



NEW EXOSKELETAL MATERIAL FROM BAHIA STATE PROVIDES NEW EVIDENCE OF GEOGRAPHIC DISTRIBUTION AND PALEOPATHOLOGY FOR QUATERNARY CINGULATES

LETÍCIA FRANCIELLE MOREIRA PALES

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.
leticiapales@hotmail.com (Corresponding author)

KLEBERSON OLIVEIRA PORPINO

Departamento de Ciências Biológicas, Universidade do Estado do Rio Grande do Norte,
59610-090, Mossoró, RN, Brazil. klebersonporpino@uern.br

CAROLINA SALDANHA SCHERER

Centro de Ciências Agrárias, Ambientais e Biológicas, Universidade Federal do Recôncavo da Bahia,
Rua Rui Barbosa, 710, 44380-000, Cruz das Almas, BA, Brazil. carolina.ss@ufrb.edu.br

ABSTRACT – The Cingulata clade has a great taxonomic diversity, and its remains are abundantly found in the fossil record of South America, represented mainly by elements from the exoskeleton. Most of the work on cingulate fossils from the Brazilian Quaternary is restricted to taxonomy, while studies on paleobiology, including pathological aspects, are still scarce. This paper describes new exoskeletal specimens and paleopathological evidence for cingulates from Quaternary deposits in Bahia State, Brazil, among the identified taxa (*Pachyarmatherium brasiliense*, *Tolypeutes* cf. *tricinctus*, *Propraopus sulcatus*, *Glyptotherium* sp., *Neuryurus* sp., *Panochthus* sp., *Hoplophorus* cf. *euphractus*, *Pampatherium humboldtii*, and *Holmesina paulacoutoi*). *Neuryurus* is recorded for the first time in the Quaternary of Bahia. Skin lesions, possibly caused by fungi or bacteria, are identified for *Panochthus* sp. and *Glyptotherium* sp. In addition, we identified lesions caused by fleas in *Glyptotherium* sp. These findings underscore disharmonious interspecific relationships involving microorganisms and parasites with glyptodonts, aligning with previous research conclusions.

Keywords: Paleobiology, Paleopathology, Cingulata, Quaternary.

RESUMO – O clado Cingulata possui uma grande diversidade taxonômica e é abundantemente encontrado no registro fóssil da América do Sul, sendo representados, principalmente, por elementos do exoesqueleto. Até o presente, a maioria dos trabalhos sobre fósseis de cingulados do Quaternário brasileiro são restritos à taxonomia, enquanto estudos sobre a paleobiologia, incluindo aspectos patológicos, ainda são escassos. Este trabalho descreve novos espécimes exoesqueléticos e evidências paleopatológicas para cingulados de depósitos do Quaternário na Bahia, Brasil. Os táxons identificados incluem *Pachyarmatherium brasiliense*, *Tolypeutes* cf. *tricinctus*, *Propraopus sulcatus*, *Glyptotherium* sp., *Neuryurus* sp., *Panochthus* sp., *Hoplophorus* cf. *euphractus*, *Pampatherium humboldtii* e *Holmesina paulacoutoi*. O registro de *Neuryurus* sp. é o primeiro para o gênero no Quaternário da Bahia. Lesões cutâneas, possivelmente ocasionadas por fungos ou bactérias, são reportadas para *Panochthus* sp. e *Glyptotherium* sp. Além disso, para *Glyptotherium* sp. identificamos lesões causadas por pulgas. Estes novos registros de relação interespecífica desarmoniosa de microorganismos e parasitas com gliptodontes reforçam as conclusões de trabalhos anteriores.

Palavras-chave: Paleobiologia, Paleopatologia, Cingulata, Quaternário.

INTRODUCTION

Cingulates are traditionally divided into three groups with family status: the extinct Glyptodontidae and Pampatheriidae, and Dasyopodidae, with living and extinct species. Additional family-level taxa recognized within cingulates include Peltephilidae and Palaeopeltidae (Mckenna & Bell, 1997)

and, more recently, Pachyarmatheriidae (*Pachyarmatherium* + *Neoglyptatelus*; Fernicola *et al.*, 2018), but their broader affinities remain elusive.

On the other hand, the latest phylogenetic proposals have demonstrated other arrangements for the clade Cingulata. Molecular phylogenies suggest a new conformation of the clade, splitting it into two groups: Chlamyphoridae and

Dasypodidae (Gibb *et al.*, 2016; Delsuc *et al.*, 2016; Mitchell *et al.*, 2016). Thus, Dasypodidae would include only the Dasypodinae, while Chlamyphoridae is divided into the subfamilies Glyptodontinae, Pamphathiinae, Euphractinae, Chlamyphorinae, and Tolypeutinae (Delsuc *et al.*, 2016; Mitchell *et al.*, 2016).

Cingulates have a great taxonomic diversity and are abundantly found in Quaternary deposits from South America, where most of their evolution occurred (Avilla *et al.*, 2012). Part of the explanation for this abundance of fossils is the disarticulation of osteoderms after the animal's death, producing numerous bones and enhancing the preservation potential (Gaudin & Wible, 2006). Externally, these osteoderms display variable ornamentation, often featuring apomorphic characters that distinguish genera and species (Paula Couto, 1979).

Their great representation in the fossil record of South America, combined with their morphological distinctiveness, has spurred investigations into the paleobiology and paleoecology of extinct cingulates (*e.g.*, De Iuliis *et al.*, 2000; Pérez-Crespo *et al.*, 2012). In this context, paleopathology - the study of diseases affecting fossils of humans and animals (Ruffer, 1914; Barbosa, 2013) - offers valuable insights into paleobiology through the interpretation of lesions caused by interspecific ecological interactions, such as changes caused by fleas, fungi, and bacteria (*e.g.*, Truman, 2005; Tomassini *et al.*, 2016), and intraspecific interactions, such as mechanical trauma resulting from fighting for territory and/or sexual partners (*e.g.*, Ferigolo, 2007).

Some works have recorded pathologies in cingulate osteoderms, most notably lesions caused by flea parasitism in *Chaetophractus vellerosus*, *C. villosus*, *Tolypeutes matacus*, *Zaedyus pichiy*, *Euphractus sexcinctus*, and *Priodontes maximus* (Ezquiaga *et al.*, 2015, 2020); *Chasicotatus ameghinoi* and *Vetelia perforata* (Tomassini *et al.*, 2016), *Glyptotherium* sp., *Panochthus* sp. and *Pachyarmatherium brasiliense* (Lima & Porpino, 2018), *Neuryurus* sp. (Perea *et al.*, 2019), *Holmesina cryptae* (Nascimento *et al.*, 2020; Moura *et al.*, 2021), and *Chaetophractus villosus*, *Tolypeutes matacus* (Boyde *et al.*, 2023). Other types of lesions, such as infections caused by fungi or bacteria, have been reported for *Panochthus* sp. (Barbosa & Luna, 2014; Lima & Porpino, 2018), *Glyptotherium* sp., *Pachyarmatherium brasiliense* (Lima & Porpino, 2018), and *Holmesina cryptae* (Moura *et al.*, 2021).

This paper describes novel exoskeletal materials from Bahia State, Brazil, belonging to several Quaternary cingulates. The analysis of these specimens provides new contributions in terms of paleobiology and past geographical distribution of the group, more specifically: (i) the first record of the genus *Neuryurus* for the State of Bahia; (ii) new records of *Pachyarmatherium brasiliense*, *Propraopus sulcatus*, *Tolypeutes* cf. *tricinctus*, *Glyptotherium* sp., *Hoplophorus* cf. *euphractus*, *Panochthus* sp., *Pamphatherium humboldtii*, *Holmesina paulacoutoi*; (iii) new evidence of parasitism and other lesions in osteoderms of glyptodonts.

GEOLOGICAL SETTING

The specimens described here come from seven tank and cave deposits in Bahia State, located in the municipalities of Guanambi, Ouro-lândia, Santaluz, and between Serra do Ramalho and Carinhanha (Figure 1). The fossiliferous sites located in the municipality of Guanambi comprise two tank-type deposits called Lagoa do Rancho (14°07'42"S and 42°53'7"W) and Lagoa das Abelhas (14°9'32"S and 42°46'22"W). These tanks are geologically positioned in the Gavião Block, intruded by the Guanambi Batholith, in Paleoproterozoic rocks (Souza *et al.*, 2003). C¹⁴ dating has been previously conducted on fossil material retrieved from these ponds, revealing ages of 22,230 ± 55 years for Lagoa das Abelhas and 16,020 ± 40 years for Lagoa do Rancho (Scherer *et al.*, 2016, 2017).

In the Municipality of Santaluz, the fossil material comes from three tank-type deposits: Lagoa Escura, Vargem Grande, and Várzea Funda. The Lagoa Escura (11°19'56"S and 39°24'49"W) and Vargem Grande (11°16'55.96"S and 39°34'30.12"W) tanks are geologically located in the Mesoarchean Santaluz Complex (Souza *et al.*, 2003; Silveira *et al.*, 2015). The tank at Várzea Funda (11°18'69"S and 39°42'81"W) is located under the granitoid rocks Riacho da Onça (Silveira *et al.*, 2015).

The Gruna do Carlinhos Cave (13°44'2.92"S and 43°49'2.05"W), situated between Serra do Ramalho and Carinhanha, occurs in Neoproterozoic rocks, which are part of the Sete Lagoas Formation, Bambuí Group (Vieira, 2007). C¹⁴ dating performed on fossil material from this cave indicates an approximate age of 15,000 years BP for certain elements of the local paleofauna (Scherer *et al.*, 2016, 2017).

Finally, the Toca dos Ossos Cave (10°55'52"S, 41°03'24"W), at Ouro-lândia Municipality, is located within the confines of a Private Natural Heritage Reserve (RPPN). This cave is renowned as a significant paleontological site, boasting a remarkable fossiliferous association (Cartelle, 1992). Geologically, the cave is situated on Miocene-aged limestones belonging to the Caatinga Formation (Ribeiro *et al.*, 2002).

MATERIAL AND METHODS

The material studied here comprises one partial carapace and 211 isolated osteoderms of fossil cingulates deposited in the Coleção de Paleontologia de Vertebrados do Museu de Zoologia e Paleontologia da Universidade Federal do Recôncavo da Bahia (UFRB-PV), Campus Cruz das Almas, Bahia.

The morphological description was based on the following Cartelle (1992), Zurita *et al.* (2006), Porpino *et al.* (2009, 2010, 2014), González-Ruiz *et al.* (2010), Oliveira *et al.* (2010), Góis *et al.* (2012), and Castro *et al.* (2013). The systematic classification follows Gibb *et al.* (2016), Delsuc *et al.* (2016), and Fericola *et al.* (2018).

