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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), *Pliodasypus* 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 tautonymy); *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).

The hairy (or woolly) long-nosed armadillo, currently referred as *Dasyopus pilosus*, is the most enigmatic species of the group. For more than one century since its description (Fitzinger 1856) only six specimens were housed in scientific collections (Burmeister 1862; Flower 1886, 1894), and even more contemporary studies were able to examine only few specimens (Wetzel & Mondolfi 1979; Wetzel 1982). However, these works clearly show strikingly different external features relative to other congeneric species: the carapace is concealed by long hair and the skull is much longer and slender (Fig. 1), leading Talmage & Buchanan (1954) to question its affinities.

With respect to the historical background of the taxon, based on a skin bought from an animal dealer in London with no locality data other than “Peru”, Fitzinger (1856:123) named this species as *Cryptophractus pilosus*. He remarked that it differs from other armadillos in having abundant hair concealing the carapace, and also detailed other external features, including the presence of 11 movable bands, the distribution of hair, and the number of digits, briefly comparing it to *D. novemcinctus*.

Ignoring the work of Fitzinger, Burmeister (1862) coined *Praopus hirsutus* for the same taxon, also defining the conspicuous hair cover as the main diagnostic character. He mistakenly attributed Guayaquil as the collection site of both specimens he examined in Lima. According to Wetzel & Mondolfi (1979), the type of *Praopus hirsutus* “is probably one of two museum exhibit mounts, either MHN [referred herein as MUSM] 26 or 27”. However, nowadays and at least since 1967, there is a single mounted skin on the exhibition of MUSM (Exhibition number 27) and Wetzel & Mondolfi (1979) did not clarify why they related Burmeister’s (1862) specimen to MUSM, considering that this museum was created only in 1918.

Later, Fitzinger (1871) expanded the description of *Cryptophractus pilosus*, but assigned its distribution to Colombia, Ecuador, Chile, and Peru. Flower (1886) reported an armadillo from unknown origin and identified it as the same taxon described by Fitzinger (1856) and Burmeister (1862), but referring it to genus *Tatusia*. Flower (1894) reported another specimen, from Maraynioc, central Peru. Gray (1865), Trouessart (1898, 1905), and Thomas (1927) adopted different binominal combinations (see below). Yepes (1928) was the first to combine *Dasyopus* with the specific epithet *pilosus*, although with incorrect gender agreement and restricting its distribution to Ecuador and Peru. Finally, Frechkop & Yepes (1949) corrected the gender agreement to *Dasyopus pilosus*. Cabrera (1958) and Mondolfi (1967) expanded the distribution of the species to Bolivia. Talmage & Buchanan (1954) erected *Cryptophractus* as a subgenus, which has been generally accepted (Wetzel & Mondolfi 1979; Wetzel 1982, 1985; Kraft 1995; Wetzel *et al.* 2007).

In this scenario, two taxonomic hypotheses might be considered: a) “*Dasyopus*” *pilosus* represents a subgenus, *Dasyopus* (*Cryptophractus*), as currently widely accepted; or b) “*Dasyopus*” *pilosus* should be placed in a different genus. This paper aims to provide: 1) an assessment of the relationships and taxonomic status of the hairy long-nosed armadillo; 2) a detailed comparative description of the external and cranial morphology; and 3) the first description of the distinctive morphological pattern of osteoderms.

Material and methods

Abbreviations: F, female; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; LSU, Louisiana State University, Museum of Zoology, Baton Rouge, USA; M, male; MSB: Mamm, Mammal Collection, Museum of Southwestern Biology, University of New Mexico, Albuquerque, USA; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; NHM, Natural History Museum, London, United Kingdom; NMW, Naturhistorisches Museum Wien, Vienna, Austria; YPM-VPPU, Princeton University Collection at Yale Peabody Museum of Natural History, New Haven, USA.

Analyzed specimens of *Dasyopus pilosus*: Eleven specimens were directly analyzed, namely MUSM 2056, skull and skin, M, Acomayo, Huánuco; MUSM 7499, skin, Parque Nacional Río Abiseo, San Martín; MUSM 7500, skull, unknown locality; MUSM 7501, skull and skin, M, Patáz, San Martín; MUSM 7502, skull and skin, F, Parque Nacional Río Abiseo, San Martín; MUSM 7503, skull and skin, M, Patáz, San Martín; MUSM 7504, skull and skin, F, Parque Nacional Río Abiseo, San Martín; MUSM 7505, skull and skin, F, Parque Nacional Río Abiseo, San Martín; MUSM 24214, disarticulated carapace, Oxapampa, Pasco; MUSM-ING 633, Concesión para la Conservación Alto Huayabamba, San Martín; MUSM-CT 1312, Yurac Rume, Amazonas. Photos of NMW 222 (holotype), skin, unknown locality; LSU 21888, skull and skin, Cordillera Colán, Amazonas; IRSNB 291536, mounted skin without tail, unknown locality (suggested as Santiago, Piura, by Frechkop & Yepes 1949);

MSB:Mamm 49990, skin, Acomayo, Huánuco. **Other referred material:** NHM 27.11.1.235, Acobamba, Junín; 94.10.1.13, Maraynoic, Huánuco; LSU 14352–14353, skins, Cordillera Carpish, Huánuco; LSU 18435, skin, Bosque Zapatogocha, Huánuco; LSU 19240–19241, skulls and skins, Bosque Taprag, Huánuco; LSU 19242, skin, Bosque Taprag, Huánuco; LSU 19243, skin and skull, Bosque Zapatogocha, Huánuco.

Measurements. For the comparative description, external and cranial measurements of dried specimens were considered. Externally, the total length was taken, as well as the length of head, carapace, tail, hind foot, and ear (Table 1). Also, the length of cephalic shield, scapular buckler, movable bands, and pelvic buckler were measured along the sagittal line (Table 2). The cranial measurements assessed were: maximum skull length, palatal length at sagittal line, rostral length, rostral ratio (i.e., rostral length divided by the maximum skull length), zygomatic width, and maximum mandibular length (Table 3). *Dasyopus pilosus* were compared to the specimens of *Dasyopus* listed in Appendix 1.

Phylogenetic analysis. To test the relationships of *D. pilosus*, we conducted a phylogenetic analysis including fossil and extant Dasypodidae. Fifty-eight morphologic characters related to the skull, mandible, and carapace were scored for the ingroup, which represents the subfamily Dasypodinae; see character, character-states definitions, and matrix in Appendices 2 and 3. Most characters were taken from previous phylogenetic analyses (Gaudin & Wible 2006; Ciancio 2010; Billet *et al.* 2011; Carlini *et al.* 2014; Castro *et al.* 2013a, 2014), some of them were modified, and new characters were also proposed. The ingroup taxa are: *Stegosimpsonia* sp. Vizcaíno (Astegotheriini; early Eocene of Argentina), *Stegotherium tauberi* González & Scillato-Yané (Stegotheriini; early Miocene of Argentina), and the extinct Dasypodini *Propraopus sulcatus* (Lund) (Pleistocene–early Holocene of South America), *Anadasypus hondanus* Carlini *et al.* (middle Miocene of Colombia), *Dasyopus bellus* (late Pliocene–late Pleistocene of North America), and *D. punctatus* (late Pleistocene–early Holocene of Brazil), besides the extant species of *Dasyopus*. The election of *Peltephilus pumilus* Ameghino (middle Miocene of Argentina) as outgroup is based on the presence of well-preserved skull and carapace (González Ruiz *et al.* 2013), and on previous phylogenetic studies that found it as the basal-most cingulate xenarthran, followed by *Stegotherium* + *Dasyopus* (Engelmann 1985; Gaudin & Wible 2006; Billet *et al.* 2011). Under maximum parsimony criterion, an exact search was conducted in the software TNT 1.1 (Goloboff *et al.* 2008). The multistate characters were treated as non-additive.

