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Article

PALEOMETRIC INSIGHTS INTO THE MICROMORPHOLOGY OF ZIPHODONT ARCHOSAUR TEETH FROM THE SANTA MARIA SUPERSEQUENCE (TRIASSIC, BRAZIL)

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ABSTRACT – The tooth enamel is the most mineralized tissue of vertebrates. This is one of the factors that make teeth very common in the fossil record. Most of the carnivorous archosaurs throughout the Mesozoic Era possessed ziphodont teeth, whose denticles are round bumps that are always located on carine, and with a symmetrical or convex-asymmetric border. In some taxa, they are strongly recurved apically. This study presents a paleometric approach to isolated archosaur teeth, integrating macro, micro and scanning electron microscopy (SEM) measurements of denticles from seven ziphodont teeth of archosaurs collected from the Santa Maria Supersequence (SMS) Triassic, Paraná Basin, Brazil. The quantitative data obtained allowed the identification of similarities and differences among the studied specimens, which were compared with published datasets, likely reflecting taxonomic diversity within the assemblage. Despite their superficial similarity, certain dental features suggest a greater diversity of diets and feeding strategies among the SMS archosauriforms. Moreover, this paper provides the first enamel thickness measurements from ziphodont teeth of the SMS, opening new perspectives for understanding enamel microstructure and its implications for archosaur taxonomy and functional morphology.

Keywords: biomechanic, denticles, Gondwana, SEM, Paraná Basin.

INTRODUCTION

The general morphology of a tooth can be subdivided into two portions: the part embedded in the gum, called the root, and the part above the gum line, named the crown. The root of the tooth can be subdivided, from inside to outside, into root canal, dentine and cementum, meanwhile the crown, into pulp chamber, dentine and enamel (Figure 1A; Rothschild & Martin, 2006; Dangelo & Fattini, 2007; Junqueira & Carneiro, 2013; Netter, 2015). For mammals, the region where the crown and root meet is called the neck or cementoenamel junction (CEJ; Schroeder & Scherle, 1988; Junqueira & Carneiro, 2013). Tooth compartmentalization may vary among, for example, fishes and some lizards, which may exhibit different subdivisions and terminology (Owen, 1840; Pough *et al*., 2013). Nevertheless, we adopt this nomenclature for the ziphodont teeth studied here.

Most carnivorous archosaurs throughout the Mesozoic Era possessed ziphodont teeth (Benton, 2004; D'Amore, 2009), characterized by long rows of relatively uniform teeth, with distal curvature, labiolingual flattening, and serrations (Benton, 2004; D'Amore & Blumensehine, 2009). Although the first iteration of this feature appeared in non-mammalian synapsids (*e.g*., Permian gorgonopsian; Whitney *et al*., 2020). At present, this kind of dentition only occurs in certain members of the squamate family Varanidae (Molnar, 2004; D'Amore, 2009).

These serrations or denticles have different classifications, depending on the consulted literature. However, these tooth surface structures can be summarized as follows:

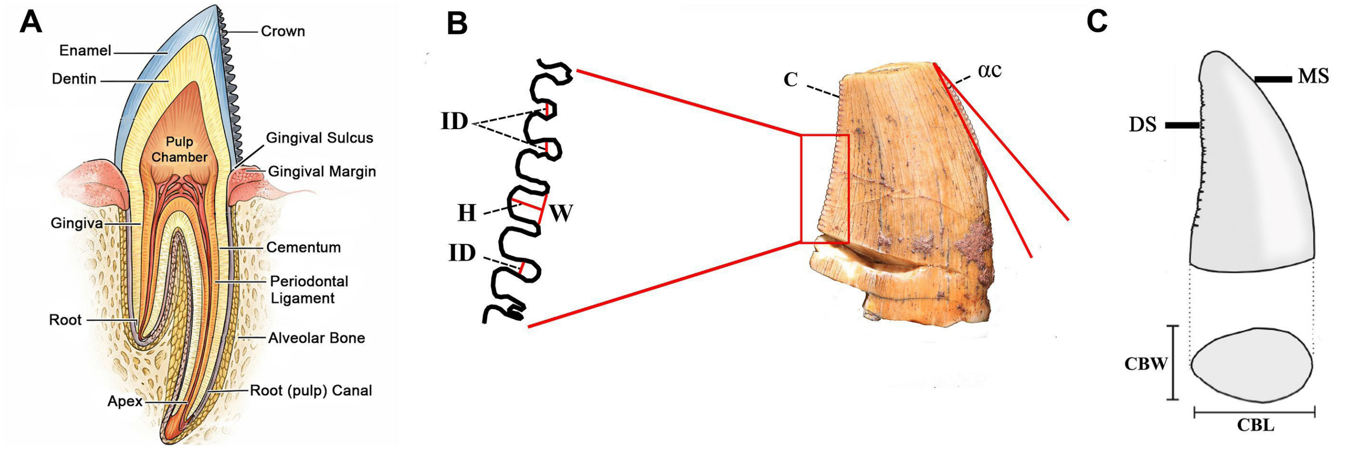

Figure 1. Illustrative diagram of the measurements taken in this study. **A**, diagram showing the constituent parts of a ziphodont tooth (adapted from Junqueira & Carneiro, 2013); **B**, micrometric measurements in an undetermined archosaur ziphodont tooth (PV-1261-T); **C**, macrometric measurements. **Abbreviations: αc**, carina's angulations; **C**, carina with denticles; **CBL**, crown base length; **CBW**, crown base width; **DS**, distal side; **H**, height; **ID**, interdenticular distance; **MS**, mesial side; **W**, width.

Serration – projection situated across the carina of a tooth, being composed by both enamel and dentine. Besides that, it can be defined as a denticles' line along the cutting edge of the crown (carina) (Sander, 1997; Brink & Reisz, 2014; Hendrickx *et al*., 2015). There are many different proposals to define a denticle, although there are two which are considered the main ones: (i) an elaborated kind of serration that corresponds to a dentine's projection covered by enamel along the carina (Currie & Padian, 1997; Brink & Reisz, 2014); (ii) a rounded bump with a symmetrical or asymmetrical convex margin, sometimes strongly apically recurved. The denticles project either perpendicularly from the crown margin or are apically inclined with a main axis oriented diagonally from the carina (Hendrickx *et al*., 2015). According to Hendrickx *et al*. (2015), the denticles are always located on the carinae, and the smallest denticles use to be positioned on the carina's base and top. These authors still stand out that the term denticle is more commonly used on theropod teeth studies. However, in this study, the denticles' definition proposed by these authors will be adopted (Hendrickx *et al*., 2015). We opted for this definition because it is better founded and more current than those previously mentioned (*e.g*., Sander, 1997; Currie & Padian, 1997).

The teeth (and their respective denticles) studied here came from the Middle-Late Triassic strata of the Santa Maria Supersequence (SMS, *sensu* Horn *et al*., 2014), of the Paraná Basin, which encompass four different Assemblage Zones (AZ) based on their tetrapods' contents (see Schultz *et al*., 2020).

In this study, measurements will be conducted along the preserved denticles of isolated archosaur teeth specimens belonging to two SMS Assemblage Zones (AZs) (*Dinodontosaurus* AZ and *Hyperodapedon* AZ) owing to gain information that contributes to their biomechanical and paleoecological knowledge. In addition, scanning electron microscopy (SEM) images will be collected to make it possible to get the enamels' thickness information.

Stratigraphic context

The Santa Maria Supersequence (SMS; Zerfass *et al*., 2003) is composed of four third order sequences, being the three most basal encompassing four tetrapod biozones (Horn *et al*., 2014). From base to the top, they are named as: Pinheiros-Chiniquá Sequence (including *Dinodontosaurus* AZ, Ladinian), Santa Cruz Sequence (encompassing the *Santacruzodon* AZ, early Carnian) and Candelária Sequence (encompassing the *Hyperodapedon*, late Carnian and *Riograndia* AZs, Norian). The Mata Sequence (Rhaetian) has no records of vertebrates so far (Schultz *et al*., 2020).

The fossil content and the absolute ages of the SMS sequences (and their respective AZs) correlate with the Middle-Late Triassic stratigraphic sequences from the Chañares and Ischigualasto formations, from Argentina (Barberena *et al*., 1985; Langer, 2005; Langer *et al*., 2007; Martínez *et al*., 2013; Ezcurra *et al*., 2017; Martinelli *et al*., 2016, 2017; Langer *et al*., 2018; Desojo *et al*., 2020b; Corecco *et al*., 2025; Scartezini *et al*., 2025), as well as, from the African layers of Omingonde (central portion of Namibia), Manda beds (Tanzania) formations (Abdala *et al*., 2013; Martinelli *et al*., 2017) and Pebbly Arkose Formation, from Zimbabwe (Griffin *et al*., 2022; Figure 2). Recently, the occurrence of a new pseudosuchian from the Pinheiros-Chiniquá Sequence (*Tainrakuasuchus bellator*) was used to reinforce the biostratigraphic correlation between the *Dinodontosaurus* AZ (Brazil) and the upper fauna of the Manda beds in Tanzania. The authors proposed an Anisian rather than a Ladinian age for the latter unit (Müller *et al*., 2025).

