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The cingulates (Mammalia: Xenarthra) from the late Quaternary of northern Brazil: Fossil records, paleoclimates and displacements in America

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ABSTRACT

This paper presents the Quaternary cingulates collected from two limestone caves in Aurora do Tocantins, northern Brazil. Osteoderms of *Euphractus sexcinctus*, *Dasypus novemcinctus*, *Propraopus sulcatus*, and *Pachyarmatherium brasiliense* were retrieved, representing an expansion on the known distribution of the taxa. The specimens are described herein, and their geographic and chronologic distributions in Brazil are reviewed. Numerical dates allied to the presence of biostratigraphically relevant taxa indicate a Late Pleistocene–middle Holocene age. Considering that *E. sexcinctus* and *D. novemcinctus* occupy the area nowadays, why did part of the past cingulate community survive and the other part became extinct? We believe that their distribution was affected by paleoclimatic shifts, especially during glacial/interglacial cycles. The colder and arid climate of the Pleistocene glacial periods favored the development of open forests and savannas in Brazil, whereas grasslands and steppes were predominant in higher latitudes. Probably, *Propraopus* and *Pachyarmatherium* (from south and north, respectively) took refuge in lower latitudes, including in Brazil. Later, during the interglacial cycle, warm and moist climates favored the development of an evergreen forest in central Brazil, leading *Propraopus* and *Pachyarmatherium* to extinction and positively selecting *E. sexcinctus* and *D. novemcinctus*.

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1. Introduction

The Cingulata includes several lineages that share a unique feature, a dorsal bony carapace. The interrelationships of its three main lineages, Dasypodidae, Pamphathiidae, and Glyptodontidae, are still debated, as well as the monophyly of the former (e.g., De Iuliis et al., 2000; Gaudin and Wible, 2006).

The Dasypodidae, commonly known as armadillos, tatús or quirquinchos, represent the group of Xenarthra with the oldest fossil record, dating back to the late Paleocene of Brazil (Paula-Couto, 1979; Scillato-Yané, 1982; Oliveira and Bergqvist, 1998; Bergqvist et al., 2004). They also show the greatest geographic distribution and diversity, achieved during the period of isolation of South America. Later, during the Great American Biotic Interchange (GABI), they dispersed and radiated into North America (McDonald,

2005; Woodburne, 2010). Currently, this group is distributed in South, Central, and North America, although its major diversity corresponds to South America (only *Dasypus novemcinctus* expand its distribution into North America). Their most conspicuous anatomical feature is the subdivision of the dorsal shield or carapace in three clearly distinguishable regions composed by bony dermal scutes or osteoderms: a scapular shield, a region of mobile bands (of variable number), and a pelvic shield (see Soibelzon et al., 2013). However, this diagnostic attribute is also present in the Pamphathiidae, representing either a homoplasy or a plesiomorphy (Gaudin and Wible, 2006; Hill, 2006). The dorsal surface of the osteoderms has a particular morphology and ornamentation that are characteristic of each genus and, in some cases are the basis for the taxonomy of the group.

2. Regional setting

The material described here was collected in two limestone caves, Gruta do Urso and Gruta dos Moura, at the municipality of

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Aurora do Tocantins (12°35'0.08''S; 46°30'58.39''W), northern Brazil (Fig. 1) during paleontological expeditions carried out from 2009 to 2013. These are part of the Neoproterozoic carbonate Bambuí Group (CPRM, 2006).

Although there is no numerical dating for the fossil cingulates described here, Electro Spin Resonance (ESR) dating of remains of a peccary (*Catagonus stenocephalus*) collected at Gruta dos Moura and in association with cingulate osteoderms, revealed a late Pleistocene age (20 ± 2 ka; Avilla et al., 2013). In addition, a stratigraphic fossiliferous level was recognized for Gruta do Urso, and its age can be inferred based also on ESR dates of fossils from the bottom and top of this level. Fossils of *Panthera onca* found at the bottom and *Morenelaphus* from the top of the fossiliferous level gave ESR dates of 22 and 3.8 ka, respectively.

Additionally, two taxa collected in the limestone caves allow us to establish the age of these fossiliferous associations. The armadillo *Propraopus sulcatus*, collected in both caves, is restricted to the Early to Late Pleistocene in South America (see Castro et al., 2013). Moreover, the equid *Equus (Amerhippus) neogaeus*, found only in the Gruta do Urso cave, is a fossil guide for the Lujanian Age in the Pampean Region, Argentina (Late Pleistocene/earliest Holocene; Cione and Tonni, 2005). Thus, it is assumed that the fossil cingulates studied here inhabited the surroundings of the Gruta do Urso and Gruta dos Moura caves sometime between Late Pleistocene and middle Holocene.

