



HISTOLOGICAL VARIATION IN OSTEODERMS *PANOCHTHUS* SP. AND *GLYPTOTHERIUM* SP. (XENARTHRA: MAMMALIA) FROM THE BRAZILIAN INTERTROPICAL REGION

SHALINE ELAIDE DE ARAÚJO

Programa de Pós-Graduação em Ciências Naturais, Universidade do Estado do Rio Grande do Norte,
Av. Professor Antônio Campos, s/n, 59610-090, Mossoró, RN, Brazil.

KLEBERSON DE OLIVEIRA PORPINO

Departamento de Ciências Biológicas, Universidade do Estado do Rio Grande do Norte,
Av. Professor Antônio Campos, s/n, 59610-090, Mossoró, RN, Brazil.

ABSTRACT – Glyptodonts are one of the most peculiar mammal groups that inhabited South America during the Pleistocene. Among the main characteristics of the group is the presence of a carapace composed of hundreds of osteoderms, which take on variable forms and external ornamentation. The fossiliferous sites of the Brazilian Intertropical Region (RIB) are rich in glyptodont fossils, of which the osteoderms are the most registered elements, possibly due to their high potential for preservation. Recently, the analysis of histological characteristics has proven useful in the differentiation of genera and species. However, the samples used are still limited and do not consider possible differences among different regions of the carapace. In this work, we evaluate possible histological variations among the osteoderms of *Glyptotherium* sp. and *Panochthus* sp. from different regions of the carapace and, based on a larger number of specimens, discuss their implications for the systematics of these genera. We found differences among osteoderms from distinct regions of the carapace for both analysed genera. Within the morphological variation described for the osteoderms of *Glyptotherium* sp., it is observed that they have more characteristics in common with the species *Glyptotherium floridanum* than with *Glyptodon reticulatus*, thus reinforcing that the Glyptodontinae findings in the RIB belong to the genus *Glyptotherium* sp. The osteoderms of *Panochthus* share a central region with common characters regardless of the position they occupy in the carapace; the main histological differences among them reside in the layers of compact bone, which show differences even in osteoderms of the same region. Caution is required when the presence of *Neuryurus* in the RIB deposits based on osteoderms is proposed, as morphological and histological characteristics of some representative of this genus overlap with some altered osteoderms (likely pathological) of the *Panochthus* sp. studied here.

Keywords: osteoderms, variation, carapace, *Glyptotherium*, *Panochthus*.

RESUMO – Os gliptodontes são considerados um dos grupos de mamíferos mais peculiares que habitaram a América do Sul durante o Pleistoceno. Entre as principais características do grupo está a presença de uma carapaça constituída de centenas de osteodermos fusionados (exceto nos indivíduos mais juvenis), os quais apresentam formatos e ornamentação externa variados. Os depósitos fossilíferos presentes na Região Intertropical Brasileira (RIB) são ricos em ocorrências de gliptodontes e os osteodermos são os elementos mais registrados, possivelmente devido ao seu alto potencial de preservação. Recentemente, a análise de características histológicas que podem ser usadas para diferenciar os gêneros ou espécies vem sendo exploradas em alguns estudos sobre o grupo. Entretanto, a amostragem utilizada ainda é limitada e não contempla possíveis diferenças entre regiões diferentes da carapaça. Dessa forma, o objetivo desse trabalho foi avaliar possíveis diferenças entre osteodermos de diferentes regiões da carapaça de *Glyptotherium* sp. e *Panochthus* sp. comparando os gêneros estudados com outros já descritos baseando-se em um maior número de exemplares e discutir suas implicações na sistemática do grupo. De acordo com os resultados obtidos existem diferenças quando comparamos osteodermos de regiões distintas da carapaça de *Glyptotherium* sp. e *Panochthus* sp. Dentro da variação morfológica observada para os osteodermos de *Glyptotherium* sp. constata-se que esses possuem mais características em comum com a espécie *Glyptotherium floridanum* do que com *Glyptodon reticulatus*, reforçando assim que os achados de Glyptodontinae presentes na RIB pertencem ao gênero *Glyptotherium* sp. É necessário cautela ao se propor a presença de *Neuryurus* nos depósitos da RIB com base em osteodermos, uma vez que foi constatada sobreposição de características morfológicas e histológicas de alguns representantes deste gênero com os osteodermos alterados de *Panochthus* sp. aqui estudados.

Palavras-chave: osteodermos, variação, carapaça, *Glyptotherium*, *Panochthus*.

INTRODUCTION

Glyptodonts are one of the most peculiar mammalian groups that inhabited South America during the Cenozoic. One of the main characteristics of the group is the presence of a carapace without transverse mobile bands, in contrast to other cingulates, such as dasypodids and pampatheres, formed by fused, thick osteoderms (except in immature individuals; Gillette *et al.*, 2016), which present distinct shapes and external ornamentation patterns that are diagnostic for both genera and species (Paula-Couto, 1979; Gillette *et al.*, 2016). They diverged from other cingulates approximately 35 million years ago according to modern estimates (Fariña *et al.*, 2013; Delsuc *et al.*, 2016).

Remains of glyptodonts are very common in the fossiliferous sites of the Brazilian Intertropical Region (BIR), where they are represented mostly by osteoderms. This is arguably a result of the osteoderms' high preservation potential due to the great number that can be produced from a single individual (Gaudin & Wible, 2006; Pereira *et al.*, 2014). Among the glyptodont genera most common in the BIR are *Panochthus* sp. (Panochthinae) and *Glyptotherium* sp. (Glyptodontinae) (Oliveira *et al.*, 2010; Porpino *et al.*, 2014).

The first species of *Panochthus* described from the BIR was *Panochthus greslebini*, based on a caudal tube collected from a tank deposit in the Jaguaratama municipality, Ceará State (Castellanos, 1942; Porpino *et al.*, 2014). Later, another species of this genus – *Panochthus jaguaribensis* – was also established based on a caudal tube from Limoeiro do Norte municipality, Ceará State (Moreira, 1965; Porpino *et al.*, 2014). In addition to these, a fair amount of isolated osteoderms and carapace fragments, as well as some postcranial material, have been assigned to these species (*e.g.* Moreira, 1971; Porpino & Bergqvist, 2002). However, there are doubts concerning some specific attributions of these elements, given that the caudal tube is the only element known so far that bears diagnostic characters for both species (Porpino *et al.*, 2014). Consequently, Porpino *et al.* (2014) suggested that all material from *Panochthus* found in the BIR, including osteoderms, should be assigned to *Panochthus* sp. unless a clear association with caudal tubes with preserved diagnostic characters can be established.

Past records of Glyptodontinae in the BIR (chiefly of isolated osteoderms) were assigned to *Glyptodon*, a genus very common in the Pleistocene deposits of southern Brazil. However, Oliveira *et al.* (2010) suggested that at least part of these records likely belong to the North American genus *Glyptotherium*, which despite possessing osteoderms similar to *Glyptodon* – its sister genus (Zurita *et al.*, 2013) – differs from the latter genus in that it has rougher external surfaces, shallower main and radial sulci and peripheral figures ranging from eight to nine.

In addition to being a traditional source of macroscopic characters for specific differentiation, isolated osteoderms and carapace fragments have recently been used as sources for mitochondrial DNA for use in molecular phylogenetic analyses (*e.g.* Delsuc *et al.*, 2016), for histological characters useful in systematics, and also to infer ontogenetic and

functional aspects of the animal (Hill, 2006; Wolf *et al.*, 2012; Pereira *et al.*, 2014).

Until now, all histological studies on glyptodont osteoderms relied on a few specimens and did not take into account potential differences across the carapace, even though glyptodont carapaces can have hundreds of osteoderms of which can bear distinctive macroscopic features (*e.g.* relative size of main figures) due to where they formed (see for instance Gillette *et al.*, 2016). Therefore, the aim of this paper is to evaluate possible histological differences between osteoderms from distinct regions of the carapace for the genera *Panochthus* and *Glyptotherium* collected in the BIR, comparing them with other specimens described in the literature and discussing their implications for use in systematics.

MATERIAL AND METHODS

Material analysed

We analysed 18 osteoderms housed in Museu Câmara Cascudo (MCC), Natal City, Brazil. They include eight osteoderms assigned to *Glyptotherium* (four from the dorsal region, two from the lateral region, and two from the region near the posterior border of the carapace) and 10 assigned to *Panochthus* (one dorsal, four from lateral regions and five bearing *ante mortem* alterations, including one from the posterior border of the carapace).

The osteoderms of *Glyptotherium* were collected at the Lajedo da Escada site (5°14'31''S, 37°44'20''W), Baraúna municipality, Rio Grande do Norte State (Figure 1). It consists of a karst deposit within an outcrop of the Jandaíra Formation, which occupies an area of nearly 5 km². This outcrop encompasses two karstic pavements separated from each other by a distance of 200 m (Carvalho *et al.*, 1966). The mammalian fossil fauna of Lajedo da Escada includes small to medium sized taxa, such as *Proechimys* sp. and *Pachyarmatherium*, as well as several large sized species, such as *Eremotherium laurillardi*, *Smilodon populator* and *Notiomastodon waringi* (Porpino *et al.*, 2009; Araújo-Júnior *et al.*, 2011). In this context, the osteoderms of *Glyptotherium* described here were found in association with postcranial bones that likely belong to a single individual (Barbosa *et al.*, 2014).

