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Osteoderm histology of Late Pleistocene cingulates from the intertropical region of Brazil

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During the Late Pleistocene, several possibly endemic cingulate species, known mostly from isolated osteoderms, carapace fragments, and caudal tubes, coexisted in the Brazilian Intertropical Region. Here, we describe the osteoderm microstructure of *Pachyarmatherium brasiliense*, as well as the glyptodonts *Panochthus greslebini*, *Panochthus jaguaribensis* and *Glyptotherium* sp., in order to provide additional species-diagnostic characters and shed light on their evolutionary relationships. *Pachyarmatherium brasiliense* lacks several derived features shared by glyptodonts and pampatheres, such as extensive bone remodeling, fibers arranged in large bundles, and relatively poorly developed layers of compact bone, thus supporting its exclusion from glyptodonts as suggested by a recent cladistic study. The osteoderm histology of *P. greslebini* resembles that of other species of *Panochthus* (e.g., *Panochthus frenzelianus*). By contrast, the presence of relatively thick layers of compact bone, the configuration and size of resorption areas, the absence of randomly oriented lateral fiber bundles, and the absence of an intermediary region between the compact and trabecular bone potentially support the exclusion of *Panochthus jaguaribensis* from the genus. Finally, osteoderms of the Brazilian specimens of Glyptodontinae share histological features with *Glyptotherium floridanus*, rather than *Glyptodon*, thus reinforcing their assignment to *Glyptotherium*. These results highlight the relevance of histological osteoderm characters in cingulate systematics, and call for further and more comprehensive studies.

Key words: Mammalia, Cingulata, Glyptodontidae, *Pachyarmatherium*, osteoderms, paleohistology, Pleistocene, Brazilian Intertropical Region.

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Introduction

The Brazilian Intertropical Region (sensu Cartelle 1999) is a Quaternary paleomastozoological province covering most of the northeastern, and some of the southeastern and mid-western Brazilian states. Fossils in this region occur predominantly in caves (e.g., Bahia, Minas Gerais, Rio Grande do Norte) and natural tanks (Moreira 1971; Porpino and Bergqvist 2002), and were likely deposited during a period of significant rainfall at the end of the Pleistocene or beginning of the Holocene (Cartelle 1999; but see Auler et al. 2006). Among the most frequent findings are the remains of cingulates, which comprise armadillos, pampatheres, and glyptodonts (Fig. 1).

At least four cingulate species appear to be endemic to the region (Fig. 2), including the glyptodonts *Panochthus greslebini* Castellanos, 1941 (but see Chimento and Agnolin 2011 for a possible occurrence outside the Brazilian Intertropical Region), *Panochthus jaguaribensis* Moreira, 1965, and *Hoplophorus euphractus* Lund, 1839 (Cartelle, 1999), as well as *Pachyarmatherium brasiliense* Porpino, Fernicola, and Bergqvist, 2009 of uncertain affinity (Porpino et al. 2009). Specimens described as *Glyptodon* also commonly occur (Cartelle 1992; Porpino et al. 2004; Alves and Barreto 2007; Dantas 2009), but may in fact belong to the North American genus *Glyptotherium* (Oliveira et al. 2010). As is generally the case for cingulates, all of these taxa are mainly represented by exoskeletal elements, particularly carapace

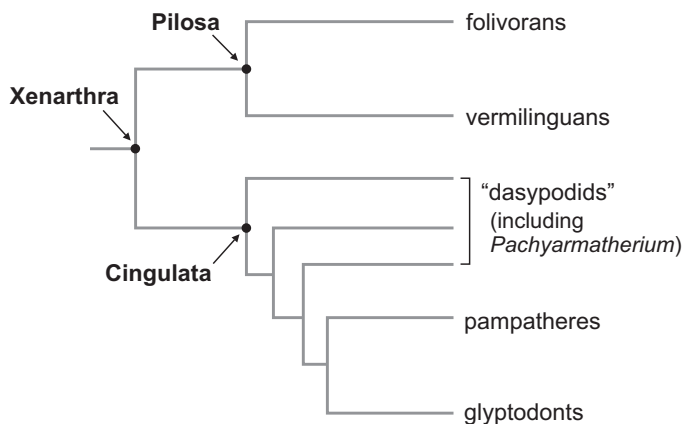


Fig. 1. Simplified cladogram showing the phylogenetic relationships of cingulates, modified from Gaudin and Wible (2006) and Porpino et al. (2009). Note that dasypodids, a group traditionally recognized in the systematics of the xenarthrans, actually represent a paraphyletic assemblage.

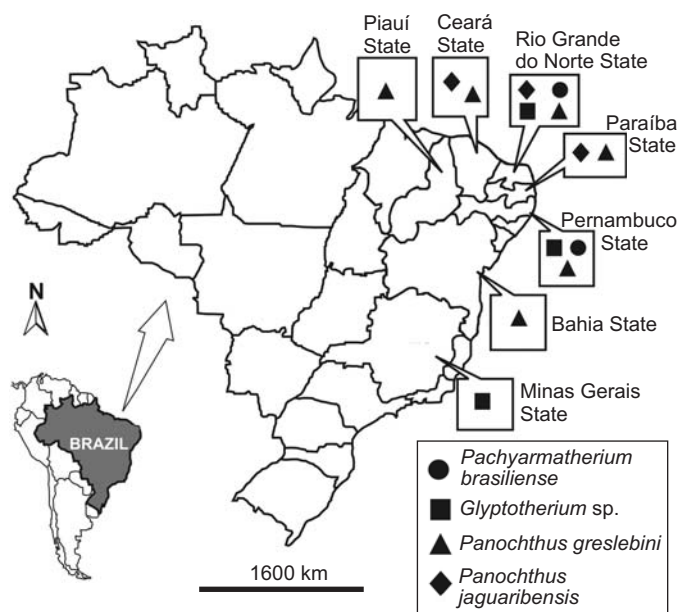


Fig. 2. Distribution of the studied species within Brazil. Based on Porpino (2009), Porpino and Bergqvist (2002), and Oliveira et al. (2010).

osteoderms, which also provide some of the most useful diagnostic features of the group.

