface of mesofemur with sparse row of long dark setae. Outer surface of mesotibia serrate. Width at mesotibial apex one-third mesotibial length.

Metathoracic legs. Posterior surface of metatrochanter with tuft of long dark setae. Anterior and posterior surface of metafemur with sparse row of long dark setae. Outer surface of metatibia serrate. Width at metatibial apex one-third metatibial length.

Male genitalia. Aedeagus length: 2.8 mm. Medially paired sclerites of genital segment elongate (Fig. 37), subequal in length to lateral sclerites. Paramere (Fig. 27) laterally flattened, gently tapered with apex subtruncated, slightly projecting dorsally. FLP endophallite (Fig. 33) reduced, appearing rounded and truncated.

Female allotype (Figs 6, 18)

Similar to male with the following exceptions: Body length 12.6 mm. Clypeofrontal carina transverse, centrally raised. Interocular surface coarsely punctate. Anterior pronotal ridge low, followed by shallow concavity.

Variation

Body length 11–19 mm. Small males with medially projecting clypeofrontal ridge instead of cephalic horn. Anterior pronotal edge medially indented more often than evenly curved. Pronotal ridge in small males low, medially notched. Elytral interstriae minutely punctate (invisible at 10×) more often than finely punctate (visible at 10×).

Distribution (Fig. 66)

Serra dos Órgãos and Serra da Mantiqueira in the Brazilian states of Minas Gerais, Rio de Janeiro and São Paulo, with recorded elevations between 1150 and 1900 m.

Natural history

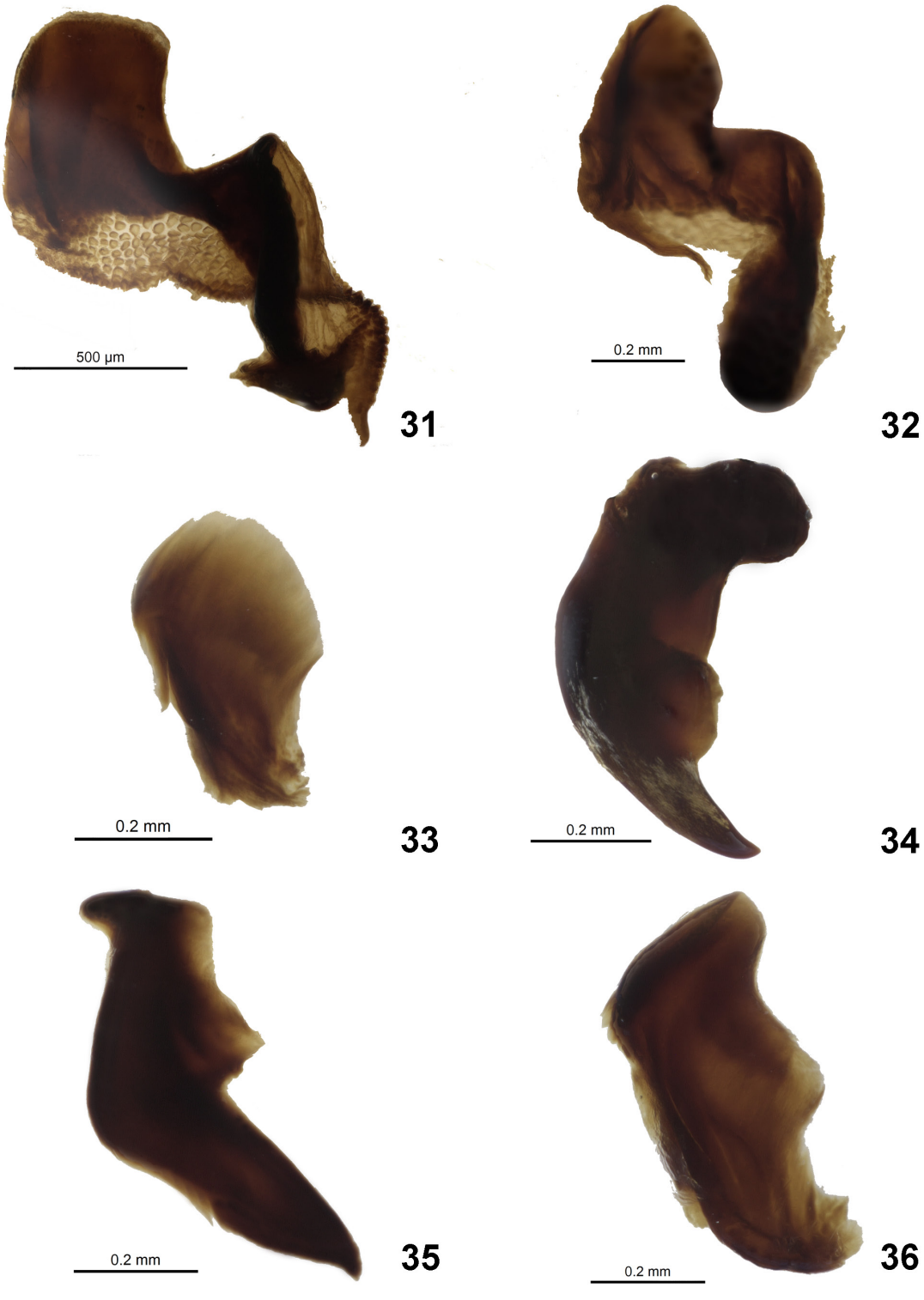
Specimens with data were collected in Atlantic Forest and quasi-primary mountain Atlantic Forest. Most specimens were collected using pitfall traps with unspecified baits. A single specimen was collected in a carrion trap and three specimens were collected in pitfall traps baited with human faeces.

Homocopris punctatissimus (Curtis, 1845)
Figs 7–8, 19–20, 28, 34, 44, 67

Copris punctatissima Curtis, 1845: 444 (original description).

Copris punctatissima – Solier 1851: 60 (synonymy). — Harold 1869a: 133 (synonym). — Martínez 1959: 87 (synonym).

[*Copris*] *punctatissimus* – Harold 1869b: 1011 (synonym). — Heyne 1900: 62 (synonym). — Gillet 1911: 62 (synonym). — Blackwelder 1944: 208 (synonym).



Figs 31–36. FLP endophallite, dorsal view. **31**. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov., specimen ♂. **32**. *Andinocopris buckleyi* (Waterhouse, 1891) gen. et comb. nov., specimen ♂. **33**. *Homocopris grossiorum* Darling & Génier sp. nov., holotype, ♂ (CEMT). **34**. *Homocopris punctatissimus* (Curtis, 1845), specimen ♂ (CMNC). **35**. *Homocopris torulosus* (Eschscholtz, 1822), neotype, ♂ (CMNC). **36**. *Homocopris williami* Darling & Génier sp. nov., holotype, ♂ (MZSP).

Copris punctatissimus – Reed 1876: 281 (synonym). — Bruch 1911: 187 (synonym).
Pinotus punctatissimus – Waterhouse 1891: 361 (diagnosis). — Luederwaldt 1929: 650 (synonym).
Copris Punctatissimus – Gutiérrez 1940: 277 (synonym).
Homocopris punctatissimus – González *et al.* 2015: 53 (bona species, ecology). — Rebolledo *et al.* 2017: 27 (distribution). — Tello *et al.* 2021: 139 (distribution). — Mondaca 2023: 222 (checklist, distribution, diagnosis, new combination).

Differential diagnosis

Dorsal ocular width subequal to one-sixth interocular distance; lateral pronotal edge broadly arcuate on anterior half in dorsal view; width of ellipse formed by lateral pronotal carina and pronotal edge approximately one-half the elliptical length; posterior pronotal surface chagrined; elytral interstriae punctation visible at 10× magnification; metasternal depression entire, limited to posterior portion of median metasternal lobe. ♂ pronotal ridge with three sets of distinct bilaterally paired tubercles in large individuals; paramere apex acutely tipped; FLP endophallite heavily sclerotized, crescent-shaped, with one end rounded and the other toothed.

Name-bearing type data

Copris punctatissimus Curtis, holotype ♀ (BMNH): [recto] "Chil" [handwritten]; [verso] "*punctatissima* | 63 Curt" [handwritten]; "63 | 49" [handwritten, white disc]; "Type" [disc with red border]; "*Copris* Curt | *punctatissima*"*;* [handwritten].

Type locality

Copris punctatissimus: Chile.

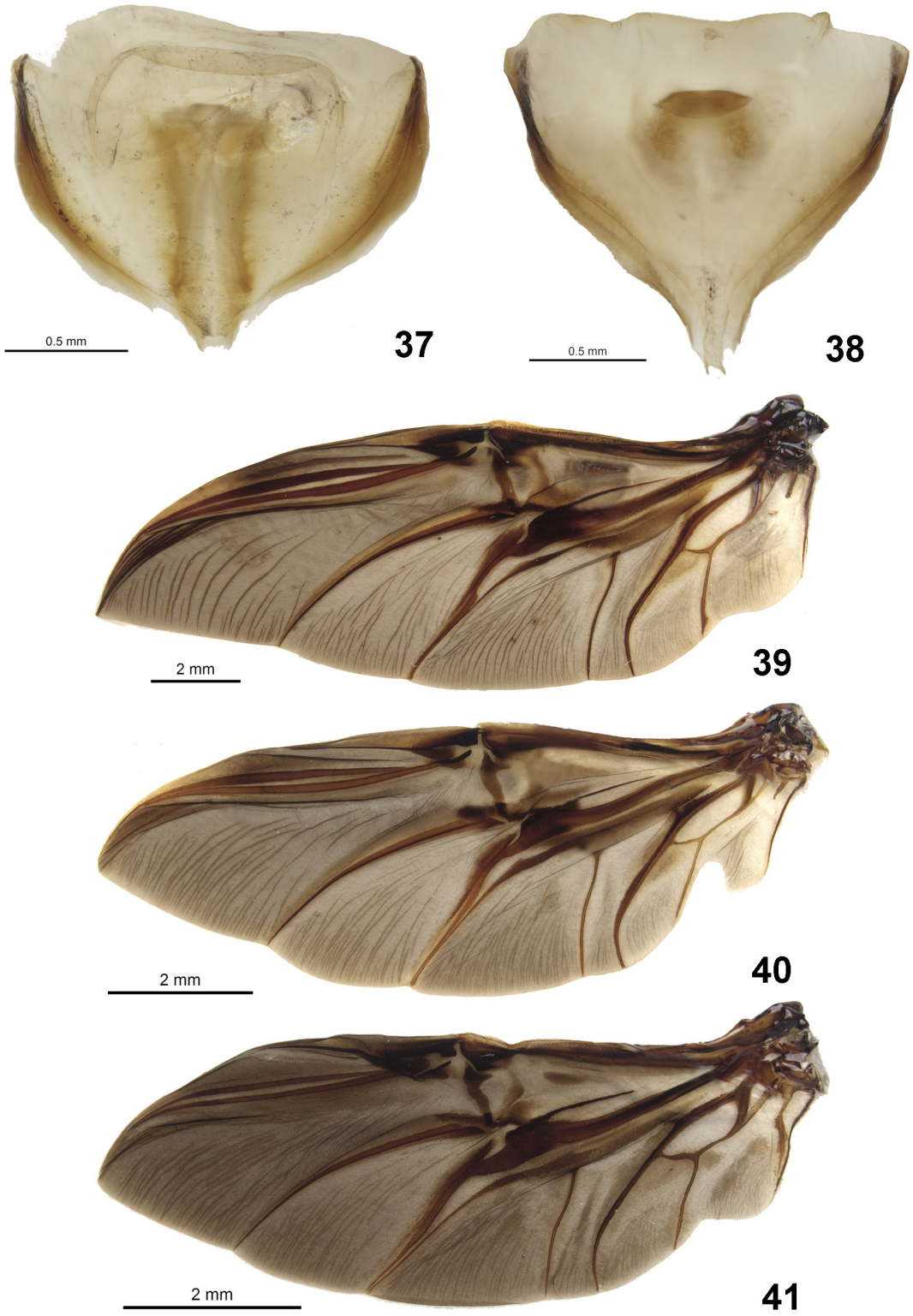
Type material

Holotype

CHILE • ♀; [recto] "Chil" [handwritten]; [verso] "*punctatissima* | 63 Curt" [handwritten]; "63 | 49" [handwritten, white disc]; "Type" [disc with red border]; "*Copris* Curt | *punctatissima*"*;* [handwritten]; (BMNH).

