UNIVERSIDADE FEDERAL DO PAMPA

JAQUELINE LOPES FIGUEIREDO

A NEW CYNODONT CONCENTRATION FROM THE BRAZILIAN TRIASSIC: INSIGHTS INTO THE GENESIS AND PALEOBIOLOGICAL SIGNIFICANCE OF A HIGHLY PRODUCTIVE FOSSIL SITE

São Gabriel
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Dissertação apresentada ao programa de Pós-graduação Stricto Sensu em Ciências Biológicas da Universidade Federal do Pampa, como requisito parcial para obtenção do Título de Mestre em Ciências Biológicas.

Orientador: Dr. Felipe Lima Pinheiro

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Dr. Francesco Battista
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Dedico este trabalho aos meus pais, João
Batista e Sandra.

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Aos meus pais, João Batista e Sandra, pelo apoio, incentivo e amor dedicados a mim. A minha família, especialmente, a minha vó Delma e a minha dinda Cleusa. Aos meus companheiros caninos, Batman e Lola, principalmente pela companhia nas tardes de estudo. Ao João, namorado e amigo, por todo o apoio e força dedicados. Amo todos vocês.

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“Às vezes eu começo uma frase sem saber como ela vai terminar. Eu só torço para que ela chegue em algum lugar”.

Michael Scott, The Office

RESUMO

É importante analisarmos as evidências bioestratinômicas para entender a história tafonômica e reconstruir a paleoecologia. Ao longo dos anos, pesquisas tafonômicas sobre os vertebrados fósseis do Triássico do Rio Grande do Sul vêm sendo publicados, mostrando a diversidade de concentrações fósseis de vertebrados. Dentre estas, reportamos uma nova concentração de cinodontes em distintos estágios ontogenéticos pertencentes à espécie *Exaeretodon riograndensis* proveniente do afloramento Várzea do Agudo, Triássico do Rio Grande do Sul. Como anteriormente proposto na literatura, a hipótese de fatores biogênicos, resultando em um acúmulo de elementos esqueletais por predadores, seria a chave para a origem de tais concentrações. Nossa nova integração de dados taxonômicos e tafonômicos, permitiu concluir que há vários fatores envolvidos na formação dos leitos de ossos do afloramento. A dinâmica do ambiente de sedimentação, além da ação acessória de outros organismos, seriam os potenciais formadores desta assembleia. A descoberta da nova assembleia de *E. riograndensis* contribui para uma melhor compreensão da paleoecologia do táxon, tal como a inferência de provável comportamento gregário, e auxilia a compreensão da peculiar abundância de vertebrados fósseis no sítio Várzea do Agudo.

Palavras-chaves: tafonomia; *Exaeretodon riograndensis*; leitos de ossos; Triássico; Paleoecologia

ABSTRACT

It is important to analyze bioestratinomic evidence to understand the taphonomic history and reconstruct paleoecology. Over the years, taphonomic research on Triassic fossil vertebrates from Rio Grande do Sul has been published, showing the diversity of fossil vertebrate concentrations. Among these, we report a new concentration of cynodonts at different ontogenetic stages belonging to the species *Exaeretodon riograndensis* from the Várzea do Agudo outcrop, Triassic of Rio Grande do Sul. As previously proposed in the literature, the hypothesis of biogenic factors, resulting in an accumulation of skeletal elements by predators, would be key to the origin of such concentrations. Our new integration of taxonomic and taphonomic data allowed us to conclude that several factors are involved in the formation of the bone beds at the outcrop. The dynamics of the sedimentary environment, along with the accessory action of other organisms, would be the potential formers of this assemblage. The discovery of the new *E. riograndensis* assemblage contributes to a better understanding of the paleoecology of the taxon, as well as the inference of probable gregarious behavior, and aids in understanding the peculiar abundance of fossil vertebrates at the Várzea do Agudo site.

Keywords: Taphonomy; *Exaeretodon riograndensis*; bonebeds; Triassic; Paleoecology

ORGANIZAÇÃO E APRESENTAÇÃO DA DISSERTAÇÃO

Esta dissertação será apresentada em formato de artigo seguindo as regras do Manual de Normatização de Trabalho Acadêmicos da Universidade Federal do Pampa. Inicialmente, será apresentada uma introdução geral, englobando os pontos importantes tratados na pesquisa. A seguir, é apresentado o artigo intitulado "*A new assemblage from the Brazilian Triassic: insights into the genesis and paleobiological significance of a highly productive fossil site*" submetido no dia 13 de junho de 2024 para a revista *Journal of South American Earth Sciences*.

SUMÁRIO

1 INTRODUÇÃO

Os cinodontes tiveram seu primeiro grande pulso de diversificação após a extinção Permo-Triássica, quando muitos grupos de tetrápodes começaram a proliferar e explorar novos ambientes (Benton, 1995; Ezcurra & Butler, 2018; Kemp, 2005; Romano et al., 2020; Sahney & Benton, 2008; Schmitt et al. 2023). Dentro dos cinodontes, o grupo dos traversodontídeos (Traversodontidae), se diversificou atingindo uma ampla distribuição global durante o Triássico Médio e Tardio (e.g., Abdala & Ribeiro, 2010; Liu & Abdala, 2014; Tolchard et al., 2021; Schmitt et al. 2023). Os traversodontídeos caracterizam-se pela presença de dentes pós-caninos expandidos lábio-lingualmente e uma profunda bacia oclusal (Kammerer et al., 2008; Liu and Abdala, 2014; Pavanatto et al. 2018).

A espécie *Exaeretodon riograndensis* é bem representada em afloramentos do Rio Grande do Sul, especificamente na Zona de Assembleia de *Hyperodapedon* Sequência Candelária), onde predominam junto do rincossauro do gênero *Hyperodapedon* (Schultz et al., 2000; Langer et al., 2007). Para *E. riograndensis* há trabalhos de descrição e tafonomia, tendo conhecidos grande parte do crânio e esqueleto pós-craniano (e.g. Abdala et al. 2002; Oliveira et al. 2007; Liparini et al. 2013, Müller et al. 2015). Além da dentição diagnóstica, *E. riograndensis* diferencia-se pelo processo angular do dentário projetado bem posteriormente e o processo suborbital do jugal bem desenvolvido (Oliveira et al. 2007).

Müller et al. 2015 descreveu uma concentração fossilífera de *E. riograndensis* em diferentes estágios ontogenéticos para o afloramento Várzea do Agudo. O estudo tafonômico de concentrações fossilíferas ajuda a compreender dados macroevolutivos, paleoecológicos e bioestratinômicos. As concentrações fósseis podem favorecer diferentes interpretações para o olhar a qual são estudadas. Pesquisas sobre a tafonomia de vertebrados fósseis do Rio Grande do Sul vem sendo desenvolvidas ao longo dos anos (eg. Holz e Barbarena, 1994; Holz e Schultz, 1998; Bertoni-Machado et al. 2006, Bertoni-Machado et al. 2008; França et al. 2011; Muller et al. 2015; Ugalde et al. 2018; Battista et al. 2022; Battista et al. 2023; Cunha et al. 2024), acrescentando informações valiosas na compreensão de sua paleoecologia.

Nesse contexto, uma prospecção a campo realizada pela equipe do Laboratório de Paleobiologia da Universidade Federal do Pampa recuperou um bloco de rocha contendo uma peculiar assembleia de vertebrados fósseis. A preparação mecânica dos espécimes revelou que todos eles eram consistentes com sua atribuição a *E. riograndensis*. De forma única, a assembleia contém exemplares adultos e minúsculos fragmentos cranianos de espécimes em estágio ontogenético inicial.

A presente dissertação, como apresentada no artigo científico submetido ao periódico *Journal of South American Earth Sciences*, avalia os fatores envolvidos na origem desta nova assembleia fóssil, com implicações na compreensão da destacada abundância de vertebrados fósseis em níveis sedimentares do afloramento Várzea do Agudo.

