



ANALYSIS OF DENTAL AND OSTEOLOGICAL ELEMENTS OF TOXODONTIDAE (MAMMALIA, NOTOUNGULATA) FROM LATE PLEISTOCENE–HOLOCENE DEPOSITS OF THE RIBEIRA OF IGUAPE VALLEY, SOUTHEASTERN BRAZIL

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ABSTRACT – The Ribeira of Iguape Valley, located in the south of São Paulo State, presents an important cave system where several preserved Quaternary faunal remains have been found, especially in the Abismo Ponta de Flecha, Abismo do Fóssil and Abismo do Juvenal caves. Although the records of toxodontids are common in the region, almost no multidisciplinary research has been done in these materials, including the potential interaction with prehistoric humans. Therefore, the objective of this work was to analyze teeth of toxodontids found in the Ribeira Valley, to understand paleontological aspects of these animals and investigate the presence of cut marks as a proxy for potential interactions with human groups. Taxonomic analysis and measurements showed that all teeth could be assigned to the species *Toxodon platensis*, deciduous teeth to the cf. *T. platensis*, and one lower molar that was suggestively associated with *Mixotoxodon larensis*. The analysis of paleopathologies identified the presence of dental enamel hypoplasia in all specimens found at Abismo Ponta de Flecha Cave, suggesting that this individual suffered from stress events during the period of tooth formation. Cut marks were identified in only two specimens of *T. platensis*, but the unusual location of these incisions and the identified weathering marks made it difficult to understand the aiming of these marks.

Keywords: enamel hypoplasia, human marks, *Mixotoxodon*, *Toxodon*.

RESUMO – O Vale do Ribeira de Iguape, localizado no sul do Estado de São Paulo, apresenta um importante sistema de cavernas no qual foram encontrados diversos restos faunísticos quaternários preservados, especialmente nas cavernas Abismo Ponta de Flecha, Abismo do Fóssil e Abismo do Juvenal. Embora os achados fósseis de toxodontes sejam frequentes na região, raros trabalhos multidisciplinares foram realizados até o presente momento nestes materiais, especialmente quanto a potencial interação destes animais com humanos pré-históricos. Portanto, o objetivo deste trabalho foi analisar os elementos dentários de toxodontídeos encontrados no Vale do Ribeira, para compreender aspectos paleontológicos destes animais e investigar a presença de marcas de corte como um indicador de potenciais interações com grupos humanos pretéritos. A análise taxonômica e as medições mostraram que todos os dentes podiam ser atribuídos à espécie *Toxodon platensis*, os dentes decíduos a cf. *T. platensis* e um molar inferior suggestivamente associado a *Mixotoxodon larensis*. A análise das paleopatologias identificou a presença de hipoplasia do esmalte dental em todos os exemplares encontrados no Abismo Ponta de Flecha, sugerindo que os espécimes analisados foram submetidos a eventos de estresse durante o período de formação dos dentes. Foram identificadas marcas de corte em apenas dois exemplares de *T. platensis*, mas a localização incomum destas incisões e as marcas de intemperismo identificadas dificultaram a compreensão do objetivo destas marcas.

Palavras-chave: hipoplasia de esmalte, marcas humanas, *Mixotoxodon*, *Toxodon*.

INTRODUCTION

The order Notoungulata is a group of native ungulates from South America. The first known fossils date from the Paleocene (Zimicz *et al.*, 2020), being restricted to the South American continent until the Miocene, when there was the Great Biotic Interchange of the Americas (GABI), which allowed their migration to North America (Woodburne, 2010; Lundelius *et al.*, 2013).

Notoungulata is considered a monophyletic group, composed of 140 genera distributed in 13 families (Cifelli, 1985; Carrillo *et al.*, 2018; Silva, 2019), of which only Toxodontidae is recorded in the Brazilian Pleistocene (Mendonça, 2007; Silva, 2019). The first records of Toxodontidae date back to the Oligocene and extend into the Upper Pleistocene (Bond *et al.*, 2006; Carrillo *et al.*, 2018). The family is currently subdivided into two subfamilies, Nesodontinae Simpson, 1945 and Toxodontinae Owen, 1845

(Nasif *et al.*, 2000; Forasiepi *et al.*, 2015; Bonini *et al.*, 2017; Silva, 2019).

Tooth morphology and the distribution of enamel bands are important diagnostic characters for the identification of Toxodontidae species (Mendonça, 2007; Silva, 2019). Toxodontidae fossils from the Brazilian Pleistocene are represented by the species *Mixotoxodon larensis* van Frank, 1957, *Trigodonops lopesi* Roxo, 1921 (= *Piauhytherium capivarae*; Silva, 2019) and *Toxodon platensis* Owen, 1837 (Rancy, 2000; Mendonça, 2007; Asevedo *et al.*, 2021), being *T. platensis* the most representative of them, having its occurrence recorded in almost all Brazilian states (Mendonça, 2007; Silva, 2019; Asevedo *et al.*, 2021).

Toxodon platensis was characterized by an herbivorous diet, with robust bodies reaching approximately 1790kg (Elissamburu, 2012; Gomes *et al.*, 2023). The skull of *T. platensis* was robust and elongated, with an elevated auditory region and large tympanic bulla. They had short necks and very muscularly developed limbs, the forelegs being shorter than the hindlegs. Their paws had three digitigrade toes that were short, stout and very wide, as seen in extant ungulates, like rhinos (Paula Couto, 1979; Mendonça, 2012; Silva, 2019).

Previous works have reported the presence of *Toxodon platensis* fossils associated with assemblages where lithics and megafauna bones with cutmarks were found (Marshall *et al.*, 1984; Tonni *et al.*, 1992; Guidón *et al.*, 1994; Politis & Gutiérrez, 1998; Politis *et al.*, 2016; Chahud *et al.*, 2023a,b; Del Papa *et al.*, 2024), but in none of these studies it was possible to identify marks that could be reliably associated

with an interaction with prehistoric human groups. Chahud *et al.* (2023b) analyzed *T. platensis* teeth that presented incisions found in the Ribeira Valley; however, the authors were unable to determine whether the marks had been produced by prehistoric human groups.

The Ribeira of Iguape Valley is located in the south of the state of São Paulo. The paleontological interest in the region is due to the exploration of caves, where many fossils from Pleistocene megafauna as well as remains of recent fauna have been found. Despite several studies pointing out the importance of the Ribeira of Iguape Valley for the understanding of the paleofauna of Brazil, as shown in the works of Paula Couto (1975), Lino *et al.* (1979), Barros-Barreto *et al.* (1982), Ghilardi *et al.* (2011), and Chahud *et al.* (2022, 2023b, c, 2024a, c), there are still few studies exploring the materials that have been collected in the region, many being restricted to identification or citation of specimens.

Among the key sites for understanding the diversity of megafauna present in the Ribeira Valley are the Abismo Ponta de Flecha Cave, the Abismo do Fossil Cave, and the Abismo do Juvenal Cave. These vertical caves are located near the municipalities of Iporanga and Apiaí, in the south of the State of São Paulo (Figure 1). The excavations revealed a large quantity of osteological materials from various groups of vertebrates, living and extinct. Among the megafauna found are representatives of the families Megatheriidae, Nothrotheriidae, Megalonychidae, Scelidotheriidae, Glyptodontidae, Felidae, and Toxodontidae (Ameghino, 1907; Paula Couto, 1975; Lino *et al.*, 1979; Barros-Barreto *et al.*,

