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The armadillo *Propraopus sulcatus* (Mammalia: Xenarthra) from the late Quaternary of northern Brazil and a revised synonymy with *Propraopus grandis*

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ABSTRACT

This paper describes new remains of *Propraopus sulcatus* from a late Quaternary cave deposit located in Aurora do Tocantins, northern Brazil. *Propraopus* was recorded in numerous late Pleistocene–early Holocene sites in South America, and its inclusiveness has been long debated. In order to address some of the controversial taxonomic questions, the osteoderms of *P. sulcatus* were qualitatively and quantitatively compared to those of related nominal species (*Propraopus grandis*, *Propraopus magnus*, *Dasyypus bellus*, and *Dasyypus punctatus*); special attention was given to the former due to the debated synonymy between both taxa. Analyses reveal that there is no morphologic, spatial, or temporal discontinuity between *P. sulcatus* and *P. grandis*. Adopting morphologic, associational, and distributional criteria to define morphospecies, we believe it is impossible to clearly separate both nominal entities. As a consequence, in agreement with previous studies, we favor their synonymization. *P. sulcatus* has nomenclatural priority over *P. grandis* and should be the valid name for the species. The scarce analyzed remains referred to *P. magnus* show concordant size and morphology with *P. sulcatus*, but the analysis of more complete material is essential to determine its synonymization. Finally, we revised and updated the geochronologic distribution of *Propraopus*.

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1. Introduction

Since the mid-19th century, the exploration of cave deposits yielded most of the available information on Brazilian Quaternary mammals (Lund, 1840; Cartelle and Hartwig, 1996; Czaplewski and Cartelle, 1998; Lessa et al., 1998; Salles et al., 1999; Santos et al., 2002; Castro and Langer, 2011; Ghilardi et al., 2011; Avilla et al., 2013). These deposits commonly protect the organic remains from normal processes of disintegration, at the same time acting as a natural trap for living animals or a burial site for their remains (Behrensmeyer and Hook, 1992).

Two karstic caves located in Aurora do Tocantins (Tocantins State, northern Brazil) (Fig. 1) were systematically explored since 2009. They yielded several macro and microfossils, attributed to marsupials (Oliveira et al., 2011; Villa Nova et al., 2011), ungulates (Avilla et al., 2011a, 2013), rodents, carnivores (Rodrigues et al., 2011; Rodriguez et al., in press), and cingulates. The latter group was the most abundant in the sites, especially because of the great

number of isolated osteoderms (Avilla et al., 2011b). The systematic value of these elements led to the identification of six taxa belonging to the three major groups of cingulates (armadillos, pampatheres, and glyptodonts) (Table 1). This paper aims to: (1) describe the osteoderms of *Propraopus sulcatus* from Aurora do Tocantins; (2) compare the osteoderms with those of closely related species in qualitative and quantitative bases; (3) compile and update the geochronologic distribution of the taxon; (4) discuss the controversial taxonomic and nomenclatural status of the species, especially focusing on the debated synonymy of *P. sulcatus* and *Propraopus grandis*.

Table 1

Fossil cingulates from caves Gruta dos Moura and Gruta do Urso, Aurora do Tocantins, Tocantins State, Brazil.

Family	Taxa	Gruta dos Moura	Gruta do Urso
Dasypodidae	<i>Dasyypus novemcinctus</i>	×	×
	<i>Euphractus sexcinctus</i>	×	×
	<i>Propraopus sulcatus</i> ^a		×
Pampatheriidae ^a	<i>Pampatherium</i> cf. <i>typum</i> ^a		×
Glyptodontidae ^a	cf. <i>Glyptotherium</i>	×	×
Incertae sedis	<i>Pachyarmatherium</i> cf. <i>brasiliense</i> ^a	×	×

^a Fossil taxon.

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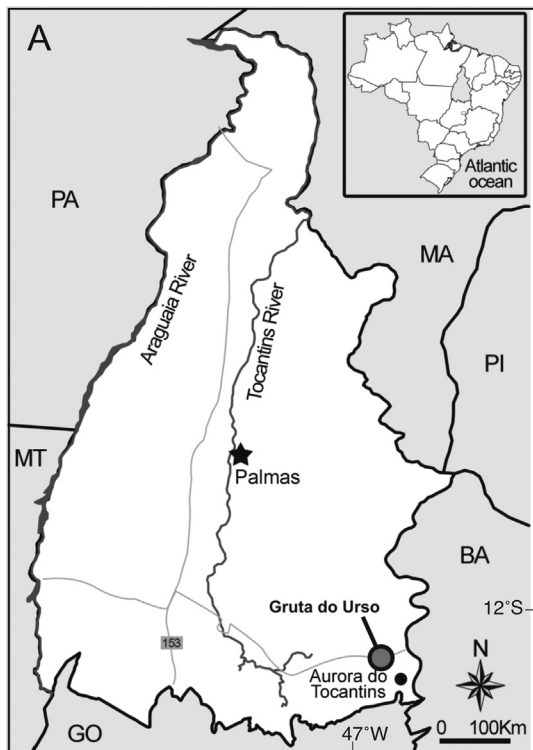


Fig. 1. Location (A) of Gruta do Urso cave, Tocantins State, Brazil ($12^{\circ}35'0.08''\text{S}$ and $46^{\circ}30'58.39''\text{W}$).