2 OBJETIVOS

2.1 Objetivo geral

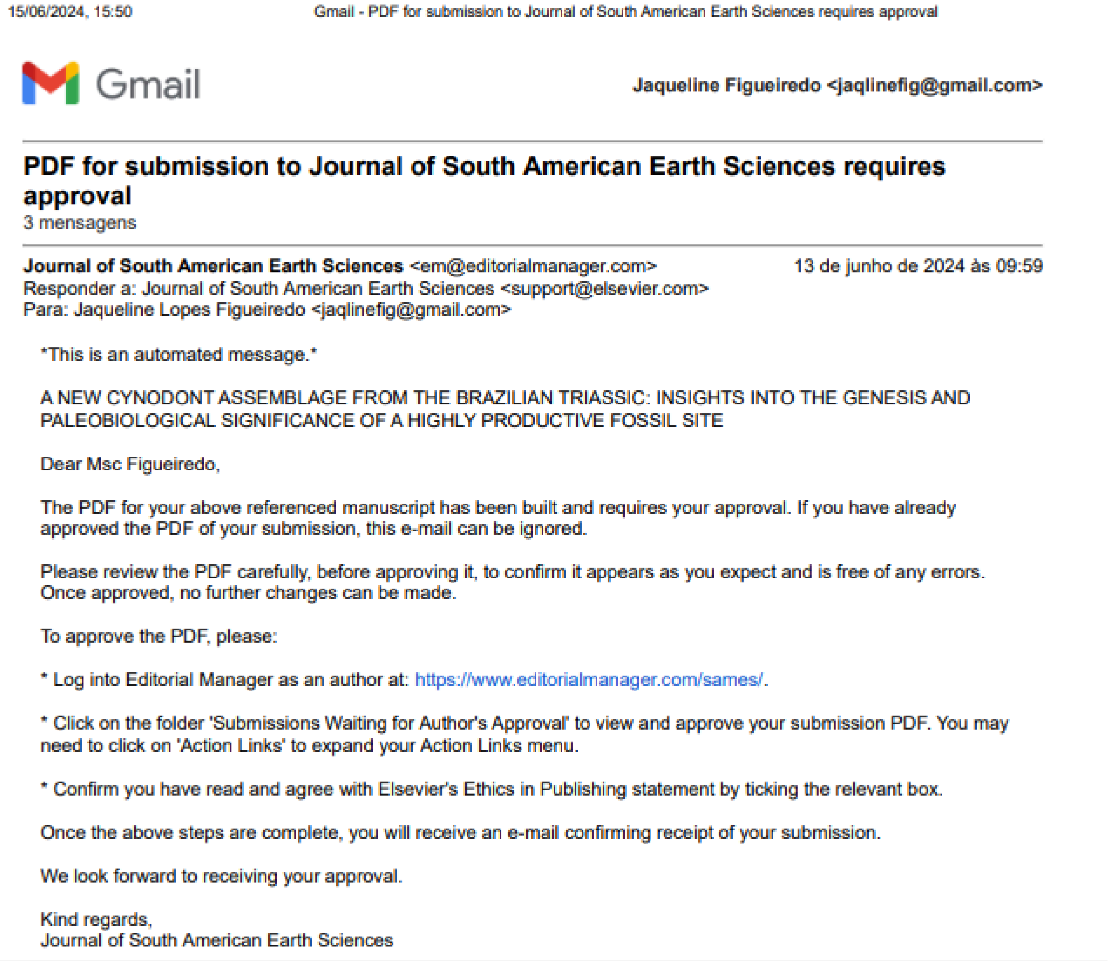
Compreender a gênese e agentes envolvidos na nova concentração fossilífera da espécie *Exaeretodon riograndensis.*

2.2 Objetivos específicos

- Descrever os indivíduos presentes na concentração fossilífera.
- Analisar a tafonomia da concentração fossilífera.
- Levantar informações sobre a paleobiologia e ontogenia da espécie *Exaeretodon riograndensis*.

3 RESULTADOS

Manuscrito submetido para o periódico *Journal of South American Earth Sciences* no dia 13 de junho de 2024.



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A NEW CYNODONT CONCENTRATION FROM THE BRAZILIAN TRIASSIC: INSIGHTS INTO THE GENESIS AND PALEOBIOLOGICAL SIGNIFICANCE OF A HIGHLY PRODUCTIVE FOSSIL SITE

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Abstract

Bonebeds, concentrations of fossilized vertebrates, provide valuable insights into paleoecological, biostratigraphic, and macroevolutionary contexts, though they are often influenced by taphonomic processes. Brazilian Triassic rocks are notable for such fossil assemblages. Among these, the Várzea do Agudo site is remarkable for its abundance of fossils of the traversodontidae cynodont Exaeretodon riograndensis. Initial studies suggested that biogenic factors, especially scavenging and predation, were key to the formation of these bonebeds. This study aims to describe a new fossiliferous concentration from this site, analyzing the taphonomic and biostratinomic processes involved in its genesis. Our findings indicate that multiple factors, including biogenic actions and environmental conditions such as floodplain dynamics, contributed to the accumulation and preservation of the abundant bonebeds. This integrative approach enhances our understanding of the paleoecology of Exaeretodon riograndensis, which was probably a gregarious animal, and the environmental context of Hyperodapedon Assemblage Zone.

Key words: Taphonomy; *Exaeretodon riograndensis*; bonebeds; Triassic; Paleoecology

1. Introduction

Bonebeds are clusters of fossilized vertebrates, containing remains of multiple individuals concentrated in limited sedimentary areas (Behrensmeyer, 1991). South Brazilian Triassic rocks frequently exhibit concentrations of fossil vertebrates that are deeply influenced by taphonomic processes, which can affect paleoecological, biostratigraphic, and macroevolutionary interpretations (e.g. Behrensmeyer, 1991; Holz & Schultz, 1998; Bertoni-Machado et al., 2008; Schultz et al., 2020; Batistta et al. 2023, 2024; Cunha et al. 2024). Biostratinomic interpretations are vital in identifying potential taphonomic biases, providing guidelines on how paleontological data can be used to resolve evolutionary and paleoecological issues (Olson 1980, 1985; Behrensmeyer and Kidwell, 1985; Behrensmeyer et al., 1991).

The taphonomic studies of fossil vertebrates from the Brazilian Triassic have been increasing since the initial research by Holz and Barberena (1994) and Holz and Schultz (1998). The discovery of monotypic and polytypic fossiliferous concentrations in Triassic outcrops of the Rio Grande do Sul State (Southern Brazil) has led to further taphonomic investigations, as seen in works byBertoni-Machado et al. (2006, 2008), França et al. (2011), Müller et al. (2015), Paes-Neto et al. (2016), Ugalde et al. (2018), Battista et al. (2023, 2024) and Cunha et al. (2024). These studies were successful in identifying a series of taphonomic biases affecting the studied samples, establishing a connection between fossil preservation and paleobiology, and enabling to make paleobiological inferences about extinct animals.

In the Brazilian Triassic, one of the greatest abundance of bonebeds is linked to the occurrence of the cynodont *Exaeretodon riograndensis* Abdala et al. 2002 at the fossil site Várzea do Agudo, Rio Grande do Sul. *E. riograndensis* is a traversodontid cynodont commonly found in the upper portion of the Santa Maria Formation (Abdala et al. 2002). Several specimens have been collected, although most remain undescribed, likely representing the most extensively surveyed tetrapod taxon within the *Hyperodapedon* Assemblage Zone (Liu and Abdala, 2014; Schultz et al., 2020).From the Várzea do Agudo site (also known as Janner site) numerous E. riograndensis skulls, jaws, isolated teeth, and postcranial materials were collected, although reports on such materials are scarce in the literature.An ongoing survey of museum collections and fieldwork has documented a total of 46 individuals of E. riograndensis to date. Currently, these data may represent only one quarter of the individuals already collected from this species (A. F. Machado, personal communication).

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Müller et al. (2015) reported a monotypic association of *E. riograndensis* from the Várzea do Agudo fossil site. Various biogenic traces, including invertebrate scavenging and vertebrate bite marks, suggested, according to the authors, extrinsic biogenic action, likely predation/necrophagy and trampling. The spatial orientation of elements, disarticulation patterns, and presence of biogenic traces indicate prolonged exposure before burial, with ecteniniid cynodonts potentially playing a role as modifier agents of the bonebed. Despite this seminal work, further studies on the Várzea do Agudo *E. riograndensis* bonebeds are needed, as several biostratinomic processes (apart or including biogenic accumulation) may have played a role in the genesis of such a productive fossil site. The aim of this work is to describe and provide interpretations regarding the origin of a new fossiliferous concentration containing individuals in various ontogenetic stages of *E. riograndensis* (Fig. 1). The discussion of possible processes involved in the genesis of this concentration holds implications for the paleobiology of the species and the paleoecology of this significant locality in the Upper Triassic of Brazil.

2. Geological setting and associated fauna

The Santa Maria Supersequence (Zerfass et al. 2003), in which the Santa Maria Formation is included, is characterized by the presence of alluvial deposits and ephemeral lacustrine red beds, accumulated mainly under arid and semi-arid conditions, but evolving to more humid conditions after the transition from the early to the late Carnian (Horn et al. 2014, Mancuso et al. 2021, Battista et al. 2023). It is divided in four third-order sequences: Pinheiros-Chiniquá, Santa Cruz, Candelária and Mata Sequences (Horn et al. 2014). The Várzea do Agudo outcrop (also known as Janner Site) is located on the outskirts of the city of Agudo, in the state of Rio Grande do Sul, Brazil. The site is one of the most productive fossiliferous localities for the Brazilian Triassic. It represents layers from the Candelária Sequence, equivalent to the upper portion of the Santa Maria Formation (Zerfass et al. 2003; Horn et al., 2014; Pretto et al. 2015; Schultz et al. 2020). Its faunistic content allows its attribution to the Hyperodapedon Assemblage Zone dated as Carnian (Langer et al. 2018) and more recently, to the *Exaeretodon* subzone (see Schultz et al. 2020). The *Hyperodapedon* Assemblage Zone (AZ) is part of the Candelária Sequence (Horn et al., 2014; Zerfass et al., 2003), which also contains the younger *Riograndia* AZ (Zerfass et al., 2003; Langer et al. 2018; Schultz et al. 2020).