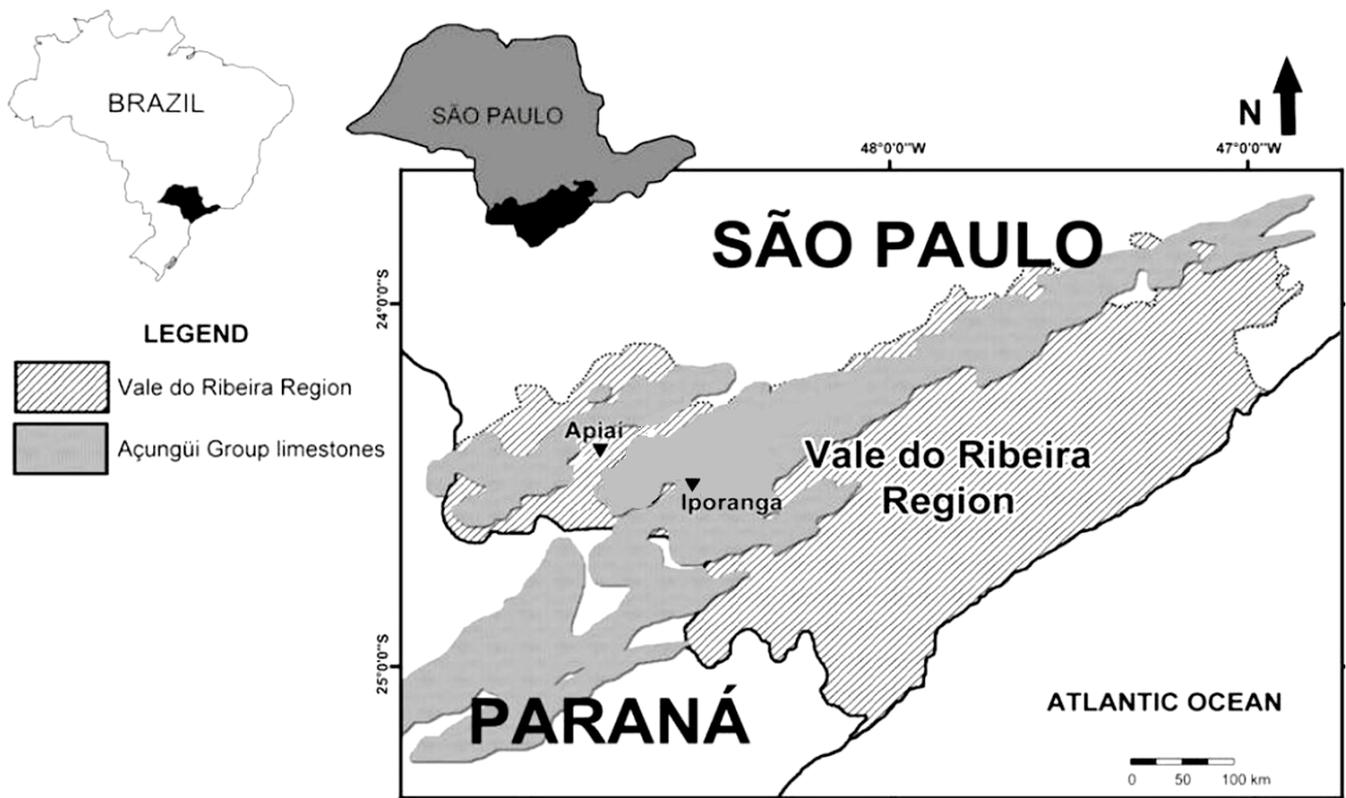


Figure 1. Location of paleontological sites in Ribeira Valley (modified from Ghilardi *et al.*, 2011).

1982; Chahud, 2022; Karmann & Ferrari, 2002; Ghilardi *et al.*, 2011; Chahud *et al.*, 2023a, c, 2024b).

The present work aims to describe the morphology, and to analyze paleopathologies and incisions found in an assemblage of Toxodontidae dental and osteological elements from the Ribeira Valley.

MATERIAL AND METHODS

The elements that were analyzed in this work were collected in different expeditions throughout the 20th and early 21st centuries in three different sites, the Abismo Ponta de Flecha Cave, the Abismo do Fóssil Cave, and the Abismo do Juvenal Cave (Figure 1). The materials from the Abismo Ponta de Flecha Cave belong to the paleontological collections curated at the Laboratory of Systematic Paleontology of the Department of Sedimentary and Environmental Geology of the Institute of Geosciences of the University of São Paulo (IGc-USP) and contain 12 specimens, including the condylar process and 11 permanent teeth, four upper and seven lower. The teeth analyzed in this work are the same as those analyzed by Chahud *et al.* (2023b), but here is a more detailed morphological description and a comparison with other specimens of Toxodontidae found in the Ribeira Valley will be made. The specimens received two valid numbering for the present study, the first related to the field collection with the acronym “PF-” and the second from the Institute of Geosciences, University of São Paulo, IGc-USP collection, “GP/2C-”.

The materials from Abismo do Fóssil Cave and the Abismo do Juvenal Cave are part of the collection of the Department of Paleontology of the Museu de Zoologia of the University of São Paulo (MZUSP), which consist of 16 teeth, of which five are deciduous upper and lower teeth and 12 are permanent upper and lower teeth. All specimens received the acronym MZUSP-PV, referring to the vertebrate paleontological collection.

For taxonomic review, the dental elements were compared with the diagnoses described and used by Roth (1898), Laurito (1993), Miño Boilini *et al.* (2006), Mendonça (2007), and Rincón (2011). The identification of potential marks produced by human action was made using the descriptions made by Lyman (1994), Labarca (2003) and Domínguez-Rodrigo *et al.* (2009).

A digital microscope, Dino-Lite AM111, and a stereomicroscope, Leica M80, were used beyond direct macroscopic examination analyses for presence or absence of enamel hypoplasia on each tooth. The stereomicroscope photos were taken using a Leica MC 170 HD camera; both equipment belong to the Laboratory of Plant Anatomy of the Department of Genetics and Evolutionary Biology of the Institute of Biosciences at the Universidade de São Paulo. The methodology used to identify enamel hypoplasia was developed by Ferigolo (2007). Ferigolo (2007) describes six different types of enamel hypoplasia defects that could be identified in the teeth of *Toxodon platensis*. The classification of enamel defects was done as follows: type 1)

a few isolated and scattered pits; type 2) vertical rows of pits (one or more, with different distances between them); type 3) mesiodistal rows of pits (one or more); type 4) very large defects such as grooves on the buccal surface of the crown, with a wavy appearance; type 5) narrow mesiodistal and/or vertical grooves, with various degrees of depth (the grooves are usually continuous rows of pits); type 6) partial or total absence of enamel in an area.

The metric analysis of the teeth was performed using a digital pachymeter, following the anatomical landmarks used and defined in the works of Roth (1898), van Frank (1957), Lucas *et al.* (1997), Fariña *et al.* (1998), Miño Boilini *et al.* (2006), Rincón (2011) and Rosa *et al.* (2011), which include the transverse and anteroposterior diameters.

SYSTEMATIC PALEONTOLOGY

Order NOTOUNGULATA Roth, 1903
Family TOXODONTIDAE Ameghino, 1889

Mixotoxodon van Frank, 1957

Mixotoxodon larensis van Frank, 1957
(Figure 2A)

Material. One lower molar (MZUSP-PV 455) (Figure 2A).

Description. Specimen MZUSP-PV 455 has a buccally-lingually broad hypoconid with the size similar to that of a trigonid; the hypoconid is projected lingually, with a lingual enamel band extending between the metaconid and the antero-lingual side of the hypoconid, but without fully covering it; it has an ento-hypoconid fold with a well-marked angulation curvilinear antero-mesially; paraconid is not anteriorly projected and does not have a meta-entoconid fold; the metaconid is covered by a band of lingual enamel, which extends to the antero-buccal border of the hypoconid; it has a band of buccal enamel that covers the protoconid postero-mesially and extends to the hypoconulid at its antero-medial border; the buccal enamel is wider than the lingual enamel. From the descriptions of lower molars by Laurito (1993) and Rincón (2011) it is possible to associate this specimen with an m2, and differentiate it from an m1, due to the paraconid not being projected anteriorly and the absence of the meta-entoconid fold.

Remarks. When comparing the specimen MZUSP-PV 455 with *Toxodon platensis* molars, including the specimens identified in the Ribeira of Iguape Valley, this specimen differs in that its hypoconid is larger than that of *T. platensis*, by the absence of the meta-entoconid fold, and by its paraconid not projected anteriorly. Specimen MZUSP-PV 455 was also compared with *Trigodonops lopesi* molars, following the descriptions found in Silva (2019). MZUSP-PV 455 differs from *Trigodonops* in that the protoconid is covered by enamel, the meta-entoconid fold is absent and the hypoflexid fold is very shallow. The measurements of the specimen MZUSP-PV 455 fall within the expected range for adult individuals of *Mixotoxodon larensis*. Only its anteroposterior diameter