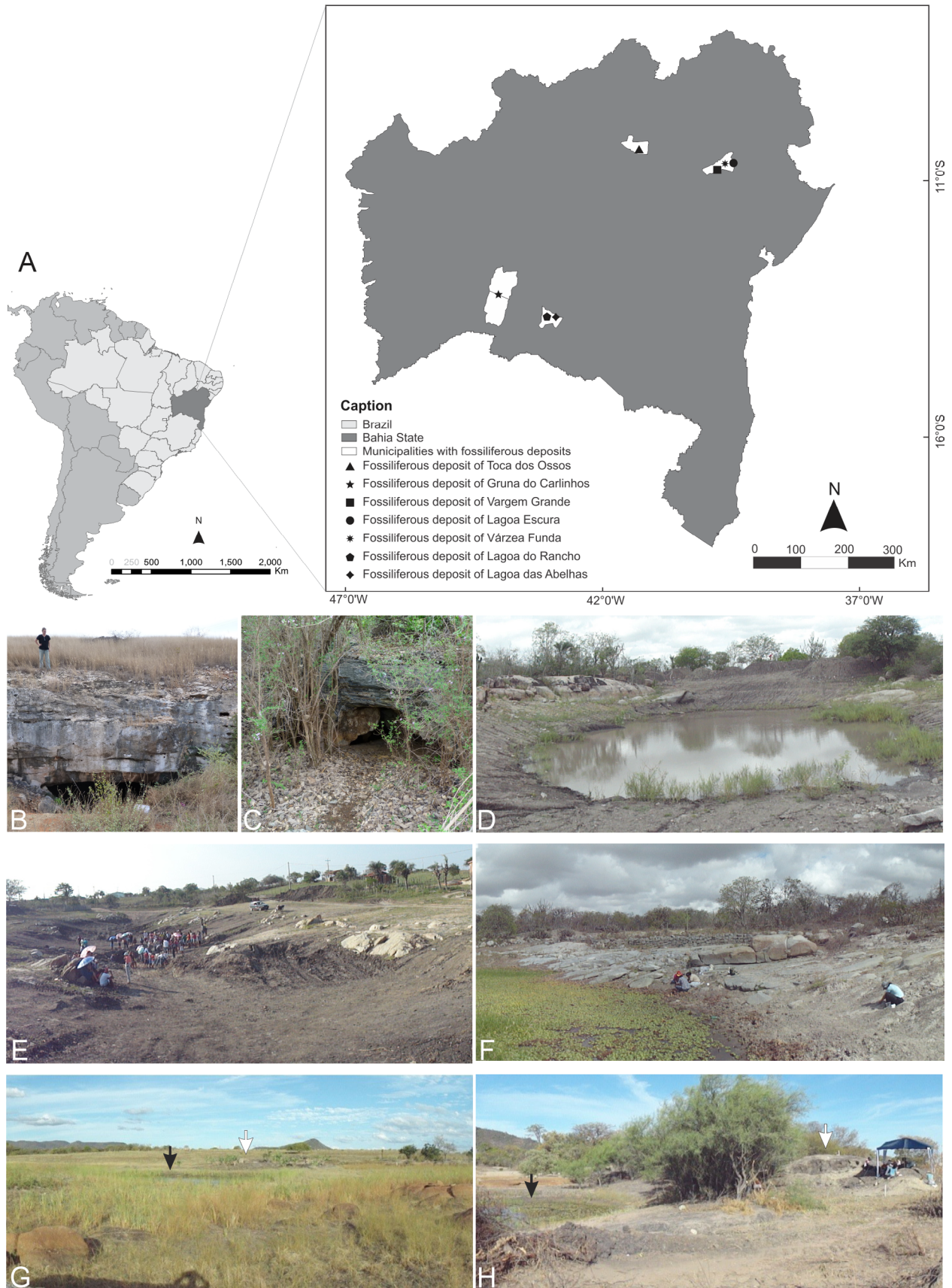


Figure 1. A, location of fossiliferous deposits in the municipalities of Santaluz (top right), Ourulândia (top left), Guanambi (bottom right) and Serra do Ramalho/Carinhanha (bottom left), in the State of Bahia, Brazil; B, entrance to Gruna do Carlinhos; C, the main entrance to Toca dos Ossos; D, Vargem Grande Tank; E, Lagoa Escura Tank; F, Várzea Funda Tank; G, Lagoa do Rancho Tank; H, Lagoa das Abelhas Tank (the white arrow marks the tailings of the tank where the fossil material was collected, and the dark arrow indicates the tank in G and H).

Paleopathological interpretations and diagnoses were established through comparisons with cases documented in the existing literature, drawing from sources such as Ferigolo (2007), Barbosa & Luna (2014), Matthias *et al.* (2016), Tomassini *et al.* (2016), and Lima & Porpino (2018). Macroscopic analysis was conducted on all specimens, and potential lesions were scrutinized using a Dino-Lite digital microscope at magnifications up to 280 times. The DinoCapture 2.0 software was employed to acquire additional information related to observed alterations, encompassing features such as signs of bone reaction or growth and microcavities.

SYSTEMATIC PALEONTOLOGY

Order CINGULATA Illiger, 1811

Family PACHYARMATHERIIDAE Fernicola *et al.*, 2018

Pachyarmatherium Downing & White, 1995

Pachyarmatherium brasiliense Porpino *et al.*, 2009
(Figures 2A–B)

Material analyzed and provenance. UFRB-PV 783, 813, 882, 909, fixed osteoderms and UFRB-PV 627, 785, fragments of fixed osteoderms, from Lagoa das Abelhas, Guanambi, Bahia, Brazil; UFRB-PV 854, 966, 983, 1043, 1176, 1178, 1562, fixed osteoderms and UFRB-PV 702, 1313, fragments of fixed osteoderms, from Lagoa do Rancho, Guanambi, Bahia, Brazil; UFRB-PV 924, fixed osteoderms, from Várzea Funda, Santaluz, Bahia, Brazil.

Taxonomic assignment and comments. Identifying these osteoderms (Figures 2A–B) as *Pachyarmatherium brasiliense* was based on the diagnosis presented by Porpino *et al.* (2009). Key features supporting this assignment include hexagonal and pentagonal osteoderms, with a rounded, pentagonal, or hexagonal main figure occupying nearly half of the total length of the osteoderm and displaced posteriorly, around which four to six peripheral figures occur. Although Martínez & Rincón (2010) suggest that *P. brasiliense* is a junior synonym of the Venezuelan species *Pachyarmatherium tenebris*, this proposition lacks substantial data support (Oliveira *et al.*, 2013). Additionally, our sample is restricted to a few isolated osteoderms, making a conclusive taxonomic decision difficult. Therefore, a comprehensive study based on more complete material is essential to address this proposed synonymy, a task beyond the scope of this paper. Consequently, the material studied here is attributed to the Brazilian species *P. brasiliense*, with documented occurrences in the states of Rio Grande do Norte (Porpino *et al.*, 2009); Sergipe (Dantas *et al.*, 2011); Pernambuco (Oliveira *et al.*, 2013); Bahia (Scherer *et al.*, 2017); Tocantins (Soibelzon *et al.*, 2015), Minas Gerais (Missagia *et al.*, 2012), and likely Venezuela (see Reyes-Céspedes *et al.*, 2022). This record extends the known distribution of *P. brasiliense* in Bahia.

Family DASYPOLIDAE Gray, 1821

Propraopus Ameghino, 1881

Propraopus sulcatus Lund, 1838
(Figures 2C–E)

Material analyzed and provenance. UFRB-PV 618, 623, fragments of mobile band osteoderms, UFRB-PV 764, 784, 786, fixed osteoderms, from Lagoa das Abelhas, Guanambi, Bahia, Brazil; UFRB-PV 633, 812, 1413, 1461, fragments of mobile band osteoderms, UFRB-PV 704, 857, 1074, fixed osteoderms, UFRB-PV 635, fragment of fixed osteoderm, from Lagoa do Rancho, Guanambi, Bahia, Brazil.

Taxonomic attribution and comments. We attribute these osteoderms (Figures 2C–E) to *Propraopus sulcatus* based on the diagnosis by Castro (2015), considering the following features: osteoderms of small thickness and size, with piliferous foramina positioned in the main groove between the main figure and one of the peripheral figures. According to Castro *et al.* (2013), *P. sulcatus* is deemed the sole valid species for the genus in South America. The authors argue that no discernible morphological, distributional, or associative criteria exist to differentiate *Propraopus grandis* and *P. sulcatus*, with the latter holding nomenclatural priority. Additionally, *Propraopus magnus* exhibits similar characteristics to *P. sulcatus*, but a potential synonymy remains unresolved due to the limited number of specimens available for the former (Castro *et al.*, 2013). Considering the above, *P. sulcatus* has records in Brazil the states of Minas Gerais (Lund, 1842), Bahia (Schimitz, 1990), Piauí (Faure *et al.*, 1999), Mato Grosso (Cartelle & Hirooka, 2005), Rio Grande do Sul (Oliveira & Pereira 2009), and Tocantins (Castro *et al.*, 2013). The present record extends the known distribution of *P. sulcatus* in Bahia.

Family CHLAMYPHORIDAE Pocock, 1924
Subfamily TOLYPEUTINAE Gray, 1865

Tolypeutes Illiger, 1811

Tolypeutes cf. tricinctus Linnaeus, 1758
(Figure 2F)

Material analyzed and provenance. UFRB-PV 444, mobile band osteoderm, from Toca dos Ossos, Ourorândia, Bahia, Brazil.

Taxonomic attribution and comments. The mobile osteoderm UFRB-PV 444 (Figure 2F) presents the typical ornamentation pattern of *Tolypeutes* sp., composed of several rounded tubercles, more prominent at the periphery and smaller at the center (Cartelle, 1992; Porpino *et al.*, 2004; Dantas, 2012). Two species are known for this genus: *Tolypeutes matacus*, prevalent in the Midwest region of Brazil, and *Tolypeutes tricinctus*, with a limited distribution in Northeastern Brazil, with fossils reported in Bahia (Cartelle,