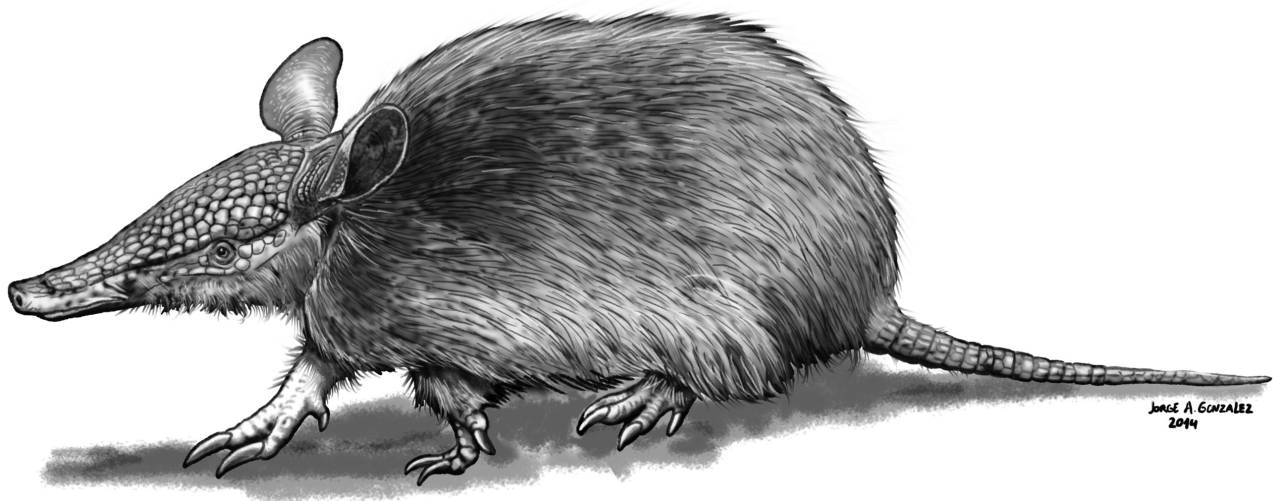


FIGURE 1. Drawing of *Cryptophractus pilosus* showing some of its external features: dense hair concealing the carapace, long and slender rostrum, cephalic shield with an acute posterior margin, more distantly separated from the base of the ears, and V-shaped occipital sulcus.

Results

A single most parsimonious tree was found in the maximum parsimony analysis (tree length = 113; Consistency Index = 0.66, Retention Index = 0.61; Fig. 2). This analysis finds support for *Stegosimpsonia* as the sister-group of Dasypodini (node A). *Anadasypus hondanus* is regarded as the most basal Dasypodini (node B), followed by

Propraopus sulcatus (node C), and *Dasypus pilosus* (node D). Subgenus *Dasypus* (*Hyperoambon*) (i.e., *D. kappleri*) is within node E, that encompasses the extinct species of *Dasypus* (*D. bellus* and *D. punctatus*) and the extant members of subgenus *Dasypus* (*Dasypus*), which resulted paraphyletic. The nodal supports for nodes B–E range from 27–44 (Jackknife, P=20, frequency differences, implicit enumeration, 100 replicates).

The numerous autapomorphies of *Dasypus pilosus* (i.e., most frequent number of completely movable bands equals to 10 [ch. 36: 3]; presence of two rows of piliferous foramina in the posterior border of buckler and/or movable osteoderms [ch. 42: 1]; absence of principal [ch. 43: 0] and radial [ch. 51: 1] sulci in the buckler osteoderms; absence of principal sulcus in movable osteoderms [ch. 53: 0]; and one or two large foramina frequently present in the anterior part of the ornamented portion of movable osteoderms [ch. 58: 0]) and its external position relative to other species of *Dasypus* (represented in node E) in the cladogram reflect the extreme difference of that species in relation to the remaining ones. Therefore, we favor the rank modification of *Cryptophractus* from subgenus to genus, revalidating the generic name originally proposed by Fitzinger (1856).

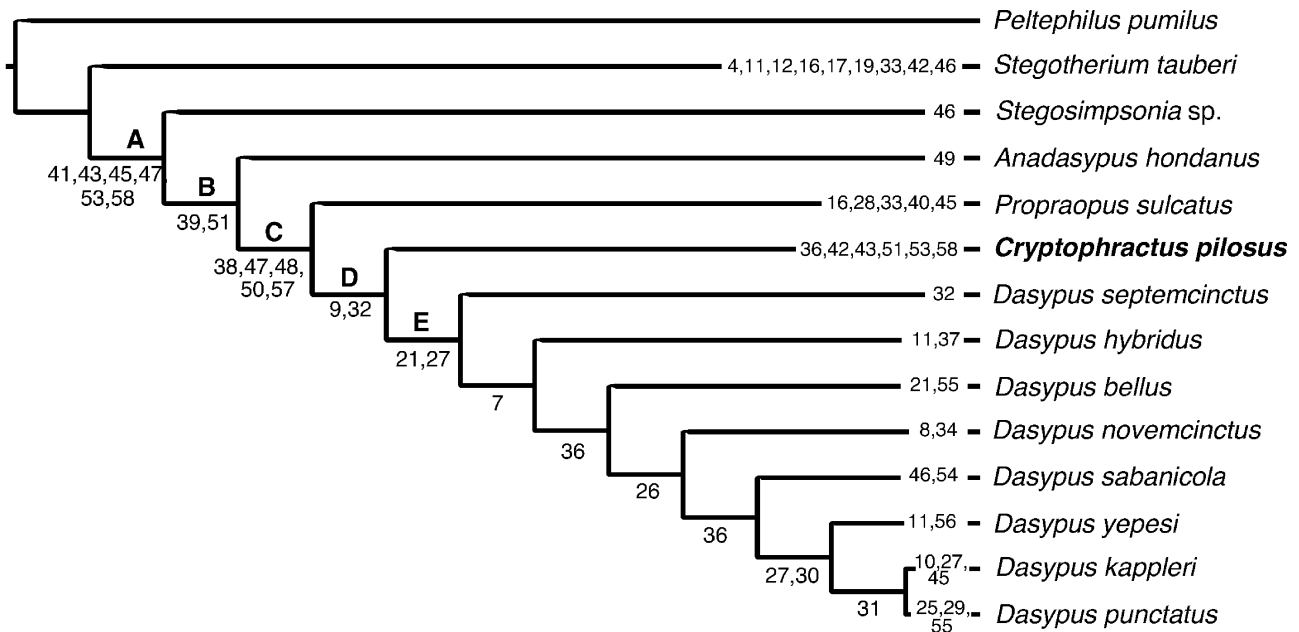


FIGURE 2. Most parsimonious tree resulting from the cladistic analysis of 58 characters (tree length = 113; Consistency Index = 0.66, Retention Index = 0.61). Capital letters represent the nodes discussed in the text; sinapomorphies given below the nodes and autapomorphies given along each branch, following the numbers assigned in Appendix 2.

Systematics

XENARTHRA Cope, 1889

Cingulata Illiger, 1811

Dasypodidae Gray, 1821

Dasypodinae Gray, 1821

Dasypodini Gray, 1821

Genus *Cryptophractus* Fitzinger, 1856 [nomen revalidatum]

Cryptophractus Fitzinger, 1856: 123.

Praopus Burmeister, 1854 [part]: Burmeister 1862:147; new species.

[*Tatusia* (*Cryptophractus*)] Cuvier, 1822 [part]: Trouessart 1898:1140; name combination and new rank.

[*Tatus* (*Cryptophractus*)] Frisch, 1775: Trouessart, 1905:814; name combination.

Tatu Blumenbach, 1779 [part]: Thomas, 1927:605; name combination.

Dasypus Linnaeus, 1758 [part]: Yepes, 1928:468; name combination.

Dasypus (*Cryptophractus*) Linnaeus, 1758: Talmage & Buchanan, 1954:84; new rank.

Type species. *Cryptophractus pilosus* Fitzinger, 1856

Diagnosis. As the species by monotypy.