Presently, there are 11 extant species of Dasypodidae in Brazil (*Tolypeutes matacus* and *Tolypeutes tricinctus* [Tolypeutinae]; *Euphractus sexcinctus* [Euphractinae]; *D. novemcinctus*, *Dasypus septemcinctus*, *Dasypus hybridus* and *Dasypus kappleri*

[Dasypodinae]; *Cabassous unicinctus*, *C. tatouay*, *C. chacoensis*, and *Priodontes maximus* [Priodontinae]), although only five are present in the studied area (i.e. *D. novemcinctus*, *D. septemcinctus*, *Euphractus sexcinctus*, *C. unicinctus* and *T. tricinctus*) (Medri et al., 2006; IUCN, 2014). However, the fossil records during the Quaternary (more precisely Late Pleistocene–Early Holocene) shows a different composition. The aims of this paper are to describe the recent discoveries on fossil Cingulata from two limestone caves Gruta dos Moura and Gruta do Urso (Aurora do Tocantins, Tocantins State, northern Brazil. Fig. 1), focusing on reviewing their fossil record in Brazil and its biogeographic importance.

3. Materials and methods

In order to identify the fossil cingulate osteoderms collected from Gruta dos Moura and Gruta do Urso, comparative morphological analyses were conducted. Thus, studies were carried out in the Coleção de Mamíferos Fósseis do Laboratório de Mastozoologia (UNIRIO-PM) and reference collections at the Universidade Federal do Estado do Rio de Janeiro, the Mammalogy and Vertebrate Paleontology collections of the Museu Nacional, Rio de Janeiro, Brazil; Fossil collection of the Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Brazil; and the División Paleontología de Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Argentina for taxonomic identification of *Chaetophractus villosus*, *Euphractus sexcinctus*, *D. novemcinctus*, and *D. hybridus*. Additionally, we used specialized literature (e.g., Scillato Yané, 1982; Oliveira et al., 2013; Soibelzon et al., 2010, 2013; Castro et al., 2013).

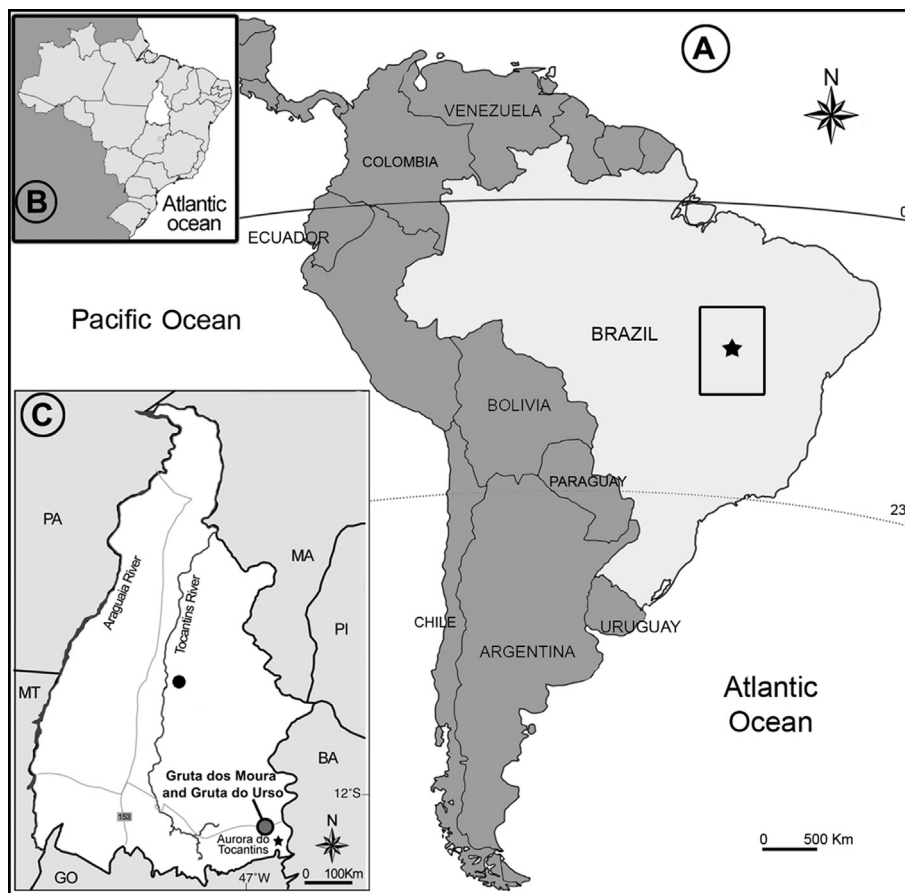


Fig. 1. A-General map of South America; B- Political map of Brazil showing the location of the Tocantins State; C- Map of the Tocantins State. The star marks the studied area and the location of the Gruta do Urso and Gruta dos Moura. The dot marks Palmas, the capital of Tocantins State.

