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Gomphocopriss ashworthi gen. et sp. nov. (Coleoptera, Scarabaeinae, Homocoprini): An additional new Chilean fossil genus and species extinct at the Pleistocene- Holocene boundary

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Abstract

Based on male and female fossil beetle remains recorded in the Pilauco deposits (northern Chilean Patagonia), a new and extinct dung beetle genus and species from an upper Pleistocene sequence (16.4 to 12.8 kyr BP) namely, *Gomphocopriss ashworthi* gen. et sp. nov. (Coleoptera, Scarabaeidae, Homocoprini) is described and illustrated. The morphological analysis of these fossil remains suggest that this extinct genus and species are placed into the tribe Homocoprini due to presence of supplementary carina in the lateral area in the pronotum. Moreover, this new taxon is separated from the extant Homocoprini species by the absence hypomeral carina (well developed in all extant species); cephalic horn in males with a distinct posterior projection apically (absent in the extant species), and the unique shapes and disposition of the pronotal lobes in major male and female. We suggest that this dung beetle genus and species became extinct in the late Pleistocene to early Holocene as a consequence of the drastic environmental changes, and the extinction of most of the large mammals, which were the organisms that provided feces for the development of their larvae.

Keywords: Dung beetles, extinction, taxonomy, Quaternary insect, palaeoentomology

Introduction

Fossil beetles are crucial for understanding the past climate,

diversity, and evolutionary processes (Hoganson *et al.*, 1989; Massafferro *et al.*, 2008). Moreover, the reliable identification and systematic placement of fossils are important tasks for modern taxonomy overall, especially for hyper-diverse groups such as scarabaeine dung beetles (Coleoptera: Scarabaeidae) (Krell, 2006; Tarasov *et al.*, 2016). Molecular and biogeographical evidence suggest that the Neotropical dung beetles underwent substantial taxonomic radiation during the Cenozoic as a consequence of the increasing size and diversity of mammals (Davis *et al.*, 2002). Nevertheless, few dung beetle fossils records (excluding ichnospecies) are as yet known for the most part of the Cenozoic, and only 23 fossil taxa can be reliably assigned to the Scarabaeinae (Tarasov *et al.*, 2016; Tello *et al.*, 2021b, 2023).

The South American dung beetle tribe Homocoprini Génier & Darling was recently established (Génier & Darling, 2024) as a member of the subfamily Scarabaeinae Latreille. This new tribe includes the extant genera *Andinocopriss* Génier & Darling, 2024 and *Homocopriss* Burmeister, 1864 (Génier & Darling, 2024). The genus *Andinocopriss* consists of *A. achamas* (Harold), inhabiting Colombia and northern Ecuador, and *A. buckleyi* (Waterhouse), occurring in southern Ecuador and northern Perú. The genus *Homocopriss* consists of four living species: *H. grossiorum* Darling & Génier, 2024, recorded from Brazil; *H. punctatissimus* (Curtis, 1845) recorded from Chile; *H. torulosus* (Eschscholtz, 1822), recorded from Chile and Argentina (González-Chang & Pinochet,

2015; Ratcliffe *et al.*, 2015; Vaz-de-Mello, 2010); and *H. williami* Darling & Génier, 2024, recorded from Brazil. All these species are distinguished morphologically from other related scarabaeines (*e.g.*, *Dichotomius* and *Copris*) by having a supplementary lateral pronotal carina and setose elytral underside (Vaz-de-Mello, 2010; Darling & Génier, 2024). These tunneler dung beetle species are associated with cattle in several forestry and livestock environments (González-Chang & Pinochet, 2015). For instance, *H. torulosus* and *H. punctatissimus* are associated with a broad dietary preference in Chilean areas, which includes feces of cattle, donkeys, guanacos, dogs, humans, horses, among others (González-Chang & Pinochet, 2015).

The fossil and biogeographic history of these species are scarce and still poorly known. Only a few fossils assigned to *H. torulosus* have been found in Pleistocene layers (16.4 to 12.8 kyr BP: Martel-Cea, 2008; Tello *et al.*, 2017). Additionally, their traces or ichnofossils-like balls are commonly recorded in several Holocene palaeosoils due to brood ball behaviour (Klemperer, 1983). Nevertheless, no dating analysis have been carried out on this material so far.