Institutional abbreviations: CAPPA/UFSM, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, Brazil; **CPEZ**, Museu Paleontológico e Arqueológico Walter Ilha, São Pedro do Sul, Brazil; **PUCRS**, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; **UFRGS**, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

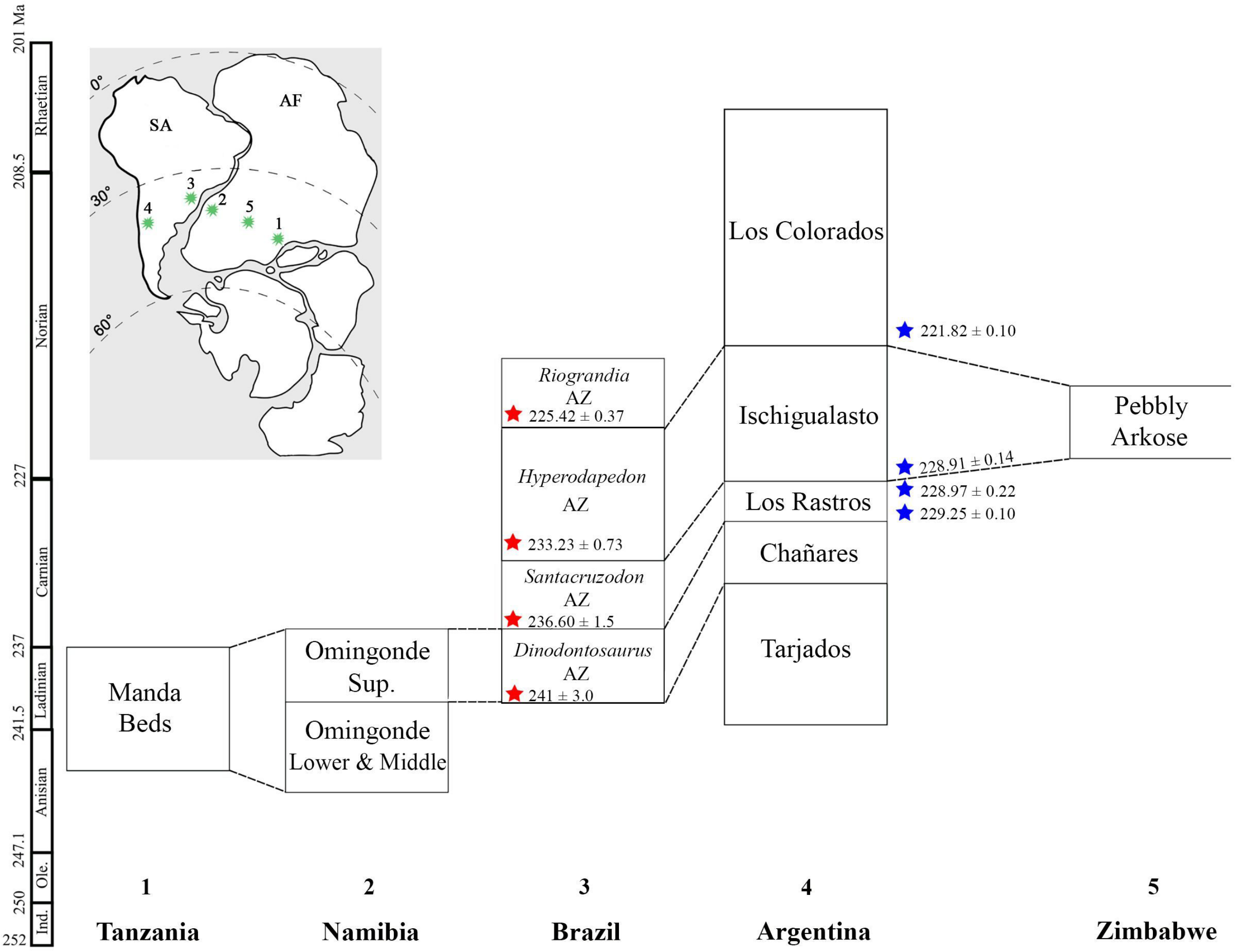

Figure 2. Simplified lithostratigraphic correlation of the Brazilian Triassic sequences (**3**) with other Gondwana units [Tanzania (**1**); Namibia (**2**); Argentina (**4**) and Zimbabwe (**5**)]. *Dinodontosaurus* and *Hyperodapedon* Assemblage Zones (3) are the focus of this study. The Brazilian unit dates (**red stars**) were obtained respectively from Philipp *et al*. (2018, 2023) and Langer *et al*. (2018), whereas the Argentinean ones (**blue stars**) are from Desojo *et al*. (2020b) and Colombi *et al*. (2021). The Argentinean (4) and Zimbabwean (5) units are geological formations. Abbreviations: **AF**, Africa; **AS**, South America; **AZ**, Assemblage Zone; **Seq.**, Sequence.

MATERIAL AND METHODS

Selected sampling

In a set of 41 samples of fossil teeth from *Dinodontosaurus* (18) and *Hyperodapedon* (23) AZs, 13 were ziphodont, and only seven specimens had their denticles preserved. All these seven specimens were from isolated elements and attributed to archosaurs (Table 1), being one from *Dinodontosaurus* AZ and six from *Hyperodapedon* AZ.

Denticles' study

The denticles of these seven sampled teeth (see Table 1) were characterized according to the Hendrickx *et al*. (2015)'s definitions. It is worth mentioning that the original proposal by Hendrickx *et al*. (2015) was made for non-avian dinosaurs of the Theropoda group, but it can also be properly applied to the non-dinosaurian specimens found on *Dinodontosaurus* and *Hyperodapedon* AZs.

Macroscopic measurements

The measurements conducted on the preserved denticles were made by using an analog caliper Vernier 0–150 mm and following the Hendrickx *et al*. (2015) and Oliveira & Pinheiro (2017) methodologies. However, it is of note that some measurements such as CH (crown height) and CA (crown angle) from Hendrickx *et al*. (2015) were not possible to be carried out because these specimens are with incomplete (apically broken) crowns. The CBL (crown base length), CBW (crown base width) and CBL/CBW (*sensu* Oliveira & Pinheiro, 2017) mensuration were conducted before the thin sections' confection (Figure 1D). The morphotypes assigned to the studied specimens follow the proposed guidelines of Oliveira & Pinheiro (2017; Table 2).

Table 1. Sample's description and provenance. **Abbreviations: AZ**, Assemblage Zone; **Ds**, *Dinodontosaurus* AZ specimen; **Hs**, *Hyperodapedon* AZ specimens; **SED**, sedimentary rock.

SPECIMENS	FOSSIL	UNIT	AZ	AGE	SED.	LOCALITY	CATALOG no.
Ds7	cf. *Prestosuchus chiniquensis*	Pinheiros-Chiniquá	*Dinodontosaurus*	Ladinian	Clayey siltite; Pelite	Sanga da Árvore, Chiniquá-RS	CPEZ-157b/229
Hs1	Undet. Archosaur	Candelária (base)	*Hyperodapedon*	late Carnian	Clayey siltite; Pelite	Sítio Pivetta, Restinga Sêca-RS	PV-1261-T
Hs13	Undet. Archosaur					Sítio Pivetta, Restinga Sêca-RS	CAPPA/UFSM 0365
Hs14	Undet. Archosaur						CAPPA/UFSM 0366
Hs15	Undet. Archosaur						CAPPA/UFSM 0367
Hs17	Undet. Archosaur						CAPPA/UFSM 0369
Hs18	Undet. Archosaur						CAPPA/UFSM 0370

Table 2. Morphotypes characterization by Oliveira & Pinheiro (2017). These were used here to improve the description of the specimens. **Abbreviations: CBL**, crown base length; **CBW**, crown base width.

Morphotype	Classification	Characteristics
I	cf. Phytosauria	Pronounced elongation.
		Total length of 32 mm.
		CBL = 12 mm.
		CBW = 12 mm.
		Pronounced symmetry between the lingual and labial faces.
		Not laterally compressed (oval shape in cross section).
II	Pseudosuchia indet.	CBL = 20 mm.
		CBW = 13 mm.
		CBL/CBW = 1.54.
		Both anterior and posterior carenae have about three denticles/mm.
		The size of denticles decreases in basal direction on the mesial margin of the tooth.
		Distal margin - Denticles remain subequal in size throughout the whole extension of the carena.
III	Pseudosuchia indet.	Mesial and distal margins are almost parallel to each other at the base.
		Tooth is posteriorly curved only in the apical portion.
		More rounded cross-section than MII.
		Distal and mesial carenae have about four denticles/mm.
		CBL/CBW = 1.43.

Microscopic measurements

For microscopic measurements, thin sections of the teeth were confectioned in longitudinal and transverse orientations, following Lamm (2013) and Cerda *et al*. (2020)'s methodologies. After that, the specimens were carbon coated and analyzed by SEM (JOEL JSM-6610LV) at the Laboratório de Geologia Isotópica (LGI), from the UFRGS. The teeth samples were analyzed by Secondary Electron Imaging (SEI) and Backscattered Electrons (BSE). The following parameters were adopted: spot size (SS = 50-60mm), voltage (12 and 15kv) and working distance (WD = 12 and 14 mm).

Microscopic measurements were conducted from photographs took by a professional camera and by a SEM's camera. For this, it was used a Canon EOS Rebel T7 photographic camera, with Sigma DG MACRO (70mm) objective that belongs to the Laboratório de Fotografia and the SEM JOEL JSM-6610LV of the LGI, both from the Geosciences Institute of the UFRGS.

The ImageJ 1,53e (Rasband, 2018) software was used for the measurements.

The following microscopic measurements were taken on the studied denticles: height (H), width (W), interdenticular distance (ID), denticles' number (no.) per mm and per 5 mm, height/width (H/W), carena's angulation (αc) and percentages of variation along the carinae (%). Whenever possible, the thickness of the layers that compound the denticles (enamel and dentine) was measured. H, W, ID and H/W are similar, respectively to DDH, DDl and idsp from Hendrickx *et al*. (2015) and to CBL/CBW from Oliveira & Pinheiro (2017), meanwhile αc resembles $F_α$ from Abler (1992; Figure 1B).