With few exceptions, such as the Eocene insectivore *Pholidocercus* (Koenigswald and Storch 1983) and the spiny mouse *Acomys* (Kraft 1995), the presence of osteoderms in xenarthrans is a unique feature among mammals (Wolf 2007). Osteoderms show a high degree of morphological and histological diversity (Hill 2006; Wolf 2007), and their external morphology has repeatedly been used in cingulate systematics (Ameghino 1889; Hoffstetter 1958; Paula Couto 1979; Carlini and Scillato-Yané 1996). By contrast, osteoderm microstructure had until recently received relatively little attention (but see Fernandez 1931), although the past five years have been marked by an increased interest in their histology (e.g., Hill 2006; Wolf 2007; Chavez-Aponte et al.

2008; Krmpotic et al. 2008; Wolf et al. 2011), which has provided important insights into cingulate ontogeny and phylogeny (Chinsamy 1997; Krmpotic et al. 2008).

Here, we describe the histology of the osteoderms of four cingulates from the Pleistocene of the intertropical region of Brazil, and discuss the implications of our results in terms of their systematics and phylogeny.

Institutional abbreviations.—MCC, Museu Camara Cascudo, Rio Grande do Norte, Brazil; UFRJ-DG...-M, fossil mammalian collection, Universidade Federal do Rio de Janeiro, Departamento de Geologia, Rio de Janeiro, Brazil.

Material and methods

The sectioned specimens were collected in tank (*Panochthus* cf. *greslebini*, *Panochthus jaguaribensis*) and cave (*Pachyarmatherium brasiliense* and *Glyptotherium* sp.) deposits in the state of Rio Grande do Norte, northeastern Brazil. With the exception of MCC 1089V, which represents a carapace fragment of *P. jaguaribensis*, they comprise uncatalogued, isolated, eroded osteoderms found in association with catalogued material (other osteoderms and, in some cases, post-crania) held at MCC. We decided to restrict our analysis to Brazilian glyptodontids and *Pachyarmatherium* because their histological features have not yet been described, while both Dasypodidae and Pampatheriidae were the subject of recent studies (Hill 2006; Krmpotic et al. 2008; Wolf et al. 2011)

The histological sections were deposited at the fossil mammal collection of the Departamento de Geologia (UFRJ) as UFRJ-DG 491-M (*Panochthus* cf. *greslebini*), UFRJ-DG 492-M (*Pachyarmatherium brasiliense*), UFRJ-DG 493-M (*Glyptotherium* sp.), and UFRJ-DG 494-M (*Panochthus jaguaribensis*). All osteoderms were embedded in polyester resin and sectioned using a diamond disc on a metallographic saw. The samples were then affixed to glass slides and ground on a lap wheel until the microstructure became evident, with the thickness of the sections varying depending on material, resistance and coloration. Thin sections were photographed under ordinary and cross-polarized light using a Nikon Eclipse E200 POL petrographic microscope. While all osteoderms were sectioned and analyzed along both their anteroposterior and transverse axes, only transverse sections were photographed. Nomenclature follows Hill (2006) and Porpino et al. (2009). The classification of glyptodonts in the Systematic paleontology section follows Fernicola (2008).

Systematic paleontology

Family incertae sedis

Genus *Pachyarmatherium* Downing and White, 1995

Type species: *Pachyarmatherium leiseyi* Downing and White, 1995; Late Pliocene–Late Pleistocene, Florida, United States.