Recent explorations of Chilean Pleistocene deposits allowed the discovery of several dung beetle fossils remains, including new and extinct species, as well as coprophilous beetles (Tello *et al.*, 2017, 2021a, 2023). Here, we analyse new fossil remains of the tribe Homocoprini found in a late Pleistocene layer from the archaeological, palaeontological, and astrophysical site Pilauco, in northwestern Chilean Patagonia. In order to establish the taxonomic placement of these fossil remains we: (1) analyse the morphological traits; (2) compare the characters with the extant species and related genus; and (3) explore palaeoecological implications of these fossils.

Material and methods

Chronostratigraphic and palaeo-archaeological evidence in Pilauco

The Pilauco site (Fig. 1A, B) contains Pleistocene-Holocene deposits ($14,300 \pm 40$ to $3,944 \pm 30$ 14C yrs BP; equivalent to 17,340 and 4,340 years BP, respectively), characterized by containing a large amount of well-preserved extinct and extant megafauna bones, plants, extant and extinct insects, human artifacts and footprints records, among others (Pino *et al.*, 2013; Tello *et al.*, 2017; Moreno *et al.*, 2019; Pino *et al.*, 2019; Abarzúa *et al.*, 2020; Pérez-Balarezo *et al.*, 2021; Tello *et al.*, 2021b).

The stratigraphy of this deposit contains three beds where these fossils have been recorded, namely, PB-7: peat with a very dark brown matrix with isolated clasts of

Andean origin up to 7 cm. It is possible to observe in this layer the largest amount of fossilized organic remains; PB-8: peat with a composition very similar to PB-7, but slightly paler in colour and with fewer fossilized organic remains; PB-9: black peat. Between the PB-8 and PB-9 beds, a sedimentological singularity of a few centimetres is observed, which indicates an abrupt transition between one bed and another. This unconformity has recently been defined as evidence of extraterrestrial impact that was the result of the impact of a distant meteorite, at ~12,800 yrs BP (Pino *et al.*, 2019).

Drawings and determination of fossil remains

Fossil beetles were recovered from PB-7 and PB-8 Pilauco's beds. The fossil remains were separated from the sedimentary matrix using the conventional flotation technique, which consists in washing the sediment and using a sieve to recover the organic remains (Tello & Torres, 2020). Additionally, some large fossil beetle remains were directly recovered from the excavation or curation process. The remains were partially cleaned using a fine brush and ethanol as a removal liquid. Afterward, the fossil remains were mounted and stored using traditional entomological techniques. The label information was registered using “/” (intra label) and “//” (between labels) as a separating in the verbatim data of the specimens examined.

The systematic, taxonomy, and morphological nomenclature follow relevant literature dealing with these genera and tribe (*e.g.*, Vaz-de-Mello, 2010; González-Chang & Pinochet, 2015; Mondaca, 2023; Génier & Darling, 2024), and the related taxa (*e.g.*, *Dichotomius*: Valois *et al.*, 2017; Cassenote *et al.*, 2020; Rossini & Vaz-de-Mello, 2020; Montoya-Molina & Vaz-de-Mello, 2021). The fossil remains were compared with multiple extant individuals deposited in the CMNC, CEKU, MNHNC, and MZUF collections.

A Canon M100 or FLEXA CAM C1 cameras, attached to a Leica SD6 stereo microscope were used to study, measure and photograph the specimens. In order to obtain a detailed photograph, we used the multiple layer procedure in Helicon Focus software. Afterward, we edited the aesthetic details in Photoshop CC2023 software.

Abbreviations

CMNC, Canadian Museum of Nature, Gatineau, Quebec, Canada (F. Génier); CEKU, Colección Ernesto Kraemer, Universidad Austral de Chile, Valdivia, Chile (C. Montalva); LNP, Laboratorio Natural Pilauco (A. Abarzúa); MNHNC, Museo Nacional de Historia Natural, Santiago, Chile (M. Elgueta); MPDO, Museo Pleistocénico de Osorno, Osorno, Chile (G. Peralta); MZUF, Museo di Storia Naturale dell'Università di Firenze, Florence, Italy (L. Bartolozzi).