4. Results

The analysis of the faunal remains presented here allows the recognition of four species in the caves of Tocantins: *E. sexcinctus*, *D. novemcinctus*, *P. sulcatus*, and *Pachyarmatherium brasiliense* (Table 1). With the exception of the South American *Pachyarmatherium* (*P. brasiliense* or *P. tenebris*, but different from the North and Central American *Pachyarmatherium leiseyi*), which previously did not have Argentinean records, all other three taxa have their austral distributional limits during the Late Pleistocene/Early Holocene in Argentina.

Table 1
Dasypodidae recognized for Gruta dos Moura and Gruta do Urso, Tocantins State, Northern Brazil.

Species	Gruta dos Moura	Gruta do Urso
<i>Dasypus novemcinctus</i>	x	x
<i>Euphractus sexcinctus</i>	x	x
^a <i>Propraopus sulcatus</i>		x
^a <i>Pachyarmatherium brasiliense</i>	x	x

^a extinct taxon. Table modified from Castro et al. (2013).

Systematic

Superorder Xenarthra Cope, 1889

Order Cingulata Illiger, 1811

Family Dasypodidae Gray, 1821

Subfamily Euphractinae Winge, 1923

Genus *Euphractus* Wagler, 1830

Euphractus sexcinctus Linnaeus, 1758

Materials and precedence. UNIRIO-PM 1165 to 1205, 1368. Gruta dos Moura and Gruta do Urso, Aurora do Tocantins, Tocantins State, Brazil.

Distribution. *Euphractus* is registered only in South America, from the Late Pleistocene to Recent (McKenna and Bell, 1997). The record in the middle Pleistocene corresponds to a fragmented right femur (MLP 69-VIII-9-5), which has dubious data of provenance (Soibelzon et al., 2010). For this reason, the biochron of the genus is considered from Late Pleistocene to Recent. It is recorded in the Late Pleistocene of Brazil in the Cavernas de Ossadas, vale do Rio das Velhas, Minas Gerais State (Paula-Couto, 1979), and Toca dos Ossos, Ouro-lândia, Bahia State (Cartelle, 1992), as well as in the early Holocene of Caverna do Urso Fossil, Ceará State (Oliveira et al., 2014) (Fig. 2) and northeastern Argentina (Corrientes Province; Francia, 2014). Presently, *Euphractus* inhabits a broad range of South American environments, from grasslands to rainforests (Redford and Wetzel, 1985), from southern Surinam into northern Argentina (Gardner, 2005).

Description and comments. The osteoderms of *Euphractus* has nearly flat central and peripheral figures (see Fig. 3). The ones from the scapular and pelvic shield are rectangular, pentagonal to hexagonal, presenting an elongated central figure surrounded by three cranial and two lateral peripheral figures (Fig. 3 A–C). Numerous hair follicle foramina are located on the posterior and lateral margins, the most developed coinciding with the central figure. The movable osteoderms (see Fig. 3 D–F) have a central figure flat as well, surrounded by lateral peripheral figures that are also flat (Scillato-Yané, 1982). Four to five hair follicle foramina are present at the posterior edge. There is a dorsal rugose transverse depression between the cranial and the caudal parts, as in *Chaetophractus* (see Soibelzon et al., 2010, 2013). The pelvic shield osteoderms are rectangular-shaped with a flattened and elongated central figure, anteriorly limited by two small cranial and two or three lateral figures, almost undivided (see Fig. 3B–C). In the posterior margin

