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THE FIRST DUNG BEETLE RETRIEVED FROM COPRINISPHAERIDAE ICHNOFOSSILS: *PHANAEUS VIOLETAE* N. SP. (COLEOPTERA: SCARABAEINAE) FROM ECUADORIAN CANGAHUA BALLS

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ABSTRACT. A previously unknown species of dung beetle is described, related to a Coprinisphaeridae ichnofossils. Its discovery demonstrates that such structures really are fossil nests of Scarabaeinae beetles. The taxonomic and phylogenetic relationships of the new species are discussed, as well as some hypotheses about the biogeographical history of the *Phanaeus chalcomelas* species group to which the fossil species is assigned. A preliminary version of both the group's track and Steiner's areal tree is represented and compared to the phylogenetic and biographic hypotheses of recent literature.
Key words: Coprinisphaeridae, Cangahua balls, first finding, associated fossil *Phanaeus*, Ecuador.

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RESUMEN. Se describe, como especie inédita, el primer hallazgo de un escarabajo asociado con un ichnofósil de la familia Coprinisphaeridae. Este descubrimiento comprueba la naturaleza de nidos fósiles de Scarabaeinae de tales estructuras. Se discute la posición taxonómica de la nueva especie y sus posibles relaciones filogenéticas, así como algunas hipótesis sobre la historia biogeográfica del grupo *Phanaeus chalcomelas*, al que se reconduce la especie fósil. Se presentan el trazo y el árbol de Steiner de las distribuciones del grupo, ambos preliminares, comparándolos con las hipótesis filogenéticas y biogeográficas de la literatura reciente.
Palabras clave: Coprinisphaeridae, bolas de cangahua, primer hallazgo, *Phanaeus* fósil asociado, Ecuador.

INTRODUCTION

"Cangahua" balls, whose name comes from the Andean Quechua word meaning "hard soil" (Sauer, 1955; Nimloss *et al*., 1995) are sub-spherical structures until now only

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supposedly interpreted as dung beetle fossil brood balls coated by a clay or soil shell (Fig. 1). Sauer (1955) described such formations as *Coprinisphaera ecuadoriensis*, relating them to brood nests of an unknown scarab beetle (Sauer 1955, 1956; see also Estrada, 1941). Halffter (1959) firstly revised the paleontological data about dung beetles at world-wide scale. Concerning the southern American reports he wrote "el hecho de que únicamente se conozcan los nidos hace difícil la determinación genérica, pero sin duda se trata de Scarabaeinae con formas de nidificación muy semejante a las que presentan en la actualidad los géneros a los que Frenguelli [*Megathopa*, *Phanaeus*, *Canthon*: Frenguelli, 1938a, 1938b, 1939 (MZ)] atribuye los fósiles". Halffter & Matthews (1966) reported that "… it seems most probable that species of *Phanaeus* or *Dichotomius,* or both, are involved in all cases". Laza (2006) wrote: "*C. ecuadoriensis* resembles brood balls constructed by Dichotomiina (tunnelers), and Canthonina (rollers)". In spite of a great amount of research, that has been recently synthesized and updated (Genise *et al*., 2000; Genise, 2004; Laza 2006; Krell, 2006; Krell & Schawaller, 2011; Genise, 2012, personal communication), it has never been possible to relate any sample of Cangahua balls –nor of any similar structure belonging to the ichnofamily Coprinisphaeridae established by Genise (2004)– to a definite taxonomic group, in the absence of the related beetle. The discovery of a fossil scarab beetle associated to a specimen of *Coprinisphaera ecuadoriensis* finally reveals the true maker of at least one representative of this ichnofamily, extensively distributed (Laza, 2006) in Southern America, Africa, Europe (NW Italy) and Asia (Pakistan).