2. Taxonomic background

Together with *Anadasypus* (middle Miocene of Colombia and Ecuador) and *Dasyopus* (?Pliocene–recent) (Carlini et al., 1997), *Propraopus* (Pleistocene–early Holocene of South America) belongs to tribe Dasypodini, one of the most basal lineages of armadillos (Gaudin and Wible, 2006; Delsuc et al., 2012).

P. grandis Ameghino, 1881, the type species of the genus, was founded based on several osteoderms from the Pleistocene of Buenos Aires Province, Argentina. Ameghino did not compare the material, which is currently lost (Scillato-Yané, 1982), with those of *Dasyopus punctatus* and *Dasyopus sulcatus*, both species named by Lund for the Pleistocene of the Lagoa Santa, Minas Gerais State, Brazil (Lund, 1840, 1842; Winge, 1915). In turn, Hoffstetter (1952, 1958) allocated *Dasyopus magnus* Wolf, 1875 (Pleistocene of Ecuador), *Dasyopus bellus* Simpson, 1929 (Pleistocene of U.S.A.), *D. punctatus*, and *D. sulcatus* within *Propraopus*, an ascription commonly accepted, except for *D. bellus*. Later, Hoffstetter (1982) considered *Propraopus* a subgenus of *Dasyopus*.

Some authors (Hoffstetter, 1952; Paula-Couto, 1979, 1982; Scillato-Yané, 1982) questioned the differentiation among *Propraopus magnus*, *P. grandis*, and *P. sulcatus*, whereas others (Oliveira and Pereira, 2009) stood for the validity of both *P. grandis* and *P. sulcatus*. Rincón et al. (2008) recognized similarities among *Propraopus punctatus*, *P. sulcatus*, *D. bellus*, and the living *Dasyopus kappleri*. Castro et al. (2013) found *Propraopus* sensu Hoffstetter (1952, 1958) to be paraphyletic, as *P. punctatus* is nested within *Dasyopus* (so *D. punctatus* should be the valid name for the species); *P. sulcatus* and *P. grandis* formed a clade, both species differing on a single character (total number of foramina in the principal sulci of movable osteoderms, which is revised herein after expanding the number of specimens analyzed). With respect to *P. magnus*, Hoffstetter (1952) mentioned that most of the material is included

in sediment matrix and lacks preparation. This situation persists nowadays (José Luis Román Carrión, personal communication), raising difficulties on their direct analysis. However, Hoffstetter (1952) provides a useful description and figures of some remains, leading to a brief comparison and taxonomic discussion. To evaluate the generic assignment of *D. bellus*, we included data relative to its osteoderms, based on the type series and several other specimens directly analyzed (Appendix 1), in the phylogenetic matrix of Castro et al. (2013). The result indicates that the species is nested within *Dasyopus*, so its allocation in genus *Propraopus* (Hoffstetter, 1958) would not be justified. Therefore, in this contribution we mostly investigate specimens attributed to *P. grandis* and to *P. sulcatus*, primarily referring to them as two different nominal entities, although the conclusion is that they are synonymous.

Abbreviations—AAC, personal collection of Alfredo A. Carlini at MLP; AMNH FM, Fossil Mammals Collection, American Museum of Natural History, New York, U.S.A.; FLMNH, Florida Museum of Natural History, Gainesville, USA; ka, thousand years; MACN and MACN-A, Colección Paleovertebrados and Colección Ameghino (respectively), Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; MCN-MA and MCN-PV, Seção de Mastozoologia and Seção de Paleontologia (respectively), Museu de Ciências Naturais, Porto Alegre, Brazil; MLP, Museo de La Plata, La Plata, Argentina; MNPA-V, Museo Nacional Paleontológico-Arqueológico, Vertebrados, Tarija, Bolivia; MNRJ, Museu Nacional, Rio de Janeiro, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; SALMA: South American Land Mammal Age; UNIRIO-PM: paleontological collection of Laboratório de Mastozoologia, Universidade Federal do Estado do Rio de Janeiro, Brazil; ka, years before present. Specimens examined for the comparative study are in Appendix 1.

3. Regional settings

The fossils described here were collected in 2009, 2011, and 2012 from a limestone cave named Gruta do Urso, at Aurora do Tocantins ($12^{\circ}35'0.08''\text{S}$; $46^{\circ}30'58.39''\text{W}$), Tocantins State, northern Brazil (Fig. 1). The excavation was controlled in order to recognize stratigraphic aspects. The geology of the study area is still poorly understood. Online notes of CPMR (Companhia de Pesquisa de Recursos Minerais) on the geology of the municipality report carbonate and terrigenous deposits of the Bambuí Group, which is Neoproterozoic (CPMR, 2006). The fossil bearing level inside the cave is composed of laminated reddish-grey loess-like sediment (for a more detailed description, see Avilla et al., 2013). All osteoderms were found isolated, although some concentrations were recognized. However, these accumulations may result of taphonomic factors (transport) acting inside the cave deposit. Moreover, the osteoderms were found all over the superficial layer of the cave deposit, which is around 200 mm thick. This superficial layer is bedded on a carbonate layer.

