

# New bioerosion traces in rhynchosaur bones from the Upper Triassic of Brazil and the oldest occurrence of the ichnogenera *Osteocallis* and *Amphifaoichnus*

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New bioerosion traces produced by insects in bones are reported from the *Hyperodapedon* Assemblage Zone of the Santa Maria Supersequence (Carnian, Brazil). The bones are assigned to a single rhynchosaur *Hyperodapedon mariensis* individual and among the traces, the ichnogenera *Osteocallis* (*Osteocallis mandibulus*, *Osteocallis infestans*, and *Osteocallis* isp.) and *Amphifaoichnus* (*Amphifaoichnus* isp.) are recognized, along with two morphotypes of indistinct traces: clusters of grooves and borings. All the traces are assigned to the action of insects exploring the rhynchosaur carcass. *Osteocallis* and associated clusters of grooves are interpreted as feeding traces, but whether they represent necrophagic or osteophagic behavior is still uncertain. The lack of direct evidence for the ethological interpretation of *Amphifaoichnus* precludes its sole correlation with osteophagy, and other possibilities, such as the construction of temporary domiciles related to feeding or sediment moisture, are discussed. The traces analyzed here indicate that the insects explored a buried carcass, challenging the automatic association of *Osteocallis* and prolonged subaerial exposure of bones, placing insects as relevant taphonomic agents that affect the preservation of vertebrate carcasses. Additionally, the first appearance record of *Amphifaoichnus* is expanded back more than 140 Ma, indicating that complex behaviors employed by insects in bone exploration were already established in the early Late Triassic, shortly after the oldest records of invertebrate bioerosion in bones on continental settings.

Key words: Rhynchosauria, ichnotaxonomy, insect, osteophagy, paleoecology, taphonomy, vertebrate carcass, Triassic, Santa Maria Supersequence, Brazil.

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## Introduction

Bioerosion traces produced by insects in bones are of great paleoecological and taphonomical importance. They are direct evidence of interaction between these arthropods and vertebrate skeletal remains, revealing aspects of their biostratinomic history. Not rarely, the environmental conditions of past ecosystems are reconstructed or corroborated based on the information gathered from the bioerosion traces found in bones and the identification of the possible producer and its behavior (e.g., Rogers 1992; Martin and

West 1995; Hasiotis et al. 1999; Gatta et al. 2021). Since the 1990s, the number of studies focusing on fossil bioerosion made by insects in bones preserved in continental settings have increased, both in paleontology and archeology (e.g., Rogers 1992; Roberts et al. 2007; Hutchet et al. 2011, 2013; Pirrone and Buatois 2016; Wrobel and Biggs 2018; Backwell et al. 2020). Consequently, a variety of recurrent morphologies have been identified, raising questions and hypotheses about the possible behaviors and producers associated with them, and also allowing for the ichnotaxonomical classification of several traces (Roberts et al. 2007; Xing et al.

2013; Pirrone et al. 2014; Pirrone and Buatois 2016; Xing et al. 2016; Paes Neto et al. 2016; Parkinson 2016; Höpner and Bertling 2017; Serrano-Brañas et al. 2018).

The oldest records of bioerosion trace fossils produced by insects in bones date from the latest Middle Triassic (Paes Neto et al. 2016), revealing that the usage of bones as a substrate by terrestrial species is nearly as old as the origin of some of the groups that show this behavior in the present (e.g., Dermestidae beetles; Zhang et al. 2018). Up until now, however, only two full articles focusing on Triassic insect bioerosion in bones were published (Leal et al. 2002; Paes Neto et al. 2016); other publications that report these traces are either abstracts or articles focusing on other subjects (Müller et al. 2015; Francischini et al. 2018; Pavanatto et al. 2018; Medeiros et al. 2019; Battista et al. 2021). Remarkably, all the mentioned records came from the Middle–Upper Triassic Santa Maria Supersequence (SMS) of Rio Grande do Sul State, southern Brazil. In this contribution, we bring novel and important data from the Brazilian SMS, contributing to the advance of ichnotaxonomical discussions and expanding knowledge about the use of bone substrate by insects in the Triassic.

*Institutional abbreviations.*—CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, Santa Maria, Brazil; IPR-PUCRS, Instituto do Petróleo e dos Recursos Naturais, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; UFRGS-PV, Laboratório de Paleontologia de Vertebrados, Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

*Other abbreviations.*—AZ, Assemblage Zone; SMS, Santa Maria Supersequence.

## Geological setting

The Paraná Basin covers an area of about 1 500 000 km<sup>2</sup> of Brazil, Uruguay, Paraguay, and Argentina and comprises a package up to 7000 m thick, ranging from Ordovician to Cretaceous (Fig. 1A, B; Milani et al. 2007). The Triassic deposits of the Paraná Basin are restricted to its southernmost portion, in the state of Rio Grande do Sul (Fig. 1A, B) and are divided into two second-order sequences (Zerfass et al. 2003): the Sanga do Cabral Supersequence (Lower Triassic) and the Santa Maria Supersequence (Middle–Upper Triassic; Fig. 1D). In this latter, four third-order sequences can be recognized from bottom to top (sensu Horn et al. 2014; Fig. 1D): Pinheiros-Chiniquá Sequence (Ladinian–Carnian), Santa Cruz Sequence (lower Carnian), Candelária Sequence (Carnian–Norian) and Mata Sequence (Rhaetian?). Except by this latter, all the SMS sequences yield a rich vertebrate fossil record, which occurs in, at least, four distinct assemblage zones (AZ). The Pinheiros-

Chiniquá Sequence comprises the *Dinodontosaurus* AZ, the Santa Cruz Sequence comprises the *Santacruzodon* AZ and the Candelária Sequence comprises both the *Hyperodapedon* AZ (at the base of the sequence) and the *Riograndia* AZ (at the top).

The fossil record of the *Hyperodapedon* AZ, the main focus of this work, is characterized by the presence and abundance of the genera *Hyperodapedon*, a rhynchosaur, and *Exaeretodon*, a traversodontid cynodont, and is mostly composed of other cynodonts (e.g., *Trucidocynodon*, *Charruodon*, and *Alemoatherium*) and archosauromorphs (e.g., *Aetosauroides*, *Rauisuchus*, *Ixalerpeton*, *Gnathovorax*, and *Saturnalia*) (Schultz et al. 2020). This faunal content is similar to what is found in the Argentinean Ischigualasto Formation (e.g., Desojo et al. 2020). Recently, Schultz et al. (2020) suggested that the *Hyperodapedon* AZ could be subdivided into a lower portion characterized by the abundance of this rhynchosaur and the lack of the traversodontid cynodont *Exaeretodon*, and an upper *Exaeretodon* sub-AZ where the abundance of *Hyperodapedon* decreases and the dominant taxa are *Exaeretodon* and the hyperodapedontine rhynchosaur *Teyumbaita*. The Ischigualasto Formation presents a similar pattern of succession with an abundance of *Hyperodapedon* in its lower portion and an abundance of *Exaeretodon* in its upper portion, allowing direct biostratigraphic correlation with the SMS. The U-Pb zircon geochronology study of Langer et al. (2018) indicated an age of  $233.23 \pm 0.73$  Ma for the most iconic outcrop with fossils of the *Hyperodapedon* AZ, the Cerro da Alemoa site, in Santa Maria City, which would place this biozone in the middle Carnian.

Lithologically, the base of the Candelária Sequence is composed mainly of trough cross bedded sandstones, interpreted as a fluvial system. This facies is overlain by red, massive or laminated mudstones, representing shallow lacustrine deposits and a transition between a lowstand and a transgressive system tract. Upwards, this sequence presents a coarsening trend with decrease in the mudstone content and increase of amalgamated sandstone, which would indicate a progressive replacement of the lacustrine system by a fluvial system (Zerfass et al. 2003).

## Material and methods

The materials described here were collected in an area smaller than 2 m<sup>2</sup> in the Buriol Site (29°39'10" S, 53°26'35" W), approximately 6 km southeast of the municipality of São João do Polêsine, in the state of Rio Grande do Sul, Brazil (Fig. 1C). It consists of hundreds of pieces of disarticulated or fragmented bones, which can be assigned to a single *Hyperodapedon mariensis* individual based on: (i) the presence of the combination of the following characters: a single groove on the ventral portion of the maxilla, the presence of teeth in the lingual surface of the dentary blade and the lack of lingual teeth in the maxilla (Langer and Schultz 2000); (ii) size correspondence between the elements; (iii) the lack

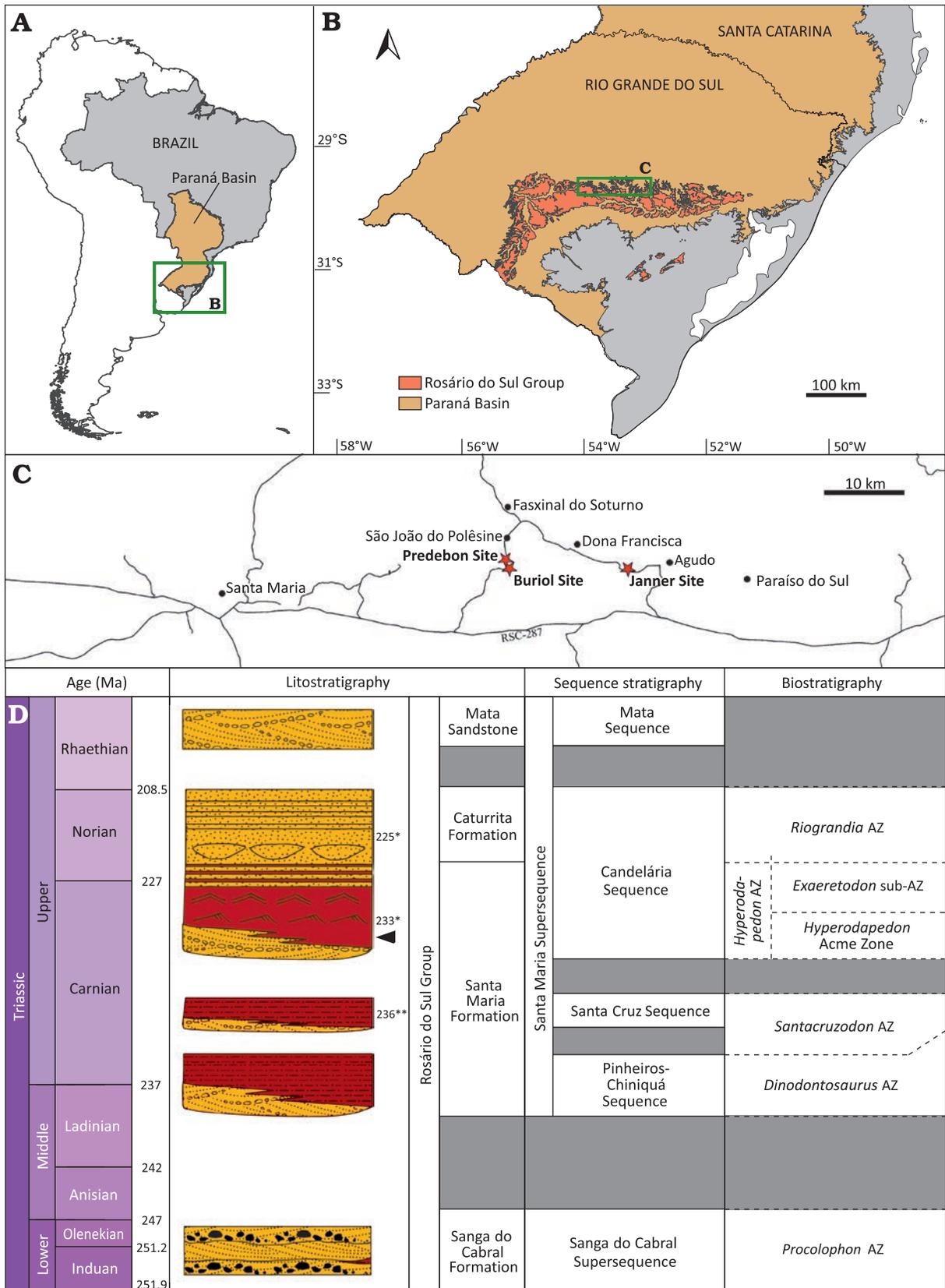


Fig. 1. Geological and geographic context. **A.** Location of the Paraná Basin in Brazil. **B.** Limits of the Triassic rocks of Rosário do Sul Group and the Triassic rocks of Paraná Basin in Rio Grande do Sul state. **C.** Location of the Buriol Site, locality of UFRGS-PV-1581-T, and nearby Predebon and Janner sites. **D.** Chrono-, lito-, and biostratigraphy of southern Brazilian Triassic (modified from Schultz et al. 2020). Arrow indicates stratigraphical position of UFRGS-PV-1581-T; \* refers to absolute ages from Langer et al. (2018); \*\* refers to absolute ages from Philipp et al. (2018).