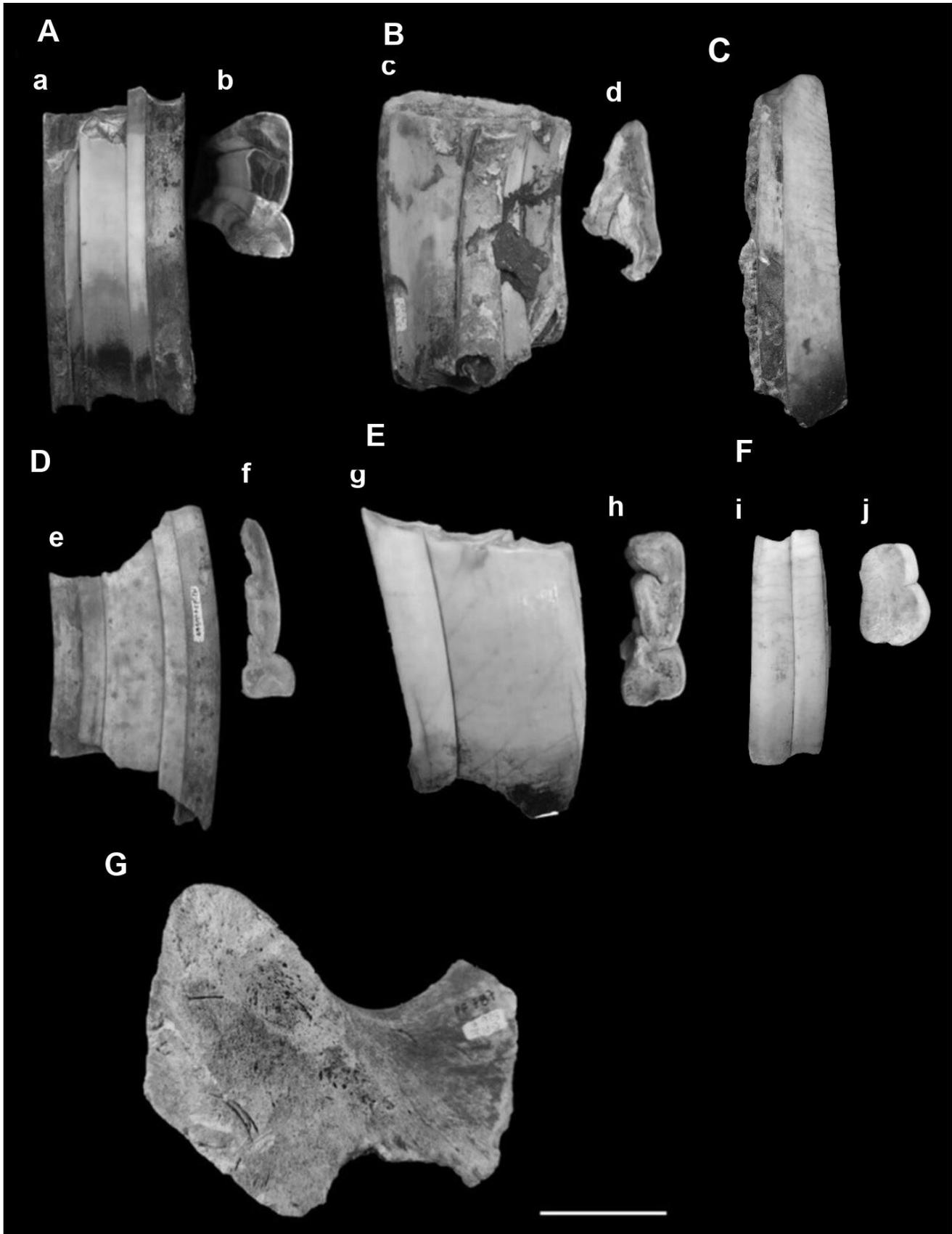


Figure 2. Toxodontidae dental and osteological elements. *Mixotoxodon larensis*, A, lower molar in lingual (a) and occlusal (b) views (MZUSP-PV 455). *Toxodon platensis*, B, upper molar in lingual (c) and occlusal (d) views (PF-993/GP/2C-533F); C, lower incisor in buccal view (MZUSP-PV 704); D, lower molar in lingual (e) and occlusal (f) views (MZUSP-PV 569); E, lower molar in buccal (g) and occlusal (h) views (PF-995/GP/2C-533C); F, lower premolar in buccal (i) and occlusal (j) views (MZUSP-PV 580); G, condylar process in lateral view (PF-787/GP/2C-526B). Scale bar = 5 cm.

is slightly larger than expected, which can be interpreted as individual intraspecific variation. Small dental variations are common in this species (Rincón, 2011; Lundelius *et al.*, 2013). The presence of this species in the State of São Paulo would be its southernmost record in the Americas, for South America its occurrence is recorded in Colombia (Porta, 1959; Villarroel & Clavijo, 2005), Venezuela (Karsten, 1886; van Frank, 1957; Royo & Gómez, 1960; Rincón, 2004; Rincón *et al.*, 2009), in northern Brazil (Paula Couto, 1982) and in northern Bolivia (Hoffstetter, 1968).

Toxodon Owen, 1837

Toxodon platensis Owen, 1837
(Figure 2B–G)

Material. Twenty six teeth and one osteological element were analyzed, 22 belonged to adult and five juvenile individuals (Figure 2), including the condylar process (PF-787/GP/2C-526B), six incisors (PF-940/GP/2C-306A; PF-1123/GP/2C-107; PF-994/GP/2C-306B; MZUSP-PV 704; MZUSP-PV866), eight premolars (PF-1214/GP/2C-316; PF-997/GP/2C-533B; PF-1368/GP/2C-312; MZUSP-PV 521; MZUSP-PV 579; MZUSP-PV 580; MZUSP-PV 662; MZUSP-PV 975) and twelve molars (PF-430/GP/2C-533D; PF-995/GP/2C-533C; PF-993/GP/2C-533F; PF-856/GP/2C-533B; GP/2C-533A; MZUSP-PV 453; MZUSP-PV 454; MZUSP-PV 569; MZUSP-PV 802).

Description. Two I1 (PF-940/GP/2C-306A and MZUSP-PV 866) have a semi-elliptical transverse shape and are very arched. The lingual surface is destitute of enamel. The buccal surface on the mesial side has an open angle that forms a corner so that this incisor forms an internal mesial surface. Both the buccal and mesial surfaces are totally covered in enamel. Three upper molars were analyzed (PF-993/GP/2C-533F, GP/2C-533A and PF-856/GP/2C-533B). Both M1 and M2 are morphologically similar, only differing by their size, M2 being larger than M1. All have a triangular shape and have three enamel bands: one that covers almost the entire buccal surface, leaving only the metaloph without enamel; another that covers the entire protoloph, but with the protocone absent from the enamel covering; and finally, a band that covers the entire anterior fold of the lingual surface. The anterior fold is very deep, dividing the molar into two lobes. Specimen PF-993/GP/2C-533F showed that the metatoloph is more anteriorly projected than the other two specimens analyzed. (Figure 2Bd).

The three lower incisors have three surfaces and are triangular. The i1 (PF-1123/GP/2C-107) has a buccal surface, a lingual surface, and a distal surface. Buccal and lingual surfaces are much wider than the distal surface, only the lingual surface is covered by a band of enamel that extends to the lateral edge but does not completely cover this side of the incisor. The distal surface is slightly concave in the middle and is covered by a thin layer of cementum. The i2 (PF-994/GP/2C-306B) is morphologically similar to the i1, only the

distal surface has a more acute angulation than the i1. As in the other incisors, only the lingual surface of i3 (MZUSP-PV 704) is covered by enamel, but in this tooth two lateral surfaces are formed, which have almost the same width and are devoid of enamel (Figure 2C).

Six teeth were identified as pm3 (PF-1368/GP/2C-312, PF-997/GP/2C-533B, MZUSP-PV 662, MZUSP-PV 580, MZUSP-PV 521, and MZUSP-PV 975), all have an oblong shape and are covered by an enamel band only on the buccal surface. The lingual surface is concave and not covered with enamel (Figure 2F). In pm4 (PF-1214/GP/2C-316) only the buccal surface is covered in enamel. The buccal surface has a fold dividing it into two lobes. In contrast, the lingual surface has a deep concave shape. The m2 (PF-995/GP/2C-533C, PF-430/GP/2C-533D, MZUSP-PV 802 and MZUSP-PV 453) have an enamel band that covers the entire buccal surface, extending to its lateral edges, it is also possible to note on this surface that the hypoflexid fold is quite deep. The lingual surface is also covered with enamel, this band in turn extends to the most lingual portion of the hypoconulid. Also, on the lingual surface the ento-hypoconid fold is very deep, while the meta-entoconid fold is more discreet (Figure 2Eh). Two teeth were associated with m3 (MZUSP-PV 454 and MZUSP-PV 569), the trigonid morphology is similar to that observed in m2, however, the talonid in these teeth is longer and extended posteriorly, in addition, the ento-hypoconid fold has a depth similar to that of the meta-entoconid fold (Figure 2Df).

Remarks. All the specimens can be referred to *Toxodon platensis* based on descriptions of tooth morphology found in Roth (1898) and Miño Boilini *et al.* (2006). The condylar process (PF-787/GP/2C-526B) was compared with the specimen illustrated by Mones & Heintz (1992) and can therefore be associated with *Toxodon platensis*. This specimen was compared with other species of megafauna, but no other species presents mandibular ramus like that of *T. platensis* and like that of specimen PF-787/GP/2C-526B. The teeth diameters were measured linearly, transverse, and anteroposteriorly, based on measurements found and suggested by Roth (1898), Fariña *et al.* (1998) and Miño Boilini *et al.* (2006). The results obtained (Table 1) were compared with the values found in the studies by the aforementioned authors. Some teeth such as PF-856/GP/2C-533B, PF-997/GP/2C-533B, PF-1214/GP/2C-316 and MZUSP-PV 704 have part of their occlusal surface fragmented or covered by incrustation, preventing an accurate measurement. The Table 1 shows that most of the analyzed specimens (n = 15) presented measurements within the expected range, according to the literature (Roth, 1898; Fariña *et al.*, 1998; Miño Boilini *et al.*, 2006). However, seven specimens presented measurements slightly greater than those found in the literature (Table 1), which could be interpreted as a small intraspecific variation. *Toxodon platensis* is a species known to have polymorphic features in its dentary (Roth, 1898; Mendonça, 2007; Silva, 2019), some authors associate this polymorphy to regional variations (Mendonça, 2007; Silva, 2019; Chahud *et al.*, 2023b).

Table 1. Toxodontidae teeth measurements (in mm). The range is based on the works of Roth (1898), van Frank (1957), Lucas *et al.* (1997), Fariña *et al.* (1998), Miño Boilini *et al.* (2006), Rincón (2011) and Rosa *et al.* (2011). **Abbreviations:** R, right; L, left; APD, anteroposterior diameter; TD, transverse diameter.