Material examined (74 ♂♂, 64 ♀♀)

CHILE • 1 ♂, 3 ♀♀; [unspecified locality]; [no date]; [anonymous]; CAS • 3 ♂♂, 2 ♀♀; same collection data as for preceding; CNC • 2 ♂♂; same collection data as for preceding; CPFA • 23 ♂♂, 9 ♀♀; same collection data as for preceding; MNHN • 2 ♂♂; same collection data as for preceding; NMPC • 2 ♂♂, 2 ♀♀; same locality as for preceding; [no date]; Clavareau; CAS. – **Región de Los Lagos** • 6 ♂♂, 3 ♀♀; 10 km E of Puyehue; [40°41′ S, 72°18′ W]; 24 Jan. 1951; Ross and Michelbacher; CAS • 2 ♂♂, 2 ♀♀; Aguas Calientes, Parque Nacional Puyehue; [40°44′20″ S, 72°18′25″ W]; 600 m; 18 Dec. 1984–8 Feb. 1985; S. and J. Peck; *Nothofagus* forest, Malaise; CMNC • 2 ♂♂; Ancud; [41°53′ S, 73°49′ W]; 30 May 1914; [anonymous]; CAS • 1 ♀; Chaitén; [42°54′50″ S, 72°42′4″ W]; Dec. 1985; L. Peña; CMNC • 1 ♂; Dalcahue, Chiloé; [42°22′23″ S, 73°39′9″ W]; Feb. 1952; Peña; CMNC • 1 ♂; Estaquilla; [41°23′30″ S, 73°50′0″ W]; 17 Jan. 1977; J. Solervicens; MNHN • 1 ♂; Fundo El Mirador, Río Chico; [41°23′42″ S, 72°49′17″ W]; 14 Feb. 2008; V.M. Diéguez; CEMT • 1 ♂; Isla Chiloé; [42°38′ S, 73°55′ W]; [no date]; [anonymous]; MNHN • 5 ♂♂, 3 ♀♀; Los Derrumbes Forest Trail, Aguas Calientes, Parque Nacional Puyehue; [40°44′ S, 72°18′ W]; 500 m; 20 Dec. 1984–8 Feb. 1985; S. and J. Peck; flight interception trap; CMNC • 2 ♀♀; Los Muermos; [41°24′ S, 73°28′ W]; 19 Jan. 1951; Ross and Michelbacher; forest; CAS • 4 ♂♂, 9 ♀♀; Pionero Forest Trail, Aguas Calientes, Parque Nacional Puyehue; [40°44′ S, 72°18′ W]; 500 m; 20 Dec. 1984–6 Feb. 1985; S. and J. Peck; carrion trap; CMNC • 1 ♂, 1 ♀; Puerto Varas; [41°19′ S, 72°59′W]; [no date]; [anonymous]; NMPC • 1 ♂, 2 ♀♀; Purranque; [40°55′ S, 73°10′ W]; Jan. 1951; [anonymous]; CAS. – **Región de Los Ríos** • 2 ♂♂, 1 ♀; 34 km WNW of La Union;



Figs 37–41. 37–38. Genital segment, dorsal view. **37**. *Homocopris grossiorum* Darling & Génier sp. nov., holotype, ♂ (CEMT). **38**. *Homocopris torulosus* (Eschscholtz, 1822), neotype, ♂ (CMNC). **39–41**. Hindwing, dorsal view. **39**. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov. **40**. *Andinocopris buckleyi* (Waterhouse, 1891) gen. et comb. nov. **41**. *Homocopris torulosus*.

[40°13′45″ S, 73°21′35″ W]; 700 m; 17 Dec. 1984–7 Feb.1985; S. and J. Peck; mixed evergreen forest, flight interception trap; CMNC • 1 ♀; Corral; [39°53′ S, 73°26′ W]; 20 Oct. 1913; R.H. Beck; CAS • 1 ♂ (alloreferent), 1 ♀; Panguipulli; [39°38′20″ S, 72°20′30″ W]; Jan. 1943; Gutiérrez; CMNC • 1 ♀; same locality as for preceding; Jan. 1952; [anonymous]; CMNC • 4 ♀♀; same locality as for preceding; Feb. 1942; Gutiérrez; CMNC • 2 ♀♀; same locality as for preceding; 1927; [anonymous]; CAS • 2 ♂♂, 1 ♀; Valdivia; [39°50′ S, 73°13′ W]; [no date]; [anonymous]; MNHN • 1 ♂, 1 ♀; same collection data as for preceding; NMPC. – **Región de Valparaíso** • 1 ♂, 2 ♀♀; Valparaíso; [33°4′ S, 71°36′ W]; [no date]; E.P. Reed; CAS. – **Región del Biobío** • 4 ♂♂, 2 ♀♀; Concepción; [36°48′ S, 73°1′ W]; [no date]; Reed; CAS. – **Región La Araucanía** • 1 ♀; 30 km NE of Villarrica; [39°8′47″ S, 72°3′32″ W]; Jan. 1965; L. Peña; CAS • 1 ♀; same locality as for preceding; Dec. 1964; L. Peña; CAS • 1 ♂ ; same locality as for preceding; 16–31 Dec. 1964; M. Rivera; CMNC • 2 ♂♂, 1 ♀; same locality as for preceding; 16–31 Dec. 1964; L. Peña; CAS • 1 ♀; Boroa Central, SE of Nueva Toltén; [39°16′ S, 73°8′ W]; 22 Jan. 2004; M. Snižek; NMPC • 1 ♂, 1 ♀; Campground, Parque Nacional Huerquehue; [39°10.026′ S, 71°43.455′ W]; 785 m; Nov.–Dec. 2005; F. Ledezma Zúñiga; CMNC • 1 ♀; Victoria; [38°14′ S, 72°21′ W]; [no date]; [anonymous]; NMPC. – **Región Metropolitana de Santiago** • 1 ♂, 2 ♀♀; Santiago; [33°29′ S, 70°39′ W]; [no date]; [anonymous]; CAS • 1 ♀; Santiago; [33°29′ S, 70°39′ W]; [no date]; [anonymous]; MNHN.

Description

Male alloreferent specimen (Figs 7, 19, 28, 34, 44)

Measurements. Body length 16.6 mm.

Head. Clypeus bidentate with broad, rounded teeth. Anteroventral clypeal tooth broad. Clypeal and genal surface rugose, demarcated by shallow notch along edge. Posterior genal angle obtuse. Frontal surface reduced, smooth. Dorsal ocular width subequal to one-sixth interocular distance. Interocular surface medially smooth. Cephalic horn emerging centrally from clypeofrontal surface, parallel sided, straight, 5.8 mm in length.

Prothorax. Anterior pronotal edge medially indented. Lateral pronotal edge broadly arcuate on anterior half in dorsal view. Anterolateral pronotal surface smooth, impunctate. Anterior inclined pronotal surface with irregular, fused rugosities. Pronotal ridge with three sets of distinct bilaterally paired tubercles. Posterior pronotal surface chagrined. Prosternal apex acutely tipped.

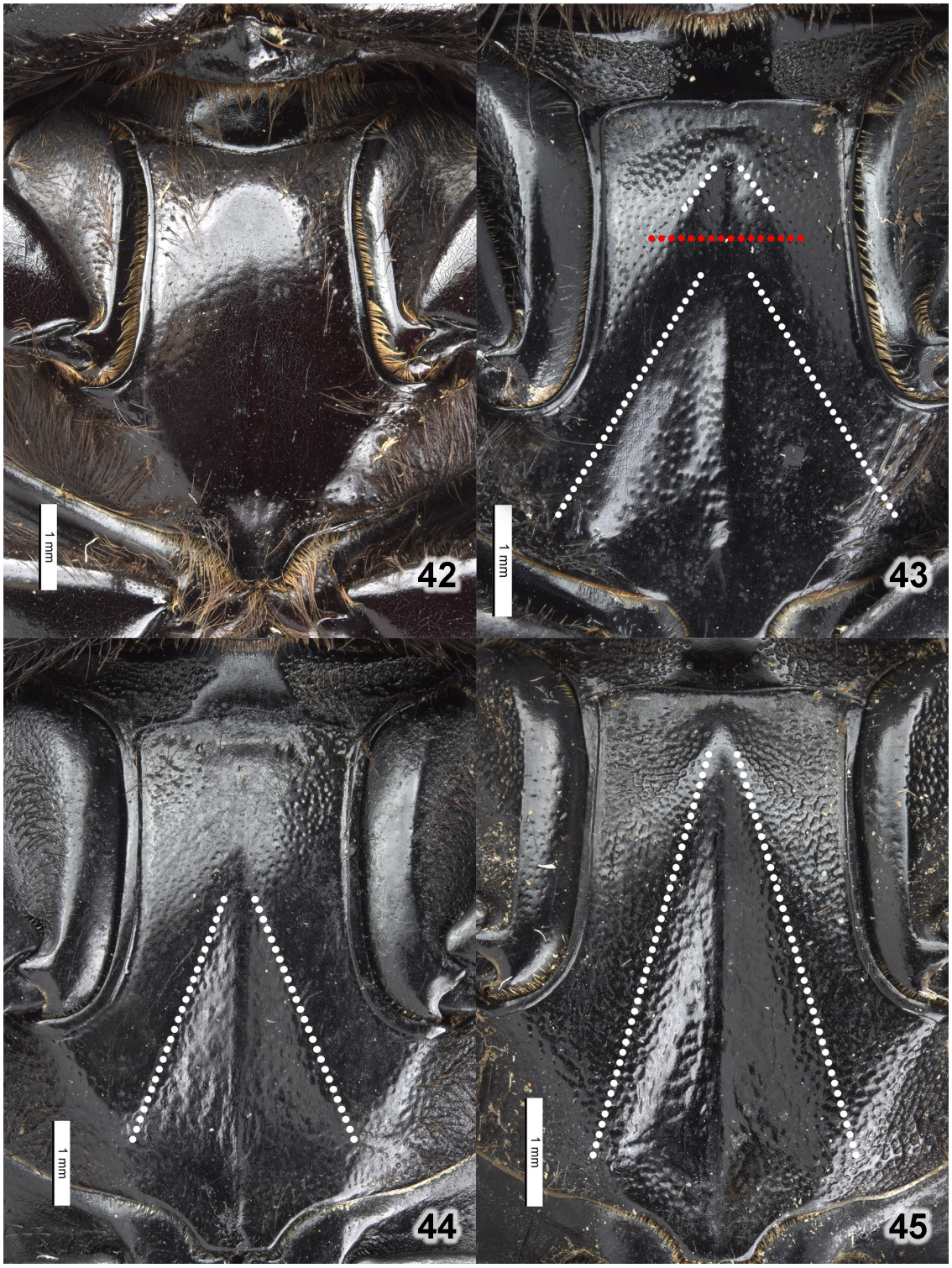
Elytra. Glossy overall. Striae 1-6 widest anteriorly; narrowing posteriorly. Third and fourth striae posteriorly joined. Eighth stria absent throughout. Ninth stria effaced along anterior quarter of elytral length. Interstriae convex, minutely punctate.

Hindwing. Membrane edge between AP and AA sinuous. AP vein entire, converging with J.

Ventrites. Meso-metasternal suture straight. Median metasternal lobe (Fig. 44) with deep posteromedial impression; anterior surface convex. Lateral metasternal lobe sparsely setose. Fifth abdominal ventrite with dense medial punctation. Pygidium coarsely punctate.

Prothoracic legs. Anterior and posterior surfaces of profemur with sparse row of long dark setae. Ventral profemoral surface finely punctate. Protibia with three distinct teeth. Protibial forespur parallel-sided, curving downward apically.

Mesothoracic legs. Posterior surface of mesotrochanter with three dark setae. Anterior and posterior surface of mesofemur with sparse row of long dark setae. Outer surface of mesotibia serrate. Width at mesotibial apex one-third mesotibial length.



Figs 42–45. Metasternum, ventral view. In specimens with a metasternal depression, the lateral depression is bordered with white dotted lines. For *Homocopris grossiorum* Darling & Génier sp. nov., a red dotted line indicates where the metasternal depression is interrupted. **42**. *Andinocopris buckleyi* (Waterhouse, 1891) gen. et comb. nov., specimen ♀ (MNHN) **43**. *Homocopris grossiorum*, holotype ♂ (MZSP). **44**. *Homocopris punctatissimus* (Curtis, 1845), specimen ♀ (NMPC). **45**. *Homocopris torulosus* (Eschscholtz, 1822), specimen ♂ (CMNC).

Metathoracic legs. Posterior surface of metatrochanter with three dark setae. Anterior and posterior surface of metafemur with sparse row of long dark setae. Outer surface of metatibia serrate. Width at metatibial apex one-third metatibial length.