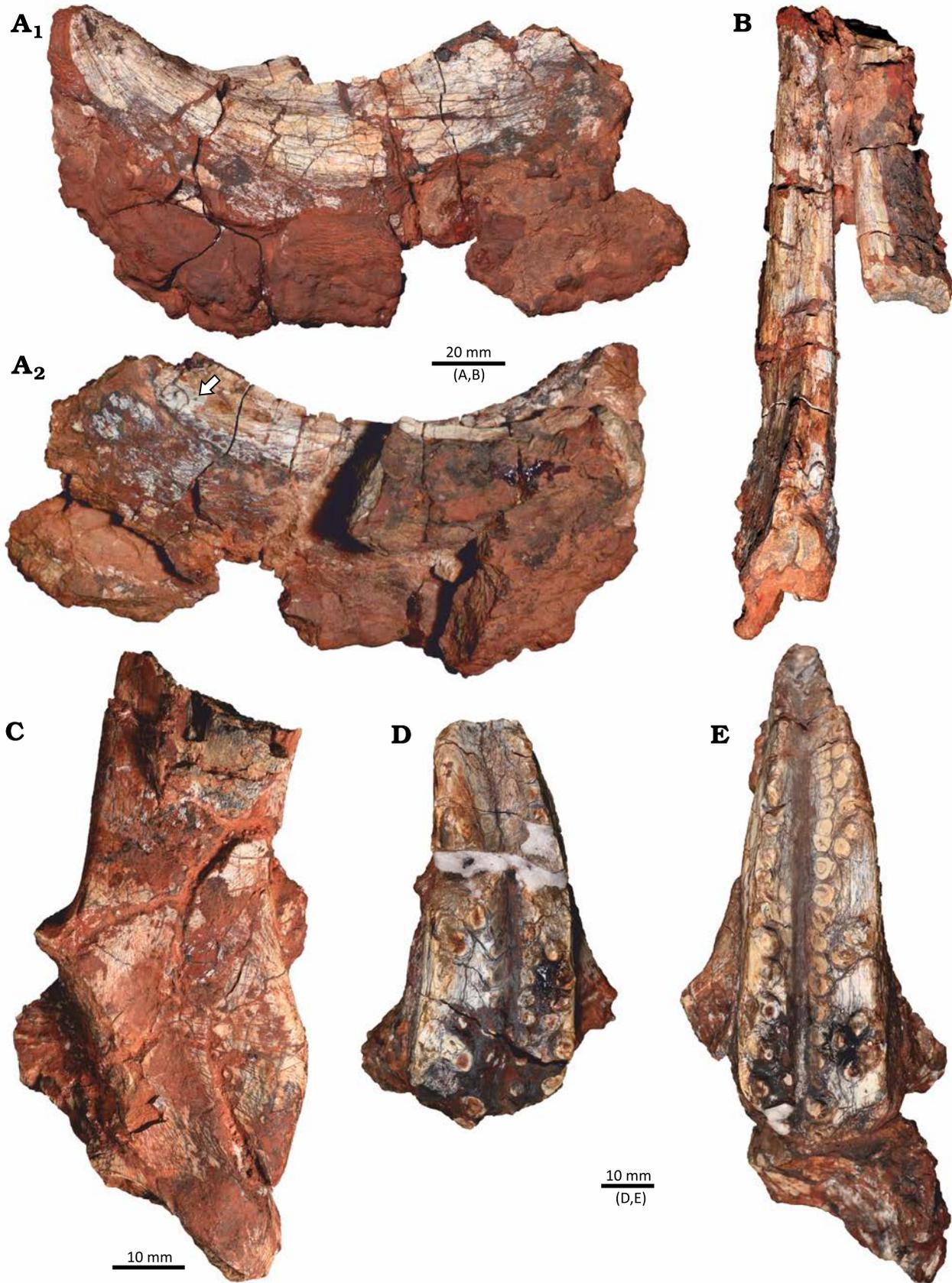


Fig. 2. Identified cranial elements of the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933) in UFRGS-PV-1581-T from Buriol Site, Brazil, *Hyperodapedon* AZ, Carnian. **A.** Left dentary in lateral view (**A<sub>1</sub>**) and medial view (**A<sub>2</sub>**) showing the dentary blade with at least one lingual tooth (arrow). **B.** Left and right dentaries in dorsal view. **C.** Partial left pterygoid in medial view. **D.** Right maxilla in ventral view. **E.** Left maxilla in ventral view.

of bone element duplication; and (iv) the lack of evidence of transportation and reworking. Some of the bone fragments are covered by a concretion, indicating that at least some of the fragmentation occurred prior to diagenesis. The better-preserved skull elements consist of the partial left and right dentaries in articulation, disarticulated partial left and right maxillae and a partial left pterygoid (Fig. 2). No bioerosion traces were found in these elements.

The identification of this material as *Hyperodapedon mariensis*, along with the faunal content of nearby sites, such as Predebon Site (Fig. 1D), suggests the record represents the lower portion of the *Hyperodapedon* AZ. Sites in this region have yielded remains of the rhynchosaur *Hyperodapedon*, the aetosaur *Aetosauroides*, the sauropodomorph *Buriolestes*, the lagerpetid *Ixalerpeton*, and the stereospondyl *Compsocerops* (Langer et al. 2007; Cabreira et al. 2016; Dias-Da-Silva et al. 2012; Roberto-Da-Silva et al. 2014; Paes Neto et al. 2021), reinforcing our interpretation.

The studied specimen received the collection numbers UFRGS-PV-1581-T and CAPP/UFMS 0383. Each of the trace-bearing fragments was numbered and will be referred to as UFRGS-PV-1581-T # (Table 1). The fossils were mechanically prepared using standard methods. In total, 520 fragments were analyzed and prospected for traces under an Opticam OPZTS stereomicroscope at magnifications of 10×, 16×, 25×, and 40×. The 29 trace-bearing bone pieces were photographed under different angles of lighting, allowing for the highlight of the traces and more accurate analyzes. For digital measurement of the traces, the software ImageJ 1.53k was used. UFRGS-PV-1581-T #3 was scanned with a SkyScan 1173 CT scan in the IPR-PUCRS. It was used 130 kv and 61 μA and 1800 slices with a voxel size of 21.9 μm were obtained. The slices were analyzed with the software 3D Slicer 5.2.1. The description of the traces followed the nomenclature and ichnotaxobases proposed by Pirrone et al. (2014).

## Results

From the 520 bone fragments analyzed, only 29 present bioerosion traces. Among them, the ichnogenera *Amphifaoichnus* and *Osteocallis*, this latter represented by at least two ichnospecies (*O. mandibulus* and *O. infestans*), were recognized due to their discrete morphology. Other traces, however, do not have a clear morphology and, in consequence, do not fall within any known ichnotaxon. Therefore, we opted to describe them using an open nomenclature (morphotypes). They are described properly below.

## Systematic palaeoichnology

Ichnogenus *Amphifaoichnus* Pirrone & Buatois, 2016

Type ichnospecies: *Amphifaoichnus seilacheri* Pirrone & Buatois, 2016, Plottier Formation, Argentina, Coniacian–lower Santonian (Upper Cretaceous).

Table 1. List of traces in each bone fragment.

Specimen	Traces
UFRGS-PV-1581-T #1	<i>Osteocallis mandibulus</i>
UFRGS-PV-1581-T #2	<i>Osteocallis mandibulus</i>
UFRGS-PV-1581-T #3 (Figs. 3A, 4A, 8A)	<i>Osteocallis mandibulus</i> ; <i>Amphifaoichnus</i> isp.; Morphotype 2 (boring)
UFRGS-PV-1581-T #4 (Fig. 3B)	<i>Amphifaoichnus</i> isp.
UFRGS-PV-1581-T #5 (Fig. 6C)	<i>Osteocallis mandibulus</i> ; Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #6 (Fig. 6E)	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #7 (Fig. 8B)	Morphotype 2 (boring)
UFRGS-PV-1581-T #8	<i>Osteocallis mandibulus</i> ; Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #9 (Fig. 8C)	Morphotype 2 (boring)
UFRGS-PV-1581-T #10 (Fig. 3C)	<i>Amphifaoichnus</i> isp.
UFRGS-PV-1581-T #11 (Fig. 4D)	<i>Osteocallis</i> isp.; Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #12 (Fig. 4C)	<i>Osteocallis infestans</i>
UFRGS-PV-1581-T #13 (Fig. 7B)	Morphotype 1 (subcircular cluster of grooves)
UFRGS-PV-1581-T #14 (Fig. 5)	<i>Osteocallis mandibulus</i> ; Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #15	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #16 (Fig. 7C)	Morphotype 1 (subcircular cluster of grooves)
UFRGS-PV-1581-T #17 (Figs. 6F, 7A)	Morphotype 1 (subcircular cluster of grooves)
UFRGS-PV-1581-T #18	<i>Osteocallis mandibulus</i>
UFRGS-PV-1581-T #19	<i>Osteocallis mandibulus</i>
UFRGS-PV-1581-T #20 (Fig. 6A)	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #21	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #22 (Fig. 6B)	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #23 (Fig. 4B)	<i>Osteocallis mandibulus</i> ; Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #24	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #25	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #26 (Fig. 6D)	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #27	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #28	Morphotype 1 (cluster of grooves)
UFRGS-PV-1581-T #29	Morphotype 1 (cluster of grooves)

*Emended diagnosis*.—Predominantly horizontal, unbranched, unlined, elongated tubes, circular or subcircular in cross-section, straight or tortuous, located at the interface between bone and sediment, but penetrating the cortical bone tissue and occasionally the trabecular bone tissue; fill consists of both unconsolidated sediment and bone chips; rough texture of the exposed surface (modified from Pirrone and Buatois 2016).