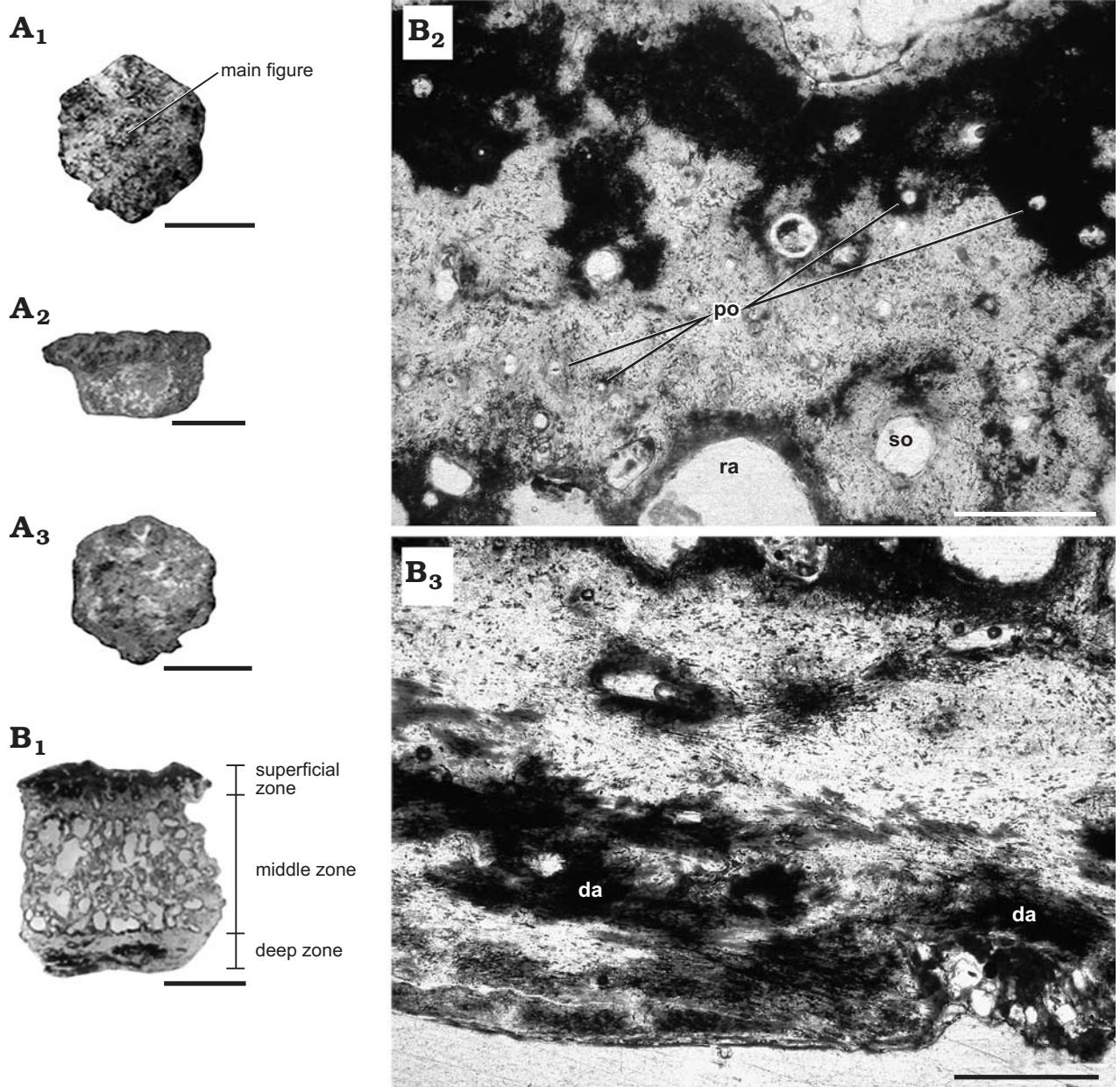


Fig. 3. Uncatalogued isolated osteoderm of the carapace of *Pachyarmatherium brasiliense* Porpino, Fernicola, and Bergqvist, 2009 from the Late Pleistocene of Lajedo da Escada site, Baraúna municipality, Rio Grande do Norte State, Brazil. **A.** Osteoderm in external view showing the superficial ornamentation (A_1), lateral (A_2) and internal (A_3) views. **B.** UFRJ-DG 492-M, internal structure of the osteoderm (B_1). Paleohistological sections viewed under a petrographic microscope, superficial layer of osteoderm (B_2), note the darker region near the top of the section and the uniform distribution of primary osteons marked by pointers; deep layer of compact bone with dark areas (B_3). Scale bars: A, 10 mm; B_1 , 3 mm; B_2 , B_3 , 1 mm. Abbreviations: da, dark areas (see text for details); po, primary osteon; ra, resorption area; so, secondary osteon.

Pachyarmatherium brasiliense Porpino, Fernicola, and Bergqvist, 2009

Fig. 3.

Material.—Uncatalogued isolated osteoderm (section UFRJ-DG 492-M) forming part of the carapace (MCC collection) from Lajedo da Escada, Baraúna municipality, Rio Grande do Norte, Late Pleistocene.

Description.—The osteoderm is hexagonal in external view. While the external surface, though eroded, bears a main

figure surrounded by peripheral figures located in the corners and separated from one another by sulci (Fig. 3A₁), the internal surface of the osteoderm is smooth and shows no perforations (Fig. 3A₃). In cross section, the osteoderm resembles turtle shells (e.g., Zangerl 1969) in being composed of well-developed superficial and deep layers of compact bone (the inner and outer tables) enclosing a central region of trabecular bone, as previously observed by Hill (2006).

The superficial layer of compact bone contributes about 25% of the total thickness of the osteoderm (Fig. 3B₁), con-