Concerning the age, mammal-bearing Brazilian cave deposits are loosely dated as late Pleistocene–early Holocene (Cartelle, 1999). This assignment is based both on the comparison to well-known Argentinean local faunas (Marshall et al., 1984; Cione and Tonni, 2005) and on several radiometric dates (Faure et al., 1999; Neves and Piló, 2003; Hubbe et al., 2007, 2009; but see; Auler et al., 2006). In the case of Aurora do Tocantins, the peccary *Catagonus stenocephalus* collected in Gruta dos Moura was ESR dated, yielding an age of 20 ± 2 ka (Avilla et al., 2013). The age can also be discussed based on the faunistic assemblage. Oliveira et al. (2011) proposed a Pleistocene age for the neighboring cave Gruta dos Moura. Although some taxa show wider biochrons, as *Pachyarmatherium* and *Catagonus* (Porpino et al., 2009; Gasparini et al., 2010), *Propraopus* is restricted to Ensenadan–Lujanian SALMAs (Pleistocene–early

Holocene) in South America (Cione and Tonni, 1999), and frequently attributed to late Pleistocene in Brazil (although not dated). Also, the faunistic association with *Pampatherium*, *Pachyarmatherium*, and *Xenorhinotherium* reinforces a late Pleistocene age for the deposit (Cartelle, 1999). Finally, time averaging cannot be discarded, and cave deposits are generally averaged over time intervals of 100–10,000 years (Behrensmeyer and Hook, 1992).

4. Systematic paleontology

Xenarthra Cope, 1889
Cingulata Illiger, 1811
Dasypodidae Gray, 1821
Dasypodinae Gray, 1821
Dasypodini Gray, 1821
Propraopus Ameghino, 1881

Type Species—*P. grandis* Ameghino, 1881 (by monotypy).

Type material—several osteoderms from the Pleistocene of Luján, Buenos Aires Province, Argentina; material presently lost (Scillato-Yané, 1982).

Emended diagnosis—Pelvic buckler almost twice longer than scapular buckler; lateral border of pelvic buckler composed by sharp projecting osteoderms, forming a denticulate border; frequently three (ranging from one to five) remarkably large (but not always) foramina in the principal sulcus of buckler osteoderms, restricted to the anterior half, never at the intersection with the radial sulci.

Distribution—Pleistocene–early Holocene of Argentina (Ensenadan–Lujanian SALMAs); Pleistocene of Brazil, Venezuela, Uruguay, and Bolivia (see below).

Comments—In the short original description of the genus and species, Ameghino (1881) only mentioned that the osteoderms of *P. grandis* are similar to *Dasypus* in shape, but with size equivalent to *Eutatus* (Eutatini, Euphractinae; late Pliocene–early Holocene), differing from this genus in having smooth surface (not rough and granulose). After gathering more material, Ameghino (1886, 1889) expanded the description of *Propraopus*, comparing it with *Dasypus* (referred therein as *Praopus* or *Tatusia*). He described that in the movable osteoderms the deep principal sulci diverge posteriorly, drawing a triangular central figure and an inverted triangle on each lateral; a longitudinal convexity is sided by small foramina on the main figure; one to four foramina pierce the mid part of each principal sulcus, and one to three foramina are in the posterior border of the osteoderm; the lateral figures bear a series of irregular transversal grooves. The buckler osteoderms are pentagonal or hexagonal, and those close to the lateral borders are longer; the central figure is convex, subcircular to elliptic in shape, sided by three or four small anterolateral peripheral figures; the principal sulcus is deeper than in *Dasypus* and show two or three foramina, not placed at the intersection between main and radial sulci; the pelvic osteoderms are larger and have more elongated main figures. The posterior caudal osteoderms are thick rhombus, and the posterior part of the tail is more compressed than in *Dasypus*. The main differences in relation to latter genus are: the most lateral part of the pelvic buckler, which is composed by sharp projecting osteoderms that form a denticulate border (not denticulate in *Dasypus*); and the much longer pelvic buckler in relation to the scapular buckler (both bucklers with almost the same length in *Dasypus*) (Ameghino, 1895). Based on mostly complete specimens, Ameghino (1889) estimated that the carapace of *P. grandis* was 70–75 cm long, about twice as *Dasypus novemcinctus*.

Analysis of an almost complete carapace (MLP 69-IX-9-9; figured by Lydekker, 1894, p. 66, plate XLIV and Hoffstetter, 1958,

p. 547, Fig. 7) allowed us to corroborate some of the Ameghino's observations. We estimate that the length, at the sagittal plane, of the pelvic buckler is around 40 cm, whereas the scapular buckler is around 22 cm long. The total length of the dorsal carapace, including seven movable bands, would be approximately 85 cm; the tail, composed of at least 12 rings and a continuous posterior part, would have about 45 cm. The presence of a denticulate border and the elongation of the lateral elements can be confirmed in other specimens (MLP 69-VIII-25-10 and MACN A 1170). On the other hand, the posterior part of the tail is indeed compressed, but this was also observed in *Dasypus* (such as *Dasypus hybridus*, AAC 7). Besides material from the Argentinean Pampean region, we also observed specimens attributed to *P. grandis* collected in other Pleistocene localities: Arroyo Toropí (Corrientes, Argentina), Tarija (Bolivia), and Rio Grande do Sul State (Brazil). Despite their geographic amplitude, the remains have size and morphology equivalent to the above described.

P. sulcatus (Lund, 1842) (Fig. 2)

D. sulcatus Lund, 1842

Type Material—syntype from Lagoa Santa karst, composed of osteoderms, cranial and postcranial fragments, some figured by Winge (1915, pl. V.3,4 and VII); lectotype not designated.