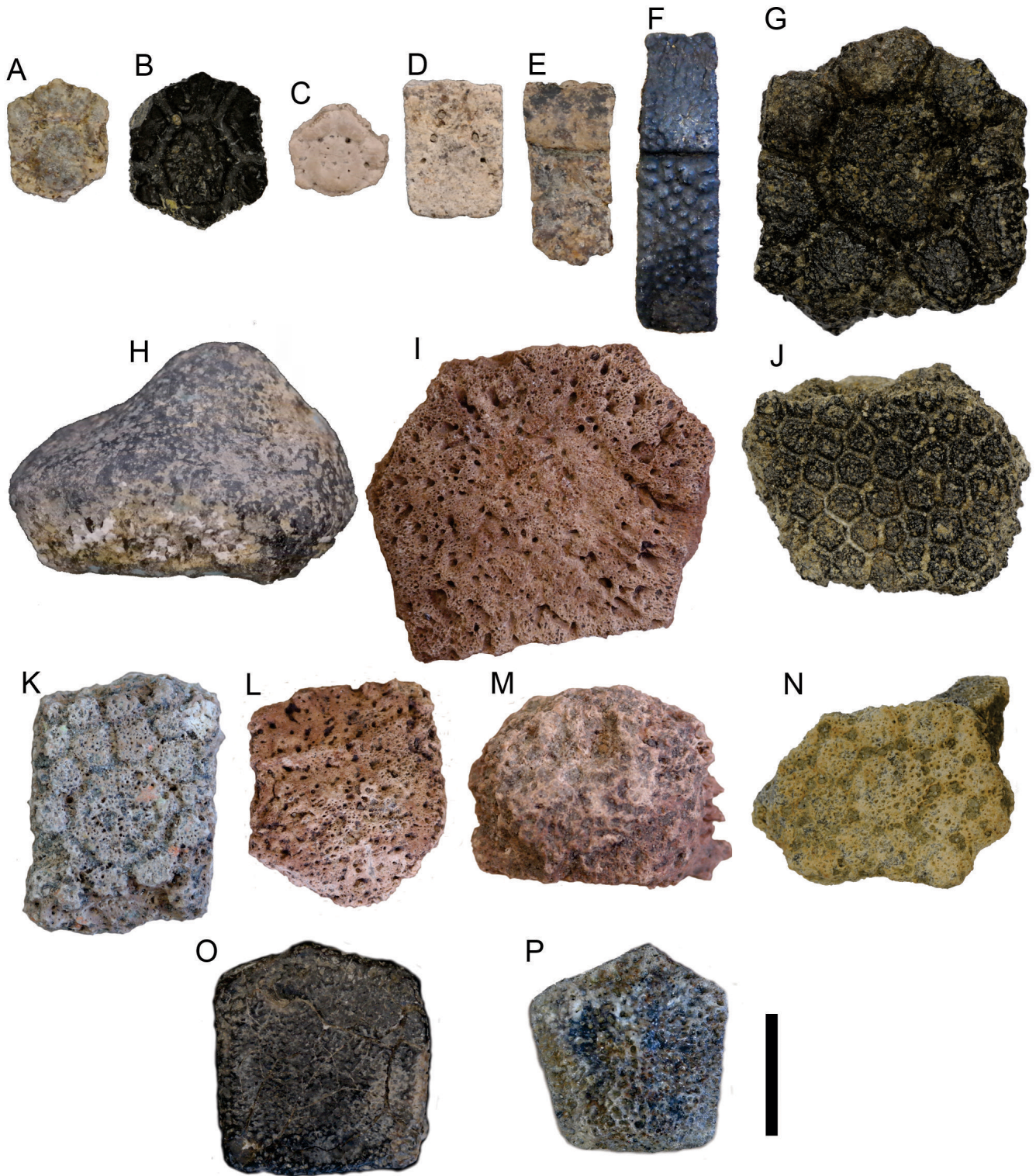


Figure 2. Isolated and fragmented cingulate osteoderms from Bahia State, Brazil (for detailed information regarding the specific provenance of each specimen, see text.). **A** and **B**, isolated osteoderms of *Pachyarmatherium brasiliense* UFRB-PV 812 and UFRB-PV 924 respectively; **C**, fixed osteoderm UFRB-PV 857 of *Propraopus sulcatus*; **D** and **E**, fragments of mobile osteoderm of *Propraopus sulcatus* UFRB-PV 623, and UFRB-PV 633, respectively; **F**, mobile osteoderm of *Tolypeutes* cf. *tricinctus* UFRB-PV 444; **G**, isolated dorsal osteoderm of *Glyptotherium* sp. UFRB-PV 921; **H**, osteoderm of the caudal ring of *Glyptotherium* sp. UFRB-PV 2110; **I**, isolated osteoderm of *Neuryurus* sp. UFRB-PV 4199; **J**, isolated osteoderm of *Panochthus* sp. UFRB-PV 528; **K**, isolated osteoderm of the lateral edge region of the carapace UFRB-PV 996 of *Panochthus* sp.; **L**, isolated caudal ring osteoderm of *Panochthus* sp. UFRB-PV 942; **M**, isolated osteoderm from the posterior region of the carapace of *Panochthus* sp. UFRB-PV 1943; **N**, isolated osteoderm of *Hoplophorus* cf. *euphractus* UFRB-PV 686; **O**, fixed osteoderm of *Pampatherium humboldtii* UFRB-PV 63; **P**, fixed osteoderm of *Holmesina paulacoutoi*. UFRB-PV 621. All osteoderms in dorsal view, except for (H) the osteoderm of the caudal ring (lateral view). Scale bar = 20 mm.

1992), Rio Grande do Norte (Porpino *et al.*, 2004), Piauí (Guérin *et al.*, 1996), and Sergipe (Dantas, 2012). The present record extends its distribution in Bahia.

Subfamily GLYPTODONTINAE Gray, 1869

Glyptotherium Osborn, 1903

Glyptotherium sp.
(Figures 2G, 3A–B)

Material analyzed and provenance. UFRB-PV 397, 928, 929, 930, 933, 984, 985, 990, 994, 1001, isolated osteoderms, UFRB-PV 687, 722, 992, 993, 1017, 1028, 1035, isolated osteoderm fragments, UFRB-PV 2110, tail ring osteoderm, UFRB-PV 545, carapace fragment from Lagoa Escura, Santaluz, Bahia, Brazil; UFRB-PV 442, isolated osteoderm, UFRB-PV 443, isolated osteoderm fragment, from Toca dos Ossos, Ouroândia, Bahia, Brazil; UFRB-PV 776, isolated osteoderm fragment, from Lagoa das Abelhas, Guanambi, Bahia, Brazil; UFRB-PV 917, 919, 921, 922, 923, 3697, isolated osteoderms, UFRB-PV 916, 918, 3651, isolated osteoderm fragments, from Várzea Funda, Santaluz, Bahia, Brazil; UFRB-PV 1289, isolated osteoderm fragment, from Lagoa do Rancho, Guanambi, Bahia, Brazil; UFRB-PV 4191, 4115, 4127, isolated osteoderms, UFRB-PV 1240, 4109, 4118, 4181, 4198, isolated osteoderm fragments, UFRB-PV 1241, carapace fragment, from Vargem Grande, Santaluz, Bahia, Brazil; UFRB-PV 4596, isolated osteoderm fragment, from Gruna do Carlinhos, Serra do Ramalho, Bahia, Brazil.

Taxonomic assignment and comments. The dorsal carapace osteoderms studied here (Figure 2G) have rosette pattern ornamentation, a highly perforated and rough outer surface featuring eight to nine trapezoidal peripheral figures, and shallow main and radial grooves. These characteristics are compatible with *Glyptotherium* sp. (Oliveira *et al.*, 2010) and differ from *Glyptodon* sp., which has osteoderms with a smoother outer surface, fewer peripheral figures, and deeper main and radial grooves (Oliveira *et al.*, 2010). Osteoderms of the caudal rings previously described for this genus are subquadrangular, with a conical protrusion in the central region, but less so than in *Glyptodon*, and do not present main or peripheral figures (Oliveira *et al.*, 2010; Zurita *et al.*, 2018), as in our material (Figure 2H). The genus *Glyptodon* has been frequently documented both in southern and northeastern Brazil (Cartelle, 1992; Kerber & Oliveira, 2008). However, a proposal by Oliveira *et al.* (2010) suggests that the records of the genus *Glyptodon* in northeastern Brazil should be reattributed to the genus *Glyptotherium*. In a broader geographical context, the records for lowland regions such as Venezuela and eastern Brazil are considered to belong to *Glyptotherium*. In contrast, those in areas parallel to the Andes are attributed to *Glyptodon* (Zurita *et al.*, 2012). In Brazil, the genus *Glyptotherium* is recorded for the states of Pernambuco, Rio Grande do Norte, Minas Gerais (Oliveira *et al.*, 2010), Paraíba (Andrade *et al.*, 2017), and Bahia (Silva *et al.*, 2019).

Thus, the current finding extends the known distribution of *Glyptotherium* in Bahia.

Description of ante-mortem alterations. We observed macroscopically a superficial erosion extending on the external surface between 20% (UFRB-PV 4115 and 4181) and 80% (UFRB-PV 545 and 722) of the area of some osteoderms (Figures 3A–B). In microscopical view, the region with superficial erosion presents a rough and irregular aspect, with a slight bone reaction (Figure 3A’); in contrast, the specimen UFRB-PV 4181 did not show a bone reaction in the microscopic analysis (Figure 3B’). In the specimens UFRB-PV 545 and 722, in addition to the erosion of the ornamentation, there is a circular hole in each osteoderm, which starts in the outer region and enters the inner layers, which, in the microscopic analysis, presented a quite polished inner surface (3A’’).

Neuryurus Ameghino, 1889

Neuryurus sp.
(Figure 2I)

Material analyzed and provenance. UFRB-PV 4232, isolated osteoderm; UFRB-PV 3664, osteoderm fragment, from Várzea Funda, Santaluz, Bahia, Brazil; UFRB-PV 4199, 4806, isolated osteoderms from Lagoa do Rancho, Guanambi, Bahia, Brazil.

Taxonomic attribution and comments. The osteoderms (Figure 2I) present a rough external surface with numerous oblique-angled foramina, the typical pattern of *Neuryurus* osteoderms (Zurita *et al.*, 2009; González-Ruiz *et al.*, 2010). Based on dermal elements, only two species are recognized for this genus, namely, *Neuryurus rudis* and *Neuryurus trabeculatus* (Zurita & Ferrero, 2009; Soibelzon *et al.*, 2010). Due to the scarcity of material and the insufficient understanding of this genus, a specific attribution of this material remains challenging. *Neuryurus* sp. is recorded in Brazil in the Rio Grande do Sul (Ribeiro *et al.*, 2007) and Pernambuco states (Silva *et al.*, 2012). The material described here extends its distribution to Bahia State.

Panochthus Burmeister, 1866

Panochthus sp.
(Figures 2J–M, 4, 5)

Material analyzed and provenance. UFRB-PV 1239, 4114, 4116, 4196, 4214, 4222, fragments of carapace; UFRB-PV 4110, 4111, 4112, 4119, 4120, 4129, 4220, isolated dorsal osteoderms; UFRB-PV 4117, 4121, 4126, osteoderms of lateral region, from Vargem Grande, Santaluz, Bahia, Brazil; UFRB-PV 3661, 3662, 3663, isolated dorsal osteoderms, from Várzea Funda, Santaluz, Bahia, Brazil; UFRB-PV 395, 528, 720, 920, 925, 938, 986, 998, 1004, 1006, 1008, 1011, 1013, 1015, 1016, 1018, 1019, 1025, 1026, 1148, 3304, 4185, 4325, 4399, 4724, isolated dorsal osteoderms; UFRB-PV 927, 931, 935, 939, 940, 987, 989, 991, 999, 1010, 1012, 1014, 1023,

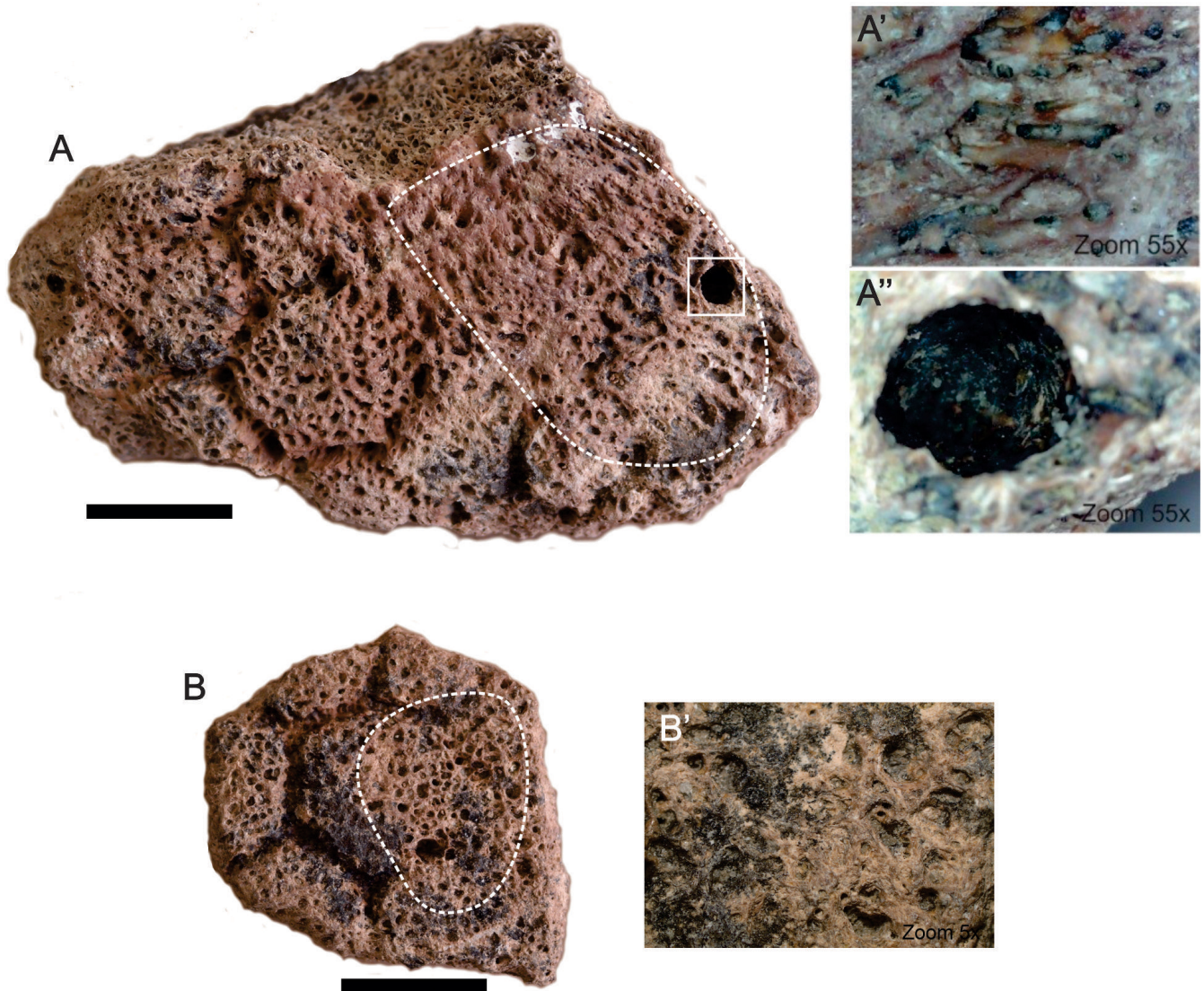


Figure 3. Osteoderms of *Glyptotherium* sp. with *ante-mortem* changes UFRB-PV 545 and UFRB-PV 4181. **A–B**, macroscopic view of surface erosion (dotted lines in white) in UFRB-PV 545 and UFRB-PV 4181, respectively; **A'–B'**, microscopic view of surface erosion in UFRB-PV 545 and UFRB-PV 4181, respectively; **A''**, microscopic view of the inside of the hole (white square in A) in UFRB-PV 545. Scale bars = 20 mm.