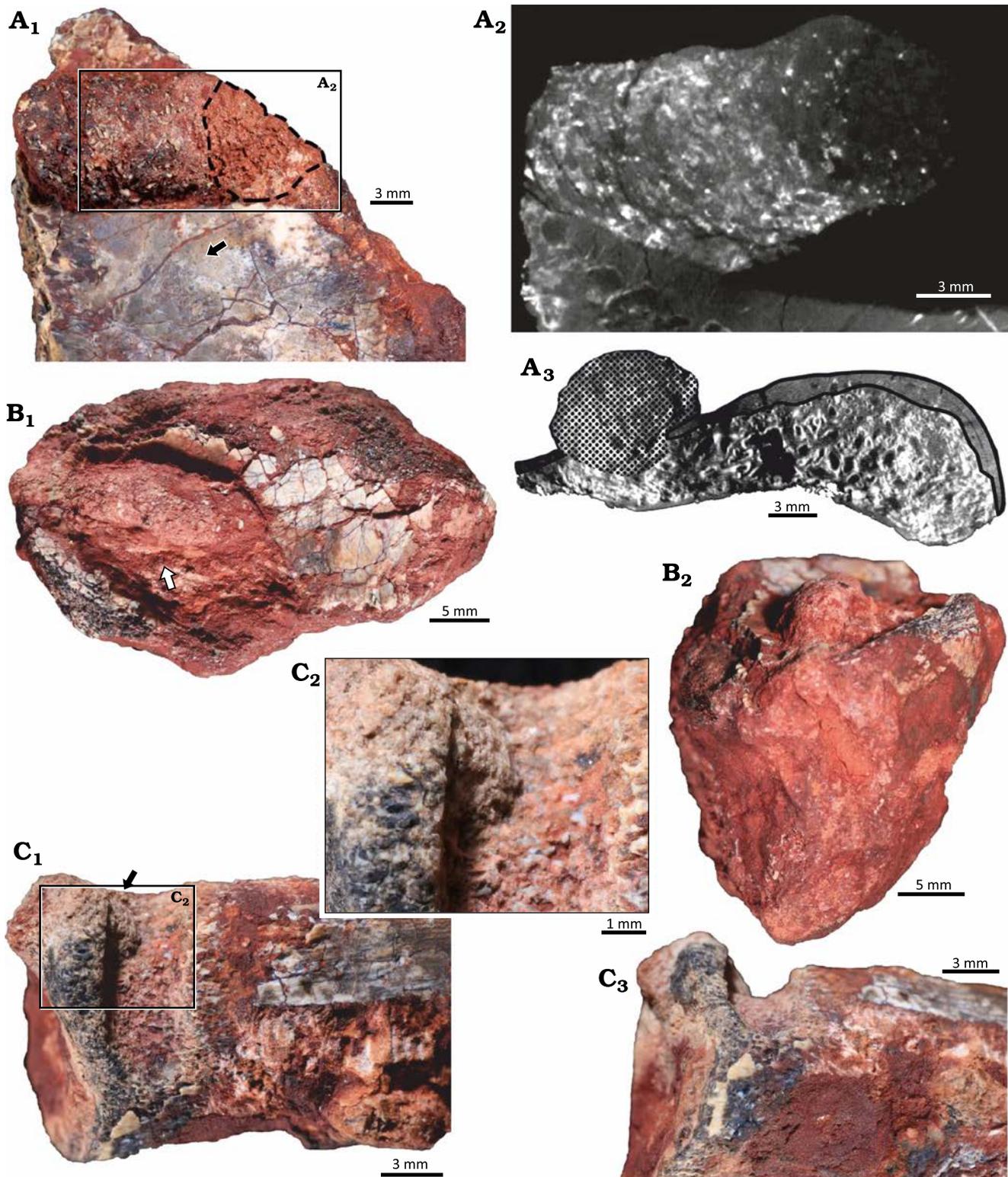


Fig. 3. Arthropod bioerosion trace fossil *Amphifaoichnus* isp. on bone fragments of the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933) from Buriol Site, Brazil, *Hyperodapedon* AZ, Carnian. **A.** UFRGS-PV-1581-T #3; A<sub>1</sub>, close up showing *Amphifaoichnus* isp. (note the bone chips) associated to a perpendicular boring (dashed outline) and feeding traces of *Osteocallis mandibulus* Roberts et al., 2007 (arrow; see also Fig. 4A<sub>1</sub>); A<sub>2</sub>, axial view of  $\mu$ CT scan showing the internal morphology of the tube, meniscate structures and the perpendicular boring; A<sub>3</sub>, coronal view of  $\mu$ CT scan showing the trace (dotted surface) and the destruction of both cortical (black outline) and trabecular bone. **B.** UFRGS-PV-1581-T #4; B<sub>1</sub>, specimen (arrow) showing the uneven distribution of bone chips in the filling; B<sub>2</sub>, specimen in transversal view showing the rounded morphology of the filling. **C.** UFRGS-PV-1581-T #10; C<sub>1</sub>, specimen in negative relief with a small portion of filling still preserved (arrow); C<sub>2</sub>, close up of filling; C<sub>3</sub>, specimen in transversal view showing the U-shape of the boring.

*Remarks.*—The original diagnosis proposed by Pirrone and Buatois (2016) only mentions the penetration of cortical bone tissue. Because the traces described below also penetrate trabecular bone, we emended the diagnosis of *Amphifaoichnus* in order to properly accommodate them in the ichnogenus.

*Amphifaoichnus* isp.

Fig. 3.

*Material.*—UFRGS-PV-1581-T #3 (Fig. 3A), UFRGS-PV-1581-T #4 (Fig. 3B), and UFRGS-PV-1581-T #10 (Fig. 3C), bone fragments assigned to *Hyperodapedon mariensis*; from Buriol Site, São João do Polêsine municipality, Rio Grande do Sul State, Brazil; base of the Candelária Sequence (vertebrate remains associated to the lower subunit of the *Hyperodapedon* AZ), SMS, Paraná Basin; middle Carnian (lower Upper Triassic).

*Description.*—Elongated, straight to slightly meandering tubes located in the interface between bone and substrate but penetrating cortical and trabecular bone (Fig. 3A<sub>3</sub>). Tubes are subcircular in cross section and are filled with sediment identical to the rock matrix and bone chips apparently unevenly distributed in the filling (Fig. 3A<sub>1</sub>, B<sub>1</sub>). Tube length is 9.6–22.2 mm and the width is 3.9–9.1 mm. At least one tube presents structures indicating a meniscate backfill (Fig. 3A<sub>2</sub>).

*Remarks.*—In opposition to *Amphifaoichnus seilacheri*, the tubes described here are not restricted to cortical bone but penetrate to trabecular bone as well. The tubes on UFRGS-PV-1581-T #3 and UFRGS-PV-1581-T #4 are preserved in positive relief, as expected for *Amphifaoichnus*, but UFRGS-PV-1581-T #10 is preserved in a negative relief (Fig. 3C). Its assignment to *Amphifaoichnus* is based on the morphological similarities to the other tubes and the presence of a small portion of fill formed by sediment and bone chips at its base and close to its boundary (Fig. 3C<sub>2</sub>). The tube on UFRGS-PV-1581-T #3 is penetrated by a boring trace, so that one of its extremities is not as well preserved, internally and externally (Fig. 3A<sub>1</sub>). The presence of meniscate structures on UFRGS-PV-1581-T #3 filling is revealed by  $\mu$ CT scan analysis and the segments are visible only in the termination which was not altered by the second boring (Fig. 3A<sub>2</sub>). *Amphifaoichnus seilacheri* is characterized by evenly distributed bone chips in the infill sorted by size, a feature visible only in cross section. On the surface of the filling in UFRGS-PV-1581-T #3 and #4 no pattern of distribution is observed, which could be indicative of unevenly distributed bone chips (Fig. 3A<sub>1</sub>, B<sub>1</sub>). However, due to the low number of available specimens of *Amphifaoichnus* in UFRGS-PV-1581-T, destructive methods were avoided, preventing the analysis of bone chip distribution in cross section. Meniscate structures are not mentioned by Pirrone and Buatois (2016), but the methods used to reveal this structure in UFRGS-PV-1581-T #3 were not applied to *A. seilacheri*. Another significant difference between the Triassic and Cretaceous specimens comprises the penetration into the trabecular bone, but this feature might be a consequence of differences between the substrates (e.g.,

thicker cortical bone tissue in the Cretaceous specimens). Considering that *Amphifaoichnus* specimens are considerably rare (up to now, restricted to the Upper Triassic of Brazil and Upper Cretaceous of Argentina) and that possible influence of taphonomic processes over the trace-bearing bones is still perplexing, new materials (fossil and recent), might bring additional information regarding ichnospecific diversity of *Amphifaoichnus* traces. A detailed discussion on the ichnotaxonomy of *Amphifaoichnus* is beyond the scope of this work and will be published elsewhere. Therefore, the traces UFRGS-PV-1581-T #3, #4, and #10 are here assigned to *Amphifaoichnus* isp.

Ichnogenus *Osteocallis* Roberts et al., 2007, sensu Paes Neto et al., 2016

*Type ichnospecies:* *Osteocallis mandibulus* Roberts et al. 2007, Maevrano Formation, Madagascar, Maastrichtian (Late Triassic).

*Diagnosis.*—Shallow trail of mandibular grooves bored into external (cortical) bone surfaces. It may present as a single trail or a network of randomly overlapping trails.

*Osteocallis mandibulus* Roberts et al., 2007

Figs. 4A, B, 5A, B, E.

*Diagnosis.*—Shallow, meandering trail of arcuate grooves (apparently paired) bored into external (cortical) bone surfaces. Occurs as single trails or network of randomly overlapping trails.

*Material.*—UFRGS-PV-1581-T #2, #5 (Fig. 6C), #8, #19, and #23 (Fig. 4B) present single trails. UFRGS-PV-1581-T #3 (Fig. 4A) and UFRGS-PV-1581-T #18 present two trails without overlapping. UFRGS-PV-1581-T #1 presents two overlapping trails and UFRGS-PV-1581-T #14 (Fig. 5A, B, E) presents three trails without overlapping. All of these bone fragments are referred to *Hyperodapedon mariensis* from Buriol Site, São João do Polêsine municipality, Rio Grande do Sul State, Brazil; Base of the Candelária Sequence (vertebrate remains associated to the lower subunit of the *Hyperodapedon* AZ), SMS, Paraná Basin; middle Carnian (lower Upper Triassic).

*Description.*—All 14 trails formed by successive mainly arcuate and apparently paired grooves on the bone surface (Figs. 4, 5A, B, E, 6C). In some cases, the grooves overlap, forming long arcuate grooves or crossing each other. Most of the trails present some degree of meandering. Trail length is 1.1–21.5 mm and the width is 0.1–4.4 mm.