The osteoderms of *Panochthus* sp. in turn were collected in a tank deposit in Lagoa do Santo site (06°15'39''S, 36°31'04''W), Currais Novos municipality, Rio Grande do Norte State (Figure 1). Until now, there has been little information obtained concerning this deposit, but its vertebrate fauna includes typical Pleistocene megafauna such as *Glyptotherium*, *Eremotherium*, *Toxodon*, *Panochthus*, *Palaeolama* and *Xenorhinotherium* (Araújo-Júnior *et al.*, 2011). This faunal composition is comparable to other tank deposits from Northeastern Brazil (Araújo-Júnior *et al.*, 2011). According to recent studies, the estimated age for such deposits is Late Pleistocene-early Holocene (Araújo-Júnior *et al.*, 2013; França *et al.*, 2014). The osteoderms from *Panochthus* sp. from the Lagoa do Santo site here described were found in association with a partial carapace (MCC 1603V; Oliveira

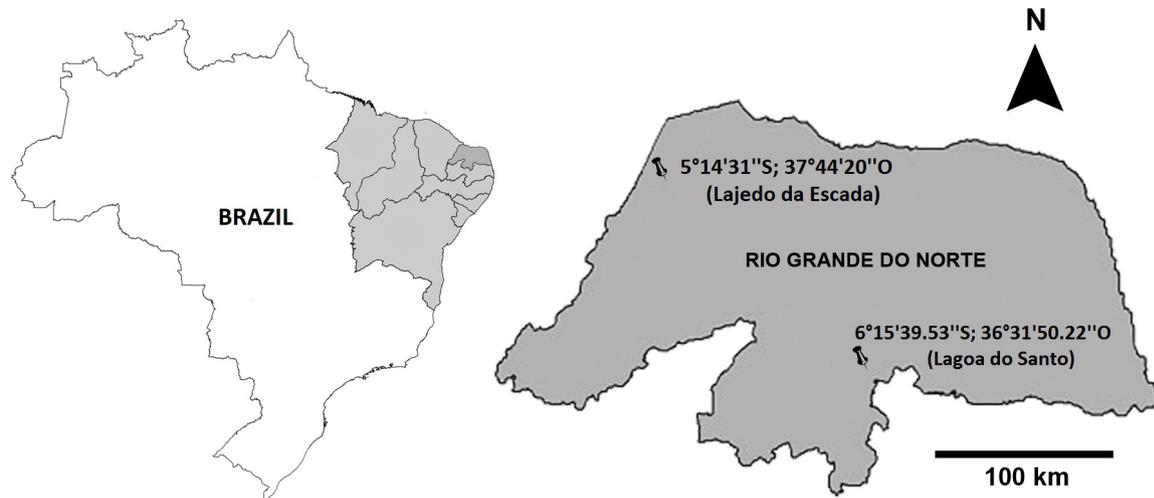


Figure 1. Location map of the Lajedo da Escada and Lagoa do Santo (Rio Grande do Norte, Brazil) fossiliferous sites.

et al., 1984) and few postcranial bones (Porpino & Bergqvist, 2002), and similar to the material of *Glyptotherium* mentioned above, may belong to a single individual.

Terminology and systematics

The taxonomic identification and systematics of the osteoderms here analysed follows Fernicola (2008), Oliveira *et al.* (2010) and Porpino *et al.* (2014). Concerning the regions of the carapace from which the isolated osteoderms studied here were derived, we follow Porpino *et al.* (2014) and Gillette *et al.* (2016) for *Panochthus* and *Glyptotherium*, respectively.

The different sections of the carapace's dorsal region, as defined by Porpino *et al.* (2014), are anterodorsal, mid-dorsal and posterodorsal; the lateral region, in turn, is divided into anterolateral, mid-lateral and posterolateral. Finally, there are the anterior, lateral and posterior borders. While the osteoderms originating from the lateral and dorsal regions for both *Panochthus* and *Glyptotherium* can be differentiated by their shape, it is difficult to assign isolated osteoderms from the dorsal and lateral regions to specific sections, particularly for *Panochthus*, where the external ornamentation of most osteoderms is indistinctly composed of small polygonal figures. The exceptions are the osteoderms from the lateral region closer to the lateral border and the osteoderms from the posterior border, which bear a main figure. In contrast, the variation in the external ornamentation of osteoderms from the dorsal region of *Glyptotherium* (see Gillette *et al.*, 2016) sometimes allow for easier identification of the section from which they belong.

According to Oliveira *et al.* (2010), the osteoderms of *Glyptotherium* are characterized by rough surfaces, perforated by several small foramina, with shallow main and radial sulci (compared to *Glyptodon*) and eight to nine peripheral figures around a flat main figure (Figure 2A). However, we follow

these authors in restricting our assignment to the generic level, as a specific identification would demand a more extensive revision of the material described so far, an aim well beyond the scope of the present paper.

With regard to *Panochthus*, Porpino *et al.* (2014) denominate the small polygonal figures present in osteoderms as small, when not associated with a main figure, and peripheral when associated with them (*e.g.* osteoderms located close to the lateral border of the carapace; Figure 2B). As mentioned earlier, in addition to osteoderms from the dorsal and lateral regions, we also described osteoderms that bear probable signs of pathological alteration (see discussion); these specimens do not exhibit the characteristic external ornamentation pattern of *Panochthus* or show residues of it but were found in association with the remaining osteoderms and the partial carapace of this genus (see above). The inclusion of these specimens was motivated by their similarity with some material assigned to *Neuryurus* in previous works (especially Zurita & Ferrero, 2009) and with the carapace material of *Panochthus* showing pathological alteration described by Barbosa & Luna (2014).

For the histological description of the osteoderms, we follow the terminology employed by Hill (2006), Wolf *et al.* (2012) and Pereira *et al.* (2014). All of these studies agree that the cingulate osteoderms present a general “*diplöe-like*” structure, which consists of a central region of trabecular bone positioned between a superficial and a deep layer of compact bone (Figure 2C).

Preparation of the histological sections

The paleohistological thin sections analysed in this study were prepared in the Laboratório Geológico de Processamento de Amostras da Faculdade de Geologia da Universidade do Estado do Rio de Janeiro (UERJ). Initially, the osteoderms were sectioned along their sagittal plane

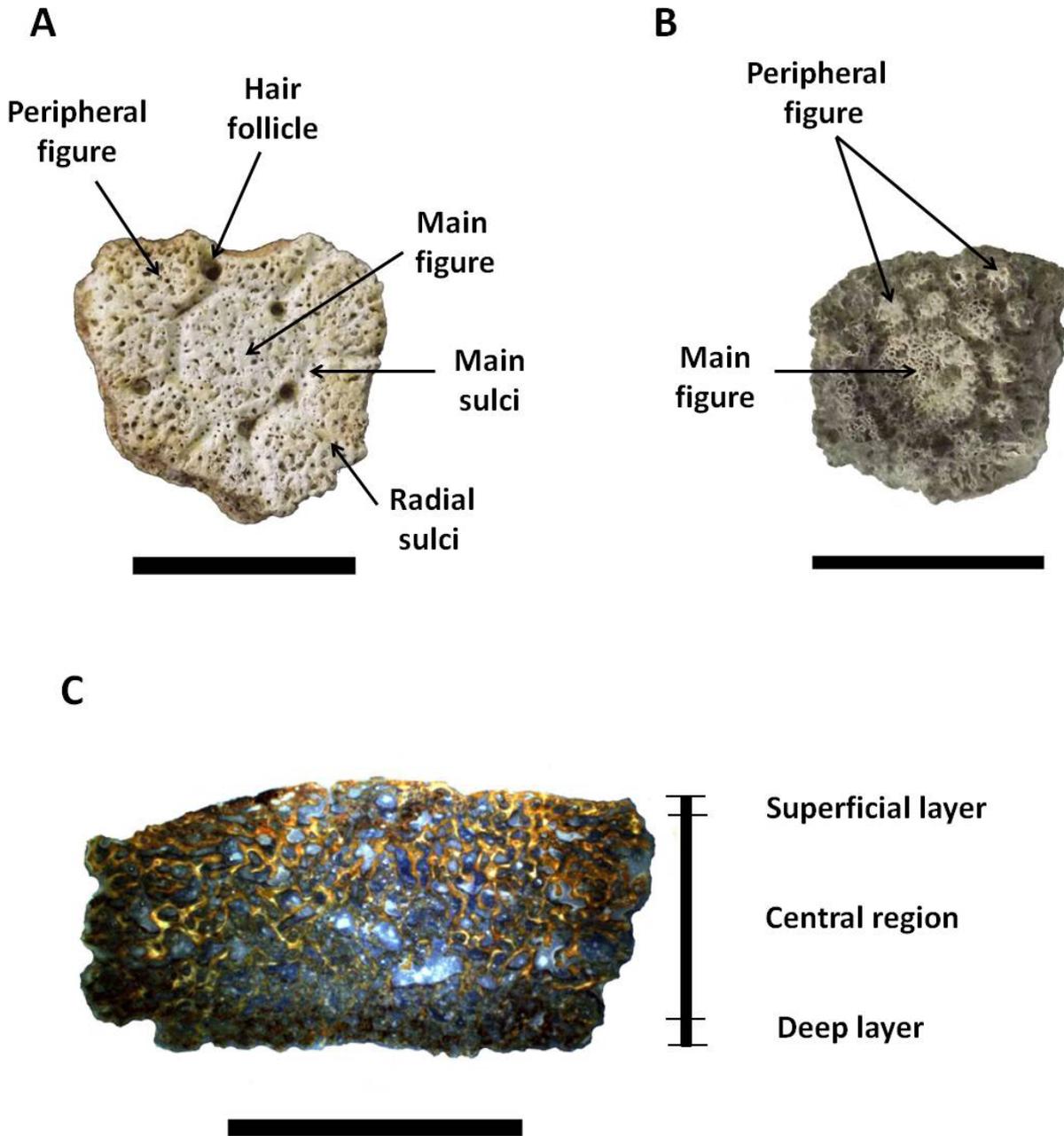


Figure 2. Terminology used for the osteoderms of *Glyptotherium* sp. osteoderms (A); *Panochthus* sp. (B) and histological terminology (C). Scale bars: A = 40 mm; B = 30 mm; C = 20 mm.

with a diamond cut-off saw, and then the sections obtained were imbedded in epoxy resin, with hardener HY951 in a 10:1 mL proportion to provide consistency and to prevent fractures. Then, the specimens were dried for 24 h. After the drying, the blocks formed by the osteoderms sections embedded into the resin were sectioned again to attain the proper size to be included in glass slides, where they were polished in 320 to 600 grit carbide sandpaper until attaining the ideal thickness for visualization under an optic microscope. The thin sections were examined using a petrographic microscope.

SYSTEMATIC PALAEONTOLOGY

Suborder GLYPTODONTIA Ameghino, 1889
 Superfamily GLYPTODONTOIDEA Gray, 1869
 Family GLYPTODONTIDAE Gray, 1869
 Subfamily GLYPTODONTINAE Gray, 1869

Glyptotherium Osborn, 1903

Glyptotherium sp.
 (Figures 3–8)

Material analysed. Osteoderms: MCC 1234-V, MCC 2601-V, MCC 2579-V, MCC 2092-V, MCC 2593-V, MCC 2096-V, MCC 2328-V and MCC 2585-V.

Osteoderms from the mid-dorsal section (dorsal region) of the carapace. Referred material: MCC 1234-V (length = 53.1 mm; width = 22.12 mm; thickness = 23.5 mm), MCC 2601-V (57.94 × 43.18 × 21.77 mm), MCC 2579-V (72.66 × 49.05 × 19.56 mm) and MCC 2092-V (50.94 × 46.05 × 21.14 mm).

Morphological description. The osteoderms are pentagonal to nearly hexagonal, with a very rough external surface, and a circular main figure surrounded by seven to eight peripheral figures; three to five hair follicle pits are observed in the confluence of the main and radial sulci (Figures 3A, C, E and G). Their internal surface is smooth, flat to gently convex, with zero to three small neurovascular foramina (Figures 3B, D, F and H). The specimen MCC 2579-V shows some small signs of bone remodelling; its main figure is poorly delimited, the sulci are barely visible and there is extensive erosion on nearly 1/3 of its internal surface, where the trabecular tissue is exposed.