Cutting forces estimates ($F_α$)

The measurements of the carina angulation (αc) were taken considering that αc, resembles $F_α$ from Abler (1992). So, according to Abler (1992)'s proposition, $F_α = F_{max.}$ x sinα/2, and the F_{max} tends to infinity (to be gigantic) as α approaches zero. Based on that, the αc measurements made it possible to infer these studied specimens cutting forces.

Statistical analysis

Statistical correlations were performed among the variables mentioned above, in an independent way between all analyses (*i.e*., H's correlation among all the specimens). Besides that, it was investigated the existence of eventual correlations among the variables in a single sample (*i.e*, H and W' relationship in the specimen H1).

Spearman's Rank Correlation was used to determine the association degree between the denticles' measurements: H, W, H/W and αc. The Spearman's Rank was preferred over Pearson's product of momentum due to its sensibility to the nonlinear and monotonic increases, as those observed when comparing continuous (H, W) with discontinuous (αc) variables (Conover, 1999; Zar, 2009).

The relationship among the denticles' measurements studied was determined by using Principal Coordinate Analysis (PCoA) with Euclidian distance (Legendre & Anderson, 1999; Cox & Cox, 2001). For these analyses, data were transformed using the square root transformation to reduce the effect of high magnitude variables, like αc.

All the statistical analyses were conducted using the software Microsoft Excel (2007)® and R (R Core Team, 2025). The vegan package was used to calculate the PCoA (Oksanen *et al*., 2022). The vector variables were determined and plotted in PCoA graphics using the "envfit" function. The function "ordisurf" with default settings was used to plot gradient lines in the PCA plot.

Abbreviations: αc, carina's angulation; **BSE**, backscattered electrons; **CBL**, crown base length; **CBW**, crown base width; **H**, height, **H/W,** height/width; **ID**, interdenticular distance; **SEI**, secondary electron imaging; **SEM**, secondary electron microscopy; **W**, width.

RESULTS

Here, we present the results of the macroscopic and microscopic measurement, cutting forces estimates ($F_α$), statistical analyses, and SEM observations. The data are organized by AZ.

Macro and microscopic measurements

Dinodontosaurus AZ

Ds7 (cf. Prestosuchus chiniquensis*; CPEZ-157b/229)*

The unique sample from the *Dinodontosaurus* AZ, in this study is attributed to a specimen of *Prestosuchus chiniquensis* (Figure 3B). This attribution is based on the tooth's size (this species represents the biggest predator known until now for this unit) and on its catalog number (CPEZ-157b/229), which identifies it as belonging to this genus. The four preserved denticles belong to the distal portion (DS) of the tooth.

The complete information about the macro and microscopic measurements, including the rest of the specimens studied, is presented in Tables 3 and 4, and S1 (Supplementary Material 1).

Hyperodapedon AZ

Hs1 (Undetermined Archosaur; UFRGS-PV-1261-T)

This specimen, like the others from the *Hyperodapedon* AZ, cannot be assigned to a less inclusive taxon. Despite that, due to the presence of some features (*e.g*., distal curvature, labiolingual flattening, serrations), typically attributed to a ziphodont dentition, they can be classified as undetermined archosaurs. Altogether 48 denticles are preserved in this specimen (Figure 3C), with 29 located on distal portion (DS) and 19, on mesial portion.

It is worth noting that in both, distal and mesial portions, there was a tendency towards an increase in the denticles' height (H) from the apical to the basal portion of the tooth. On distal portion there is a 101% increase between the H of denticle no. 1 (more apical) and that of denticle no. 28 (more basal). On mesial portion, the H's difference along the carina was lower than on DS, being represented by a 66.9% increase between the denticle no. 1 and the denticule no. 14 (Table S1). Right after the denticule no. 14 from MS, the denticles start to reduce their height, basally, which agrees with Hendrickx *et al*. (2015) observation, for theropod dinosaurs, who found that smaller denticles tend to typically occur at the bases and tops of the carinae.

Hs13 (Undetermined Archosaur; CAPA/UFSM 0365)

In this specimen (Figure 3D), thirteen denticles have been preserved and all are located on mesial portion (MS). It is worth noting that the height of the denticles (H) tends to decrease towards the basal portion of the tooth (~46.75%; Table S1), which is consistent with the observations of Hendrickx *et al*. (2015).

Hs14 (Undetermined Archosaur; CAPA/UFSM 0366)

Only four denticles have been preserved in this tooth, and all are located on mesial portion (MS; Figure 3E). The results obtained are presented in Tables 3, 4 and S1. The small number of preserved denticles does not allow any further conclusions about this specimen.

Hs15 (Undetermined Archosaur; CAPA/UFSM 0367)

In this specimen, fifteen denticles have been preserved, all of which are located on the distal portion (DS; Figure 3F).

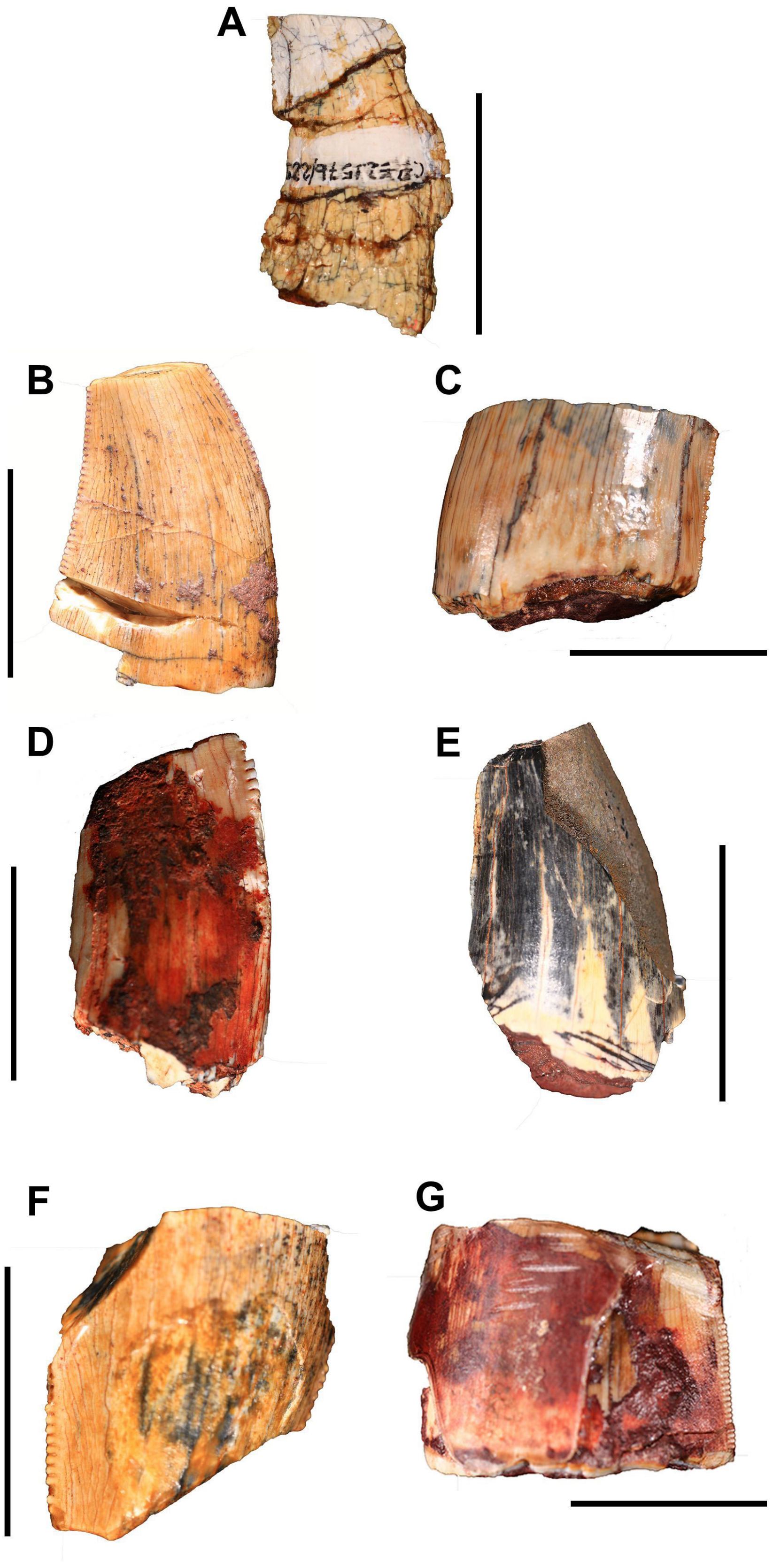

Figure 3. A, Pictures from the measured teeth from *Dinodontosaurus* AZ of *Prestosuchus chiniquensis*. **B–G**, *Hyperodapedon* AZ of undetermined archosaurs. **A**, Ds7 - CPEZ-157b/229; **B**, Hs1 (UFRGS-PV-1261-T); **C**, Hs13 (CAPPA/UFSM 0365); **D**, Hs14 (CAPPA/UFSM 0366); **E**, Hs15 (CAPPA/UFSM 0367); **F**, Hs17 (CAPPA/UFSM 0369); **G**, Hs18 (CAPPA/UFSM 0370). Scale bars = 10 mm.

Table 3. Macroscopic measurements (mm) taken in this study. The morphotypes column follows the Oliveira & Pinheiro (2017) proposal. **Abbreviations: Ds**, *Dinodontosaurus* AZ specimen; **Hs**, *Hyperodapedon* AZ specimens. *This specimen is broken, so the measurements must be interpreted with caution.

