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ISOLATED ARCHOSAURIFORM TEETH FROM THE UPPER TRIASSIC CANDELÁRIA SEQUENCE (*HYPERODAPEDON* ASSEMBLAGE ZONE, SOUTHERN BRAZIL)

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ABSTRACT – We describe isolated teeth found in the locality "Sítio Piveta" (*Hyperodapedon* Assemblage Zone, Candelaria Sequence, Upper Triassic of the Paraná Basin). The material consists of five specimens, here classified into three different morphotypes. The morphotype I is characterized by pronounced elongation, rounded base and symmetry between lingual and labial surfaces. The morphotype II presents serrated mesial and distal edges, mesial denticles decreasing in size toward the base, distal denticles present until the base and asymmetry, with a flat lingual side and rounded labial side. The morphotype III, although similar to morphotype II, has a greater inclination of the posterior carinae. The conservative dental morphology in Archosauriformes makes difficult an accurate taxonomic assignment based only on isolated teeth. However, the specimens we present are attributable to "Rauisuchia" (morphotype II and III) and, possibly, Phytosauria (morphotype I). The putative presence of a phytosaur in the Carnian *Hyperodapedon* Assemblage Zone would have impact in the South American distribution of the group. The taxonomic assignments proposed herein contribute to the faunal composition of the *Hyperodapedon* Assemblage Zone, a critical unit on the study of the Upper Triassic radiation of archosaurs.

Key words: Paraná Basin, Santa Maria Supersequence, Phytosauria, Rauisuchia, dentition.

RESUMO – Descrevemos, aqui, dentes isolados encontrados na localidade "Sítio Piveta" (Zona de Associação de *Hyperodapedon*, Sequência Candelária, Triássico Superior da Bacia do Paraná). O material consiste de cinco exemplares, aqui classificados em três diferentes morfótipos. O morfótipo I é caracterizado por pronunciado alongamento, base arredondada e simetria entre a superfície lingual e labial. O morfótipo II apresenta bordas mesial e distal serrilhadas, dentículos mesiais diminuindo de tamanho em direção à base, dentículos distais presentes até a base e assimetria, com um lado lingual achatado em relação ao lado labial. O morfótipo III, embora semelhante ao II, apresenta uma inclinação mais pronunciada na carena posterior. A morfologia dentária conservativa dentro de Archosauriformes torna difícil uma atribuição taxonômica acurada baseada apenas em dentes isolados. Ainda assim, os espécimes aqui descritos são atribuíveis a "Rauisuchia" (morfótipos II e III) e, possivelmente, Phytosauria (morfótipo I). A possível presença de Phytosauria na Zona de Associação de *Hyperodapedon* (Carniano) teria impacto na distribuição deste grupo na América do Sul. As atribuições taxonômicas propostas aqui contribuem na composição faunística da Zona de Associação de *Hyperodapedon*, uma unidade sedimentar crítica para a compreensão da irradiação dos arcossauros no Triássico Superior.

Palavras-chave: Bacia do Paraná, Supersequência Santa Maria, Phytosauria, Rauisuchia, dentição.

INTRODUCTION

As observed in the geological record, some vertebrate remains are more likely to preserve as fossils, because their constituent tissues have comparatively greater resistance to biostratinomic and diagenetic processes. This is particularly the case for teeth, which compose a substantial portion of the fossil record of vertebrates (*e.g.* Rauhut & Werner, 1995; Zinke, 1998; Heckert, 2004; Larson & Currie, 2013; Sues & Averianov, 2013; Hendrickx *et al.*, 2015). In areas where other osteological elements are rare or absent, the dental record may provide important information about the faunal composition of a locality. Here, we describe isolated archosauriform teeth from an Upper Triassic outcrop of the Candelária Sequence (*Hyperodapedon* Assemblage Zone, Rio Grande do Sul State, Southern Brazil). In addition to reporting novel tooth morphotypes for the Brazilian Triassic, this study emphasizes the importance of greater detail in dental anatomical descriptions, in order to refine the identification of isolated teeth. Besides, our results contribute to the record of non-dinosaurian archosauriforms of the *Hyperodapedon* Assemblage Zone (**AZ**), where the occurrence of the group is scarce when compared with the underlying *Dinodontosaurus* AZ, more expressive in the record of basal archosaurs.