Male genitalia. Aedeagus length: 4.6 mm. Medially paired sclerites of genital segment truncated. Paramere (Fig. 28) with apex acutely tipped. FLP endophallite (Fig. 34) heavily sclerotized, crescent-shaped, with one end rounded, another toothed.

Female (Figs 8, 20)

As male alloreferent with the following exceptions: body length 20.0 mm. Clypeal teeth deeply notched. Clypeofrontal carina transverse, centrally raised. Entire anterior pronotal surface with irregular, fused rugosities. Anterior pronotal ridge low, followed by shallow concavity. Protibial forespur straight throughout.

Variation

Body length 15–22 mm. Small males with medially projecting clypeofrontal ridge instead of cephalic horn. Pronotal ridge in small males low, medially notched. Large ♀♀ with bi-tubercular clypeofrontal.

Distribution (Fig. 67)

Chile in the Región de los Lagos, Región de Los Ríos, Región de Valparaíso, Región del Biobío, Región la Araucanía and Región Metropolitana de Santiago. Recorded elevations from 500 m to 785 m.

Natural history

Examined specimens with data were collected in unspecified forest type, mixed evergreen forest and *Nothofagus* Blume forest. Data for the material examined indicate that specimens were collected in pitfall traps baited with unspecified carrion and flight interception traps. A few specimens were collected in Malaise traps. No recorded trapping events from dung in the material examined, certainly due to a lack of data.

Homocopris torulosus (Eschscholtz, 1822)
Figs 9–10, 21–22, 29, 35, 38, 41, 45, 47, 49, 54, 61, 67

Copris torulosa Eschscholtz, 1822: 29 (original description).
Copris valdiviana Philippi, 1859: 661 (original description).
Pinotus torulosus var. *minor* Luederwaldt, 1925: 68 (original description) (uncertain status, see remarks below).
Pinotus Dahli Landin, 1955: 5 (original description) **syn. nov.**

Copris (*Homocopris*) *torulosa* – Burmeister 1846: [3] (mention).
Copris torulosa – Solier 1851: 60 (monograph).
Copris torulosus – Redtenbacher 1868: 55 (distribution).
Pinotus torulosus – Harold 1869a: 133 (monograph); 1869b: 1011 (catalogue). — Waterhouse 1891: 361 (comment). — Bruch 1911: 187 (catalogue). — Gillet 1911: 62 (catalogue). — Joseph 1929: 31 (nidification). — Gutiérrez 1940: 277 (monograph). — Pereira 1941: 267 (checklist). — Blackwelder 1944: 208 (checklist). — Lange 19476: 313 (misidentification).
[*Copris*] *valdivianus* – Harold 1869b: 1011 (synonymy). — Heyne 1900: 62 (synonym). — Gillet 1911: 62 (synonym).
Copris valdivianus – Harold 1869a: 133 (synonym). — Reed 1876: 281 (synonym). — Bruch 1911: 187 (synonym).
[*Pinotus*] *torulosus* – Reed 1876: 281 (catalogue). — Heyne 1900: 62 (diagnosis, distribution).

Pinotus valdivianus – Waterhouse 1891: 361 (comment).
Pinotus (*P.*) *torulosus* var. *valdivianus* – Luederwaldt 1929: 649 (monograph).
Pinotus torulosus var. *Minor* – Luederwaldt 1929: 649 (monograph). — Gutiérrez 1940: 280 (monograph). — Blackwelder 1944: 208 (checklist). — Mondaca 2023: 223 (synonym).
Pinotus (*P.*) *torulosus* – Luederwaldt 1929: 650 (monograph).
Pinotus torulosus var. *valdivianus* – Gutiérrez 1940: 279 (monograph). — Blackwelder 1944: 208 (checklist).
Pinotus torulosus minor – Lange 1947: 313 (biology, distribution).
Dichotomius (*D.*) *torulosus* – Martínez 1959: 87 (catalogue).
Dichotomius torulosus – Halffter & Matthews 1966: 7 (biology). — Halffter 1977: 242 (nidification). — Halffter & Edmonds 1982: 89 (biology). — Zunino 1983: 541 (classification). — Klemperer 1983: 61 (ecology). — Cabrera Walsh & Gandolfo 1996: 586 (nidification).
[*Dichotomius* (*D.*) *torulosus*] var. *minor* – Vaz-de-Mello 2000: 193 (checklist).
[*Dichotomius* (*D.*) *torulosus*] var. *valdivianus* – Vaz-de-Mello 2000: 193 (checklist).
Homocopris torulosus – Vaz-de-Mello *et al.* 2010: 192 (new combination). — Jerez 2015: 1 (biology). — Ratcliffe *et al.* 2015: 197 (checklist). — González *et al.* 2015: 53 (ecology). — Tarasov & Génier 2015: 21 (phylogeny). — Tarasov & Dimitrov 2016: 7 (phylogeny). — Rebolledo *et al.* 2017: 27 (faunistic). — Tello *et al.* 2017: 61 (fossil); 2021: 139 (distribution). — Mondaca 2023: 223 (checklist, distribution).
Copris valdiviana – Mondaca 2023: 223 (synonymy).
Pinotus dahli – Mondaca 2023: 223 (synonym).

Differential diagnosis

Dorsal ocular width subequal to one-sixth interocular distance; lateral pronotal edge angular on anterior fourth in dorsal view; width of ellipse formed by lateral pronotal carina and edge approximately one third the elliptical length; posterior pronotal surface chagrined; elytral interstriae punctation visible at 10× magnification; metasternal depression entire, extending into anterior portion of median metasternal lobe. ♂ pronotal ridge with three sets of distinct bilaterally paired tubercles in large individuals; paramere apex acutely tipped; FLP endophallite elongate, bent, with internal angle adjacent to sclerotized extension.

Name-bearing type data

Copris torulosus Eschscholtz, neotype ♂, here designated (CMNC) (Fig. 54): "CHILE:Malleco | 17kmWAngol,800m | 8.XII.84-16.II.85 | S&JPeck,FIT | mixed *Nothofagus*"; "WORLD | SCARAB. | DATABASE | WSD00035423" [barcode label]; "Southern Neotropical Scarabs | database # AS2599338 | *Homocopris torulosus* | (Eschscholtz, 1822) ♂ | DET: A.B.T.Smith 2005" [with black border]; "N E O T Y P E ♂ | *Copris* | *torulosus* | Eschscholtz, 1822 | des. Génier & Darling, 2021" [on red card with black border.].

Pinotus torulosus var. *minor* Luederwaldt: no type material examined.

Pinotus dahli Landin, allotype ♂ (MZLU) (Fig. 57): "Chile" [handwritten]; "Allotypus" [red card with black border]; "*Pinotus Dahli* m. | allotype ♂ | B. O. Landin det" [partly handwritten]; "Photo 2018 | by MZLU"; "MZLU | Type no | 2775:2" [partly red]; "MZLU | 2018 | 001" [green paper]; "ZML.2005 | 202" [green paper]; "WORLD | SCARAB. | DATABASE | WSD00035268" [barcode label]; "Southern Neotropical Scarabs | database # AS2607242 | *Homocopris torulosus* | (Eschscholtz, 1822) ♂ | DET: A.B.T.Smith 2006"; "*Homocopris* ♂ | *torulosus* | (Eschscholtz, 1822) | det. Génier & Darling, 2018".

Type locality

17 km W Angol (800 m), Malleco, Chile.

Type material

Neotype of *Copris torulosus* (present designation)
CHILE • ♂ (Fig. 54); "CHILE:Malleco | 17kmWAngol,800m | 8.XII.84-16.II.85 | S&JPeck,FIT | mixed *Nothofagus*"; "WORLD | SCARAB. | DATABASE | WSD00035423" [barcode label]; "Southern Neotropical Scarabs | database # AS2599338 | *Homocopris torulosus* | (Eschscholtz, 1822) ♂ | DET: A.B.T.Smith 2005" [with black border]; "N E O T Y P E ♂ | *Copris* | *torulosus* | Eschscholtz, 1822 | des. Génier & Darling, 2021" [on red card with black border]; CMNC.

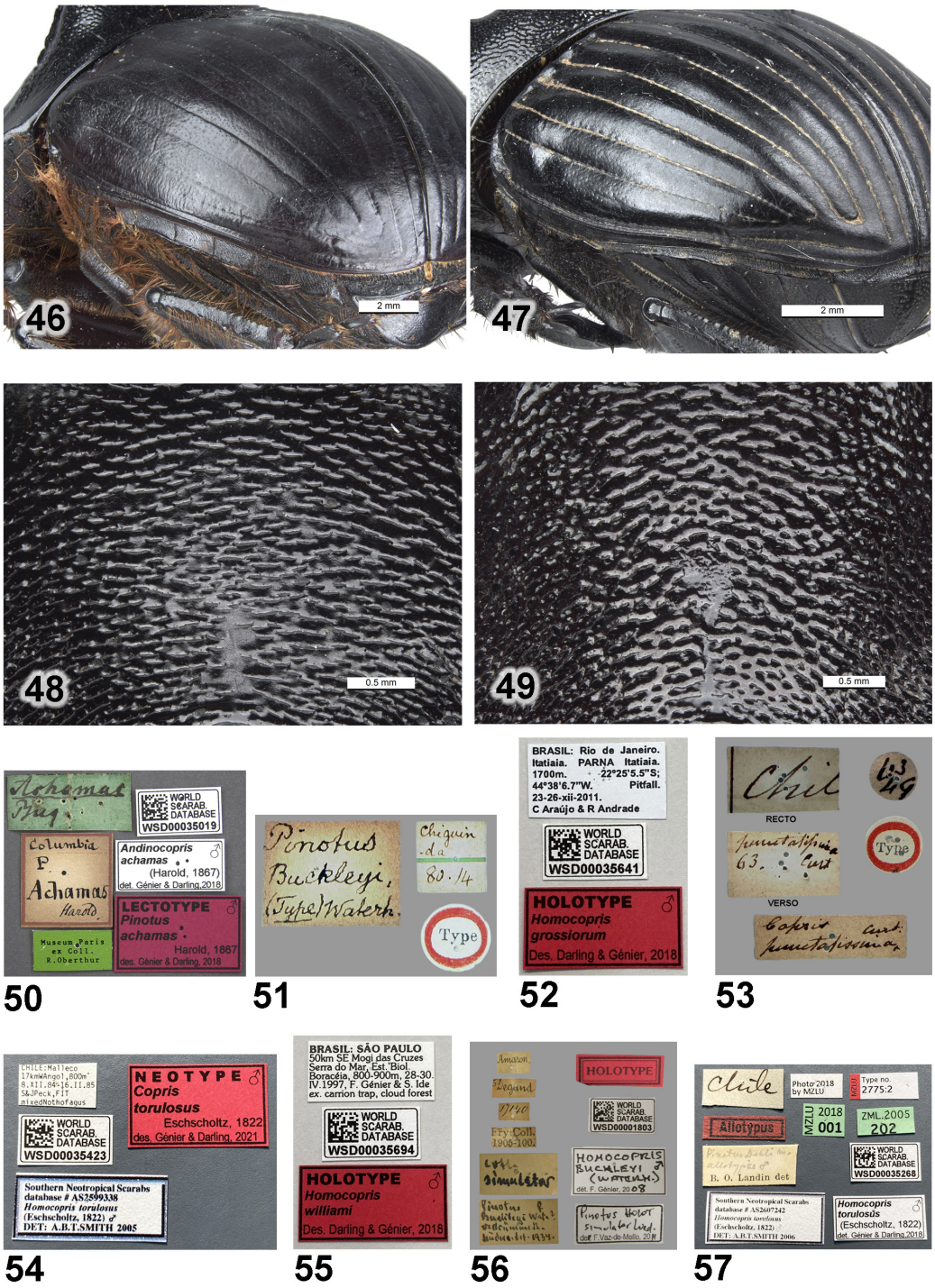
Allotype of *Pinotus dahli*
CHILE • ♂ (Fig. 57); "Chile" [handwritten]; "Allotypus" [red card with black border]; "*Pinotus Dahli* M. | allotype ♂ | B. O. Landin det" [partly handwritten]; "Photo 2018 | by MZLU"; "MZLU | Type no | 2775:2" [partly red]; "MZLU | 2018 | 001" [green paper]; "ZML.2005 | 202" [green paper]; "WORLD | SCARAB. | DATABASE | WSD00035268" [barcode label]; "Southern Neotropical Scarabs | database # AS2607242 | *Homocopris torulosus* | (Eschscholtz, 1822) ♂ | DET: A.B.T.Smith 2006"; "*Homocopris* ♂ | *torulosus* | (Eschscholtz, 1822) | det. Génier & Darling, 2018"; MZLU.