The Várzea do Agudo, outcrop (Agudo municipality, Rio Grande do Sul State, Brazil) (29839010.8900 S, 53817034.2000 W) (Fig. 1) is characterized by usually massive reddish layers, which mostly encompass siltstones, overlied by light colored cross-bedded sandstones. The site can be divided into three portions: (1) the lowermost portion, composed of non fossiliferous massive and laminated burgundy-colored mudstone, with the presence of carbonate nodules and crusts; (2) the middle portion, characterized by orange/red siltstones and fine sandstones, is the most productive in vertebrate fossil remains; (3) the upper portion, formed by light-colored fine sandstone layers bearing cross-bedded stratification and occasional fine-grained intraclasts, is clearly set apart from the lower layers by an erosional surface (Pretto et al. 2015; Pretto et al. 2019), being similar to those strata referred to the Caturrita Formation.

The middle portion of the outcrop has yielded remains of few rhynchosaurs, probably from the genus *Hyperodapedon* (Huxley, 1859), the proterochampsid *Stenoscelida aurantiacus* Müller et al. 2022, the sauropodomorph dinosaurs *Bagualosaurus agudoensis* Pretto et al. 2019 and *Pampadromaeus barberenai* Cabreira et al. 2011, the pseudosuchian *Dynamosuchus collisensis* Müller et al., 2020, as well as the cynodonts *Exaeretodon riograndensis* Abdala et al. 2002 (Oliveira et al. 2007, Liparini et al. 2013)*Trucidocynodon riograndensis* Oliveira et al. 2010 and recently Siriusgnathus niemeyerorum Pavanatto et al. 2018 (Roese-Miron et al. 2024) . The traversodontid cynodont *E. riograndensis* accounts for approximately 50% of the occurrences in the outcrop, matching the occurrence of the same genus in the upper portion of the Ischigualasto Formation in Argentina (Müller et al. 2015; Desojo et al. 2020).The predominance of *Exaeretodon* and the presence of *Hyperodapedon* allow the correlation of the *Exaeretodon* subzone of the *Hyperodapedon* AZ with the upper levels of the Argentine Ischigualasto Formation that also yields an *Exaeretodon* subzone (Pavanatto et al., 2015; Pretto et al. 2018; Müller et al. 2015; Langer et al. 2007; Schultz et al. 2020; Desojo et al. 2020).

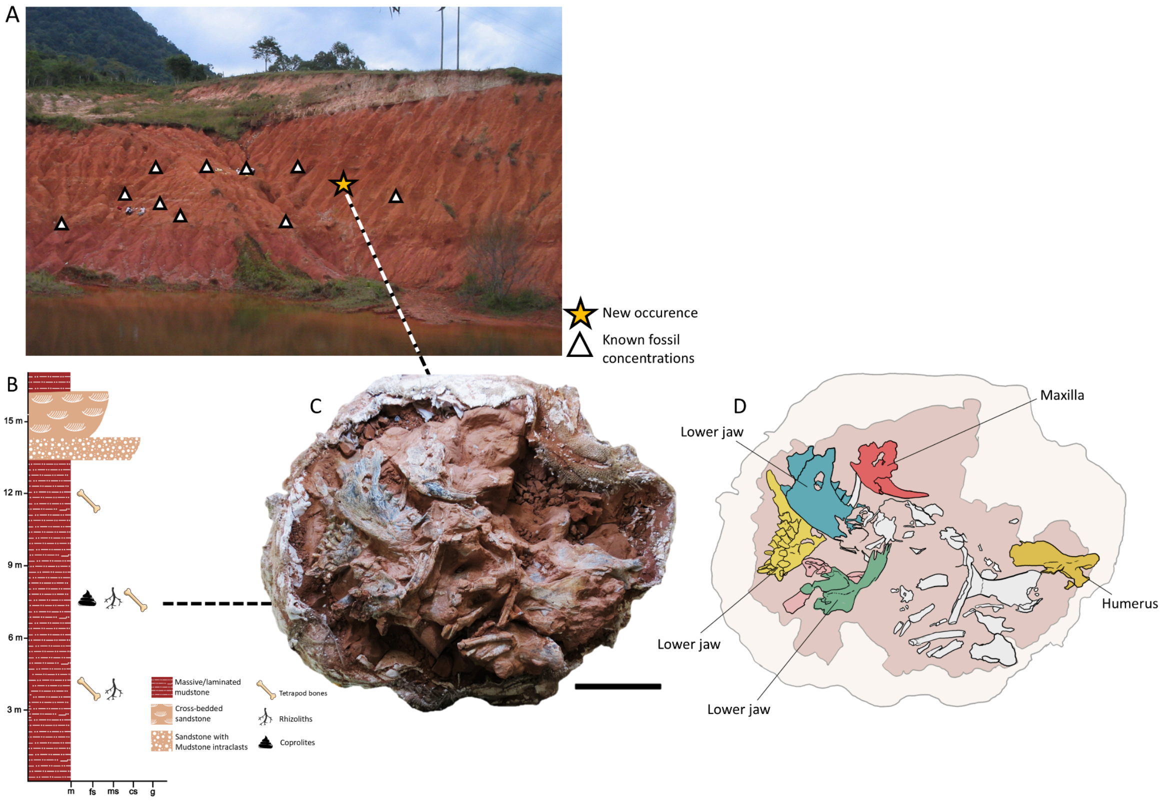

Figure 1. A, photograph of the Várzea do Agudo fossil site, depicting the occurrence of known fossil concentrations and the exact spot where the new assemblage was collected; B, stratigraphic profile of the outcrop. Dashed line indicates the level from which the new assemblage was collected; C, D, plaster jacket before complete preparation and interpretative drawing, exhibiting the bone elements within the matrix. Only a few fossil elements were highlighted, being the most easily identifiable in the sample before mechanical preparation. A, photograph by C. L. Schultz, used under permission; B, modified from Pretto et al. (2015).

3. Material and methods

The studied material, CAPPA-UFSM 0263, consists of an association of 7 cranial elements, 12 isolated teeth, 2 humeri, 1 vertebra, 25 rib fragments and 98 undetermined fragments (some of the breakage happened during preparation), see Table 1 and 2 and Figures 1-4. The fragments classified as indeterminate are tiny pieces for which it was not possible to determine their anatomical position. The fossil concentration was collected from the middle portion of the Várzea do Agudo outcrop, where the elements were clustered in an area of about 1 m² (Fig.1). The associated jaws were partially exposed, while other cranial elements were covered by sediment and overlapped by the rib fragments. A plaster jacket was made in the field, with the aim of preserving the integrity of the fossil assemblage while still embedded in the rock matrix. The specimens were mostly isolated through mechanical preparation. Photographs of the material were taken before the bones were removed from the plaster jacket (Fig. 1C, D), allowing to track the elements in their original position within the matrix before isolation. After the preparation of the bones from the matrix, a survey of taphonomic and taxonomic data was conducted using methods similar to those of Bertoni-Machado & Holz (2006), Bertoni-Machado et al. (2008), Müller et al. (2015), and Battista et al. (2023). bone representativity (Müller et al. 2015), orientation of the bones in the matrix, degree of disarticulation (Hill, 1979), modifications on the bone surface (Behrensmeyer, 1978), Minimum Number of Individuals count (MNI: Badgley, 1986), Voorhies Group count (Voorhies, 1969, sensu Behrensmeyer, 1975), and hydraulic equivalence analysis (Behrensmeyer, 1975).

Voorhies (1969) identified three groups to analyze the different hydraulic behaviors and susceptibility to fluvial transport (Battista et al. 2023). The VG I group consists of fossil elements that are immediately removed (such as ribs and vertebrae), the gradually removed elements belong to the VG II group (long bones), and finally, the elements that are the most difficult to remove are part of the VG III group (skulls and mandibles). In their research, Battista et al. (2023) propose the inclusion of additional groups, such as the IFR group (indeterminate fragments). These indeterminate fragments consist of bone fragments whose anatomical origin is uncertain, and whose fragmentation may be of anthropogenic origin or pre-burial fragmentation. We chose to include the small indeterminate fragments in Voorhies Group I. This is based on the assumption that small-sized materials with evidence of pre-final burial fragmentation would have hydraulic behavior equivalent to elements with high transportability. The fact that it is not easy to distinguish anthropogenic fragmentation from pre-burial breakage in this particular assemblage may generate artifacts to our analysis. However, most of the fracture surfaces of the indeterminate fragments were covered by sediment, indicating that the breakage occurred before the final burial.