<i>Toxodon platensis</i>					
Teeth	Specimen	Measure TD	Range	Measure APD	Range
I1	PF-940/GP/2C-306A (L)	27.50	–	–	–
	MZUSP-PV 866 (L)	32.69	–	–	–
M1	PF-993/GP/2C-533F (L)	30.23	28-30	63.4	40-65
M2	PF-856/GP/2C-533B (L)	~29.44	29-45	64.68	51-72
	GP/2C-533A (R)	29	29-45	65.39	51-72
i1	PF-1123/GP/2C-107 (L)	21.90	21-22	–	–
i2	PF-994/GP/2C-306B (R)	22.20	22	–	–
i3	MZUSP-PV 704 (R)	~31.02	–	–	–
pm3	PF-1368/GP/2C-312 (R)	13.30	12-14	26.30	20-26
	PF-997/GP/2C-533B (L)	14.26	12-14	~25.17	20-26
	MZUSP-PV 662 (R)	14.14	12-14	23.70	20-26
	MZUSP-PV 975 (R)	14.87	12-14	26.89	20-26
	MZUSP-PV 521 (R)	20.79	12-14	37.90	20-26
	MZUSP-PV 580 (R)	16.67	12-14	26.20	20-26
pm4	PF-1214/GP/2C-316 (R)	~18.40	17-18	~32.79	22-32
m2	PF-995/GP/2C-533C (R)	14.32	14-20	47.54	34-50
	PF-430/GP/2C-533D (L)	14.47	14-20	45.55	34-50
	MZUSP-PV 802 (L)	22.89	14-20	57.19	34-50
	MZUSP-PV 453 (R)	21.15	14-20	49.75	34-50
m3	MZUSP-PV 569 (L)	19.82	16-19	67.84	50-65
	MZUSP-PV 454 (R)	19.79	16-19	–	50-65
<i>Mixotoxodon larensis</i>					
Teeth	Specimen	Measure TD	Range	Measure APD	Range
m2	MZUSP-PV 455 (L)	24.88	19 - 26	54.14	44 - 52

cf. *Toxodon platensis* Owen, 1837
(Figure 3)

Material. Specimens MZUSP-PV 585, MZUSP-PV 586, MZUSP-PV 516, MZUSP-PV 522, MZUSP-PV 976.

Description. It is possible to note in the material that the molars had not yet erupted at the time of death of this individual. Specimens MZUSP-PV 585, MZUSP-PV 586 and MZUSP-PV 516 have their occlusal surface totally or partially covered by dental bone, indicating that they would still erupt (Figure 3A, D, E). The incisor (MZUSP-PV 976) is triangular, with a slightly concave medial wall without enamel. Its buccal surface is covered by a longitudinal band of enamel. The lingual surface completes the triangle and is slightly arched with a thin band of enamel in the inflection zone of the arch. The upper premolar (MZUSP-PV 522) is triangular

with the metacone quite arched buccally (Figure 3B). On its lingual surface, the protoloph is strongly turned posteriorly, with a deep anterior fold and an intermediary lobe. The posterior fold is large and concave. The buccal surface is covered in enamel from the metacone to the paracone, while on the lingual surface only the protoloph is covered in enamel. The lower molar (MZUSP-PV 516) presents a very deep hypoflexid fold on its buccal surface. The hypoconulid is covered by the dentary with only the lingual portion visible (Figure 3A). On its lingual surface the ento-hypoconulid fold is shallow, while the meta-entoconid fold is deep. The metaconid is also covered by the dentary. The tooth is covered by enamel from the mesial portion of the talonid, on the buccal surface, extending to the paraconid and connecting to the lingual surface without interruptions. The enamel extends across the entire lingual surface to the posterior

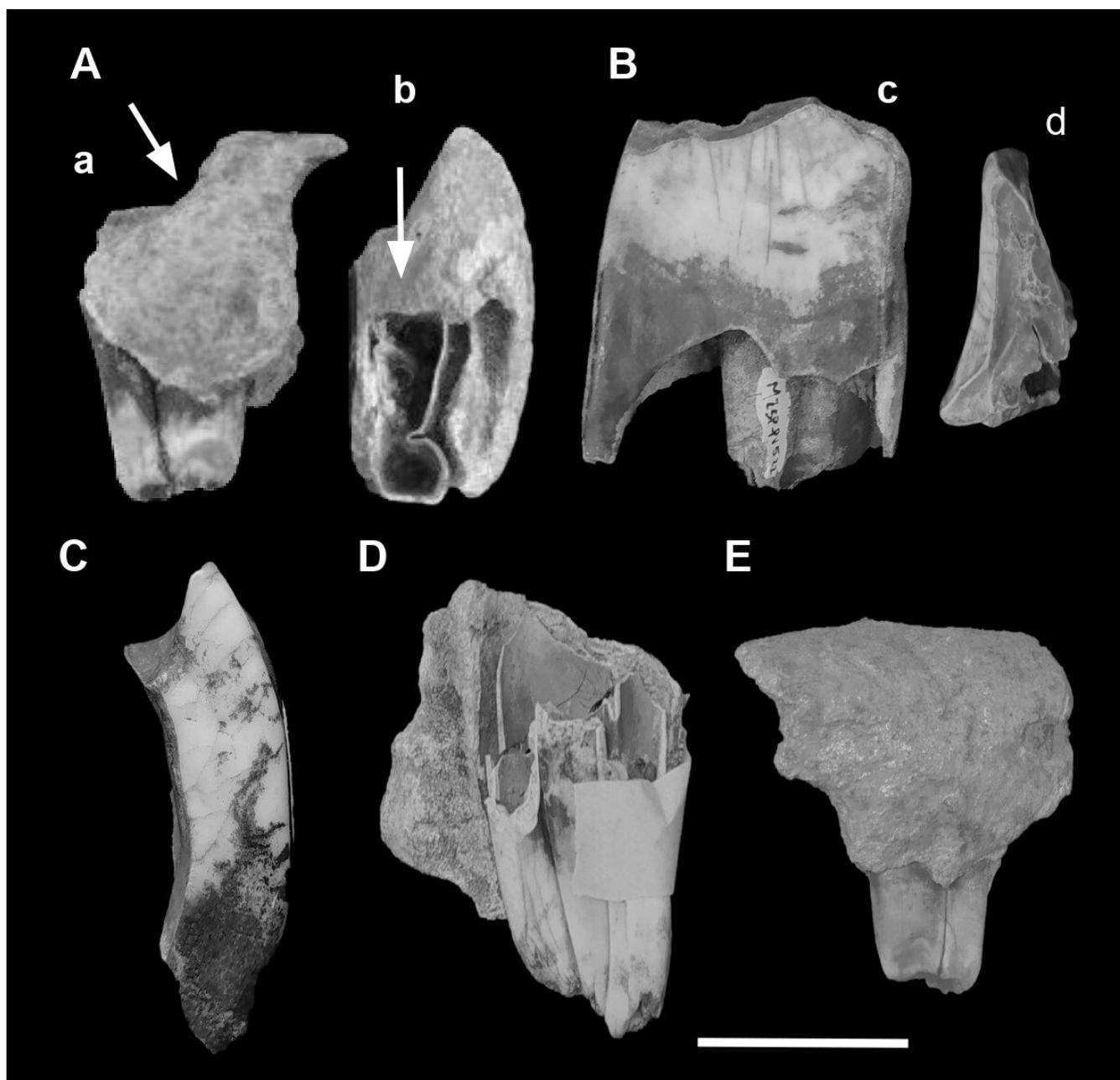


Figure 3. cf. *Toxodon platensis* deciduous teeth. **A**, lower molar in buccal (**a**) and occlusal (**b**) views (MZUSP-PV 516), arrows indicate the part of the occlusal surface that is being partially covered by the dentary; **B**, upper premolar in buccal (**c**) and occlusal (**d**) view (MZUSP-PV 522); **C**, incisor in lateral view (MZUSP-PV 976); **D**, lower molar in lingual view (MZUSP-PV 585); **E**, lower molar completely covered by the dentary in buccal view (MZUSP-PV 586). Scale bar = 5 cm.

portion of the hypoconulid (Figure 3Ab). The lower molar (MZUSP-PV 585) is quite fragmented and fragile, but from what can be analyzed on the buccal surface, the hypoflexid fold is well marked (Figure 3D), as in MZUSP-PV 516. The lingual surface, on the other hand, is quite fragmented and has not preserved many diagnostic features, it is only possible to see that the tooth presents the ento-hypoconulid and meta-entoconid folds. The enamel covering on the lingual surface is similar to specimen MZUSP-PV 516, but it is not possible

to identify the enamel covering on the buccal surface due to the fragmentation and because it is attached to the dentary.

Remarks. Few papers report and describe deciduous teeth of *Toxodon* (Roth, 1895, 1898; Agnolin & Chimento, 2011; Braunn *et al.*, 2021). It should be noted that none of the previous studies measured the dimensions of deciduous teeth. Due to the lack of more detailed diagnoses of juvenile individuals of *Toxodon platensis*, we prefer to associate the individuals described in this study as cf. *T. platensis*. Due to

the difficulty in precisely identifying which types of teeth are present in the materials of juvenile *T. platensis* individuals, the measurements of these specimens were placed in a separate table (Table 2). As with the adult specimens, the approximate values in the table are due to the occlusal surface of the specimens being fragmented or covered up.