1027, 1029, 1942, 2208, 2230, osteoderm fragments; UFRB-PV 744, 745, 1000, 1002, 1003, 1005, 1007, 1021, 1024, 1030, 1242, 2015, 4388, carapace fragments; UFRB-PV 4870, partial carapace; UFRB-PV 942, 943, 1022, osteoderm of the caudal ring; UFRB-PV 996, 1243, 4183, osteoderms of the lateral region; UFRB-PV 1943, 4395, 4397, osteoderm of the posterior region, from Lagoa Escura, Santaluz, Bahia, Brazil. **Taxonomic attribution and comments.** The partial carapace and dorsal isolated osteoderms (Figure 2J) are ornamented with small polygonal figures distributed without orientation. The lateral osteoderms (Figure 2K) are from the portion closer to the lateral border and bear a rosette pattern, in which the main figure is larger than the peripheral ones (Porpino *et al.*, 2014). In addition, there are osteoderms from the posterodorsal border (Figure 2L), which have a convex central figure covering most of the osteoderm, and from the caudal

rings (Figure 2M), which have a pentagonal shape, without ornamentation (see Porpino *et al.*, 2014).

The distribution of the genus *Panochthus* encompasses Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Ferreira *et al.*, 2015). For Brazil, the species *Panochthus tuberculatus* are recorded for the southern region (Ribeiro & Scherer, 2009), and *Panochthus greslebini* and *Panochthus jaguaribensis* for the Northeast (Porpino & Bergqvist, 2002; Ribeiro & Carvalho, 2009; Porpino *et al.*, 2014). The exoskeletal materials described here are not amenable to specific identification due to the diagnostic characters of species of the genus *Panochthus* occurring in northeastern Brazil being restricted to the caudal tube (Porpino *et al.*, 2014). Thus, the present record extends the distribution of *Panochthus* in Bahia.

Description of *ante-mortem* alterations. The partial carapace UFRB-PV 4870 presented 14 macroscopic alterations located

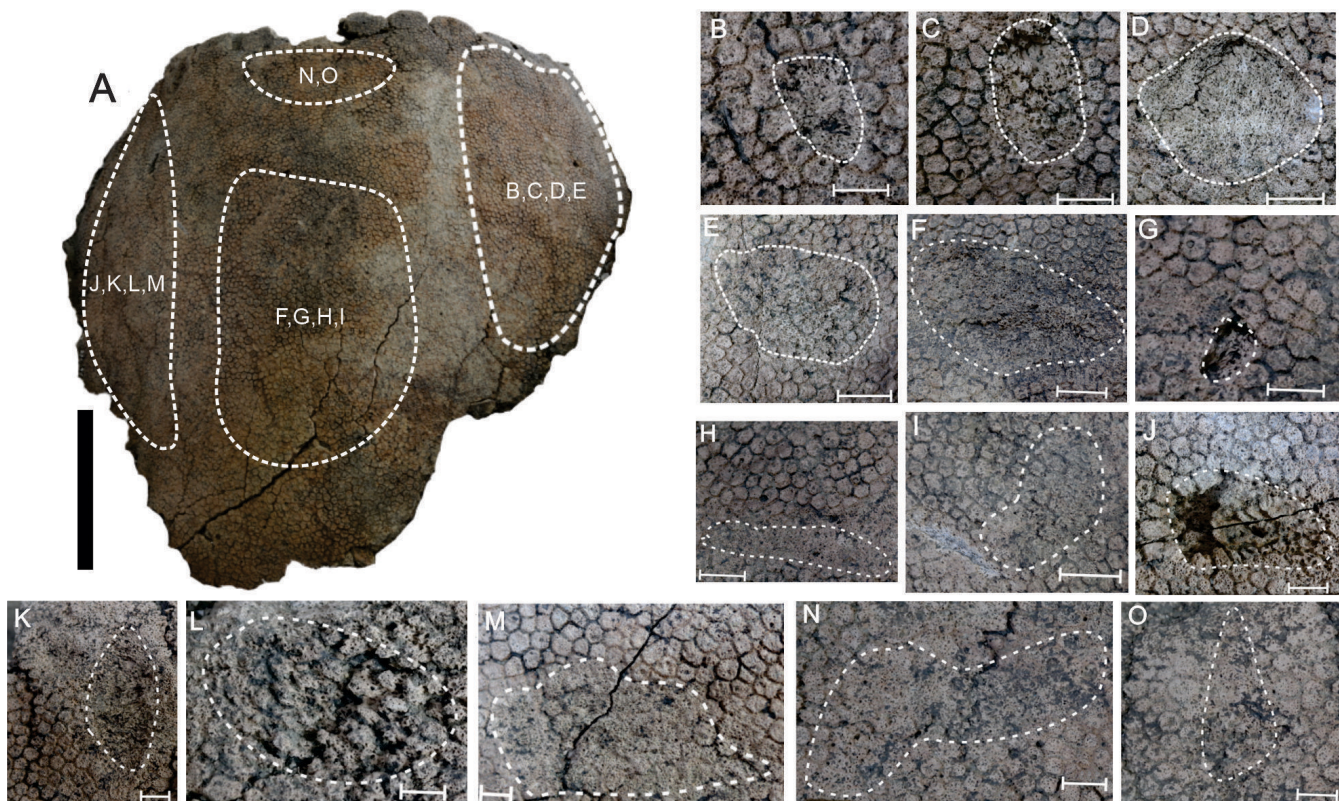


Figure 4. Carapace fragment of the posterodorsal region UFRB-PV 4870 of *Panochthus* sp. with *ante-mortem* alterations **A**, Dorsal view of UFRB-PV 4870 showing the location of the lesions (white dotted line); **B**, lesion 1; **C**, lesion 2; **D**, lesion 3; **E**, lesion 4; **F**, lesion 5; **G**, lesion 6; **H**, lesion 7; **I**, lesion 8; **J**, lesion 9; **K**, lesion 10; **L**, lesion 11; **M**, lesion 12; **N**, lesion 13; and **O**, lesion 14. Scale bars: A = 50 mm; B–O = 10 mm.

posteriorly and laterally, with a porous appearance, sometimes associated with loss of ornamentation. For a better description of the *ante mortem* alterations, we decided to identify them by numbers (see Figure 4).

Lesions 1, 3, 5, and 10 (Figures 4B, D, F, and K) are focal losses of ornamentation, forming circular craters of irregular appearance; they are probable pittings in the early (Figure 4B), intermediate (Figure 4D) and advanced stages (Figure 4F and K). In microscopic view, the interior of the pitting presents a twisted aspect, characterizing bone reaction.

Lesions 2, 4, 6, 7, 8, 9, 11, 12, 13, and 14 (Figures 4C, E, G–O) correspond to superficial erosions with different extensions; the obliteration of the ornamentation with a porous and irregular appearance characterizes them. In the microscopic observation, only lesions 2, 6, 7, and 12 showed bone reactions associated with loss of ornamentation.

Among the isolated osteoderms, osteoderm fragments, and carapace fragments, we observed, macroscopically, a superficial erosion that extends on the surface between 10% (in UFRB-PV 395, 1026, 4110, 4325, and 1016) and 50% (in UFRB-PV 986, 1029 and 4119) of the area, hindering the visualization of the typical osteoderm ornamentation (Figures 5A–C). In specimens UFRB-PV 4325 and 986 the loss of ornamentation is characterized by a sloping crater formation with severe exposure of the spongy tissue (Figure 5B). Microscopic examination of some specimens with superficial erosion revealed a slight bone reaction in the affected region

(Figure 5B'). In contrast, specimens UFRB-PV 395, 4110, and 4119 did not show a bone reaction in the microscopic analysis (Figure 5A').

The specimen UFRB-PV 1016 showed macroscopically focal loss of ornamentation at the center of the osteoderm, where an early-stage pitting was observed macroscopically (Figure 5C). Under microscopic view, we observed a twisted aspect at the center of this cavity, indicative of a bone reaction (Figure 5C').

Hoplophorus Lund, 1834

Hoplophorus cf. *euphractus* Lund, 1834
(Figure 2N)

Material analyzed and provenance. UFRB-PV 686, 688 isolated osteoderms from Lagoa Escura, Santaluz, Bahia, Brazil.

Taxonomic attribution and comments. The osteoderms UFRB-PV 686 and 688 (Figure 2N) bear ornamentation characterized by a main figure surrounded by small peripheral figures (7–8), forming a rosette pattern. While the number of peripheral figures in these osteoderms is fewer than that described for *Hoplophorus euphractus* (9–12; Porpino *et al.*, 2010), UFRB-PV 686 and 688 have a lesser thickness (14.7 mm) compared to the osteoderms of *Panochthus* (average of 28.3 mm), and *Glyptotherium* (average of 31.5 mm) studied