*Remarks.*—The grooves that compose the trails are not always arcuate, with some trails also presenting straight grooves. *Osteocallis leonardii* (Collareta et al. 2023) presents both straight and arcuate grooves as well, but in opposition to the materials referred herein to *O. mandibulus*, the grooves are predominantly straight. In some of the trails it is difficult to ascertain if the grooves are indeed paired, especially when their overlapping results in long arcuate grooves. This makes the precise measurement of individual grooves nearly

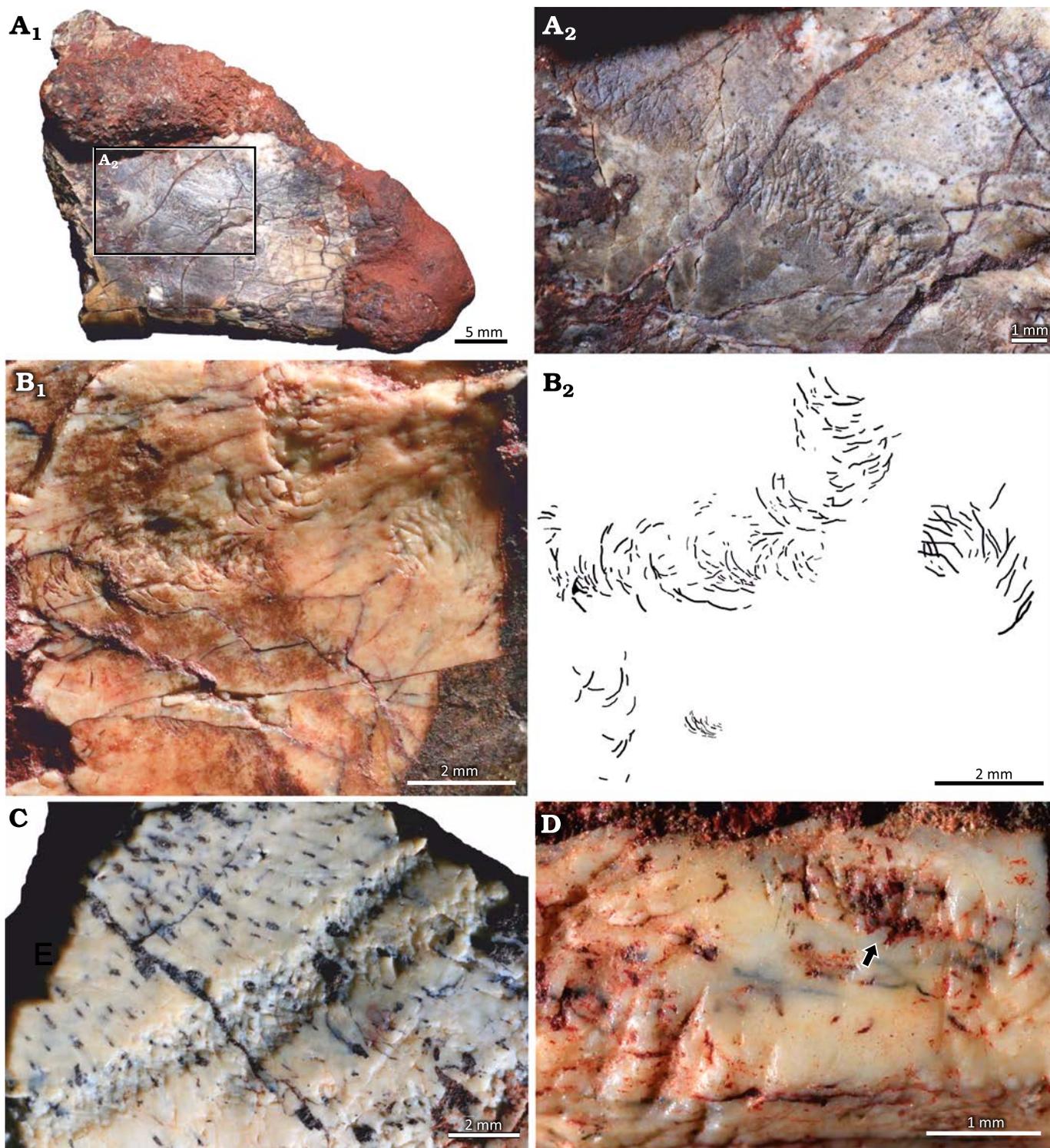


Fig. 4. Feeding traces of *Osteocallis* on bone fragments of the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933) from Buriol Site, Brazil, *Hyperodapedon* AZ, Carnian. **A.** UFRGS-PV-1581 #3; **A<sub>1</sub>**, *Osteocallis mandibulus* Roberts et al., 2007, associated to arthropod bioerosion trace fossil *Amphifaoichnus* isp.; **A<sub>2</sub>**, details of one of the trails. **B.** UFRGS-PV-1581 #23; **B<sub>1</sub>**, *Osteocallis mandibulus* associated to a cluster of grooves in crescent shape; **B<sub>2</sub>**, schematic drawing highlighting the grooves. **C.** UFRGS-PV-1581-T #12 showing two overlapping *Osteocallis infestans* Paes Neto et al., 2016. **D.** UFRGS-PV-1581-T #11 showing *Osteocallis* isp. (arrow) associated to a cluster of larger grooves.

impossible. UFRGS-PV-1581-T #14 was found covered by a thin layer of iron oxide that served as a natural cast, allowing for the observation of the traces in a positive relief (Fig. 5A, B). Trails on UFRGS-PV-1581-T #5, #11, #14, and #23 are

associated to clusters of grooves (Figs. 4B, D, 5A, B, 6C). In UFRGS-PV-1581-T #14 a cluster is overlapping one of the trails. The only association of trails with other borings occurs in UFRGS-PV-1581-T #3 (Fig. 4A<sub>1</sub>).

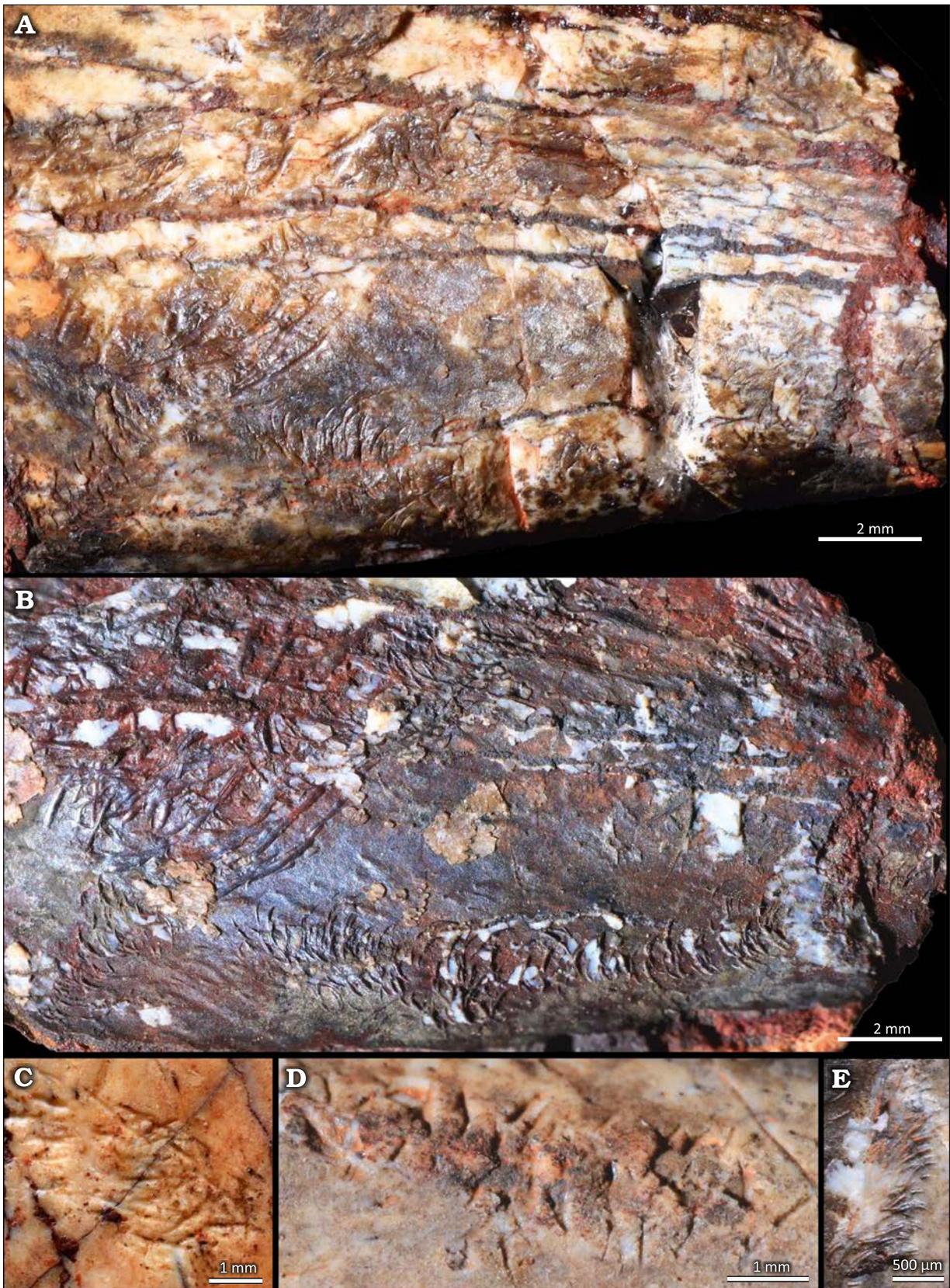


Fig. 5. A suite of traces in the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933), UFRGS-PV-1581-T #14, bone fragment from Buriol Site, Brazil, *Hyperodapedon* AZ, Carnian. **A.** Two feeding traces of *Osteocallis mandibulus* Roberts et al., 2007, overlapped by a cluster of larger grooves. **B.** Natural cast formed by a cover of iron oxide showing the grooves in positive relief. Image mirrored to facilitate comparison. **C, D.** Clusters of grooves on different surfaces of the same bone fragment. **E.** Small *Osteocallis mandibulus* close to the trails shown in A and B.

*Osteocallis infestans* Paes Neto et al., 2016

Fig. 4C.

**Diagnosis.**—Shallow to moderately deep, meandering trail of generally straight overlapping thick grooves excavated into the cortical bone surfaces. Grooves are randomly orientated, often overlapping other grooves which are either perpendicular or parallel to one another. The intensity of the grooves culminates in an irregular furrow-like morphology for the trail.

**Material.**—UFRGS-PV-1581-T #12 (Fig. 4C), a bone fragment referred to *Hyperodapedon mariensis* from Buriol Site, São João do Polêsine municipality, Rio Grande do Sul State, Brazil; Base of the Candelária Sequence (vertebrate remains associated to the lower subunit of the *Hyperodapedon* AZ), SMS, Paraná Basin; middle Carnian (lower Upper Triassic).

**Description.**—Two overlapping, moderately deep trails formed by randomly oriented, overlapping grooves culminating in a furrow-like morphology. Isolated grooves outside of the furrow appear to be arcuate, but the intense overlapping prevents the precise observation of groove morphology. The length of the trails ranges from 8.37–14.38 mm and the width ranges from 0.33–1.47 mm.

**Remarks.**—Both trails described here are considerably narrower than the holotype of *O. infestans* (which came from the *Exaeretodon* sub-AZ of the *Hyperodapedon* AZ) and the grooves are not as thick. As in the holotype, some areas outside of the furrow present isolated grooves. The furrow-like morphology is readily distinguishable from what is seen in *O. mandibulus* (Fig. 4C).

*Osteocallis* isp.

Fig. 4D.