PALEOPATHOLOGY

All teeth were analyzed for the existence of paleopathologies and it was possible to identify the presence of the enamel hypoplasia in the specimens from the Abismo Ponta de Flecha Cave. Dental enamel hypoplasia is common in several, recent and fossil vertebrate groups and is characterized as a discontinuity in the secretory activity of the ameloblasts during the enamel formation process. This interruption might

be caused by local factors, such as mechanical trauma, or by systemic physiological stress (Ferigolo, 2007; Braunn *et al.*, 2014).

All enamel defects were photographed, and, from the obtained images, they were compared with the descriptions listed in the Material and Methods section (Figure 4). It was possible to identify that defect type 2 (vertical rows of pits) was the most representative, being observed in all specimens (Table 3). Types 4 and 6 (very large defects such as grooves on the buccal surface of the crown and partial or total absence of enamel in an area) are the least representative (Figure 4), being observed in three specimens (Table 3).

Based on the results obtained, it can be noted that the upper dentition had a lower number of teeth affected by enamel hypoplasia ($n = 3$) compared to the lower dentition ($n = 7$). Despite this, the large number of defects identified in the teeth of the Abismo Ponta de Flecha Cave suggests that

Table 2. Measurements (in mm) of deciduous teeth of cf. *Toxodon platensis*. **Abbreviations:** APD, anteroposterior diameter; TD, transverse diameter.

Teeth	Specimen	Measure TD	Measure APD
dI	MZUSP-PV 976 (L)	13.12	–
dm	MZUSP-PV 516 (L)	~13.07	~27.84
	MZUSP-PV 585 (L)	~12.40	~32.43

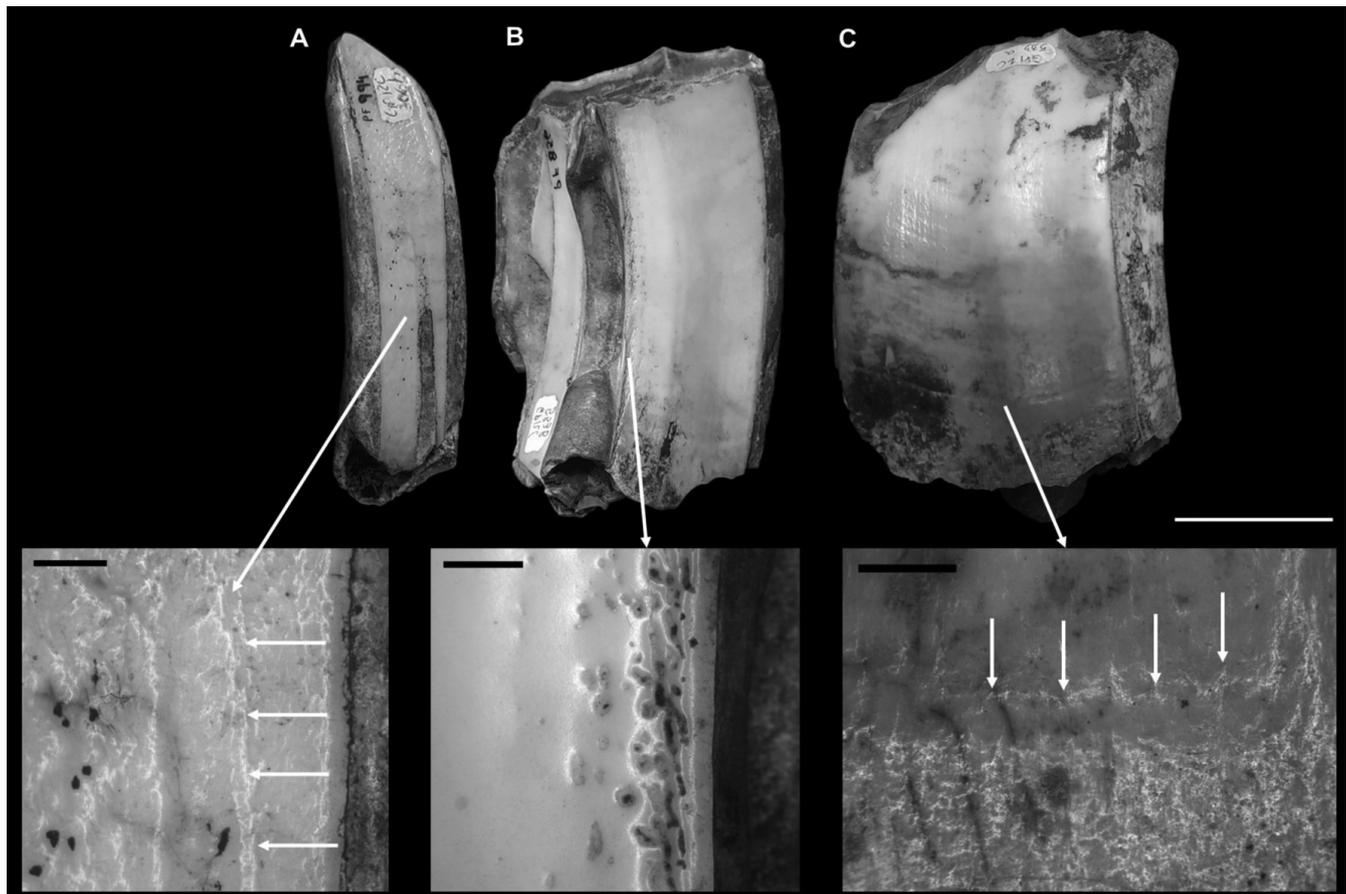


Figure 4. Defects found in the teeth of *Toxodon platensis*. **A**, lower incisor (PF-994/GP/2C-306B), in detail is the type 6 defect; **B**, upper molar in lingual view (PF-856/GP/2C-533B), in detail is the type 5 defect; **C**, upper molar in buccal view (GP/2C-533A), in detail is the type 4 defect. Black scale bars = 2 mm; white scale bar = 3 cm.

Table 3. Data from *Toxodon platensis* specimens with evidence of enamel hypoplasia.

Specimen	Tooth Type	Type of Hypoplasia
PF-940/GP/2C-306A	I1	2
MZSP-PV 866	I1	Absence
MZSP-PV 976	dI	Absence
MZSP-PV 522	dM	Absence
PF-993/GP/2C-533F	M1	1, 2, 4
PF-856/GP/2C-533B	M2	1, 2, 5
GP/2C-533A	M2	2, 4, 5
PF-1123/GP/2C-107	i1	1, 2
PF-994/GP/2C-306B	i2	2, 6
MZSP-PV 704	i3	Absence
PF-1368/GP/2C-312	pm3	2
PF-997/GP/2C-533B	pm3	2
MZSP-PV 662	pm3	Absence
MZSP-PV 975	pm3	Absence
PF-1214/GP/2C-316	pm4	1, 2
MZUSP-PV 521	pm3	Absence
MZUSP-PV 580	pm3	Absence
MZSP-PV 516	dm	Absence
MZUSP-PV 585	dm	Absence
PF-995/GP/2C-533C	m2	1, 2, 3
MZUSP-PV 453	m2	Absence
PF-430/GP/2C-533D	m2	2, 3
MZSP-PV 802	m2	Absence
MZSP-PV 455	m2	Absence
MZUSP-PV 569	m3	Absence
MZUSP-PV 454	m3	Absence

in this case, the individual suffered from physiological stress events, such as infections or malnutrition, during the period of dental formation (Ferguson, 2007; Braunn *et al.*, 2014).

In ungulates, enamel hypoplasia has been associated with major episodes of nutritional deficiency, often indicating a scarcity of food resources (Dobney & Ervynck, 2000). Some authors associate the appearance of enamel hypoplasia defects with stress events in the neonatal phase, such as abandonment of young by females or during the period of replacement of maternal milk by grasses in the diet (Dobney & Ervynck, 2000; Franz-Odenaal *et al.*, 2003; Byerly, 2007).

Specimens PF-997/GP/2C-533B and MZUSP-PV 454 were dated by Neves *et al.* (2007) and Hubbe *et al.* (2013), respectively, and the authors found that these individuals

lived around the late Pleistocene, approximately 11,000 years BP. Chahud *et al.* (2023b) tried to understand the supposed paleoenvironment of the Ribeira of Iguape Valley at the of the late Pleistocene, the authors suggest that the region was a transitional environment including forest and open fields. The works of MacFadden (2005) and Dantas *et al.* (2017) show that *Toxodon* would have been adapted to inhabit this type of environment. Thus, it is possible to suggest that the Ribeira Valley environment was not the main causative agent of the hypoplasia in the individuals from the Abismo Ponta de Flecha Cave, since the specimen from the Abismo of Fossil Cave inhabited the region at approximately the very same time (~11,000 years BP) as the one from the Abismo Ponta de Flecha Cave and did not have the disease.