FIGURE 3. Collection sites of *Cryptophractus pilosus* in Peru. Armadillos, collection sites; gray shade, integrated area of distribution; black circles, Department Capitals.

***Cryptophractus pilosus* Fitzinger, 1856 [nomen revalidatum]**

Cryptophractus pilosus Fitzinger, 1856:123. Holotype NMW 222; type locality Peru.

Praopus hirsutus Burmeister, 1862:147. Possibly MUSM 27 (see above); type locality “Guayaquil”, Peru.

[*Tatusia* (*Cryptophractus*)] *pilosus*: Trouessart, 1898:1140; name combination.

[*Tatus* (*Cryptophractus*)] *pilosus*: Trouessart, 1905:814; name combination.

Tatu pilosa: Thomas, 1927:605; name combination.

Dasypus pilosa: Yepes, 1928:468; name combination with incorrect gender agreement.

Dasypus pilosus: Frechkop & Yepes, 1949:27; gender agreement correction.

Dasypus (*Cryptophractus*) *pilosus*: Talmage & Buchanan, 1954:84; name combination.

Holotype. NMW 222, mounted skin (Fitzinger 1856).

Type locality. Montane Peru (restricted by Wetzel & Mondolfi 1979).

Distribution. Montane cloud forests and subparamo of Peruvian Andes, in the departments of San Martín, La Libertad, Huánuco, Junín, Amazonas (Grimwood 1969; Wetzel & Mondolfi 1979; Wetzel *et al.* 2007) and expanded herein to Pasco (Fig. 3). The specimens examined were generally collected close to water bodies, between 2,600 to 3,400 m above the sea level.

Diagnosis. Dense hair covering the whole carapace, obscuring it; cephalic shield narrow and elongate, loosely delimited anteriorly, with acute posterior margin more distantly separated from the base of the ears, and V-shaped occipital sulcus; greater number of completely movable bands (9 to 11); osteoderms with no sulci, numerous foramina (more than 30), and frequently two larger foramina placed anteriorly in the movable osteoderms; rostrum and palate longer and narrower (rostral ratio 0.66 on average; see Wetzel & Mondolfi [1979] for description on how to take this measure); condylar process of mandible lower and sessile; and minute teeth.

Comparative description. Externally, *Cryptophractus pilosus* has the whole carapace covered by a thick coating of rigid, long, yellow to light-brown hairs that completely conceal the carapace, but for the antero-lateral margin of the scapular buckler (Fig. 4). The same type of hair is present in the cheeks and proximal portion of the limbs; shorter and less abundant hair covers the ventral surface of the body, where brownish transversal lines in the skin are in continuation to the movable bands. These areas also show some flat isolated osteoderms within the skin. *Cryptophractus pilosus* has five digits in the feet and four in the hands; a vestigial fifth digit is externally visible only in *D. kappleri* (but see Costa & Vizcaíno 2010). The ears are large and conical, covered with pebbly skin, whereas the eyes are a small slit.

The external measurements (Table 1) agree with previous observations on the species (Fitzinger 1871; Flower 1886; Frechkop & Yepes 1949; Wetzel & Mondolfi 1979; Wetzel 1985). Only three adult specimens analyzed have weight data (MUSM 7501=2.30 kg; MUSM 7504=1.40 kg; MUSM 7505=1.85 kg), being on the upper range or slightly heavier than *D. septemcinctus* (1.45–1.80 kg), *D. hybridus* (2.04 kg) and *D. sabanicola* (1.00–2.00 kg) (Hamlett 1939; Wetzel & Mondolfi 1979). The average total length also indicates that *C. pilosus* is larger than these species and *D. yepesi*, whereas is smaller than *D. novemcinctus* and *D. kappleri* (Wetzel & Mondolfi 1979). As observed in *D. novemcinctus* (McBee & Baker 1982), apparently the males (MUSM 2056, 7501) of *C. pilosus* are slightly larger than the females (MUSM 7504, 7505), as shown in Tables 1–3.

TABLE 1. External lengths of *Cryptophractus pilosus* (mm), taken from dried specimens. Averages calculated excluding the juvenile specimens.

	Total	Head	Carapace	Tail	Hind foot	Ear
MUSM 2056	750	112	287	261	70	50
MUSM 7499	—	117	237	—	—	35
MUSM 7501	648	125	266	268	80	43
MUSM 7502*	—	—	186	181	53	43
MUSM 7503*	413	80	159	162	56	33
MUSM 7504	593	116	205	245	71	41
MUSM 7505	650	122	233	260	75	42
MUSM-ING 633	—	—	231	253	71	—
MUSM-CT 1312*	—	—	167	146	—	—
Average	660	118	236	243	74	44

*juvenile specimens.

TABLE 2. Carapacial measurements of *Cryptophractus pilosus* (mm), taken along the sagittal line.

Specimen	Specimen	Scapular Buckler	Movable Bands	Pelvic Buckler
MUSM 2056	80.7	70.7	98.4	118.2
MUSM 7499	70.9	71.3	73.4	92.5
MUSM 7501	~90	67.5	94.0	104
MUSM 7502*	~73	~49	~65	~72
MUSM 7503*	67.6	45.6	59.0	54.7
MUSM 7504	67.4	57.0	~61	~87
MUSM 7505	~85	55.2	77.3	100.9
MUSM-ING 633	63.6	59.2	89.	81.8
MUSM-CT 1312*	—	48.4	~65	53.2

*juvenile specimens.

TABLE 3. Cranial measurements of *Cryptophractus pilosus*. **Abbreviations:** **MSL**, maximum skull length; **PL**, palatal length at sagittal line; **RL**, rostral length; **R ratio**, rostral ratio (=RL/MSL); **ZW**, zygomatic width; **ManL**, maximum mandibular length. Averages calculated excluding the juvenile specimens.

Specimen	MSL	PL	RL	R ratio	ZW	ManL
MUSM 2056	109.4	80.5	75.2	0.69	35.1	90.6
MUSM 7500	110.7	75.5	71.8	0.65	36.2	90.4
MUSM 7501	109.3	79.4	72.3	0.66	34.5	88.2
MUSM 7502*	89.0	~61	54.8	0.62	31.1	68.0
MUSM 7503*	69.8	51.1	43.4	0.62	24.1	61.0
MUSM 7504	99.9	68.6	65.2	0.65	32.1	80.9
MUSM 7505	105.9	~69	66.1	0.62	35.0	86.2
Average	102.9	68.6	65.7	0.64	33.6	83.6

*juvenile specimens.

With respect to the carapace, the cephalic shield is narrow and elongate, roughly rhomboid, and the osteoderms does not form rosettes; the posterior end is acute, more distantly separated from the base of the ears, and has a V-shaped occipital sulcus; anteriorly, the osteoderms become gradually irregular in shape, loosely articulated to each other, and arranged in lines parallel to the sagittal plan. The morphology of the cephalic shield differs from that of *Dasypus* spp., as was illustrated by Frechkop & Yepes (1949) and Kraft (1995). The pelvic buckler is variably longer than the scapular buckler (Table 2). The latter has a round anterior border (angular only in *D. kappleri*). The number of completely movable bands ranges from 9 to 11 (n=8). Besides of being more numerous than in *Dasypus* spp. (Hamlett 1939; Wetzel & Mondolfi 1979; Vizcaíno 1995), each band is anteroposteriorly shorter. Also our observation on a dry carapace (MUSM-ING 633) suggests limited mobility among the four anterior bands, which seem to be fused with each other. The cylindrical tail corresponds to 65–76% of the head-body length, similarly to *D. kappleri* and *D. novemcinctus* and much longer than the other species of *Dasypus*; its posterior third gradually tapers, whereas the proximal two-thirds is partitioned in 7–11 rings (n=8), each composed of two rows of osteoderms with scarce hairs on the posterior margin of each ring.