Specimens	D/mm	CBL	CBW	CBL/CBW	Morphotype
Ds7	2	20.00	12.00	1.60	-
Hs1	4	12.00	8.00	1.50	MII
Hs13	4	19.00	14.00	1.36	MIII
Hs14	4–5	15.50	12.00	1.29	MII
Hs15	3–4	17.00	13.00	1.31	MIII
Hs17	3–4	11.00	7.00	1.57	MIII
Hs18	3–4	10.00*	12.00	1.67*	MII

Table 4. Microscopic measurements (mm) intervals taken in this study**. Abbreviations: αc**, carina's angulation; **Ds**, *Dinodontosaurus* AZ specimen; **DS**, distal side; **H**, height; **Hs**, *Hyperodapedon* AZ specimens; **ID**, interdenticular distance; **MS**, mesial side; no. /5mm, number of denticles per 5 mm length; **T.S.**, teeth side; **W**, width.

Specimens	T.S.	H	W	H/W	No./5mm	ID	αc
Ds7	DS	0.04–1.11	0.80–1.06	0.53–1.16	5	0.21–0.29	4.67°
Hs1	DS	0.19–0.38	0.14–0.23	0.98–2.01	16	0.06–0.11	9.67°
	MS	0.17–0.29	0.14–0.22	0.96–1.76	17	0.06–0.15	26.83°
Hs13	DS	0.22–0.42	0.14–0.24	1.31–1.83	22	0.03–0.04	7.29°
Hs14	MS	0.41–0.46	0.32–0.34	1.20–1.39	14	0.04–0.06	10.14°
Hs15	DS	0.47–0.72	0.34–0.45	1.04–1.99	10	0.04–0.10	9.15°
Hs17	DS	0.26–0.37	0.26–0.34	0.76–1.43	14	0.07–0.10	15.95°
	MS	0.16–0.31	0.19–0.40	0.54–1.26	10	0.09–0.15	12.07°
Hs18	DS	0.21–0.29	0.16–0.24	1.13–1.50	20	0.03–0.06	9.14°

Again, the height (H) is bigger on the denticles from the middle of the carina (denticles no. 6–9), as suggested by Hendrickx *et al.* (2015). In general, the H15 specimen denticles' height varied approximately 54.72% between the smaller H (0.466 mm, denticle no. 1) and bigger H (0.721 mm, denticle no. 8).

Hs17 (Undetermined Archosaur; CAPA/UFSM 0369)

Altogether, fifteen denticles have been preserved in this specimen, being nine located on distal portion (DS) and seven on mesial portion (MS; Figure 3G).

On the distal portion, there is a 43.19% increase in height from denticle no. 1 (H) and denticle no. 6. On the mesial portion, on the other hand, the H's difference along the carina was bigger than that observed on DS. On that portion, it was verified to be a 98.71% increase between the denticle's no. 3H and the denticle's no. 2H (Table S1).

Hs18 (Undetermined Archosaur; CAPA/UFSM 0370)

Twenty denticles have been preserved in this tooth, all being located on its distal portion (DS; Figure 3H). In this specimen, there is an increase of approximately 40.98% between the denticle's no. 12 H and the denticle's no. 3 H (Table S1).

Cutting forces estimates (F_α)

Based on αc results presented in Table 4 and considering that these measurements were obtained in a manner similar to the F_α of Abler (1992), it is possible to infer that the specimens Ds7 (αc = 4.67°) and H13 (αc = 7.29°) exhibited the highest cutting forces among the analyzed samples. In contrast, specimen Hs17 (DS = 15.95° and MS = 12.07°) likely had the lowest F_α.

Enamel thickness measurements

With a scanning electron microscope (SEM), it was possible to determine the dental enamel thickness of the specimens studied. Since the enamel of the Ds7 (CPEZ-157b/229) had been previously removed for conducting isotopic studies, it was not possible to measure its thickness. The thickness of the dental enamel of Hs1, Hs13, Hs14, Hs15, Hs17 and Hs18 specimens vary respectively between: 69 and 92 µm; 212 and

240 µm; 60 and 76 µm; 80 and 110 µm; 14 and 23 µm and 60 and 120 µm. SEM analyses also made it possible to observe structures similar to dentin's deposition layers (like von Ebner lines) on Hs13, and Hs14 (Figure 4A).

Statistical analyses

Correlations among the variables were conducted both for all specimens combined and for each specimen separately. The results obtained are presented below.

A high positive correlation (rho=0.85) was observed between H and W variables when correlated the measured data as a set, which did not happen in the specimens individually. No significant correlation ($p > 0.80$) was observed between the interdenticular distances (ID) and the other variables (H and W), when they were considered as a set. However, this is not valid to the correlation conducted per specimen. The specimen Hs13 has positive correlations between its ID and the variable H (rho = 0.90) and the H/W ratio (rho = 0.81).

High negative correlations (rho > -0.80) were detected on Ds7 and Hs14 and on the distal portion of Hs17 specimens. The Ds7 sample's ID has negative correlations with H (rho = -1.00) and W (rho = -1.00). The Hs14 sample's ID are negatively correlated with H (rho = -1.00), as well as, with their H/W ratios (rho = -0.85), and not with their W. Both correlations must be analyzed with parsimony since these specimens (Ds7 and Hs14) have just few denticles preserved (see Table S2) which can interfere in the statistical results. The ID of the distal portion of Hs17, by its turns, is also negatively correlated to H (rho = -0.84), just like the Ds7 and Hs14. It is observed that no other correlation, positive or negative, was detected in the other samples analyzed.

The height and width measurements of the Ds7 specimen's denticles (cf. *Prestosuchus chiniquensis*) are notably bigger compared to the *Hyperodapedon* AZ's specimens (Figure 5). Nonetheless, the H/W ratio is lower than that of the other samples. It is worth noting that these results must be interpreted

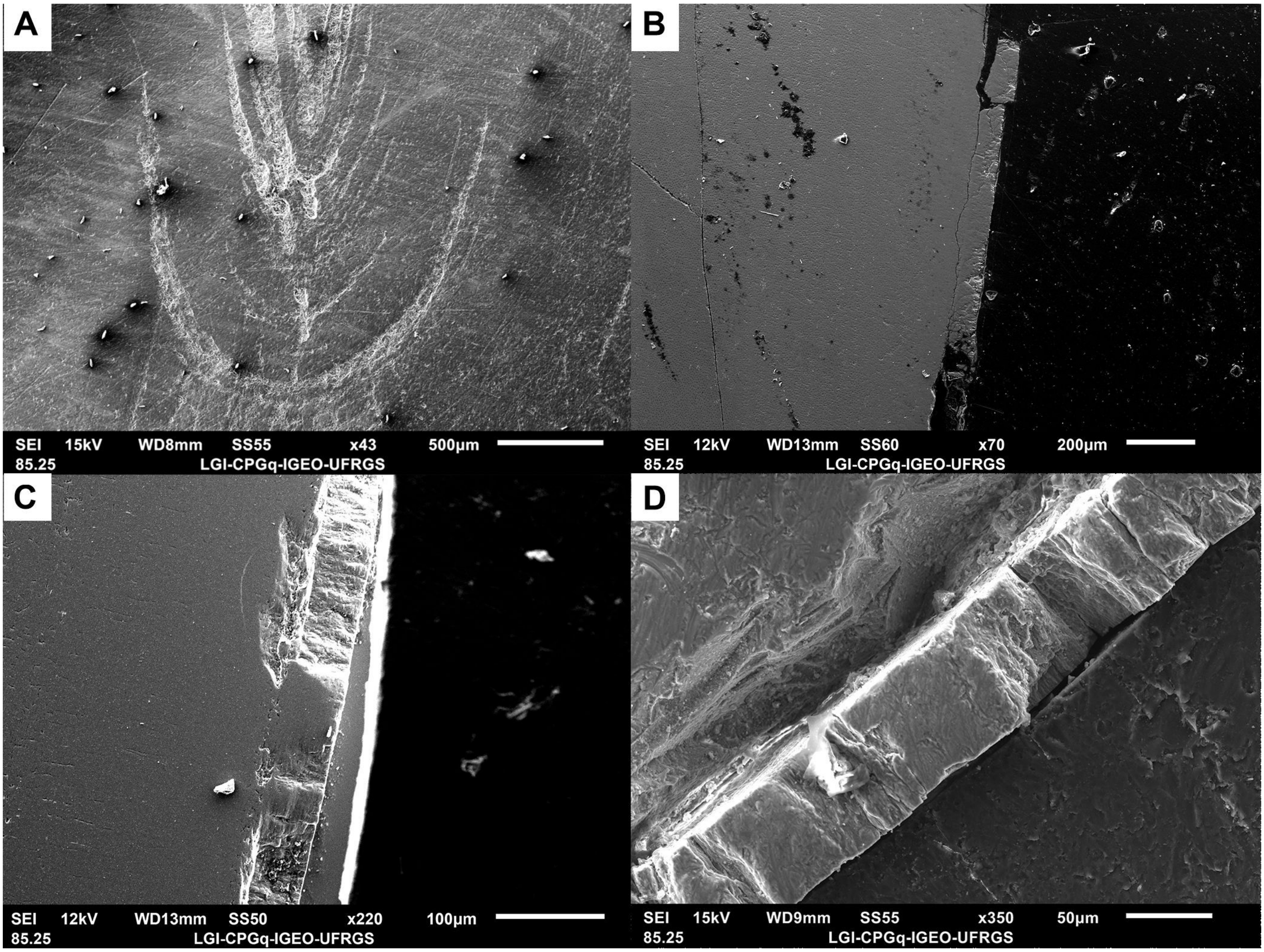

Figure 4. SEM images from the analyzed teeth. **A**, Structures resembling dentin's deposition layers (like von Ebner lines) on Hs14, CAPPA/UFSM 0366 specimen. **B**, Enamel thickness from the undetermined archosaur on Hs1, UFRGS-PV-1261-T. **C**, Hs13, CAPPA/UFSM 0365. **D**, Hs14 - CAPPA/UFSM 0366.