Histological description. Overall, the osteoderms show parallel fibre bundles in the deep layer, although in some points, small sets of fibres without clear orientation are

observed as well as osteocytes and primary osteons (Figures 4A and B). Towards the central region of trabecular bone, there are resorption areas filled with iron oxide (Figures 4C and D), which occupy this entire region and stretch until the lower limits of the superficial layer of compact bone. In addition, this central region also presents some primary and secondary osteons (Figures 4E and F). Near the superficial layer of compact bone, fibre bundles with varied orientations appear; at some points, these fibres have a somewhat oblique orientation. The superficial layer of compact bone shows several osteocytes and fibre bundles, most of which are oriented parallel to the external surface (Figures 4G and H); some primary and secondary osteons, as well as a few resorption areas, are also present.

Osteoderms from the lateral region. Referred material: MCC 2593-V (42.37 × 36.83 × 19.24 mm) and MCC 2096-V (55.59 × 46.54 × 22.28 mm).

Morphological description. The osteoderms of the lateral region differ from the dorsal region in that they have a more hexagonal-rectangular to clearly rectangular shape (Figures 5A and C). Their external surfaces have small foramina and a rough aspect, like in the dorsal osteoderms, a well-delimited central figure surrounded by eight to nine peripheral ones,

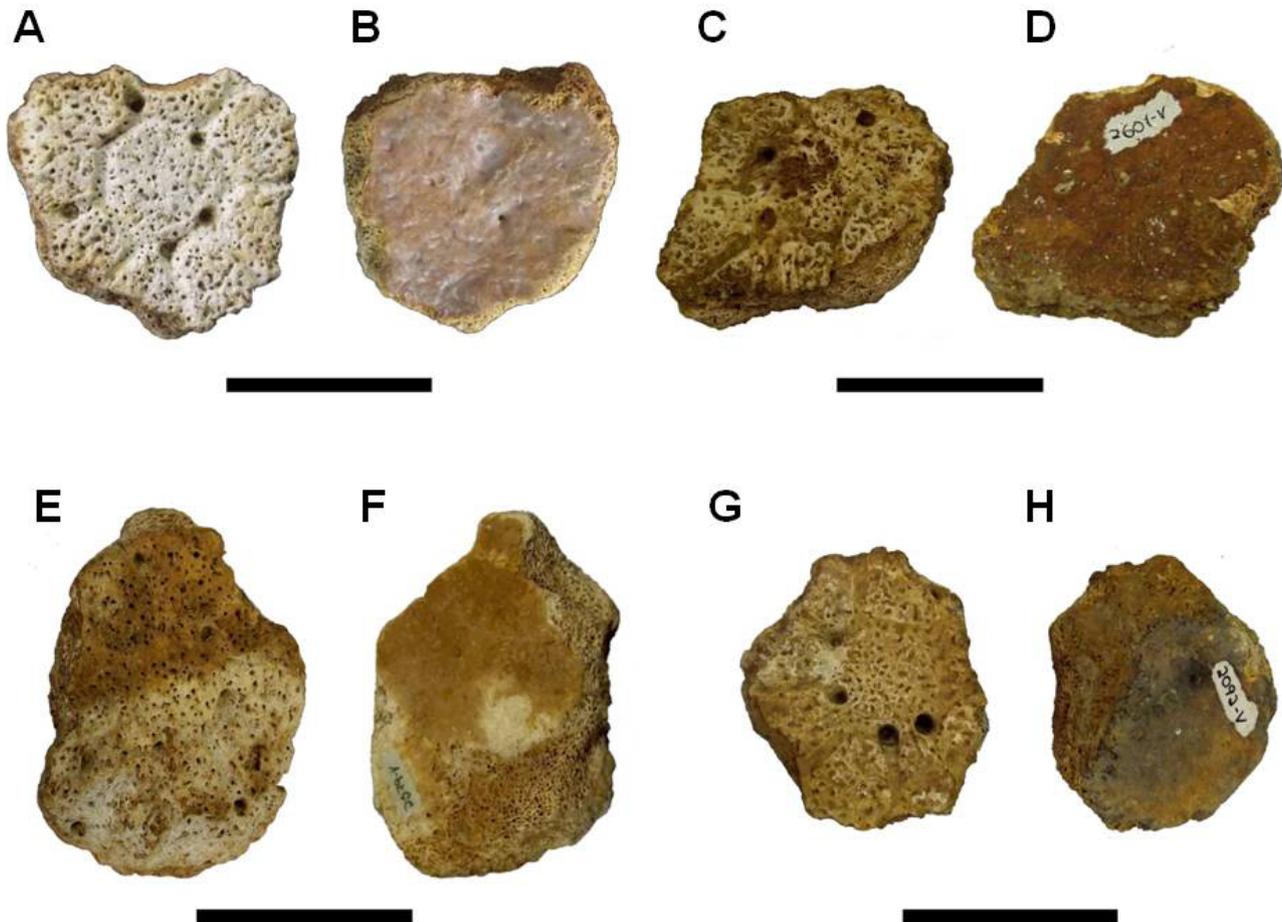


Figure 3. Osteoderms from the dorsal region of *Glyptotherium* sp.: MCC 1234-V in external (A) and in internal (B) views; MCC 2601-V in external (C) and in internal (D) views; MCC 2579-V in external (E) and internal (F) views; MCC 2092-V in external (G) and internal (H) views. Scale bars = 40 mm.

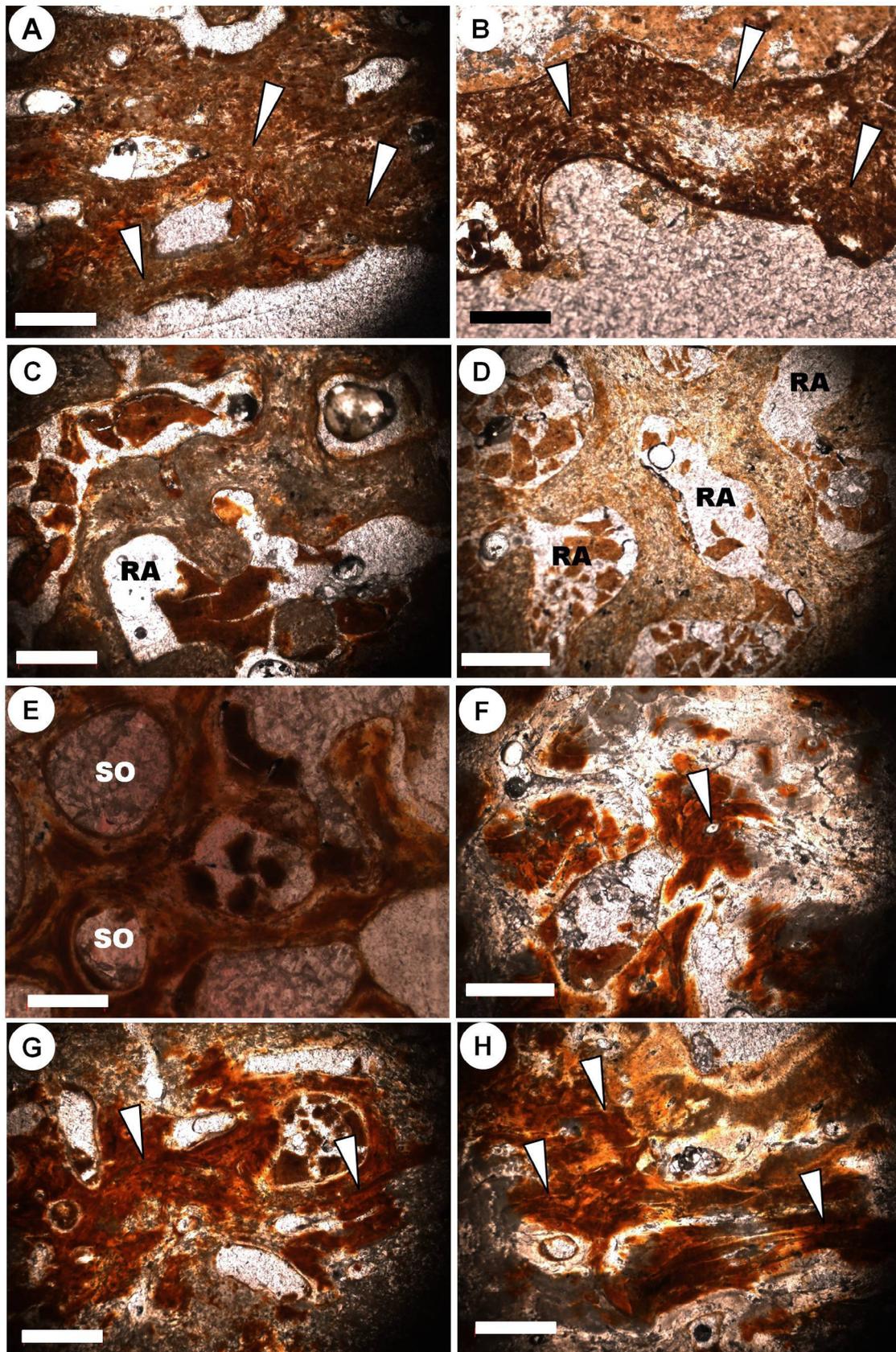


Figure 4. Histological sections of osteoderms from the dorsal region of *Glyptotherium* sp.: **A**, fibre bundles aligned parallel to the deep layer of compact bone on MCC 1234-V (white arrows); **B**, fibre bundles aligned parallel to the deep layer of compact bone in MCC 2579-V; **C**, resorption area in the central region of MCC 2601-V; **D**, resorption areas in the central region of MCC 1234-V; **E**, secondary osteons in the central region of MCC 2579-V; **F**, primary osteon in the compact surface layer of MCC 2601-V (white arrow); **G**, fibre bundles aligned parallel to the compact surface layer of MCC 1234-V (white arrows) and **(H)** osteoderm MCC 2579-V (white arrows). **Abbreviations:** RA, reabsorption area; SO, secondary osteon. Scale bars = 200 µm.