Comments—Although Lund (1842) named the species, the detailed description was given later by Winge (1915). Compared with *D. novemcinctus*, the latter author noted that *P. sulcatus* was three times longer, with heavier hands and feet. With respect to the osteoderms, Winge (1915) noted that these have deeper sulci and more convex figures; the buckler osteoderms show one to four foramina in the principal sulcus (either one or two on each side, or a single central foramen); neurovascular foramina tend to be in longitudinal lines in the main figure, which is displaced toward the posterior margin of most buckler osteoderms, although some of them may have more developed posterior figures; the movable osteoderms have wrinkled peripheral figures, and one to five foramina pierce each principal sulci, which form a lageniform (bottlenecked) main figure; one or two piliferous foramina are present in the posterior border; the caudal osteoderms have more curved sulci, with more numerous and deeper ramifications, and the longitudinal crest is either delicate or absent. These features led Winge to speculate that *P. sulcatus* would have less hair than *D. novemcinctus*, but longer and more rigid.

Winge (1915) also stated that the angular process of mandible is less evident and the incision between this and the condylar process is shallower, almost unnoticeable, than in *D. novemcinctus*. The humerus has a more prominent supinatory crest. The ulna has a shorter anconeal process, with a more curved posterior border. The ungual phalanges are thicker and more curved. Unfortunately, our specimens do not preserve cranial or postcranial remains in order to compare those features.

Studied Material—The specimens (UNIRIO-PM 1120–1164) are housed at the paleontological collection of the Laboratório de Mastozoologia of Universidade Federal do Estado do Rio de Janeiro, Brazil. Besides fragmented elements, it includes 51 mostly complete isolated osteoderms, 28 from the bucklers, 17 movable, and six from the caudal sheath. Because of the concordance between the morphology of these osteoderms and those of the syntype of *P. sulcatus*, we attributed them to this taxon.

Description—The ornamented external surface of the buckler osteoderms are smooth to finely wrinkled. Most are hexagonal and bear two or three foramina in the principal sulcus (ranging from one to four). These foramina are restricted to the anterior half of the osteoderm and are never located at the intersection between the

principal and the radial sulci. The main figure is convex, subcircular to polygonal, and displaced posteriorly up to be close to the margin of the osteoderm. Neurovascular perforations are either randomly distributed or tend to be in longitudinal lines in the main figure. Radial sulci separate commonly five peripheral figures (ranging from four to six), which are bigger and more delimited in the anterolateral zone. The depth of the sulci varies among elements. Most movable osteoderms are incomplete, lacking the anterior, non-ornamented, portion and most preserve the wrinkled horizontal depression. The ornamented portion has two anteriorly separated deep principal sulci that diverge posteriorly, frequently forming a lageniform main figure that has neurovascular perforations arranged in two longitudinal lines. The total number of foramina in these sulci is commonly four, ranging from two to six. The peripheral (=lateral) figures are remarkably wrinkled. The posterior border usually has a single piliferous foramen, located in one of the corners, but two or three foramina may be present.

Comparison and discussion—The comparisons were primarily based on direct observation of specimens housed in several museums (Appendix 1), but also based on the specialized literature. An updated qualitative comparison of the osteoderms referred to *P. sulcatus*, *P. grandis*, and taxa once attributed to genus *Propraopus* is given in Tables 2 and 3. For a more comprehensive taxonomic sample, see Castro et al. (2013). In Fig. 3, buckler and movable osteoderms of the nominal taxa considered in the comparisons are illustrated.

Table 2
Comparison of buckler osteoderms of *Propraopus sulcatus* with other nominal species of Dasypodini. Abbreviations: p.s., principal sulcus; r.s., radial sulcus.

Taxon	Foramina in the p.s., min–max (most frequent)	Foramen in the intersection between p.s. and r.s.	Distribution of foramina in the p.s.
<i>Propraopus sulcatus</i>	1–4 (3)	Absent	Restricted to the anterior half
<i>Propraopus grandis</i>	2–5 (3)	Absent	Restricted to the anterior half
<i>Dasypus bellus</i>	3–6 (4)	Rarely present	Few or none on the posterior half
<i>Dasypus punctatus</i>	6–16 (10)	Present	All over

Table 3
Comparison of movable osteoderms of *Propraopus sulcatus* with other nominal species Dasypodini. Abbreviations: p.b., posterior border; p.s., principal sulcus.

Taxon	p.s. anteriorly connected	Foramina in the p.s., min–max (most frequent)	Foramina in the p.b., min–max (most frequent)
<i>Propraopus sulcatus</i>	Absent	2–8 (4)	1–3 (2)
<i>Propraopus grandis</i>	Absent	2–7 (5)	1–3 (2)
<i>Dasypus bellus</i>	Rarely present	5–18 (10)	1–4 (2)
<i>Dasypus punctatus</i>	Rarely present	9–18 (12)	4–7 (5)

The first comparisons were with the syntype of *P. sulcatus* from Lagoa Santa, which was described and partially figured by Winge (1915, pl. V.3.4 and VII). As can be depicted from their description (see above), the morphology and ornamentation of the osteoderms from Aurora do Tocantins agree with those observed in the syntype. Their sizes are also consistent. For instance, the largest buckler osteoderm from Tocantins is 17.6 mm long, whereas among those figured for Lagoa Santa it is approximately 17.5 mm. The same is observed for the movable osteoderms: the longest ornamented portion from Tocantins has 41.4 mm, whereas it is approximately 39.0 mm long in the figured

elements from Lagoa Santa. The concordance between the studied osteoderms and the syntype of *P. sulcatus* led us to their attribution to this taxon. Thus, *P. sulcatus* in Tables 2 and 3 represents the observations of osteoderms from Aurora do Tocantins and Lagoa Santa.