HUMAN ACTIVITY

Two specimens from the Abismo Ponta de Flecha Cave show incisions compatible with marks made by humans: a lower premolar (PF-997/GP/2C-533B) and the condylar process (PF-787/GP/2C-526B). In both materials it was also possible to identify the presence of marks of abiotic origin that probably suffered later post depositional reworking within the galleries. The images taken with the digital microscope showed elongated incisions with a transverse orientation, V-shaped section, some having microstriation inside and a shoulder effect (Figure 5), corroborating previous findings of these types of marks (Lyman, 1994; Labarca, 2003; Domínguez-Rodrigo *et al.*, 2009). The marks found in both elements had a low angulation, which might indicate skillful tissue removal, possibly using less force (Bello & Soligo, 2008). The location of these marks on the tooth base of specimen PF-997/GP/2C-533B, might suggest that the likely objective of the incisions was to extract the tooth from the mandible. Two elements can be used to differentiate ancient from recent cuts (the latter made when removing the fossil

or during transport): recent cut marks have the color of the subcortical bone, interrupt post-depositional factors such as weathering cracks, manganese staining or trampling, and have an elevation of the cortex at the edge of the trace (Gibert & Jimenez, 1991; Labarca, 2003; Perez *et al.*, 2005). As can be seen in figures 5A, B and C, the incisions show concretion and sediment encrusted inside, showing that such cut marks were not produced when the material was collected or transported by the researchers. On the other hand, the abiotic marks are close to each other, and shallow, with open shapes and wide base, they intersect, and some are parallel, with variable in length and width (Figure 5D).

Although the incisions considered as being of anthropic origin based on the morphology described in the literature (Lyman, 1994; Labarca, 2003; Domínguez-Rodrigo *et al.*, 2009), their location on dental elements and the identified taphonomic changes (manganese infiltrations and filled weathering cracks) made it difficult to interpret if such incisions were made *perimortem* or on the already weathered bone.

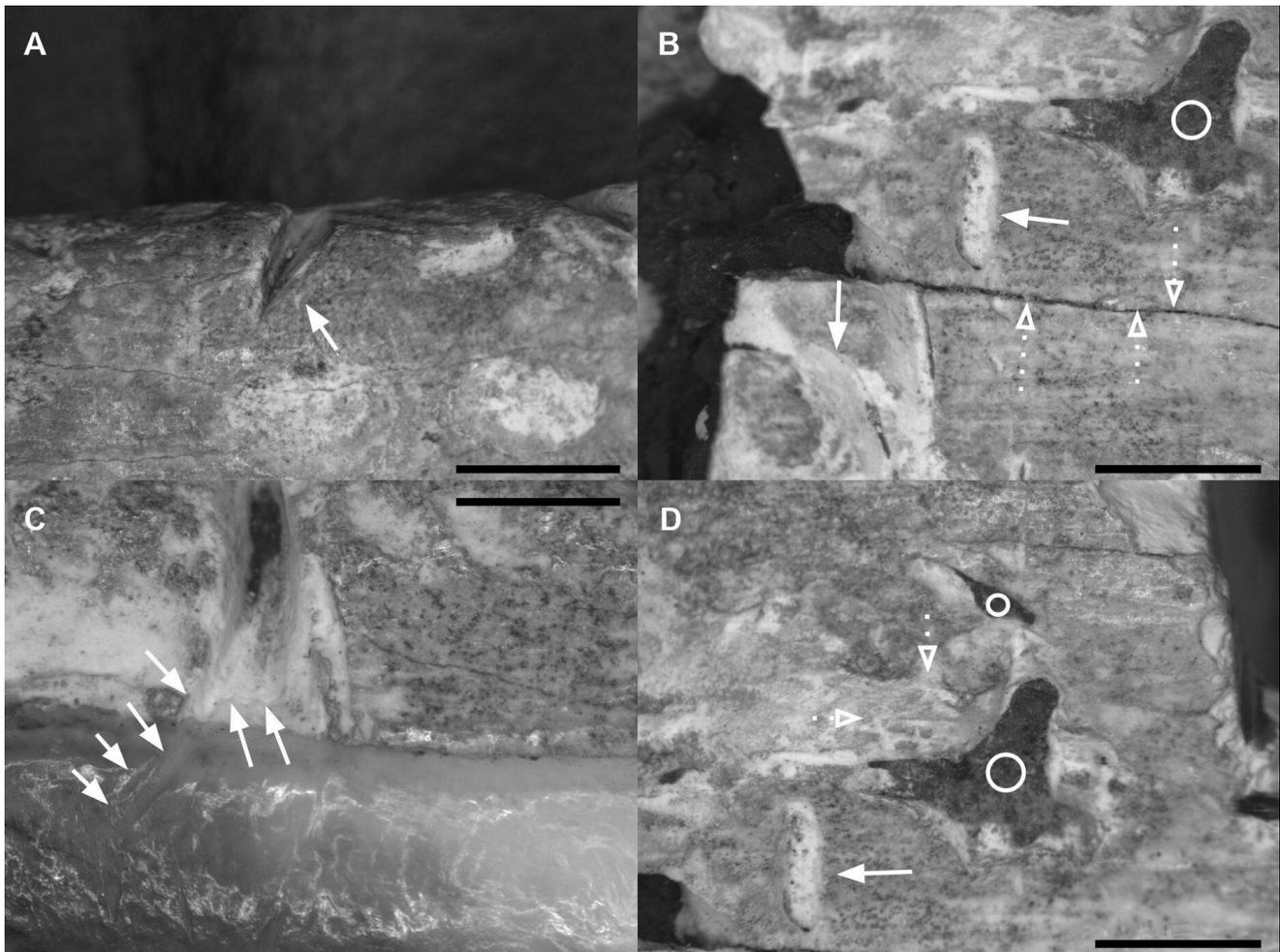


Figure 5. Incisions found in pm3 (PF-997/GP/2C-533B) of *Toxodon platensis*. **A**, cut mark, the arrow indicates the cut mark with its V-shape; **B**, cut mark and weathering mark filled with sediment and concretion, the arrow indicates the cut mark, the circle indicates a region with concretion and the dashed arrows indicate weathering marks filled with sediments; **C**, cut mark, arrow indicates microstriation; **D**, reworking mark with concretion, the arrow indicates the cut mark, the circle indicates regions with concretion and the dashed arrows indicate reworking marks. Scale bars = 2 mm.

CONCLUSIONS

The identification of the dental and osteological elements of Toxodontidae found in Ribeira of Iguape Valley contributed to the better understanding of the diversity of this family in the region, especially on dental taxonomy. Furthermore, the presence of a paleopathology associated with tooth enamel in specimens from Abismo Ponta de Flecha Cave was also investigated. Although there are few materials of juvenile individuals of cf. *Toxodon platensis* recorded in this study, the presence of these specimens in the Ribeira of Iguape Valley region demonstrates the importance of the paleontological sites from this area, since there are few sites in South America that reported juvenile individuals of that genus. It was also possible to propose a wider range of *Mixotoxodon larensis*, which had never been observed in such southern latitudes in the Americas.

Finally, the analysis of the incisions on the dental and osteological elements allowed us to identify possible interactions of past human groups with these animals, being the first record of ancient cut marks observed in *Toxodon platensis*. However, it was not possible to identify whether the marks were produced when the animal was slaughtered or on the dried carcass.