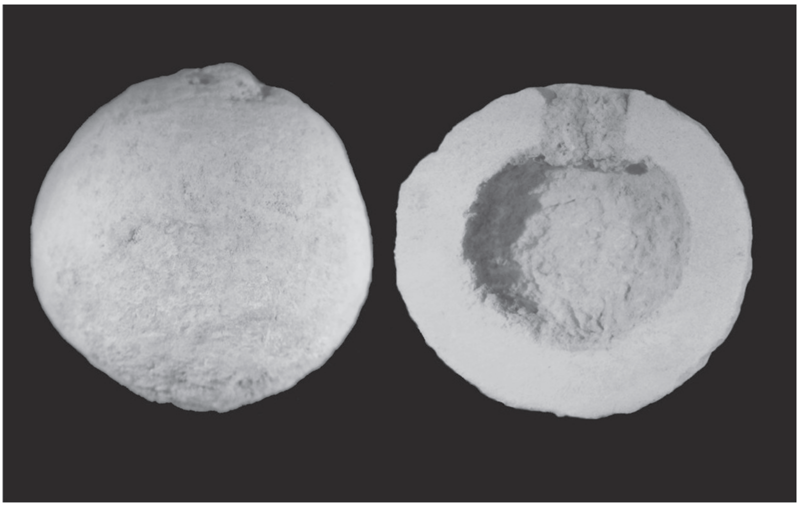

Figure 1. Cangahua balls (*Coprinisphaera ecuadoriensis*) from Quito, Ecuador, calle Rither deposit, complete (left) and opened (right).

MATERIAL AND METHODS

In 1986 I personally collected several samples of Cangahua balls that had been exposed by an excavation bordering Rither street in Quito, Ecuador, very near the type locality: Sauer (1955) had originally described the Ecuadorian ichnospecies *Coprinisphaera ecuadoriensis* from specimens collected in the city of Quito, in Vargas street. Both deposits have been destroyed in order to built new houses.

In 1987 some of the cangahua balls I had collected the previous year were examined using X rays, which revealed no significant inclusions. Later, some specimens were opened by meridian oriented cuts, and one of them showed the presence of the anterior part of a beetle. Due to personal reasons the research was suspended, and all the material was shelved until summer 2012, when the specimen was re-examined and the beetle parts removed from the inner sediment of the ball. The remains showed to clearly belong to an unknown species of the genus *Phanaeus* MacLeay (Coleoptera: Scarabaeinae) as defined by Edmonds (1972, 1994; Edmonds & Zídek, 2012), herein described.

RESULTS

***Phanaeus violetae*, n. sp.**

(Figure 1)

Holotype, ♀: a near complete head from a *Coprinisphaera ecuadoriensis* specimen. Careful examination of it's the interior sediments has not revealed any other body fragments.

Type locality: Ecuadorian intermountain valley "Callejón Andino", 2900 m, Quito, Rither street, M. Zunino coll., October 1986. Artificially exposed Cangahua formation (Upper Pleistocene according to Laza, 2006).

Type repository: the type specimen and the relative ichnofossil will be deposited in the Museo de Historia Natural "Gustavo Orces V.", Escuela Politécnica Nacional, Quito, Ecuador.

This new species is dedicated to the loving memory of our late Mexican colleague and friend Violeta Halffter (1934–2012), who dedicated all her scientific life to Scarab beetles, and named after her.

Description (terminology based on Edmonds, 1972, 1994; Philips *et al*., 2004; Edmonds & Zídek, 2012)

Maximum width 7.7 mm (Fig. 2); dorsal surface brownish black, posterior ¾ of the surface of paraocular area of parietals coppery red, as well as the semi lunar areas

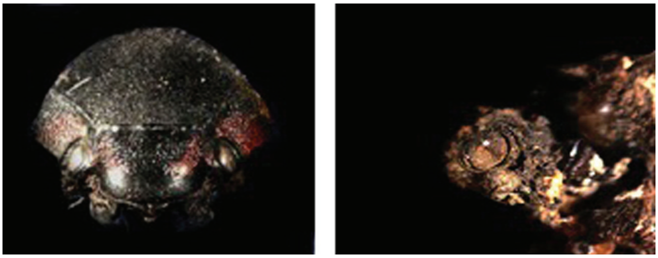

Figure 2. *Phanaeus violetae*, holotype, dorsal view (left); the same, antennal club, apical view (right).

close to the lateral, well marked branches of the occipital ring, and a small spot near to the inner margin of the eye; anterior margin of the clypeus very weakly bidentate; clypeal process rounded, narrow, its surface showing a short row of strong punctures. Lateral clypeal carinae very evident. Paraocular ridge well distinct. Cephalic carina robust, barely but evidently tridentate, each tooth flattened at the apex. Antennal club as characteristic of the genus.