Paratype de *Pinotus dahli*
CHILE • 1 ♀; same locality as for allotype; [no date]; [anonymous]; MZLU.

Other material examined (163 ♂♂, 206 ♀♀)

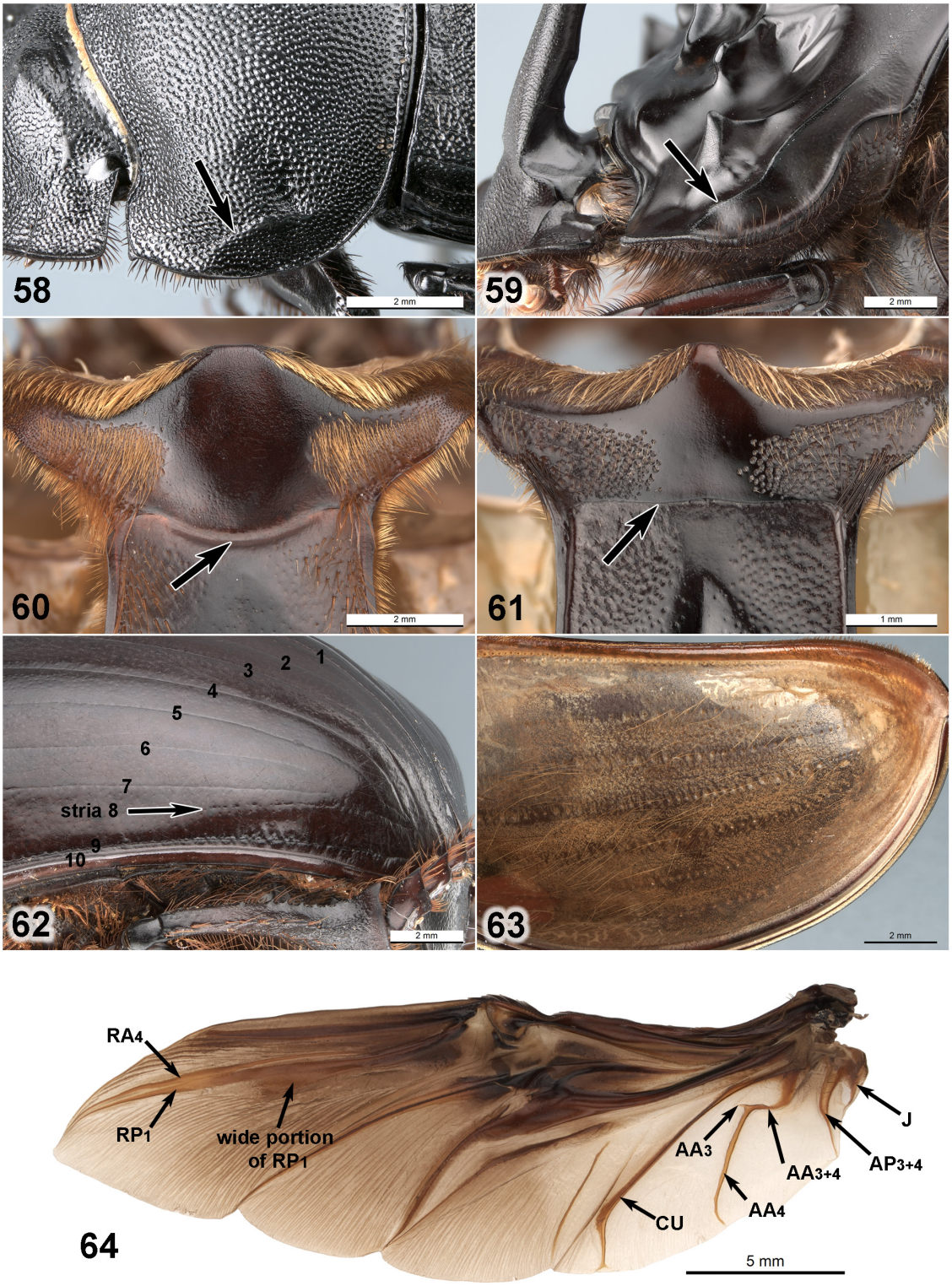
ARGENTINA – **Río Negro** • 1 ♂; El Bolsón; [41°58′ S, 71°32′ W]; Nov. 1967; [anonymous]; CPFA • 1 ♀; same locality as for preceding; [no date]; A. Kovács; NMPC • 1 ♀; same locality as for preceding; 1956; A. Kovács; NMPC • 1 ♂; same locality as for preceding; Dec. 1956; [anonymous]; NMPC.

CHILE • 6 ♂♂, 1 ♀; [unspecified locality]; 1907; M.J. Rivera; MNHN • 1 ♂; same locality as for preceding; [no date]; M.J. Rivera; CMNC. – **Región de Los Lagos** • 1 ♂, 2 ♀♀; 11 km NW of Castro, Isla Chiloé; [42°24′ S, 73°51′ W]; 200 m; 27 Dec. 1984–1 Feb. 1985; S. and J. Peck; ravine second growth forest, carrion trap; CMNC • 1 ♂, 9 ♀♀; 13 km W of Entre Lagos; [40°37′30″ S, 72°44′0″ W]; 200 m; 21 Dec. 1984–8 Feb. 1985; S. and J. Peck; forest remnant, carrion trap; CMNC • 2 ♀♀; 34 km E of Puerto Montt, Lago Chapo; [41°25′ S, 72°35′ W]; 300 m; 24 Dec. 1984–2 Feb. 1985; S. and J. Peck; second growth *Nothofagus*, carrion trap; CMNC • 1 ♂; Ahori Alto; 21–23 Feb. 1988; 70 m; L. Masner; CNC • 1 ♀; Repucura forest trail, Anticura, Parque Nacional Puyehue; [40°40′ S, 72°10′30″ W]; 500 m; 19 Dec. 1984–6 Feb. 1985; S. and J. Peck; forest, carrion trap; CMNC • 1 ♂; Terao, 10 km S of Chonchi, Isla Chiloe; [42°43′1″ S, 73°38′47″ W]; 45 m; 12–13 Feb. 2005; [anonymous]; yellow pan trap; CMNC • 1 ♂; [unspecified locality]; 30 Jan. 2007; [anonymous]; CMD • 1 ♀; same locality as for preceding; 10 Feb. 2007; [anonymous]; CMD. – **Región de Los Ríos** • 3 ♂♂, 3 ♀♀; 34 km WNW of La Union; [40°13′45″ S, 73°21′35″ W]; 700 m; 17 Dec. 1984–7 Feb. 1985; S. and J. Peck; mixed evergreen forest, carrion trap; CMNC • 3 ♂♂; Corral; [39°53′ S, 73°26′ W]; 14 Oct. 1913; R.H. Beck; CAS • 1 ♂; same locality as for preceding; 16 Oct. 1913; R.H. Beck; CAS • 1 ♂, 1 ♀; same locality as for preceding; 20 Oct. 1913; R.H. Beck; CAS • 1 ♂; Panguipulli; [39°38′20″ S, 72°20′30″ W]; Jan. 1952: [anonymous]; CMNC • 1 ♂; same locality as for preceding; 1927; [anonymous]; CAS • 2 ♂♂, 3 ♀♀; Valdivia; [39°50′ S, 73°13′ W]; [no date]; [anonymous]; MNHN. – **Región del Biobío** • 1 ♀; 4 km SE of Recinto; [36°52′ S, 71°36′ W]; 700 m; 17 Dec. 1976; H.F. Howden; CMNC • 2 ♀♀; 40 km E of San Carlos; [36°33′ S, 71°34′ W]; 24 Dec. 1950; Ross and Michelbacher; CAS • 5 ♂♂, 4 ♀♀; 60 km SE od Chillan, Thermas Road; [36°54′ S, 71°33′ W]; 1300 m; 7 Dec. 1984–19 Feb. 1985; S. and J. Peck; beech forest, flight interception trap; CMNC • 1 ♂; Arauco; [37°15′ S, 73°19′ W]; 15 Apr. 1965; Sanfeliu; CMNC • 1 ♀; Concepción; [36°48′ S, 73°1′ W]; [no date]; [anonymous]; CAS • 1 ♂, 1 ♀; Contulmo; [38°1′ S, 73°14′ W]; 28 Mar. 1940; D.S. Bullock; CAS • 1 ♀; same locality as for preceding; 7 Jan. 1967; Sanfeliu; CNC • 1 ♂; same locality as for preceding; 10 Feb. 1967; T. Cekalovic; CNC • 7 ♂♂, 4 ♀♀; same locality as for preceding; 10 Mar. 1969; Sanfeliu; CNC • 7 ♂♂, 1 ♀; same locality as for preceding;



Figs 46–57. 46–49. Elytral striae, posterolateral view. **46**. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov., lectotype, ♂ (MNHN). **47**. *Homocopris torulosus* (Eschscholtz, 1822), neotype, ♂ (CMNC). Anterior pronotal surface. **48**. *Homocopris grossiorum* Darling & Génier sp. nov., holotype, ♂ (CEMT). **49**. *Homocopris torulosus*, neotype, ♂ (CMNC). **50–57**. Type specimen labels. **50**. *Pinotus achamas* Harold, 1867. **51**. *Pinotus buckleyi* (Waterhouse, 1891). **52**. *Homocopris grossiorum*. **53**. *Copris punctatissimus* (Curtis, 1845). **54**. *Copris torulosus* Eschscholtz, 1822. **55**. *Homocopris williami* Darling & Génier sp. nov. **56**. *Pinotus simulator* Luederwaldt, 1936. **57**. *Pinotus dahli* Landin, 1955.