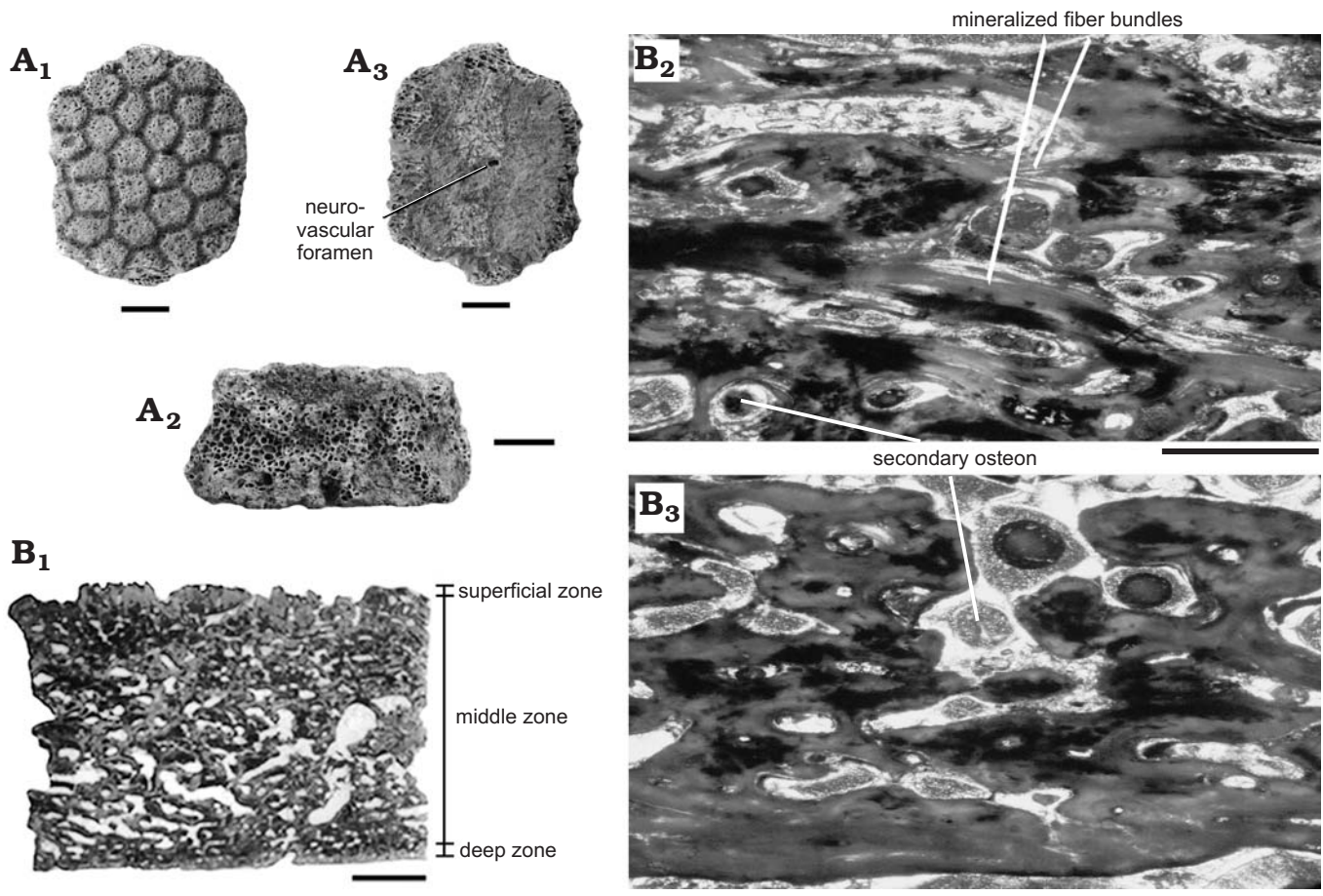


Fig. 4. Uncatalogued isolated osteoderm of the carapace of *Panochthus* cf. *greslebini* Castellanos, 1941 from the Late Pleistocene of Lagoa do Santo, Currais Novos municipality, Rio Grande do Norte State, Brazil. **A.** Osteoderm in external (A_1), lateral (A_2), and deep (A_3) views. **B.** UFRJ-DG 491-M; internal structure of the osteoderm (B_1). Paleohistological sections viewed under a petrographic microscope, superficial compact bone (B_2); thin deep layer of compact bone and trabecular bone with some resorption areas (B_3). Some possible mineralized fiber bundles also occur. Scale bars: A, 10 mm; B_1 , 5 mm; B_2 , B_3 , 1 mm.

tains numerous aligned primary osteons (Fig. 3 B_2), and itself consist of two distinct zones: (i) a dark superficial layer for which internal details are difficult to observe owing to its color; (ii) a lighter deep layer, including some resorption areas and secondary osteons. No fibre bundles were observed in the superficial layer. The central region of the osteoderm is relatively thin and consists of spongy, trabecular bone showing some resorption areas (“erosion rooms” sensu Main et al. 2005). Although this region has undergone some remodeling by secondary osteons, primary osteons also occur. Like the superficial layer, the deep layer of compact bone also displays a dark zone, but, unlike in the former, the dark areas occur as isolated spots (Fig. 3 B_3). As a whole, the deep layer of compact bone is thicker than the superficial one, and contains fiber bundles oriented horizontally and obliquely relative to the surface. There is only one secondary osteon, and primary osteons are completely absent. Marginal fibers are present, but very narrow.

Stratigraphic and geographic range.—Late Pleistocene of northeastern Brazil.

Family Panochthidae Castellanos, 1927

Genus *Panochthus* Castellanos, 1941

Type species: *Glyptodon tuberculatus* Owen, 1945; Pleistocene, Buenos Aires, Argentina.

Panochthus cf. *greslebini* Castellanos, 1941

Fig. 4.

Material.—Uncatalogued isolated osteoderm (section UFRJ-DG 491-M) forming part of the carapace (MCC collection) from Lagoa do Santo, Currais Novos municipality, Rio Grande do Norte, Late Pleistocene.

Description.—In external view, the osteoderm is pentagonal, with a rugose surface ornamented with about 40 hexagonal figures separated from one another by shallow sulci (Fig. 4 A_1). By contrast, the internal surface is smooth, gently concave, and perforated by a vascular foramen near the center, as well as several small pits (Fig. 4 A_2).

In cross section, the osteoderm is predominantly composed of trabecular bone enclosed by thin superficial and deep layers of compact bone (Fig. 4B). The figures orna-