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REFERENCES

- Agnolin, F.L. & Chimento, N.R. 2011. Afrotherian affinities for endemic South American “ungulates”. *Mammalian Biology*, **76**:101–108. doi:10.1016/j.mambio.2010.12.001
- Ameghino, F. 1907. Notas sobre una pequeña colección de huesos de mamíferos procedentes de las grutas calcarias de Iporanga, en el Estado de São Paulo, Brazil. *Revista do Museu Paulista*, **III**:59–124.
- Asevedo, L.; Pansani, T.R.; Cordeiro, V.M.; Silva-Caminha, S.A.F.; Paixão, J.S.; Cozzuol, M.A. & Dantas, M.A.T. 2021. Diversity of Pleistocene megamammals from Southern Amazon, Mato Grosso state, Brazil. *Journal of South America Earth Sciences*, **112**:103552. doi:10.1016/j.jsames.2021.103552
- Barros-Barreto, C.N.G.; de Blasiis, P.A.D.; Dias-Neto, C.M.; Karmman, I.; Lino, C.F. & Robran, E.M. 1982. Abismo Ponta de Flecha: Um projeto arqueológico, paleontológico e geológico no médio Ribeira de Iguape, SP. *Revista de Pré-História*, **3**:195–215.
- Bello, S.M. & Soligo, C. 2008. A new method for the quantitative analysis of cutmark micromorphology. *Journal of Archaeological Science*, **35**:1542–1552. doi:10.1016/j.jas.2007.10.018
- Bond, M.; Madden, R.H. & Carlini, A.A. 2006. A new specimen of Toxodontidae (Notoungulata) from the Urumaco Formation (upper Miocene) of Venezuela. *Journal of Systematic Palaeontology*, **4**:285–291. doi:10.1017/S1477201906001854
- Bonini, R.A.; Schmidt, G.I.; Reguero, M.A.; Cerdeño, E.; Candela, A.M. & Solís, N. 2017. First record of Toxodontidae (Mammalia, Notoungulata) from the late Miocene–early Pliocene of the southern central Andes, NW Argentina. *Journal of Paleontology*, **91**:566–576. doi:10.1017/jpa.2016.160
- Braunn, P.R.; Ferigolo, J. & Ribeiro, A.M. 2021. Enamel microstructure of permanent and deciduous teeth of a species of notoungulate *Toxodon*: Development, functional, and evolutionary implications. *Acta Palaeontologica Polonica*, **66**:449–464. doi:10.4202/app.00772.2020
- Braunn, P.R.; Ribeiro, A.M. & Ferigolo, J. 2014. Microstructural defects and enamel hypoplasia in teeth of *Toxodon* Owen, 1837 from the Pleistocene of Southern Brazil. *Lethaia*, **47**:418–431. doi:10.1111/let.12063
- Byerly, R.M. 2007. Palaeopathology in late Pleistocene and early Holocene Central Plains bison: dental enamel hypoplasia, fluoride toxicosis and the archaeological record. *Journal of Archaeological Science*, **34**:1847–1858. doi:10.1016/j.jas.2007.01.001
- Carrillo, J.; Amson, D.; Jaramillo, E.C.; Sánchez, R.; Quiroz, L.; Cuartas, C.; Rincón, A.F. & Sánchez-Villagra, M.R. 2018. *The Neogene Record of Northern South American Native Ungulates*. Washington D.C., Smithsonian Institution Scholarly Press, 79 p.
- Chahud, A. 2022. Comments on a small sabretooth cat in the Abismo Ponta de Flecha Cave, Vale do Ribeira, southeastern Brazil. *Carnets Geologie*, **22**:1–6. doi:10.2110/carnets.2022.2201
- Chahud, A.; Costa, P.R.O.; Figueiredo, G.F. & Okumura, M. 2023a. Quaternary ungulates of the Abismo Ponta de Flecha Cave, Ribeira of Iguape Valley, Southeast Brazil: Zooarchaeological and Palaeoenvironmental aspects. *Journal of South American Earth Sciences*, **121**:104107. doi:10.1016/j.jsames.2022.104107
- Chahud, A.; Costa, P.R.C. & Okumura, M. 2022. Cingulata of the Abismo Ponta de Flecha Cave (Pleistocene–Holocene), Ribeira de Iguape Valley, Southeastern Brazil. *Revista Brasileira de Paleontologia*, **25**:322–330. doi:10.4072/rbp.2022.4.06
- Chahud, A.; Pereira, G.C.; Costa, P.R.O. & Okumura, M. 2023b. Presença de Scelidotheriinae no Abismo Ponta de Flecha, sudeste do Brasil. *Revista Biociências (Taubaté)*, **29**:43–51.
- Chahud, A.; Pereira, G.C.; Costa, P.R.O. & Okumura, M. 2023c. Uma nova ocorrência de Megalonychidae Gervais, 1855 do Quaternário do Vale do Ribeira de Iguape, sudeste do Brasil. *Acta Biológica Paranaense*, **52**:1–8. doi:10.5380/abp.v52i1.93095

- Chahud, A.; Pereira, G.C.; Costa, P.R.O. & Okumura, M. 2024a. A new record of ground sloth in the Ribeira de Iguape valley, southeastern Brazil. *Carnets Geologie*, **24**:83–89. doi:10.2110/carnets.2024.2404
- Chahud, A.; Pereira, G.C.; Costa, P.R.O. & Okumura, M. 2024b. Um Megatheriidae Owen, 1843 do Abismo Ponta de Flecha (Quaternário), Vale do Ribeira de Iguape, sudeste do Brasil. *Acta Biológica Catarinense*, **11**:11–19. doi:10.21726/abc.v11i2.2174
- Chahud, A.; Pereira, G.C. & Okumura, M. 2024c. Novos dados sobre um espécime de *Catonyx cuvieri* Lund, 1839 do Abismo Iguatemi, limite Pleistoceno-Holoceno, Vale do Ribeira de Iguape, São Paulo, Brasil. *Boletim Paranaense de Geociências*, **82**:1–12.
- Cifelli, R.L. 1985. South American ungulate evolution and extinction. In: F.G. Stehli & S.D. Webb (eds) *The great American biotic interchange*, Springer, p. 249–266.
- Dantas, M.A.T.; Cherkinsky, A.; Bocherens, H.; Drefahl, M.; Bernardes, C. & França, L.M. 2017. Isotopic paleoecology of the Pleistocene megamammals from the Brazilian Intertropical Region: feeding ecology ($\delta^{13}\text{C}$), niche breadth and overlap. *Quaternary Science Reviews*, **170**:152–163. doi:10.1016/j.quascirev.2017.06.030
- Del Papa, M.; Reyes, M.; Poiré, D.G.; Rascovan, N.; Jofré, G. & Delgado, M. 2024. Anthropogenic cut marks in extinct megafauna bones from the Pampean region (Argentina) at the last glacial maximum. *Plos One*, **19**:e0304956. doi:10.1371/journal.pone.0304956
- Dobney, K. & Ervynck, A. 2000. Interpreting developmental stress in archaeological pigs: the chronology of linear enamel hypoplasia. *Journal of Archaeological Science*, **27**:597–607. doi:10.1006/jasc.1999.0477
- Domínguez-Rodrigo, M.; De Juana, S.; Galan, A.B. & Rodríguez, M. 2009. A new protocol to differentiate trampling marks from butchery cut marks. *Journal of Archaeological Science*, **36**:2643–2654. doi:10.1016/j.jas.2009.07.017
- Elissamburu, A. 2012. Estimación de la masa corporal en géneros del Orden Notoungulata. *Estudios Geológicos*, **68**:91–111. doi:10.3989/egol.40336.133
- Fariña, R.A.; Vizcaino, S.F. & Bargo, M.S. 1998. Body mass estimations in Lujanian (late Pleistocene-early Holocene of South America) mammal megafauna. *Mastozoología Neotropical*, **5**:87–108.
- Ferigolo, J. 2007. Paleopatologia em mamíferos. *Icnologia*, **1**:88–107.
- Forasiepi, A.M.; Cerdeño, E.; Bond, M.; Schmidt, G.I.; Naipauer, M.; Straehl, F.R.; Martinelli, A.G.; Garrido, A.C.; Schmitz, M.D. & Crowley, J.L. 2015. New toxodontid (Notoungulata) from the early Miocene of Mendoza, Argentina. *Paläontologische Zeitschrift*, **89**:611–634. doi:10.1007/s12542-014-0233-5
- Franz-Ondendaal, T.A.; Lee-Thorp, J.A. & Chinsamy, A. 2003. Insights from stable light isotopes on enamel defects and weaning in Pliocene herbivores. *Journal of Biosciences*, **28**:765–773. doi:10.1007/bf02708437
- Ghilardi, A.M.; Fernandes, M.A. & Bichuette, M.E. 2011. Megafauna from the Late Pleistocene-Holocene deposits of the Upper Ribeira karst area, southeast Brazil. *Quaternary International*, **245**:369–378. doi:10.1016/j.quaint.2011.04.018
- Gibert, J. & Jiménez, C. 1991. Investigations into cut-marks on fossil bones of Lower Pleistocene age from Venta Micena (Orce, Granada province, Spain). *Human Evolution*, **6**:117–127.
- Gomes, V.S.; Lessa, C.M.B.; Oliveira, G.R.; Bantim, R.A.M.; Sayão, J.; Bocherens, H.; Araújo-Júnior, H.I. & Dantas, M.A.T. 2023. Seasonal variations in diet ($\delta^{13}\text{C}$) and climate ($\delta^{18}\text{O}$) inferred through toxodonts enamel teeth during the Late Pleistocene in the Brazilian intertropical region. *Journal of South American Earth Sciences*, **121**:104148. doi:10.1016/j.jsames.2022.104148
- Guidon, N.; Parenti, F.; Da Luz, M.D.F.; Guérin, C. & Faure, M. 1994. Le plus ancien peuplement de l'Amérique: le Paléolithique du Nordeste brésilien. *Bulletin de la Société préhistorique française*, **91**:246–250. doi:10.3406/bspf.1994.9732
- Hoffstetter, R. 1968. Nuapua, un gisement de vertèbres pleistocènes dans le chaco bolivien. *Bulletin du Muséum National D'Histoire Naturelle*, **40**:823–836.
- Hubbe, A.; Hubbe, M. & Neves, W.A. 2013. The Brazilian megamastofauna of the Pleistocene/Holocene transition and its relationship with the early human settlement of the continent. *Earth-Science Reviews*, **118**:1–10. doi:10.1016/j.earscirev.2013.01.003
- Karmann, I. & Ferrari, J.A. 2002. Carste e cavernas do Parque Estadual Turístico do Alto Ribeira (PETAR), SP: sistemas de cavernas com paisagens subterrâneas únicas. In: C. Schobbenhaus; D.A. Campos; E.T. Queiroz & M. Berbert-Born (eds.) *Sítios geológicos e paleontológicos do Brasil*, Departamento Nacional de Produção Mineral, p. 401–413.
- Karsten, H. 1886. *Géologie de l'ancienne Colombie Bolivarienne, Vénézuéla, Nouvelle Grenade et Ecuador*. Berlin, R. Friedlander & Sohn, 95 p.
- Labarca, R. 2003. Relación hombre-mastodonte en el semiárido chileno: El caso de Quebrada Quereo (IV Region, Coquimbo). *Boletín del Museo Nacional de Historia Natural*, **52**:151–175.
- Laurito, C.A. 1993. Análisis Topológico y Sistemático del Toxodonte de Bajo de los Barrantes, Provincia de Alajuela, Costa Rica. *Revista Geológica de América Central*, **16**:61–68.
- Lino, C.F.; Dias-Neto, C. M.; Trajano, E.; Gusso, G.L.N.; Karmann, I. & Rodrigues, R. 1979. Paleontologia das Cavernas do Vale do Ribeira, Exploração I Abismo do Fóssil (SP-145): Resultados parciais. In: SIMPÓSIO REGIONAL DE GEOLOGIA, 2, 1979. *Atas*, Rio Claro, Sociedade Brasileira de Geologia, p. 257–268.
- Lucas, S.G.; Alvarado, G.E. & Vega, E. 1997. The Pleistocene mammals of Costa Rica. *Journal of Vertebrate Paleontology*, **17**:413–427. doi:10.1080/02724634.1997.10010985
- Lundelius, E.L.; Bryant, V.M.; Mandel, R.; Thies, K.J. & Thoms, A. 2013. The first occurrence of a toxodont (Mammalia, Notoungulata) in the United States. *Journal of Vertebrate Paleontology*, **33**:229–232. doi:10.1080/02724634.2012.711405
- Lyman, R.L. 1994. *Vertebrate Taphonomy*. Cambridge, Cambridge University Press, 522 p.
- MacFadden, B.J. 2005. Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late quaternary of south and Central America. *Quaternary Research*, **64**:113–124. doi:10.1016/j.yqres.2005.05.003
- Marshall, L.G.; Berta, A.; Hoffstetter, R.; Pascual, R.; Reig, O.A.; Bombin, M. & Mones, A. 1984. Mammals and Stratigraphy: Geochronology of the continental mammal-bearing Quaternary of South America. *Palaeovertebrata*, **14**:1–76.
- Mendonça, R.N.S. 2007. *Revisão dos toxodontes pleistocênicos brasileiros considerações sobre Trigononops lopesi (Roxo, 1921) (Notoungulata, Toxodontidae)*. Programa de Pós-Graduação em Zoologia, Universidade de São Paulo, M.Sc. Thesis, 104 p.