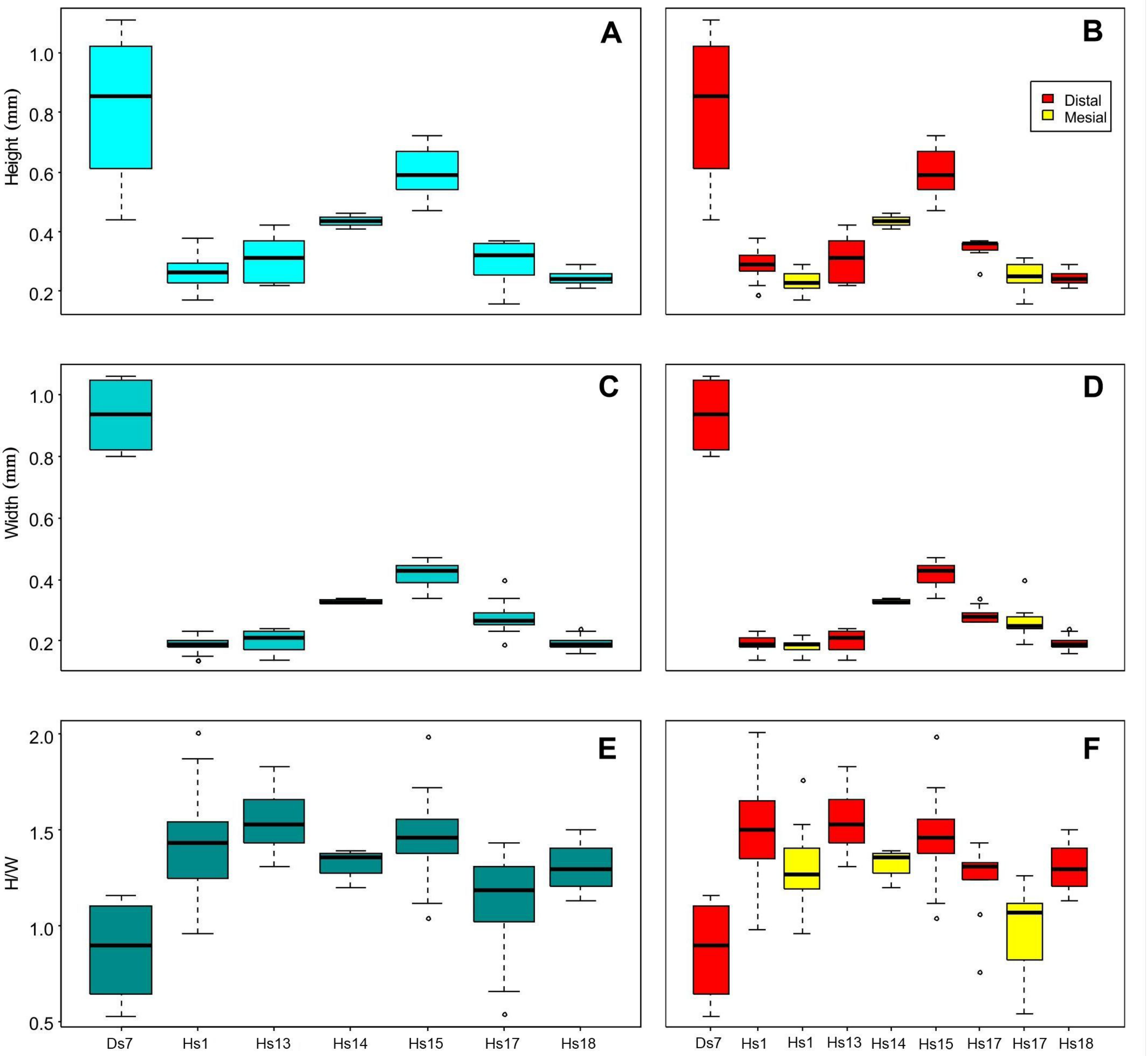

Figure 5. Summary of teeth measures across specimens. Boxplot showing **A–B**, height, **C–D**, width, **E–F**, height/width ratio teeth measures, regardless of tooth side (left panel) and considering mesial and distal tooth side (right panel). Most measures were taken from distal side of the teeth, whereas mesial side was preserved and measured only in specimens Hs1, Hs14 and Hs17.

with parsimony due to the quantity of preserved denticles in that specimen.

The PCoA results allow observing that the αc can be the responsible to the high difference between the mesial and distal portions' measurements conducted on Hs1 specimen (Figure 6). This sample is the most different. The carine angle is the variable with the higher correlation to axis 1, where nearly 50% of the variation in the measurements is concentrated. Based on these results, it is possible to observe that the specimen Ds7, Hs14, Hs15 and Hs17 presents smaller numbers of denticles/5mm (5 to 17) in relation to Hs13 and Hs18 samples (20 to 22), as can be seen in detail, on Table 4.

Other data related to the realized correlations can be seen on Tables S2 and S3, and R script attached on Supplementary Material 2 and 3.

DISCUSSION

Morphological comparisons

By comparing the morphological diversity of the studied here (Figure 7) with those illustrated in Hendrickx *et al*. (2015, figs. 4 and 8), the following similarities can be observed.

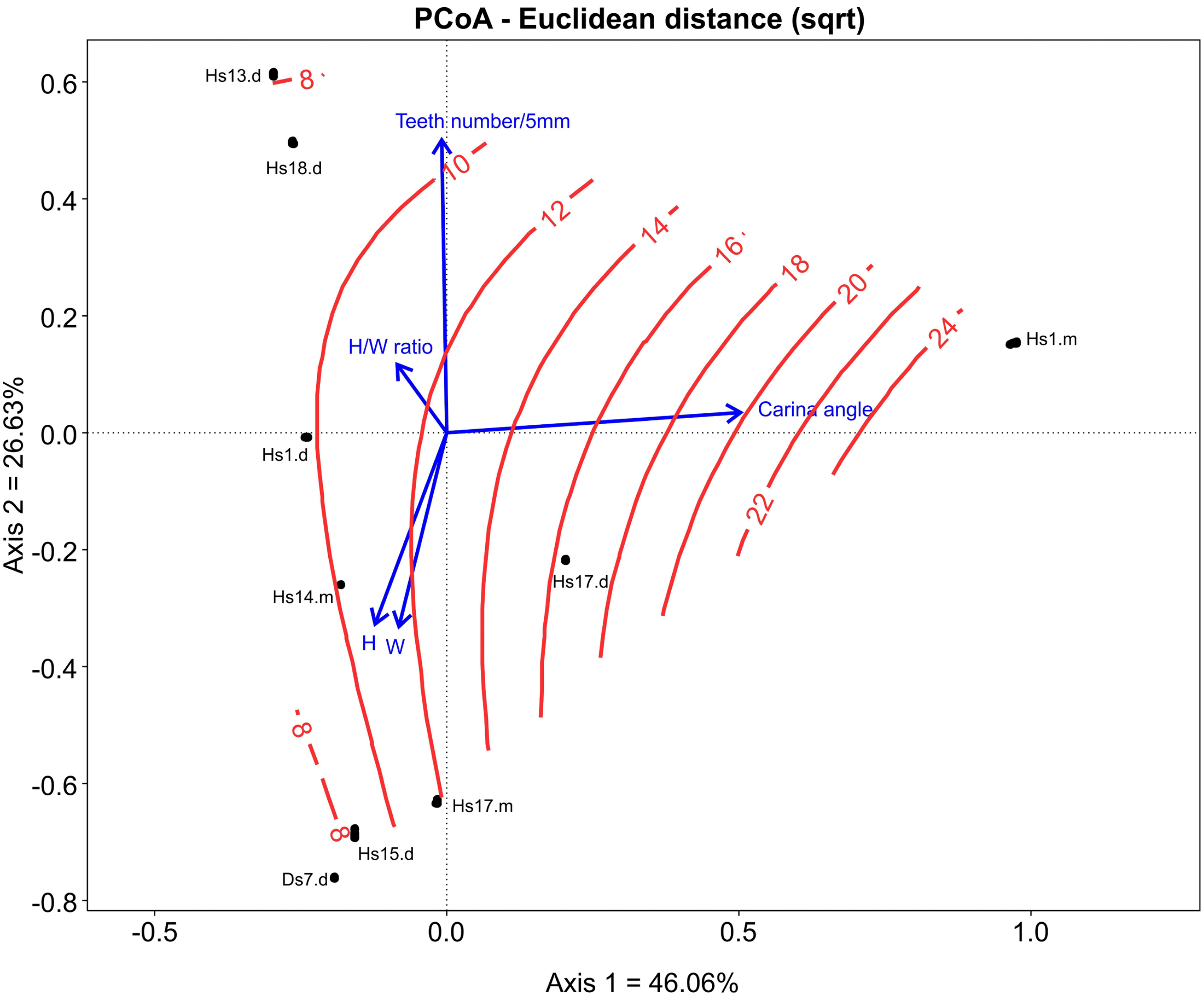

Figure 6. Principal Coordinate Analysis. Axis 1 synthesizes almost 50% of all variation. Main variables influencing relationship between specimens are almost orthogonal, carina angle and number of teeth/5mm. Red gradient lines represent the variation in carina angle throughout samples.