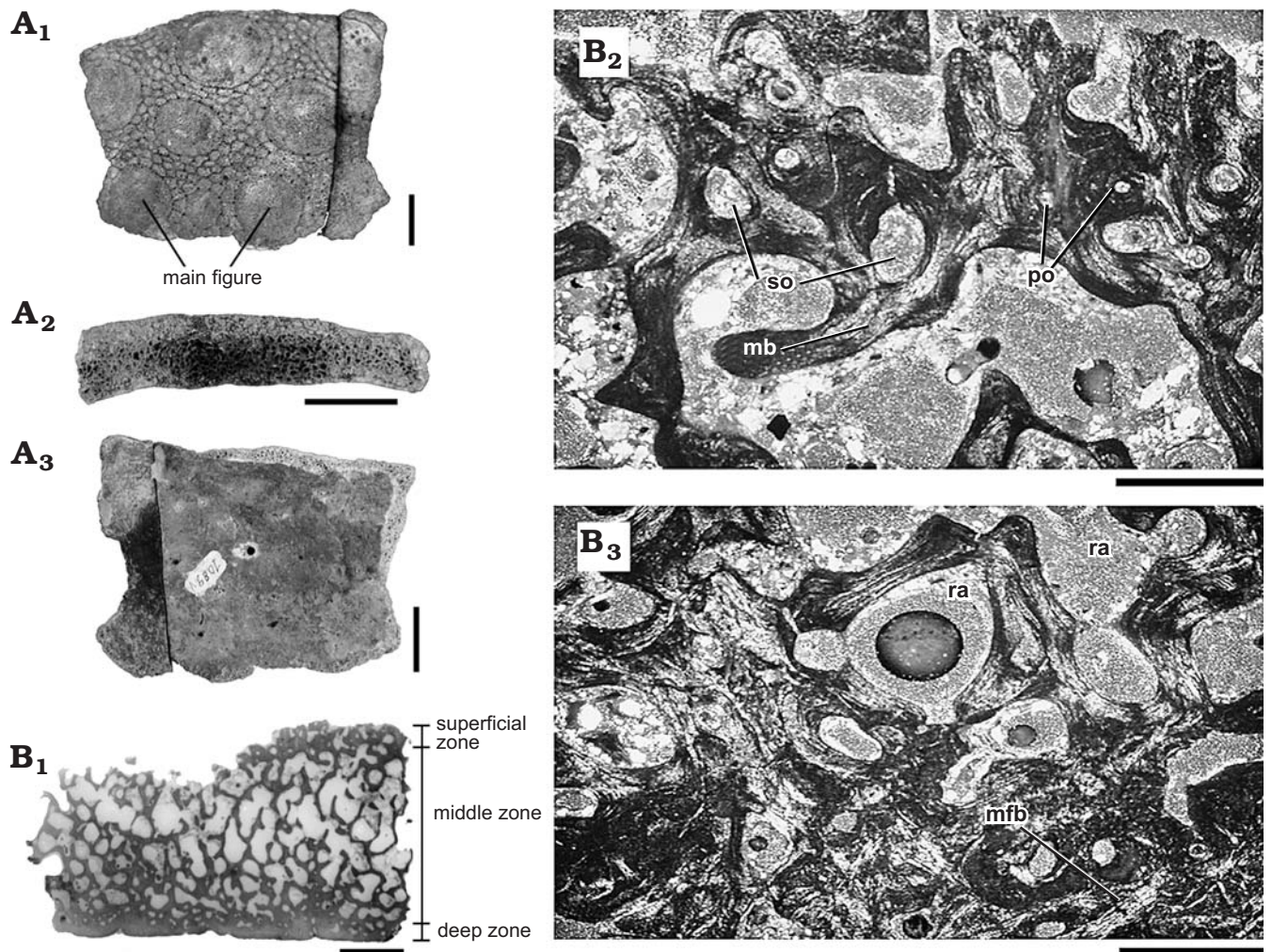


Fig. 5. Carapace fragment of *Panochthus jaguaribensis* Moreira, 1965 from the Late Pleistocene of Lagoa do Santo site, Currais Novos municipality, Rio Grande do Norte State, Brazil. **A.** MCC 1089V, carapace fragment in external view showing the superficial ornamentation (A_1), lateral (A_2) and deep (A_3) views. **B.** UFRJ-DG 494-M; internal structure of the osteoderm (B_1). Paleohistological sections viewed under a petrographic microscope, superficial compact bone with primary osteons, secondary osteons and mineralized fiber bundles (B_2); deep layer of compact bone and trabecular bone with some resorption areas (B_3). Some possible mineralized fiber bundles also occur. Scale bars: A, 30 mm; B_1 , 5 mm; B_2 , B_3 , 1 mm. Abbreviations: mfb, mineralized fiber bundles; po, primary osteon; ra, resorption area; so, secondary osteon.

menting the external surface give an irregular appearance to the superficial layer of compact bone. Primary bone is hardly identifiable owing to remodeling caused by osteoclasts, but some primary osteons are present. Near the external surface, there are mineralized collagen fiber bundles predominantly oriented parallel to the osteoderm surface (Fig. 4B₂), although some are oriented obliquely. Further towards the center of the osteoderm, the collagen fibers show less organization and the bone exhibits signs of extensive remodeling, such as vascular channels enclosed by concentric bone lamellae, indicating bone resorption and subsequent re-deposition.

Between the superficial layer of compact bone and the central trabecular bone there is an intermediate region which cannot be characterized as either compact or trabecular, and includes primary osteons and some small areas of resorption (Fig. 4B₁). Below the latter, the trabecular bone is thick and shows large cavities, with primary osteons occurring in the trabeculae. Finally, the thin deep layer of

compact bone contains narrow collagen fibers running parallel to the osteoderm surface (Fig. 4B₃), as well as a few primary osteons.

Stratigraphic and geographic range.—Late Pleistocene of northeastern Brazil.

Panochthus jaguaribensis Moreira, 1965

Fig. 5.

Material.—Carapace fragment (MCC 1089V, section UFRJ-DG 494-M) from Lagoa do Santo, Currais Novos municipality, Rio Grande do Norte, Late Pleistocene.

Description.—MCC 1089V represents a small fragment of the carapace of *Panochthus jaguaribensis*. In external view, the fragment is covered by several tiny, quadrangular to hexagonal figures, as well as some large, flat, subcircular main figures delimited by thin sulci with several small pits (Fig.