The morphology and ornamentation of the osteoderms are described here for the first time confirming that it is unique in relation to all extant armadillos (Fig. 4 and 5). They lack principal or radial sulci. The foramina of the buckler osteoderms are arranged in a central circle bounding a nearly circular central figure, which have small neurovascular foramina inside it. A second row of similar foramina forms a posterior semicircle. The total number of foramina per osteoderm (including some confluent ones) is about 30 in the scapular and 35 in the pelvic osteoderms. The pelvic elements have bigger and more lacerated foramina. Scapular semimovable osteoderms have a semicircular arch of foramina in the mid part and at least two rows of foramina in the posterior border, together forming a nearly circular figure. Pelvic semimovable and movable osteoderms have one or two large foramina anteriorly. The foramina are distributed within an inverted “V” pattern in the formers, and their size decrease posteriorly. The foramina in the movable osteoderms are arranged in two posteriorly divergent lines, which are connected distally by a semicircular arc, forming a triangular principal figure; a circular figure is limited anteriorly by an additional, but inverted, semicircular arc of foramina at mid-length; the posterior margin is copious of foramina, arranged in two or three rows; the size of the foramina also decrease posteriorly. The observations on two specimens (MUSM 24214 and MUSM-ING 633) indicate that, despite the great size of the foramina in the osteoderms, a single hair comes out of each foramen.

The horn scales are thicker than in *Dasypus* spp., with irregular borders and numerous perforations for hair emersion. Several depositional layers are visible from inside to outside. Each buckler osteoderm is covered by a central scale and about six peripheral scales that also cover part of adjoining osteoderms. In movable osteoderms the principal figure is covered by a triangular and a circular scale, and inverted triangles cover the peripheral figures of two adjoining elements (Fig. 5).

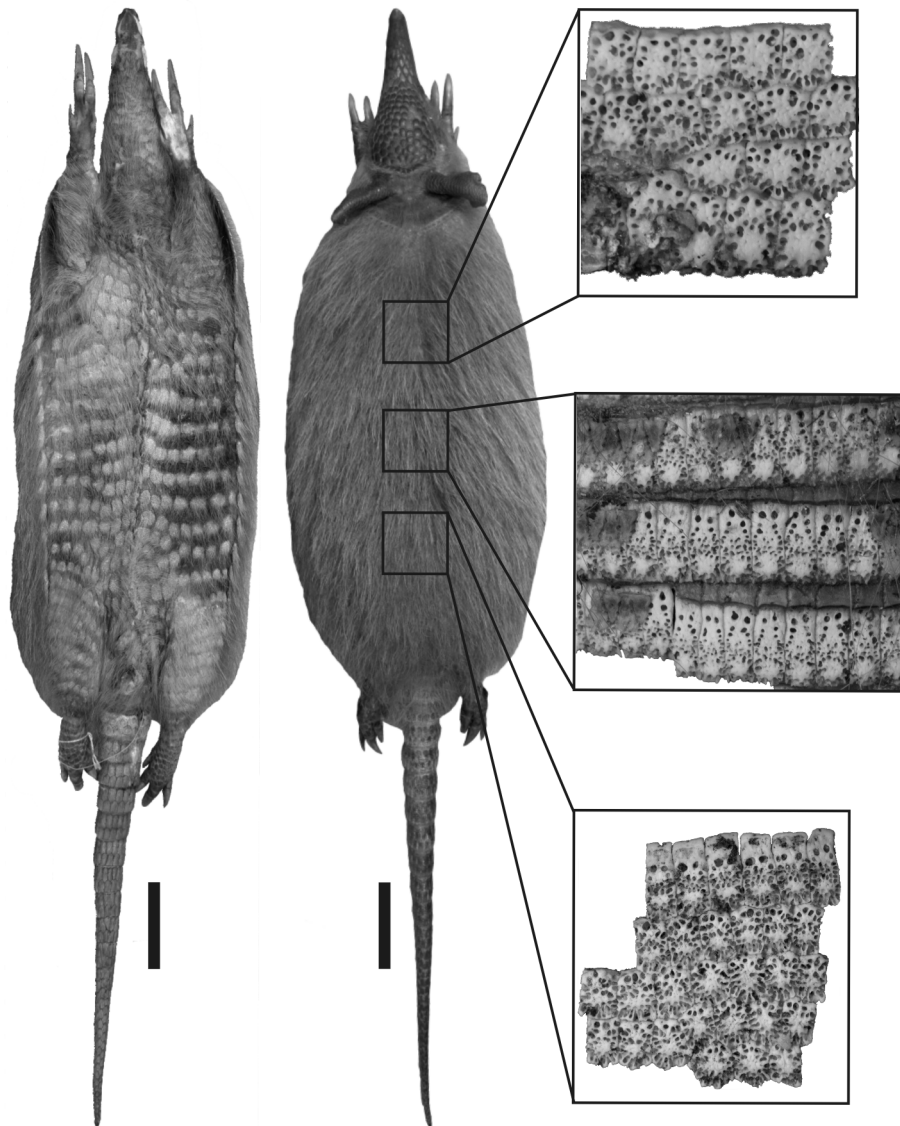


FIGURE 4. Skin of *Cryptophractus pilosus* in ventral (MUSM 7501) and dorsal (MUSM 7505) views, and detail of osteoderms from different areas of the carapace (MUSM 24214) in the boxes. Top box, scapular osteoderms; middle box, movable osteoderms; and bottom box, pelvic semimovable and pelvic osteoderms. Scale bars equal 50 mm.

The skull of *Cryptophractus pilosus* is unique in having the longest and narrowest rostrum of all extant armadillos. The lateral margins of the rostrum are sub-parallel in dorsal view but its anterior tip is slightly broader (Fig. 6A). A delicate sagittal crest is present in most of the adult specimens (e.g., MUSM 7504), a rare feature in *Dasypus* spp. Anterior to the interorbital constriction the frontals are delicately vaulted by the development of frontal sinuses. The anterior processes of the frontals are more elongated than in *Dasypus* to contact the longer nasal bones.