**Material.**—UFRGS-PV-1581-T #11 (Fig. 4D), a bone fragment referred to *Hyperodapedon mariensis* from Buriol Site, São João do Polêsine municipality, Rio Grande do Sul State, Brazil; Base of the Candelária Sequence (vertebrate remains associated to the lower subunit of the *Hyperodapedon* AZ), SMS, Paraná Basin; middle Carnian (lower Upper Triassic).

**Description.**—A trail formed by successive straight and arcuate, mainly non-paired grooves bored on the surface of the bone. Trail length is 3.29 mm and the width ranges from 0.25–1.48 mm.

**Remarks.**—The preservation of the trail prevents its ichnospecific classification, because it is not possible to ensure that the grooves are mainly arcuate and paired. The grooves do not appear to be organized in parallel rows and regularly spaced as seen in *Osteocallis leonardii*. The trail is closely associated with an irregular cluster of randomly oriented grooves (Fig. 4D).

## Morphotype 1: clusters of grooves

Figs. 6, 7.

**Material.**—UFRGS-PV-1581-T #5, #6, #8, #11, #13–#15, #17, #20–#29.

**Description.**—The clusters consist of straight and/or arcuate grooves bored on the surface of the cortical bone without forming discrete trails. In most cases the grooves are randomly oriented and scattered over large areas of the bone surface. When densely concentrated, the grooves give the bone an etched appearance, similar to traces reported both from fossil (Kaiser 2000; Britt et al. 2008; Backwell et al. 2020) and modern (Backwell et al. 2012) bones (Fig. 6B, E). Subparallel grooves appear in at least three different clusters, two of them in UFRGS-PV-1581-T #17 (Fig. 6F).

At least three subcircular concentrations of grooves were observed; they resemble the pits reported by Laudet and Antoine (2004: fig. 2B), Britt et al. (2008: fig. 1D), and Parkinson (2022: fig. 2E, F) but, unlike the pits, they do not form a depression on the bone surface (Fig. 7). The subcircular clusters on UFRGS-PV-1581-T #13 and #16 are formed by grooves with a preferential orientation whereas in the cluster on UFRGS-PV-1581-T #17 the grooves are not easily distinguishable, especially in the center of the concentration (Fig. 7A). The lengths of the subcircular clusters range from 2.90–5.26 mm, being 1.1–1.8× greater than the diameters, which range from 1.74–4.78 mm. The subcircular cluster on UFRGS-PV-1581-T #13 is associated with an irregular cluster of grooves that may be a partial subcircular cluster destroyed by the fragmentation of the bone, since it is located exactly on the edge of the fragment (Fig. 7B). This would be the only case of subcircular clusters occurring together. The subcircular cluster on UFRGS-PV-1581-T #17 is associated with an elongated cluster similar to a trail, but with grooves oriented parallel to the large axis of the cluster, as opposed to *Osteocallis*, where the grooves are mainly perpendicular to the trail length (Fig. 7A).

Some clusters are formed by arcuate and paired grooves identical to the morphology seen in *O. mandibulus*, but the lack of a preferential orientation and successiveness prevent their classification as trails and therefore their assignment to this ichnogenus (e.g., UFRGS-PV-1581-T #20; Fig. 6A). Clusters of grooves are associated with trails in UFRGS-PV-1581-T #5, #11, #14, and #23. In UFRGS-PV-1581-T #14, the cluster overlaps a trail and is formed by grooves with a length that reaches over 2 mm and a width of ~0.2 mm, whereas the largest grooves in the trail have a length of ~0.4 mm and a width of ~0.06 mm (Fig. 5A, B). The trail on UFRGS-PV-1581-T #23 is associated with a cluster mainly composed by straight grooves forming a crescent shape that resembles the subcircular clusters described above (Fig. 4B).

## Morphotype 2: borings

Fig. 8.

**Material.**—UFRGS PV-1581-T#3, #7, #9.

**Description.**—The borings are channel-like structures with at least one rounded termination (Fig. 8). Three borings were identified, their length ranging from 4.34–7.84 mm and their width ranging from 3.0–7.0 mm. They are straight to slightly tortuous with only one defined round termination

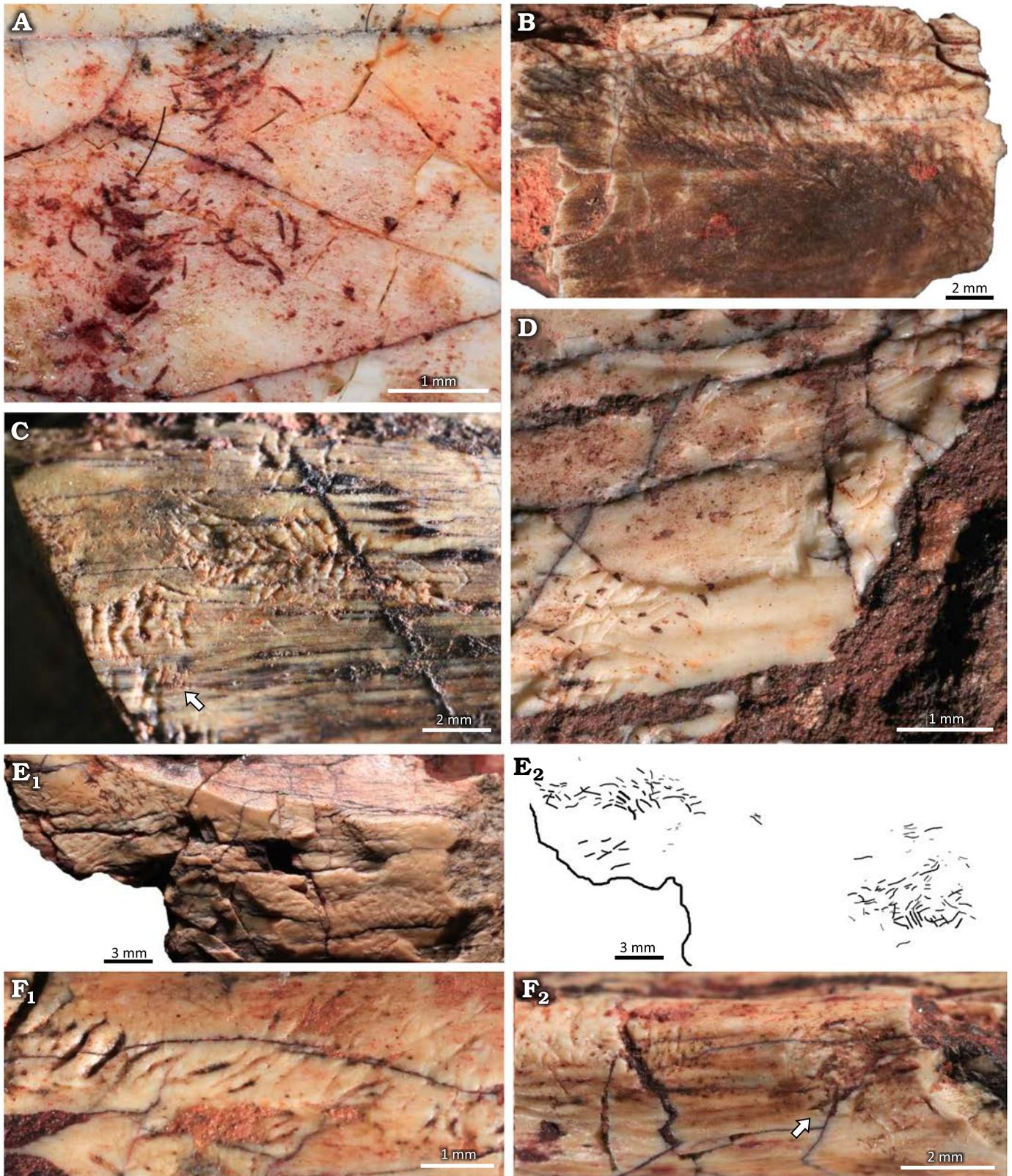


Fig. 6. Clusters of grooves on bone fragments of the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933) from Buriol Site, Brazil, *Hyperodapedon* AZ, Carnian. **A.** UFRGS-PV-1581-T #20, arcuate and paired grooves, similar to feeding traces of *Osteocallis mandibulus* Roberts et al., 2007, but without forming a trail. **B.** UFRGS-PV-1581-T #22, densely concentrated grooves, giving the bone surface an etched appearance. **C.** UFRGS-PV-1581-T #5, straight and arcuate grooves closely associated to an incipient *Osteocallis mandibulus* (arrow). **D.** UFRGS-PV-1581-T #26, straight and arcuate grooves and some isolated grooves. **E.** UFRGS-PV-1581-T #6, dentary fragment; E<sub>1</sub>, two clusters of grooves; E<sub>2</sub>, schematic drawing. **F.** UFRGS-PV-1581-T #17; F<sub>1</sub>, subparallel grooves; F<sub>2</sub>, subparallel grooves associated to a subcircular cluster of grooves (arrow).