20 Dec. 1969; T. Cekalovic; CNC • 1 ♀; Hulpencillo; [36°47′ S, 73°5′30″ W]; 20 Mar. 1964; T. Cekalovic; CNC • 2 ♂♂, 2 ♀♀; Invernada; [36°52′30″ S, 71°34′30″ W]; Mar. 1970; L.E. Peña; PMOC • 1 ♂, 1 ♀; Las Trancas; [36°54′ S, 71°40′ W]; 1 Feb. 1974; L.E. Peña; PMOC • 1 ♂, 1 ♀; Las Trancas, Curico; [36°54′ S, 71°30′ W]; 1 Mar. 1979; L.E. Peña; CMNC • 1 ♂; Los Castaños, Chillán, El Carmen; [36°37′30″ S, 72°5′0″ W]; 21 Nov. 2003; M. Snižek; NMPC • 1 ♂; Mulchén; [37°43′ S, 72°14′ W]; Jan. 1935; Gutiérrez; CMNC • 2 ♂♂; same locality as for preceding; Dec. 1935; Gutiérrez; CMNC • 3 ♂♂, 1 ♀; Recinto; [36°48′ S, 71°44′ W]; 1 Mar. 1971; [anonymous]; CPFA • 2 ♂♂, 2 ♀♀; Talcahuano; [36°45′ S, 73°6′ W]; 1841; Jacquinot; MNHN. – **Región del Maule** • 1 ♂; Fundo Malcho, Cordillera Parral; [36°19′ S, 71°25′ W]; Dec.1956; M. Rivera; CNC • 2 ♂♂, 2 ♀♀; same locality as for preceding; May 1957; [anonymous]; CPFA • 1 ♀; same locality as for preceding; 1 May 1957; [anonymous]; CPFA • 1 ♂; same locality as for preceding; 11–20 Nov. 1964; M. Rivera; CNC • 2 ♀♀; Romehual, Cordillera Parral; 5–10 Nov. 1960; [anonymous]; CPFA • 1 ♂, 3 ♀♀; Vilches Alto, Talca; [35°36′ S, 71°4′ W]; Dec. 1973; J. Valencia; CMNC. – **Región La Araucanía** • 2 ♂♂; 10 mi NE of Pucón; [39°15′30″ S, 71°46′0″ W]; 12 Jan. 1951; Ross and Michelbacher; CAS • 7 ♂♂, 7 ♀♀; 11 km W of Angol; [37°49′30″ S, 72°47′0″ W]; 1000 m; 9 Dec. 1984–16 Feb. 1985; S. and J. Peck; boggy mixed forest remnant, carrion trap; CMNC • 1 ♂, 1 ♀; 15 km W of Victoria; [38°15′ S, 72°31′ W]; 200 m; 28–31 Dec. 1976; S. Peck; dung; BDGC • 6 ♂♂, 11 ♀♀; same locality as for preceding; 28–31 Dec. 1976; S. Peck; carrion; CMNC • 10 ♂♂, 27 ♀♀; same locality as for preceding; 28–31 Dec. 1976; S. Peck; dung; CMNC • 1 ♂; same locality as for preceding; 28–31 Dec. 1976; S. Peck; carrion; CNC • 21 ♂♂, 17 ♀♀; same locality as for preceding; 28–31 Dec. 1976; S. Peck; dung; CNC • 2 ♀♀; same locality as for preceding; 28 Dec. 1976; H.F. Howden; CNC • 1 ♀ (alloreferent of *Copris torulosus*), 5 ♂♂, 8 ♀♀; 17 km W of Angol; [37°48′ S, 72°51′30″ W]; 800 m; 8 Dec. 1984–16 Feb. 1985; S. and J. Peck; mixed *Nothofagus*, flight interception trap; CMNC • 2 ♀♀; 20 km E of Manzanar; [38°26′30″ S, 71°31′0″ W]; 1100 m; 19–25 Dec. 1976; S. Peck; dung; CNC • 1 ♂; 20 km E of Temuco; [38°46′ S, 72°22′ W]; 8 Jan. 1951; Ross and Michelbacher; CAS • 1 ♂, 2 ♀♀; 21 km NE of Pucón, Lago Caburga; [39°11′ S, 71°49′ W]; 600 m; 15 Dec. 1984–10 Feb. 1985, S. and J. Peck; mixed forest remnant, flight interception trap; CMNC • 2 ♂♂, 1 ♀; 22 km E of Temuco; [38°40′ S, 72°15′30″ W]; Jun.–Jul. 1951; M.G. Smith; CAS • 1 ♂; same locality as for preceding; 2 Jan. 1951; Ross and Michelbacher; CAS • 1 ♂, 1 ♀; 30 km NE of Villarrica; [39°8′47″ S, 72°3′32″ W]; Jan. 1965; L. Peña; CAS • 1 ♀; same locality as for preceding; 16–31 Dec. 1964; L. Peña; CAS • 1 ♀; 4 km W of Victoria; [38°14′ S, 72°24′30″ W]; 300 m; 26–27 Dec. 1976; H.F. Howden; CNC • 3 ♂♂, 6 ♀♀; 40 km W of Angol, Parque Nacional Nahuelbuta; [37°49’30″ S, 73°0′30″ W]; 1200–1500 m; 9 Dec. 1984–17 Feb. 1985; S. & J. Peck; flight interception trap; CMNC • 1 ♀; 6 km W of Curacautín; [38°25′ S, 71°58′ W]; 750 m; 12 Dec. 1984–16 Feb. 1985; S. and J. Peck; grazed *Nothofagus* remnant, carrion trap; CMNC • 1 ♀; 9 km S of Pucón, Parque Nacional Volcán Villarrica; [39°22′ S, 71°57′30″ W]; 900 m; 15 Dec. 1984–10 Feb. 1985; S. and J. Peck; *Nothofagus* grove on ash, carrion trap; CMNC • 1 ♀; along road near Río Picoiquén, Cotoco, Parque Nacional Nahuelbuta; [37°45.812′ S, 72°59.314′ W]; 980 m; 15 Feb. 2004; A. Smith, M. Paulsen and J. Mondaca; CMNC • 1 ♀; Boroa Central, SE Nueva Toltén; [39°16′ S, 73°8′ W]; 22 Jan. 2004; M. Snižek; NMPC • 1 ♀; Collipulli; [37°57′ S, 72°26′ W]; 15 Feb. 1967; Mendez; CNC • 1 ♀; Crest of Sierra Nahuelbuta, W of Angol; [37°50′ S, 72°52′ W]; 1200 m; 13 Jan. 1951; [anonymous]; CAS • 2 ♀♀; Curacautín; [38°26′ S, 71°53′ W]; 20 Jul. 1950; [anonymous]; CAS • 3 ♀♀; same locality as for preceding; 7 Apr. 1971; P. Ramírez; CMNC • 3 ♂♂, 8 ♀♀; Flor del Lago, 15 km NE of Villarrica; [39°10′ S, 72°10′ W]; 300 m; 14 Dec. 1984–10 Feb. 1985; S. and J. Peck; *Nothofagus* forest, carrion trap; CMNC • 6 ♂♂, 13 ♀♀; same locality as for preceding; 14 Dec. 1984–10 Feb. 1985; S. and J. Peck; *Nothofagus* forest, flight interception trap; CMNC • 1 ♀; Manzanar; [38°28.071′ S, 71°41.873′ W]; 800 m; 1–3 Feb. 2005; S. Bilý; NMPC • 8 ♂♂, 7 ♀♀; Monumento Natural Contulmo, Purén; [38°1′ S, 73°10′ W]; 350 m; 11 Dec. 1984–13 Feb. 1985; S. and J. Peck; mixed evergreen forest, flight interception trap; CMNC • 1 ♀; Parque Nacional Nahuelbuta; [37°48′ S, 73°0′ W]; 1200 m; 9 Sep. 1966; E.I. Schlinger and E.I. Erwin; *Nothofagus* and *Araucaria* association; CAS • 1 ♀; Pucón; [39°16′ S, 71°58′ W]; 9–16 Nov. 1989; S.A. Marshall; dung trap near lake; CMNC • 1 ♀; Quepe; [38°52′ S, 72°37′ W]; 31 Oct. 1965;



Figs 58–64. 58. *Copris victorini* Boheman, 1857, pronotum oblique view. **59**. *Sulcophanaeus carnifex* (Linnaeus, 1758), pronotum oblique view. **60**. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov., meso-metasternal suture, ventral view. **61**. *Homocopris torulosus* (Eschscholtz, 1822), meso-metasternal suture, ventral view. **62**. *A. achamas*, left elytron, oblique view. **63**. *H. torulosus*, elytron underside. **64**. *Sulcophanaeus carnifex*, hindwing.

T. Cekalovic; CNC • 2 ♀♀; S Melipeuco; [38°52′ S, 71°41′30″ W]; 23 Jan. 2004; M. Snižek; NMPC • 4 ♂♂, 5 ♀♀; Salto de la Princesa, 20 km E of Curacautín; [38°28′30″ S, 71°40′30″ W]; 1000 m; 12 Dec. 1984–16 Feb. 1985; S. and J. Peck; *Nothofagus* forest, flight interception trap; CMNC • 3 ♂♂, 2 ♀♀; Selva Obscura; [38°22′ S, 72°10′ W]; 6 Oct. 1967; C. Oyarzo; CNC • 2 ♂♂, 2 ♀♀; Sendero Lemu Mau, Monumento Natural Contulmo; [38°74′ S, 73°11.13′ W]; 410 m; 8–24 Dec. 2002; Thayer and Newton; (FMHD #2002-062); *Nothofagus obliqua-Eucryphia cordifolia* with fern and bamboo understory, carrion trap, octopus; CMNC • 1 ♀; Temuco; [38°45′ S, 72°36′ W]; Jan. 1906; [anonymous]; CAS • 1 ♂; same locality as for preceding; Jan. 2004; [anonymous]; CMD • 1 ♂; same locality as for preceding; Feb. 2002; [anonymous]; CMD • 4 ♂♂, 4 ♀♀; same locality as for preceding; 16 Nov. 1926; [anonymous]; CAS • 1 ♀; Termas del Río Blanco, Curacautín; [39°6′30″ S, 71°37′0″ W]; 3 Feb. 2004; M. Snižek; NMPC • 1 ♂; Victoria; [38°14′ S, 72°21′ W]; [no date]; [anonymous]; MNHN • 1 ♀; same locality as for preceding; [no date]; F. Schneider; NMPC.

Description

Male neotype (Figs 9, 21, 29, 35, 38, 47, 49)

Measurements. Body length 13.9 mm.

Head. Clypeus bidentate with broad, rounded teeth. Anteroventral clypeal tooth broad. Clypeal and genal surface rugose, clypeogenal suture demarcated by shallow notch. Posterior genal angle obtuse. Frontal surface reduced, smooth. Dorsal ocular width subequal to one-sixth interocular distance. Interocular surface medially smooth. Cephalic horn emerging centrally from clypeofrontal surface, tapering apically, straight, 2.9 mm in length.

Prothorax. Anterior pronotal edge medially indented. Lateral pronotal edge angular on anterior fourth in dorsal view. Anterolateral pronotal lobe surface with irregular transverse rugulae. Anterior pronotal declivity surface (Fig. 49) with transverse irregular, fused punctures. Pronotal ridge with three sets of distinct bilaterally paired tubercles. Posterior pronotal surface chagrined. Prosternal apex acutely tipped.

Elytra (Fig. 47). Glossy overall. Striae 1–6 widest anteriorly; narrowing posteriorly. Third and fourth striae posteriorly joined. Eighth stria absent throughout. Ninth stria effaced along anterior quarter of elytral length. Interstriae convex, minutely punctate.

Hindwing (Fig. 41). Membrane edge between AP and AA sinuous. AP vein entire, converging with J.

Ventrites. Meso-metasternal suture straight. Median lobe of metasternum (Fig. 45) with deep impression extending throughout the entire length. Lateral metasternal lobe sparsely setose. Fifth abdominal ventrite with dense medial punctation. Pygidium coarsely punctate.

Prothoracic legs. Anterior and posterior surfaces of profemur with sparse row of long dark setae. Ventral profemoral surface finely punctate. Protibia with three distinct teeth. Protibial forespur parallel-sided, curving downward apically.

Mesothoracic legs. Posterior surface of mesotrochanter with three dark setae. Anterior and posterior surfaces of mesofemur with sparse row of long dark setae. Outer surface of mesotibia serrate. Width at mesotibial apex one-third mesotibial length.

Metathoracic legs. Posterior surface of metatrochanter with three dark setae. Anterior and posterior surfaces of metafemur with sparse row of long dark setae. Outer surface of metatibia serrate. Width at metatibial apex one-third metatibial length.

Male genitalia. Aedeagus length: 4.1 mm. Medially paired sclerites of genital segment short (Fig. 38). Paramere (Fig. 29) with apex acutely tipped. FLP endophallite (Fig. 35) elongate, bent, with internal angle adjacent to sclerotized extension.

Female alloreferent specimen (Figs 10, 22)

Similar to male with the following exceptions: clypeal teeth separated by V-shaped notch. Clypeofrontal carina width one-third interocular distance. Entire anterior pronotal surface with irregular, fused rugosities. Anterior pronotal ridge low, followed by shallow concavity. Protibial forespur apex sharply tapered, curving inward.

Variation

Body length 13–20 mm. Small males with medially projecting clypeofrontal ridge instead of cephalic horn. Pronotal ridge in small males low, medially notched.

Distribution (Fig. 67)

Chile in Región de los Lagos, Región de Los Ríos, Región de Valparaíso, Región del Biobío, Región del Maule, Región la Araucanía, Región Metropolitana de Santiago) and Argentina (Río Negro). Recorded elevations vary from 45 m to 1500 m. Rebolledo *et al.* (2017) report an elevation range from 0 m to 2000 m.

Natural history

Examined specimens were collected in beech forest, boggy mixed forest remnants, forest remnants, grazed *Nothofagus* remnants, mixed evergreen forest, mixed forest remnants, mixed *Nothofagus*, *Nothofagus* and *Araucaria* Juss. association, *Nothofagus* forest, *Nothofagus* grove on ash, *Nothofagus obliqua–Eucryphia cordifolia* with fern and bamboo understorey, second growth ravine forest and second growth *Nothofagus*. Attracted to pitfall traps baited with unspecified carrion and octopus carrion, unspecified dung and flight interception traps. A single specimen collected in a yellow pan trap.

Remarks

Copris valdivianus Philippi, 1859 was described from an unspecified number of male and female syntypes. This name was synonymized by Harold (1869a) under *Pinotus torulosus* (= *H. torulosus*), which he also considered a senior synonym of *Copris punctatissimus*. Luederwaldt (1929) later treated *C. valdivianus* as a variety of *P. torulosus*. José Mondaca recently published a checklist of Scarabaeoidea of Chile (Mondaca 2023) in which *C. valdivianus* is synonymized with *H. torulosus*. This synonymy is based on a putative male syntype deposited in the Paris Museum. “It is very probable that the specimen from Paris is the syntype of *C. valdiviana* since the specimen studied by Philippi is not found in the MNNC-Santiago. It is also not in the Prague Museum which also has some types of Philippi. It is probable that the possible syntype reached the Paris Museum through Philibert Germain. The locality written on the original label agrees with what was indicated by Philippi in the original publication and the spelling printed on the original label also agrees with that of the author of the species, therefore this only known specimen closest to the syntype that we have available.” (José Mondaca pers. com.).