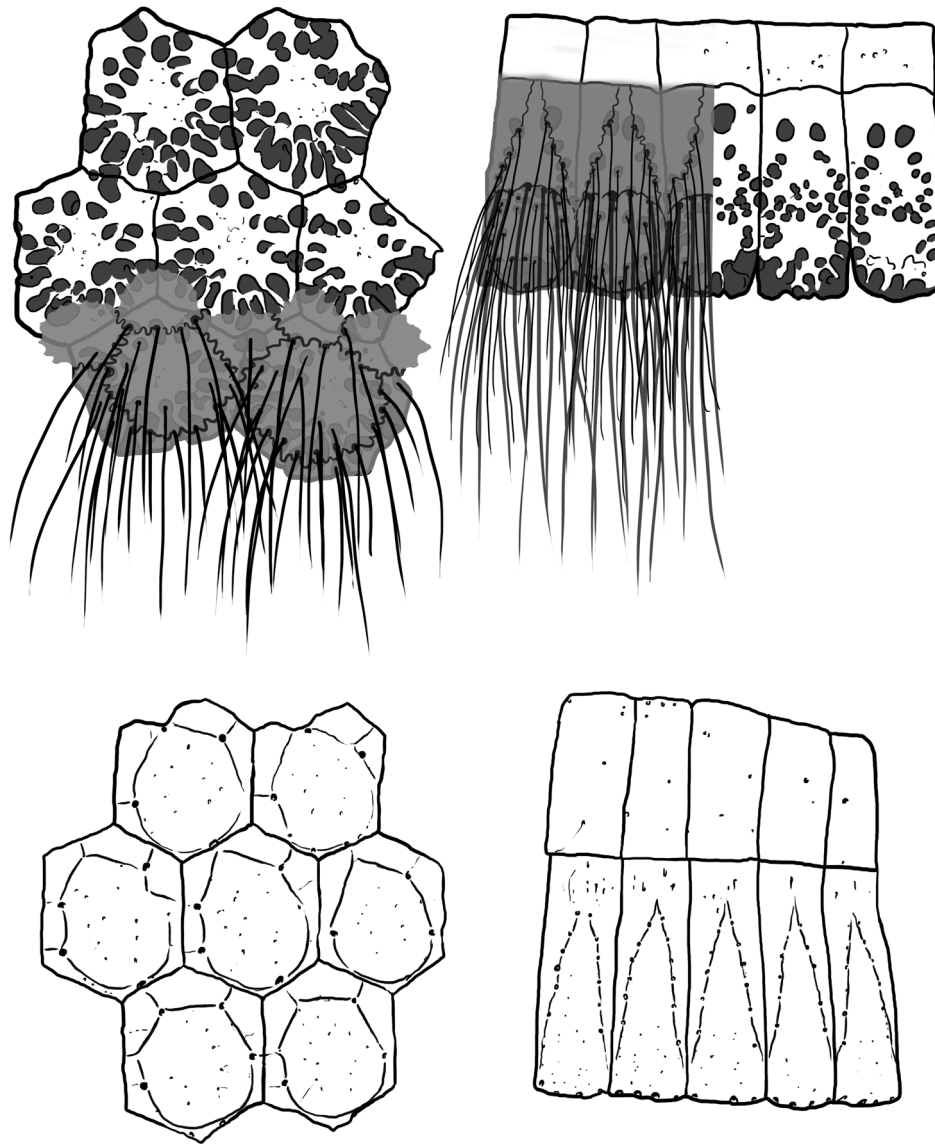


FIGURE 5. Drawing of buckler and movable osteoderms of *Cryptophractus pilosus* (top) and *D. novemcinctus* (bottom). Gray shades represent the disposition of the horn scales.

In the ventral aspect of the skull (Fig. 6B), the maxillae, and occasionally the premaxillae, are concave along the sagittal line. The palate corresponds to 68–74% (70% on average, n=7) of the maximum skull length, including juveniles, confirming the observations of Wetzel & Mondolfi (1979). In relation to *D. novemcinctus*, the increase of the palatal length in *C. pilosus* is achieved by the extension of the maxillae and premaxillae, whereas the palatines remain proportionally equal. The palatines are flat, with a heart-shaped anterior border and rounded lateral margins. The posterior border of the palate, comprising palatines and pterygoids, is indented medially with a contour varying from a long and narrow “V” to bell-shaped. This condition differs from *D. kappleri*, which has a straight and roughly square internal nasal aperture. The free border of the pterygoids has a sharp ventral projection, forming a triangular outline in lateral view. The glenoid articulation is oval and flat, with a ventrally projecting postglenoid process. The foramen ovale and the transverse canal foramen are separated in all available specimens, whereas these are confluent in some specimens of *Dasypus* spp.

In lateral view (Fig. 6C), the dorsal contour of the rostrum is approximately straight, as in *D. hybridus* and *D. septemcinctus*, whereas it is markedly sigmoid in the other *Dasypus* species. The zygomatic arch is dorso-ventrally thinner than in *D. novemcinctus* and the crest for insertion of masseter muscle is weaker. The lacrimal is proportionally smaller, as in *D. hybridus*, and possesses one or exceptionally two lacrimal foramina. The

morphology of the contact between the petrosal and the squamosal varies from a shallow occipital groove in the youngest specimen (MUSM 7503) to an occipital canal with different degrees of closure in the adults, as described for *D. novemcinctus* (Wible 2010). Five specimens (MUSM 7500, 7501, 7503, 7504, and 7505) preserve the ectotympanic and the ossicles of the middle ear. Adults present an ossified entotympanic that partially covers the ventral part of the petrosal, running medially to the ectotympanic from its the posterior part until the alisphenoid-ptyergoid suture (Fig. 7); only in MUSM 7503, a juvenile, the ossification of the entotympanic has a middle gap between two ossifications. In *D. novemcinctus*, the only extant *Dasypus* with detailed studies on the auditory region, the entotympanic is poorly developed, composed by small isolated ossifications (Patterson *et al.* 1989; Wible 2010). The same pattern was observed in *D. septemcinctus* (MNRJ 10062; Fig. 7).

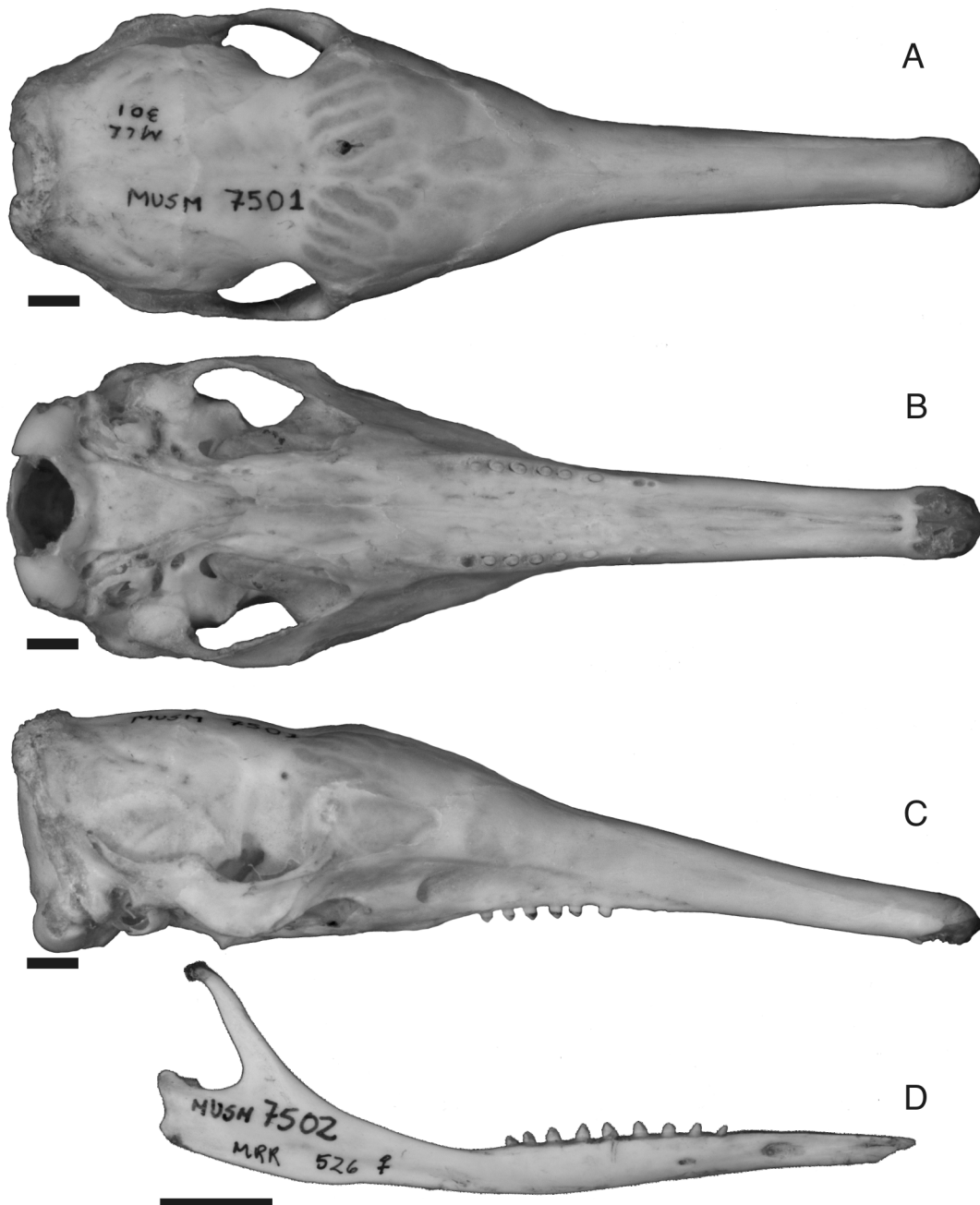


FIGURE 6. Skull of *Cryptophractus pilosus* (MUSM 7501) in dorsal (A), ventral (B), and lateral (C) views, and right mandibular ramus (MUSM 7502) in lateral view (D). Scale bars equal 10 mm.