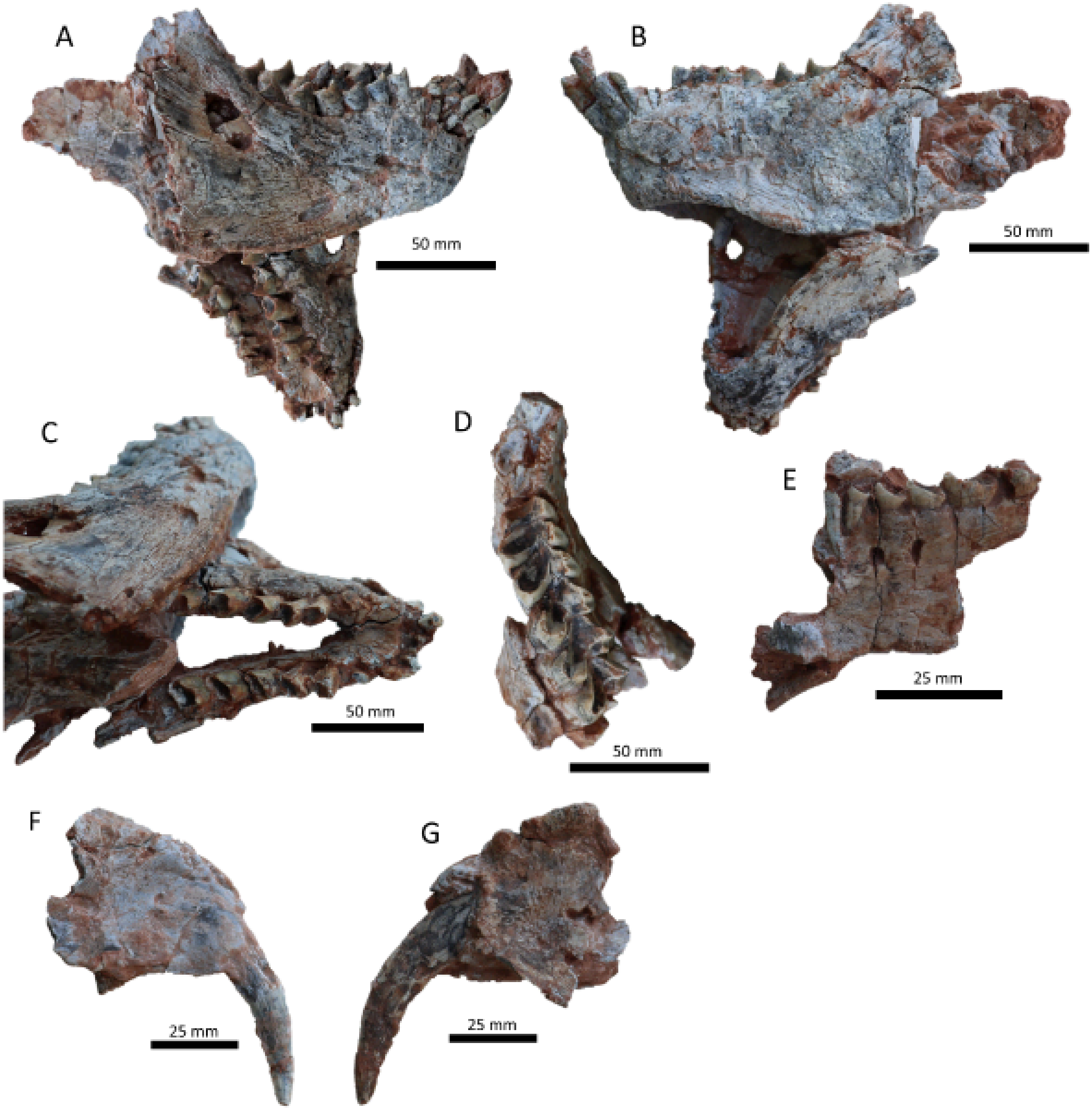

Figure 2. Representative cranial and mandibular materials present in the assemblage. A, intertwined mandibles, with mandible I represented in right lateral view; B, same as in A, but with mandible I represented in left lateral view; C, same as in A and B, but with mandible II in occlusal view; D, left maxilla in occlusal view; E, left dentary in lateral view; F, right maxilla in lateral view; G, right maxilla in medial view.

Institutional abbreviations: CAPPA-UFSM, Centro de Apoio à Pesquisa Paleontológica, Universidade Federal de Santa Maria, São João do Polêsine, Brazil; UFRGS-PV, Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

4. Results

4.1. Bone representation and Minimum Number of Individuals (MNI)

The studied assemblage is classified as monotypic and monospecific because it includes only identifiable fossil elements from a single species (see Discussion). To determine the MNI (Badgley, 1986), identifiable cranial and postcranial elements were analyzed. The elements used in the count include:

- Two associated mandibles (Fig. 2A, B, C).
- Two humerus (right humerus: Fig.2A and B; left humerus: Fig.4A and B).
- One vertebra (Fig. 4C, D).
- One maxilla (Fig. 2D).
- A fragment of an upper canine (Fig. 2F, G).
- A third, smaller mandible than the associated ones (Fig. 2E).
- Small maxillary fragments (Fig. 3A, B, C, D).

Based on the representativity of the bones in the skeleton and the size differences of the elements, a minimum of four individuals was identified in the assemblage (see Table 1 and Table 2). The two large mandibles, the maxilla fragment, two humeri, vertebra, smaller mandible fragments, and upper canine may belong to three adult individuals. Finally, the right and left small maxillary fragments may belong to an individual in an early ontogenetic stage. See Table 1.

Table. 1

Ontogenetic category	**Bone element**	**Voorhies Group**	**Weathering stage**	**Bioerosion**	**Diagenetic remarks**
Adult 1	Mandible 1	Group III	Stage 1 (0 - 3 years)	Yes	-
	Left humerus	Group II	Stage 1 (0 - 3 years)	Yes	-
	Right humerus	Group II	Stage 1 (0 - 3 years)	Yes	-
	Vertebra	Group II	Stage 1 (0 - 3 years)	Yes?	Carbonatic crust cover

	Fragmented canine	Group I	Stage 1 (0 - 3 years)	No	-
Adult 2	Mandible 2	Group III	Stage 1 (0 - 3 years)	Yes	-
	Maxilla 1	Group III	Stage 1 (0 - 3 years)	Yes	-
Adult 3	Mandible 3	Group III	Stage 1 (0 - 3 years)	No	-
Early juvenile	Frag. small maxilla 1	Group III	Stage 1 (0 - 3 years)	Yes	-
	Frag. small maxilla 2	Group III	Stage 1 (0 - 3 years)	No	-
Indeterminate	Indeterminate fragments	IFR*	Stage 1 (0 - 3 years)	No	-

* see text as this elements were considered indeterminate

Table 2. Representativity of skeletal elements in the assemblage

Bones	Number of specimens	Percentage
Skull fragments	7	7.38%
Isolated teeth	12	8.05%
Humerus	2	1.34%
Vertebra	1	0.67%
Fragmented ribs	25	16.67%
Indeterminate fragments	98	65.67%

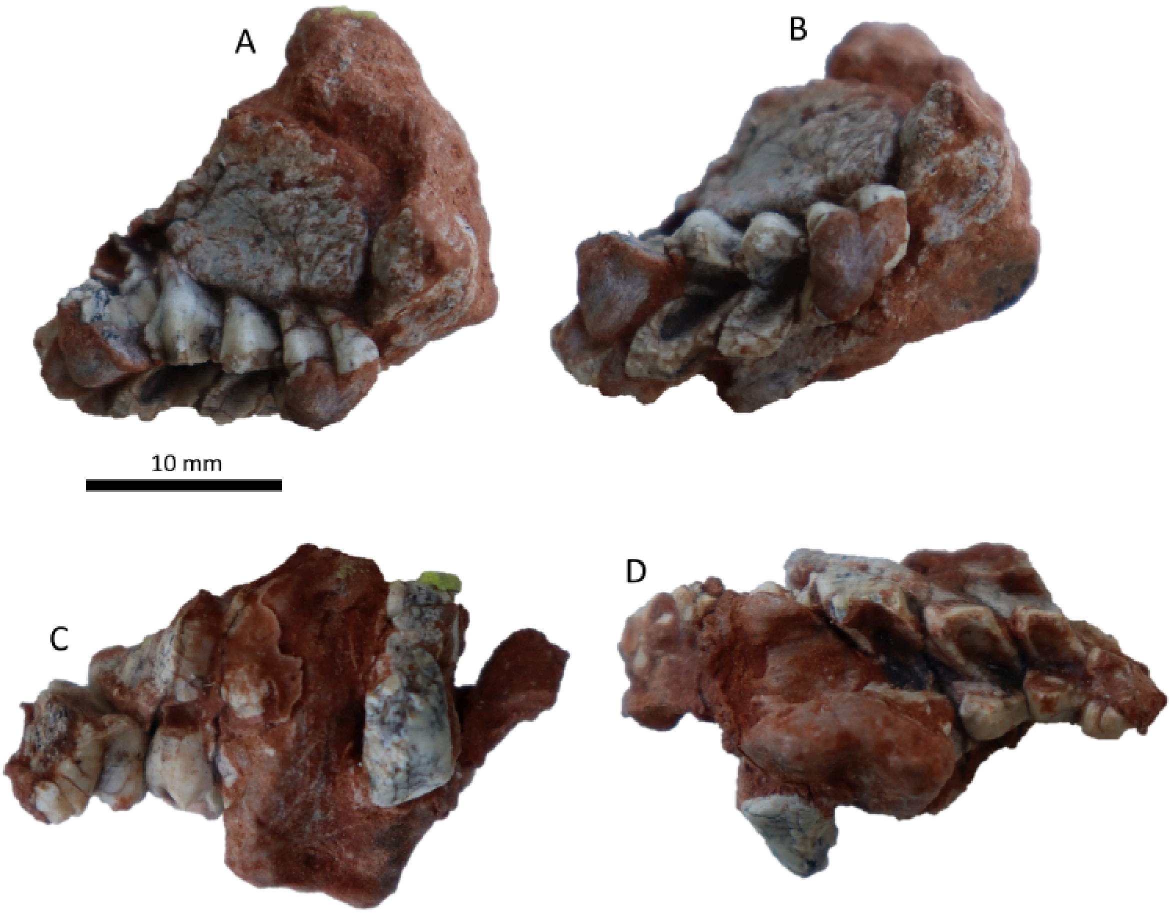

Figure 3. Tiny maxilla fragments belonging to a juvenile. A-B, right maxilla in lateral view and in occlusal view; C-D, left maxilla in lateral view and in occlusal view.