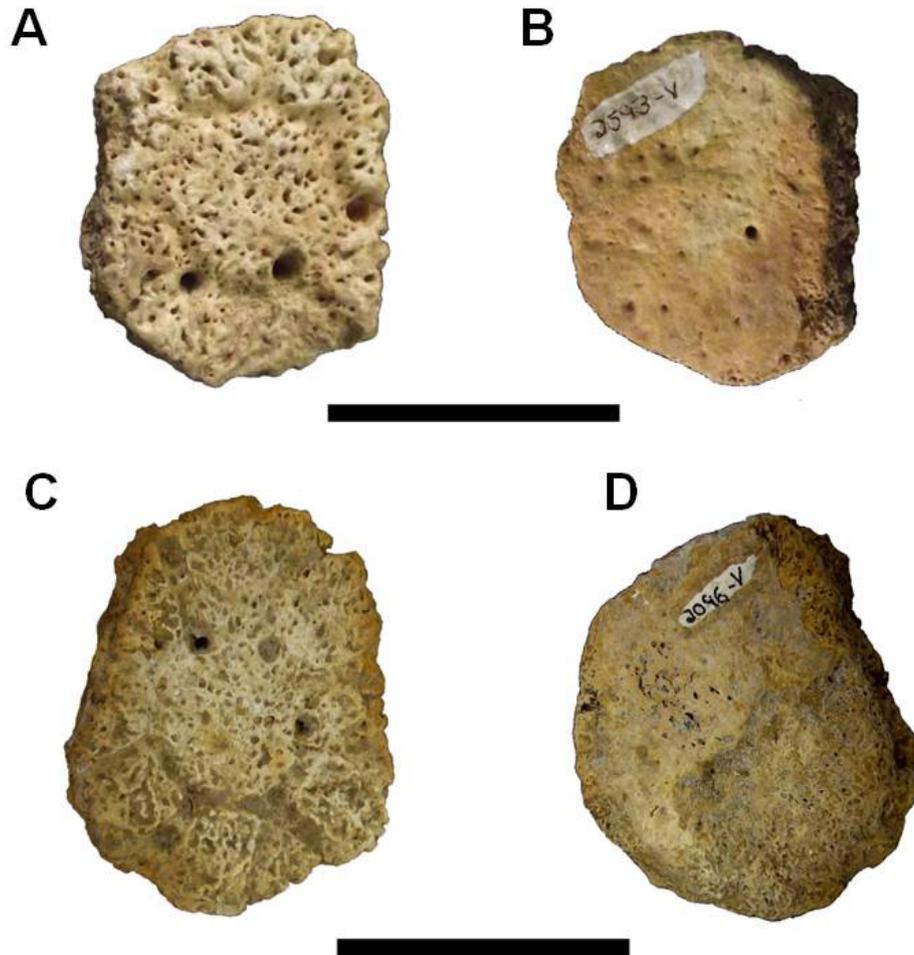


Figure 5. Osteoderms from the lateral region of *Glyptotherium* sp.: MCC 2593-V in external (A) and in internal (B) views; MCC 2096-V in external (C) and in internal (D) views. Scale bars: A–B = 30 mm; C–D = 4 cm.

and three hair follicle pits at the intersection of the main and radial sulci. Their internal surface is smooth to gently convex, with up to nine neurovascular foramina (Figure 5B), although they may be absent (Figure 5D). The specimen MCC 2096-V has an eroded area that occupies nearly half of the internal surface where the trabecular bone is exposed.

Histological description. The deep layer of compact bone has fibre bundles, most of which have an orientation parallel to the external surface; in this layer, there are several osteocytes and primary and secondary osteons randomly distributed (Figures 6A and B). The central region shows several resorption areas, osteocytes and secondary osteons (Figures 6C and D). The superficial layer of compact bone, in most cases, presents obliquely oriented fibre bundles, but some have a parallel orientation; some osteocytes, in addition to primary and secondary osteons, are present in this layer (Figures 6E and F).

Osteoderms of the posterodorsal section near the posterior border of the carapace. Referred material: MCC 2328-V (50.50 × 45.31 × 36.48 mm) and MCC 2585-V (44.80 × 41.17 × 37.97 mm).

Morphological description. These osteoderms differ from those in the lateral and mid-dorsal section in that they are

pentagonal and have an external surface without discernible figures. In addition, there is a well-marked depression at the centre of their external surface, which is strongly perforated by foramina and very rough (Figures 7A and C). In one of the lateral borders of specimen MCC 2585-V, there is a well-developed hair follicle pit filled with sediment (Figure 7C). The internal surface varies from smooth to slightly convex, or slightly concave in some points in specimen MCC 2585-V (Figures 7B and D), and there are two to nine neurovascular foramina.

Histological description: The superficial compact bone layer bears fibre bundles with mostly oblique orientations, although some regions present varied orientations (Figures 8A and B), as well as several osteocytes, some primary osteons and resorption areas. In the central region, resorption areas are abundant, showing the long axis in the sagittal plane, and most filled with iron oxide; there are some osteocytes and secondary osteons in this region as well (Figures 8C and D). The superficial layer of compact bone shows fibre bundles oriented obliquely (Figures 8E and F), although in some places they are oriented parallel to the external surface; osteocytes and secondary osteons are scarce in this layer.

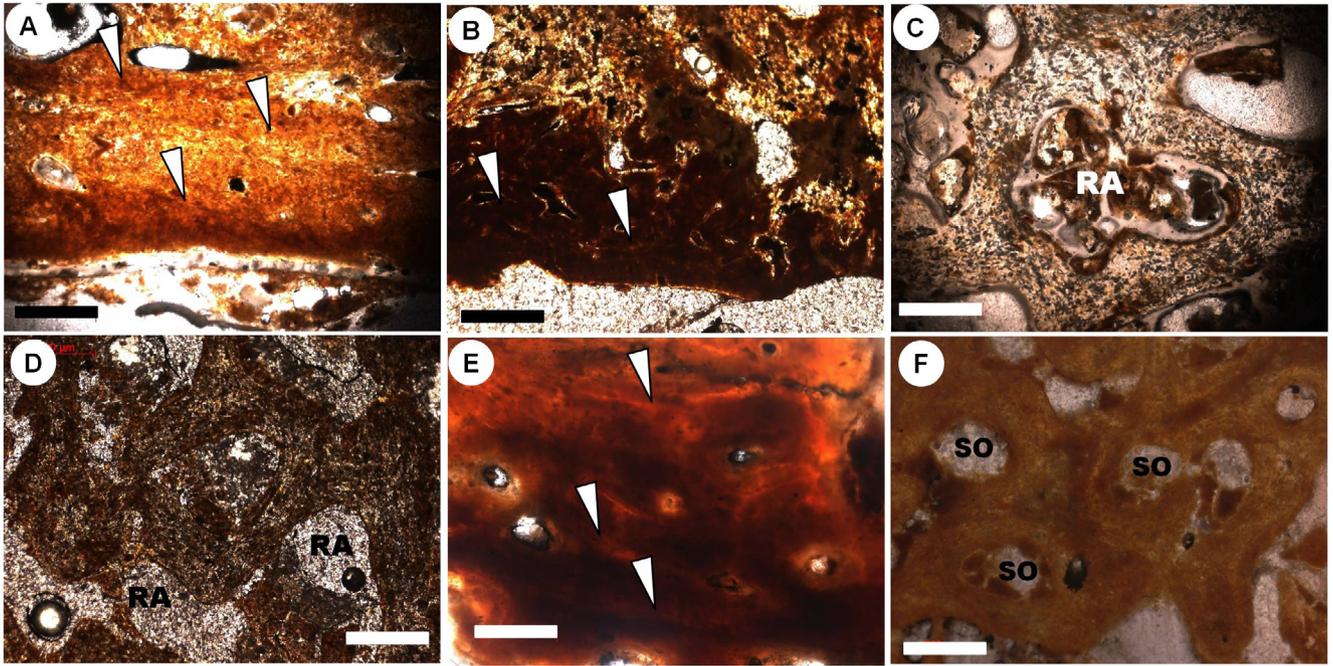


Figure 6. Histological sections of osteoderms from the lateral region of *Glyptotherium* sp.: **A**, fibre bundles in the deep layer of compact bone in MCC 2593-V (white arrows); **B**, fibre bundles with parallel alignment in the compact deep layer of MCC 2096-V (white arrows); **C**, resorption area in the central region of MCC 2593-V; **D**, resorption areas in the central region of MCC 2096-V; **E**, fibre bundles with parallel alignment in the layer of compact surface in MCC 2593-V (white arrows); **F**, secondary osteons in the compact surface layer of MCC 2096-V. **Abbreviations:** RA, reabsorption areas; SO, secondary osteons. Scale bars = 200 µm.

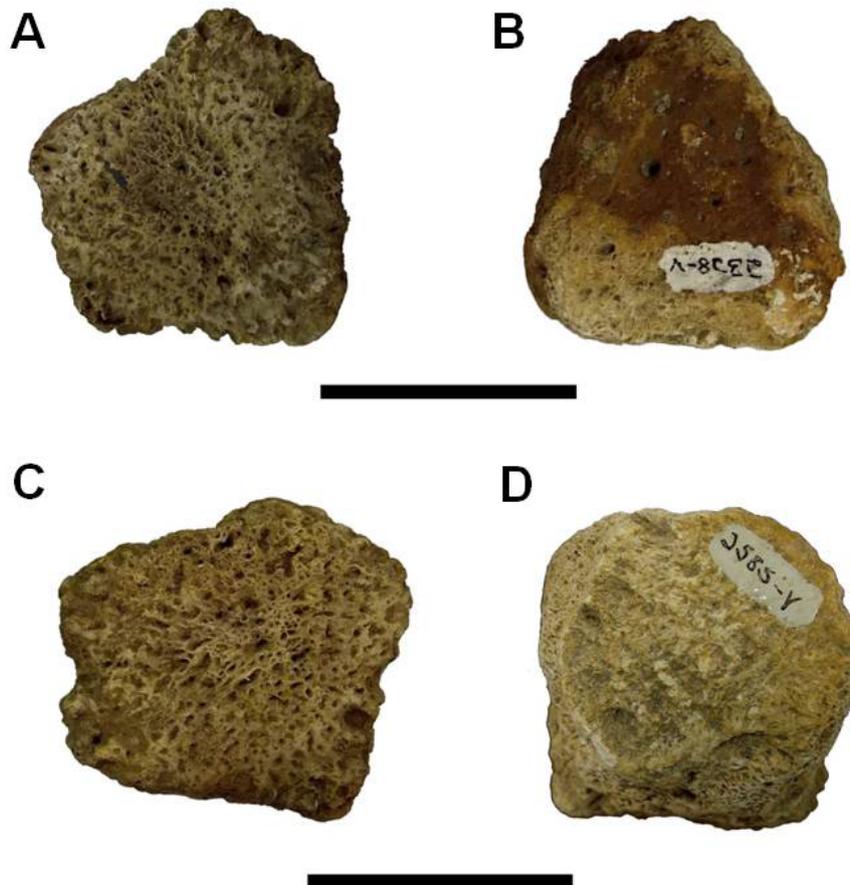


Figure 7. Osteoderms from the region near the posterior border of the *Glyptotherium* sp. carapace: MCC 2328-V in external (**A**) and internal (**B**) views; MCC 2585-V in external (**C**) and in internal (**D**) views. Scale bars = 40 mm.