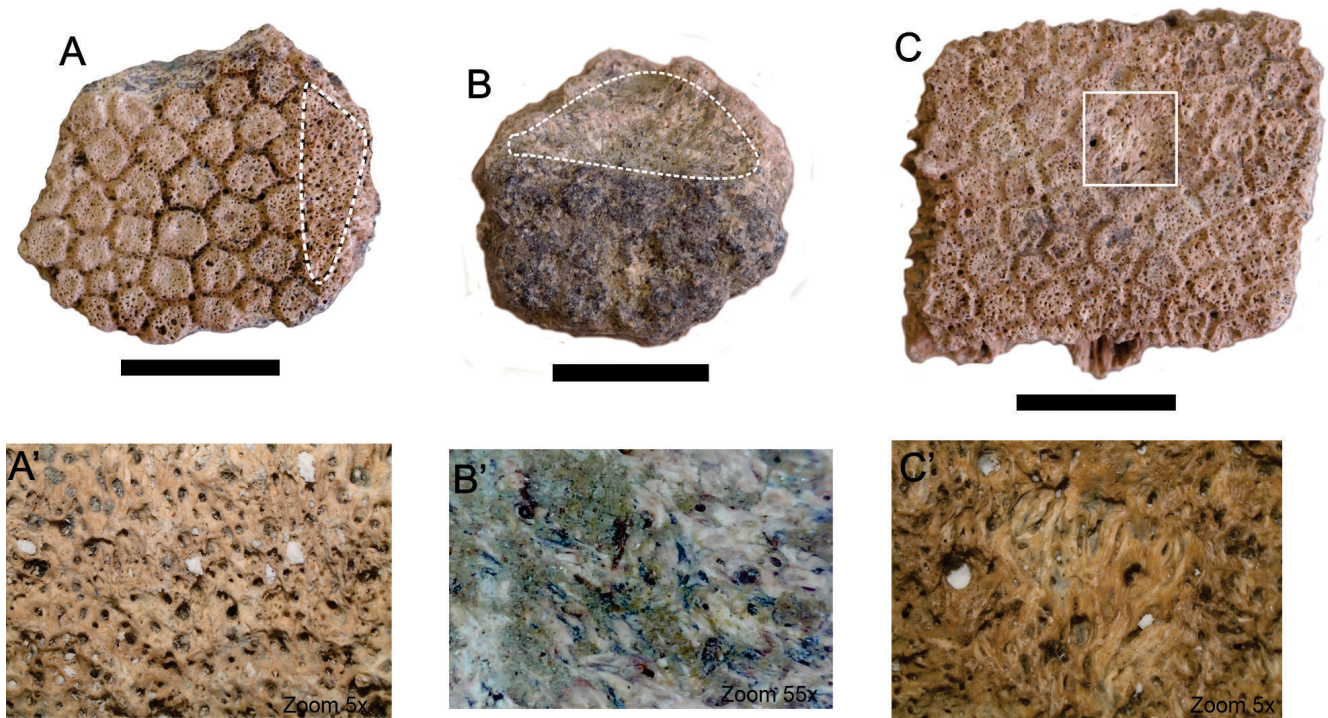


Figure 5. Isolated osteoderms of *Panochthus* sp with *ante-mortem* alterations. **A** and **B**, macroscopic view of surface erosions (white dotted lines) in osteoderms UFRB-PV 395 and UFRB-PV 986, respectively; **A'**–**B'**, microscopic view of surface erosion; **C**, macroscopic view of pitting in osteoderm UFRB-PV 1016; **C'**, microscopic view of the pitting in the osteoderm UFRB-PV 1016. Scale bars = 20 mm.

here. Additionally, a second row of peripheral figures around the row circumjacent to the main figure in UFRB-PV 686 distinguishes it from *Glyptotherium*. In Brazil, *Hoplophorus* occurs in Quaternary deposits in the states of Amazonas, Rondônia, São Paulo, Minas Gerais, Bahia, Ceará, Paraíba, Pernambuco, Piauí, and Rio Grande do Norte (Paula Couto, 1979; Cartelle, 1999; Porpino *et al.*, 2010; Silva *et al.*, 2010; Ghilardi *et al.*, 2011). Thus, the present record extends the distribution of *Hoplophorus* in Bahia.

Subfamily PAMPATHERIINAE Paula Couto, 1954

Pampatherium Ameghino, 1875

Pampatherium humboldtii Lund, 1839 (Figure 2O)

Material analyzed and provenance. UFRB-PV 429, 432, fixed osteoderms from Toca dos Ossos, Ouro-lândia, Bahia, Brazil; UFRB-PV 630, fixed osteoderm; UFRB-PV, 1046, 1047, 1051, 1159, 1673, fragments of fixed osteoderms, from Lagoa do Rancho, Guanambi, Bahia, Brazil; UFRB-PV 926, fixed osteoderm, from Lagoa Escura, Santaluz; UFRB-PV 4590, fixed osteoderm; UFRB-PV 4563, 4683, fragments of fixed osteoderms from Gruna do Carlinhos, Serra do Ramalho, Bahia, Brazil; UFRB-PV 810, fragment of fixed osteoderm, from Lagoa das Abelhas, Guanambi, Bahia, Brazil.

Taxonomic attribution and comments. The species *Pampatherium humboldtii* and *Pampatherium typum* occur in Brazil (Cartelle, 1992; Guérin & Faure, 2008; Kerber &

Oliveira, 2008; Oliveira & Pereira, 2009). The osteoderms described in this study (Figure 2O) exhibit characteristics that align with *P. humboldtii*. These features include few foramina and striae (more pronounced than in *P. typum* and less than in *Holmesina paulacoutoi*), a central longitudinal elevation, and poorly defined lateral depressions – more than in *P. typum*, where they are indistinguishable and less than in *Holmesina paulacoutoi* (see Góis, 2013). In addition, the studied osteoderms are thicker than those of *P. typum*, which is considered the smallest and least robust species of *Pampatherium* (see Góis, 2013).

Pampatherium humboldtii has a distribution in Brazil, for the states of Bahia (Cartelle, 1992), Mato Grosso (Cartelle, 1992), Minas Gerais (Lund, 1839), Piauí (Guérin & Faure, 2008), Rio Grande do Sul (Oliveira & Pereira, 2009). Thus, the present record extends the distribution of *Pampatherium humboldtii* in Bahia.

Holmesina Simpson, 1930

Holmesina paulacoutoi Cartelle & Bohorquez, 1985 (Figure 2P)

Material analyzed and provenance. UFRB-PV 430, 431, 433, 434, 439, fixed osteoderms, UFRB-PV 440, a fragment of fixed osteoderm, from Toca dos Ossos, Ouro-lândia, Bahia, Brazil. UFRB-PV 621, fixed osteoderm, UFRB-PV 628, fragment of fixed osteoderm, from Lagoa das Abelhas, Guanambi, Bahia, Brazil. UFRB-PV 696, 698, 859, 1160, 1171, fragments of fixed osteoderms, from Lagoa do Rancho,

Guanambi, Bahia, Brazil; UFRB-PV 934, 1088, fragments of fixed osteoderms, from Lagoa Escura, Santaluz, Bahia, Brazil.

Taxonomic attribution and comments. The species *Holmesina paulacoutoi*, *Holmesina major* (Oliveira *et al.*, 2009), *Holmesina rondoniensis* (Góis *et al.*, 2012), and *Holmesina cryptae* (Moura *et al.*, 2019) are reported for Brazil. The osteoderms described here (Figure 2P) have features consistent with *H. paulacoutoi*, including more pronounced ornamentation than in *H. cryptae*, a well-developed longitudinal central elevation (poorly developed in *H. major* and comparatively low in *H. cryptae*), and shallow lateral depressions (deep in *H. major*) (see Góis, 2013; Moura *et al.*, 2019). There are no osteoderms described for *H. rondoniensis* for comparison. In Brazil, *Holmesina paulacoutoi* is reported for the states of Bahia (Cartelle, 1992), Ceará (Bergqvist *et al.*, 1997), Paraíba (Bergqvist *et al.*, 1997), Pernambuco (Silva *et al.*, 2010), and Rio Grande do Norte (Porpino *et al.*, 2004).

PALEOPATHOLOGICAL ASPECTS

The changes described here as pathological show evidence that they were produced in life (differing from taphonomic changes), as most of our specimens with ulcerative lesions showed signs of bone remodeling like those already reported in previous works on *ante-mortem* alterations in fossil cingulates (Barbosa & Luna, 2014; Lima & Porpino, 2018). The orchestration of bone remodeling primarily relies on the metabolic interplay of osteoclasts and osteoblasts, safeguarding bone structure in response to fractures or micro-injuries (Junqueira & Carneiro, 2013). Notably, these lesions are confined to the external surface of the osteoderm.

On the other hand, we observed two osteoderms with characteristics that might be misconstrued as *ante-mortem* lesions. Specimens UFRB-PV702 (*Pachyarmatherium brasiliense*) and UFRB-PV795 (*Glyptotherium* sp.) displayed erosion encompassing the entire external surface, accompanied by internal erosion, rounding of the lateral

edges, and a whitish coloration. Additionally, the osteoderms were friable, releasing a fine, chalk-like residue upon handling (Figure 6A). These features align with patterns indicative of *post-mortem* changes: the whitish coloration, coupled with dust release upon contact, suggests acid corrosion (Lima & Porpino, 2018), while the rounding of the lateral edges suggests mechanical abrasion during transportation or reworking (Araújo-Júnior *et al.*, 2013). Besides, it is worth mentioning that these osteoderms were collected in the same deposit where we find osteoderms with pathologies, and a conspicuous disparity in the morphology of alterations exists between the latter and those we attribute to taphonomic modification.

Ulcerative lesions

We observed ulcerative lesions on the partial carapace (Figures 4C, E, G–J, L–O) and isolated osteoderms (Figures 3A'–B'; 5A'–B') of *Panochthus* sp. (UFRB-PV 395, 986, 1016, 1029, 4110, 4119, 4120, 4325), as well as in isolated osteoderms of *Glyptotherium* sp. (UFRB-PV 545, 722, 4115, 4181). Similar lesions have been described for ankylosaurid dinosaurs (Matthias *et al.*, 2016), crocodiles (Wolf, 2007), and the cingulates *Glyptotherium* sp., *Pachyarmatherium brasiliense*, *Panochthus* sp. (Barbosa & Luna, 2014; Lima & Porpino, 2018), and *Holmesina cryptae* (Moura *et al.*, 2021).

Ulcerative lesions are characterized by erosion of the external surface of the osteoderm. They can manifest in two types based on their depth: lesions restricted to the surface and lesions in the form of craters (pitting). The latter type can penetrate the trabecular region but does not reach the internal surface of the osteoderm (Matthias *et al.*, 2016).

There are five pitting lesions in the material studied here, which occur only in *Panochthus* sp., one in the osteoderm UFRB-PV 1016 (Figure 5C), and the other four in the partial carapace UFRB-PV 4870. These lesions are distributed on the external surface of the specimens (Figures 4B, D, F, and K) and exhibit varying sizes, indicating different stages of ulceration (initial, intermediate, and advanced), as observed in osteoderms of *Glyptotherium* sp. by Lima & Porpino (2018) and in *Holmesina cryptae* (mainly in the early stage, according

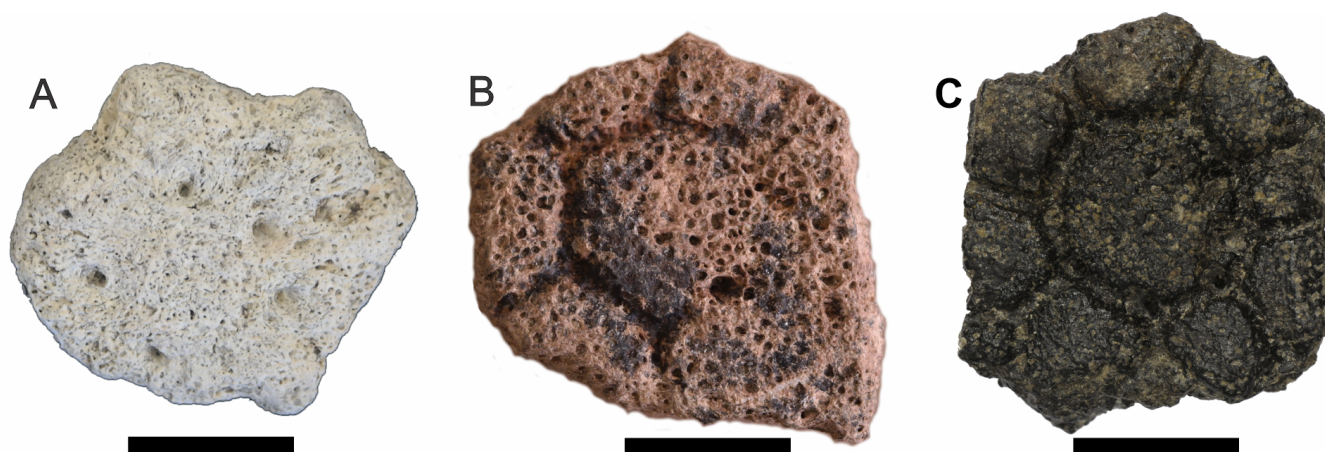


Figure 6. Osteoderms of *Glyptotherium* sp with *ante-mortem* and taphonomic alterations. **A**, taphonomically altered osteoderm UFRB-PV 795 in external view; **B**, osteoderm with pathology (superficial erosion) UFRB-PV 4181; **C**, osteoderm without alterations UFRB-PV 921 Scale bar = 20 mm.

to Moura *et al.*, 2021). Ulcerative lesions are secondary manifestations resulting from opportunistic infections caused by microorganisms. Truman (2005), for instance, describes infectious changes in *Dasyurus novemcinctus*, attributing them to bacterial attack, specifically by the causative agent of leprosy, *Mycobacterium leprae*. Another likely agent is sporotrichosis caused by the opportunistic fungus *Sporothrix schenckii* (Wenker *et al.*, 1998).