Because of the debated similarities with *P. grandis*, this is the object of detained comparisons. With respect to size, it is usually accepted that *P. grandis* is the largest Dasypodini, but extensive numerical comparisons have not been published. To assess this issue, we measured the most complete osteoderms from Aurora do Tocantins and compared with those attributed to *P. grandis* collected in the same region and inferred age where the type material was recovered (i.e., Buenos Aires Province, Argentina; Appendix 1). Measurements were made using calipers with 0.1 mm accuracy and include length (A–P), width (L–M), and thickness (Th); for the movable osteoderms, width and thickness were taken at the horizontal depression (see Fig. 2).

The dimensions of 33 buckler osteoderms (of uncertain position) were compared with 29 (11 scapular and 18 pelvic) from Buenos Aires Province (Table 4). The performance of Student's *t*-Tests ($P < 0.05$; unpaired two-tailed) indicates that all three dimensions are not significantly different between the species. Extant and fossil Dasypodini exhibit in the same carapace a considerable variation on size of buckler osteoderms: the pelvic elements are approximately 20% larger than the scapular ones. Consistently, in the case of the remains of *P. grandis* considered here, the scapular osteoderms are 12.6 (± 1.6) mm long, whereas the pelvic osteoderms are 15.0 (± 3.6) mm long. It is also congruent with the measurements of Ameghino (1886), who described that the scapular and pelvic osteoderms of *P. grandis* are about 9–10 mm and 13–14 mm long, respectively.

Table 4
Measurements (mm) of buckler osteoderms of *Propraopus sulcatus* from Aurora do Tocantins ($n = 33$) and of specimens referred to *P. grandis* from Buenos Aires Province ($n = 29$). Abbreviations: A–P, length; L–M, width; Th, thickness.

Taxon	A–P mean (\pm SD)	L–M mean (\pm SD)	Th mean (\pm SD)
<i>Propraopus sulcatus</i>	13.1 (± 1.8)	12.8 (± 2.2)	5.5 (± 1.2)
<i>Propraopus grandis</i>	14.1 (± 3.2)	13.1 (± 3.1)	5.1 (± 0.9)

As for the movable osteoderms, the length of its non-ornamented part is highly variable upon the position in the carapace, although few are entirely preserved in the remains from Aurora do Tocantins. For those reasons, we only consider the dimensions of the ornamented portion (Table 5), which may correspond to half of the total length in *P. grandis* (Ameghino, 1886). We measured 12 osteoderms of *P. sulcatus* and 53 of *P. grandis*, except for the thickness: as most elements of the latter taxon are preserved articulated (i.e., in carapace fragments), only five osteoderms had this dimension measured. Our observations also agree with those of Ameghino (1886): the ornamented parts of the osteoderms of the anterior-most movable ring are approximately 35–40 mm long and 13–14 mm wide, whereas those from the posterior-most ring are much shorter, about 16–18 mm long and 13 mm wide. As in the case of the buckler osteoderms, Student's *t*-Tests ($P < 0.05$; unpaired two-tailed) revealed that all three dimensions are not significantly different between the nominal species. The measurements of buckler and movable osteoderms are also concordant with those of *P. grandis* from Rio Grande do Sul, southern Brazil (Pitana and Ribeiro, 2007).

Table 5

Measurements of movable osteoderms of *Propraopus sulcatus* from Aurora do Tocantins ($n = 12$) and of specimens referred to *P. grandis* from Buenos Aires Province ($n = 53$, except for thickness, which $*n = 5$). Abbreviations: A–P.OP, length of the ornamented portion; L–M.HD, width of horizontal depression; Th.HD, thickness of horizontal depression.

Taxon	A–P.OP mean (\pm SD)	L–M.HD mean (\pm SD)	Th.HD mean (\pm SD)
<i>Propraopus sulcatus</i>	33.4 (\pm 3.7)	14.1 (\pm 1.3)	3.5 (\pm 0.4)
<i>Propraopus grandis</i>	31.4 (\pm 5.7)	13.3 (\pm 1.7)	3.4 (\pm 0.8)*

We also contrasted the few measurements available for the postcranial elements of the syntype of *P. sulcatus* (from Lagoa Santa, given by Winge, 1915) with those of *P. grandis* (Table 6). Some measurements of *P. magnus* (given by Hoffstetter, 1952)

were also included in this table, and are commented on below. Despite possible ontogenetic differences that may occur, these dimensions are similar between the nominal taxa. As a result, based on the osteoderms and some postcranial remains, we conclude that size is not a good criterion to differentiate specimens referred to *P. grandis* and *P. sulcatus*.