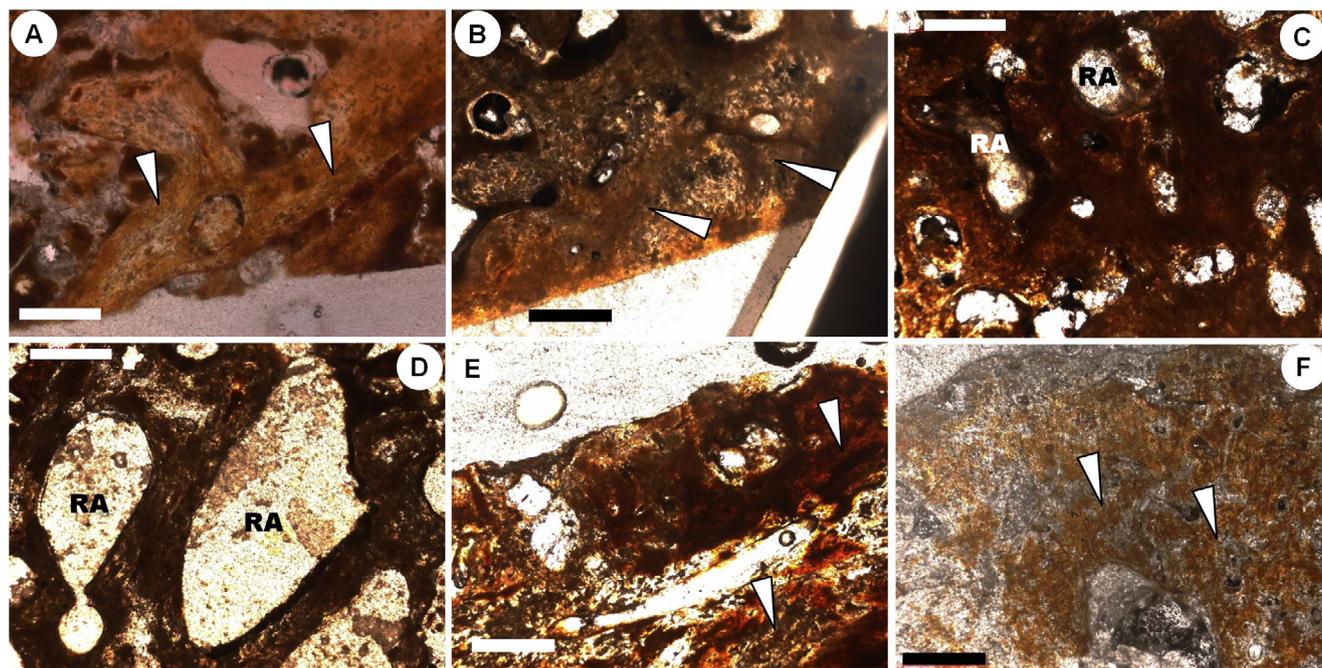


Figure 8. Histological sections of osteoderms located near the posterior border of the *Glyptotherium* sp. carapace: **A**, fibre bundles aligned obliquely in the deep compact bone layer of the MCC 2328-V (white arrows); **B**, fibre bundles aligned obliquely in the compact surface layer of MCC 2585-V (white arrows); **C**, resorption area in the central region of the MCC 2328-V; **D**, resorption area in the central region of MCC 2585-V; **E**, fibre bundles aligned obliquely in MCC 2328-V (white arrows); **F**, fibre bundles in the MCC 2585-V surface compact layer (white arrows). **Abbreviation:** RA, resorption areas. Scale bars = 200 µm.

Family PANOCHTHIDAE Castellanos, 1927
Subfamily PANOCHTHINAE Burmeister, 1866

Panochthus Burmeister, 1866

Panochthus sp.
(Figures 9–14)

Material analysed. Osteoderms: MCC 1616-V, MCC 3254-V, MCC 3255-V, MCC 3256-V, MCC 3257-V, MCC 3258-V, MCC 3259-V, MCC 3660-V, MCC 3261-V and MCC 3262-V.

Osteoderm from the dorsal region. Referred material: MCC 3259-V (length = 60.84 mm; width = 55.97 mm; thickness = 22.70 mm).

Morphological description. The osteoderm of the dorsal region here analysed is nearly hexagonal, with a badly eroded surface, showing signs of abrasion (*e.g.* rounded edges; Figure 9A). The internal surface shows depressions converging to the centre of the specimen, with 17 neurovascular foramina, most of which are in the centre of this region (Figure 9B).

Histological description. The deep layer of compact bone shows most of the fibre bundles obliquely aligned, and some resorption areas and several osteocytes are also present (Figure 10A). Towards the central region, the amounts of resorption areas –which are vertically elongated – gradually increase. In addition to the reabsorptions areas (Figure 10B), the central region is also characterized by a high number of osteocytes and fibre bundles with varied orientations and some secondary osteons. Towards the superficial layer of compact

bone, the number of reabsorption areas diminishes, while osteocytes and primary osteons increase; in this superficial layer, the fibre bundles are obliquely aligned (Figure 10C).

Osteoderms from the lateral region. Referred material: MCC 3258-V (47.44 × 35.76 × 19.80 mm), MCC 3255-V (36.07 × 35.48 × 22.44 mm), MCC 3660-V (39.05 × 29.42 × 23.00 mm), MCC 3257-V (32.93 × 35.29 × 23.31 mm).

Morphological description. The osteoderms vary from roughly hexagonal to rectangular. Their external surface is rough, with small polygonal figures (Figures 11A and E) or with a circular main figure surrounded by seven to eight small figures (peripheral figures; Figures 11C and G); the latter are osteoderms close to the lateral border. The internal surface of all of the osteoderms are smooth to gently convex (not discernible in MCC 3255-V due to extensive erosion) and, when present, the neurovascular foramina are few (one to two) (Figures 11B, D, F and H).

Histological description. In the deep layer of compact bone, most fibre bundles are parallel in alignment (Figure 12A); in this layer, there are several osteocytes and primary and secondary osteons (Figure 12B). Towards the central region, the fibre bundles have varied orientations, and small resorptions areas become common. In the central region, these reabsorptions areas are abundant (Figure 12C), larger and horizontally elongated; some osteocytes and primary and secondary osteons are also observed (Figure 12D). Towards the superficial layer of compact bone, parallel fibre bundles appear (Figure 12E), although in some portions they are more obliquely oriented; this region also presents

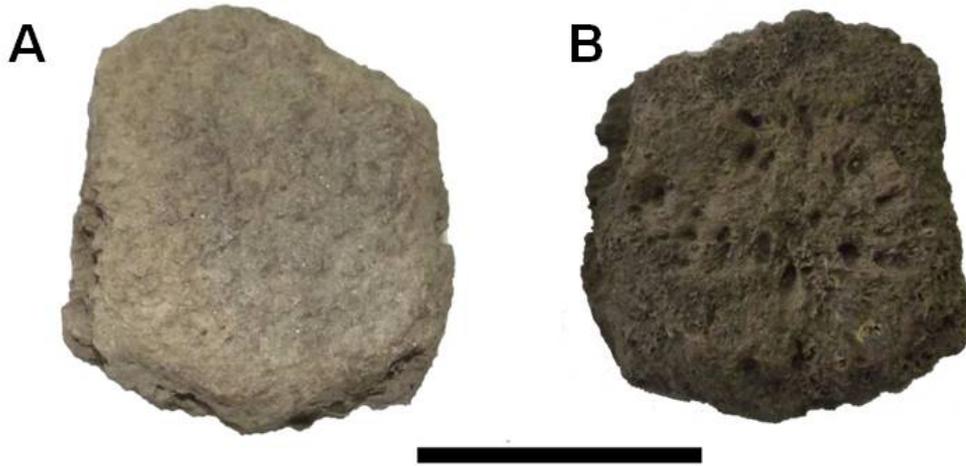


Figure 9. Osteoderms from the dorsal region of the *Panochthus* sp. carapace. MCC 3259-V in external (A) and internal (B) views. Scale bar = 40 mm.

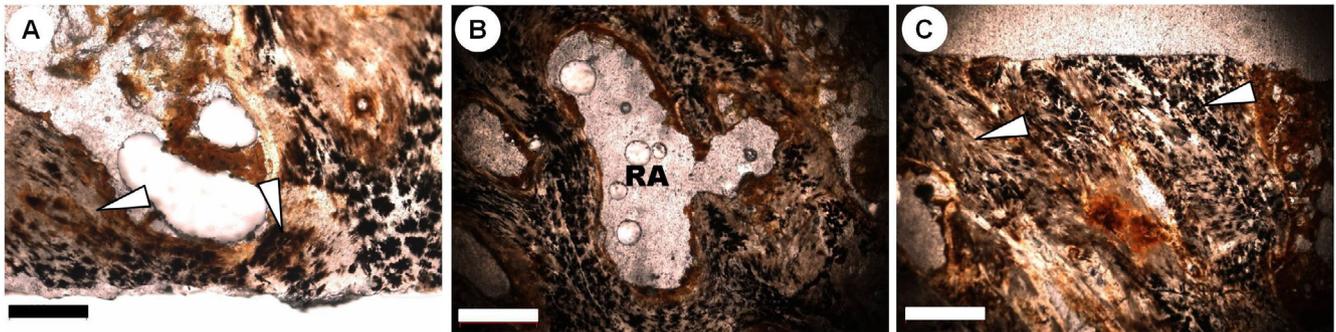


Figure 10. Histological sections of the osteoderms from the dorsal region of the *Panochthus* sp. carapace: A, fibre bundles with oblique alignment in the deep compact bone layer of MCC 3259-V (white arrows); B, resorption areas of in the central region of MCC 3259-V (white arrows); C, fibre bundles with oblique alignment in the compact surface layer of MCC 3259-V (white arrows). **Abbreviations:** RA, resorption areas. Scale bars = 200 μ m.

several osteocytes and some primary and secondary osteons (Figure 12F).

Osteoderms with *ante mortem* alterations. Referred material: MCC 3262-V (43.98 \times 36.69 \times 21.18 mm), MCC 3254-V (38.64 \times 32.33 \times 21.40 mm), MCC 3261-V (40.61 \times 31.97 \times 17.27 mm), MCC 3256-V (38.00 \times 26.20 \times 18.11 mm) and MCC 1616-V (42.27 \times 35.77 \times 21.19 mm).

Morphological description. The osteoderms 3262-V (Figures 13A and B), 3254-V (Figures 13C and D), MCC 3261-V (Figures 13E and F) and MCC 3256-V (Figures 13G and H) are rectangular and likely belong to the lateral region of the carapace; their external surfaces are eroded, with a very porous aspect due to the exposition of trabecular bone. In lateral view, these osteoderms preserve their original serrated morphology. Their internal surfaces are smooth to slightly convex, with several neurovascular foramina, among which one to five foramina are larger. The osteoderm MCC 1616-V (Figures 13I and J) clearly belongs to the posterior border of the carapace, likely from its more lateral sections. It is more quadrangular, with a posteriorly displaced main figure with a rounded outlined along its posterior edge. For the remaining altered osteoderms, their external surfaces are very porous, with an eroded aspect; at the centre of the main figure, there is a very rough depression (Figure 13I). Its internal surface, in turn, is smooth with around

ten neurovascular foramina of different sizes (Figure 13J).