Pitting reported for ankylosaurid dinosaurs has been attributed to dermatitis caused by fungal infections (Matthias *et al.*, 2016). Other studies mention ulcerative lesions in exoskeletal material of fossil cingulates, such as *Panochthus*, with attributions to an infectious process of undetermined causes (Barbosa & Luna, 2014) and potential bacterial or fungal infections (Lima & Porpino, 2018). Recently, Moura *et al.* (2021) reported ulcerative lesions in osteoderms of *Holmesina cryptae*, suggesting that the lesions caused by fleas and fungi identified in the same material are probably precursors of the former.

On the other hand, some authors have observed that pathological changes in carapaces might stem from mechanical trauma incurred during territorial disputes or fights for sexual partners (Alexander *et al.*, 1999), which may facilitate the development of infectious processes. Ferigolo (2007), for example, describes lesions akin to those observed in the studied material in a carapace fragment of *Glyptodon* sp., linking them to traumas resulting from intraspecific fighting over territorial disputes (see also Blanco *et al.*, 2009). The author emphasizes that an internal bone callus supports the trauma hypothesis (Ferigolo, 2007). However, it was impossible to observe the presence or absence of a bony callus in the carapace studied here, as it contains a sediment block embedded in its inner surface. Consequently, it is challenging to discriminate among potential causes for the observed lesions, including those produced during intraspecific fights or predation, as well as bacterial or fungal infections, among other possibilities.

Ectoparasitism

Specimens UFRB-PV 545 and 722 (*Glyptotherium* sp.), in addition to displaying superficial erosion of the ornamentation, exhibit holes with smooth inner walls. Some features suggest that these holes are bioerosion (Pirrone *et al.*, 2014) produced in life, likely by the action of ectoparasites. They occur as a single hole per osteoderm, differing from *post-mortem* perforations made by scavenging larvae, where several cavities are observed in a small area (Pirrone *et al.*, 2014). Moreover, the described holes are exclusively located on the outer surface of the osteoderms, which would have been exposed to attacks by ectoparasites during the animal's life.

Similar marks have been previously documented in fossil and living cingulates (*e.g.*, Ezquiaga *et al.*, 2015; Tomassini *et al.*, 2016; Di Nucci *et al.*, 2017) and were attributed to fleas of the genus *Tunga*, which includes a living species capable of producing bioerosion in osteoderms of living armadillos (Ezquiaga *et al.*, 2015). Injury by fleas of the genus *Tunga*, whether in osteoderms or other tissues, occurs when fertilized adult females penetrate the integument of their hosts, and

their abdomen enlarges into a structure known as neosoma (Linardi & De Avelar, 2014).

In addition, a recent analysis of the 3D morphology of these lesions showed that other mechanisms besides flea infiltration into the osteoderm are involved in forming this lesion (Boyde *et al.*, 2023). The flea perforates the osteoderm, and the subsequent development of the neosoma triggers a local inflammatory response in the host, leading to bone resorption and the creation of space for the neosoma (Boyde *et al.*, 2023).

Previously documented flea marks on *Pachyarmatherium brasiliense* and *Glyptotherium* sp. osteoderms were characterized as circular, with the external opening diameter larger than the internal one or with equal diameters, occurring isolated in most cases (Lima & Porpino (2018)). In the examined material, the external opening diameter mirrors that of the internal region, and the inner walls of the cavities exhibit a smooth, polished appearance.

Cavities with similar morphology were described in the osteoderms of *Holmesina cryptae*, including individual unbranched, circular to elliptical holes with a tapered cone shape and a smooth interior. They were attributed to flea marks (Nascimento *et al.*, 2020) in line with previous work on other cingulates (Tomassini *et al.*, 2016; Lima & Porpino, 2018). Additionally, Moura *et al.* (2021) established new ichnospecies of the genus *Karethraichnus*, *K. minimum*, for these marks.

The morphology of the cavities studied here agrees with the diagnosis of the ichnogenus *Karethraichnus*, which is characterized by circular to subcircular cavities that penetrate bone (Zonneveld *et al.*, 2015). Furthermore, the measurements of the cavities of the material presented here (5-6 mm in diameter) fall within the range observed for the diameter of this ichnogenus (0.5 to 8.0 mm; Zonneveld *et al.*, 2015).

Moura *et al.* (2021) noted morphological similarities between the bioerosions present in the osteoderms of *Holmesina cryptae* and those reported by Lima & Porpino (2018) for *Pachyarmatherium brasiliense* and *Glyptotherium* sp. and by Perea *et al.* (2019) for *Neuryurus* sp. Still, these are more tubular and different in size from *Karethraichnus minimum*. Thus, the authors consider that these lesions may belong to cf. *Karethraichnus fale*. The holes described here are similar to *Karethraichnus fale*, which has a cylindrical shape with an axis perpendicular to the surface. However, unlike some instances in which *K. fale* penetrates fully through turtle shell plates (Zonneveld *et al.*, 2015), such a condition is not observed in our osteoderms. This discrepancy can be attributed to variations in bone substrate thickness, considering that turtle plates are relatively thin compared to osteoderms of larger cingulates, such as glyptodonts.

The marks in our specimens bear resemblance to the bioerosions attributed to the ichnospecies *Karethraichnus lakkos* in its advanced stage, characterized by being cylindrical, deep, and narrow (*K. kulindros* Zonneveld *et al.*, 2015 is considered a junior synonym of *K. lakkos* by Wisshak *et al.*, 2019). However, these marks diverge from the early stage of *K. lakkos*, which are shallow and hemispherical

(Zonneveld *et al.*, 2015), and also differ from *Karethraichnus zaratan*, which assumes a hemispherical shape (Sato & Jenkins, 2020). In our material, the cavities have a smaller diameter than the depth, differing from *K. lakkos*. Also, the holes in our material are larger (5–6 mm in diameter) than those observed in *K. minimum* (2.4–3.6 mm). Given this, we attribute the cavities observed here to *Karethraichnus* isp. as our material bears morphological features reported for both *K. lakkos* (in its advanced stage) and *K. fiale*. A review of all material attributed to bioerosion by fleas is necessary to clarify this issue in fossils of glyptodonts and pachyarmateriids, which is beyond the scope of the present work.

CONCLUSIONS

We present new findings of several fossil cingulates in Bahia State, Brazil, including: *Pachyarmatherium brasiliense*, *Propraopus sulcatus*, *Tolypeutes* cf. *tricinctus*, *Glyptotherium* sp., *Hoplophorus* cf. *euphractus*, *Panochthus* sp., *Pampatherium humboldtii*, *Holmesina paulacoutoi*, and *Neuryurus* sp. Notably, the discovery of *Neuryurus* in the Quaternary of Bahia represents its first documented occurrence in this state, reinforcing its presence in Northeast Brazil during this period.

Additionally, we identified lesions associated with dermatitis in *Panochthus* sp. and *Glyptotherium* sp. We attribute the flea marks on *Glyptotherium* sp. to the ichnogenus *Karethraichnus* isp. These novel records underscore disharmonious interspecific relationships between parasites and glyptodonts, aligning with and reinforcing prior research findings.

ACKNOWLEDGMENTS

We express our gratitude to D. Peretti, F. Lima, F. Barbosa, and H.I. Araújo-Júnior for their insightful suggestions on earlier drafts of this article. Additionally, we thank the anonymous reviewers for their valuable comments and recommendations that significantly contributed to the enhancement of the manuscript. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

REFERENCES

- Alexander, R.M.; Fariña, R.A. & Vizcaíno, S.F. 1999. Tail blow energy and carapace fractures in a large glyptodont (Mammalia, Xenarthra). *Zoological Journal of the Linnean Society*, **126**:41–49. doi:10.1111/j.1096-3642.1999.tb00606.x
- Andrade, L.C.D.; Oliveira, É.V. & Souza, B.I.D. 2017. Novos achados de Xenarthra em um depósito de tanque do Pleistoceno da Paraíba, nordeste do Brasil. *Revista de Geologia*, **30**:33–46.
- Araújo-Júnior, H.I.; Porpino, K.O.; Ximenes, C.L. & Bergqvist, L.P. 2013. Unveiling the taphonomy of elusive natural tank deposits: a study case in the Pleistocene of northeastern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **378**:52–74. doi:10.1016/j.palaeo.2013.04.001
- Avilla, L.; Bernardes, C.; Mothé, D. & Asevedo, L. 2012. A megafauna de mamíferos do Pleistoceno do Brasil. In: Y. Hasui; C.D.R. Carneiro; F.F.M. Almeida & A. Bartorelli (eds.) *Geologia do Brasil*, Beca, p. 777–785.
- Barbosa, F.H.S. 2013. *Análise paleopatológica em megafauna pleistocênica do Lajedo da Escada, Baraúna, Rio Grande do Norte, Brasil*. Programa de Pós-Graduação em Geociências, Universidade Federal de Pernambuco, Dissertação de Mestrado, 99 p.
- Barbosa, F.H.S. & Luna, C. 2014. Lesiones en la coraza y endoesqueleto de un ejemplar de *Panochthus* Burmeister, 1866 (Mammalia, Glyptodontia) de la Provincia de Córdoba, Argentina. *Revista del Museo Provincial de Ciencias Naturales “Dr. Arturo Umberto Illia”*, **1**:9–26.
- Bergqvist, L.P.; Gomide, M.; Cartelle, C. & Capilla, R. 1997. Faunas-loais de mamíferos pleistocênicos de Itapipoca/Ceará, Taperoá/Paraíba e Campina Grande/Paraíba. Estudo comparativo, bioestratigráfico e paleoambiental. *Geociências*, **6**:23–32.
- Blanco, R.E.; Jones, W.W. & Rinderknecht, A. 2009. The sweet spot of a biological hammer: the centre of percussion of glyptodont (Mammalia: Xenarthra) tail clubs. *Proceedings Biological Sciences*, **276**:3971–3978. doi: 10.1098/rspb.2009.1144
- Boyde, A.; Mills, D.; Abba, A.M. & Ezquiaga, M.C. 2023. Fleas and lesions in armadillo osteoderms. *Journal of Anatomy*, **242**:1029–1036. doi:10.1111/joa.13842
- Cartelle, C. 1992. *Edentata e megamamíferos herbívoros extintos da Toca dos Ossos (Ourolândia, Bahia, Brasil)*. Programa de Pós-Graduação em Morfologia, Universidade Federal de Minas Gerais, Tese de Doutorado, 516 p.
- Cartelle, C. 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. *Mammals of the Neotropics*, **3**:27–46.
- Cartelle, C. & Hirooka, S. 2005. The first record of *Pteronura brasiliensis* (Gmelin, 1788) (Carnivora, Mustelidae) from the Pleistocene. *Arquivos do Museu Nacional Rio de Janeiro*, **63**:595–598.
- Castro, M. 2015. Sistemática y evolución de los armadillos Dasypodini (Xenarthra, Cingulata, Dasypodidae). *Revista del Museo de La Plata Sección Paleontología*, **15**:1–50.
- Castro, M.C.; Avilla, L.S.; Freitas, M.L. & Carlini, A.A. 2013. The armadillo *Propraopus sulcatus* (Mammalia: Xenarthra) from the late Quaternary of northern Brazil and a revised synonymy with *Propraopus grandis*. *Quaternary International*, **317**:80–87. doi:10.1016/j.quaint.2013.04.032
- Dantas, M.A.T. 2012. *Contribuição ao conhecimento da megafauna pleistocênica da região intertropical brasileira*. Programa de Pós-Graduação em Ecologia, Conservação e Manejo de Vida Silvestre, Universidade Federal de Minas Gerais, Tese de Doutorado, 105 p.
- Dantas, M.A.T.; Porpino, K.D.; Bauermann, S.G.; Prata, A.D.N.; Cozzuol, M.A.; Kinoshita, A. & Baffa, O. 2011. Megafauna do Pleistoceno Superior de Sergipe, Brasil: registros taxonômicos e cronológicos. *Revista Brasileira de Paleontologia*, **14**:311–320. doi:10.4072/rbp.2011.3.10
- De Iuliis, G.; Bargo, M.S. & Vizcaíno, S.F. 2000. Variation in skull morphology and mastication in the fossil giant armadillos *Pampatherium* spp. and allied genera (Mammalia: Xenarthra: Pampatheriidae), with comments on their systematics and distribution. *Journal of Vertebrate Paleontology*, **20**:743–754. doi:10.1671/0272
- Delsuc, F.; Gibb, G.C.; Kuch, M.; Billet, G.; Hautier, L.; Southon, J. & Poinar, H.N. 2016. The phylogenetic affinities of the extinct