Systematic position: according to Edmonds (1994 and personal communication, 2012; Edmonds & Zídek, 2012) and taking into account the shape of cephalic carina, clypeal process, and paraocular ridge, *Phanaeus violetae* appears to be very near the extant *Phanaeus achilles* Boheman; both are members of a monophyletic unit, the *chalcomelas* species group, which also includes *P. chalcomelas* (Perty), *P. cambeforti* Arnaud, *P. lecourti* Arnaud and *P. meleagris* Blanchard. (Edmonds 1994; Edmonds & Zídek 2012; Price 2007). The *chalcomelas* species group was included by Edmonds (1994) in the newly described subgenus *Notiophanaeus*; Edmonds & Zídek (2012) follow the same systematic arrangement. On the ground of extensive phylogenetic analyses, Price (2007) firstly reconsidered the taxonomic structure of the subgenus, later (2009) elevated such taxon to generic level, drastically restricted its specific composition, and included the *chalcomelas* species group in the newly defined genus *Phanaeus*. Independently of their different macrotaxonomic arrangement, it is noteworthy that all mentioned authors consider the group as a taxonomically and phylogenetically coherent unit –even if the Price's 2009 survey omitted *P. cambeforti*–.

DISCUSSION

As regards the geographical and ecological distribution of the group, *P. achilles* is limited to "desert scrub regions of southwestern Ecuador and northern Peru" (Edmonds & Zídek, 2012); *P. chalcomelas* is found in the "Amazon Basin from Guaiana to Bolivia" (*ibid.*); *P. meleagris* from "Eastern slopes (Yungas) of Andes from Peru to Venezuela" (*ibid*.); *P. lecourti* is reported in the "Yungas of Bolivia and Peru" (*ibid*.); *P. cambeforti* from the "Amazon Basin from Guiana to Colombia and Peru" (*ibid*.). The wide geographic distribution of such relatively small species group must be underlined, as well as its ecological range extending from arid scrub to pluvial forest. The finding of *P. violetae* in the Callejón Andino and its possible age apparently do not refute the biogeographical scenario proposed by Price (2009), who did not consider (Fig. 3.), who maintains that "the ancestral distribution for the *hermes* group is the Andes, and this group is recovered as sister to the *chalcomelas* group, also an Andean species group", based on a DIVA analysis. In the frame of Price's interpretation –different for several aspects from "Edmonds' ecogeographic hypotheses"–, the extinction of *P. violetae*, as well as the subsequent dispersion/speciation within the

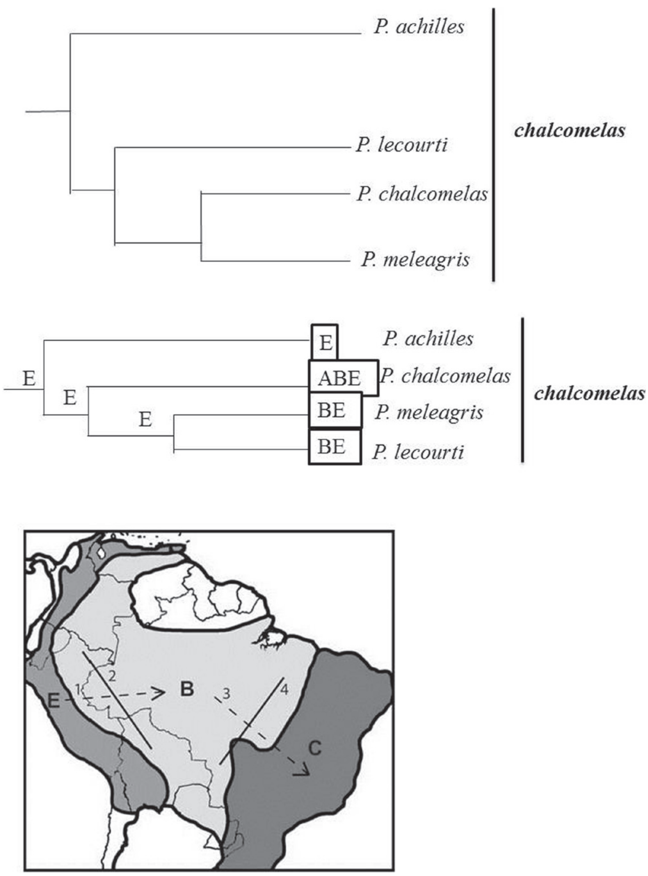

Figure 3. Phylogenetic relationships within the *chalcomelas* species group (top), relative ancestral areas (middle) and biogeographical map (modified from Price, 2009).

group, could be imputed to the effect of glaciations. As Smith *et al.* (2008) stressed, the timing of the local Last Glacial Maximum in different sectors of the tropical Andes remain controversial. However, it seems clear that at least in Ecuador and Peru multiple glaciations occurred before the Last Glacial Maximum.