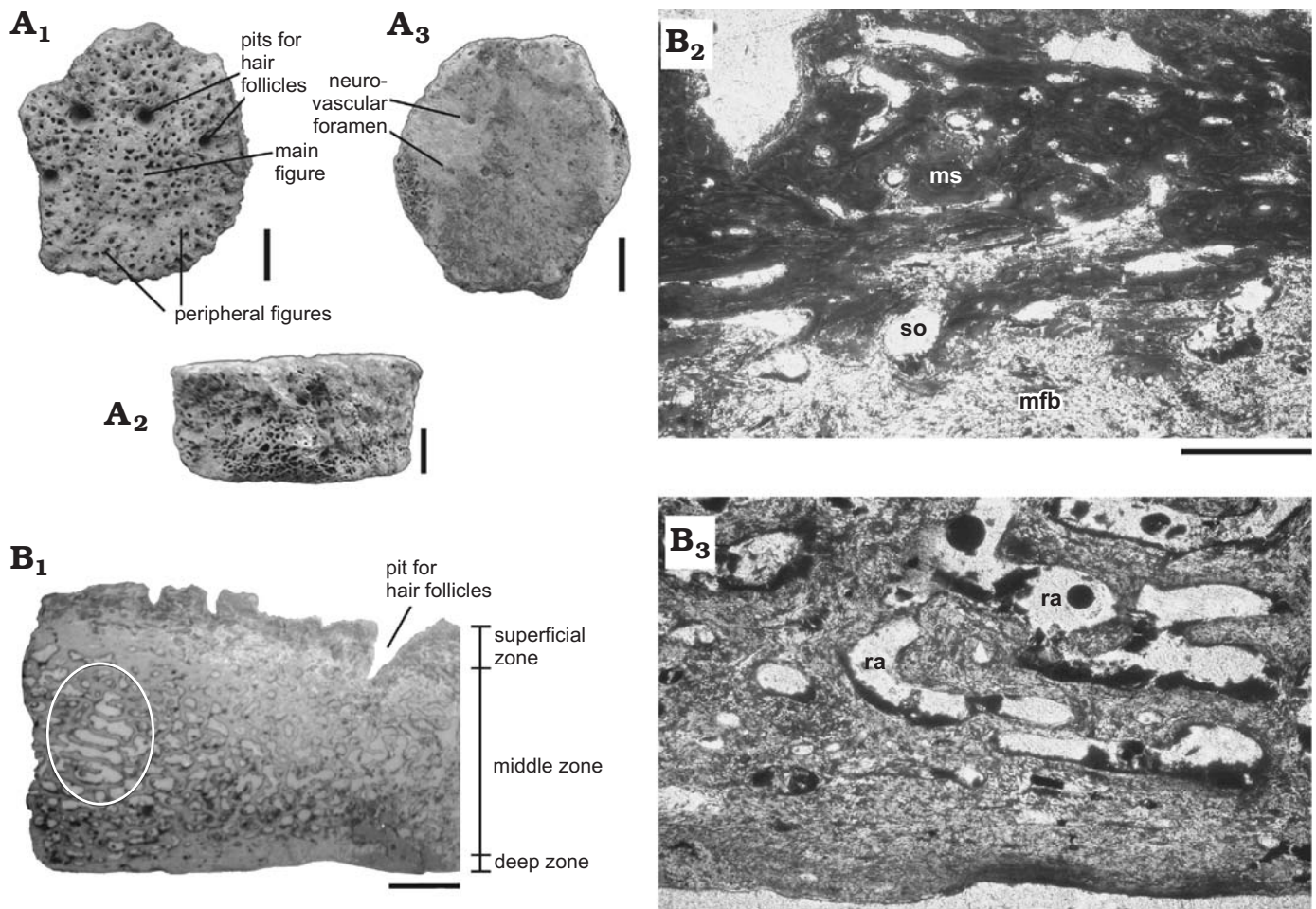


Fig. 6. Uncatalogued isolated osteoderm of the carapace of *Glyptotherium* sp. from Late Pleistocene of Lajedo da Escada site, Baraúnas municipality, Rio Grande do Norte State, Brazil. **A.** Osteoderm in external (A_1), lateral (A_2), and deep (A_3) views. **B.** UFRJ-DG 493-M; internal structure of the osteoderm (B_1), note the shelf-like structure (ellipse). Paleohistological sections viewed under a petrographic microscope; superficial (B_2) and deep (B_3) layers. Scale bars: A, 10 mm; B_1 , 5 mm; B_2 , B_3 , 1 mm. Abbreviations: ms, mosaic-like region; mfb, mineralized fiber bundles; ra, resorption area; so, secondary osteon.

$5A_1$). The internal surface is concave and perforated by large neurovascular foramina (Fig. $5A_3$).

In cross section, there are two weakly developed layers of compact bone adjacent to the external and internal surfaces (Fig. $5B_1$, B_2). The superficial layer of compact bone is highly vascularized and contains some randomly distributed primary and secondary osteons. Near the surface, there are narrow collagen fibers with no preferential orientation (Fig. $5B_1$). The central region of the osteoderm is composed of thin trabeculae with both primary and secondary osteons, outlining large and rounded resorption areas. Toward the center of the osteoderm, the resorption areas become smaller and more elongated. At its greatest extent, the deep layer of compact bone is thicker than the superficial one, but becomes thinner toward the periphery and has fewer osteons than the latter. Collagen fibers run obliquely or perpendicularly to the internal surface (Fig. $5B_3$). They seem to originate from outside the osteoderm, and therefore probably represent Sharpey fibers.

Stratigraphic and geographic range.—Late Pleistocene of northeastern Brazil.

Family Glaptodontidae Gray, 1869

Genus *Glyptotherium* Osborn, 1903

Type species: Glyptotherium texanum Osborn, 1903; Late Pliocene–Early Pleistocene, Texas, United States.

Glyptotherium sp.

Fig. 6.

Material.—Uncatalogued isolated osteoderm (section UFRJ-DG 493-M) forming part of the carapace (MCC collection) from Lajedo da Escada, Baraúna municipality, Rio Grande do Norte, Late Pleistocene.

Description.—In external view, the osteoderm is hexagonal, bearing a roughly textured surface with hundreds of small, shallow, subcircular or irregularly-shaped pits. In the center of the external surface, the main figure is surrounded by seven slightly smaller peripheral figures, separated by well-defined sulci (Fig. $6A_1$). Four large, deep perforations, probably piliferous foramina or glandular pits, occur at the intersection of the radial sulci with the main sulcus. The surface of the

peripheral and the main figures are flat. The internal surface is gently concave and perforated by several small foramina (Fig. 6A₃).

In cross section, the microstructure of the osteoderm is porous and highly vascularized. The superficial and deep layers of compact bone are darker than other areas of the osteoderm and poorly developed (Fig. 6B₁). The superficial layer of compact bone contains numerous primary osteons and is characterized by a mosaic-like structure (Fig. 6B₂). Near the external surface, mainly on the left side, narrow collagen fibers occur and are predominantly oriented parallel to the surface, although some are slightly oblique. Pits which likely housed hair follicles appear as deep excavations (Fig. 6B₁).