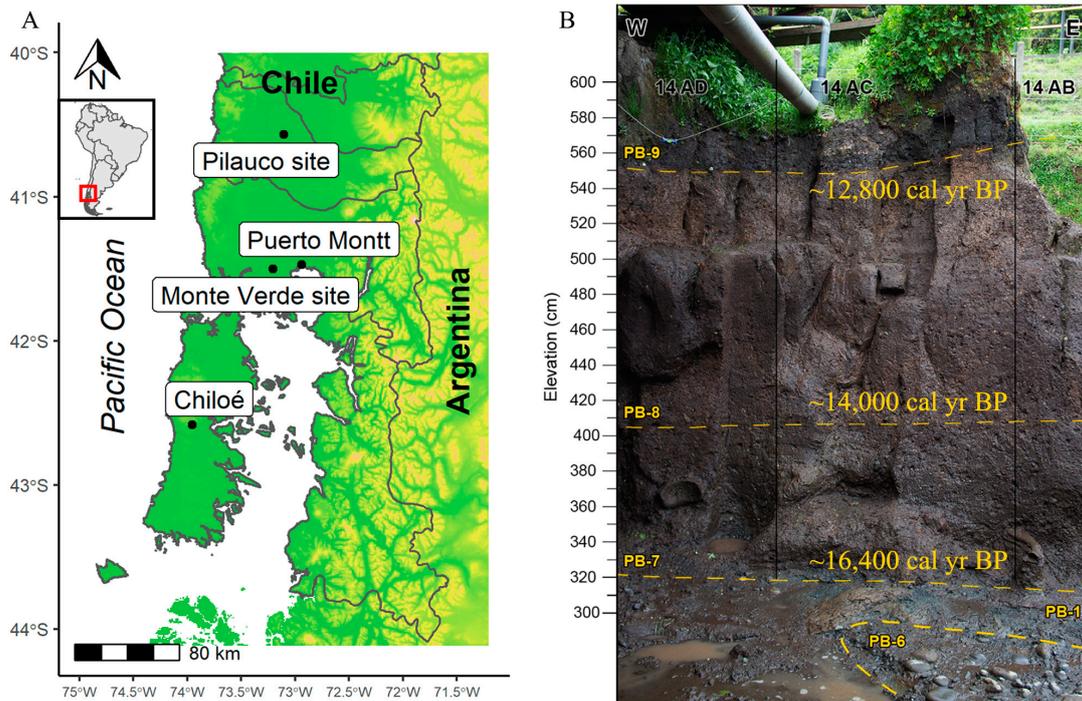


FIGURE 1. Type locality of *Gomphocopris ashworthi* gen. et sp. nov. **A**, Shaded elevation map shows the Pilauco site. **B**, Representation of the profile of a grid of the Pilauco site. Figures were modified based on Figure 1 in Tello *et al.* (2023).

Systematic palaeoentomology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Family Scarabaeidae Latreille, 1802

Subfamily Scarabaeinae Latreille, 1802

Tribe Homocoprini Génier & Darling, 2024

Genus *Gomphocopris* Tello, Pino, Rossini & Verdú gen. nov.

(Figs 2–4)

Type material. Holotype, adult specimen, male. [1] Label a) Cuad. 13AD / n°14 // Prof.: 378–400 / PB-7 // leg.: P. Matissine & F. Tello. Label b) PILAUCO / MHMOP/PI/13AD-RVXNNH. Paratype, adult specimen, female. [2] Label a) Cuad. 13AD / P002 // Prof.: 360–378 / PB-7 // leg.: P. Matissine & F. Tello. Label b) PILAUCO / MHMOP/PI/13AD-HBKEGL. [3] Label a) Cuad. 16AA // Prof.: 410 / PB-8 // leg.: F. Tello. Label b) PILAUCO / MHMOP/PI/16AA-TCPGEF. Other materials, males, cephalic horns. [4] Label a) Cuad. 15B // Prof.: 427 / PB-8 // leg.: Dominique von Bennewitz // Fecha: 19.I.2016. Label b) PILAUCO / MHMOP/PI/15B-QEAEGQ. [5] Label a) Cuad. 16A // Prof.: 430–431 / PB-8 // leg.: F. Tello // Fecha: 09.XI.2021. Label b) PILAUCO / MHMOP/PI/16A-TJZVZF.

Etymology. *Gomphocopris* is a combination of the words of Ancient Greek: “*Gompho*” γόμφος (gómphos)

and “*copris*” κόπρος (*kópros*). The former refers to the extinct Gomphoteriidae (Mammalia) family, which are the most representative fossils found in the Pilauco site. Genus is masculine.