Nevertheless, in my opinion biogeographic processes involving the *chalcomelas* species group shall be deeply investigated when a greater amount of accurate distributional data will be available. In fact, only in this case the true barycentres of extant areals and detailed tracks and distribution areas trees can be drawn and compared to phylogenetic hypotheses. This opinion is supported by both the track and the distribution areas' Steiner tree that have been drawn, even if in a very preliminary way, starting from the areals' geometric centres. The group's track (Fig. 4,

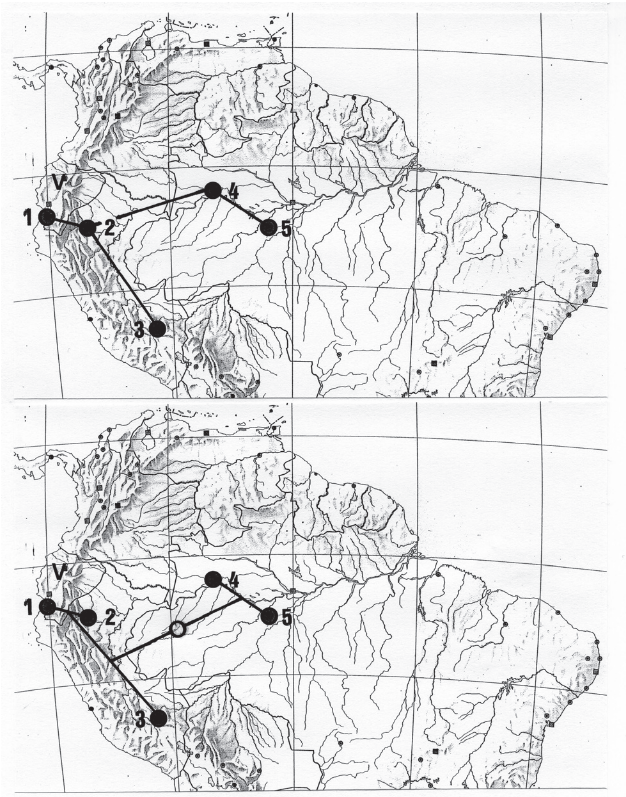

Figure 4. Preliminary track (top) and distribution areas Steiner tree (bottom) of the *chalcomelas* species group (see main text). V: *Phanaeus violetae* (unique locality); 1: *P. achilles* (distribution area's centre); 2: *P. meleagris* (the same); 3: *P. lecourti* (the same); 4: *P. cambeforti* (the same); 5: *P. chalcomelas* (the same).

top) corroborates Price's hypothesis only if the track is oriented by its baseline (which roughly corresponds to the lowest and less transversally extended point of the Andes, the Huancabamba depression, or by the cladogram's root, two criteria that have been strongly criticized by Zunino (from a discussion see: Zunino & Zullini 1995 and 2003, Zunino 2000). The distribution areas' Steiner tree (Fig. 4, bottom), also very preliminary, showed a West Amazonian root, even taking into account the distribution of the *Phanaeus hermes* species group, sister of *chalcomelas* according to Price (2009). The Steiner tree implies an Amazonian primary ancestral area for the whole group, followed by a westward dispersion and colonization of the actual Andean piedmont (the extant Yungas) and finally of the high Andean elevations. Glaciations and ancient Amazonian area fragmentation events (see Lynch, 1988; for a further discussion and extensive bibliography see Morrone, 2009) could be interpreted as causal factors of the extinction of *P. violetae,* the present distribution of *P. achilles*, and the speciation resulting in the extant species distributed along the Yungas (*P. meleagris* and *P. cambeforti*), and in the Amazonian basin/Guyana (*P. chalcomelas* and *P. lecourti*).

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