GEOLOGICAL SETTING

The specimens described in this study were collected from the outcrop "Sítio Piveta", São João do Polêsine municipality (Candelária Sequence, Paraná Basin, 29º39'34.2"S; 53º25'47.4"W). This outcrop is characterized by an association of mudstones and early diagenetic carbonates, deposited in a system of shallow lakes and floodplains of ephemeral rivers (Zerfass *et al.,* 2003; Langer *et al*., 2007; Dias da Silva *et al.,* 2011). Together with the nearby (but not necessarily correlate) "Sítio Buriol" outcrop, this locality has already yielded remains of "rauisuchians", rhynchosaurs, the aetosaur *Polesinesuchus aurelioi* (Roberto-Da-Silva *et al.,* 2014), the sauropodomorph *Buriolestes schultzi* and the lagerpetid *Ixalerpeton polesinensis* (Cabreira *et al*., 2016). The occurrence of the rhyncosaur genus *Hyperodapedon* justifies the inclusion of Buriol-Piveta complex in the Carnian *Hyperodapedon* AZ (Zerfass *et al*., 2003; Dias da Silva *et al*., 2011, 2012).

MATERIAL AND METHODS

The studied material consists of five specimens in sequential numbering (UNIPAMPA 281A, 281B, 281C, 281D and 281E). Specimen 281A is worn in its apical extremity, while 281C and 281D are broken apically. Specimens 281B and 281E are well-preserved, allowing a complete analysis of their morphology. All specimens are deposited in the fossil collection of the Laboratório de Paleobiologia, Universidade Federal do Pampa (**UNIPAMPA**).

The description of specimens took into consideration the measures summarized in Figure 1. Analyses of minute structures, such as the surfaces of carinae and denticles, were carried out with the support of a stereoscopic microscope. The morphological analysis considered:

- Total size of the tooth, as measured from the basal to apical extremities (**TS**);
- Number of denticles per millimetre (serration density, **SD**);

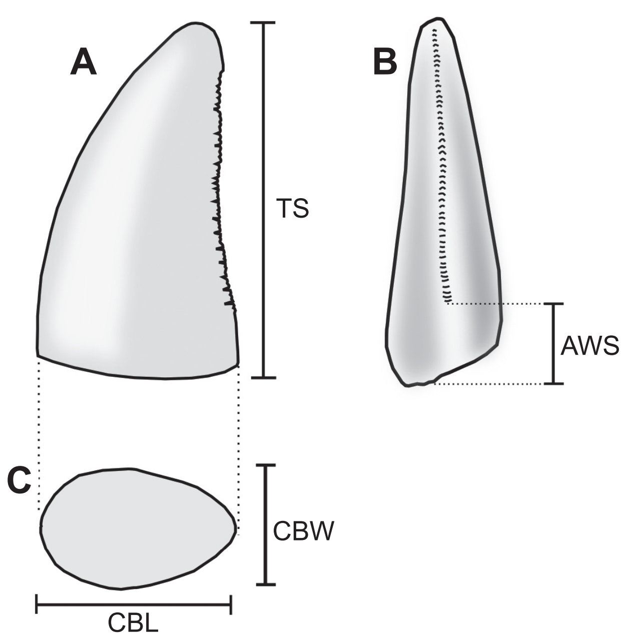

Figure 1. Schematic drawing of a ziphodont tooth in **A,** labial; **B**, distal and **C,** basal views, demonstrating the measures considered in this study. **Abbreviations: AWS**, area without denticles; **CBL**, crown base length; **CBW**, crown base width; **TS**, total size.

- Crown base length (**CBL**), equivalent to the fore-aft basal length (**FABL**) of some authors (*e.g*. Zinke, 1998; Smith & Dodson, 2003; Larson & Currie, 2013);
- Analysis of denticle shapes (square, rectangular or subquadrangular);
- Shape of the basal cross section (leaf shape or oval shape);
- Crown base width (**CBW**), roughly similar to the tooth basal width (**BW**) of some authors (*e.g*. Zinke, 1998; Smith & Dodson, 2003; Larson & Currie, 2013);
- Extension of the area without denticles, if present (both in the apical and basal portions);
- Presence or absence of enamel wrinkles;
- Symmetry;
- Size of the grooves present in denticles;
- Orientation of denticles;
- Degree of labiolingual compression (**CBL/CBW**).