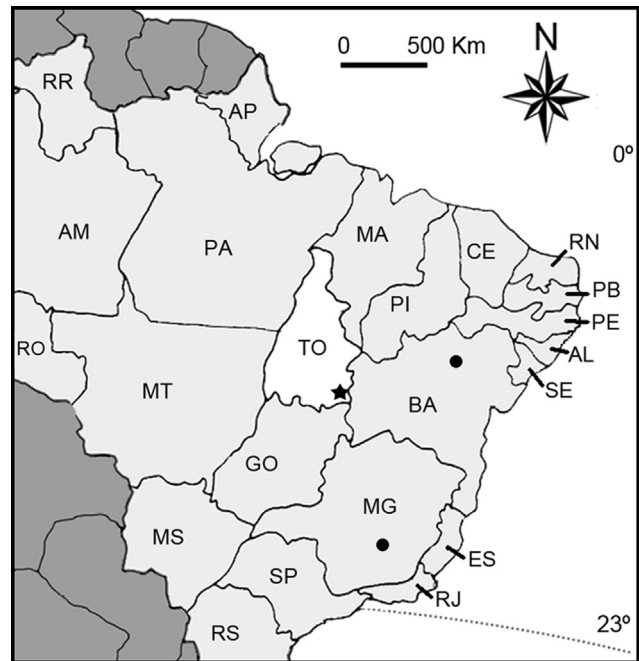


Fig. 2. Quaternary records for *Euphractus sexcinctus* in Brazil. The star marks the new record presented on this contribution. The dots mark previous records. AL, Alagoas State; AM, Amazonas State; AP, Amapá State; BA, Bahia State; CE, Ceará State; ES, Espírito Santo State; GO, Goiás State; MA, Maranhão State; MG, Minas Gerais State; MS, Mato Grosso do Sul State; MT, Mato Grosso State; PA, Pará State; PE, Pernambuco State; PB, Paraíba State; PI, Piauí State; RJ, Rio de Janeiro State; RR, Roraima State; RN, Rio Grande do Norte State; RO, Rondonia State; RS, Rio Grande do Sul State; SE, Sergipe State; SP, São Paulo State; and TO, Tocantins State.

and towards the outer side, there are two to three hair follicle foramina.

Subfamily Dasypodinae Gray, 1821

Genus *Dasypus* Linnaeus, 1758

Dasypus novemcinctus Linnaeus, 1758

Materials and precedence. UNIRIO-PM 1323 to 1356 Gruta dos Moura and Gruta do Urso, Aurora do Tocantins, Tocantins State, Brazil.

Distribution. The genus *Dasypus* is the only extant Dasypodinae and it is recorded since the late Pliocene of North America (*Dasypus bellus*; Klippel and Parmalee, 1984), early Pleistocene of the Pampean Region in Argentina (*Dasypus* sp., Soibelzon et al., 2010), Pleistocene of Mexico (Carbot-Chanona, 2010), and the late Pleistocene of Bolivia, Uruguay, Brazil (*Dasypus punctatus*), and Venezuela (Scillato-Yané, 1982; Paula-Couto, 1983; Marshall et al., 1984; Rincón et al., 2008). The oldest record of *Dasypus novemcinctus* surely correspond to South America, but the geographical provenance and age (late Pleistocene or early Holocene) is dubious until now (see Scillato-Yané, 1982; Paula-Couto, 1983; Marshall et al., 1984). It has a wide geographical distribution in the American continent, as *D. novemcinctus* is the only Xenarthra present in North America. *D. novemcinctus* occurs west of the Andes from Colombia into northern Peru, and east of the Andes in Colombia, Venezuela, Trinidad and Tobago, and the Guianas, southward through Ecuador, Brazil, Peru, Bolivia, Paraguay, Uruguay, and northern Argentina (IUCN, 2014). It usually occupies a wide variety of forest and savanna habitats (Gardner, 2005), including agroecosystems (Wetzel et al., 2007). According to McNab (1980), the distribution of *Dasypus* in temperate climates is limited both by food availability and physiological factors. Also, Abba et al. (2012) argue that the

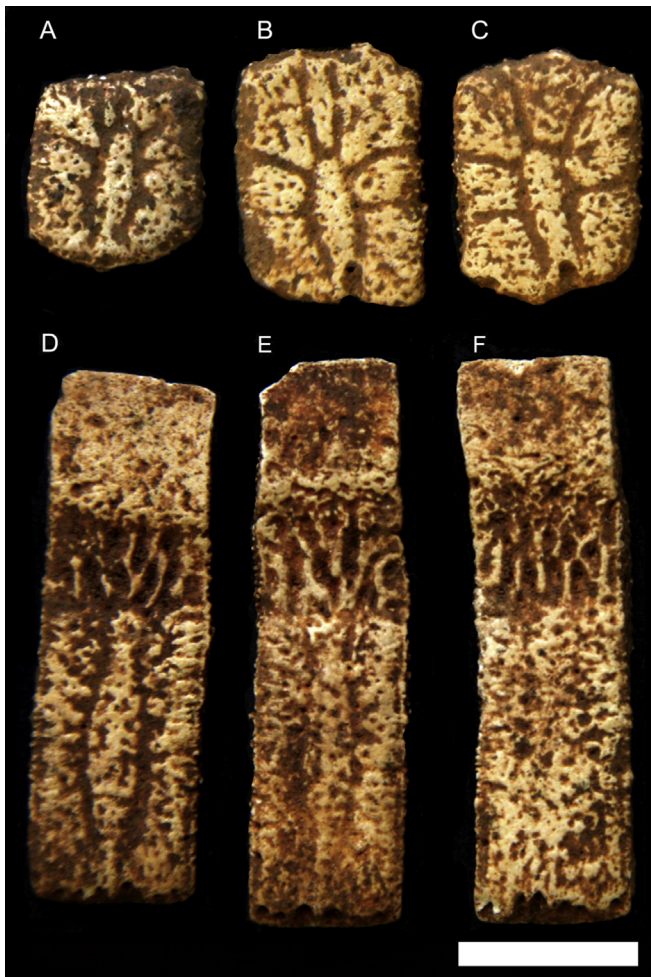


Fig. 3. Isolated fossil osteoderms of the carapace of *Euphractus sexcinctus* from Gruta do Urso, Tocantins (UNIRIO PM 1165–1205). A: a buckler osteoderm from scapular shield; B and C: a buckler osteoderm from the pelvic shield; D, E and F movable osteoderms; note the great development of the rough transverse depression between the cranial and the caudal part. Scale bar = 10 mm.