The type material of *Pinotus dahli* Landin, 1956 (holotype ♀, allotype ♂) was studied. We were unable to find any differences supporting the validity of this species. We therefore propose the following new synonymy, the second epithet being valid: *Pinotus dahli* Landin, 1956 = *Homocopris torulosus* (Eschscholtz, 1822) syn. nov.

We were unable to study type material of *Pinotus torulosus* var. *minor* Luederwaldt, 1925. Gutiérrez (1940) state that two males and four females from Chile and a single male specimen from Espírito Santo,

Brazil, are deposited in the MZSP. The syntype series is probably a mixed series of *H. torulosus* and *H. grossiorum* if properly labelled. We have requested images of these syntypes, and we should be able to confirm the synonymy with *H. torulosus* once we obtain them.

Homocopris williami Darling & Génier sp. nov.
urn:lsid:zoobank.org:act:94FAF15A-7945-460D-BF15-69FB3D05CBD0
Figs 11–12, 23–24, 30, 36, 55, 66

Pinotus torulosus – Lange 1947: 313 (distribution).

Differential diagnosis

Dorsal ocular width subequal to one-sixth interocular distance; anteromedial pronotal edge curvature tends to be continuous; posterior pronotal surface uniformly punctate; elytral interstriae punctation tends to be visible at 10× magnification; metasternal depression divided anteriorly. ♂ pronotal ridge with two sets of distinct bilaterally paired tubercles in large individuals; paramere apex evenly rounded; FLP endophallite elongate, with two indentations along right edge.

Etymology

Williami is the Latin singular genitive form of William. This species is named in honour of the second author's brother, William Darling.

Name-bearing type data

Holotype ♂ (MZSP) (Fig. 55): "BRASIL: SÃO PAULO | 50km SE Mogi das Cruzes | Serra do Mar, Est. Biol. | Boracéia, 800-900m, 28-30. | IV.1997, F. Génier & S. Ide | *ex*. carrion trap, cloud forest"; "WORLD | SCARAB. | DATABASE | WSD00035694" [barcode label]; "HOLOTYPE ♂ | *Homocopris* | *williami* | Des. Darling & Génier, 2018" [on red card with black border].

Type locality

Estação Biológica de Boracéia, 23°38′55″ S, 45°52′20″ W, 800–900 m, Salesópolis, Serra do Mar Mountains, São Paulo, Brazil.

Type material

Holotype

BRASIL • ♂ (Fig. 55); São Paulo, Salesópolis, Estação Biológica de Boracéia, 50 km SE of Mogi das Cruzes, Serra do Mar; [23°38′55″ S, 45°52′20″ W]; 800–900 m; 28–30 Apr. 1997; F. Génier and S. Ide; cloud forest, dung trap; MZSP.

Allotype

BRASIL • ♀; same collection data as for holotype; MZSP.

Other material examined (55 ♂♂, 32 ♀♀)

Paratypes

BRAZIL – **Rio de Janeiro** • 5 ♂♂; Nova Friburgo, Upper Macaé River ("Haut Rio Macaé"); [22°23′ S, 42°28′ W]; Apr. 1884; P. Germain; MNHN • 1 ♂; unspecified locality]: [no date]; [anonymous]; MNHN. – **Rio Grande do Sul** • 2 ♀♀; Nova Prata; [28°47′ S, 51°36′ W]; 30 Sep. 2001; C. Arioli; CEMT • 1 ♂, 4 ♀♀; São Francisco de Paula; [29°26′49″ S, 50°34′45″ W]; 14 Jan. 2008; L. Audino; human dung; CEMT. – **Santa Catarina** • 1 ♂, 2 ♀♀; Bom Jardim da Serra; [28°20′30″ S, 49°37′30″ W]; Dec. 2001; C. Arioli; CEMT • 3 ♂♂; same locality as for preceding; Jan. 2002; C. Arioli; CEMT • 1 ♂, 1 ♀; same locality as for preceding; 28 Dec. 2001; C. Arioli; CEMT • 4 ♀♀; same locality as for preceding;

3 Jan. 2002; C. Arioli; CEMT • 1 ♂; Campos Novo; [27°23′ S, 51°12′ W]; Feb. 2011; R.C. Campos; pitfall trap; CEMT • 1 ♂; same locality as for preceding; Feb. 2013; R.C. Campos; pitfall trap; CEMT • 1 ♂, 1 ♀; Monte Castelo; [26°43′ S, 50°19′ W]; 881 m; 6 Aug. 2012; A.L. Brandl; mata nativa, pitfall trap; CEMT •1 ♂; Seara, Nova Teutônia; [27°11′ S, 52°23′ W]; [no date]; F. Plaumann; CAS • 1 ♂; same locality as for preceding; Jun.; F. Plaumann; CAS • 2 ♂♂; same locality as for preceding; Sep.; F. Plaumann; CAS • 1 ♂; same locality as for preceding; Nov.; F. Plaumann; CAS • 1 ♂; same collection data for preceding; GHCM • 1 ♂; Urubici; [27°59′ S, 49°35′ W]; 25 Nov. 2012; J.A. Bogoni; pitfall trap; CEMT • 1 ♂, 1 ♀; Urubici; [28°8′21″ S, 49°37′51″ W]; 1300 m; 17 Dec. 2015; P.G. da Silva; pitfall trap: human feces; CEMT • 1 ♀; Urubici; [28°9′32″ S, 49°37′49″ W]; 1600 m; 20 Nov. 2015; P.G. da Silva; pitfall trap: human feces; CEMT • 1 ♂; same locality as for preceding; 17 Dec. 2015; P.G. da Silva; pitfall trap: human feces; CEMT • 2 ♂♂; same locality as for preceding; 23 Apr. 2016; P.G. da Silva; pitfall trap: human feces; CEMT. – **São Paulo** • 1 ♂, 1 ♀; same collection data as for holotype; CEMT • 8 ♂♂, 2 ♀♀; same locality as for holotype; 28–30 Apr. 1997, F. Génier and S. Ide; cloud forest, carrion trap; CMNC • 12 ♂♂, 8 ♀♀; same locality as for holotype; 28–30 Apr. 1997; F. Génier and S. Ide; cloud forest, dung trap; CMNC • 1 ♂; same locality as for holotype; 28–30 Apr. 1997; F. Génier and S. Ide; cloud forest, feces trap; CMNC • 1 ♀; Salesópolis, Estação Biológica de Boracéia; [23°38′55″ S, 45°52′20″ W]; 22 Sep. 1965; [anonymous]; CEMT • 1 ♂; same locality as for preceding; 6 Oct. 1965; [anonymous]; dung; CEMT • 1 ♀; same locality as for preceding; 21 Sep. 2012; A. Díaz; Atlantic Forest, human feces; CEMT • 1 ♂; Santo André, Estação Biológica do Alto da Serra; [23°47′ S, 46°18′ W]; Apr. 1926; [anonymous]; MZSP • 1 ♂; São Miguel Arcanjo, Parque Estadual Carlos Botelho; [24°3′59″ S, 47°59′39″ W]; 580 m; 13 May 2012; M. Boutefeu; *Tapirus* feces; CEMT • 1 ♂; same locality as for preceding; 15 May 2012; M. Boutefeu; *Tapirus* feces; CEMT • 1 ♂; São Miguel Arcanjo, Parque Estadual Carlos Botelho; [24°3′40″ S, 47°58′44″ W]; 806 m; 29 Jan. 2012; E. Bovy (1); human feces; CEMT • 3 ♀♀; São Miguel Arcanjo, Parque Estadual Carlos Botelho; [24°3′46″ S, 47°58′44″ W]; 823 m; 29 Jan. 2012; E. Bovy (2); human feces; CEMT • 2 ♂♂; [no date]; [anonymous]; MNHN.

Description

Male holotype (Figs 11, 23, 30, 36)

Measurements. Body length 15.1 mm.

Head. Clypeus bidentate with broad, rounded teeth. Anteroventral clypeal tooth broad. Clypeal and genal surface rugose, clypeogenal suture demarcated by shallow notch. Posterior genal angle obtuse. Frontal surface reduced, smooth. Dorsal ocular width subequal to one-sixth interocular distance. Interocular surface medially smooth. Cephalic horn emerging centrally from clypeofrontal surface, tapering apically, gently curved, 4.7 mm in length.

Prothorax. Anteromedial pronotal edge curvature continuous. Lateral pronotal edge angular on anterior fourth in dorsal view. Anterior inclined pronotal surface with fine, transverse rugosities. Pronotal ridge with two sets of distinct bilaterally paired tubercles. Posterior pronotal surface uniformly punctate. Prosternal apex acutely tipped.

Elytra. Glossy overall. Striae 1–6 widest anteriorly; narrowing posteriorly. Third and fourth striae posteriorly joined. Eighth stria absent throughout. Ninth stria effaced along anterior quarter of elytral length. Interstriae convex, finely punctate.

Hindwing. Membrane edge between AP and AA sinuous. AP vein entire, converging with J.

Ventrites. Meso-metasternal suture straight. Surface of median metasternal lobe with uneven texture and deep, anteriorly divided impression. Lateral metasternal lobe densely setose. Fifth abdominal ventrite with sparse medial punctation. Pygidium coarsely punctate.

Prothoracic legs. Anterior and posterior surfaces of profemur with dense row of long dark setae. Ventral profemoral surface finely punctate, sparsely setose. Protibia with three distinct teeth. Protibial forespur apically tapered, curving inward.

Mesothoracic legs. Posterior surface of mesotrochanter with tuft of long dark setae. Anterior and posterior surfaces of mesofemur with sparse row of long dark setae. Outer surface of mesotibia serrate. Width at mesotibial apex one-third mesotibial length.

Metathoracic legs. Posterior surface of metatrochanter with tuft of long dark setae. Anterior and posterior surfaces of metafemur with sparse row of long dark setae. Outer surface of metatibia serrate. Width at metatibial apex one-third metatibial length.

Male genitalia. Aedeagus length: 3.5 mm. Medially paired sclerites of genital segment elongate, subequal in length to lateral sclerites. Paramere (Fig. 30) laterally flattened, slightly tapering from base to apex with apex evenly rounded. FLP endophallite (Fig. 36) elongate with two indentations along right edge.

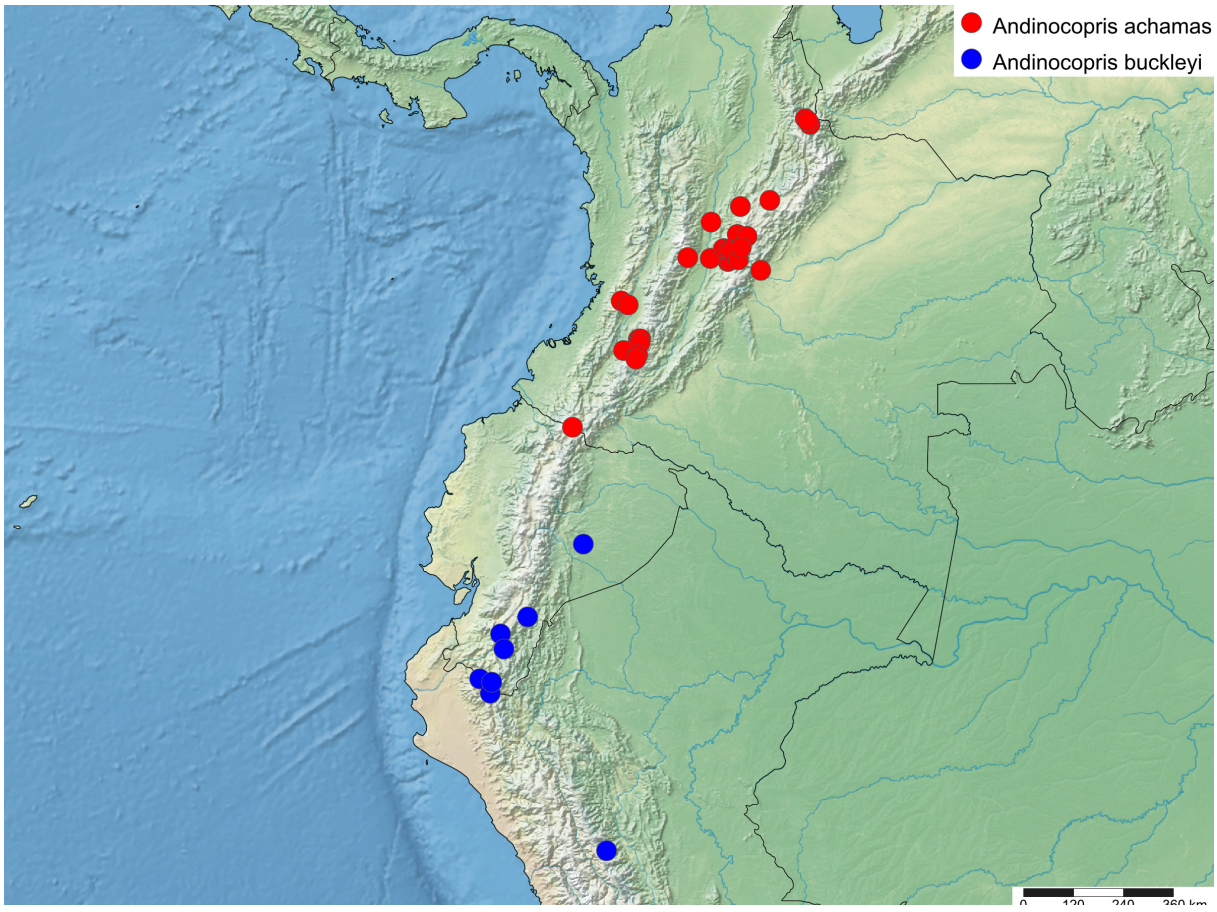


Fig. 65. *Andinocopris achamas* (Harold, 1867) gen. et comb. nov. and *Andinocopris buckleyi* (Waterhouse, 1891) gen. et comb. nov., distribution map. Legend and scale bar included in the top and bottom right corners, respectively.

