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Reassessment of the hairy long-nosed armadillo “*Dasypus*” *pilosus* (Xenarthra, Dasypodidae) and revalidation of the genus *Cryptophractus* Fitzinger, 1856

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Abstract

The hairy long-nosed armadillo, currently referred as *Dasypus* (*Cryptophractus*) *pilosus*, is an enigmatic species endemic to montane cloud forests and subparamo of Peruvian Andes. Its strikingly different external features, which include the carapace concealed by abundant hair, the presence of more movable bands, and a slender skull, have raised questions regarding its taxonomic status as subgenus or as genus. This paper assesses this issue based on a cladistic study and provides a detailed comparative description of the species, including the first account on the distinctive ornamentation of its osteoderms. Based on several unique characters in the carapace, skull, mandible, and teeth, as well as on the external phylogenetic position relative to other *Dasypus*, we favor the assignment of the hairy long-nosed armadillo to other genus. As result, we revalidate the original generic epithet, so that the valid name of the species is *Cryptophractus pilosus* Fitzinger, 1856.

Key words: Peru, Cingulata, Dasypodinae, woolly armadillo, Peruvian Andes

Introduction

The long-nosed armadillos (genus *Dasypus* Linnaeus) are the most widespread and taxonomically diverse living xenarthran, with seven extant species (Wetzel 1985; Wilson & Reeder 2005; Aguiar & da Fonseca 2008), besides two extinct species that date back to the late Pliocene–late Pleistocene of North America (*D. bellus* Simpson) and late Pleistocene of Brazil (*D. punctatus* Lund) (Castro *et al.* 2013a, 2014). Along with *Anadasypus* Carlini, Vizcaíno & Scillato-Yané (middle Miocene of Colombia and late Miocene of Ecuador; Carlini *et al.* 1997; Carlini *et al.* 2014), *Pliodasyphus* Castro, Carlini, Sánchez & Sánchez-Villagra (late Pliocene of Venezuela, Castro *et al.* 2014), and *Propraopus* Ameghino (middle Pleistocene–early Holocene of South America; Castro *et al.* 2013b), *Dasypus* is part of tribe Dasypodini, one of the most basal lineages of cingulate xenarthrans according to morphological and molecular phylogenetic analyses (Gaudin & Wible 2006; Delsuc *et al.* 2012).

Traditionally, the extant species of *Dasypus* recognized are: *Dasypus novemcinctus* Linnaeus (type species of the genus by Linnean tautonomy); *Dasypus septemcinctus* Linnaeus; *Dasypus hybridus* (Desmarest); *Dasypus pilosus* (Fitzinger); *Dasypus kappleri* Krauss; *Dasypus sabanicola* Mondolfi; and *Dasypus yepesi* Vizcaíno (Wilson & Reeder 2005; Wetzel *et al.* 2007; see Feijó & Cordeiro-Estrela 2014 for latter species). Three subgenera are widely accepted: *Cryptophractus* (for *D. pilosus*), *Hyperoambon* (for *D. kappleri*), and *Dasypus* (for the remaining species) (Wetzel & Mondolfi 1979; Kraft 1995).

conclusions of Delsuc *et al.* (2012) towards the classification of the fairy armadillos (*Chlamyphorus truncatus* and *Calyptophractus retusus*, mentioned above) in two distinct genera. In this sense, the ancient divergence between *D. novemcinctus* and *D. kappleri* (11 ± 2 My) draws attention that genus *Dasypus* as currently established encompasses more molecular (and morphological) variation than the other genera of armadillos.

Accordingly, we acknowledge that the alteration of ranks proposed here (monospecific subgenus to genus) is subject of different interpretations. However, taking into account: a) the morphological distinctiveness of the species; b) its external phylogenetic position relative to the original concept of *Dasypus*; and c) the taxonomic criteria applied to define other genera of armadillos, we favor the revalidation of the former generic name *Cryptophractus*. This proposition better reflects the degree of difference among the taxa and is more equivalent with other genera of extant armadillos. As result, the valid name for the species is *Cryptophractus pilosus* Fitzinger, 1856. Nonetheless, in future works, it would be important to complement or contrast the results obtained herein with molecular data.

Conclusions

The description presented herein shows the great distinction of the hairy long-nosed armadillo compared to its related species. The external features, as well as the morphology of the carapace, skull, teeth, and the ornamentation of osteoderms are unique among armadillos. The cladistic analysis of Dasypodinae revealed an external phylogenetic position of the species relative to other *Dasypus*. It supports an assignment to a genus other than *Dasypus*, leading to the revalidation of the original generic epithet *Cryptophractus*. Therefore, the valid name of the hairy long-nosed armadillo is *Cryptophractus pilosus* Fitzinger, 1856.

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APPENDIX 1. Specimens of *Dasypus* examined for comparative study.