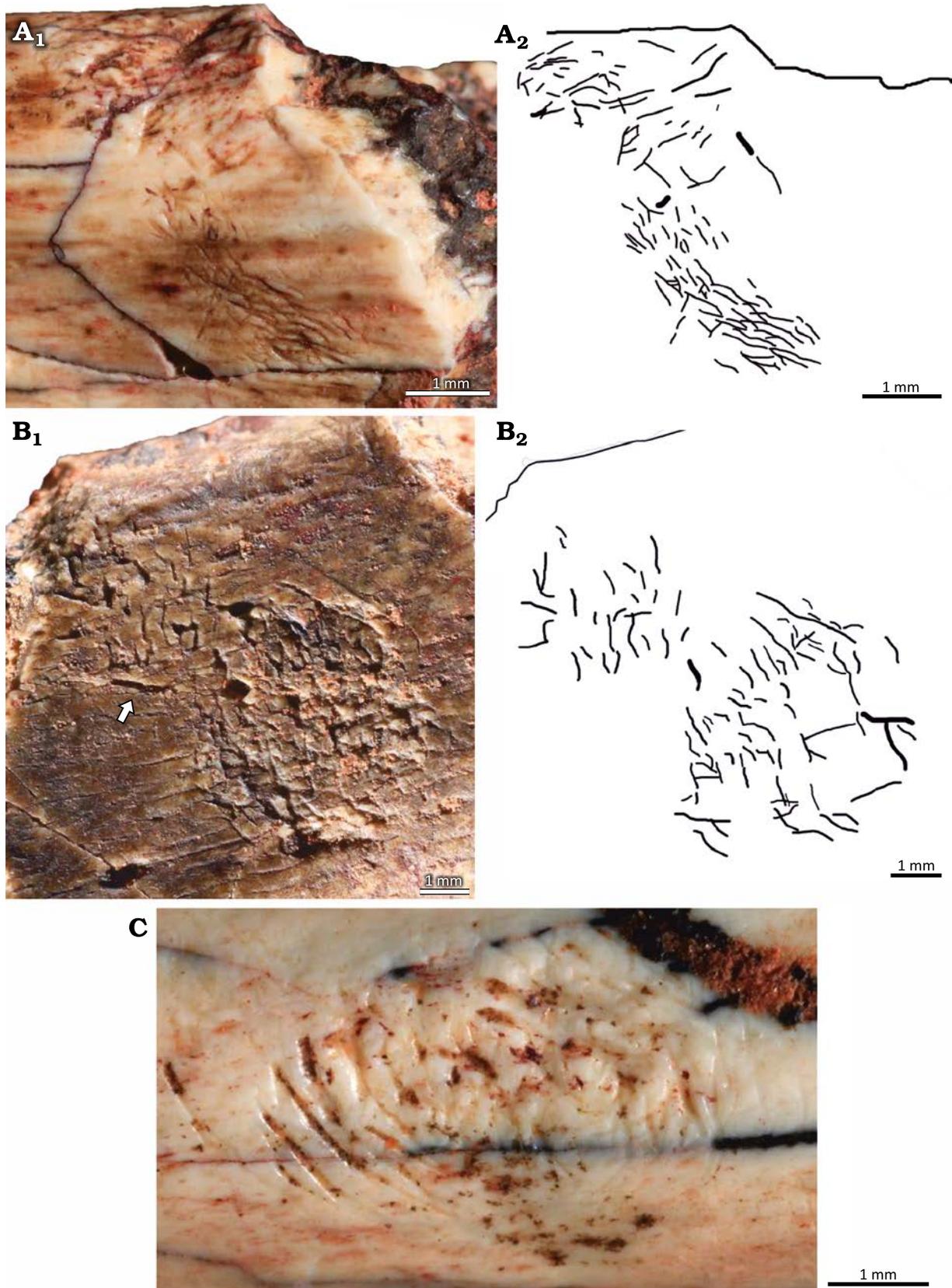


Fig. 7. Subcircular clusters on bone fragments of the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933) from Buriol Site, Brazil, *Hyperodapedon* AZ, Carnian. **A.** UFRGS-PV-1581-T #17; A<sub>1</sub>, subcircular cluster connected to a cluster of grooves; A<sub>2</sub>, schematic drawing. **B.** UFRGS-PV-1581-T #13; B<sub>1</sub>, subcircular cluster associated to an irregular cluster of grooves (arrow), possibly a partially preserved subcircular cluster; B<sub>2</sub>, schematic drawing. **C.** UFRGS-PV-1581-T #16 showing an isolated subcircular cluster of grooves.

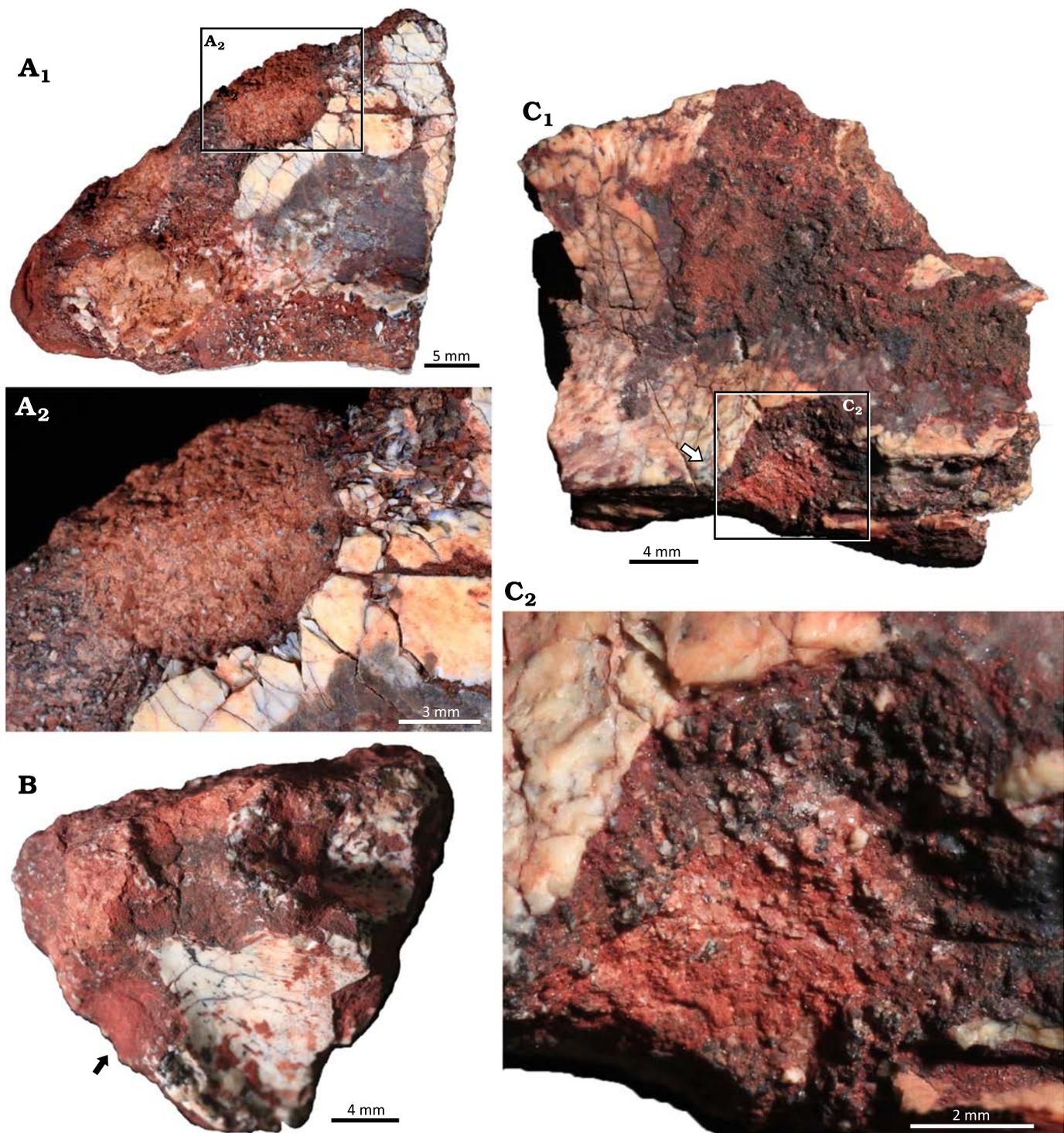


Fig. 8. Indiscrete borings on bone fragments of the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933) from Buriol Site, Brazil, *Hyperodapedon* AZ, Carnian. **A.** UFRGS-PV-1581-T #3; A<sub>1</sub>, a boring in the opposite face of the arthropod bioerosion trace fossil *Amphifaoichnus*, but also penetrating it; A<sub>2</sub>, close up view showing the presence of bone chips in the base of the boring. **B.** UFRGS-PV-1581-T #7 showing a boring with one rounded termination. **C.** UFRGS-PV-1581-T #9; C<sub>1</sub>, an elongated boring with a rounded termination and bone chips scattered on the base; C<sub>2</sub>, close up view highlighting the bone chips scattered on the base.

and U-shaped cross section. The boring on UFRGS PV-1581-T #3 is perpendicular to the *Amphifaoichnus* trace that occurs in the opposite surface of the bone, but it penetrates it as well (Fig. 8A). The borings on UFRGS PV-1581-T #7 and #9 are not associated with other bioerosion traces (Fig. 8B,

C<sub>1</sub>). Bone chips are scattered over the base of the borings on UFRGS PV-1581-T #3 and #9 (Fig. 8A<sub>2</sub>, C<sub>2</sub>). The borings differ from UFRGS PV-1581-T #10 as they are not as elongated, with a length-width ratio varying from 1.09–1.44, whereas in UFRGS PV-1581-T #10 the ratio is 2.43. Also,

no indication of fill is present in any of the borings. These morphological differences preclude their classification as *Amphifaoichnus*. The borings differ from *Cuniculichnus variabilis* Hopner and Bertling, 2017, for the lack of tapering ends; also, there is no indication of a succession of types from holes to notches and tunnels.

## Discussion

**Tracemaker identity.**—The identification of a tracemaker for bioerosion traces in bones allows a series of paleoecological and taphonomic inferences that expand their importance as a source of paleontological information. However, caution is necessary in such identification because different tracemakers may produce identical structures when behaving similarly (Bromley 1996). Furthermore, actualistic experiments focusing on bioerosion in bones are still scarce and when dealing with materials as old as the Triassic, many ethological changes yet undiscovered may have occurred between groups of organisms.

Bioerosion traces made in bones deposited in continental settings are mainly attributed to insects, especially dermestid beetles (e.g., Kitching 1980; Rogers 1992; Martin and West 1995; Britt et al. 2008) and termites (e.g., Watson and Abbey 1986; Kaiser 2000; Fejfar and Kaiser 2005; Backwell et al. 2020). Trace morphologies as those present on UFRGS-PV-1581-T, such as isolated and clustered grooves, have been reproduced in experiments using both termites (Backwell et al. 2012) and dermestids (Parkinson 2022) and, consequently, are not a precise source of information of the identity of the tracemaker. Other traces reported in this contribution (*Amphifaoichnus* and *Osteocallis*) do not support less inclusive assignments as well. Pirrone and Buatois (2016) did not assign *Amphifaoichnus* to a specific producer, but hypothesized that the tracemaker may have been a coleopteran with a heavily sclerotized body and well-developed mandibles capable of destroying bone tissue. This caution is reinforced by the lack of actualistic experiments reproducing *Amphifaoichnus* structures. Contributions reporting the occurrence of *Osteocallis* in continental fossil bones do not assign the traces to a specific producer either, only relating them to the action of insects (Roberts et al. 2007; Paes Neto et al. 2016; Perea et al. 2020). The materials referred to *Osteocallis leonardii* are attributed to the grazing action of polyplacophorans (Collareta et al. 2023), but the lack of evidence for transportation in UFRGS-PV-1581-T makes it highly unlikely that the tracemakers were marine organisms. Even though grooves have been observed in actualistic experiments, both isolated or organized in clusters, trails (as seen in *Osteocallis*) are yet to be reproduced.

The presence of the two groups of insects usually related to bioerosion in bones on continental settings is also an important point to consider. Molecular phylogenetics suggest that the origin of Coleoptera occurred in the earliest Permian and the divergence of Dermestidae in the Late

Triassic (e.g., Zhang et al. 2018). Therefore, dermestid beetles may have been components of the ecosystems contemporaneous to the deposition of the SMS. In contrast, the diversification of termites would have occurred in the Late Jurassic (Bourgignon et al. 2014), thus, their presence in the Carnian strata of the Candelária Sequence would be unlikely. Even though molecular analyses recognized dermestid beetles in Late Triassic ecosystems, their presence by itself is not sufficiently supportive for identifying them as producers of the traces analyzed herein, since the Dermestidae family presents a wide range of feeding strategies and the behavior of Triassic species could differ considerably from what is observed on extant necrophagic species of the genus *Dermestes*. Also, other still unknown Triassic arthropods could behave similarly to what is observed in dermestids today and produce the traces.

The identification of the tracemakers of UFRGS-PV-1581-T to less inclusive taxonomic levels is difficult, but the morphology of the traces strongly points toward terrestrial arthropods as the producers. In addition, records of *Skolithos serratus* both in the Buriol (HF and PD-D, personal observation) and Predebon (about 1 km far from the former) sites are interpreted as burrows excavated by tiger beetle larvae (Nascimento and Netto 2019), attesting to the presence of insects in these ecosystems. Therefore, considering the information presented above, we are able to assign the traces found in UFRGS-PV-1581-T to terrestrial insects.

**Ethological remarks.**—UFRGS-PV-1581-T a wide array of traces with at least four distinct morphotypes identified. This diversity may reflect the presence of more than one biological species exploring the rhynchosaur carcass, a behavioral complexity among the tracemakers, possible ontogenetic changes in the carcass exploitation behavior or even a combination of these possibilities. In order to better understand the possible scenarios behind bone modification in UFRGS-PV-1581-T specimens, an analysis of the conditions in which the traces were produced and their ecological meaning is required.