Concerning qualitative differences, Oliveira and Pereira (2009) pointed out differences between *P. grandis* and *P. sulcatus*, proposing autapomorphies for the latter. However, our sample indicates that some of these characters (e.g., strongly denticulate borders; subpolygonal main figure of buckler osteoderms; foramina usually concentrated in the posterior half of the movable osteoderms) are variably present in both species. This is the case of the rugose external surface, a feature also present in *P. grandis* (e.g., MACN 17989, 8959, 10085), as denoted

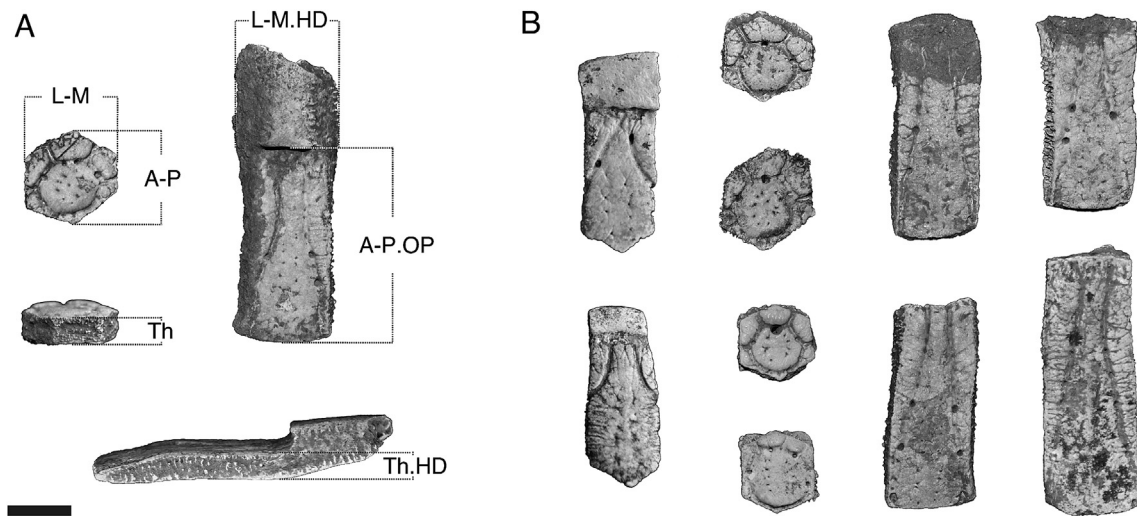


Fig. 2. Osteoderms of *Propraopus sulcatus* from Gruta do Urso cave, Tocantins State, Brazil. (A) Evaluated measurements; (B) Diversity of caudal, buckler, and movable osteoderms. Abbreviations: A–P, length; A–P.OP, length of the ornamented portion; L–M, width; L–M.HD, width of horizontal depression; Th, thickness; Th.HD, thickness of horizontal depression. Scale bar = 10 mm.

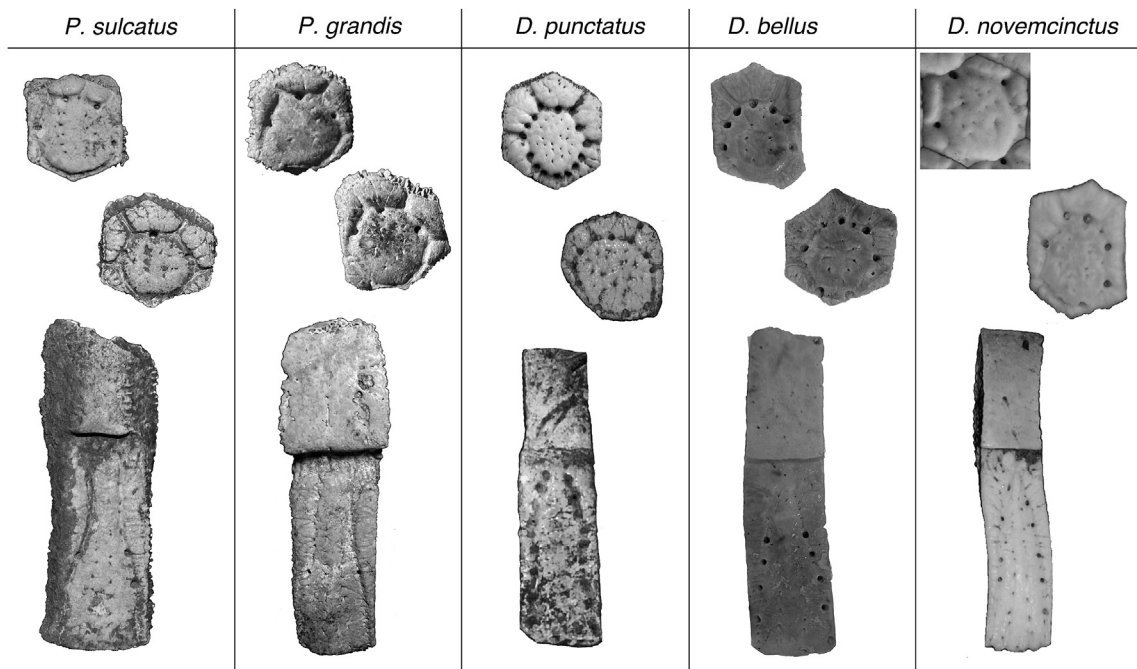


Fig. 3. Buckler and movable osteoderms of the nominal taxa considered in the comparisons (not to scale).

by Ameghino's description (1886) and illustration (1889, plate LXVII).