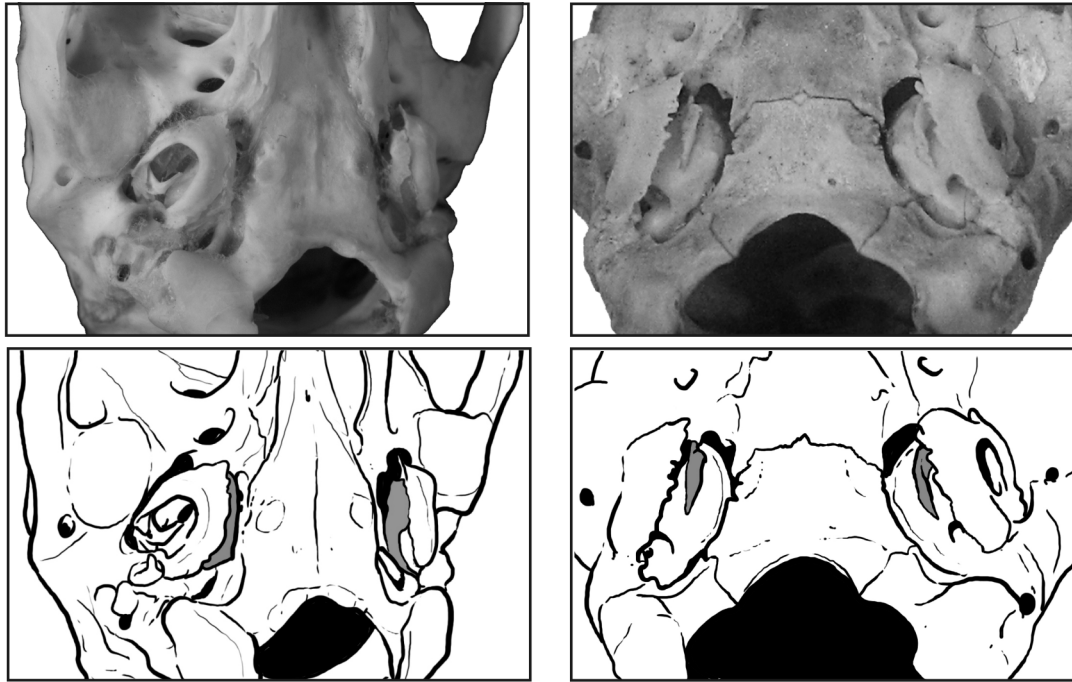


FIGURE 7. Comparison of the ear region of *Cryptophractus pilosus* (left) and *Dasypus septemcinctus* (right), showing different degrees of entotympanic ossification (gray shades in the drawings) in both taxa.

The slender mandible (Fig. 6D) shows a straighter horizontal ramus, much slender than in extant related species. The angular process is blunt and the condylar process is lower and sessile (whereas it has a neck with variable development in *Dasypus*).

Table 3 shows some cranial measurements of *Cryptophractus pilosus*. They are consistent with previous observations on the species (Wetzel & Mondolfi 1979; Wetzel 1985). The skull length and the zygomatic width are only smaller than in *D. kappleri* and than the largest specimens of *D. novemcinctus*. With respect to the rostral ratio (=length of the rostrum/maximum skull length), excluding juvenile specimens, it varies between 0.62 and 0.69, with an average of 0.66. According to data presented by Wetzel & Mondolfi (1979), this ratio is slightly higher than that of *D. kappleri* (0.64 on average) and sensibly exceeds those of *Dasypus* (*Dasypus*) group, which are mostly below 0.62 in *D. novemcinctus* and about 0.56 in *D. septemcinctus*, *D. hybridus*, and *D. sabanicola*; the rostral ratio of *D. yepesi* (0.55, calculated for MLP 30-III-90-8) agrees with the other small species.

Like in *Dasypus* (Ciancio *et al.* 2012), the peg-like molariforms of *Cryptophractus pilosus* have an anterior-posterior beveled occlusal relief (Figs. 6C and 6D). However, the teeth are substantially smaller (with approximately 1 mm long and 0.7 mm wide) and subcylindrical (instead of prismatic with subrectangular cross-sections). There are 7 to 8 upper and 7 to 9 lower molariforms, a tooth count higher than the 5/6 observed by Wetzel (1985). The dental series occupy only a short portion of the maxilla and mandible, leaving an extensive edentulous anterior section, longer than the dental series itself. Closed or aborted alveoli are highly frequent in the material analyzed. Previous studies in *Dasypus* spp. showed that a thin enamel layer is present in the apical portion of deciduous and permanent teeth, but is lost soon after the eruption; also the two real cusps (labial and lingual), are worn leaving secondary labial and lingual borders (Martin 1916; Ciancio *et al.* 2010). Further studies are required to confirm the presence of dental enamel in *C. pilosus*.

A single specimen (MUSM 24214) has appendicular and axial elements preserved, mostly with unfused epiphyses, suggesting an immature condition of the skeleton. It includes three thoracic and five lumbar vertebrae, sacrum, right femur, tibia-fibula, astragalus, calcaneus, navicular, plantar sesamoid, metatarsals, and phalanges. Anatomical comparisons were made among these elements and those of *Dasypus* species (including a young juvenile specimen of *D. septemcinctus*), except for *D. sabanicola*. Figure 8 compares equivalent postcranial elements of *C. pilosus* and *D. novemcinctus*. In *C. pilosus*, the lumbar vertebrae have shorter neural spines and metapophyses and, in lateral view, the angle formed between these apophyses is wider. The morphology of the

xenarthrous articulations is concordant with the description of Gaudin (1999). The synsacrum is proportionally longer, composed of seven vertebrae (varying from seven to nine in *Dasypus* spp.), although the irregular posterior margin of the transverse processes of the last one suggests the presence of an eighth posteriorly incorporated element. The iliac crest is more recurved and more laterally projected, as wide as the ischia. The femur is slenderer; oddly a hair pierces the posterior surface of the shaft. The tibia and fibula are not yet fused at their distal ends, as observed in adults of *Dasypus*. Compared to *D. novemcinctus* and *D. hybridus*, the astragalus of *C. pilosus* has a longitudinal separation in the tibial facet, the neck lacks ridges on the dorsal surface, and the sustentacular and navicular facets are larger. Both calcaneal heel and head are proportionally broader, the ectal facet extends further over the calcaneal heel, and laterally the peroneal process is incipient. Jasinski & Wallace (2014) hypothesized that a greater development of this process (as present in *D. novemcinctus*) may be related to semifossorial habits. No differences were observed in the remaining elements.