Diagnosis. *Gomphocopris* gen. nov. is distinguished from extant Homocoprini genera by the following combination of characters: (1) male with one pronotal lateral lobe (Fig. 3C); (2) male cephalic horn with a distinct posterior projection apically (absent or inconspicuous in the other genera) (Fig. 3A, B); (3) male and female without hypomeral carina (Fig. 4A, B). The carina is present in all species of *Andinocopris* and *Homocopris*. In *Andinocopris* it is shorter, about half the hypomeral width, in *Homocopris* is complete, separating the hypomeron in two parts (Fig. 4C); (4) male and female with an elongated and entirely connected supplementary carinae dividing the pronotum of the hypomeron, the surface between carina rhomboidal in shape (just connected in the anterior margin in *H. torulosus*) (Fig. 2E, F).

Locality and horizon. Chile, Región de Los Lagos, Osorno City (40°34’S, 73°07’W). Upper Pleistocene sequence between PB-7 and PB-8 beds; 16,000 to 14,420 cal yrs BP (Pino *et al.*, 2019; Hogg *et al.*, 2020). The age of each material are: MHMOP/PI/13AD-RVXNNH ~15,400 to 15,000 cal yrs BP; MHMOP/PI/13AD-HBKEGL ~16,000 to 15,400 cal yrs BP; MHMOP/PI/16AA-TCPGEF ~14,800 cal yrs BP; MHMOP/PI/15B-QEAEGQ; ~14,400 cal yrs BP and MHMOP/PI/16A-TJZVZF ~14,420 cal yrs BP.