Tables 2 and 3 qualitatively compare specimens referred to *P. sulcatus* and *P. grandis*, and other two species formerly attributed to *Propraopus* (i.e., *D. bellus* and *D. punctatus*). In the buckler osteoderms of *P. sulcatus* and *P. grandis*, there are most frequently three foramina in the principal sulcus, restricted to its anterior half, and not located at the intersection with radial sulci. This morphology is quite different from that of *D. punctatus* (about ten foramina distributed all over the principal sulcus, at least some at the intersection with the radial sulci) and, to a minor extent, of *D. bellus* (frequently four foramina in the principal sulcus, few or none in its posterior half, rarely at the intersection with the radial sulci). *P. grandis*, *P. sulcatus*, and *D. bellus* coincide in the most frequent number of foramina in the posterior border, which is two (ranging from one to four in the latter, and one to three in the formers), in contrast to five in *D. punctatus*. The main disparity in relation to *D. bellus* is the number foramina in the principal sulci of movable osteoderms (frequently ten, in contrast to four in *P. sulcatus* and five in specimens attributed to *P. grandis*). This character links the North American species to *D. punctatus* and living species of *Dasylops* (see Castro et al., 2013). Also, some elements of *D. bellus* and *D. punctatus* have the principal sulci connected anteriorly, a condition absent in *Propraopus*. Overall, Tables 2 and 3 show that specimens referred to *P. sulcatus* and to *P. grandis* generally agree in all evaluated issues.

On the other hand, we observed slight differences between both nominal species that may be more or less accentuated according to the position of the osteoderm in the carapace. As indicated by Oliveira and Pereira (2009), the main figure of movable osteoderms is more commonly lageniform in specimens referred to *P. sulcatus* than to *P. grandis*, although the sulci may diverge straightly in both taxa. Another possible dissimilarity is that some of the movable osteoderms of *P. sulcatus* figured by Winge (1915) have a single centrally positioned foramen anterior to the principal sulci, a feature not observed in the specimens attributed to *P. grandis*. The number of foramina in the principal sulcus of movable osteoderms may be higher in *P. sulcatus*, ranging from 2 to 8, whereas it ranges from 2 to 7 in elements referred to *P. grandis*.

5. Distribution and environmental aspects

Fossils attributed to *Propraopus* are widely distributed in South America, also in terms of altitude (from sea level in Buenos Aires area to about 2800 m in Ecuador). In Argentina, *P. grandis* or *P. cf. grandis* are present in the Ensenadan–Lujanian SALMAs of the Pampean Region and Mesopotamia (Cione and Tonni, 2005; Francia et al., 2010). The following occurrences are loosely dated as Pleistocene. In Bolivia (Tarija and Ñuapua), they were attributed to *P. cf. grandis* or *P. cf. sulcatus* (Marshall et al., 1984; Marshall and Sempere, 1991), whereas in Uruguay *Propraopus* sp. was identified in the Dolores and Sopas Formations (Ubilla and Perea, 1999). In Ecuador, Hoffstetter (1952) recognized *P. magnus*, although questioning its validity, and in Venezuela Rincón et al. (2008) identified *P. sulcatus* in Mene de Inciarte tar pits, the northernmost locality known so far for the genus. In the late Pleistocene–early Holocene of Brazil, *Propraopus* sp. was found in Rio Grande do Norte (Porpino, 1999). *P. sulcatus* or *P. cf. sulcatus* were recorded in the states of Minas Gerais (Lund, 1842), Bahia (Schimitz, 1990), Piauí (Faure et al., 1999), Mato Grosso (Cartelle and Hirooka, 2005; mistakenly referred as *P. punctatus*), and recently in the southernmost Rio Grande do Sul (Oliveira and Pereira, 2009). *P. grandis* is only recorded in the latter state, from the coast to the west limit with Uruguay and Argentina (Pitana and Ribeiro, 2007). There is

also a possible occurrence (cf. *Propraopus*) in the Amazon (Paula-Couto, 1983).

Among these, some were collected in directly dated deposits. It is the case of the locality Toca do Serrote do Artur, Piauí State, which yielded two Holocene dates (8.490 ± 120 ka and 6.890 ± 60 ka; Faure et al., 1999). In Rio Grande do Sul State, the fossiliferous levels in Touro Passo arroyo and in Sanga da Cruz were dated approximately 15 ka, whereas the deposits by the coastal plain are as old as 120 ka (revised by Pitana and Ribeiro, 2007). In Uruguay, the Dolores Formation was dated 11.650 ± 130 ka, and the Sopas Formation between 43 and 45 ka (Ubilla and Perea, 1999). These ages agree with the Ensenadan–Lujanian distribution of *P. grandis* in the Argentinean Pampean region. It means that localities that record the nominal species *P. sulcatus* (Piauí State), *P. grandis* (Argentinean Pampean region), or both (Rio Grande do Sul State) are encompassed in the late Pleistocene–early Holocene.

Concerning the environmental aspects, the abundance of large cingulates in the Ensenadan of Argentina suggests the existence of grasslands and steppes. The same biome continued in the Lujanian, but relatively drier (Carlini and Scillato-Yané, 1999). This condition is similar to that estimated for the late Pleistocene of Rio Grande do Sul (Pitana and Ribeiro, 2007). In Gruta do Urso cave, the association of *Propraopus*, *Pampatherium*, Glyptodontidae, and *Pachyarthrum* suggests the presence of open environments during this time as well.