Female allotype (Figs 12, 24)

Similar to male with the following exceptions: Body length 14.3 mm. Clypeofrontal carina transverse, centrally raised. Interocular surface chagrined. Anterior pronotal ridge low, followed by shallow concavity.

Variation

Body length 13–19 mm. Small males with medially projecting clypeofrontal ridge instead of cephalic horn. Anteromedial pronotal edge evenly curved more often than indented. Pronotal ridge in small males low, medially notched. Elytral interstriae finely punctate (visible at 10×) more often than minutely punctate (invisible at 10×).

Distribution (Fig. 66)

Serra do Mar and Serra Geral Mountains in the Brazilian states of Rio de Janeiro, São Paulo, Santa Catarina, and Rio Grande do Sul, with recorded elevations from 800 to 1600 m.

Natural history

Specimens with data were collected in cloud and sub-montane Atlantic Forest. Some specimens came to carrion and dung traps, pitfall traps baited with human faeces and faeces of *Tapirus* Brisson, 1762 at elevations between 580 m and 1600 m.

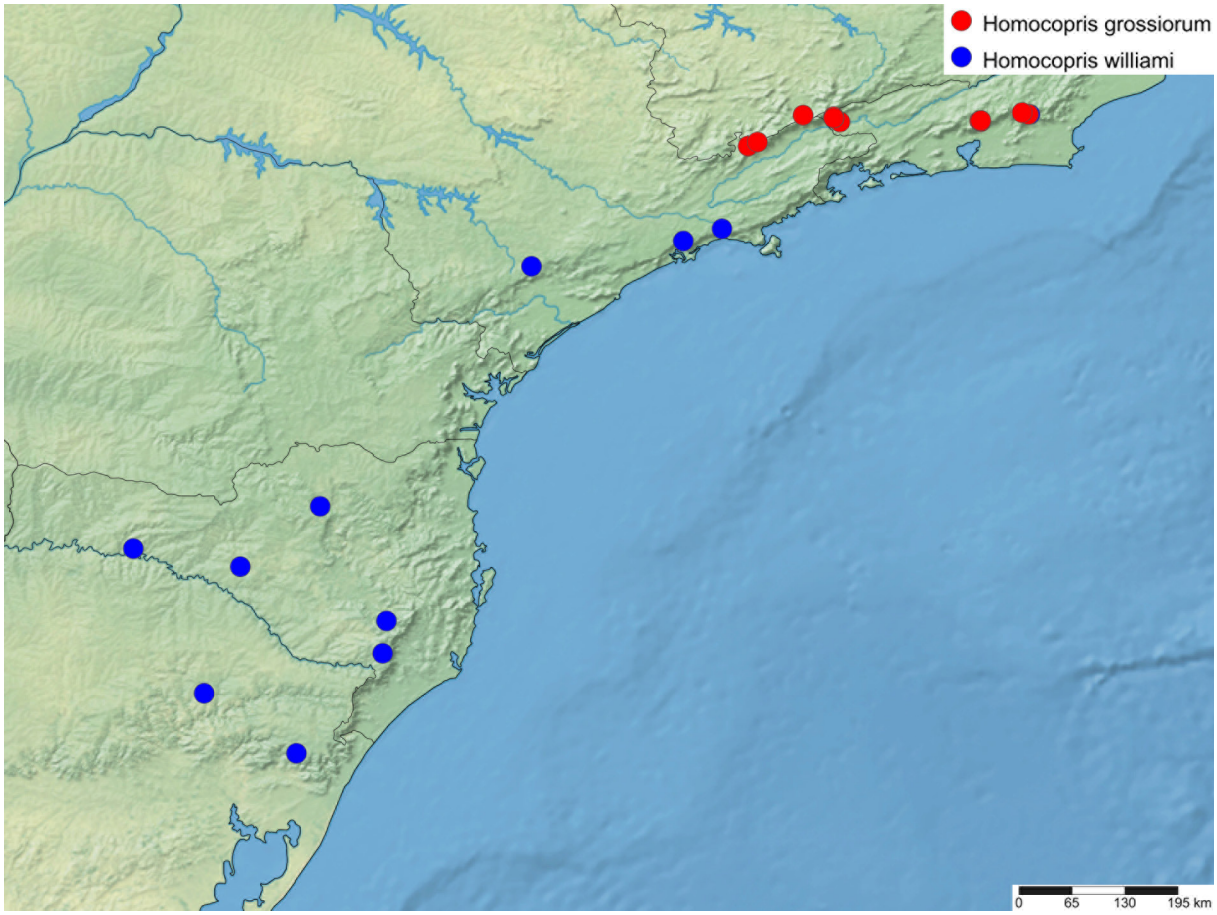


Fig. 66. *Homocopris grossiorum* Darling & Génier sp. nov. and *Homocopris williami* Darling & Génier sp. nov., distribution map. Legend and scale bar included in the top and bottom right corners, respectively.

Identification key to species of Homocopris Burmeister, 1846 and Andinocopris gen. nov.

1 Dorsal ocular width greater than one quarter of interocular distance; lateral pronotal carina and pronotal edge joined anteriorly and posteriorly, forming a closed ellipse in lateral view (Figs 13–16); meso-metasternal suture posteriorly arcuate between mesocoxae (Fig. 60). Metasternum broadly flat (Fig. 42), some individuals with a narrow and shallow longitudinal sulcus. ♂ pronotal armament forming an overhanging ridge or bifurcating projection in large individuals (Figs 13, 15). Colombia, Ecuador, Peru .....***Andinocopris*** gen. nov. 2

– Dorsal ocular width approximately one sixth of interocular distance; lateral pronotal carina and pronotal edge only joined anteriorly, forming an open ellipse in lateral view (Figs 17–24); meso-metasternal suture approximately straight between median coxae (Fig. 61); metasternum with a large median depression (Figs 43–45). ♂ pronotal armament forming bilaterally paired tubercles along an inclined ridge in large individuals (Figs 5, 7, 9, 11). Chile, Argentina, Brazil ....***Homocopris*** Burmeister, 1846 3

2. Elytral interstriae flat (Fig. 46). Fifth abdominal ventrite with dense setigerous punctation. Body length: 20–34 mm. Colombia, Ecuador (Carchi) ..... ***A. achamas*** (Harold, 1867)

– Elytral interstriae slightly convex. Fifth abdominal ventrite smooth. Body length: 15–20 mm. Ecuador, Peru .....***A. buckleyi*** (Waterhouse, 1891)

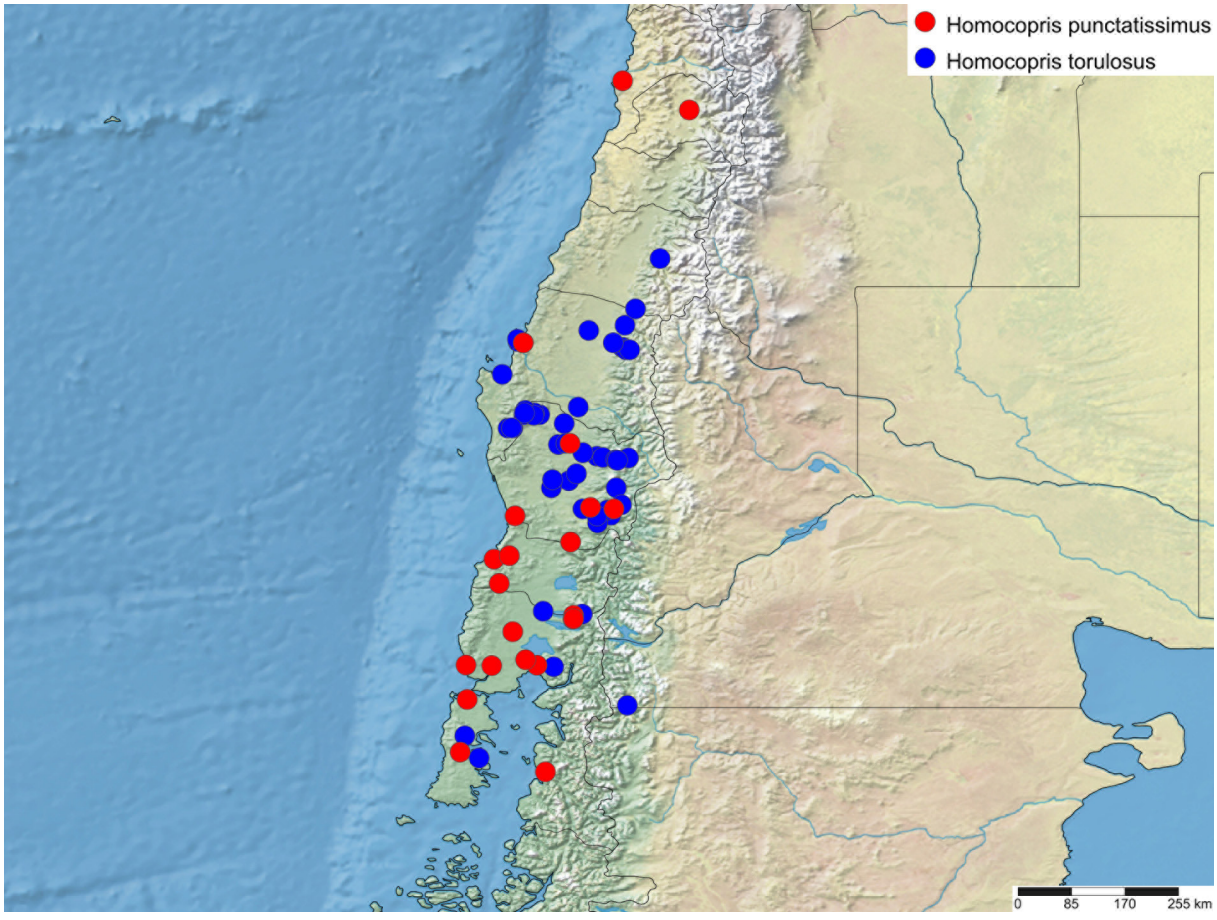


Fig. 67. *Homocopris punctatissimus* (Curtis, 1845), and *Homocopris torulosus* (Eschscholtz, 1822), distribution map. Legend and scale bar included in the top and bottom right corners, respectively.