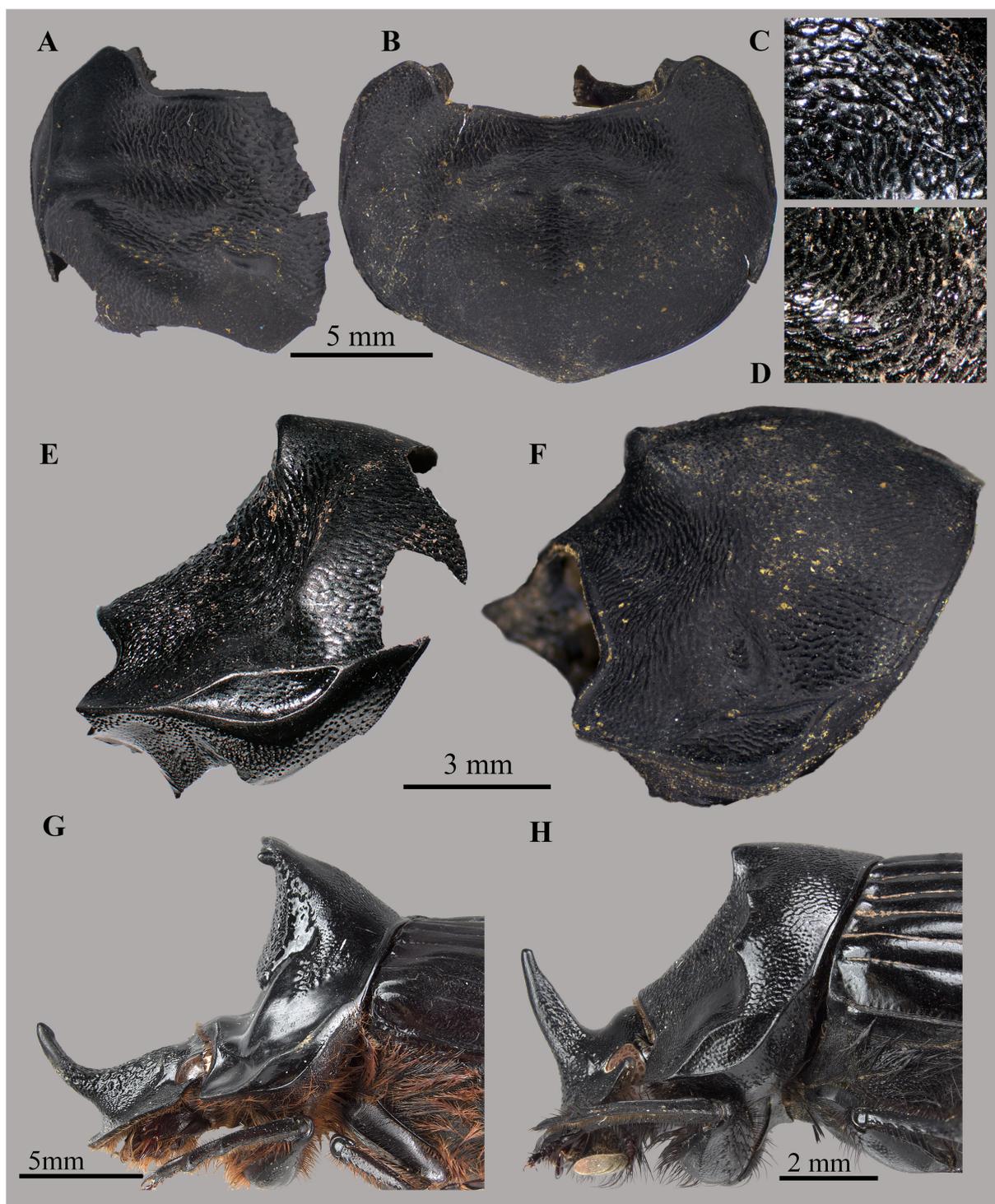


FIGURE 2. *Gomphocopris ashworthi* gen. et sp. nov., holotype and paratype, compared with modern species: **A**, Dorsal view of male. **B**, Dorsal view of female. **C**, Surface of pronotal excavation of male. **D**, Female. **E**, Lateral view of male. **F**, Lateral view of female. **G**, Lateral view of *Andinocopris achamas*, male modern specimen. **H**, Lateral view of *Homocopris torulosus*, male modern specimen.

***Gomphocopris ashworthi* Tello, Pino, Rossini & Verdú sp. nov.**

(Figs 2A–F, 3A–F, 4A, B)

Etymology. The specific name *ashworthi* honours Allan

C. Ashworth for his notable contributions to Chilean Quaternary palaeoentomology.

Description. Male. Holotype. Maximum width (pronotum): ~19.80 mm. Colour black. *Head.* Clypeus unknown. *Pronotum.* Wider than long. Anteromedian