The Ds7 specimen (cf. *Prestosuchus chiniquensis*) has subquadrangular mesioapical denticles with planar external margins, similar to those observed in the teeth of *Acrocanthosaurus atokensis* (fig. 8F of Hendrickx *et al*., 2015), a theropod dinosaur from the clade Carcharodontosauridae. The H1 specimen's denticles (undetermined archosaur) are subquadrangular distocentral with wide interdenticular chambers (ID) like those of an undetermined Tyrannosauridae (fig. 8J of Hendrickx *et al*., 2015). The Hs13 specimen (undetermined archosaur) has apically domed denticles, which seem like those of an undetermined Abelisauridae (fig. 4K of Hendrickx *et al*., 2015). The denticles of the Hs14 specimen (undetermined archosaur) have short interdenticular sulci like the *Erectopus superbus* (fig. 8G of Hendrickx *et al*., 2015), an allosauroid theropod. The Hs15 specimen (undetermined archosaur) has apically inclined and bilobate mesioapical denticles that are similar to those of *Megalosaurus bucklandi* (fig. 8D of Hendrickx *et al*., 2015), a megalosaurid theropod. The denticles of the Hs17 specimen (undetermined archosaur) have similar morphology to those of the Hs14 sample, and, by consequence, to the *Erectopus superbus*, but they have greater ID than that (Tables 4 and S2). The Hs18 sample (undetermined archosaur), by its turns, have proximodistally subrectangular distocentral denticles, which seem like those of the *Afrovenator abakensis* (fig. 8C of Hendrickx *et al*., 2015), another theropod dinosaur from the clade Megalosauridae.

The similarity between the denticle morphology of cf. *Prestosuchus chiniquensis* and that of the theropod *Acrocanthosaurus atokensis* suggests that these species may have interacted with their prey in comparable ways. However, their overall paleoecological roles were certainly not identical, given major anatomical and functional differences (*e.g*., quadrupedal

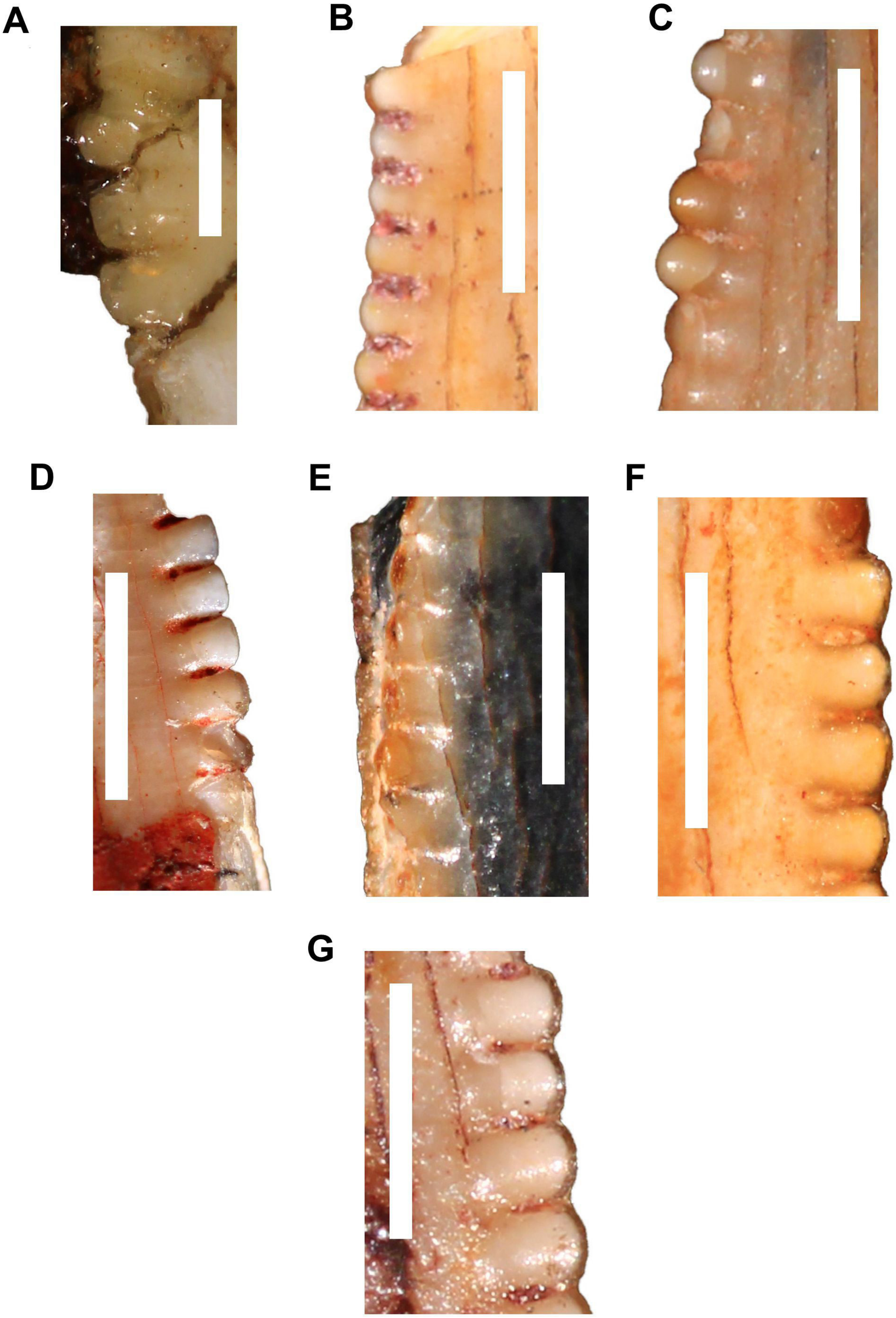

Figure 7. Morphological diversity of denticles in isolated teeth from Santa Maria Supersequence. A, subquadrangular mesioapical denticles with planar external margins in an isolated tooth of cf. *Prestosuchus chiniquensis* (Ds7 - CPEZ-157b/229). **B**, subquadrangular distocentral denticles with wide interdenticular chambers in an isolated tooth of an indet. archosaur (Hs1 – UFRGS-PV-1261-T). **C**, apically domed morphology of denticles from an isolated tooth of an indet. archosaur (H13 - CAPPA/UFSM 0365). **D**, **F**, distocentral denticles with short interdenticular sulci and shallow interdenticular slits from an isolated tooth of an indet. archosaurs (Hs14 - CAPPA/UFSM 0366 and Hs17 - CAPPA/UFSM 0369). **E**, apically inclined and bilobate mesioapical denticles in an isolated tooth of an indet. archosaur (H15 - CAPPA/UFSM 0367). **G**, Proximodistally subrectangular distocentral denticles in an isolated tooth of an indet. archosaur (H18 - CAPPA/UFSM 0370). Scale bars = 1 mm.

versus bipedal posture, with *A. atokensis* having its forelimbs free to handle prey) that would have influenced prey capture and feeding behavior.

Both *Acrocanthosaurus atokensis* and *Prestosuchus chiniquensis* exhibit feeding adaptations consistent with active macropredators. A functional morphology study of the neck muscles of *Acrocanthosaurus* showed that it had exceptional dorsoventral neck movements that enabled downward and backward tearing motions, which suggests "slash-and-pull" predation style (Snively & Russell, 2007; Eddy & Clarke, 2011). In *Prestosuchus*, the laterally compressed, serrated teeth and robust cranial architecture indicate strong shearing forces adapted for cutting flesh (Mastrantonio *et al*., 2019; Lacerda *et al*., 2016), and the tall neural spines and muscular neck and back also suggest substantial pulling strength during feeding (Roberto-da-Silva *et al*., 2018; Mastrantonio *et al*., 2024), impaling in a "bite-and-pull" or "bite-and-shake" feeding strategy. Some studies suggested that the feeding behavior of *Acrocanthosaurus* relied on the coordinated use of jaws, neck, and forelimbs to restrain and dismember large prey, producing deep, slicing wounds rather than bone-crushing bites (Currie & Carpenter, 2000; Senter & Robins, 2005). Similar behavior was proposed for the *Prestosuchus*, that had powerful forelimbs that could be used to aid in grasping or manipulating prey, which was supported by sensory adaptations consistent with an active predatory lifestyle (Mastrantonio *et al*., 2019). Although separated by tens of millions of years and distinct evolutionary histories, both taxa converged functionally toward a similar flesh-shearing feeding mechanism, emphasizing power and tearing efficiency over bone-crushing or swallowing prey whole (Nesbitt, 2011; Desojo *et al*., 2020a), which is supported by their similar denticles morphology observed in this study.

Since the samples from *Hyperodapedon* AZ could not be assigned to a genus-level taxonomy, it is not possible to establish phylogenetic correlations between the denticles morphotypes analyzed here and those of the taxa to which they show morphological similarity, namely the specimens reported by Hendrickx *et al*. (2015). Nevertheless, the substantial morphological diversity observed among the sampled denticles is consistent with the known diversity of this AZ, which includes at least five different taxa with distinct ethologies. According to the currently known archosauromorph species from the *Hyperodapedon* AZ (c. N = 18; Schultz *et al*., 2020), these teeth could be attributed to Dinosauria (*e.g*., *Gnathovorax cabrerai*, *Buriolestes schultzi*), Ornithosuchidae (*Dynamosuchus collisensis*), Protherochampsia (*e.g*., *Proterochampsa nodosa*) or Rauisuchia (*Rauisuchus tiradentes*), due to their sizes, which agrees with the diversity indicated by the morphologies of the denticles.