- Mendonça, R.N.S. 2012. *Diversidade de toxodontes pleistocênicos (Notoungulata, Toxodontidae): uma nova visão*. Programa de Pós-Graduação em Zoologia, Universidade de São Paulo, Ph.D. Thesis, 166 p.
- Miño-Boilini, Á.R.; Cerdeño, E. & Bond, M. 2006. Revisión del género *Toxodon* Owen, 1837 (Notoungulata: Toxodontidae) en el Pleistoceno de las provincias de Corrientes, Chaco y Santa Fe, Argentina. *Spanish Journal of Palaeontology*, **21**:93–103. doi:10.7203/sjp.21.2.20483
- Mones, A. & Heintz, N. 1992. Catalogue of the Conrad Møller Collection of Cenozoic Mammals from Uruguay. *Contributions from the Paleontological Museum, University of Oslo*, **375**:1–14.
- Nasif, N.L.; Musalem, S. & Cerdeño, E. 2000. A new toxodont from the late Miocene of Catamarca, Argentina, and a phylogenetic analysis of the Toxodontidae. *Journal of Vertebrate Paleontology*, **20**:591–600. doi:10.1671/0272-4634(2000)020[0591:ANTFTL]2.0.CO;2
- Neves, W.; Hubbe, A. & Karmann, I. 2007. New accelerator mass spectrometry (AMS) ages suggest a revision of the electron spin resonance (ESR) Middle Holocene dates obtained for a *Toxodon platensis* (Toxodontidae, Mammalia) from southeast Brazil. *Radiocarboni*, **49**:1411–1412. doi:10.1017/S003382220004323X
- Paula Couto, C. 1975. Mamíferos fósseis do Quaternário do sudeste brasileiro. *Boletim Paranaense de Geociências*, **33**:89–132.
- Paula Couto, C. 1979. *Tratado de Paleomastozoologia*. Rio de Janeiro, Academia Brasileira de Ciências, 596 p.
- Paula Couto, C. 1982. Fossil mammals from the Cenozoic of Acre, Brazil. V. Notoungulata Nesodontinae (II), Toxodontinae and Haplodontheriinae, and Litopterna, Pyrotheria and Astrapotheria (II). *Iheringia, Série Geologia*, **7**:5–43.
- Perez, V.R.; Godfrey, L.R.; Nowak-Kemp, M.; Burney, D.A.; Ratsimbazafy, J. & Vasey, N. 2005. Evidence of early butchery of giant lemurs in Madagascar. *Journal of Human Evolution*, **49**:722–742. doi:10.1016/j.jhevol.2005.08.004
- Politis, G.G. & Gutiérrez, M.A. 1998. Gliptodontes y cazadores-recolectores de la región pampeana (Argentina). *Latin American Antiquity*, **9**:111–134.
- Politis, G.G.; Gutiérrez, M.A.; Rafuse, D.J. & Blasi, A. 2016. The arrival of *Homo sapiens* into the Southern Cone at 14,000 years ago. *PLoS ONE*, **11**:e0162870. doi:10.1371/journal.pone.0162870
- Porta, J. 1959. Nueva subespecie de Toxodóntido del Cuaternario de Colombia. *Boletín de Geología*, **3**:55–61.
- Rancy, A. 2000. Fossil Mammals of the Amazon as a Portrait of a Pleistocene environment. In: J.F. Eisenberg & K.H. Redford (eds.) *Mammals of the Neotropics: Ecuador, Peru, Bolivia, Brazil*, Vol. 3, University of Chicago Press, p. 20–26.
- Rincón, A.D. 2004. Los mamíferos fósiles del Pleistoceno de la cueva del Zumbador (fa. 116), Estado Falcón, Venezuela. *Boletín de la Sociedad Venezolana de Espeleología*, **37**:18–26.
- Rincón, A.D. 2011. New remains of *Mixotoxodon larensis* Van Frank 1957 (Mammalia: Notoungulata) from Mene de Inciarte tar pit, north-western Venezuela. *Interciencia*, **36**:894–899.
- Rincón, A.D.; Parra, G.E.; Prevosti, F.J.; Alberdi, M.T. & Bell, C.J. 2009. A preliminary assessment of the mammalian fauna from the Pliocene-Pleistocene El Breal de Orocuál locality, Monagas State, Venezuela. *Museum of Northern Arizona Bulletin*, **65**:593–620.
- Rosa, R.A.R.; Guzmán-Gutiérrez, J.R. & Ortega-Hurtado, M.C. 2011. A new occurrence of toxodonts in the Pleistocene of México. *Current Research in the Pleistocene*, **28**:29–30.
- Roth, S. 1895. Rectificaciones sobre la dentición del *Toxodon*. *Revista del Museo de La Plata*, **6**:333–356.
- Roth, S. 1898. Catálogo de los mamíferos fósiles conservados en el Museo de La Plata: Grupo Ungulata. *Revista del Museo de La Plata*, **8**:33–160.
- Royo y Gomez, J. 1960. El yacimiento de vertebrados pleistocenos de Muaco, Estado Falcón, Venezuela, con industria lítica humana. In: INTERNATIONAL GEOLOGICAL CONGRESS, 21, 1960. *Report*, Norden, p. 154–157.
- Silva, A.K.B. 2019. *Toxodontídeos (Mammalia, Notoungulata) Pleistocênicos dos Estados de Pernambuco e Piauí, Nordeste do Brasil: Aspectos Sistemáticos e Paleoecológicos*. Programa de Pós-Graduação em Geociências, Universidade Federal de Pernambuco, Ph.D. thesis, 132 p.
- Tonni, E.P.; Alberdi, M.T.; Prado, J.; Bargo, M.S. & Cione, A.L. 1992. Changes of mammal assemblages in the Pampean region (Argentina) and their relationship with the Plio-Pleistocene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **95**:179–194. doi:10.1016/0031-0182(92)90140-Z
- Van Frank, R. 1957. A fossil collection from northern Venezuela. 1, Toxodontidae (Mammalia, Notoungulata). *American Museum Novitates*, **1850**:1–38.
- Villarrol, C. & Clavijo, J. 2005. Los mamíferos fósiles y las edades de las sedimentitas continentales del Neógeno de la Costa Caribe Colombiana. *Revista de la Academia Colombiana de Ciencias*, **29**:345–356.
- Woodburne, M.O. 2010. The Great American Biotic Interchange: dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution*, **17**:245–264. doi:10.1007/s10914-010-9144-8
- Zimicz, A.N.; Fernández, M.; Bond, M.; Chornogubsky, L.; Arnal, M.; Cárdenas, M. & Fericola, J.C. 2020. *Archaeogaia macachae* gen. et sp. nov., one of the oldest Notoungulata Roth, 1903 from the early-middle Paleocene Mealla Formation (Central Andes, Argentina) with insights into the Paleocene-Eocene South American biochronology. *Journal of South American Earth Sciences*, **103**:102772. doi:10.1016/j.jsames.2020.102772

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