Grooves and striae are possibly the most recurrent traces produced by insects in bone, occurring isolated, in clusters, forming trails and associated with a variety of other traces (e.g., Kaiser 2000; Laudet and Antoine 2004; Fejfar and Kaiser 2005; Roberts et al. 2007; West and Hasiotis 2007; Britt et al. 2008; Backwell et al. 2012; Paes Neto et al. 2016; Perea et al. 2020; Parkinson 2022). Britt et al. (2008) interpreted grooves (referred to as “scratches”) as probing traces, differing from *Osteocallis*, which would be a more complex feeding trace. In UFRGS-PV-1581-T grooves are observed isolated, in clusters and forming trails, sometimes with more than one morphotype occurring in association. Most of the clusters are formed by straight and non-paired grooves, but clusters of arcuate and paired grooves are also observed and are likely produced by the same organism as *Osteocallis*. If we consider the interpretation of Britt et al. (2008), the occurrence of feeding traces (including *Osteocallis*) would be

concentrated on areas of higher nutritional value, while probing traces could occur in any portion of the bones. In the five fragments (UFRGS-PV-1581-T #5, #8, #11, #14, and #23) that present both clusters of grooves and *Osteocallis*, the grooves forming the clusters are larger and morphologically distinct, being predominantly straight and non-paired. The clusters and the trails target the same bone region, which may be indicative of both being feeding traces. The difference in size and shape of the grooves points to two distinct trace makers, or at least two different ontogenetic states.

Even though *Osteocallis* is usually interpreted as a feeding trace, it is still debatable if it represents a necrophagic or osteophagic aculate. Hopner and Bertling (2017) stated that the intentionality in the production of *Osteocallis* is highly speculative, whilst West and Hasiotis (2007) interpreted traces very similar to *Osteocallis* (referred to as “scallop”) as grazing traces (Pascichnia) of insects feeding on the periosteum rather than the bone. Considering this interpretation, the feeding traces in UFRGS-PV-1581-T (*Osteocallis* and associated clusters of grooves) could be concentrated in regions of the bone where the periosteum was still preserved. Collareta et al. (2023) relates *Osteocallis leonardii* to polyplacophoran algal grazing, but consider carrion scavenging and bone consumption as possible scenarios as well. The reproduction of *Osteocallis* in controlled experiments or its observation in present ecosystems might help elucidate the nature of the feeding behavior it represents.

*Amphifaoichnus* was assigned to the Fodinichnia ethological group by Pirrone and Buatois (2016) based on the presence of bone chips in the infilling, which would indicate bone consumption. Britt et al. (2008) interpreted bone fragments in the matrix next to bioeroded bones as relicts of frass (insect feces), therefore associating the traces to osteophagy as well. Paik (2000), on the other hand, while attributing the presence of bone fragments in the matrix subjacent to bioeroded bones to the action of carrion insects, did not conclude that they were used for food. The presence of bone chips in the sediment close to bioeroded bones or within the filling of bioerosion traces might not be direct evidence for bone consumption, because the bone chips, even when removed from its source by the action of insects, could have been deposited without being ingested. The frass of insects that feed on wood, for instance, is composed not only of excrements, but also material loosened from the tree without being consumed (Nuorteva and Kinnunen 2008). The excrements differ from the loosened material by being roughly homogeneous in size and shape, and by being enveloped in a thin film (Nuorteva and Kinnunen 2008). Also, excrements of some species of insects might present identifiable surface features, such as the grooves in the excrements of *Sphinx pinastri* (Lepidoptera) larvae (Nuorteva and Kinnunen 2008: pl. 1B). In addition to the absence of any surface features indicating consumption, bone chips in UFRGS-PV-1581-T present no consistency in shape or sorting by size, meaning that there is no strong evidence for interpreting them as in-

sect frass. Therefore, the osteophagical behavior is not clear for *Amphifaoichnus* traces.

Other invertebrate traces from nearby sites as well as the Buriol site may help reveal the behavior behind the production of *Amphifaoichnus*. Specimens of *Skolithos serratus* resemble UFRGS-PV-1581-T #10, both being circular in cross section and of roughly the same width. The interpretation for *Skolithos serratus* is that they are burrows excavated by tiger beetle larvae (Coleoptera, Cicindelidae), which prey by positioning themselves in the entrance of the burrow and ambushing other invertebrates (Nascimento and Netto 2019 and references therein). The burrows would also function as domiciles, protecting the beetles in larval stage and their pupae until reaching the adult stage. The difference in substrates of *S. serratus* (sediment) and *Amphifaoichnus* (both sediment and bone) is not sufficient to discard the possibility of both traces being produced by the same organism, as Pirrone and Buatois (2016) stated that modes of penetration and behavioral strategies may be independent of the type of substrate. A more significant difference may be the type of filling, since *S. serratus* is passively filled by sediment and *Amphifaoichnus* is actively backfilled, presenting a meniscate pattern. This could represent a difference in the purpose of the structures, therefore indicating different tracemakers or different behaviors of the same tracemaker. Another ichnogenus found in Buriol and other sites nearby is *Taenidium*, which also presents meniscate backfilling. This trace is usually attributed to deposit feeders and is interpreted as Fodinichnia, but Savrda et al. (2000) have discussed the problems with these attributions when no clear evidence indicating feeding behavior is present. For the *Taenidium* of SMS, Netto (2007) adopted a different explanation, relating the vertical orientation of the burrows to a low water table forcing the organisms to excavate deeply until reaching more humid conditions within the substrate. It is possible that, when excavating the substrate, the organisms would encounter the bones and pass through them, rather than deviating. A similar hypothesis was defended by Rogers (1992), who interpreted bioerosion in dinosaur bones from the Two Medicine Formation (Cretaceous of USA) as the result of chance encounters during subterranean excavations of puparial chambers by dermestid beetles. This hypothesis could be reinforced for UFRGS-PV-1581-T if the orientation of the bone fragments matched those of *Taenidium*, but this information was not possible to infer during the material collection. Regardless, carcasses tend to increase moisture in the soil (Quagiotto et al. 2019), therefore the buried bones could attract burrowing insects, functioning as a humidity island within the dry sediment.

The occurrence of *Amphifaoichnus* and *Osteocallis* in the same bone fragment might be another useful tool for understanding the possible behaviors associated with the traces. Being a feeding trace, *Osteocallis* would not necessarily be restricted to chance encounters, but instead could be linked to a more recurrent ecological relationship between insects and vertebrate carcasses. In this sense,

*Amphifaoichnus* could represent a temporary domicile used by the insects when feeding on the bones or the remaining soft tissues. In fact, the trails in UFRGS-PV-1581-T #3 are directly connected to *Amphifaoichnus*, reinforcing the hypothesis that these traces were produced by the same trace maker employing different behaviors.

The lack of direct evidence precludes the certain attribution of any of the above-mentioned behaviors to the production of *Amphifaoichnus*. Actualistic experiments might help solving the origin of this trace in the future, but at this moment its function and relation to necrophagic or osteophagic behavior is uncertain.

The ethological meaning of subcircular clusters of grooves is also an intriguing question. Similar morphologies reported from the fossil record present, besides the grooves, depressions on the surface of the bones and are interpreted as incipient borings or pits (Laudet and Antoine 2004; Britt et al. 2008; Parkinson 2022). Laudet and Antoine (2004) interpreted these traces as incipient dermestid pupal chambers, whilst for Britt et al. (2008) they are attempts at penetration into the trabecular bone. The only subcircular cluster with a depression is the one in UFRGS-PV-1581-T #17, but it is irregular and considerably different from the incipient borings. It is possible that the subcircular clusters do not reflect a specific behavior, being only a coincident morphology. Another explanation is that they represent an even more incipient stage of abandoned borings or pits.

**Taphonomic remarks.**—The presence of *Osteocallis* is usually associated with subaerial exposure of skeletal remains, since dermestid beetles, the insect group most commonly associated with bioerosion in bones, act over exposed carcasses during the dry stage of decomposition. Müller et al. (2015) reported a trail of grooves attributable to *Osteocallis* in *Exaeretodon* remains from the Janner Site (*Exaeretodon* sub-AZ of the *Hyperodapedon* AZ, Fig. 1C), and used this occurrence as an argument supporting the idea that the bones were subaerially exposed. Francischini et al. (2018), Fontoura et al. (2018) and Perea et al. (2020) also associated the presence of *Osteocallis* with subaerial exposure of the bony substrate. Paes Neto et al. (2016) defended a pre-burial origin for trails of grooves in bones from the Janner Site as well, but the presence of bioturbation structures in the adjacent sediment raised the possibility that the traces were produced underground and that the trace makers could be soil burying insects like beetles from the families Histeridae, Silphidae, and Staphilinidae.

On the other hand, the compound morphology of *Amphifaoichnus* indicate that the bony substrate should be at least partially buried when the trace was produced. Therefore, the association between *Amphifaoichnus* and *Osteocallis*, as seen in UFRGS-PV-1581-T #3, might be additional evidence supporting a post-burial origin for trails of grooves on the bone surface. Indeed, bioerosion in buried bones has been reported before (Rogers 1992; Huchet et al. 2011) and is strongly supported in the case of dinosaurs from

the Djadokhta and Barun Goyot formations (Cretaceous of Mongolia; Saneyoshi 2011), where bioturbation structures are directly connected to borings in bones, sometimes passing through them and continuing in the circumjacent sediment. In these cases, the burrows are lined with fine bone material for a short distance after passing through the bone, demonstrating a clear association of burrows and borings (Kirkland et al. 1998). In the same locality, invertebrate bioturbations are found, including meniscate back-filled burrows (Fastovsky et al. 1997). Roberts et al. (2007) commented that some of the traces associated to *Osteocallis* in the bones from the Kaiparowits Formation (Cretaceous of USA) are meniscate back-filled burrows. Burrows with meniscate backfilling and bone chips were also reported by Paik (2000) in sediments subjacent to bioeroded bones. Pirrone and Buatois (2016) noted similarities between these traces and *Amphifaoichnus*, stating, however, that their attribution to this ichnogenus would depend on a reevaluation of the material. Even though burrows are often associated with bored bones, Paik (2000) defended a subaerial scenario for the bioerosions. Based on the evidences of this and previous contributions, the automatic association of *Osteocallis* and subaerial exposition might be problematic and a post-burial origin for trails of grooves on the bone surface may be considered as a plausible scenario as well (Fig. 9).

Adopting a post-burial hypothesis for the origin of *Osteocallis*, it is worth questioning if the morphology seen for this trace in the fossil record is affected by a preservational bias. As seen in UFRGS-PV-1581-T #10, the sediment filling of *Amphifaoichnus* might not be preserved, resulting in a simple and concave bioerosion trace on the surface of the bone. Xing et al. (2013) described that, in cases where the convex tunnels of *Taoteichnus* are detached from the bone, it is possible to observe shallow grooves. Thorne and Kimsey (1983) reported a similar observation in actualistic experiments with termites in Panama. It is possible that *Osteocallis* originally presented a convex structure covering the trails on the bone surface that was not preserved. In this case, its association with *Amphifaoichnus* might indicate that both traces would represent a similar behavior with very distinct levels of bone destruction. This hypothesis still lacks clear and direct evidence, but its consideration might guide actions of prospection (both field and collections) and caution in preparation of materials that may eventually lead to a confirmation.