Histological description. Overall, the histology of the altered osteoderms is characterized by a deep layer containing fibre bundles with no discernible preferential direction (Figure 14A), several osteocytes, some primary and secondary osteons (Figure 14B), and some small resorption areas. Towards the central region, there are large resorption areas (Figure 14C), which possess the typical trabecular aspect of this region. In addition, there are some osteocytes, primary and secondary osteons (Figure 14D). Towards the superficial layer of compact bone, the resorption areas diminish in both size and quantity. In the superficial layer, there are several osteocytes, some osteons and resorption areas (Figure 14E) and fibre bundles with no preferential alignment (Figure 14F).

DISCUSSION

All osteoderms evaluated in this paper present a “*diploë-like*” structure, which consists of a central region of trabecular bone sandwiched between superficial and deep layers of compact bone, as in other previously described osteoderms of cingulates (*e.g.* Hill, 2006; Wolf, 2007; Wolf *et al.*, 2012; Pereira *et al.*, 2014; Asakura *et al.*, 2017). In addition, we noted that the specimens studied present extensive bone remodelling,

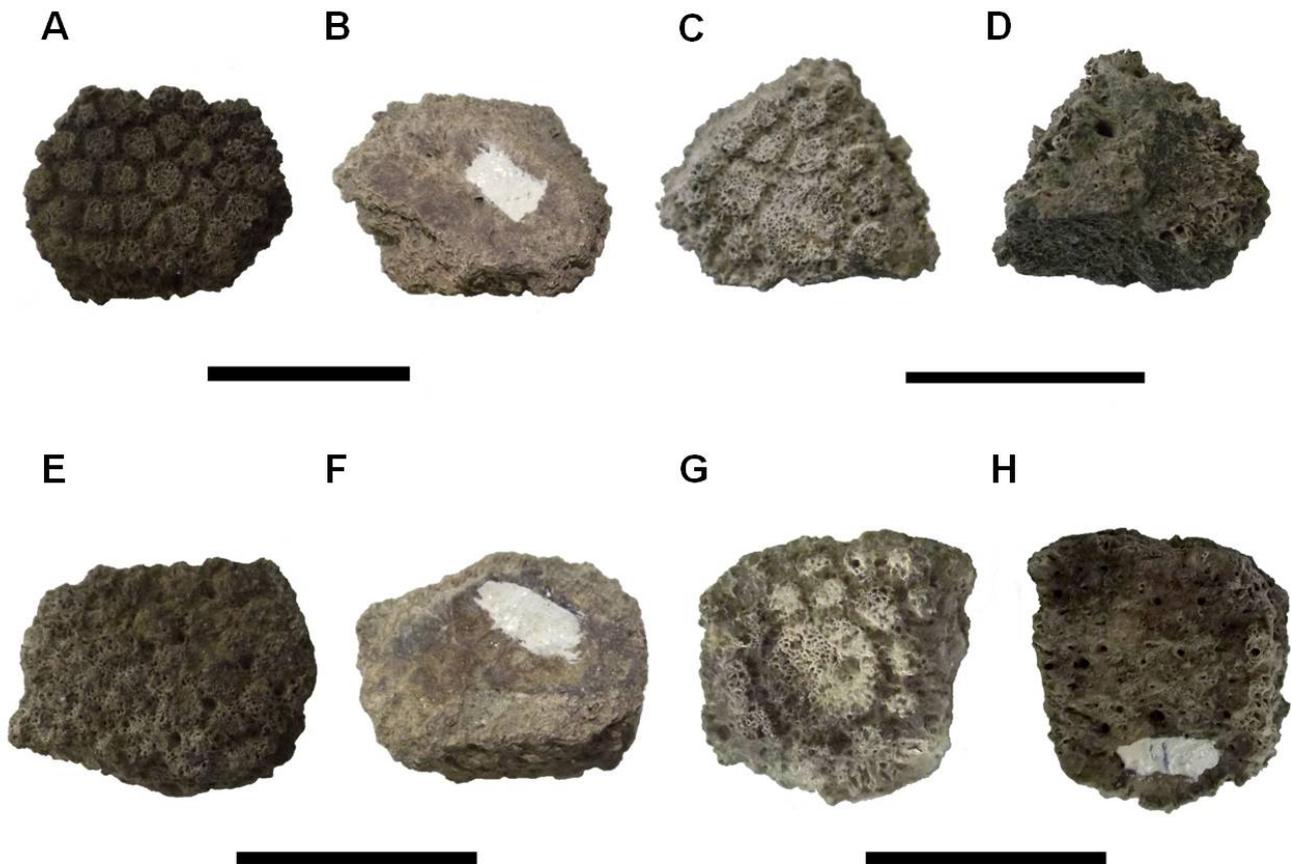


Figure 11. Osteoderms from the lateral region of the *Panochthus* sp. carapace. MCC 3258-V in external (A) and internal (B) views; MCC 3255-V in external (C) and internal (D) views; 3660-V in external (E) and internal (F) views; MCC 3257-V in external (G) and internal (H) views. Scale bars = 30 mm.

which seems a remarkable characteristic of glyptodont osteoderms (Wolf, 2007). Comparing the osteoderms of the genera here analysed, we observe that those of *Glyptotherium* show layers of thicker compact bone than in *Panochthus*, while those of the latter have a more porous aspect.

The osteoderms of *Glyptotherium* sp. here analysed share a central region dominated by a large resorption area, with few primary and secondary osteons. On the other hand, there are differences between the superficial and deep layers of compact bone among osteoderms from different regions of the carapace. Osteoderms from the mid-dorsal section of the dorsal region exhibit fibre bundles with a parallel alignment in both layers of compact bone, while the osteoderms from the lateral region have both parallel and obliquely aligned fibre bundles in the deep and superficial layers, respectively. The osteoderms from the posterodorsal section near the posterior border, in turn, have obliquely aligned fibre bundles in both layers of compact bone.

The specimens from the dorsal region of the *Glyptotherium* sp. studied here (MCC 1234-V, MCC 2601-V, MCC 2579-V, MCC 2092-V) are similar to those analysed by Pereira *et al.* (2014), which are also from the same region of the carapace and study location (Lajedo da Escada). The specimens evaluated here show, in their deep layer of compact bone, fibre bundles with dominantly parallel alignment, some primary and secondary osteons, a central region with several

resorption areas and several osteocytes and secondary osteons; in addition, their superficial layer of compact bone shows fibre bundles with parallel alignment and some osteocytes and osteons. These histological patterns concur with those described by Pereira *et al.* (2014), except for the deep layer of compact bone for which there is no available information regarding the orientation of the fibre bundles in the mentioned paper, precluding a more complete comparison.

The osteoderms from the lateral region and those closer to the posterior border of the carapace show some differences when compared with osteoderms from the dorsal region, as described by Pereira *et al.* (2014). The osteoderms from the lateral region have fibre bundles with parallel and oblique alignment in the deep and superficial layers of compact bone, respectively. The osteoderms from the posterodorsal section near the posterior border of the carapace bear obliquely oriented fibre bundles in both layers. This pattern is different from the osteoderms of the dorsal region (including the one described by Oliveira *et al.*, 2014), which present fibre bundles with parallel alignment in both layers.

Curiously, the osteoderms from the posterodorsal section near the posterior border described here are histologically similar to the *Glyptotherium floridanum* exemplar described by Hill (2006), although they differ from the latter in external morphology because they are not from comparable regions. They share obliquely aligned fibre bundles in the

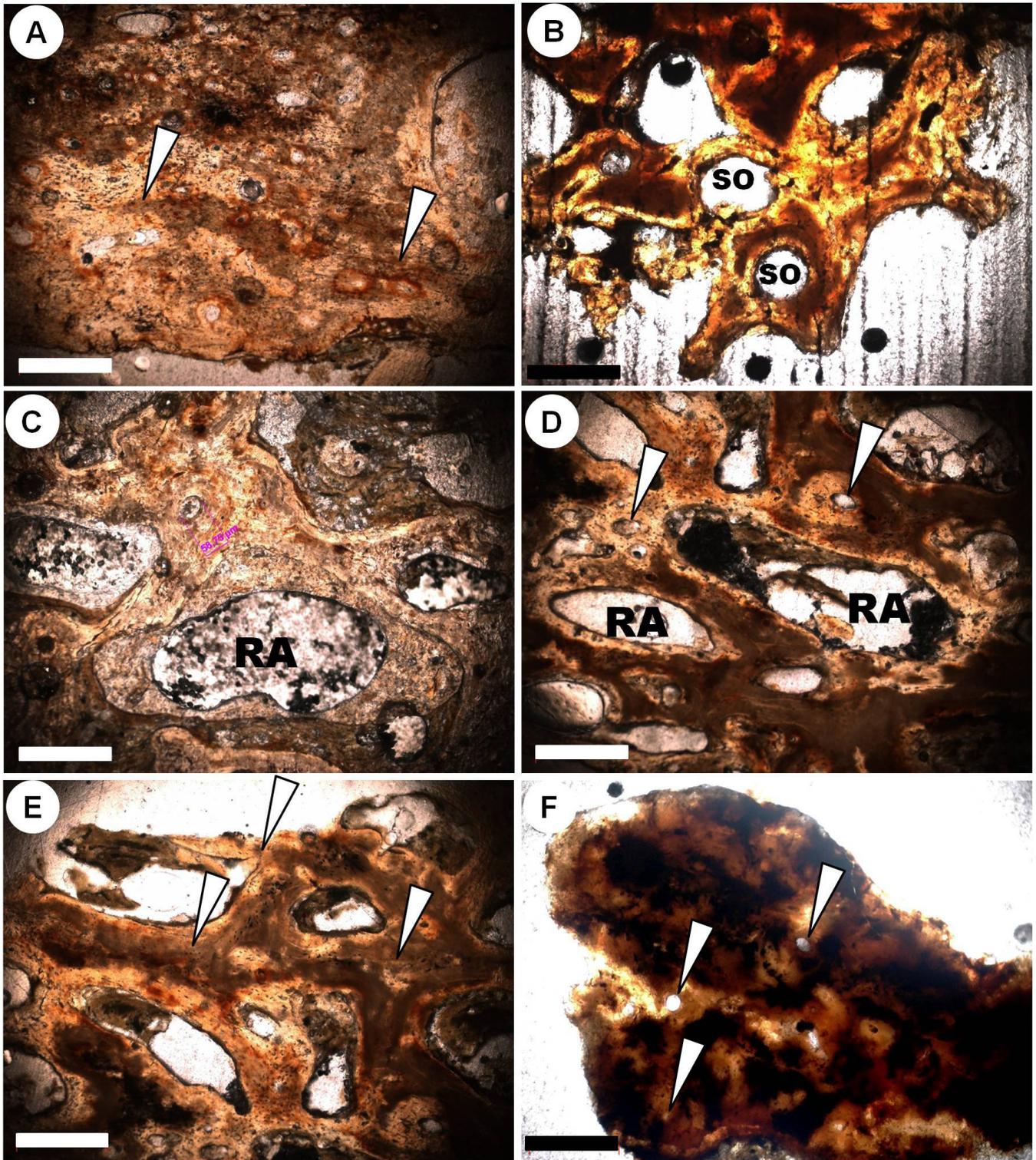


Figure 12. Histological sections of osteoderms from the lateral region of the *Panochthus* sp. carapace. **A**, fibre bundles aligned parallel to the deep compact layer of MCC 3660-V (white arrows); **B**, secondary osteons in the deep compact layer of MCC 3258-V; **C**, resorption areas in the central region of MCC 3255-V (white arrows); **D**, primary osteons in the central region of MCC 3660-V (white arrows); **E**, fibre bundles with parallel alignment in the compact surface layer of MCC 3660-V (white arrows); **F**, primary osteons in the compact surface layer of MCC 3257-V (white arrows). **Abbreviations:** RA, reabsorption areas; SO, secondary osteon. Scale bars = 200 µm.