Considering the aforementioned taxa, we can discard some sauropodomorph dinosaurs (*e.g*., *Pampadromaeus barberenai* and *Bagualosaurus agudoensis*), since it possessed leaf-shaped teeth with denticles angled approximately 45º relative to the distal margin of the tooth (Langer *et al*., 2019), which suggests omnivory or some degree of herbivory, a morphology not observed in our sample set. The blade-like shape of specimens Hs1, Hs14, Hs15, and Hs17 is comparable to the "blade-like" morphology observed in *Gnathovorax cabrerai* (Pacheco *et al*., 2019) and *Dynamosuchus collisensis* (Müller *et al*., 2020), although the latter is more conical teeth than *Gnathovorax*. Based on the tooth size and the number of denticles per 5 mm (~25; Lautenschlager & Rauhut, 2014), *Rauisuchus tiradentes* could be a good candidate for samples Hs13 (~22 denticles per 5 mm) and Hs18 (~20 denticles per 5 mm; see Figure 7C–G and Table S1). Despite that, caution is advised, as only a few teeth (n = 2) are certainly known to belong to *R. tiradentes* (Lautenschlager & Rauhut, 2014). However, it is not possible to affirm that each analyzed morphotype corresponds to distinct taxa. Ontogeny and tooth position are factors that should be evaluated to achieve a more precise taxonomic identification. Therefore, it is necessary to conduct studies on taxa whose teeth still are associated with their jaws and mandibles, and, if possible, that include different ontogenetic stages. Such studies would enable comparative analyses of denticle morphotypes, their correlation with morphotypes observed on the isolated teeth, and the identification of new morphotypes potentially attributable to previous unknown species.

Paleometric and biomechanical observations

Comparing the statistical correlations of this study with those based on Hendrickx *et al*. (2015)'s figs. 4 and 8, we verified the statistical correlation between H and W for the Hs13 specimen is 0.90. This specimen's ID also has high positive correlation (0.90) with H, but this correlation should be considered with parsimony since only six denticles had been measured in this sample. The Hs17 specimen's ID, in an opposite way of the Hs13, presents a high negative correlation with H (-0.84), but again, the number of denticles preserved were lower than the statistical ideal ($5 \leq n \geq 15$ measurements, *e.g*., Medri, 2011; Bussab & Morettin, 2017). Thus, it also needs to be analyzed with caution. The other correlations obtained in this research should be seen with parsimony due to the small number of measurements.

Besides that, it was observed that there is a tendency of high correlation (0.85) between all the H and W variables. It means that as the denticles increase in height they tend to become wider, which is due to a relatively homogeneous growth of these. That fact, in principle, does not imply a taxonomic differentiation. In general, the correlations conducted on Hendrickx *et al*. (2015)'s studied specimens were also resultant of few measurements (Tables S2 and S3). The only correlation that can be statistically considered relevant in this research (> 8 measurements) can be seen between H/W ratio and ID (-0.85). Thus, the higher the H/W ratio is, lower the ID would be, which may be related to the tooth's growth speed and/or to the fact of processing the correlation of samples from different species. The correlation among such variables, in this preliminary approach, does not provide sufficient support for taxonomic classifications but rather details the structural characteristics of the teeth. However, future studies including a greater number of identified individuals at species level will allow these variables to be tested with broader taxonomic perspectives.

According to Hendrickx *et al.* (2015), the denticles tend to be smaller on the apical and basal portions of the tooth. In general, on Hs1 specimen (DS) the H values only increase. The same is true to its MS, but, from denticle no. 14 on, the H values tend to decrease, which agrees with Hendrickx *et al.* (2015) observation. The Hs15 sample best illustrates the statement of these authors, as it shows an increase in H values in the apical-basal direction, followed by a decrease along the carina. This sample is important because it suggests that the pattern proposed by Hendrickx *et al.* (2015) for theropod dinosaurs could represent a plesiomorphic condition within the group, since a similar feature can already be observed in Triassic archosaurs. The Hs14, Hs17 and Hs18 specimens do not have any pattern related to their H values. These measures are variable along the carina lines of these samples. It is interesting that on Ds7 and Hs14 these values are almost constant, but considering that there are only four preserved denticles, this observation must be taken with parsimony.

Two findings are possible in light of these observations: (i) the fact that most of the studied samples present poorly preserved apical portions or even absents, may have resulted in the observed correlations or non-correlations, due to the number of preserved denticles; (ii) the fact that Hendrickx *et al.* (2015) have been proposed that the denticles' height tends to be smaller on apical and basal portions based on theropod dinosaurs' teeth, a distinct group of that approached in this study, can be the cause of the differences observed on these correlations (or the miss of them) among this study specimens.

Based on the αc measured in the Ds7 specimen (4.67°) that belongs to the *Prestosuchus chiniquensis*' species and considering its similarity with F_{α} from Abler (1992), it is possible to propose elevated bite forces' values to this specimen. According to Abler (1992), the F_{max} tends to infinity (to be gigantic) as α approaches zero. In an analogy with modern knives, it is mentioned that those with minor angulations (~10° to 15°) tend to be sharper and therefore used to be used to activities that demand higher cutting precision, such as professional kitchen knives and razor blades. As the knives' angulation increases (> 25°) these applications become for heavier activities, like for example, machetes, cleavers and axes. Thus, the greater the angle of the knife is, more durable its blade tends to be (McCreight, 1985; Watson, 1997; Kertzman & Shackleford, 2016).

Following this analogy, the cf. *Prestosuchus chiniquensis* (Ds7), in addition to having the highest bite force (F_{α}), would be what would generate a more accurate cut among the studied samples; however, it would be subject to lower tooth durability. In an opposite way, the undetermined archosaur (Hs17) should have the lowest F_{a}, but the greater resistance of the tooth to wear (Figure 8). The Ds7 sample is the one that has the biggest CBL and CBW difference (8 mm; Table 3). Therefore, it is the most laterally compressed, which reinforces the previously proposed statements (precise cut and less durability). Studies focusing on the understanding of tooth replacement in Pseudosuchia dental exchange comprehension (the only one correctly identified specimen Ds7) must be conducted to verify the possibility of the existence of a high tooth replacement rate (polyphyodonty) throughout the individual's life, as occurs in crocodiles (Poole, 1961; Kieser *et al*., 1993), sharks (Lauer *et al*., 1990; Whitenack *et al*., 2010) and even in non-mammalian cynodonts (Luo *et al*., 2004; Martinelli & Bonaparte, 2011). Such studies would make it possible to relate the αc, F_{α}, and wear resistance to the tooth replacement rate of this group and, consequently, extends these findings to other taxa.

A dynamical testing device to quantify cutting performance of shark teeth was performed by Corn *et al*. (2016). They found that tiger (*Galeocerdo cuvier*) and silky (*Carcharhinus falciformis*) sharks possess sharp but rapidly dulling teeth, likely related to their high tooth replacement rates and hard-prey diets (*e.g*., turtles and crustaceans). In contrast, sixgill sharks (*Hexanchus griseus*) exhibited low cutting efficiency but no dulling, consistent with slower tooth replacement rates and prey swallowed whole. These results illustrate a "sharp versus durable" trade-off in tooth morphology, analogous to the pattern proposed here for archosaur teeth (low αc = sharper, less durable). Similarly, Massare's (1987) tooth morphology–prey type guilds for Mesozoic marine reptiles show that rounded, high-αc teeth were adapted to crush hard prey, whereas sharper, low-αc teeth were suited for piercing or cutting. Prosauropod dinosaurs, such as *Plateosaurus*, also display high-αc, coarsely denticulate teeth consistent with herbivory (Galton, 1985; Sander, 1997). Altogether, these comparisons support our interpretation that αc correlates with feeding strategy: high αc with resistance and hard-food diets, and low αc with cutting efficiency and soft-food diets.

The morphofunctional diversity of basal dinosaurs was investigated in comparison to the actual Squamata and Crocodylia, to get diet information (Ballell *et al*., 2022). Among this sample set, those teeth with small αc (based on the observation of that paper's figures) have bigger strength stress indices (> MPA – Von Mises stress). On the contrary, those teeth with bigger αc tend to better distribute the forces imposed on them. This agrees with the hypothesis presented here that says that teeth with small αc tend to be less resistant, but more efficient to the cut, meanwhile those with bigger angle (αc) are mechanically more resistant to the wearing, but less efficient to the cut (*e.g*., of soft tissues). Thus, it is possible to suggest that those teeth with lower αc (less resistant) were used to grip and rip, meanwhile those with bigger αc (more resistant), could have been used to puncture and grip their prey. This observation can be made based on an analogy with sharks (grip and rip); crocodiles and *Tyrannosaurus* (puncture and grip) teeth (Abler, 1992; D'Amore, 2009).