4.2. Orientation of the bones in the matrix, disarticulation and fragmentation

. All the bones were associated and closely packed. The fossil elements were chaotically arranged within the matrix, lacking a preferential orientation. Even so, the taphonomic study was conducted after the bones had already been completely isolated, and unfortunately, the preparation was not meticulous enough to track the azimuthal orientation of the isolated elements. Therefore, a more categorical analysis of possible orientation patterns was not possible. None of the identified and isolated elements in the taphocoenosis exhibited an anatomical pattern of articulation. Fragmented and abraded specimens are the norm in the collected sample. In terms of abrasion, there are no apparent differences between the taphonomic signatures of the whole and fragmentary elements. The upper and lower postcanine teeth present in the mandibles and maxillae remain inserted in their alveoli and retain their cusps, even though the loss of maxillary/mandibular teeth are observed in specimens that were probably subjected to a longer exposure before final burial (e.g. Schmitt et al., 2023).

Although part of the fragmentation appears to have an anthropogenic origin, especially considering that the mechanical preparation of the material was not properly documented, most of the fracture surfaces show total or partial coverage by sediments, indicating breakage prior to the final burial.

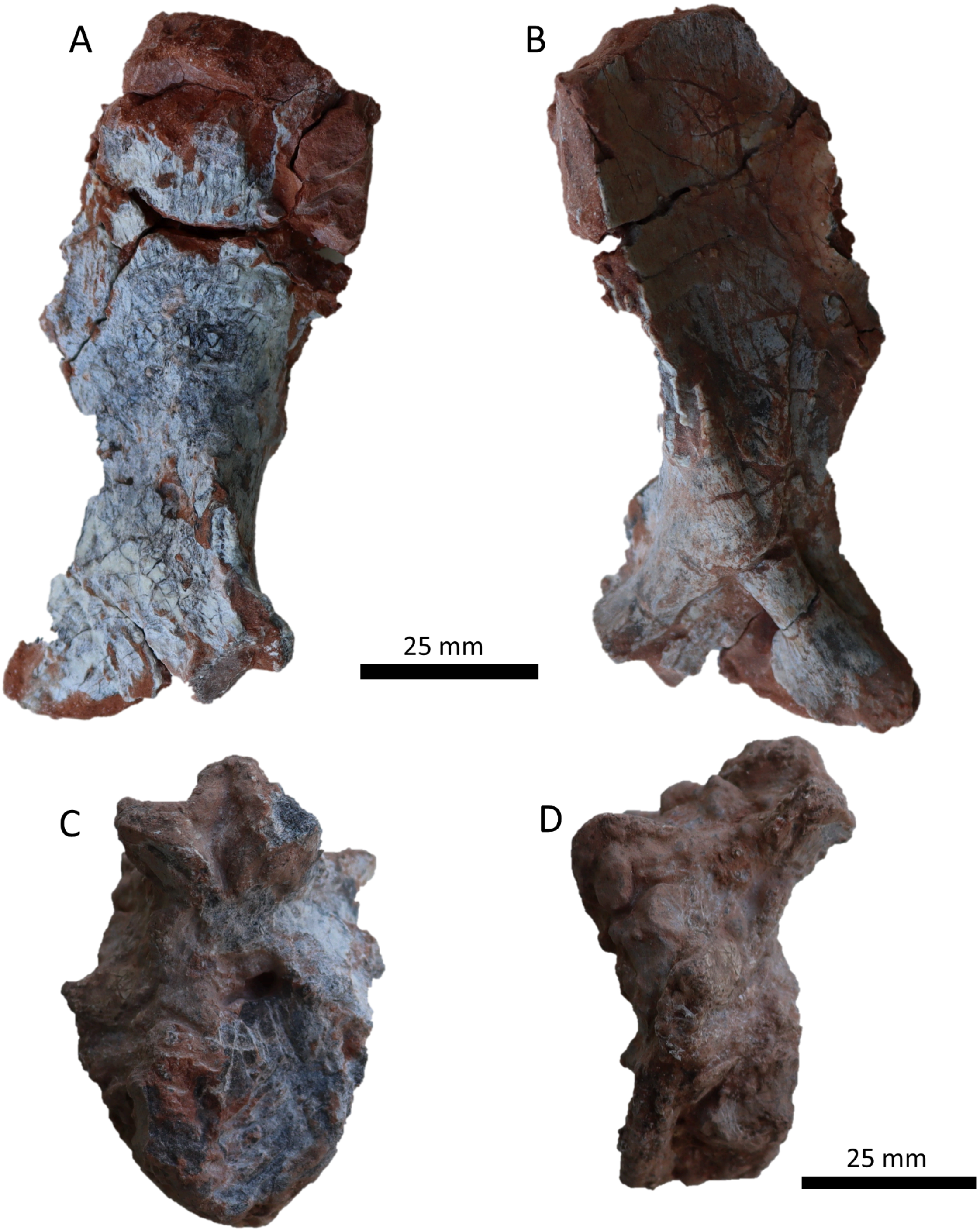

Figure 4. Representative postcranial bones. The left humerus in dorsal view Fig.4A and in ventral view Fig.4B The vertebra in posterior view Fig. 4C and in right lateral view Fig. 4D. .

4.3. Voorhies Groups and hydraulic equivalence

The three Voorhies groups are represented in the assemblage (Fig. 5), in order of abundance: Group I (rib fragments and vertebra), Group III (mandibles and skull fragments) and Group II (humeri and vertebra). For a more detailed analysis, a “indeterminate fragments group” or IFR (as proposed by Battista et al., 2023) was created for the grouping of fragments whose anatomical identification was not possible. In the new assemblage, the IFR are formed mainly by small, fragmentary elements of dubious anatomical identification, they range from 5 mm to 1 cm.

Noteworthily, the pattern of relative abundance of each group may be influenced by the fact that anatomically equivalent elements vary greatly in size (due to the association of individuals at different ontogenetic stages).

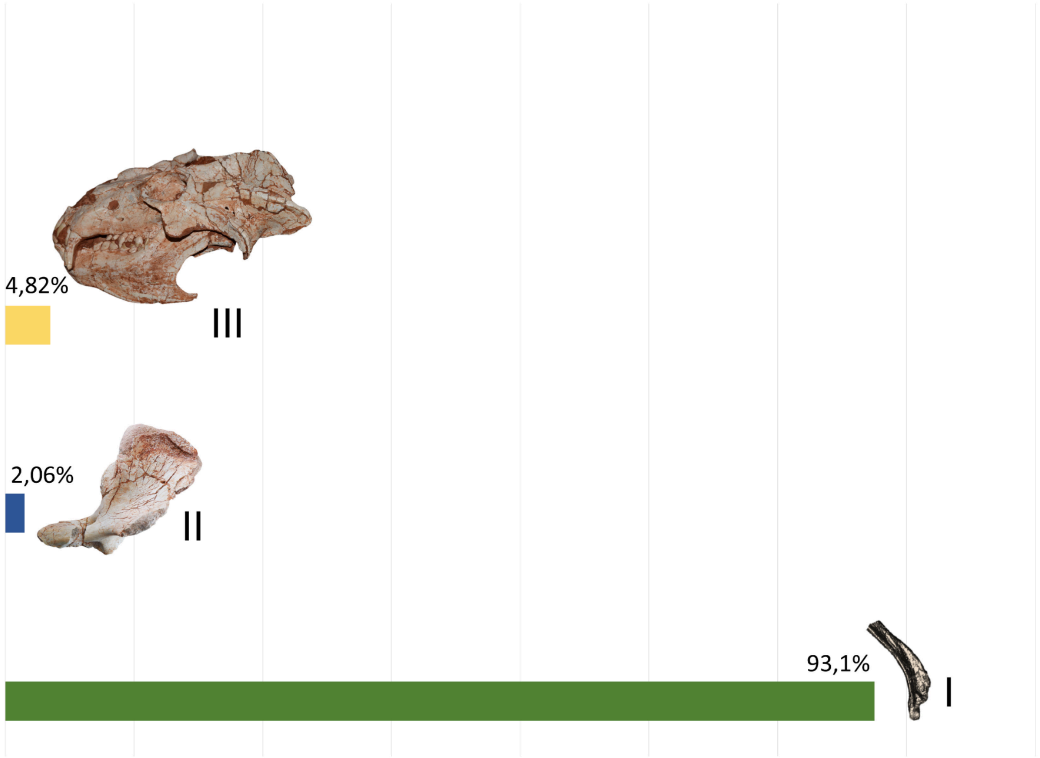

Figure 5. Representativeness of Voorhies groups in the new assemblage. Photographs by Leonardo Kerber.