The central region of the osteoderm is composed of trabecular bone with small to medium-sized resorption areas and some secondary osteons. One section in particular stands out for being composed of a vertical sequence of transversely elongated, parallel resorption areas (Fig. 6B₁). The deep layer of compact bone is thinner than the superficial one, especially on the sides (Fig. 6B₃), and contains some primary and secondary osteons.

Discussion

Our results reveal a range of characters potentially useful for both species diagnosis and phylogenetic analyses of intertropical Brazilian cingulates. Although originally described as an armadillo (Dasypodoidea) by Downing and White (1995), Vizcaíno et al. (2003) later assigned *Pachyarmatherium* to Glyptodontoidea based on both the absence of movable bands in the carapace, as seen in armadillos and pampatheres, and the presence of very thick osteoderms, as seen in glyptodonts. However, *Pachyarmatherium* does not show any of the postcranial features shared by pampatheres and glyptodonts, and instead retains the ancestral cingulate morphology also seen in dasypodids (Porpino et al. 2009; Fig. 1). Similarly, the external morphology of the osteoderms of *Pachyarmatherium* closely resembles that of dasypodine armadillos, such as *Dasypus* and *Propraopus* (see Ameghino 1889; Hill 2006; Vickaryous and Hall 2006), although it is also almost identical to that of the basal glyptodont *Neoglyptatelus* (Carlini et al. 1997). Like the armadillos *Dasypus* (Hill 2006) and *Chaetophractus* (Krmptotic et al. 2008), but unlike glyptodonts and pampatheres, *Pachyarmatherium brasiliense* is characterized by very thick superficial and deep layers of compact bone (Fig. 3B). In contrast to the extensive bone remodeling typical of derived glyptodonts (Wolf 2007; Wolf et al. 2011), bone remodeling in *Pachyarmatherium* is limited, as also seen in dasypodids. Finally, *Pachyarmatherium* differs from pampatheres in lacking collagen fiber bundles organized into broad, decussating strands at the margin of the osteoderm (see Wolf 2007). Taken together, the absence of any of the derived features characterizing glyptodonts and pampatheres thus supports the exclusion of *P. brasiliense* from both taxa, as previously suggested by Porpino et al.

(2009). A similar conclusion was recently reached regarding *Neoglyptatelus* by Carlini (2008a).

The genus *Panochthus* comprises several species ranging from the early to the late Pleistocene (including *Panochthus greslebini* from northeastern Brazil). The latter differ in features relating to the caudal tube, but share a strikingly similar carapace morphology (see Cruz et al. 2011; Zurita et al. 2011b), thus making specific assignments of isolated carapace material difficult. Although the osteoderm here assigned to *Panochthus* cf. *greslebini* was collected in association with a large carapace fragment and several other identical isolated osteoderms, no caudal tube was recovered, and we therefore decided to refrain from firmly diagnosing the specimen to the species level.

The osteoderms of *Panochthus* cf. *greslebini* and *Panochthus frenzelianus* (Hill 2006) closely resemble each other in both their external and internal morphology. In addition to the features typical of derived glyptodonts (extensive bone remodeling, fibers arranged in large bundles, and thinner layers of compact bone relative to the region of trabecular bone), both species share an intermediate region between the superficial layer of compact bone and the central region of trabecular bone. This intermediate region is characterized by numerous primary osteons and some small resorption areas, and is better developed in *P. cf. greslebini*, thus potentially representing an additional diagnostic feature differentiating the two taxa besides their diverging caudal tube morphologies (see Castellanos 1941). However, a more comprehensive analysis including more taxa, as well as comparisons of osteoderms from different areas of the carapace, will be needed to assess its reliability.

Panochthus jaguaribensis was originally described based on an isolated caudal tube from Ceará State, Brazil (Moreira 1965). A second caudal tube from a tank deposit in Paraíba State was later referred to the same species (Moreira 1971). The referred material was found in association with a caudal tube of *P. greslebini*, as well as several carapace fragments and isolated osteoderms bearing two distinctive external ornamentation patterns: (i) small, randomly distributed figures; and (ii) a main figure surrounded by small figures, interpreted to represent *P. greslebini* and *P. jaguaribensis*, respectively (Moreira 1971). Based on these interpretations, an additional carapace fragment from Rio Grande do Norte State was later also assigned to *P. jaguaribensis* (Oliveira et al. 1982; Porpino and Bergqvist 2002: fig. 2A).

The ornamentation pattern of *P. jaguaribensis* strikingly differs from that of most other species traditionally assigned to *Panochthus*, such as *P. tuberculatus* and *P. subintermedius* (Moreira 1971; Porpino and Bergqvist 2002; Porpino 2009), in which the presence of a main figure is restricted to a few longitudinal rows close to the lateral, anterior and posterior borders of the carapace (Castellanos 1941; Cruz et al. 2011). This, together with some differences in caudal tube ornamentation (e.g., a more slender outline, less prominent tubercles on the lateral and terminal figures) led Moreira (1971) to place *P. jaguaribensis* in the new genus *Parapanochthus*.

Porpino and Bergqvist (2002) criticized this new allocation, arguing that the Ensenadan species *Panochthus intermedius* also presents well-developed, large main figures. However, as in other species of *Panochthus*, the main figures in *P. intermedius* are limited to the anterior and posterior portions of the carapace, and decrease in size towards the mid-dorsal region (Castellanos 1941; Zurita et al. 2011b). By contrast, the carapace fragments of *P. jaguaribensis* (see Moreira 1971; Porpino and Bergqvist 2002; Porpino 2009) are thought to belong to the mid-dorsal region (Moreira 1971; Porpino 2009), and display fully developed main figures which are more closely spaced and proportionally larger than in *P. intermedius* (Porpino 2009). Nevertheless, it is possible that the isolated osteoderms and carapace fragments referred to *P. jaguaribensis* by Moreira (1971) and Porpino and Bergqvist (2002) may be dubious. While the isolated osteoderms resemble elements forming longitudinal rows near the lateral border of the carapace in *P. tuberculatus* (e.g., Burmeister 1870–1874) and *P. intermedius* (Zurita et al. 2011b), the main figures of the supposedly mid-dorsal carapace fragments of *P. jaguaribensis* share intriguing similarities with the cephalic shield of other species of *Panochthus*. This new interpretation calls for a detailed revision of *P. jaguaribensis*.