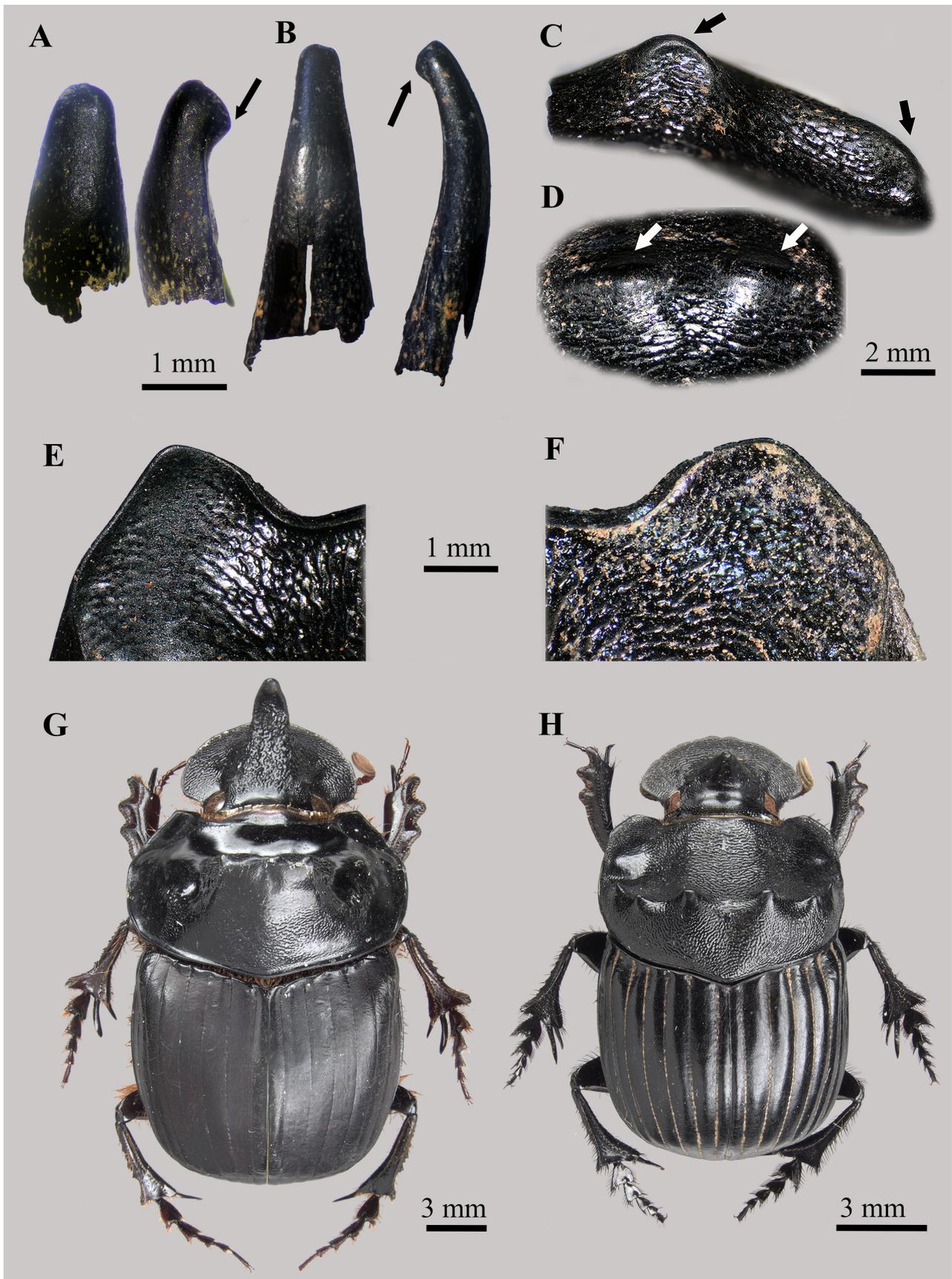


FIGURE 3. Details of *Gomphocoprpris ashworthi* gen. et sp. nov. compared with modern species. **A, B**, Male clypeal tubercles in dorsal and lateral view. Arrows indicates the apex behind expanded. **C**, Central and lateral lobes of the pronotum in male. **D**, Central lobes of the pronotum in females. **E, F**, Male and female anterior angles of the pronotum, respectively. **G**, Dorsal view of *Andinocoprpris achamas*, male modern specimen. **H**, Dorsal view of *Homocoprpris torulosus*, male modern specimen.

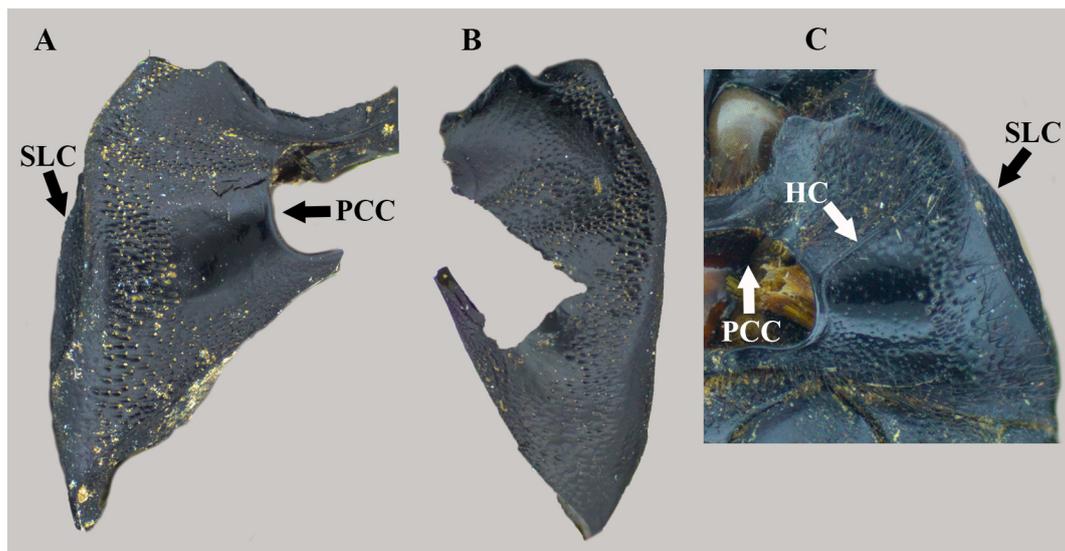


FIGURE 4. Hypomer area of the *Gomphocoprish ashworthi* gen. et sp. nov. compared with modern species. **A**, Female. **B**, Male. **C**, Hypomer area of extant *Homocoprish torulosus*, male specimen. SLC, supplementary lateral carina; PCC, procoxal cavities. HC, hypomer carina of *Homocoprish torulosus*, male modern specimen.