- glyptodonts. *Current Biology*, **26**:155–156. doi:10.1016/j.cub.2016.01.039
- Di Nucci, D.L.; Ezquiaga, M.C. & Abba, A.M. 2017. *Tunga penetrans* in Giant anteater (*Myrmecophaga tridactyla*) from Argentina. *Veterinary Parasitology: Regional Studies and Reports*, **10**:82–84. doi:10.1016/j.vprsr.2017.08.012
- Ezquiaga, M.C.; Linardi, P.M.; De Avelar, D.M. & Lareschi, M. 2015. A new species of *Tunga* perforating the osteoderms of its armadillo host in Argentina and redescription of the male of *Tunga terasma*. *Medical and Veterinary Entomology*, **29**:196–204. doi:10.1111/mve.12106
- Ezquiaga, M.C.; Rios, T.A.; Gallo, J.A. & Abba, A.M. 2020. Evidencias de pulgas en xenartros de Argentina: nuevos registros geográficos de corazas de armadillos perforadas. *Notas Sobre Mamíferos Sudamericanos*, **2**:1–8. doi:10.31687/sarem NMS.20.0.04
- Faure, M.; Guérin, C. & Parenti, F. 1999. The Holocene Megafauna from Toca do Serrote do Artur (São Raimundo Notato Archaeological Area, Piauí, Brazil). *Comptes Rendus de l'Académie des Sciences, Series IIA, Earth and Planetary Sciences*, **329**:443–448.
- Ferigolo, J. 2007. Paleopatologia em mamíferos. In: I.S. Carvalho & A.C.S. Fernandes (eds.) *Iconologia*, Sociedade Brasileira de Geologia, p. 88–107.
- Fernicola, J.C.; Rinderknecht, A.; Jones, W.; Vizcaíno, S.F. & Porpino, K.O. 2018. A new species of *Neoglyptatelus* (Mammalia, Xenarthra, Cingulata) from the Late Miocene of Uruguay provides new insights on the evolution of the dorsal armor in cingulates. *Ameghiniana*, **55**:233–253. doi:10.5710/AMGH.02.12.2017.3150
- Ferreira, J.D.; Zamorano, M. & Ribeiro, A.M. 2015. On the fossil remains of *Panochthus* Burmeister, 1866 (Xenarthra, Cingulata, Glyptodontidae) from the Pleistocene of southern Brazil. *Anais da Academia Brasileira de Ciências*, **87**:15–27. doi:10.1590/0001-3765201520140012
- Gaudin, T.J. & Wible, J.R. 2006. The phylogeny of living and extinct armadillos (Mammalia, Xenarthra, Cingulata): a craniodental analysis. In: M.T. Carrano; T.J. Gaudin; R.W. Blob & J.R. Wible (eds.) *Amniote Paleobiology, Perspectives on the evolution of Mammals, Birds and Reptiles*, The University of Chicago Press, p. 153–198.
- Gibb, G.C.; Condamine, F.L.; Kuch, M.; Enk, J.; Moraes-Barros, N.; Superina, M.; Poinar H.N. & Delsuc, F. 2016. Shotgun mitogenomics provides a reference phylogenetic framework and timescale for living xenarthrans. *Molecular Biology and Evolution*, **33**:621–642. doi:10.1093/molbev/msv250
- Góis, F. 2013. *Análisis morfológico y afinidades de los Pamphathiidae (Mammalia, Xenarthra)*. Facultad de Ciencias Naturales y Museo Universidad Nacional de La Plata, Tese de Doutorado, 263 p.
- Góis, F.; Scillato-Yané, G.J.; Carlini, A.A. & Ubilla, M. 2012. Una nueva especie de *Holmesina* Simpson (Xenarthra, Cingulata, Pamphathiidae) del Pleistoceno de Rondônia, sudoeste de la Amazonia, Brasil. *Revista Brasileira de Paleontologia*, **2**:211–227. doi:10.4072/rbp.2012.2.09
- González Ruiz, L.R.; Zurita, A.E.; Fleagle, J.; Scillato-Yané, G.J.; Dozo, M.T. & Zamorano, M. 2010. The southernmost record of a Neuryurini Hoffstetter, 1958 (Mammalia, Xenarthra, Glyptodontidae). *Paläontologische Zeitschrift*, **85**:155–161. doi:10.1007/s12542-010-0083-8
- Guérin, C.; Curvello, M.A.; Faure, M.; Huguency, M. & Mourer-Chauviré, C. 1996. The Pleistocene fauna of Piauí (Northeastern Brazil). Palaeoecological and biochronological implications. *Fundamentos*, **1**:55–103.
- Guérin, C. & Faure, M. 2008. La biodiversité mammalienne au Pléistocène supérieur – Holocène ancien dans la Région du Parc National Serra da Capivara (SE du Piauí, Brésil). *Fundamentos*, **7**:80–93.
- Ghildardi, A.M.; Fernandes, M.A. & Bichuette, M.E. 2011. Megafauna from the Late Pleistocene-Holocene deposits of the Upper Ribeira karst area, southeast Brazil. *Quaternary International*, **2**:369–378. doi:10.1016/j.quaint.2011.04.018
- Junqueira, L.C. & Carneiro, J. 2013. *Histologia básica*. 13. ed. Rio de Janeiro, Guanabara Koogan, 488 p.
- Kerber, L. & Oliveira, É.V. 2008. Novos fósseis de vertebrados para a Sanga da Cruz (Pleistoceno Superior), Alegrete, RS, Brasil. *Revista Pesquisas em Geociências*, **35**:39–45. doi:10.22456/1807-9806.17935
- Lima, F.C.G. & Porpino, K.O. 2018. Ectoparasitism and infections in the exoskeletons of large fossil cingulates. *PLoS One*, **13**:e0205656. doi:10.1371/journal.pone.0205656
- Linardi, P.M. & de Avelar, D.M. 2014. Neosomes of tungid fleas on wild and domestic animals. *Parasitology Research*, **113**:3517–3533. doi:10.1007/s00436-014-4081-8
- Lund, P.W. 1839. Blik paa Brasiliens dyreverden for sidste jorgdomvaeltning. Anden afhandling: Pattedyrene (Lagoa Santa d. 16 de novbr. 1837). *Det Kongelige Danske 90 Videnskabernes Selskabs Naturvidenskabelige og Mathematisk Afhandlinger*, **8**:61–144.
- Lund, P.W. 1842. Blik paa Brasiliens Dyreverden for Sidste orgdomvaeltning. Fjerde Afhandling: Fortsaettelse af Pattedyrene. Lagoa Santa den 30te. *Det Kongelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematisk Afhandlinger* **9**:137–208.
- Martinez, J.N. & Rincón, A.D. 2010. Los Xenarthra Cingulata del noroeste del Perú. In: CONGRESO PERUANO DE GEOLOGÍA, 15, 2010. *Publicación Especial de la Sociedad Geológica del Perú*, p. 432–435.
- Matthias, A.; McWhinney, L.A. & Carpenter, K. 2016. Pathological pitting in ankylosaur (Dinosauria) osteoderms. *International Journal of Paleopathology*, **13**:82–90. doi:10.1016/j.ijpp.2016.02.006
- McKenna, M. C.; Bell, S.K. 1997. *Classification of mammals: above the species level*. New York, Columbia University Press, 631 p.
- Missagia, R.V.; Dantas, M.A.T.; Dutra, R.P. & Cozzuol, M.A. 2012. Primeiro registro de *Pachyarmatherium brasiliense* Porpino, Bergqvist & Fernicola, 2009 (Mammalia: Cingulata) em grutas calcáreas de Lagoa Santa, Minas Gerais, Brasil. In: SIMPÓSIO BRASILEIRO DE PALEONTOLOGIA DE VERTEBRADOS, 8, 2012. *Boletim de Resumos*, Recife, p. 51.
- Mitchell, K.J.; Scanferla, A.; Soibelzon, E.; Bonini, R.; Ochoa, J. & Cooper, A. 2016. Ancient DNA from the extinct South American giant glyptodont *Doedicurus* sp. (Xenarthra: Glyptodontidae) reveals that glyptodonts evolved from Eocene armadillos. *Molecular Ecology*, **25**:3499–3508. doi:10.1111/mec.13695
- Moura, J.F.; Góis, F.; Galliari, F.C. & Fernandes, M.A. 2019. A new and most complete pamphathere (Mammalia, Xenarthra, Cingulata) from the Quaternary of Bahia, Brazil. *Zootaxa*, **3**:401–444. doi:10.11646/zootaxa.4661.3.1
- Moura, J.F.; Nascimento, C.S.I.; de Barros, G.E.; Robbi, B. & Fernandes, M.A. 2021. Damaged armour: Ichnotaxonomy and paleoparasitology of bioerosion lesions in osteoderms of Quaternary extinct armadillos. *Journal of South American Earth Sciences*, **109**:103255. doi:10.1016/j.jsames.2021.103255