Table 3. Representativity of Voorhies groups in the assemblage

Voorhies Group	Number of specimens
Group I: rib fragments and vertebra	26
Group II: humerus	2
Group III: skull elements and isolated teeth	23
IFR: tiny bone fragments	98

4.4. Modifications on the bone surface and bioerosion traces

The jaws, maxillae, humeri, and vertebra belonging to larger individuals are the best-preserved bones, compared to smaller elements, like the anatomically unidentified fragments. The surfaces of some fossils, for example the isolated vertebra (Fig. 4C, D), are associated with carbonatic (possibly paedogenic in nature) concretions that are difficult to extract, and their further preparation would potentially damage the material. This differs from other postcranial elements such as the humeri and cranial bones, all of which display excellent preservation of their surfaces. The ribs are highly fragmented, some of the damage being attributable to mechanical preparation. However, photographs of the assemblage prior to preparation reveal that most ribs were fragmented when in situ. This allows to establish that most bone elements of the assemblage are in stage 1 of weathering (as proposed by Behrensmeyer, 1978), with the predominance of cracks on the bone surfaces.

The bone elements exhibit numerous traces of bioerosion, most of which can be reliably attributed to the osteophagic activity of insects or bite marks (Paes-Neto et al. 2018). The traces are systematized in Table 3 and Figure 6.

Thirteen traces were found on bones of the assemblage: erosion of extremities (not counted), irregular bone erosion (2), circular or irregular pits (8), lenticular pit (1) and straight grooves (2).

Irregular surface bone destruction: Present on the large maxilla and mandibles. Additionally, erosion of extremities are observed in the vertebra and humerus. In the maxilla (Fig. 6A), the irregular trace is ‘channel-like’ (Fig. 6C1), with generally straight and irregular margins, and associated fractures. Nonetheless, occasional scalloped margins are also observed. Nearby traces are also irregular in general morphology (Fig. 6C). A similar shallow trace is observed in mandible 1 (Fig. 6B), with similar width but its morphology is generally more groove-like and elliptical in plain view (Fig. 6D). The bioerosion morphology is more similar to Morphotype 3 of Paes-Neto et al. (2018), rather than other known ichnotaxa with similar morphology (e.g. Cubiculum Roberts et al., 2007). Additionally, the weathering stage at the bottom surface appears to not show parallel cracks as in the non-modified bone surface.

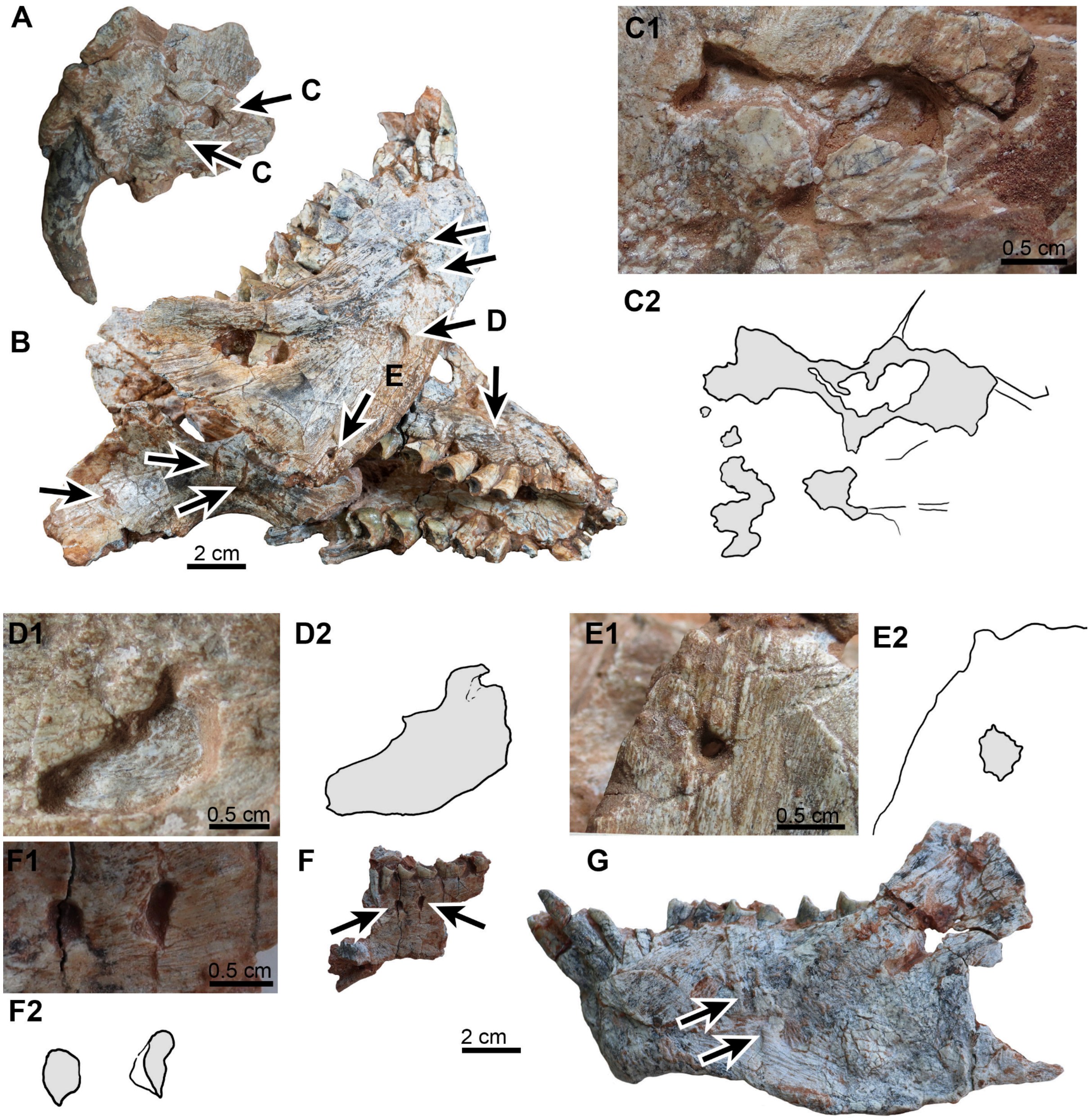

Figure 6. Suite of bone bioerosions in the A, maxilla I; B, mandible I; F, small maxilla and G, mandible II, with details and interpretative drawings: C, 'Groove-like' bone destruction and associated pits; D, Elliptical bone destruction; E, Circular hole; F, Circular and lenticular pits.

Table 3. Bioerosion traces

Specimen	Morphotype	Trace	Interpretation
Mandible 1	Bone destruction	Shallow bone destruction	Insect

Mandible 1	Pit	Elliptical pit	Insect
Mandible 1	Pit	Elliptical pit	Insect
Mandible 1	Pit	Pit	Insect
Mandible 1	Pit	Circular pit	Insect
Mandible 2	Pit	Elliptical pit	Insect?
Maxilla 1 canine	Bone destruction	Groove bone destruction	Ambiguous
Maxilla 1	Pit	Circular pit	Insect?
Maxilla 1	Irregular	Irregular traces	Insect?
Dentary frag.	Pit	Lenticular pit	Bite trace
Dentary frag.	Pit	Circular pit	Ambiguous
Right Humerus	Erosion of extremity	Bone extremities eroded	Insect?
Right Humerus	Groove	Two straight grooves	Bite trace
Vertebra	Erosion of extremity	Bone extremities (neural spine) eroded	Insect?

4.5. Diagenetic remarks

In general, the cranial elements are well preserved and have a whitish coloration. One of the mandibles appears to have undergone plastic deformation, probably as a result of sedimentary compression. The sedimentary compression of fossil elements from this site has already been reported by Müller et al. (2020), and Stefanello et al. (2018).

The vertebra has a more grayish coloration and is covered by a thick concretionary matrix (as reported above), being similar to that aspect found in CAPPA/UFSM 0029, a skull of *Trucidocynodon riograndensis* also collected from the Várzea do Agudo site (Oliveira et al., 2010; Stefanello et al., 2018). This concretionary matrix, of carbonatic nature, appears to be the result of pedogenic action on the bone elements.

5. Discussion

5.1. Taxonomic attribution and ontogenetic remarks

As complete skulls are missing from the assemblage, it was not possible to access, in the new material, some relevant diagnostic cranial features for Brazilian traversodontids. Typical features of *Exaeretodon riograndensis* present in bones of the assemblage includes upper postcanine teeth possessing an occlusal basin on the labial half of the occlusal surface, a central main labial cusp, and anterior and posterior accessory labial cusps, which form a vertical cutting plane with wear; three lower incisors; absence of a diastema between the lower post canines and lower canines; and the presence of a diastema between the upper postcanines and upper canines. Other elements, as humerus, vertebrae and ribs resemble those of *E. riograndensis* and other traversodontids (e.g. Liu et al., 2017), and are compatible in size with the larger dentigerous bones.