The external morphology of MCC 1089V resembles that carapace fragments previously assigned to *P. jaguaribensis* (Moreira 1971: fig. 3; Porpino and Bergqvist 2002: fig. 2A). In terms of histology, *P. jaguaribensis* shares with *Panochthus* cf. *greslebini* and *Panochthus frenzelianus* several features typical of derived glyptodonts: thin superficial and deep layers of compact bone bordering a thick (representing about 80% of the total thickness) central region of trabecular bone, as well as extensive bone remodeling, with primary bone being largely absent (Hill 2006; Wolf 2007). There is only a single area in the section of *P. cf. greslebini* where the mineralized collagen fibers are diffuse, a typical feature of primary bone according to Chinsamy (1997).

The comparison of *P. cf. greslebini* and *P. frenzelianus* with *P. jaguaribensis* also revealed some marked differences between them. *P. jaguaribensis* lacks both lateral fiber bundles oriented in random directions, and an intermediate region between the superficial layer of compact bone and the trabecular bone. Instead, *P. jaguaribensis* is marked by thinner trabeculae outlining larger, rounded and more uniformly distributed resorption areas in the central region, as well as a thicker deep layer of compact bone than in the other two species. Taken together with its distinctive dorsal carapace morphology, the lack of histological characters shared with *P. cf. greslebini* and *P. frenzelianus* may thus potentially support the exclusion of *P. jaguaribensis* from *Panochthus*, as suggested by Moreira (1971; see also Porpino 2009), pending, however, a revision of the material assigned to this species.

Although originally assigned to *Glyptodon* (Winge 1915; Paula Couto 1979; Dantas 2009), all glyptodontine (Glyptodontiade, Glyptodontinae) specimens from the intertropical region of Brazil were recently referred to the North American genus *Glyptotherium* (Oliveira et al. 2010). The external or-

nammentation of the osteoderm attributed here to *Glyptotherium* sp., though eroded, is similar to osteoderms from both North (e.g. Gillette and Ray 1981) and South America (Carlini et al. 2008b; Oliveira et al. 2010) previously attributed to this genus. The layers of compact bone and the mineralized fiber bundles of the *Glyptotherium* specimen studied here are thicker than in *Glyptodon reticulatus*, but resemble those of *Glyptotherium floridanum* (Hill, 2006), thus supporting the referral of the Brazilian material to *Glyptotherium* (Oliveira et al. 2010). In terms of their external morphology, the carapace osteoderms of *Glyptodon* and *Glyptotherium* differ only in some subtle details, such as the number of peripheral figures and the relative development of the radial and main sulci (Carlini et al. 2008a; Oliveira et al. 2010). The latter may be difficult to observe in eroded specimens, thus making differences in osteoderm microstructure a potentially useful source of additional diagnostic characters. However, as in other glyptodonts, the superficial ornamentation of the osteoderms in both genera varies according to the position they occupy in the carapace, and it is possible that histological features may be subject to a similar kind of variation.

All of the glyptodontine osteoderms analyzed by Hill (2006) were from the mid-trunk region (Hill 2006: 1443), which we interpret to correspond to the mid-dorsal region of the carapace (sensu Porpino 2009; Cruz et al. 2011). The specimen described here likely comes from the same region of the carapace, and resembles those of Hill (2006) in its near-isodiametric and hexagonal outline, instead of being anteroposteriorly elongate as in the lateral regions of carapace, as well as the relatively small size of the main figure compared to that found on the posterodorsal and lateralmost osteoderms (see Lydekker 1894 and Duarte 1997 for descriptions and illustrations of *Glyptodon* osteoderms, and Gillette and Ray 1981 for *Glyptotherium*; for a comparison between the two, see Carlini et al. 2008b and Oliveira et al. 2010). In addition, both the present material and the specimens analyzed by Hill (2006) lack some of the typical juvenile stage characters of glyptodontine glyptodonts, such as convex main and peripheral figures and smooth lateral surfaces (Zurita et al. 2011a), indicating that they belonged to relatively mature individuals. This suggests that the histological differences described here are not the result of intra-individual or ontogenetic variation, and may therefore be significant in a systematic context. More comprehensive analyses of histological variation across the carapace and different ontogenetic stages, as well as the incorporation of some of the characters discussed here into a broad cladistic study are needed to corroborate this preliminary conclusion.

Conclusions

Together with previous work (Hill 2006; Wolf 2007; Krmptotic et al. 2008; Wolf et al. 2011), our study shows that osteoderm microstructure may hold relevant information regarding the relationships of cingulates, and provide charac-

ters diagnostic at the species level. Our results may support the exclusion of *Pachyarmatherium* from glyptodonts, based on the absence of histological features present in both basal (*Propalaeohoplophorus*) and derived glyptodonts (extensive bone remodeling, fibers arranged in large bundles, and undeveloped layers of compact bone relative to the region of trabecular bone). Relatively thick layers of compact bone and the pattern and size of resorption areas, as well as the absence of both randomly oriented lateral fiber bundles and an intermediary region between the compact and trabecular bone, potentially support the placement of *Panochthus jaguaribensis* in a distinct genus (*Parapanochthus*), pending a revision of the carapace material previously attributed to *P. jaguaribensis*. Finally, the characteristics shared between the glyptodontine osteoderm analysed here and *Glyptotherium floridanus* support the referral of the Brazilian glyptodontine material to *Glyptotherium*.

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