presence and distribution of *Dasypus* is limited by rainfall, increasing their probability of occurrence in areas with higher pluviometric precipitation. Paula-Couto (1979) commented that the Danish naturalist P.W. Lund collected remains of *D. novemcinctus* and *Dasypus hybridus* in caves of the valley of Rio das Velhas (Minas Gerais State); such remains of the former species are described and figured by Winge (1915). Other records range from Pleistocene to early Holocene of Acre (*D. cf. novemcinctus*; Paula-Couto, 1983), Ceará (*D. aff. novemcinctus*; Oliveira et al., 2014) and Bahia (*D. novemcinctus*; Castro, 2014) (Fig. 4).

Description and comments. The buckler osteoderms of the species included in the subfamily Dasypodinae are hexagonal to pentagonal, with a large central figure occupying almost its entire surface and small peripheral figures developed on its cranial edge (Fig. 5A and B). Those located in the movable bands have a central figure delimited by two diverging sulci towards the back, giving the typical lageniform appearance of Dasypodinae (Fig. 5C–E). The horny scales are common to two or three osteoderms, unlike the Euphractinae (Scillato-Yané, 1982). The osteoderms of the scapular and pelvic shields of *Dasypus* are small, isodiametric, and hexagonal. Following Soibelzon et al. (2013) the central figure is sub-circular and, although it is displaced backwards, occupies almost the entire surface, surrounded by four to five small peripheral

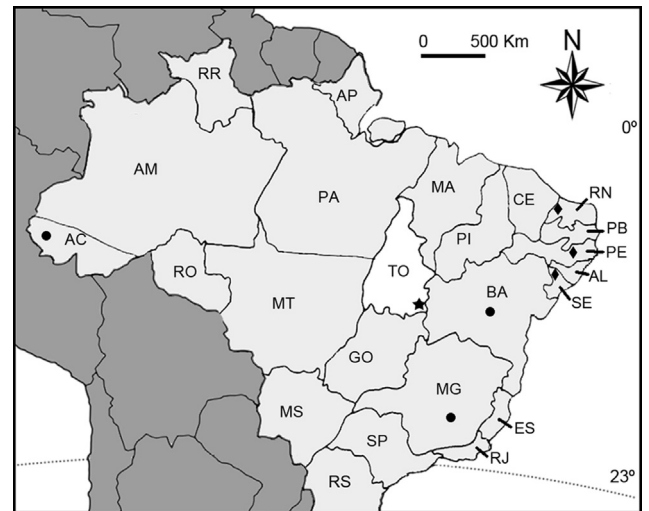


Fig. 4. Quaternary records for *Dasypus novemcinctus* (dots) and *Pachyarmatherium brasiliense* (diamond) in Brazil. The star marks the new records presented on this contribution. AC, Acre State.

figures. In the sulci between the central figure and the peripheral figures, there are three to four small glandular foramina. The osteoderms of the mobile bands are antero-posteriorly elongated; the central figure is delimited by two diverging sulci towards the



Fig. 5. Isolated fossil osteoderms of the carapace of *Dasypus novemcinctus* from Gruta do Urso, Tocantins (UNIRIO PM 1323–1356). A: buckler osteoderm from scapular shield; B: a buckler osteoderm from the pelvic shield; C, D, E: Movable osteoderms. Scale bar = 10 mm.

back, giving the typical lageniform shape. There are glandular foramina on those sulci. On its posterior edge, two to four hair follicle foramina grow (Fig. 5 C–E). The ornamentation of the exposed surface continues in the separation area between the cranial and caudal parts. The movable osteoderms of *D. novemcinctus* has a mean length of 20 mm and mean width 6 mm (*D. hybridus* has the mean length 12.5 mm and mean width 5.1 mm; Soibelzon et al., 2013) while the fixed ones have a mean length of 9 mm and mean width 6 mm (*D. hybridus* has mean length 7 mm and mean width 5 mm).

Genus *Propraopus* Ameghino, 1881

***Propraopus sulcatus* (Lund, 1842)**

Materials and precedence. UNIRIO-PM 1120 and 1164. Castro et al. (2013) assigned 51 mostly complete isolated osteoderms, 28 from the bucklers, 17 movable, and six from the caudal sheath to this species collected at Gruta do Urso.