The suborbital process of the jugal bone is not accessible for examination, as it was not preserved. The assessment of this feature would be useful to exclude closely-related taxa, such as *Siriusgnathus niemeyerorum* Pavanatto et al. 2018 and *Santagnathus mariensis* Schmitt et al. 2024. The larger jaw of the material we present here has seven lower postcanines, with the last one being an emerging replacement tooth. This condition differs from known specimens of *S. niemeyerorum*, which bear eight lower postcanines (Pavanatto et al., 2018). The canines are fragmented, and there are three lower incisors on each side, which also differs from the number displayed by *S. niemeyororum* (Pavanatto et al., 2018). The specimens exhibit diastemata between the postcanine and canine teeth, both in the upper and lower jaws, a feature not present in S. mariensis (Schimitt et al., 2023). . One of the two associated larger jaws features six lower postcanines, fragmented canines, and three fragmented lower incisors. A large maxilla fragment has seven upper postcanines, with the seventh appearing in eruption as a replacement tooth. The maxillary canine is fragmented, with only its root being observable. The associated mandibles vary in the number of upper postcanine teeth, differing from the number described by Liparini et al. (2007), which mentions the presence of five lower postcanine teeth and a sixth as a replacement tooth. We propose a seventh lower postcanine tooth as a replacement tooth, as described by Abdala et al. (2002) for the mandible, suggesting a potential indicator of ontogenetic variation in these cynodonts.

As such, all fossil elements within the assemblage are here attributed to the species *E. riograndensis* (Abdala et al., 2002) and represent more than one individual of different ontogenetic stages. Among the identified elements, the association represents: three mandibles and three maxillae, twelve isolated teeth, one vertebra, two humeri, twenty five fragmented ribs and several indeterminate fragments. The genus *Exaeretodon* Cabreira, 1943 has dozens of specimens already recorded at the Várzea do Agudo site, indicating the abundance of the genus at the locality (Müller et al. 2020). As detailed above, our taxonomic attribution was mainly based on representativity of the species in the outcrop and in dental characters, especially with regard to the premaxillary/maxillary and dentary postcanines, which are characteristic of the species.

The three ontogenetic categories identified in the assemblage are: i) adult: two associated mandibles, a fragment of a maxilla, right and left humeri and one vertebra; ii) juvenile: one mandible; iii) early juveniles: two tiny fragments of maxillae.

Erosion of extremities: Bone destruction is observed in the left humerus and in the vertebra extremities (Fig. 4) being patterns similar to those documented by insect bone bioerosion (see Backwell et al. 2012). However, we emphasize that both of these elements show a considerable coverage of concretionary matrix and, in some areas, have sustained damage caused by mechanical preparation. Therefore, we recommend caution in interpreting these features as unequivocal evidence of osteophagic activity.

Pits: Irregular, circular and lenticular pits are observed in the maxilla 1 (1, Fig. 6C), mandible 1 (3, Fig. 6E), mandible 2 (1, Fig. 6G), dentary (2, Fig. 6F), and in the right humerus situated between the two intertwined mandibles. These traces present around 0.6 mm of diameter and usually present scalloped margins (Fig. 6E).

However, one preserves a more homogeneous outline (Fig. 6F) being in close proximity with a teardrop-shaped pit of similar size. Two larger elliptical pits are observed in mandible 1 (Fig. 6B) being found associated with the bone destruction described above (Fig. 6D) and a hole (Fig. 6E). Smaller circular pits are also observed in the mandible 2 and in the humerus (Fig. 6B). Circular and irregular pits are compatible with insect traces (Britt et al., 2008; Saneyoshi et al. 2011; Paes-Neto et al., 2016)

Straight grooves: Two paired large straight grooves are observed in the humerus (Fig. 6B), being almost 10 mm in length by 5 mm in largest width. The extremities of these grooves are less wide than its mid-portion.

5.2. Ethologic and taphonomic significance of fossil traces

Bone surface destruction and erosion of extremities are patterns commonly observed in extant insect biorosions in bones (e.g. Backwell et al., 2012; Zanetti et al., 2014; Holden et al., 2013). The elliptical bone destruction is very similar to extant invertebrate bone bioerosions, like those of gastropods (Dirks et al. 2015) and insects (Backwell et al., 2012; Zanetti et al., 2014; Holden et al., 2013) but it lacks bioglyphs or any associated traces of their mouth parts. The irregular 'channel-like' bone destruction is somewhat similar to this, but its non-scalloped margins associated with fractures may indicate that breakage or collapse of the external surface may have occurred. In this scenario, the agency of vertebrate bite marks may be considered, although no conclusive evidence is present to support this. Circular to irregular pits and holes are also a common pattern regarding insects (Backwell et al., 2012; Zanetti et al., 2014; Holden et al., 2013), but lenticular traces are typical patterns of teeth marks (Rinehart et al. 2006). Other commonly trace related to bite marks are the presence of grouped straight grooves, like the pair observed in the humerus.

None of these traces can be attributed to named traces (like *Cubicullum* or *Nihilichnus*) but their association indicates that both invertebrates and vertebrates have acted as biostratinomy agents in the sample. It is not possible to establish if vertebrates acted prior the invertebrate traces, but it is possible to assume that the later act after the carcasses were already subaerially exposed due to the difference between the weathering stage of the 'elliptical bone destruction'. Insects have been reported as the sole invertebrate agent in other Late Triassic reports (Paes-Neto et al. 2016; Cunha et al. 2024) including from the same fossil site (Müller et al. 2015), being thus likely the producers of the bone destruction, pits and holes. Our results indicate that at least some of the traces were produced while the caracesses were not yet buried. Also, the absence of healing on the bone surface indicates that all traces are post mortem. The potential vertebrate traces, like the lenticular pits and straight grooves, indicate the action of a small - to midsize agent, compatible in size with the ecteniid cynodont *Trucidocynodon* and the ornithosuchid archosaur *Dynamosuchus* (see Müller et al. 2015; 2021).

5.3. Taphonomic interpretations of the new assemblage

Different and, sometimes, complementary taphonomic processes can act in the genesis of a fossil concentration. Macrovertebrate bonebeds can be either: a) biogenic: intrinsic or extrinsic; or b) physical: hydraulic or sedimentary. Intrinsic biogenic concentrations result from the behavior or activity of individuals present in the concentration, while extrinsic ones result from the feeding behavior or collecting activity of other animals (Rogers et al., 2007). An extrinsic concentration was, for instance, proposed for the *Exaeretodon* assemblage described by Müller et al. (2015). Furthermore, hydraulic physical concentrations are the result of the activity of surface flows or waves.

Interpreting the genesis of a bonebed can be a challenging task, and different hypotheses can arise to explain the biostratinomic concentration of bones. Those hypotheses are often related to mainly geologic causes (e. g. hydraulic transport) or a biogenic origin (accumulation of skeletal remains by carnivores). This is often the case for those peculiar bonebeds where skull or skull/mandibular fragments are the main components of the assemblage, when an extrinsic cause may be needed to explain the lack of natural representativity of bones.

Our association is similar to other concentrations reported for different strata of the Brazilian Triassic (Bertoni-Machado et al., 2008; Battista et al. 2023) and for the same outcrop (Müller et al., 2015). Similarities include a comparable depositional floodplain environment, the abundance of cranial elements, and traversodontid cynodonts as the main recovered taxa. In particular, the new assemblage is similar to the one described by Müller et al. (2015), as it was recovered in the same locality (and probably the same level) and is composed of elements in distinct ontogenetic stages belonging to the traversodontid species *Exaeretodon riograndensis*. In addition, a similar pattern of disarticulation, abrasion, fragmentation and bone modification was detected in both fossil concentrations.

As such, we will focus our discussion on the main possible causes for the occurrence of a concentration with such characteristics.

5.3.1 Hydraulic *transport hypothesis*

Patterns of orientation and spatial distribution of fossils are usually related to the environmental energy levels to which the bioclasts are exposed (Toots, 1965). In most cases, random orientation does not result from hydraulic transport, as organic remains deposited at the bottom of the water body and subject to a directional or oscillatory flow tend to assume a preferred orientation determined by their shape and center of mass (Toots, 1965). In spite of that, random orientation can be produced by sediment traps characteristic of high-energy environments or by the activity of burrowing organisms that are characteristic of low-energy environments (Toots, 1965).

The abundant presence of cranial elements and of elements belonging to all the three Voorhies Groups (elements in different sizes and densities), as well as apparently the random orientation of fossil elements, and the interpreted low-energy sedimentary environment for the stratigraphic level from where the assemblage was recovered (see above), dismiss the hypothesis of hydraulic transport as playing a major role in the genesis of the studied assemblage. This is also the case for the concentrations described and interpreted by Bertoni-Machado et al. (2008) and Müller et al. (2015). As such, we discard hydraulic transport/selection as a major factor to explain the *Exaeretodon* bone accumulation described here.