- Nascimento, C.S.I.; Moura, J.F.; Robbi, B. & Fernandes, M.A. 2020. Lesions in osteoderms of pampatheres (Mammalia, Xenarthra, Cingulata) possibly caused by fleas. *Acta Tropica*, **211**:105614. doi:10.1016/j.actatropica.2020.105614
- Oliveira, É.V.; Barreto, A.M.F. & Alves, R.S. 2009. Aspectos sistemáticos, paleobiogeográficos e paleoclimáticos dos mamíferos quaternários de Fazenda Nova, PE, nordeste do Brasil. *Journal of Geoscience*, **5**:75–85. doi:10.4013/gaea.2009.52.04
- Oliveira, É.V. & Pereira, J.C. 2009. Intertropical cingulates (Mammalia, Xenarthra) from the Quaternary of Southern Brazil: systematics and paleobiogeographical aspects. *Revista Brasileira de Paleontologia*, **12**:167–178. doi:10.4072/rbp.2009.3.01
- Oliveira, É.V.; Porpino, K.O. & Barreto, A.F. 2010. On the presence of *Glyptotherium* in the Late Pleistocene of Northeastern Brazil, and the status of “*Glyptodon*” and “*Chlamydotherium*”. Paleobiogeographic implications. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, **258**:353–363. doi:10.1127/0077-7749/2010/0116
- Oliveira, E.V.; Porpino, K.O. & Silva, F.M. 2013. New material of *Pachyarmatherium* from the late Pleistocene of northeastern Brazil: insights into its morphology and systematics. *Paläontologische Zeitschrift*, **87**:505–513. doi:10.1007/s12542-013-0166-4
- Paula Couto, C. 1979. *Tratado de Paleomastozoologia*. Rio de Janeiro, Academia Brasileira de Ciências, 590 p.
- Perea, D.; Verde, M.; Montenegro, F.; Toriño, P.; Manzueti, A. & Roland, G. 2019. Insect trace fossils in glyptodonts from Uruguay. *Ichnos*, **27**:1–10. doi:10.1080/10420940.2019.1584562
- Pérez-Crespo, V.A.; Arroyo-Cabrales, J.; Alva-Valdivia, L.M.; Morales-Puente, P. & Cienfuegos-Alvarado, E. 2012. Diet and habitat definitions for Mexican glyptodonts from Cedral (San Luis Potosí, México) based on stable isotope analysis. *Geological Magazine*, **149**:153–157. doi:10.1017/S0016756811000951
- Pirrone, C.A.; Buatois, L.A. & Bromley, R.G. 2014. Ichnotaxobases for bioerosion trace fossils in bones. *Journal of Paleontology*, **88**:195–203. doi:10.1666/11-058
- Porpino, K.O. & Bergqvist, L.P. 2002. Novos achados de *Panochthus* (Mammalia, Cingulata, Glyptodontoidea) no Nordeste do Brasil. *Revista Brasileira de Paleontologia*, **4**:51–62.
- Porpino, K.O.; Fernicola, J.C. & Bergqvist, L.P. 2009. A new cingulate (Mammalia: Xenarthra), *Pachyarmatherium brasiliense* sp. nov., from the Late Pleistocene of Northeastern Brazil. *Journal of Vertebrate Paleontology*, **29**:881–893. doi:10.1671/039.029.0305
- Porpino, K.O.; Fernicola, J.C. & Bergqvist, L.P. 2010. Revisiting the intertropical Brazilian species *Hoplophorus euphractus* (Cingulata, Glyptodontoidea) and the phylogenetic affinities of *Hoplophorus*. *Journal of Vertebrate Paleontology*, **30**:911–927. doi:10.1080/02724631003765735
- Porpino, K.O.; Fernicola, J.C.; Cruz, L.E. & Bergqvist, L.P. 2014. The intertropical Brazilian species of *Panochthus* (Xenarthra, Cingulata, Glyptodontoidea): a reappraisal of their taxonomy and phylogenetic affinities. *Journal of Vertebrate Paleontology*, **34**:1165–1179. doi:10.1080/02724634.2014.863203
- Porpino, K.O.; Santos, M.F.C.F. & Bergqvist, L.P. 2004. Registro de mamíferos fósseis no Lajedo de Soledade, Apodi, Rio Grande do Norte, Brasil. *Revista Brasileira de Paleontologia*, **7**:349–358. doi:10.4072/rbp.2004.3.06
- Reyes-Céspedes, A.E.; Carlini, A.A. & Carrillo-Briceño, J.D. 2022. New record of *Pachyarmatherium* (Cingulata: Pachyarmatheriidae) from the Late Pleistocene in Venezuela. *Anartia*, **35**:7–13. doi:10.5281/zenodo.7951590
- Ribeiro, A.D.F.; Pereira, C.P. & Magalhães, A.C.F. 2002. *Mármora Bege Bahia em Ourulândia-Mirangaba-Jacobina, Bahia: geologia, potencialidade e desenvolvimento sustentável*. Salvador, Companhia Baiana de Pesquisa Mineral, 53 p.
- Ribeiro, A.M.; Scherer, C.D. & Pitana, V.G. 2007. Mamíferos do Pleistoceno do Rio Grande do Sul, Brasil: Estado atual do conhecimento. In: WORKSHOP QUATERNÁRIO DO RS – INTEGRANDO CONHECIMENTOS, 2007. Canoas, Resumos, p. 25.
- Ribeiro, A.M. & Scherer, C.S. 2009. Mamíferos do Pleistoceno do Rio Grande do Sul, Brasil. In: A.M. Ribeiro; S.G. Bauermann & C.S. Scherer (eds.) *Quaternário do Rio Grande do Sul: Integrando Conhecimentos*, SBP, p. 171–192.
- Ribeiro, R.C. & Carvalho, I.S. 2009. Megafauna do Quaternário tardio de Baixa Grande, Bahia, Brasil. *Anuário do Instituto de Geociências*, **32**:42–50. doi:10.11137/2009_2_42-50
- Ruffer, M.A. 1914. Studies in palaeopathology in Egypt. *The Journal of Pathology and Bacteriology*, **18**:149–162.
- Sato, K. & Jenkins, R.G. 2020. Mobile home for pholadoid boring bivalves: First example from a late Cretaceous sea turtle in Hokkaido Japan. *Palaaios*, **35**:228–236. doi:10.2110/palo.2019.077
- Scherer, C.S.; Moraes, S.S. & Oliveira, T.V. 2016. *Projeto FIOLE salvamento paleontológico: Uma ponte entre a universidade e a sociedade*. Salvador, UFBA, 154 p.
- Scherer, C.S.; Pales, L.F.M.; Rosa, M. & Silva, S.A. 2017. Chronological, taphonomical, and paleoenvironmental aspects of a Late Pleistocene mammalian fauna from Guanambi, Bahia, Brazil. *Journal of South American Earth Sciences*, **79**:95–110. doi:10.1016/j.jsames.2017.07.016
- Schmitz, P.I. 1990. O povoamento pleistocênico do Brasil. *Revista de Arqueologia Americana*, **1**:9–32.
- Silva, F.M.; Filgueiras, C.F.C.; Barreto, A. & Oliveira, E.V. 2010. Mamíferos do Pleistoceno Superior de Afrânio, Pernambuco, nordeste do Brasil. *Quaternary and Environmental Geosciences*, **2**:1–11. doi:10.5380/abequa.v2i1-2.14182
- Silva, F.M.; Oliveira, E.V. & Porpino, K.O. 2012. Presença de *Neuryurus* (Cingulata, Glyptodontidae) em Fazenda Nova, Brejo da Madre de Deus, Estado de Pernambuco, Brasil. In: SIMPÓSIO BRASILEIRO DE PALEONTOLOGIA DE VERTEBRADOS, 8, 2012. *Boletim de Resumos*, SBP, p. 174.
- Silva, R.C.; Berbert-Born, M.; Bustamante, D.E.F.; Santoro, T.N.; Sedor, F. & Avilla, L.S. 2019. Diversity and preservation of Pleistocene tetrapods from caves of southwestern Bahia, Brazil. *Journal of South American Earth Sciences*, **90**:233–254. doi:10.1016/j.jsames.2018.12.004
- Silveira, C.J.S.D.; Frantz, J.C.; Marques, J.C.; Queiroz, W.J.A.D.; Roos, S. & Peixoto, V.M. 2015. Geocronologia U-Pb em zircão de rochas intrusivas e de embasamento na região do Vale do Jacurici, Cráton São Francisco, Bahia. *Brazilian Journal of Geology*, **45**:453–474. doi:10.1590/2317-488920150030233
- Soibelzon, E.; Avilla, L.S. & Castro, M. 2015. The cingulates (Mammalia: Xenarthra) from the late Quaternary of northern Brazil: Fossil records, paleoclimates and displacements in America. *Quaternary International*, **377**:118–125. doi:10.1016/j.quaint.2015.02.052

- Soibelzon, E.; Miño-Boilini, Á.R.; Zurita, A.E. & Krmpotic, C.M. 2010. Los Xenarthra (Mammalia) del Ensenadense (Pleistoceno inferior a medio) de la región pampeana (Argentina). *Revista Mexicana de Ciencias Geológicas*, **3**:449–469.
- Souza, J.D.; Melo, R.C. & Kosin, M. (coord.). Mapa geológico do estado da Bahia. Versão 1.1. Salvador: CPRM, 2003. Escala 1:1.000.000.
- Tomassini, R.L.; Montalvo, C.I. & Ezquiaga, M.C. 2016. The oldest record of flea/armadillos interaction as example of bioerosion on osteoderms from the late Miocene of the Argentine Pampas. *International Journal of Paleopathology*, **15**:65–68. doi:10.1016/j.ijpp.2016.08.004
- Truman, R.W. 2005. Leprosy in wild armadillos. *Leprosy Review*, **76**:198–208.
- Vieira, L.C. 2007. *A Formação Sete Lagoas (Grupo Bambuí) e as variações paleoambientais no final do Proterozóico*. Programa de Pós-Graduação em Geofísica, Universidade de São Paulo, Tese de Doutorado, 258 p.
- Wenker, C.J.; Kaufman, L.; Bacciarini, L.N. & Robert, N. 1998. Sporotrichosis in a nine-banded armadillo (*Dasypus novemcinctus*). *Journal of Zoo and Wildlife Medicine*, **29**:474–478.
- Wisshak, M.; Knaust, D. & Bertling, M. 2019. Bioerosion ichnotaxa: review and annotated list. *Facies*, **65**:1–39. doi:10.1007/s10347-019-0561-8
- Wolf, D. 2007. Osteoderm histology of extinct and recent Cingulata and Phyllophaga (Xenarthra, Mammalia): Implications for biomechanical adaptation and systematic. *Hallesches Jahrbuch für Geowissenschaften*, **23**:145–151.
- Zonneveld, J.P.; Bartels, W.S.; Gunnell, G.F. & McHugh, L.P. 2015. Borings in early Eocene turtle shell from the Wasatch Formation, South Pass, Wyoming. *Journal of Paleontology*, **89**:802–820. doi:10.1017/jpa.2015.61
- Zurita, A.E. & Ferrero, B.A. 2009. New species of *Neuryurus* Ameghino (Mammalia, Glyptodontidae) from the late Pleistocene of the Mesopotamic region of Argentina. *Geobios*, **42**:663–673. doi:10.1016/j.geobios.2009.03.003
- Zurita, A.E.; Gillette, D.D.; Cuadrelli, F. & Carlini, A.A. 2018. A tale of two clades: comparative study of *Glyptodon* Owen and *Glyptotherium* Osborn (Xenarthra, Cingulata, Glyptodontidae). *Geobios*, **51**:247–258. doi:10.1016/j.geobios.2018.04.004
- Zurita, A.E.; Miño-Boilini, A.; Francia, A. & Arenas-Mosquera, J. E. 2012. The Pleistocene Glyptodontidae Gray, 1869 (Xenarthra: Cingulata) of Colombia and some considerations about the South American Glyptodontinae. *Revista Brasileira de Paleontologia*, **15**:273–280. doi:10.4072/rbp.2012.3.04
- Zurita, A.E.; Soibelzon, E. & Carlini, A.A. 2006. *Neuryurus* (Xenarthra, Glyptodontidae) in the Lujanian (late Pleistocene-early Holocene) of the Pampean region. *Neues Jahrbuch für Geologie und Paläontologie-Monatshefte*, **2006**:78–88. doi:10.1127/njgpm/2006/2006/78
- Zurita, A. E.; Soibelzon, E.; Scillato-Yané, G. J. & Cenizo, M. 2009. The earliest record of *Neuryurus* Ameghino (Mammalia, Glyptodontidae, Hoplophorinae). *Alcheringa*, **33**:49–57. doi:10.1080/03115510802618250

Received in 03 February, 2023; accepted in 18 September, 2023