- Dasypus novemcinctus*: MCN 99, 986, 2788, 2836, 3021; MZUSP 7996, 10431, 13800, 13801, 20189; MN 5789, 26915, 27945, 42850, 75225, 30687, 24465, 10044, 51653, 5006.
- Dasypus septemcinctus*: MZUSP 5111, 8111, 19983, 19984; MN 2366, 2367, 2370, 2693, 4291, 10062, 10071, 10091, 23989, 23997.
- Dasypus kappleri*: MZUSP 8950, 24798; AMNH 136251, 136253, 267011, 76573; MN 20581, 26931, 42853, 42854.
- Dasypus hybridus*: MLP 1-I-03-65, 3-X-96-1, 1-I-03-67, 1-I-03-69, 1-I-03-70, 3-X-94-3.
- Dasypus sabanicola*: Photos of MEBRG 965 (holotype); MLP 22-II-00-6.
- Dasypus yepesi*: MLP 30-III-90-8 (holotype), 30-III-90-1, 30-III-90-2, 30-III-90-3, 30-III-90-4, 30-III-90-5, 30-III-90-6, 30-III-90-7, 10-III-90-4.
- Dasypus punctatus*: ZMK 1/1845:13767 (lectotype); MN 552-V; MCN 009, 014.
- Dasypus bellus*: AMNH FM 23542 (holotype), 23543–23546, 92263; FLMNH 224700, 201289, 61906, 2910, 2478.

APPENDIX 2. List of characters and character states used in the cladistic analysis.

1. Number of upper teeth: 5 (0); 6 (1); 7 (2); 8 (3); or 9 (4). (Modified from Gaudin & Wible 2006, ch. 1)
2. Number of lower teeth: 6 (0); 7 (1); 8 (2); or 9 (3). (Modified from Gaudin & Wible 2006, ch. 2)
3. Coronoid process shape: elongated (0); or small (1). (Billet *et al.* 2011, ch. 14)
4. Distal extent of coronoid process relative to condylar process: dorsal to (0); or ventral to (1). (Billet *et al.* 2011, ch. 15)
5. Shape of mandibular condyle in dorsal view: narrow, greatest anteroposterior length more than one and a half times greater than the greatest width (0); greatest width and the anteroposterior length roughly equivalent (1); or wide, greatest width more than one and a half times the greatest anteroposterior length (2). (Gaudin & Wible 2006, ch. 24)
6. Dorsal surface of mandibular condyle in posterior view: convex transversely (0); or flat (1). (Modified from Gaudin & Wible 2006, ch. 27)
7. Mandibular condyle: roughly sessile (0); or separated from the ascending ramus by a distinct neck (1).
8. Length of nasal bone: short, <twenty-five percent of the GSL (0); ≥twenty-five percent, <thirty percent of the GSL (1); ≥thirty percent, <thirty-five percent of the GSL (2); or elongated, ≥thirty-five percent of the GSL (3). (Gaudin & Wible 2006, ch. 37)
9. Lateral expansion of the maxilla, anterior to the root of the zygomatic arch: absent (0); modestly developed (1); highly developed (2).
10. Maxillary/palatine suture shape: rectangular, with angular anterolateral corners (0); or U-shaped with rounded anterolateral corners (1). (Modified from Gaudin & Wible 2006, ch. 55)
11. Median palatine suture: flat (0); raised to form a midline crest along the posterior half of the suture (1); or raised to form a midline crest along the entire length (2). (Gaudin & Wible 2006, ch. 58)
12. Maxillary foramen: (0) distinct from caudal palatine foramen; or (1) linked in a groove with caudal palatine foramen. (Billet *et al.* 2011, ch. 51)
13. Orbitosphenoid participation in sphenopalatine/caudal palatine foramen: present (0); or absent (1). (Gaudin & Wible 2006, ch. 74)
14. Orbital muscular crest: absent (0); or present (1). (Modified from Billet *et al.* 2011, ch. 63)
15. Zygomatic process of maxilla: forms the anterior margin of the infratemporal fossa (0); or excluded from the anterior margin of the infratemporal fossa by the jugal/lacrimal contact (1). (Modified from Gaudin & Wible 2006, ch. 84)
16. Depth of jugal (posterior to descending process): approximately uniform depth throughout its length (0); maximum depth in the anterior half, narrower posteriorly (1); or maximum depth in posterior half, narrower anteriorly (2). (Gaudin & Wible 2006, ch. 85)
17. Ventral process on zygomatic arch: absent (0); or present as elongated, mediolaterally compressed process on the posterior half of the jugal (1). (Modified from Gaudin & Wible 2006, ch. 86)
18. Dorsal edge of zygomatic arch profile from a lateral perspective: concave with a sharp break slope near jugal-squamosal suture (0); or straight and horizontal (1). (Modified from Billet *et al.* 2011, ch. 69)
19. Distinct groove for Eustachian (auditory) tube on basisphenoid: absent (0); or present (1). (Gaudin & Wible 2006, ch. 108)
20. Large vascular foramen (transverse canal foramen of Wible & Gaudin (2004)) located immediately anterior or ventral to foramen ovale: absent (0); or present (1). (Billet *et al.* 2011, ch. 83)
21. Entoglenoid process: present as a distinct ridge near the squamosal/alisphenoid suture (typically contacting the ectotympanic) (0); or present as in state (0) but sharper and longer (1). (Billet *et al.* 2011, ch. 86)