5.3.2 *Extrinsic biogenic hypothesis and selection by predators/scavengers*

The taphonomic studies of Bertoni-Machado et al. (2008) and Müller et al. (2015) propose predator/scavenger selection as the genesis of some Brazilian

Triassic bonebeds that are, in some ways, similar to the one we present here. An extrinsic biogenic control for the fossil accumulation would explain why cranial elements make up for the most part of the assemblages, as they tend to be less nutritious than postcranial bone elements and more difficult to be carried by scavenging animals (Behrensmeyer, 1991). Thus, cranial elements end up being discarded by predators and scavengers, accumulating and concentrating in the floodplains (Bertoni-Machado & Holz, 2006).

White and Diedrich (2012) monitored the current activity of hyenas on an exposed elephant carcass as a model to predator/scavenger bone modifications, with implications on the biostratinomic history of fossil assemblages. The authors report modifications on the bone surfaces and the absence of transport of bone elements by the hyenas, who fed on the carcass at the exposure site. The exposure of the elephant skeleton was ended by the seasonal flooding of that particular environment.

Haynes (1991) notes the presence of skulls and hip bones as the most abundant elements in mass death or serial predation sites in Africa, being this also the case of sites in North America. Elements of the upper limb bones are better represented than the bones of the lower limbs, while elements such as vertebrae and ribs are not as well represented at these sites (Haynes, 1991). Haynes (1991) also notes that trampling marks and spiral or complete fractures are commonly observed on lower limb bones, whereas predator tooth marks are less frequent.

According to Rogers et al. 2007, extrinsic fossil concentrations formed by the action of predators/scavengers can be separated into two categories: a) serial predation; b) intentional selection/transport of skeletal materials. Serial predation, proposed by Haynes (1988), can be diagnosed by the presence of temporal mixing, abundance of bone processing indicators, presence of cranial elements, as well as an environment conducive to the accumulation of prey. Haynes (1988) presents cases of mass death sites and cumulative sites, sometimes as aresult from serial predation. Cumulative sites are not the result of just one event; they accumulate over time. The bones found in these sites exhibit varying degrees of weathering and may show signs of gnawing marks. Meanwhile, concentrations formed by intentional selection/transport of skeletal material display, as a rule, extensive evidence of chewing, abundance of bone chips and cranial elements, and an environment conducive to prey accumulation (Rogers and Kidwell, 2007).

Among the cataloged specimens of *E. riograndensis* from the Várzea do Agudo site (e.g. Müller et al. 2020), there is generally a higher presence of skulls and mandibles compared to postcranial elements. The collection of postcranial materials at the Várzea do Agudo outcrop presents a significant challenge, due to the degree of disarticulation and chaotic preservation pattern of these fossils. In many cases, the postcranial elements are scattered over large areas, complicating the process of comprehensive recovery, particularly when using plaster jackets. This dispersion, along with the fragmentary nature of the remains, demands a meticulous approach to minimize the loss of information and ensure the proper recovery of the specimens. The fossil concentration presented here is characterized by the presence of cranial and postcranial elements and by belonging to an environment conducive to predation. However, the other characteristics cited by Rogers and Kidwell (2007) and Haynes et al. (1988) do not fit. The fossil elements of the concentration do not show clear evidence of temporal mixing (e.g. clearly distinct taphonomic signatures) or the presence of bone chips. However, the action of scavengers/burrowers is not ruled out; it is probably, however, an accessory characteristic linked to other events that together caused the formation of this concentration.

One extrinsic factor that likely influenced the fossil concentration in question is trampling. This is supported by the presence of fractures that suggest pre-burial fragmentation, exhibiting patterns typically associated with trampling. Such evidence points to a densely populated floodplain environment.

5.3.3 *Alternative hypothesis*

When integrating taphonomic information from the new assemblage, along with other specimens reported for the same site, it is possible to consider the Várzea do Agudo site as a cumulative death site, where its formation occurs through the accumulation over considerably long time spans, with carcasses being exposed for some time and buried by successive massive sediment deposition events on the floodplain. The time averaging of the different levels would thus be controlled by cyclic river channel overflows. In a humid climate, these floodplain overflows would occur at short enough intervals to not produce significantly different taphonomic signatures in the individual elements of the bonebeds. Therefore, a single event did not kill all the animals present in each particular concentration, suggesting that a more holistic and integrative model should be invoked to explain the exceptional abundance of fossil yields, beyond simple biogenic sorting and accumulation (see Haynes, 1988).

Some other fossil specimens found in the Várzea do Agudo site, as reported in the literature, show relevant taphonomic features that may be useful to a more integrative approach. The partial skeleton of the sauropodomorph *Bagualosaurus agudoensis* shows evidence of insect osteophagy, weathering on the fossil elements (stages 2 and 3 of Behrensmeyer, 1978) and diagenetic modifications such as compression (Paes-Neto et al. 2016; Pretto et al. 2019). Pretto et al. (2019) propose that the loss of bone elements and the unusual position of the carcass may be the result of scavenger activity, but there is no evidence of tooth marks, although there is evidence of insect bone destruction (Paes et al. 2016). The presence of nodular concretions in the fossil elements of *Bagualosaurus agudoensis* (Pretto et al., 2019) and *E. riograndensis* UFRGS-PV-1177-T was also reported (Paes et al. 2016), both possibly suggesting the presence of galleries of burrows around the carcasses after final burial. Recent reports indicate that insect activity may occur in both subaerial and buried remains in the Late Triassic (Cunha et al. 2024), being thus equally possible that insects were important agents while the carcass were exposed subaerially and within the active taphonomic zone of the Triassic deposits.

The presence of individuals from such distinct ontogenetic classes, in abundant monotypic associations without obvious signs of transport, seems to indicate that the fossil site is reminiscent of a typical habitat/feeding area for *Exaeretodon*. The abundance of this animal, a potential prey, would certainly attract the presence of predators or scavengers, such as *Trucidocynodon* and *Dynamosuchus*, both predators being reported for the site. Thus, the abundance of the taxon, combined with the presence of different age classes, may be justified by the accumulation of skeletal elements of dead animals during the intervals between the cyclic sedimentary loads resulting from flood events in the riverine plain.

Predation can also be an accessory factor in generating carcass concentrations in habitats such as swamps, ponds, and puddles of water, where scavengers and predators may drag dead animals away from the death site (Behrensmeyer and Boaz, 1980). According to Bertoni-Machado & Holz(2006), the predatory activities in the Schoenstatt outcrop would be favored by the presence of ephemeral and/or seasonal waterholes, such as lakes and ponds, controlled by the water table. The Schoenstatt outcrop, interpreted as a floodplain, created a habitat rich in vegetation that grew around a lake, attracting both herbivores and carnivores. During episodes of lake overflow and storms, alluvial sheet sedimentation would occur, creating a chaotic mix of isolated bones that remained on the lake's edge and, finally, burying them and protecting the bones from aerial exposure and from further action of scavengers. As above, the taphonomic model proposed by Bertoni-Machado et al. (2006) recognizes that this particular kind of fossil concentrations may have more than one player at work, being generated by both biotic and abiotic factors. This more holistic approach recognizes the complexity that may be involved in the genesis of bonebeds.

The integration of the taphonomic data and particular signatures of the new fossil assemblage allows us to propose that similarly complex factors may have taken place during its origin. As such, an alternative origin, not restricted to biogenic accumulation by predators and scavengers, may be considered by integrating more comprehensive data on similar occurrences in the same locality (e.g. Müller et al. 2015). It is striking that most traversodontid remains are found in similar associations like those concentrations found at Várzea do Agudo Site, including other Middle-Late Triassic taxa like *Massetognathus*, *Santacruzodon*, *Syriusgnathus* and *Santagnathus* in Brazil (e.g. Beroni-Machado et al. 2008; Pavanatto et al. 2018; Schmitt et al. 2024; Battista et al. 2023, 2024) and *Ruberodon* in India (Ray, 2014). These associations may be more related to possible gregarious behavior of these cynodonts rather than any taphonomic bias as proposed by previous authors. The possible occurrence of gregarious behavior has already been proposed by Battista et al. (2024) for the cynodont Santacruzodon.

6. Conclusion

Although our study focuses on an isolated fossil concentration, its investigation and the recognition that similar taphonomic signatures have been reported for other concentrations in the Várzea do Agudo locality allow us to make more specific inferences at the fossil concentration level and more general ones at the locality level, although the latter are more speculative and require a more integrative taphonomic study at the Várzea do Agudo site.

The integration of taphonomic signatures from the new concentration allows us to infer that it underwent modifications due to the action of predators and insects, was probably buried by seasonal floods, and that *Exaeretodon riograndensis* displayed gregarious behavior.

It seems likely that the wet floodplain environment, abundant in vegetation (evidenced by the common rhizoliths), attracted herbivorous and carnivorous cynodonts (as in the case of *Trucidocynodon*), rhynchosaurs, sauropodomorphs, and other archosaurs, such as the possible scavenger *Dynamosuchus*. The accumulation of bone elements from the natural mortality of gregarious herbivores, heavily modified by the action of scavengers and insects, was buried by seasonal flash floods, enough to overflow the fluvial channel. Thus, although the action of scavengers and carrion-feeders may have affected the fossil concentration, other factors need to be considered to understand its genesis.

7. Aknowledgements

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