The study of distribution of forces conducted by Ballell *et al.* (2022) allowed inferring that those dinosaurs with mechanically weaker teeth (*Herrerasaurus*, *Eodromaeus*, *Buriolestes* and *Eoraptor*) had their diets based on softer substances, as for an example, meet. So, they would have had a predominantly carnivorous diet. The more resistant teeth, in their turn, would have had, according to these authors, a food source based on harder materials like plants and insect exoskeletons. It is also

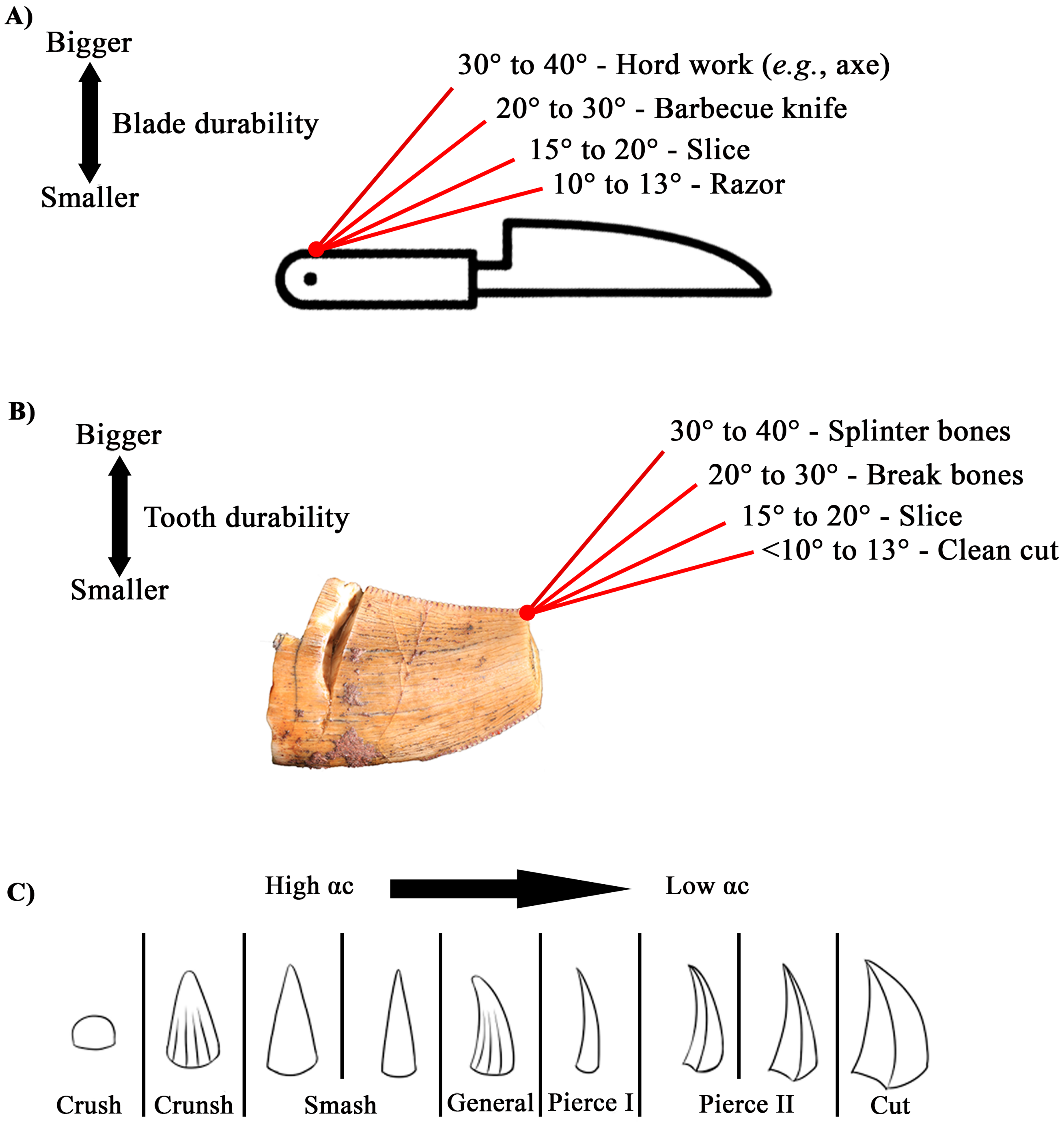

Figure 8. Different knife-angle utilities associated with **A**, blade durability, adapted from Watson (1997), and **B**, a comparative proposal for tooth use and durability. **C**, tooth morphology-prey-type guilds adjusted according to the αc (adapted from Massare, 1987).

possible that these teeth were used to break/smash bones; however, this hypothesis was not raised by these authors. The denticle's morphology of these studied samples suggest that their owners must have had diets preferably composed by meet as same as proposed by Ballell *et al*. (2022) for *Herrerasaurus*, *Eodromaeus*, *Buriolestes* and *Eoraptor*. Based on this observation and on the analogy with knives proposed here, it is possible to suggest similar biomechanical behaviors for cf. *Prestosuchus chiniquensis* (Ds7) and *Eoraptor* teeth (high F_α, precise cut and less tooth durability), as well as, for the undetermined archosaur (Hs17) and those of the *Eodromaeus* genus (low F_α, less precise cut and more tooth durability). However, owing to confirm these taxa possible diets and biomechanical similarities, it is necessary to realize complementary studies.

Enamel thickness measurements aimed at inferring feeding strategies or dietary preferences are common in studies involving fossil mammals (*e.g.*, Janis & Fortelius, 1988; Smith *et al*., 2003; Lucas *et al*., 2008; Rabenold & Pearson, 2011). Among the clade Archosauria, on the other hand, the crocodilians generally have thicker enamel than dinosaurs, with thicker regions toward the apex of the crown (Sellers *et al*., 2019; Cullen *et al*., 2023). Despite the apex of the crowns not preserved among the samples studied it was possible to infer some correlations. It is well established for mammals that those who have thickest enamel tend to feed on more abrasive and/or hard foods/particles (*e.g*., grasses, mollusks), so thick enamels tend to provide greater resistance to teeth (like observed on archosaurs). It is also commonly associated with the habit of grazing and with hypsodonty (Fortelius, 1982; Janis & Fortelius, 1988; Hummel *et al*., 2011; Melo *et al*., 2019).

Therefore, based on its greater enamel thickness, the undetermined archosaur Hs13 (212 to 240 μm; Figure 4C) would have had the most abrasive and/or hard diet, among those studied here, as well as the most weather-resistant tooth (*e.g*., against abrasion, corrosion). In contrast, the undetermined archosaur Hs14 (14 to 23 μm; Figure 4D), would have consumed less abrasive and/or softer food items, and possessed the least weather-resistant tooth. Considering Sellers *et al*. (2019) and Cullen *et al*. (2023) observations, the Hs13 specimen would have a greater affinity with the Crocodylia (Pseudosuchia) clade (perhaps *Rauisuchus*), while the Hs14 specimen, with Dinosauria (perhaps *Gnathovorax*). Both clades were already recorded in the *Hyperodapedon* AZ, which corroborates that hypothesis. Since these specimens are not classified at the species level, it is not possible to infer more precise ecological relationships. This reinforces, once again, the need for studies including a larger number of specimens, preferentially teeth preserved within jaws and/or mandibles to obtain more information about the paleodiet of the SMS taxa.

A study on tooth enamel microstructure in *Revueltosaurus* (Aetosauriformes) and *Krzyzanowskisaurus* (synonymized with *Revueltosaurus* by Irmis *et al*., 2007) conducted by Heckert & Miller-Camp (2013) showed that these species possessed relatively thick enamel for teeth of their size, with thickness ranging from about 5 to 152 μm. This range falls within the enamel thickness observed in the samples of the present study, except for the Hs13 specimen (212 and 240 μm). Both groups are also recorded in *Hyperodapedon* AZ and could be potential candidates as the owners of the isolated teeth analyzed here. It is worth noting that, for instance, *Aetosauroides scagliai* exhibits, according to Paes Neto *et al*. (2021), some features typical of predatory archosaurs, such as the recurved ziphodont teeth and a mandibular articulation aligned with the tooth row, but was probably omnivorous, which could be another potential fit among our isolated teeth.

The preliminary paleometric insights of this study are valuable because they offer a new perspective on isolated teeth and pave the way for future investigations into predation styles and diagenetic processes. Micrometric measurements, in particular, can provide important information about the depositional context in which fossils were preserved, as similarly proposed by Dauphin (2025) in her study of the Pliocene–Pleistocene fauna from Malawi.

CONCLUSIONS

The present study on isolated archosaur teeth from the Santa Maria Supersequence demonstrates that parametric analyses (CBL, CBW, D/mm, αc, and enamel thickness) can provide paleoecological and taxonomic insights. The integration of macro- and micromorphological data, supported by SEM observations, revealed consistent correlations among denticle geometry, enamel thickness, and inferred feeding behavior.

The morphometric parameters enabled the recognition of two denticle morphotypes comparable to those proposed by Oliveira & Pinheiro (2017), suggesting that these variables can serve as reliable tools for the taxonomic assessment of isolated teeth. In turn, the αc measurements proved to be useful indicators of cutting efficiency and tooth resistance, supporting biomechanical and dietary interpretations consistent with data from extant and extinct vertebrates.

The variation in enamel thickness, ranging from thin (Hs14) to very thick (Hs13) specimens, also reflects potential differences in feeding strategies and food hardness, reinforcing the ecological diversity of the archosaurs from the Santa Maria Supersequence.

Although the isolated nature of the samples prevents precise taxonomic attribution, these results demonstrate that quantitative dental parameters can contribute to reconstructing feeding behavior and ecological roles. Future studies involving teeth still attached to jaws or mandibles will be essential for refining taxonomic identification and validate the applicability of this approach to other Triassic taxa.

DATA AVAILABILITY STATEMENT

All supplementary data are available in Figshare: https://doi.org/10.6084/m9.figshare.31471975.

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AUTHOR CONTRIBUTIONS

Leonardo Corecco: writing – original draft, methodology, conceptualization, investigation, formal analysis, software, data curation. Vitor Paulo Pereira: writing – original draft, methodology, conceptualization, review. Fernando Erthal: writing – original draft, methodology, conceptualization, formal analysis, software, review. Cesar Leandro Schultz: writing – original draft, methodology, conceptualization, investigation, data curation, resources. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

DECLARATION OF AI USE

We have not used AI-assisted technologies to create, review, or any part of this article.

ETHICS

This work did not require ethical approval, collecting licenses, or previous authorizations.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1 Denticule's measurements

Table S2 Denticule's measurements

Table S3 Denticule's measurements (Hendrickx *et al*., 2015)

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