By the end of the Lujanian SALMA, as happened with most giant Xenarthra, *Propraopus* became extinct. The region of Aurora do Tocantins is currently covered by humid savannah (Cerrado biome; Avilla et al., 2013). The increasingly wet and warm climate, which can be related to climatic changes by the Pleistocene–Holocene boundary (de Vivo and Carmignotto, 2004), could have influenced the extinction of *Propraopus*, as proposed for the peccary *C. stenocephalus* (Avilla et al., 2013).

6. Taxonomic conclusions

Different from the biological concept of species (inbreeding organisms), in paleontology we are practically restricted to adopt the morphologic concept, that is taxa readily separable by evident morphological differences. Simpson (1951) suggests the adoption of morphological, associational, and distributional criteria to non-arbitrarily define morphospecies. The author proposes a practical procedure that consists in considering the two (or more) lots of associated specimens as samples of different populations and to estimate their morphological variation. If the estimations indicate no significant mean difference, the samples should be interpreted as representative of a single population and hence taxonomic grouped. Thereby, the presence of morphological, geographic and/or temporal discontinuity (i.e., non-overlapped variation between compared populations) bases the definition of morphospecies.

In our study case, following the procedure proposed by Simpson (1951), we morphologically contrasted the specimens from Aurora do Tocantins do Tocantins, attributed to *P. sulcatus*, with those referred to *P. grandis* from the Argentinean Pampean region. We found no significant difference in the measurements of the osteoderms. With respect to the qualitative features, we found minor differences (see above) that, based on an articulated carapace (MLP 69-IX-9-9), are variably accentuated according to the position in the carapace. They may be also related to population differences, which can be expected for a taxon with such a vast geographic distribution (Fig. 4). Clearly, there is no morphologic discontinuity between *P. sulcatus* and *P. grandis*. The comparison of the geochronologic distributions of both taxa reveals that there is no temporal or spatial discontinuity



Fig. 4. Updated geographic distribution of *Proptraopus* in the late Pleistocene of South America, highlighting Gruta do Urso cave (rhombus). Black dots represent other occurrences of *P. sulcatus*, considering synonymization with *P. grandis* proposed herein; the triangle corresponds to *P. magnus*.

either. All the specimens of *P. grandis* and *P. sulcatus* are late Pleistocene–early Holocene in age, and the presence of both supposed valid taxa in Rio Grande do Sul shows a geographic continuity.

From the characters of the osteoderms, we believe it is impossible to clearly separate both nominal species. As a consequence, corroborating the propositions of Hoffstetter (1952) and Paula-Couto (1982), we favor the synonymization of *P. sulcatus* and *P. grandis* (**syn. nov.**). *P. sulcatus* (Lund, 1842) has nomenclatural priority over *P. grandis* Ameghino, 1881 and is the valid name for the species. In this case, the emended diagnosis given herein for the genus is applicable to *P. sulcatus*. The status of *P. grandis* as the type species of the genus remains unchanged, although this is now regarded as a junior synonym of *P. sulcatus* (ICZN, 1999; article 67.1.2).

With respect to *P. magnus*, Hoffstetter (1952, pp. 117) concludes that his description of osteoderms and postcranial remains belonging to this species does not provide any reason to separate it from *P. sulcatus* and *P. grandis*. He opted for keeping the name as valid, although clarifying that later authors could define them as synonyms, or that the Ecuadorian form represents a subspecies. Our evaluation of his description and of the few elements figured suggests that the three nominal species have concordant size (Table 6) and morphology, favoring the synonymization of *P. magnus* as well. However, analysis of more complete remains of this taxon is essential to decisively address this question. Fig. 4 gives an updated geographic distribution for genus *Proptraopus* in the late Pleistocene of South America, incorporating the synonymization proposed herein.

Table 6

Measurements of postcranial elements of *Proptraopus sulcatus* from Lagoa Santa karst (Winge, 1915) compared with specimens referred to *P. grandis* from Argentinean Pampean region (MACN 17989 and MACN-A 10989) and to *P. magnus* from Ecuadorian Andes (Hoffstetter, 1952).

	<i>P. sulcatus</i>	<i>P. grandis</i>	<i>P. magnus</i>
Width of axis on the articular surface for atlas	39.0	37.0	
Width of the trochlea of humerus	30.0	32.0	30.0
Maximum width of metacarpal III	18.0	20.6	
Maximum diameter of the head of femur	32.5	32.0	
Maximum length of metatarsal II	33.0		39.0
Maximum length of metatarsal IV	42.5		38.0

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Appendix 1. Specimens examined for the comparative study.

Proptraopus sulcatus: UNIRIO-PM 1120–1164; photos in Winge (1915: pl. V.3,4 and VII)

Dasyopus novemcinctus: MCN-MA 99, 986, 2788, 2836, 3021, MZUSP 7996, 10431, 13800, 13801, 20189.

Dasyopus punctatus: MN 552-V, MCN-PV 009, 014.

Dasyopus bellus: AMNH FM 23542 (holotype), 23543–46 (paratypes), 23583–85, 45746, 96330, FLMNH 2478, 82206, 130011, 224700.

Proptraopus grandis: MACN 1610, 1630, 7027, 17989, MACN-A 1170, 10989, 11108, MLP 58-IX-3-26, 69-IX-9-9, 90-V-1-4, FLMNH 932404, 91288; MNPA-V 187 (not updated old numeration; specimen figured by Takai et al., 1984).

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