Distribution. Considering the synonymy between *P. sulcatus* and *Propraopus grandis*, the species is known for the Pleistocene–early Holocene of Argentina, Brazil, Venezuela, Uruguay, and Bolivia (Castro et al., 2013) (Fig. 7).

Description and comments. Following Castro et al. (2013), the exposed surface of the buckler osteoderms is smooth to finely wrinkle. Most are hexagonal, and the central figure is subcircular to polygonal, and displaced posteriorly up to be close to the margin of the osteoderm. Radial sulci separate commonly five peripheral figures, and those located at the anterolateral zone are larger and more delimited. In the sulci between the central figure and the peripheral ones are two or three small glandular foramina. These foramina are restricted to the cranial portion of the osteoderm and are never located in the intersection between the principal and the radial sulci (Fig. 6 A and B). Most of the movable osteoderms

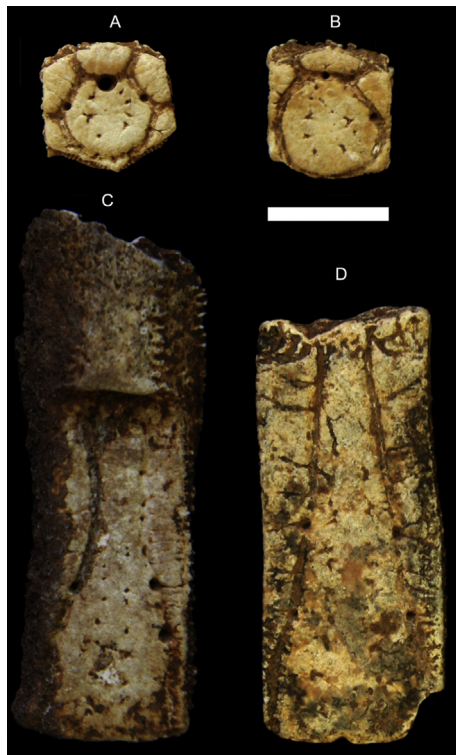


Fig. 6. Isolated fossil osteoderms of the carapace of *Propraopus sulcatus* from Gruta do Urso, Tocantins (UNIRIO PM 1121–1164). A–B: buckler osteoderm, C–D: Movable osteoderms. Scale bar = 10 mm.



Fig. 7. Quaternary records for *Propraopus sulcatus* in Brazil. The star marks the new records presented on this contribution. The dots mark previous records.

exhumed at the cave are fragmented (Fig. 6 C and D), lacking the cranial portion (Fig. 6 D), but preserving the transverse depression and the caudal portion. The exposed surface has a central figure delimited by a sulci, with the typically Dasypodinae lageniform shape, and commonly has four foramina in the sulci. The posterior border usually has one to three piliferous foramina (Fig. 6 C and D).

CINGULATA incertae sedis

Genus *Pachyarmaterium* Downing and White 1995

***Pachyarmaterium brasiliense* Porpino et al., 2009.**

Materials and precedence. UNIRIO-PM 1315, 1316. Gruta dos Moura and Gruta do Urso, Aurora do Tocantins, Tocantins State, Brazil.

Distribution. *Pachyarmaterium brasiliense* is restricted to the Northeastern region of Brazil, from the states of Rio Grande do Norte, Pernambuco and Sergipe (Oliveira et al., 2013; Porpino et al., 2009; Dantas et al., 2011) (Fig. 4). Additionally, Missagia et al. (2012) presented a new record of the species for the classical paleontological site of Lagoa Santa caves in the Minas Gerais State. Thus, the distribution of *P. brasiliense* is now extended to Northern (this contribution) and Southeastern Brazil (Minas Gerais State; Missagia et al., 2012). Moreover, Bostelmann et al. (2008) also recorded *Pachyarmaterium* in Rio Grande do Sul State in Brazil, and also in Uruguay, but they did not indicate to which species this record belongs. Here, the records for *P. brasiliense* from south-eastern, northeastern and northern regions of Brazil (Fig. 4) are considered.

Description and comments. *Pachyarmaterium* and its type species, *Pachyarmaterium leiseyi*, were based on numerous remains from Florida, USA (Downing and White, 1995). The taxon was later recorded in the late Pliocene–early Pleistocene of numerous sites in the USA and Costa Rica (Valerio and Laurito, 2011). With respect to its affinities, these authors recognized the morphology of osteoderms as similar to that of glyptodonts, whereas the mandible and postcranium as resembling those of armadillos, and provisionally attributed the taxon to Dasypodoidea. Later, *Pachyarmaterium* was related both to Dasypodoidea (Rincón and White, 2007; Rincón

et al., 2008; Oliveira et al., 2012, 2013) and to Glyptodontoidea Glyptatelinae (McKenna and Bell, 1997; Vizcaíno et al., 2003); Porpino et al. (2009) found it as the sister group of pampatheres + glyptodonts; whereas Oliveira et al. (2013) suggested that *Pachyarmatherium* is a Dasypodini. We believe that this issue is not clearly solved and that the features indicating a close relationship between *P. brasiliense* and Dasypodini may represent symplesiomorphies. Thus, we preferred to recognize *P. brasiliense* as a cingulate *incertae sedis*.