superficial and deep layers of compact bone, differing only in the number of primary osteons, which are few in the specimens here analysed but copious in the specimens described by Hill (2006). These results suggest caution

when searching for histological characters useful for taxonomic decisions and phylogenetic inference based on isolated osteoderms, especially when no carapace positional information is available.

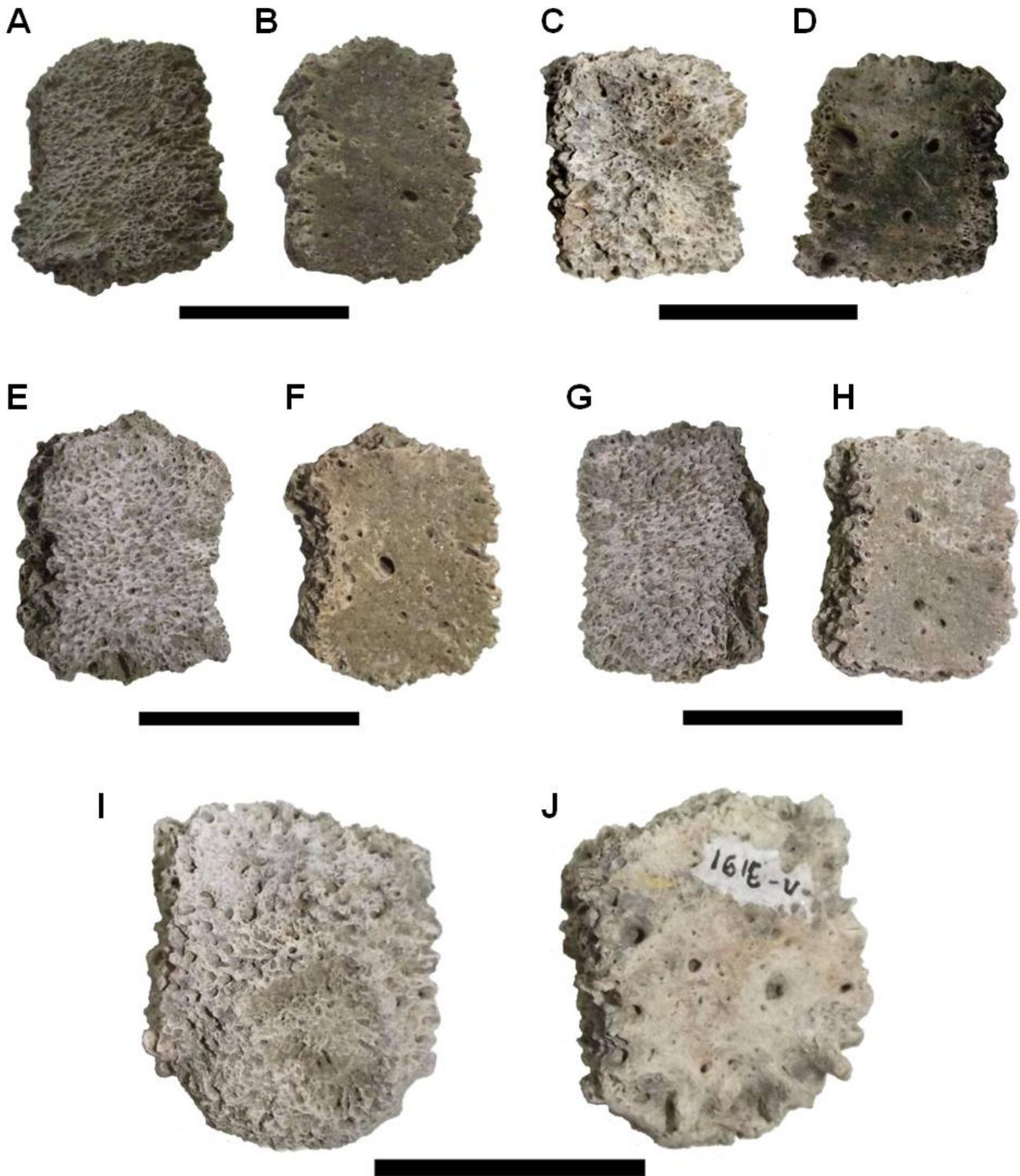


Figure 13. Altered osteoderms of *Panochthus* sp. MCC 3262-V in external (A) and internal view (B); MCC 3254-V in external (C) and internal (D) views; MCC 3261-V in external (E) and internal (F) views; MCC 3256-V in external (G) and internal (H) views; MCC 1616-V from the posterior border in external (I) and in internal (J) views. Scale bars = 30 mm.

A comparison between the osteoderms of *Glyptotherium* described here and the osteoderm of *Glyptodon reticulatus* studied by Hill (2006) shows that the exemplars of the former taxon do not exhibit the coexistence of fibre bundles without discernible or perpendicular alignment in the deep and superficial layers, respectively, in contrast to *G. reticulatus*. This

difference offers additional potential evidence to differentiate *Glyptotherium* and *Glyptodon* in addition to the macroscopic distinctive characters (see, for example, Oliveira *et al.*, 2010) and concurs with Oliveira *et al.* (2010) and Pereira *et al.* (2014) in assigning the Glyptodontinae specimens of the Lajedo da Escada Site to *Glyptotherium* rather than *Glyptodon*.

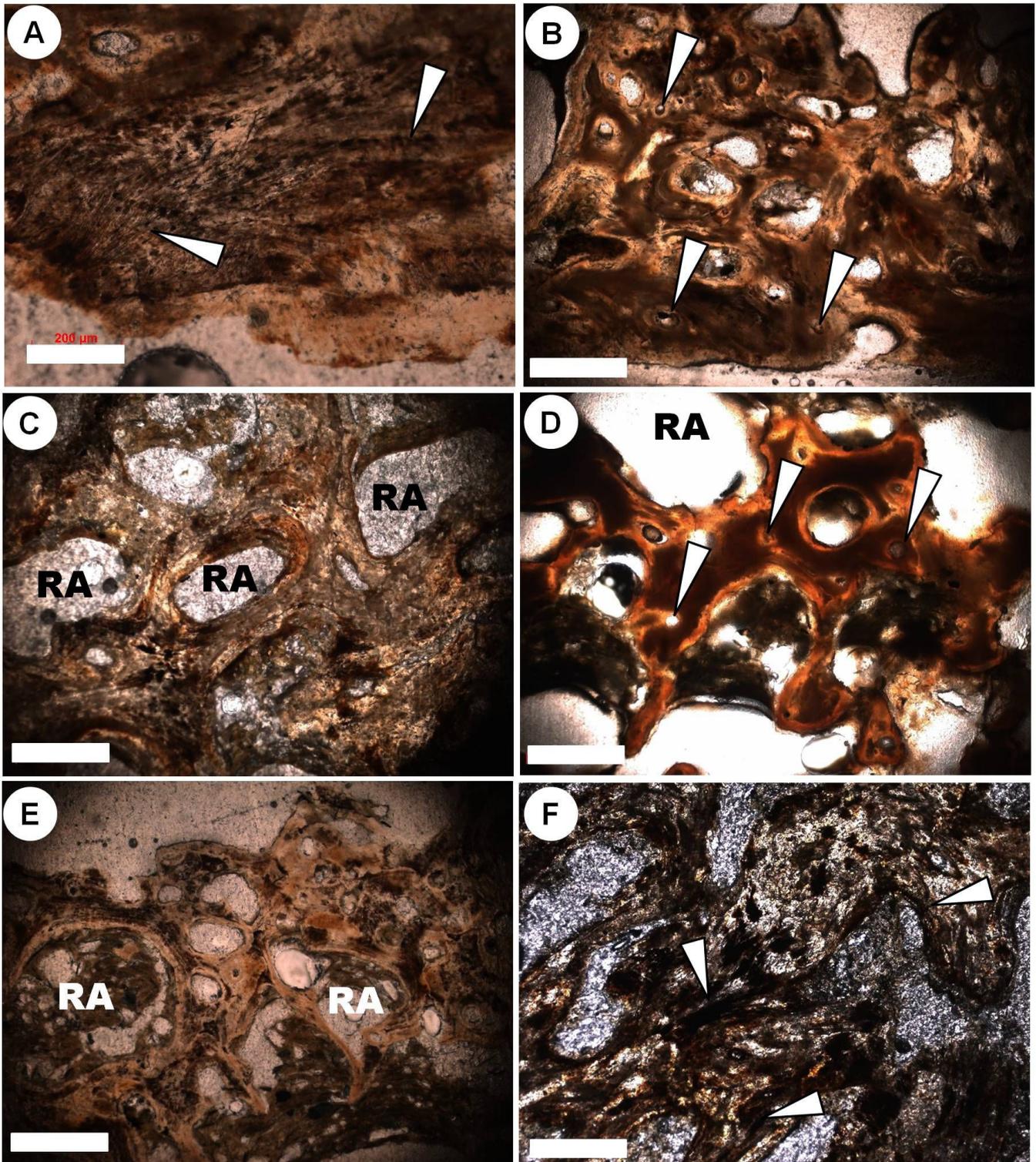


Figure 14. Histological sections of the altered osteoderms of *Panochthus* sp. **A**, Fibre bundles with no preferential alignment in the deep compact layer of MCC 3262-V (white arrows); **B**, primary osteons in the deep compact layer of MCC 3261-V (white arrows); **C**, resorption areas in the central region of osteoderm MCC 3254-V; **D**, primary ossicles in the central region of MCC 3256-V (white arrows); **E**, resorption areas in the superficial compact bone layer; **F**, fibre bundles without preferential alignment in the compact surface layer of MCC 3256-V. **Abbreviations:** RA, reabsorption areas; SO, secondary osteon. Scale bars = 200 μ m.