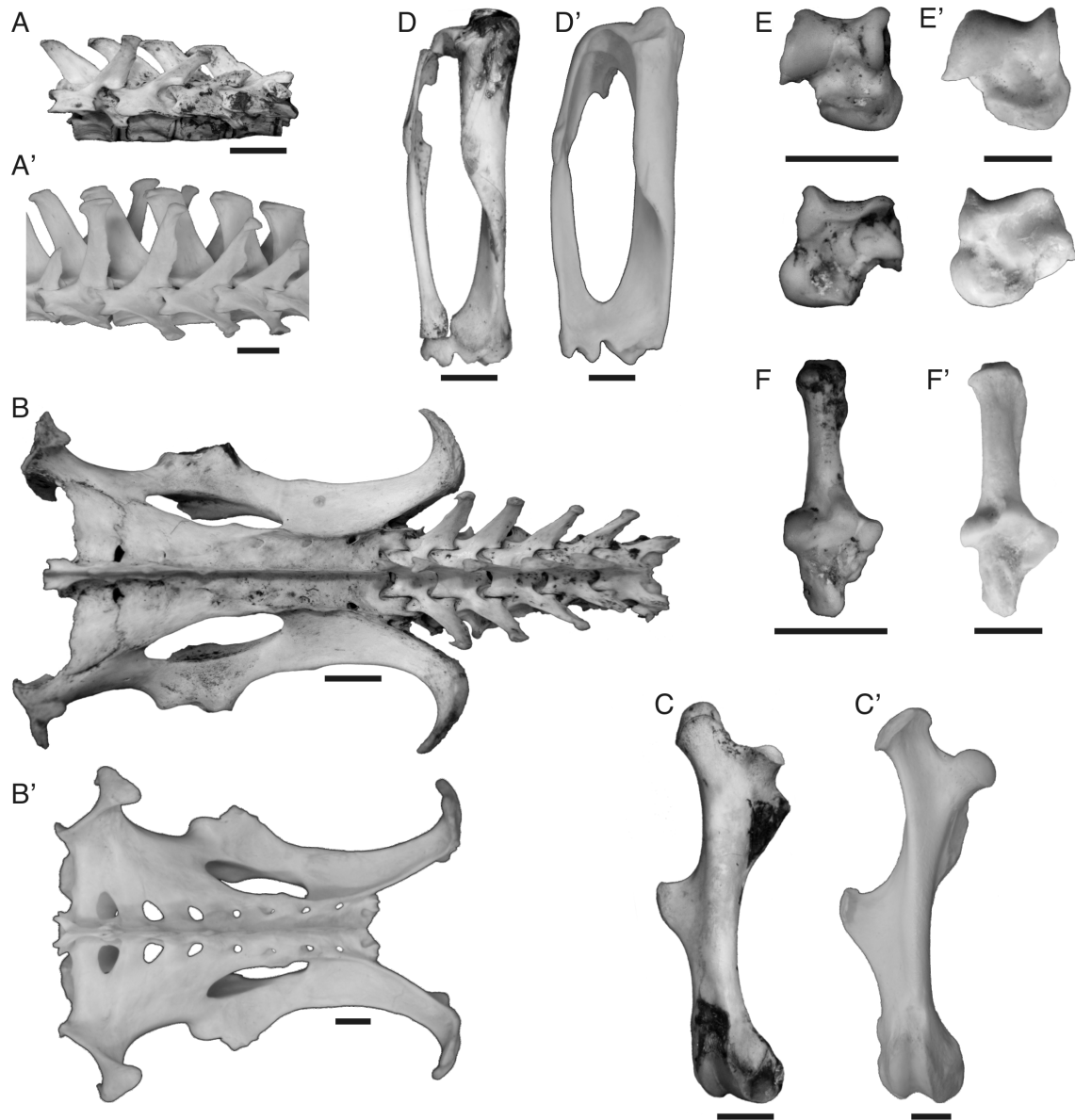


FIGURE 8. Comparison of the postcranial elements of *Cryptophractus pilosus* and *Dasypus novemcinctus*, which is represented by ('). (A), lumbar vertebrae; (B), synsacrum; (C), femur; (D), tibia-fibula; (E), astragalus; and (F), calcaneum. Scale bars equal 10 mm.

Habitat and biology. The predicted distribution of *C. pilosus* (NatureServe 2014) includes a narrow montane strip in Peru from Amazonas to Junín Departments. Consequently, due to deforestation of montane habitats the conservation status of *C. pilosus* is vulnerable (Pacheco 2002; Superina & Abba 2010). Its ecology and behavior are completely unknown (Wetzel *et al.* 2007). In this regard we report the occurrence of multiple embryos in the species based on the observation of a female with four embryos (MUSM 7504). Also, a tick identified as *Ixodes* sp. was found attached to the skin of other specimen (MUSM 7499).

With respect to diet, it is predominantly based on insects in *D. sabanicola* and in *D. novemcinctus* (Mondolfi 1967, McBee & Baker 1982, Smith & Redford 1990). Numerous morphological adaptations for myrmecophagy (=termitophagy) were recognized in *D. novemcinctus* (Moeller 1968; Wetzel & Mondolfi 1979; Smith & Redford 1990; Charles *et al.* 2013). In *C. pilosus*, some of these characters are even more accentuated, such as a longer and narrower rostrum, the shorter dental series composed of minute teeth, frequent closed/aborted alveoli in adults, and lower and sessile mandibular condyle. These features suggest a predominantly ant and termite-eating diet, although no direct observations of feeding activity has been recorded. Also, the skull, mandible, and teeth of the mid-sized fossil armadillo *Stegotherium* (early–middle Miocene of Patagonia) shows similarities to *C. pilosus*. Although phylogenetic studies support a close relationship between this genus and Dasypodini (Engelmann 1985; Gaudin & Wible 2006; and the present cladistic analysis), the resemblances between *Stegotherium* and *C. pilosus* might reflect a convergence related to their feeding habits, as a myrmecophagous diet was also inferred for the former (Vizcaíno 1994).

Discussion

The peculiar external and cranial morphology of *Cryptophractus pilosus* led previous authors to question its relations with congeneric taxa, placing the species in a separate subgenus or in a separate genus (Fitzinger 1856; Talmage & Buchanan 1954; Wetzel & Mondolfi 1979). The only exception was the allometric cranial analysis of Moeller (1968) that regarded a closer relationship between *C. pilosus* and *D. septemcinctus* than either to *D. novemcinctus*, a proposition later rejected (see Wetzel & Mondolfi 1979).

Although controversial (e.g., Benton 2000; Kuntner & Agnarsson 2006; de Queiroz & Donoghue 2013), we present here an attempt to conciliate the rank-based nomenclature and the proposed phylogeny for the taxa under study. The original concept of *Dasypus* proposed by Linnaeus (1758) includes *D. novemcinctus* and *D. septemcinctus*. Transposing this fundamental concept to our cladogram, genus *Dasypus* corresponds to node E, the least-inclusive group that comprises the two above-mentioned species. In this context, *Anadasypus hondanus*, *Propraopus sulcatus*, and *Cryptophractus pilosus* may be interpreted as a paraphyletic array of ‘stem Dasypodini’, each one deserving distinct generic status.

It is clear that the establishment of supraspecific ranks depends on the taxonomist’s criterion and that these taxa go through problems of equivalence among distinct zoological groups. In the present case, what is the difference between a genus and subgenus that contains a single species? How much difference justifies the separation of a genus? Examining an example among living armadillos, well summarized by Delsuc *et al.* (2012), the pink fairy armadillo *Chlamyphorus truncatus* Harlan and the Chacoan fairy armadillo *Calyptophractus retusus* (Burmeister) are nowadays widely accepted as two distinct monospecific genera (Wetzel *et al.* 2007; Delsuc *et al.* 2012). They were originally part of the same genus (*Chlamyphorus*), but several authors supported their separation aiming to reflect the degree of morphological difference between them (Gray 1865; Fitzinger 1871; Moeller 1968), which is the same purpose that we present here.

Although some characters of *Cryptophractus pilosus* can be intuitively attributed to natural selection related to its restricted niche (e.g., cranial enlargement and dental reduction, potential adaptations to myrmecophagy), other features (e.g., greater ossification of the entotympanic and greater number of movable bands) are potentially plesiomorphic and do not seem to be adaptive.