Two species of *Pachyarmatherium* are recognized in South America: *P. tenebris* from the late Pleistocene of Venezuela and Perú (Rincón and White, 2007; Martínez and Rincón, 2010) and *P. brasiliense* from the late Pleistocene–early Holocene of Brazil (Porpino et al., 2009). However, some authors considered *P. tenebris* as a senior synonym of *P. brasiliense* (Martínez and Rincón, 2010). Taking into account that *P. tenebris* is based on very few osteoderm samples and only scarce skeletal elements (Oliveira et al., 2013), at this time, we recognize the specimen from Aurora do Tocantins as *P. brasiliense*.

The carapace of *Pachyarmatherium* is divided into two buckler shields, separated by a single transversal row of imbrication (Downing and White, 1995). The osteoderms (Fig. 8) have a polygonal main figure displaced caudally and three to six peripheral figures, defined by broad sulci. One to four foramina are present at the intersection between the main sulcus and the radial sulci. Also, a thick layer of spongy bone is present in the middle zone, resulting in a great thickness in relation to the length of the osteoderm, and the articular borders are spiculate.

5. Discussion

The numerical dating obtained from different taxa (*Catagonus*, *Morenelaphus*, and *Panthera*) and the presence of taxa with biostratigraphic importance (i.e., *Equus (A.) neogeus*) allow us to determine that the fossil cingulates described here inhabited northern Brazil during the Late Pleistocene/middle Holocene. These new materials expand the geographic distribution of Dasypodidae into the northern region (Tocantins State) of Brazil, and demonstrate that at least two of the species that inhabit the region

nowadays were present since the Late Pleistocene. However, it also imposes a question: why did some of this cingulate community survived and others went extinct? Cartelle (1999) suggests that Pampean mammals (Argentina) with records in the Ensenadan age (Early to Middle Pleistocene; Soibelzon et al., 2008), such as *P. sulcatus*, took refuge in lower latitudes of South America (including Brazil), probably escaping from the arid and colder conditions that predominated during glacial periods at the higher latitudes (see Soibelzon and Tonni (2009) for more about Ensenadan paleoclimates). The same explanation could be used to understand the presence of typical Blancan/Irvingtonian (early-mid Pliocene to Middle Pleistocene) North/Central American mammals, such as *Pachyarmatherium*, in the late Pleistocene of South America. Thus, both immigrants, *P. sulcatus* (from the south) and *Pachyarmatherium* (from the north), became extinct in deference to *D. novemcinctus* and *E. sexcinctus*, typical Brazilian taxa without records in North and Central Americas during the Pleistocene, and with doubtful records in the South American Late Pleistocene of the Uruguay, Argentina and Bolivia, in the case of the former.

The vegetation physiognomy in Central–North Brazil is well-known and gives important information about paleoenvironment and climate changes in the last 17ka (Ledru, 1993; de Vivo and Carmignotto, 2004). Thus, during Last Glacial Maximum (17ka) the climate of Central–North Brazil appears to have been cooler and perhaps drier than today but not sufficiently to completely eliminate the forests (Ledru, 1993; de Vivo and Carmignotto, 2004). Evergreen forests would leave space for mosaic of open forests and, in areas with poor soils, savannas could be established (de Vivo and Carmignotto, 2004). At this time, dry and cold conditions prevailed in the Pampean Region of Argentina (Tonni et al., 1999) with development of grassland or steppe environments (de Vivo and Carmignotto, 2004); similar paleoclimates conditions were proposed for North and Central Americas (Harmon et al., 1978). The climate in lower latitudes of Brazil may have favored the displacement of *P. sulcatus* and *Pachyarmatherium*, from South and North respectively, as a kind of “escape” to lower latitudes. At the beginning of the Holocene, the climate became moister but remained cold until 8.5 ka, a typical Temperate climate, associated with records of *Araucaria* forests in Central Brazil (Ledru, 1993). After this, the climate became warmer while remaining moist (Ledru, 1993), related with the Thermal Maximum of the Holocene (TMH, ca. 7.5–4.5 BP). Probably, this association of warm and moist climate favored the development of an evergreen forest in central Brazil (de Vivo and Carmignotto, 2004) and led *P. sulcatus* and *Pachyarmatherium* to extinction, and positively selected *D. novemcinctus* and *E. sexcinctus* in this biome, given that the precipitation regimen is the most important variable that explains the current distribution of the latter two species (Abba et al., 2012). The Cerrado (or Brazilian savanna) climate is typical of the rather moister savanna regions of the world, with an average precipitation of 800 ± 2000 mm in over 90% of the area, and a very strong dry season during the southern winter (Ratter et al., 1997). Following Ledru (2002), the earliest record of Cerrado-type vegetation dates to 32 ka. Nevertheless, vegetation resembling present-day cerrados does not occur prior to 7 ka in central Brazil and 10 ka in northern Brazil; after 4 ka, the climate became moister, essentially resembling modern conditions. de Vivo and Carmignotto (2004) proposed that during TMH, tropical savannas could maintain their floristic identity but they were more densely packed, with marked reduction of grassland areas with the development of evergreen forest and dense savannah in central and northern Brazil. The southern part of South America had a temperate climate, with the development of temperate formations (de Vivo and Carmignotto, 2004).