With regard to the inferred closer affinity among *Glyptotherium*, *Doedicurus* and *Glyptodon*, which form the Glyptodontinae clade (sensu Fernicola, 2008; see also Fernicola & Porpino, 2012), we observed that the *Glyptotherium* osteoderms described here and the *Doedicurus*

and *Glyptodon* osteoderms previously described (e.g. Hill, 2006) share a markedly remodeled central region with several large resorption areas, in contrast to *Panochthus* (Hill, 2006; Pereira *et al.*, 2014; this work). This observation provides potential new evidence supporting this clade.

All osteoderms for *Panochthus* described here share a central region with several horizontally elongated resorption areas, bearing some osteocytes and primary and secondary osteons. The altered osteoderms (including the one from the posterior border) are histologically very similar in that they have superficial and deep compact bone layers with fibre bundles without preferential orientation. However, the osteoderms from the dorsal and lateral regions show differences when their compact bone layers (superficial and deep) are compared. Most of the fibre bundles of specimen MCC 3259-V (dorsal region) are obliquely oriented, while the osteoderms of the lateral region have fibre bundles aligned parallel to the external surface.

The osteoderm from dorsal region 3259-V shares some characters with the *Panochthus frenzelianus* exemplar described by Hill (2006), which is also likely from the same region of the carapace, including fibre bundles in the deep layer of compact bone that are mostly obliquely oriented and a central region with a great amount of resorption areas. Conversely, the superficial compact bone layer in MCC 3259-V shows fibre bundles with oblique alignment rather than parallel, as in *P. frenzelianus* (Hill 2006). This difference may indicate a possible interspecific variation that could be useful in distinguishing these species, considering that the coexistence of parallel and obliquely aligned fibre bundles in the superficial and deep layers of compact bone as described for the specimens of *P. frenzelianus* in Hill (2006) was not observed in any of the *Panochthus* sp. osteoderms described here.

Curiously, MCC 3259-V shows differences with respect to the osteoderm from the dorsal region described by Pereira *et al.* (2014), which is from the same deposit. The exemplar described by Pereira *et al.* (2014) has parallel fibre bundles in both the superficial and deep layers of compact bone, in contrast to the pattern observed in MCC 3259-V, in which the fibre bundles are obliquely aligned in both layers. Surprisingly, the histological pattern of MCC 3259-V is very similar to that of specimen MCC 1089-V described by Pereira *et al.* (2014), which is likely a fragment of the cephalic shield found in the same deposit (see Porpino *et al.*, 2014). Both show obliquely aligned fibre bundles in the superficial and deep layers of compact bone and a central region with a less porous aspect and smaller resorption areas, compared to other osteoderms of *Panochthus* sp. described here and in Pereira *et al.* (2014). This observation implies that the histological pattern for distinct parts of the exoskeleton (*i.e.* a carapace and cephalic shield), at least in this genus, may coincide in some instances, even if their external morphology is strikingly different.

In regard to the histological pattern of the osteoderms with *ante mortem* alterations, we noted that they share several features such as fibre bundles without preferential alignment, few osteocytes and osteons in the deep and superficial layers of compact bone, and a highly porous central region with great resorption areas. It is possible that the fibre bundles lack a discernible orientation in the more superficial parts of these specimens due to the erosive process that eroded their surfaces, creating a more rough and porous aspect (Barbosa &

Luna, 2014). In fact, these erosive processes may have eroded most of the superficial layer of compact bone, exposing, in the most superficial areas of the osteoderms, the intermediate zone (observed in the remaining osteoderms of *Panochthus* described here) just below the superficial compact layer, which is characterized by fibre bundles with no preferred alignment (Pereira *et al.*, 2014).

The osteoderms of *Panochthus* sp. recently described by Asakura *et al.* (2017) are histologically similar to the osteoderms of the lateral region of this genus described here, in that they have superficial and deep layers of compact bone with fibre bundles that have a parallel orientation and few osteons. In addition, they also share a porous central region, with great resorption areas. In comparison to the osteoderms described here from the dorsal region and the altered ones, the osteoderms described by Asakura *et al.* (2017) show some differences, part of which may be due to alteration (in the case of the altered ones). However, the differences observed with regard to the non-altered osteoderms described here is difficult to ascertain because a) Asakura *et al.* (2017) did not specify the region of the carapace from which the osteoderms they study come from; and b) there is currently no sound basis in assigning isolated osteoderms to the species of *Panochthus* occurring in the Brazilian Intertropical Region (*i.e.* *P. greslebini* and *P. jaguaribensis*) unless, as stated earlier, a clear association between isolated specimens with caudal tubes (or parts of the caudal tube preserving the diagnostic characters) is clearly established (see Porpino *et al.*, 2014).

Curiously, the histological organization described by Asakura *et al.* (2017) for specimens of *Neuryurus* sp., including fibre bundles with no preferred orientation in the superficial and deep layers of compact bone and a central region with elongated resorption areas, is similar to that of specimens bearing *ante mortem* alterations described here, although the description offered by those authors is not equally detailed for all specimens they studied. The altered specimens of *Panochthus* sp. described here do not show the typical external ornamentation pattern of the genus due to an extensive erosive process that gave their external surfaces a very rough aspect, and several foramina (likely representing the trabecular tissue exposure). At first glance, this rough and porous aspect bears a resemblance to the external surface of *Neuryurus* osteoderms, which are characterized by the absence of polygonal figures and by the presence of several foramina (Ameghino, 1889; Zurita *et al.*, 2006; Zurita & Ferrero, 2009). It is worth noting, however, that the altered osteoderms of *Panochthus* studied here were found in association with the partial carapace MCC 1603V, as stated above (see Oliveira *et al.*, 1984; Porpino *et al.*, 2014, fig. 5G). The specimen MCC 1603 bears osteoderms with the diagnostic external ornamentation pattern of the genus, but show, in some parts, osteoderms with eroded ornamentation alongside osteoderms with intact ornamentation (like in the carapace described by Barbosa & Luna, 2014). Therefore, it is more parsimonious to infer that the altered osteoderms described here belong to *Panochthus* and are likely part of this mentioned carapace rather than to *Neuryurus*. This conclusion

is reinforced by the fact that there is no additional evidence of the latter genus in the deposit from which the material was collected (e.g. osteoderms of the caudal armor, which are clearly distinct from the homologous elements of *Panochthus*; see, for instance, Ameghino, 1889, pl. LXI).

In addition, when we compared the ornamentation pattern of the *Neuryurus rudis* (the type-species of *Neuryurus*) osteoderms figured by Ameghino (1889), those of a partial carapace of *Neuryurus* sp. described by Zurita *et al.* (2006) and the one figured by Asakura *et al.* (2017) with the altered osteoderms described here, we noted that, despite some similarities, the latter presents a much rougher external aspect with larger foramina that resemble the trabecular tissue. In contrast, the osteoderms described by Zurita *et al.* (2006) and Asakura *et al.* (2017) show some tubercles in the external surface not observed in the altered specimens examined here. In the face of these macroscopic differences, one reasonable explanation is that a likely pathological process eroded most of the superficial layer of compact bone in the altered osteoderm of *Panochthus*. This erosion exposed the intermediate zone between the superficial layer of compact bone and the central region of trabecular bone (see above), which have fibre bundles without a preferred alignment, as in the superficial layer of compact bone in the *Neuryurus* osteoderms described by Asakura *et al.* (2017).

Conversely, there is an intriguing similarity between the altered osteoderms described here and those of *Neuryurus trabeculatus* (Zurita & Ferrero, 2009) in terms of the external surface, which is also very similar to trabecular tissue and differs from the specimens of *Neuryurus* previously described, such as those in Ameghino (1889), Zurita *et al.* (2006) and Asakura *et al.* (2017). This peculiar external morphology of the altered osteoderms described here and those of *N. trabeculatus* is remarkably similar to that of some pathologically affected *Panochthus* osteoderms described and figured by Barbosa & Luna (2014). At first glance, this similarity suggests the possibility that *N. trabeculatus* is a pathologically affected individual of *Panochthus*, like the altered osteoderms described here. However, there are some differences, such as the presence of large foramina along the internal surface of the osteoderms assigned to *N. trabeculatus*, which are not observed in both the altered and non-altered *Panochthus* osteoderms described here. Therefore, while it is reasonable to infer that the osteoderms MCC 3262-V, MCC 3254-V, MCC 3261-V, MCC 3256-V and MCC 1616-V are pathologically altered specimens of *Panochthus*, detailed comparisons, including histological information not yet available to *N. trabeculatus*, are necessary in order to figure out the implication for these similarities in our understanding of the latter species.

CONCLUSIONS

Our analysis shows that there are histological variations among osteoderms from different regions of the carapace in *Glyptotherium* and *Panochthus*. The osteoderms from the lateral and dorsal regions of *Glyptotherium* sp. show

histological differences relative to the osteoderms of *G. floridanum* previously described. Conversely, the osteoderms closer to the posterior border are similar in *Glyptotherium* sp. and *G. floridanum*. This evidence suggests that specific differentiation based on histological patterns should be proposed with caution. Our analysis also shows histological characters shared by *Glyptotherium* sp., *Glyptodon* and *Doedicurus*, which reinforces the phylogenetic affinities among these taxa, as suggested in some current phylogenetic analyses. In addition, we found histological differences in the osteoderms of *Glyptotherium* and *Glyptodon reticulatus* that show the potential of these sorts of features in order to distinguish *Glyptotherium* from *Glyptodon*, considering that most macroscopic differences in osteoderms are subtle.

With regard to the osteoderms of *Panochthus* sp., we observed that they bear a central region with common characters regardless of the position they occupy in the carapace. The altered osteoderms of this genus studied here share very similar compact layers, especially in having fibre bundles with no preferred alignment, in contrast to osteoderms from the dorsal region, which show obliquely aligned fibre bundles in the compact layers of bone. These altered osteoderms also differ from the non-altered osteoderms of the lateral region, which possess fibre bundles with parallel alignment in the mentioned layers. Intriguingly, the histological pattern of these altered osteoderms is similar to the one observed in osteoderms of *Neuryurus* recently described, though macroscopic differences exist. The likely explanation for this similarity is that some pathological processes may have eroded the superficial layers of compact bone in these altered osteoderms, exposing the fibre bundles without preferred alignment, which are characteristic of the intermediate layer between the superficial layer of compact bone and the central region.

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