3. Posterior pronotal surface uniformly punctate. Metasternal impression divided anteriorly (Fig. 43). ♂ anterior inclined pronotal surface with fine, transverse rugosities (Fig. 48); one or two sets of bilaterally paired tubercles transversely spread along pronotal ridge in large individuals (Figs 5, 11); paramere apex broad, rounded (Figs 27, 30). Brazil 4
– Posterior pronotal surface unevenly punctate-rugulate (Fig. 49). Metasternal impression entire (Figs 44–45). ♂ anterior inclined pronotal surface with irregular, fused rugosities (Fig. 49); three sets of bilaterally paired tubercles transversely spread along pronotal ridge in large individuals (Figs 7, 9); paramere apex acutely tipped (Figs 28–29). Argentina (Río Negro), Chile 5

4. Anterior pronotal edge tends to be medially indented. Elytral interstriae punctation tends not to be visible at 10× magnification. ♂ pronotal ridge with a single medial pair of distinct tubercles in large individuals (Fig. 5). Paramere apex unevenly rounded, projecting dorsally (Fig. 27). FLP endophallite reduced (Fig. 33). Brazil (Minas Gerais, Rio de Janeiro, São Paulo) .... ***H. grossiorum*** Darling & Génier sp. nov.
– Anterior pronotal edge evenly curved. Elytral interstriae punctation tends to be visible at 10× magnification. ♂ pronotal ridge with two pairs of distinct tubercles in large individuals (Fig. 11). Paramere apex evenly rounded (Fig. 30). FLP endophallite elongate (Fig. 36). Brazil (Rio de Janeiro, São Paulo, Santa Catarina, Rio Grande do Sul) ...***H. williami*** Darling & Génier sp. nov.

5. Lateral pronotal edge angular on anterior fourth in dorsal view (Figs 9–10); width of ellipse formed by lateral pronotal carina and edge approximately one third the elliptical length (Figs 21–22). Metasternal depression extending into anterior portion of median metasternal lobe (Fig. 45). ♂ cephalic horn length never exceeding interocular distance. FLP endophallite elongate, bent, with internal angle adjacent to sclerotized extension (Fig. 35). Argentina (Río Negro), Chile .... ***H. torulosus*** (Eschscholtz, 1822)
– Lateral pronotal edge broadly arcuate on anterior half in dorsal view (Figs 7–8); width of ellipse formed by lateral pronotal carina and edge approximately one-half the elliptical length (Figs 19–20). Metasternal depression limited to posterior portion of median metasternal lobe (Fig. 44). ♂ cephalic horn length up to twice the interocular distance in large individuals; FLP endophallite crescent-shaped, with one end rounded and the other toothed (Fig. 34). Chile ..... ***H. punctatissimus*** (Curtis, 1845)

Discussion

The only species belonging to the genera reviewed here that has been included in a phylogenetic analysis is *Homocopris torulosus* (Tarasov & Génier 2015; Tarasov & Dimitrov 2016). In their morphological phylogeny, Tarasov & Génier (2015) recovered the species *H. torulosus* in a clade including the Neotropical genera *Ontherus* Erichson, 1847, *Uroxys* Westwood, 1842 and *Canthidium* Erichson, 1847. Subsequently, Tarasov & Dimitrov (2016) analysis based on molecular data recovered *H. torulosus* in a clade including *Ontherus* and *Leotrichillum* Vaz-de-Mello, 2008, *Trichillum* Harold 1868 and *Trichillidium* Vaz-de-Mello, 2008. Interestingly, none of these analyses found a close relationship between *Homocopris* and *Dichotomius*, two genera that were historically considered as closely allied. Phylogenetic trees presenting *Homocopris* as closely related to *Ontherus* and other genera presently included in the subtribe Scatimina Vaz-de-Mello, 2008 of Ateuchini Perty, 1830 (*Leotrichillum*, *Trichillum* and *Trichillidium*) are most likely inaccurate, resulting from a lack of data from closely related taxa or lack of some morphological character coding or gene sampling.

While studying the internal and external morphology of *Homocopris*, we found an interesting combination of characters that could shed some light on the placement of *Homocopris*. Species of the genera *Andinocopris* gen. nov. and *Homocopris* possess a very interesting feature: the presence of a lateral pronotal carina which is fused to the lateral pronotal edge anteriorly and, in the case of *Andinocopris*, also posteriorly (Figs 13–16). This structure is seen in very few genera of Scarabaeinae. In searching

for scarabaeines with a similar structure (Fig. 58), we found it in a group of *Copris* from southern South Africa. These species belong to the Afrotropical *Copris* group 17 as defined by Cambefort & Nguyen-Phung (1996). Both species belonging to this group, *C. caelatus* Fabricius, 1794 and *C. victorini* Boheman, 1857, are restricted to the cool moist or dry areas of the Highveld (*C. caelatus*) or the highlands bordering the south coast (*C. victorini*) of South Africa (Davis *et al.* 2020). It is beyond the scope of this work to provide an extensive phylogenetic analysis and we are cautious about a possible relationship between the South African species of *Copris* and *Homocopris*. The two species (*C. caelatus* and *C. victorini*) are true *Copris* and fit the tribe Coprini Kolbe, 1805 in its narrow sense as recently redefined by Tarasov & Dimitrov (2016). However, we wish to keep in mind the presence of a lateral pronotal carina for these *Copris* species in further studies as it could help in the polarization of characters if this is typical of an ancestral coprine lineage. This lateral pronotal carina is also present in one other New World species (Fig. 59). This species is the odd *Sulcophanaeus carnifex* (Linnaeus, 1758), which is endemic to the island of Jamaica (Edmonds 2000). In this case, this character might not be the result of homoplasy, but could rather support a relationship between the members of the genus *Homocopris* and at least *S. carnifex* in the genus *Sulcophanaeus* Olsoufieff, 1924 and tribe Phanaeini Hope, 1838.

In their morphological phylogeny of Phanaeini, Philips *et al.* (2004) found *S. carnifex* and *S. faunus* (Fabricius, 1775), two large, entirely black species with a very long cephalic horn, in a distinct clade. More recently, Gillett & Toussaint (2020) also recovered *S. faunus*, along with *Bolbites onitoides* Harold, 1868 basal to all other Phanaeini. Gillett & Toussaint's molecular phylogeny did not include *S. carnifex* therefore we are unable to confirm its relationship with *S. faunus* based on molecular data. Edmonds (2000) suggested that the distribution of *S. carnifex* in Jamaica "is undoubtedly that of a relict of ancient South American origin". We agree with this statement, and we suggest that a putative close relationship between *S. carnifex* and *Homocopris* could be further supported by the following characters: a rather large body size, the presence of a large cephalic horn in well-developed males, a complete lack of metallic sheen, a short transverse ridge on the ventral surface of the clypeus, a metasternal median longitudinal sulcus (well-developed in *Homocopris* and vestigial in some individuals of *Andinocopris* gen. nov.) and the presence of a lateral pronotal carina (Fig. 59). We also investigated the elytral morphology, the hindwing venation and the endophallus, and these charcters are also similar, with some exceptions, in *S. carnifex* and *Homocopris*. The elytral morphology, and specifically the lateral striae configuration are similar in *Andinocopris*, *Homocopris* and *Sulcophanaeus carnifex*. The first similarity is the configuration of the elytral basal edge, which is rounded and distinctly protruding combined with the basal portion of the elytral striae more deeply impressed. The second similarity is the presence of a vestigial stria 8 perceptible and connected to the fifth elytral striae on the apical declivity in both *S. carnifex* and some individuals of *A. achamas* (Fig. 62). The configuration of striae 9 and 10 cannot be assessed as these elytral striae are smooth and ill-defined in *S. carnifex*. For wing venation, there are two notable differences, 1) the AA3 is connected to Cu in *H. torulosus*, as opposed to the AA3 being atrophied in *S. carnifex*, 2) RP1 is rather narrow and sharply defined throughout (Fig. 41) in *H. torulosus* as opposed to being wide basally and partially fused to RA4 apically in *S. carnifex* (Fig. 64). In fact, the configuration of RP1 and RA4 in *H. torulosus* is identical to the species of the genus *Copris* studied (*C. costaricensis*). It should also be noted that this pattern also differs from the configuration seen in species belonging to the tribe Dichotomiini as recently redefined by Tarasov & Dimitrov (2016). The endophallus of both species is also similar. We prepared the endophallus of both species in their normal extroverted position (in copula) to have a clear view of the overall shape and the positioning and shape of the endophallites. Both have a bifurcate enlargement basally, with the endophallus projecting in opposite direction followed by an enlargement of the membrane covered with a finely rugose surface on the opposite side of the bifurcate enlargement, followed by the superior right peripheral endophallite (SRP) followed by the FLP endophallite and finally the apical complex of the axial-subaxial and associated endophallites. The single notable difference found is the presence of a set of small paired flat endophallite between the SRP and the FLP in *S. carnifex*. The aedeagus has notable

differences, primarily the shape of the basoventral emargination which is angular in *Homocopris* and semicircular in *S. carnifex* and the shape of the parameres which have a large rugulate membranous fold dorsally in *Homocopris*, this is absent in *S. carnifex* but the latter has a sharp posteriorly oriented lobate projection on the basal third of the dorsal edge.

There seem to be two ways to approach the problem of classifying *Homocopris*. The first is to view *Homocopris* not as closely related to *Dichotomius*, but as a derived Phanaeine adapted to colder environments in the Neotropical region. This view is not well supported by the morphology and molecular data. However, and interestingly, it could be supported by the fact that the nidification pattern of *D. torulosus* belongs to group II in which females use soil to coat the brood ball (Joseph 1929), such pattern is seen in Phanaeini in the New World (Halffter & Edmonds 1982). It should be pointed out however that Halffter & Edmonds (1982) list some *Dichotomius* with similar pattern II nesting. All other species belonging to Dichotomiini, in which nidification is known, have a simpler nidification (group I). Therefore using the nidification pattern does not clearly support such relationship as this behavior have seemingly evolved independently in several groups (Phanaeini, some species of *Dichotomius*, *Ontherus* and *Catharsius* for example). It should be noted that pattern II is quite complex and build in different ways depending on the group. Until the nidification of the taxa listed above is thoroughly investigated we cannot completely rule out the phylogenetic information it can carry. We are unaware of any publications dealing with the nidification of *Andinocopris* gen. nov., therefore we are unable to discuss further any possible relationship of this genus with members of the Phanaeini or Dichotomiini. The configuration of the secondary sexual characters in *A. achamas*, especially the shape of the cephalic horn in males and tubercles in females resemble the configuration seen in some species of *Dichotomius*, however, the presence of long semierect setae on the underside of elytra clearly keep *Andinocopris* closely related to *Homocopris* when combined with the presence of a lateral pronotal carina.

The second approach is to view *Homocopris* and *Andinocopris* gen. nov., which essentially differs from *Homocopris* by what we consider generic level characters such as the absence of a metasternal longitudinal sulcus and the configuration of the secondary sexual characters, as a basal group which arose from the ancestral "Dichotomiine" clade which evolved in South America. These ancestral Dichotomiines would have evolved into current members of the tribe Dichotomiini, Eucraniini and Phanaeini. This scenario would make *Homocopris* and *Andinocopris* a relictual group in the Neotropics. Since we cannot confidently assign *Homocopris* and *Andinocopris* to any of the currently existing tribes, and to avoid making the Dichotomiini and Phanaeini polyphyletic, we propose here a new tribe, Homocoprini, to include both New World genera *Homocopris* and *Andinocopris*.

Homocoprini tribe nov.
urn:lsid:zoobank.org:act:A86B4671-86B5-41A2-B468-611826BCD7C9

Type genus

Homocopris Burmeister, 1846, present designation.

Differential diagnosis

The only group of Scarabaeinae with a lateral pronotal carina combined with a setose elytral underside.

Description

Typical tunneler overall body shape. Size moderate to large; secondary sexual characters present and located on dorsum of head and pronotum; integument rather thin and flexible; antennal club elongate oval, symmetrical; internal surface of first segment of antennal club pubescent; distal edge of epipharynx straight; anterior pronotal membrane covering entire width of head insertion; lateral pronotal declivity with a strong carina connected to the lateral pronotal edge anteriorly, surface between carina and lateral edge flat and

upright (slightly concave and overlapping only in *A. achamas*); posterior portion of pronotal lateral edge at most slightly sinuate; elytra with eight visible striae, stria eight absent or vestigial in some specimens of *A. achamas* (Fig. 62), stria 9 absent on basal fifth, distinct from stria 10 throughout; elytral internal surfaces with long semi erected setae; tarsal claws present; meso and metatibiae with four edges in mid cross section, expanding from base to apex and lacking transverse ridges on external surface; hindwings with AA3 connected to Cu and RP1 narrow and sharply defined throughout; apodeme of metasternal-metacoxal membrane present; unguinotarsal axillary lamellae present; medial endophallite absent.

Genera included

Andinocopris gen. nov. and *Homocopris* Burmeister, 1846.

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Author's contribution

FG: conceptualization, imaging, species description, data digitization, generic concept, discussion. JD: specimen dissections, imaging, species description.

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