Another point to examine is the divergence time estimates of Xenarthra presented by Delsuc *et al.* (2012). Based on molecular clocks, these estimates ultimately reflect the amount of molecular difference between taxa. It is noticeable that *Dasypus novemcinctus* / *Dasypus kappleri* show equivalent divergence estimates (11 ± 2 My) than *Tamandua* / *Myrmecophaga* (13 ± 2 My), and higher than *Euphractus* / *Chaetophractus* + *Zaedyus* (8 ± 2 My), taxa widely recognized as having a genus rank. A “fairly ancient estimate of divergence” (17 ± 3 My) supported the

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)

22. Medial extension and distal expansion of tympanohyal: absent (0); or medial extension present, but unexpanded distally (1). (Modified from Gaudin & Wible 2006, ch. 128)
23. Position of ectotympanic and fissura Glaseri: ectotympanic posterior to the glenoid fossa, Glaserian fissure well posterior of the foramen ovale (0); or ectotympanic medial to the glenoid fossa, Glaserian fissure immediately posterior to the foramen ovale (1). (Modified from Gaudin & Wible 2006, ch. 106)
24. Width of foramen magnum: narrow, maximum width less than or equal to one half the maximum width of the occiput (0); or wide, maximum width greater than one half the maximum width of the occiput (1). (Gaudin & Wible 2006, ch. 159)
25. Relative position of infraorbital foramen versus anterior border of the lacrimal: infraorbital foramen anterior (0); or both at same position or infraorbital foramen posterior (1). (Castro *et al.* 2013a, ch. 2)
26. Dorsal contour of the rostrum in lateral view: nearly straight (0); or sigmoid (1). (Castro *et al.* 2013a, ch. 3)
27. Length of upper tooth row (with all molariforms erupted) in relation to the maxillary length at ventral midsagittal line: less than 50% (0); 50–60% (1); 60–70% (2); or over 70% (3). (Modified from Castro *et al.* 2013a, ch. 4)
28. Posterior palatal recess: long and narrow (0); long and broad (1); short and broad (2); or straight (3). (Modified from Castro *et al.* 2013a, ch. 5)
29. Posterior palatal angle (measured between the posterior-most point of the interpalatine suture and the posterior-most medial free border of the palate): less than 80° (0); or over 80° (1). (Castro *et al.* 2013a, ch. 6)
30. Posterolateral border of palate strongly keeled: absent (0); or present (1). (Castro *et al.* 2013a, ch. 7)
31. Condition of palatine: with longitudinal wrinkle and/or lateral narrowing (0); or completely flat (1). (Castro *et al.* 2013a, ch. 8)
32. Length of infraorbital canal in relation to antero-posterior dimension of lacrimal: less than 40% (0); 40–60% (1); or over 60% (2). (Castro *et al.* 2013a, ch. 9)
33. Width of temporal fossa in relation to cranial width at the level of the frontoparietal suture: less than 9% (0); or 9% and over (1). (Castro *et al.* 2013a, ch. 10)
34. Average rostral ratio: 0.58 and lower (0); or over 0.58 (1)
35. Continuous ossified entotympanics corresponding to more than 50% of the ectotympanic's length: present (0); or absent (1)
36. Most frequent number (mode) of completely movable bands: 7 (0); 8 (1); 9 (2); 10 (3); or more than 10 (4).
37. Occipital sulcus in the cephalic shield: absent (0); semicircular (1); roughly straight (2); or V-shaped (3).
38. Longitudinal keel in the main figure of osteoderms: absent (0); or present (1). (Modified from Carlini *et al.* 2013, ch. 19)
39. Differentiation of the carapace: movable bands and pelvic buckler (0); scapular buckler, movable bands, and pelvic buckler (1). (Modified from Ciancio 2010, ch. 2).
40. Margins of the carapace: straight (0); denticulate (1). (Modified from Ciancio 2010, ch. 4).
41. Texture of the external surface of osteoderms: with numerous punctuations (0); without punctuations (1).
42. Two rows of piliferous foramina in the posterior border of buckler and/or movable osteoderms: absent (0); or present (1).
43. Principal sulcus in buckler osteoderms: absent (0); or present (1).
44. Foramina in principal sulcus of buckler osteoderms: restricted to cranial half (0); or all over the sulcus (1). (Castro *et al.* 2013a, ch. 11)
45. Remarkably large foramina in at least some buckler osteoderms: absent (0); or present (1). (Modified from Castro *et al.* 2013a, ch. 12)
46. Number of piliferous foramina in the buckler osteoderms: never more than 5 (0); at least some osteoderms with more than 5 and less than 17 (1); or more than 17 (2). (Modified from Castro *et al.* 2013a, ch. 13)
47. Main figure of buckler osteoderms: approximately lageniform (0); subcircular (1); or absent (2). (Modified from Carlini *et al.* 2013, ch. 20)
48. Outer contour of buckler osteoderms: mostly quadrangular (0); or mostly hexagonal (1). (Carlini *et al.* 2013, ch. 21)
49. Posterior border of buckler osteoderms: straight and/or V-shaped (0); or rounded (1). (Castro *et al.* 2014, ch. 21)
50. Distribution of peripheral figure(s) in buckler osteoderms: only anterior and lateral (0); or anterior, lateral, and posterior (1). (Castro *et al.* 2014, ch. 22)
51. Radial sulcus in the buckler osteoderms: present (0); or absent (1). (Castro *et al.* 2014, ch. 25)
52. Main figure of buckler osteoderms: almost reaching the borders, occupying more than 80% of the total width, (0); or occupying less than 80% of the total width (1).
53. Principal sulcus in movable osteoderms: (0) absent; or (1) present.
54. Principal sulci in ornamented portion of movable osteoderms: anteriorly free in all osteoderms (0); or anteriorly connected in some osteoderms (1). (Castro *et al.* 2013a, ch. 15)
55. Total number of foramina in the principal sulcus/sulci of movable osteoderms: less than 13 (0); or at least some osteoderms with more than 13 (1). (Castro *et al.* 2013a, ch. 17)
56. Number of piliferous foramina in the posterior border of movable osteoderms: never more than 3 (0); or at least some osteoderms with 4 or more (1). (Castro *et al.* 2013a, ch. 18)
57. Sulci of movable osteoderms: diverging and becoming confluent with the lateral margin (0); or reaching the posterior border of the osteoderm (1). (Castro *et al.* 2014, ch. 23)
58. One or two large foramina in the anterior part of the ornamented portion of movable osteoderms: frequently present (0); or absent (1). (Modified from Castro *et al.* 2014, ch. 20)

APPENDIX 3. Characters-taxon matrix used in the cladistic analysis. (?) missing data; (-) not applicable; (&) and; (/) or; (A) 0&1; (B) 1&2; (C) 2&3; (D) 0&1&2; (E) 1&2&3; (F) 2&3&4; (G) 0/1/2.

<i>Peltephilus pumilus</i>	22102	00200	00?00	00110	00001	03101	00101	4010?	000-1	020A-	1-0--	1-0
<i>Stegosimpsonia sp</i>	?????	?????	?????	?????	?????	?????	?????	??100	10110	10000	11100	101
<i>Stegotherium tauberi</i>	DC110	00311	21000	21100	10000	000?0	00010	4?100	010-1	2200-	100--	1-0
<i>Anadasypus hondanus</i>	?????	?????	0?11?	???11	11?1?	0?000	0?1??	??11?	10100	00010	00100	001
<i>Propraopus sulcatus</i>	3?001	10?11	0?111	10011	11?00	??1?0	000??	0?011	10101	01101	01100	011
<i>Cryptophractus pilosus</i>	CF001	10321	00111	000A1	111A1	0000A	01111	33010	110-0	21101	110--	1-0
<i>Dasypus bellus</i>	2C0??	?1?21	???11	???11	1??11	0?G?0	??1??	2?01?	10110	11101	01111	111
<i>Dasypus punctatus</i>	32?0?	11?21	0??1?	10???	????0	13101	1????	??01?	10110	11101	01111	111
<i>Dasypus novemcinctus</i>	FF001	11221	A0111	A001A	01111	12210	01110	21010	10110	11101	01110	111
<i>Dasypus septemcinctus</i>	EE001	10021	00111	0001A	01?11	02000	02100	01010	10110	11101	011?0	111
<i>Dasypus hybridus</i>	EB001	11121	10111	0001A	01111	02000	01100	02010	10110	11101	01110	111
<i>Dasypus kappleri</i>	CF001	11B20	00111	1001A	011A1	11311	11110	13010	10111	11101	01110	111
<i>Dasypus sabanicola</i>	ED001	11121	00111	A0010	0??11	12210	01100	1?010	10110	01101	01100	111
<i>Dasypus yepesi</i>	C2001	11B21	10111	A0010	01111	13211	01100	11010	10110	11101	01110	011