portion widely excavated (Fig. 2A, E). Surface of pronotal excavation with irregular transverse and longitudinal wrinkles (Fig. 2A, C). Anterior angles rounded with granulation inconspicuous, almost smooth (Fig. 2C). Disc distinctly convex, surface densely coated with shallow punctures (Fig. 2A, E). Lateral lobule rounded, longer than wider (Fig. 3E). Central protuberance with two separated lobules; the apex of the lobe smooth; lobe frontal surface with a narrow smooth bulge (Fig. 3E). Supplementary lateral carina elongated, always joined in both anterior and posterior margins to the carina that divides the pronotum from the hypomer (supplementary carina: Fig. 2E). *Hypomer*. Excavated anteriorly and lacking transverse carina medially (Fig. 4B). Anterior portion almost entirely covered with scattered setiferous punctures. Medial portion smooth, except for ocellate punctures along circumnotal ridge. Additional materials: male horns. Clypeofrontal region with a median or high conical horn (only known for males), with the apex expanded behind, forming a bulge in lateral view (Fig. 3A, B). Female. Paratypes (2). Maximum width of pronotum: 14.40 mm. Colour black. *Head*. unknown. *Pronotum*. Wider than longer. Anterior portion slightly excavated (Fig. 2B, F). Surface of pronotal excavation with irregular transverse and longitudinal wrinkles (Fig. 2D). Lateral area with a weak knob (located over the supplementary carina). Anterior angles rounded with distinct transversal granules (Fig. 3D). Disc distinctly convex, surface densely covered with shallow punctures (Fig. 2B). Supplementary lateral carina elongated, always joined in both anterior and posterior margins to the carina that divides the pronotum

from the hypomer (Fig. 2F). *Hypomer*. Excavated anteriorly and lacking transverse carina medially (Fig. 4A). Anterior portion almost entirely with scattered setiferous punctures. Medial portion smooth, except for ocellate punctures along circumnotal ridge.

Key to extant and extinct genera of Homocoprini

- 1 Lateral pronotal carina and lateral pronotal edge joined anteriorly and posteriorly, forming a closed ellipse in lateral view (Fig. 2E)..... 2
- 1' Lateral pronotal carina and lateral pronotal edge only joined anteriorly, forming an open ellipse in lateral view (Fig. 2H). Argentina, Brazil, and Chile.....
.....*Homocoprish* Burmeister, 1864
- 2 ♂ Pronotal armament forming an overhanging ridge or bifurcating projection in large individuals (Fig. 2G); hypomer carina present. Colombia, Ecuador, and Perú...
.....*Andinocoprish* Génier & Darling, 2024
- 2' ♂ Pronotal disc protuberance with two smooth transverse tubercles, with additional small tubercles on lateral declivities; hypomer carina absent. Chile.....
.....*Gomphocoprish* gen. nov. [extinct]

Discussion

Taxonomic placement of Gomphocoprish ashworthi gen. et sp. nov.

This new fossil species is placed into the Homocoprini based on the presence of a lateral pronotal carina, which is shared with the modern taxa of this tribe (Génier & Darling, 2024). In addition, the novel morphological traits recorded under our examinations *i.e.*, lack of the pronotal

hypomeral carina, the clypeal horn with apex expanded behind, forming a bulge in lateral view, and the number and shape of pronotal lobes, shows substantial morphological dissimilarities with the modern *Homocoprini* genera. This different combination of characters prompted us to place these fossils into a new genus and species. Thus, *Gomphocopris* **gen. nov.** shares the shape of the supplementary carina of the pronotum with *Andinocopris* (*i.e.*, edge joined anteriorly and posteriorly, forming a closed ellipse in lateral view), but differs from the other *Homocoprini* genera by lacking the transverse carina that divides the pronotal hypomeron.