The climatic instability before 4 ka might explains why Pleistocene records of *D. novemcinctus* and *E. sexcinctus* are rare in South

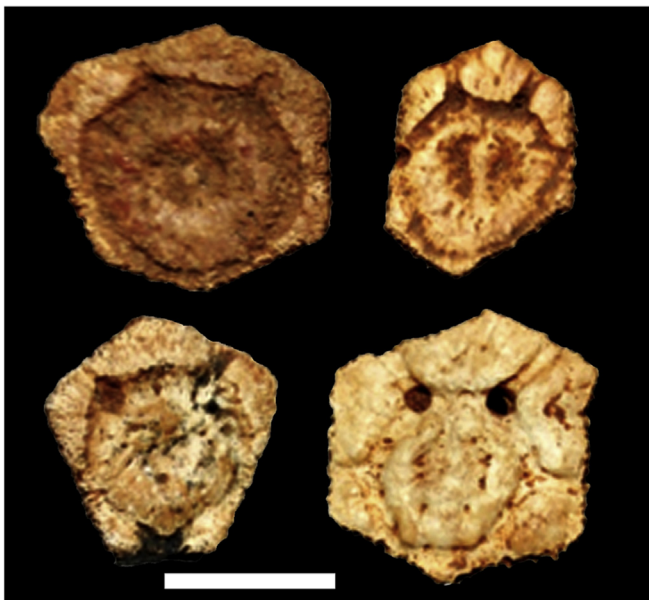


Fig. 8. Isolated buckler osteoderms of the carapace of *Pachyarmatherium brasiliense* from Gruta do Urso, Tocantins (UNIRIO PM 1315–1316). Scale bar = 10 mm.

America. Probably both species were very rare during the Pleistocene in South America, and because climate conditions were so unstable (glacial–interglacial cycles), they were only able to expand their geographic distribution after 4 ka, in response to climatic stability. This is in accordance with the earliest records of *D. novemcinctus* in the United States (current boreal limits of its geographic distribution), which is from Miller's Cave (Llano County, Texas), dated 3008 ± 410 BP (Shapiro et al., 2015). Although taphonomic biases related to their small size cannot be discarded as cause of their infrequent presence in the Pleistocene record of South America, in the fossiliferous beds where they are recorded their presence is conspicuous due to the numerous osteoderms that form the carapace.

Propaopus came from the south and *Pachyarmatherium* from the north, probably explaining the absence of the former in Gruta dos Moura cave. The dating for the fossil assemblage of this cave is 22 ka, which is earlier than the earliest dating for the deposit in the Gruta do Urso cave. Thus, probably *P. sulcatus* arrived later than *Pachyarmatherium* in the region of Aurora do Tocantins during the late Pleistocene, after the Last Glacial Maximum.

6. Conclusions

The examination of the collected remains in the limestone caves in Aurora do Tocantins shows the presence of *D. novemcinctus*, *E. sexcinctus*, *P. sulcatus*, and *P. brasiliense* in northern Brazil. The first two species inhabit the region nowadays, while the other two are only known as fossils. Two taxa, *E. sexcinctus* and *P. sulcatus*, have a wide temporal and geographic distribution from the early Pleistocene to the Holocene of South America, while the other two, *D. novemcinctus* and *Pachyarmatherium*, also extended to Central America and North America.

Global paleoclimates influenced the distribution of mammals, especially during glacial/interglacial cycles. Pleistocene climates were predominantly colder and arid than present day, which favored the development of open forests and savannas in Brazil, and grassland and cold steppes in the southern part of South America. Probably, *Propaopus* and *Pachyarmatherium*, took refuge in lower latitudes of South America (including Brazil). During the short interglacial cycles, warm and moist climate favored the developed of an evergreen forest in central Brazil, led *Propaopus* and *Pachyarmatherium* to extinction, and positively selected *D. novemcinctus* and *E. sexcinctus* in this biome. The results of this work indicate that future investigations in northern Brazil will increase the knowledge on fossil mammals and temporal and biogeographic distributions in South America.

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Appendix A. Supplementary data

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