It is important to consider, however, that the presence of *Osteocallis* and *Amphifaoichnus* in the same bone fragment is not necessarily indicative of coeval production. The skeletal remains may have been utilized as a substrate in distinct times, both subaerially exposed and/or after burial. This hypothesis would indicate either the presence of at least two phases of the bone taphonomic history or of a certain kind of species able to modify both exposed and buried bones.

**Paleoecological and evolutionary remarks.**—The succession of organisms exploring terrestrial vertebrate carcasses

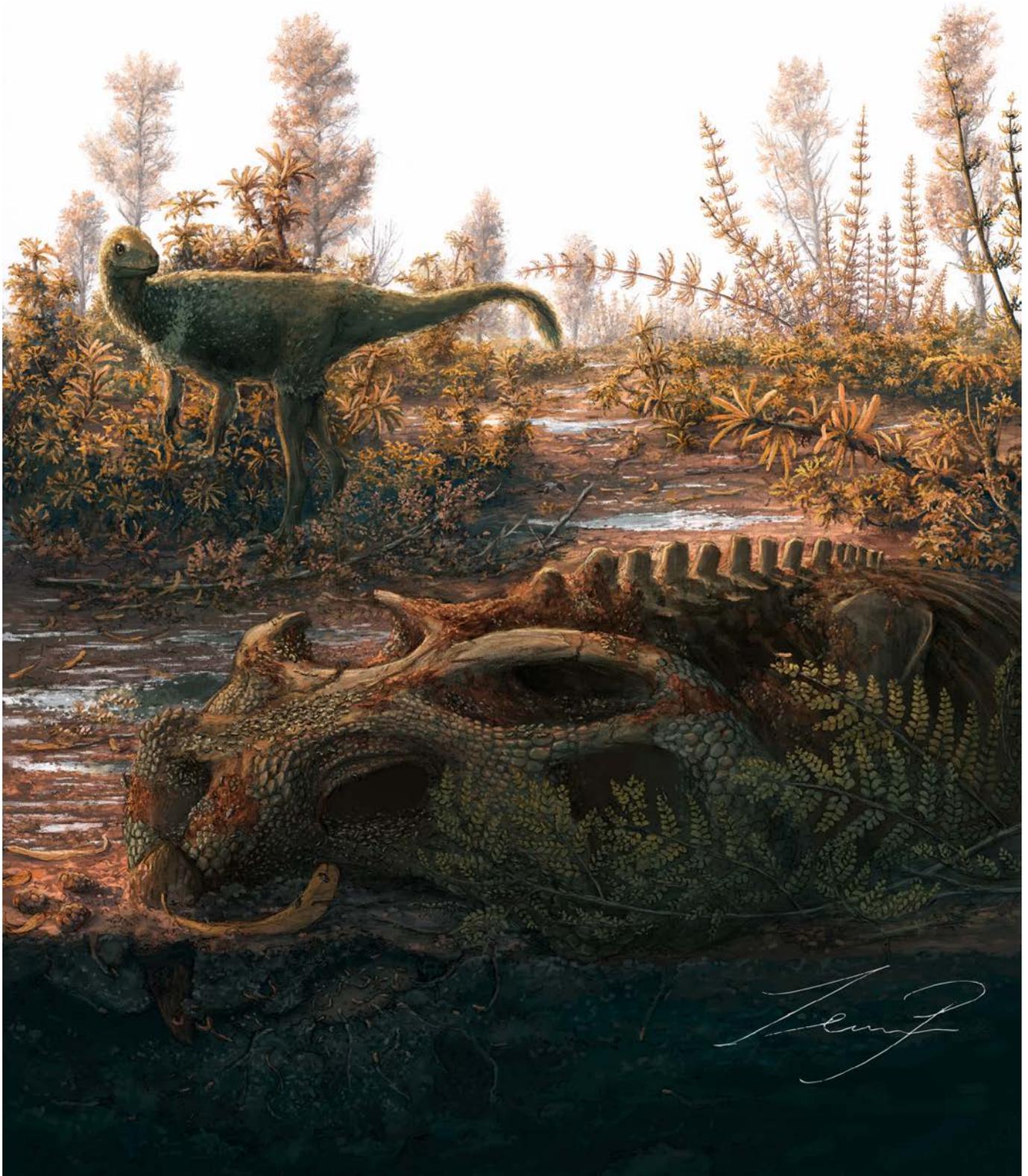


Fig. 9. Reconstruction of insect exploration on bone fragments of the rhynchosaurid archosauromorph *Hyperodapedon mariensis* (Tupi Caldas, 1933) in UFRGS-PV-1581-T. Insect activity is depicted as occurring both in exposed and buried portions of the carcass (see the text for other hypotheses). Reconstruction by Zein de Paula.

is well described in the literature and insects are important components in most of the stages of the decomposition process (e.g., Bornemissza 1957; Smith 1986). The abundance

and diversity of species occurring in carcasses decrease in the last stages of decomposition as the nutrients become less available and their exploration is more difficult (Payne

1965). Therefore, adaptations for the exploration of the remaining tissues still present in the dry stage of the carcass decay, like fur, skin and other keratinous elements, are important for necrophagous insects competing for resources. In this sense, osteophagy and other uses of the bone substrate would be behaviors capable of prolonging the value of carcasses as a resource, because vertebrate skeletons can remain exposed for more than a decade depending on the environmental conditions (Behrensmeyer 1978). The morphological complexity of *Amphifaoichnus*, a trace composed by the modification of both bone and sediment, suggests a certain degree of specialization of the tracemaker for bone exploration and, along with the other traces in UFRGS-PV-1581-T, demonstrates that in the ecosystems of the base of the Candelária Sequence the carcasses were explored by insects in latter decomposition stages, where nutrients were scarce and difficult to access. This hypothesis is further strengthened by the evidences of exploration of buried bones, which would expand the availability and duration of resources for organisms with such adaptations.

The record of bioerosion in bones from the SMS indicates that not only rhynchosaur remains were a resource for insects exploring carcasses, but also the remains of dicynodonts (Paes Neto et al. 2016; Medeiros et al. 2019), cynodonts (Müller et al. 2015; Paes Neto et al. 2016; Pavanatto et al. 2018), and dinosaurs (Paes Neto et al. 2016; Francischini et al. 2018). Considering that several groups of tetrapods are represented in the record of bioerosion in bones from the SMS, it is possible to infer that decaying carcasses were an important resource in these Carnian–Norian ecosystems, which would explain the adaptations allowing the exploration of these resources by insects.

To this moment, the fossil record shows that the exploration of bones by insects on continental settings arose during the Middle Triassic (Paes Neto et al. 2016) and was associated with large terrestrial tetrapods. Today, insects are responsible for much of the weight reduction seen in carcasses during the decomposition process (Payne 1965). However, there is much yet to be discovered about the bone destruction promoted by the action of insects during carcass decay, both in past and recent ecosystems. Actualistic studies have mainly focused on establishing identifiable morphologies to aid in the recognition of trace makers for bioerosion in bones (Roberts and Rogers 2003; Backwell et al. 2012; Holden et al. 2013; Parkinson 2022) or on the forensic value of bone modification by insects (Zanetti et al. 2014, 2015a, b, 2019a, b; Charabidzé et al. 2022). Therefore, many taphonomic and paleoecological implications of the emergence of bone modification behavior by insects are yet to be discussed.

*Amphifaoichnus* shows an elevated level of bone destruction, indicating that the action of insects could be an important factor influencing the preservation of vertebrate skeletons and consequently the fossil record. The burial of bones is an important event aiding in their preservation, since buried bones would be more protected from weathering and the action of organisms (scavenging and trampling).

Considering that *Amphifaoichnus* is probably the result of insects modifying buried bones, even in this favorable scenario the preservation of vertebrate skeletons could be negatively affected. The taphonomical importance of insects in the exceptional preservation of dinosaurs has been recently discussed by Drumheller et al. (2022). In their taphonomic model, invertebrates and microorganisms would be responsible for the removal of internal soft tissues, allowing for the desiccation of dermal tissue and favoring the preservation of both skin and bones. However, if the removal of bone by insects is added to this model, especially in the level seen in *Amphifaoichnus*, invertebrates might constitute an important factor over the preservation of these carcasses. Therefore, the emergence of the bone modifying behavior by insects in the Late Triassic may have influenced the fossil record of the whole Mesozoic.

UFRFS-PV-1581-T represents the oldest records of the ichnogenera *Amphifaoichnus* and *Osteocallis*. Since the specimens of *Amphifaoichnus* described by Pirrone and Buatois (2016) came from the Upper Cretaceous of Argentina, the records of the SMS extend the occurrence of this ichnogenus in more than 140 Ma, positioning it along with the first records of bioerosion in bones by insects and indicating that this morphology, although complex, emerged shortly after the bone modifying behavior. The records of *Osteocallis* reported by Paes Neto et al. (2016) come from the same biozone of the Candelária Sequence as UFRGS-PV-1581-T, however, they come from a portion of the Janner Site (Agudo municipality) characterized by the abundance of the cynodont *Exaeretodon*, representing the *Exaeretodon* sub-AZ of Schultz et al. (2020), the upper portion of the *Hyperodapedon* AZ. The Buriol Site, where UFRGS-PV-1581-T was collected, is considered to represent the lower portion of the *Hyperodapedon* AZ, therefore the records of *Osteocallis* described here are slightly older. Ecologically, the emergence of new ichnogenera in the early Late Triassic might represent a diversification of behaviors producing bioerosion traces in bones in comparison to the record of the Middle Triassic (Paes Neto et al. 2016), which is mainly composed of indiscrete borings and the only ichnogenus described is *Cubiculum*.

## Conclusions

The material analyzed here represents new records of bioerosion in bones from the SMS and contribute to the knowledge of the diversity and complexity of bone exploration in Late Triassic ecosystems. The record of *Amphifaoichnus* is expanded back more than 140 Ma, showing that complex bone exploration behavior was present in Carnian insects, as evidenced by tunnels made on bone-sediment interface. This is indicative of the presence of specialized organisms and the importance of tetrapod carcasses as a resource for other components of the fauna. These new records also contribute to the taphonomic discussion regarding bioerosion,

indicating that the automatic association between insect traces in bones and prolonged subaerial exposure is problematic due to the existence of evidence pointing to the possibility of bioerosion in buried remains. Furthermore, the level of bone destruction seen in *Amphifaoichnus* might indicate that insects were relevant taphonomic agents preventing the preservation of vertebrate carcasses even in sub-surface conditions. The association of *Amphifaoichnus* to osteophagic behavior is questioned on the basis of a lack of direct evidence for this behavior. Other possible behaviors, such as the construction of temporary domiciles related to feeding or sediment moisture, are discussed based on the co-occurrence of *Amphifaoichnus* and *Osteocallis* and the presence of invertebrate burrows (*Taenidium barreti* and *Skolithos serratus*) in the Buriol and Predebon sites. New research might be key to advance the discussions brought here and to comprehend the potential of bioerosion in bones as a tool for studying paleoecology and taphonomy. Therefore, continuing work on bioerosion traces in bone is necessary to help us understand the evolutionary processes that influenced the evolution of bone exploration by insects.

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