It should be noted that this new genus and species could have had a sympatric distribution with the extant *H. punctatissimus* and *H. torulosus* species during the Pleistocene—and possibly to early Holocene—both species currently inhabiting the Mediterranean forest and the southern temperate forests (Mondaca, 2023). Additionally, both the extant *Homocopris* species shared the following morphological characteristics with *Gomphocopris*: major males with the anterior pronotal area strongly excavated, and females with slight or no depression; all genera shared a similar punctuation type on the pronotal anterior angles, *i.e.*, almost smooth in major males versus densely transversely granulated in females; and, share similar disposition and types of punctuation on the pronotal disc *i.e.*, surface of pronotal excavation with transversal wrinkles, posterior disc distinctly convex, and surface with dense shallow punctures, but *G. ashworthi* also have both longitudinal and transversal wrinkles.

Nevertheless, the combination of the characteristics *i.e.*, lacking carina in the hypomeral area and apical projections of the median bulge, is rather unique among the modern *Homocoprini* fauna. Additionally, *G. ashworthi* have both transversal and longitudinal wrinkles in the pronotum. Furthermore, the pronotum size of both male and female *G. ashworthi* are considerably bigger than both Chilean *Homocopris* species. For instance, the average size of the maxim width of the pronotum of male and female specimens of Chilean *Homocopris* are 11.5 (\pm 0.6) mm and 11.3 (\pm 1.0) mm, respectably as opposed to 14.4–19.8 mm of *Gomphocopris*.

Palaeoecological and biogeographical considerations

The South American Pleistocene-Holocene transition occurrence was one of the major and recent changes in climate, environmental, and biotic conditions (Moreno & León, 2003; Barnosky *et al.*, 2004; Pino *et al.*, 2019; Gómez *et al.*, 2022). These drastic changes induced the last major animal extinction process (before the Anthropocene species decline), resulting in the loss of most of the large mammals (Brook & Barnosky, 2012; Villavicencio *et al.*, 2016). Recent studies showed that the extinction of Pleistocene megafauna could induce

a collateral extinction of dependent organisms such as megafauna-intestinal nematodes (Beltrame *et al.*, 2020) and dung beetles (Tello *et al.*, 2021b, 2023). This perspective has been understudied so far but offers an interesting approach to understand the extinction of large mammal-dependent species, such as dung beetles. For instance, both extinct *Onthophagus pilauco* Tello *et al.*, and *Scybalophagus brellenthinae* Tello *et al.*, were found in an equivalent layer to *G. ashworthi*, suggesting that the dung beetles were more diverse in the Pleistocene (Tello *et al.*, 2021b, 2023). Thus, it seems to be reasonable to propose an equivalent explanatory hypothesis for the extinction of the *G. ashworthi* *i.e.*, this species became extinct in the late Pleistocene to early Holocene as a consequence of the loss of the dung resources formerly provided by the large extinct mammals faunas.

Members of the genus *Homocopris* are forest dwellers and are known to feed and breed on different kinds of excrement (González-Chang & Pinochet, 2015) rather than occupying steppe habitats thought to dominate the landscape during the Pleistocene. It is likely that this ecological plasticity would have helped these species to escape the extinction. Thus, it is possible to suggest that *Homocopris* could have used the dung of guanacos in the lower and middle Holocene; meanwhile, after the arrival of European colonization, this species used the human related dung sources (*e.g.*, dung of modern horses, cows, and others). Moreover, the expansion of the forests and the continuity of dung resources in the Holocene could have been beneficial for these dung beetles associated to forest habitats.

It is worth asking why *G. ashworthi* became extinct while *H. torulosus* and *H. punctatissimus* have been successful species in the extant ecosystems. A possible explanation for this extinction could be the interspecific competition in the palaeoenvironment, which increased due to the reduction of the amount and diversity of dung resources when the megafauna was extinct, *i.e.*, a collateral extinction. It should also be noted that *Homocopris torulosus* has been collected on several occasions in carrion traps in Chile (Génier & Darling, 2024). This would add another alternative food source when feces were not available. It suggests that *G. ashworthi* could have been a strict non ruminant dung feeder and could only use non ruminant dung for nest construction. Additionally, the combination of the drastic events which occurred during the Pleistocene-Holocene transition such as the climate change (Moreno *et al.*, 2015), increases of human activities (Dillehay *et al.*, 2019; Prates & Perez, 2021), and an admissible asteroid impact (Pino *et al.*, 2019) could have been synergistic factors that induced the extinction of these coleopteran groups. Nevertheless, additional detailed studies are needed to understand the evolutionary process that drove the extinction of these dung beetle species.

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