The measurement of these parameters followed the methodology described Godefroit & Cuny (1997), Zinke (1998), Brusatte *et al*. (2007), Smith & Dodson (2003), Tavares (2011) and Brink *et al.* (2015).

RESULTS

The morphological analysis allowed the classification of specimens in three different morphotypes, distinct from each other in features such as the symmetry between lingual and labial faces, presence or absence of serrations and presence of grooves in the region of denticles. The terminology here used to describe teeth follows standard dental nomenclature. In accordance to the proposition of Heckert (2004), we use the terms labial, lingual, basal, and apical to describe features that are, respectively, lateral, medial, low and high on a given tooth crown. For some specimens, the lack of wear surfaces and other diagnostic features make impossible to infer if these belong to mandibular, maxillary or premaxillary dentition. Although the absolute value of measurements is meaningless for the classification of reptile teeth, the reason CBL/CBW is a good estimate of the labiolingual compression degree of specimens (Godefroit & Cuny, 1997), being here used with taxonomic purposes. The specimens here described also vary considerably in the extension of areas without denticles. According to D'Amore (2009), for theropod dinosaurs those areas probably would not enter into contact with the substrate. Curved teeth frequently have large "dead-spaces" or voids and tend to be less denticulate mesially, as shown in some of the morphotypes described herein (Table 1).

Other feature that can also be used in the analysis of isolated teeth is the presence enamel wrinkles, characterized by small undulations in the tooth crown. Enamel wrinkles are often used as a diagnostic character in the taxonomic assignment of theropod teeth, especially in the absence of quantitative traits to describe specimens (Brusatte *et al.*, 2007). Canale *et al.* (2009), for instance suggested that isolated teeth originally referred as post-Cenomanian carcharodontosaurids, most probably belonged to abelisaurids, an assumption mostly based on the presence of well-demarcated enamel wrinkles. Except for the morphotype I, the specimens we report do not

Table 1. Measurements (in mm) of specimens.

Specimen	CBW	Total size	Serration density		CBL	Area without serration	CBL/CBW
			M	D		M	
281A	12	32	-		12	-	1
281B	11	29	4	4	15	7	1,36
281C	9	-	-		10	-	1,11
281D	13	33	3	3	20	15	1,54
281E	7	25	4	4	10	15	1,43

show enamel wrinkles as well demarcated as in some other previously described Triassic archosauriform teeth.

Morphotype I
cf. Phytosauria
(Figure 2)

Represented only by specimen 281-A (Figure 2), morphotype I is characterized by a pronounced elongation, with a total length of 32 mm, rounded base measuring 12 mm (CBW), and pronounced symmetry between the lingual and labial faces. The specimen is not laterally compressed, having an oval shape in cross section along its whole apicobasal extension. The base has 12 mm in length (CBL). The presence and morphology of serrations (*e.g.* serration density and shape of denticles) are difficult to estimate due to intense tooth wear in the apical portion, which probably took place during the lifetime of the animal. The wear surfaces are located mainly in its mesial surface, having flat elliptic shape, with their main axis running longitudinally through the distal portion of the crown. This specimen shows distal enamel wrinkles.

Morphotype II
"Rauisuchia" indet.
(Figure 3)

Specimen 281-B. This specimen (Figures 3A–F) has serrated mesial and distal edges, both presenting serration density of four denticles per millimetre in all their extension. It has total length of 29 mm, labiolingual width (CBW) of 11 mm and length of crown base measuring 15 mm (CBL). The apical portion of the tooth is slightly broken but probably had a rounded morphology. The basal section of the specimen is leaf shaped, meaning that the tooth has a wider curved margin at the mesial margin and a sharp distal edge, with smooth outlines at the labial and lingual margins. The mesial

Figure 2. Tooth belonging to morphotype I. Specimen 281-A in **A**, labial; **B**, mesial; **C**, lingual; **D**, distal and **E**, basal views. Scale bar = 20 mm.

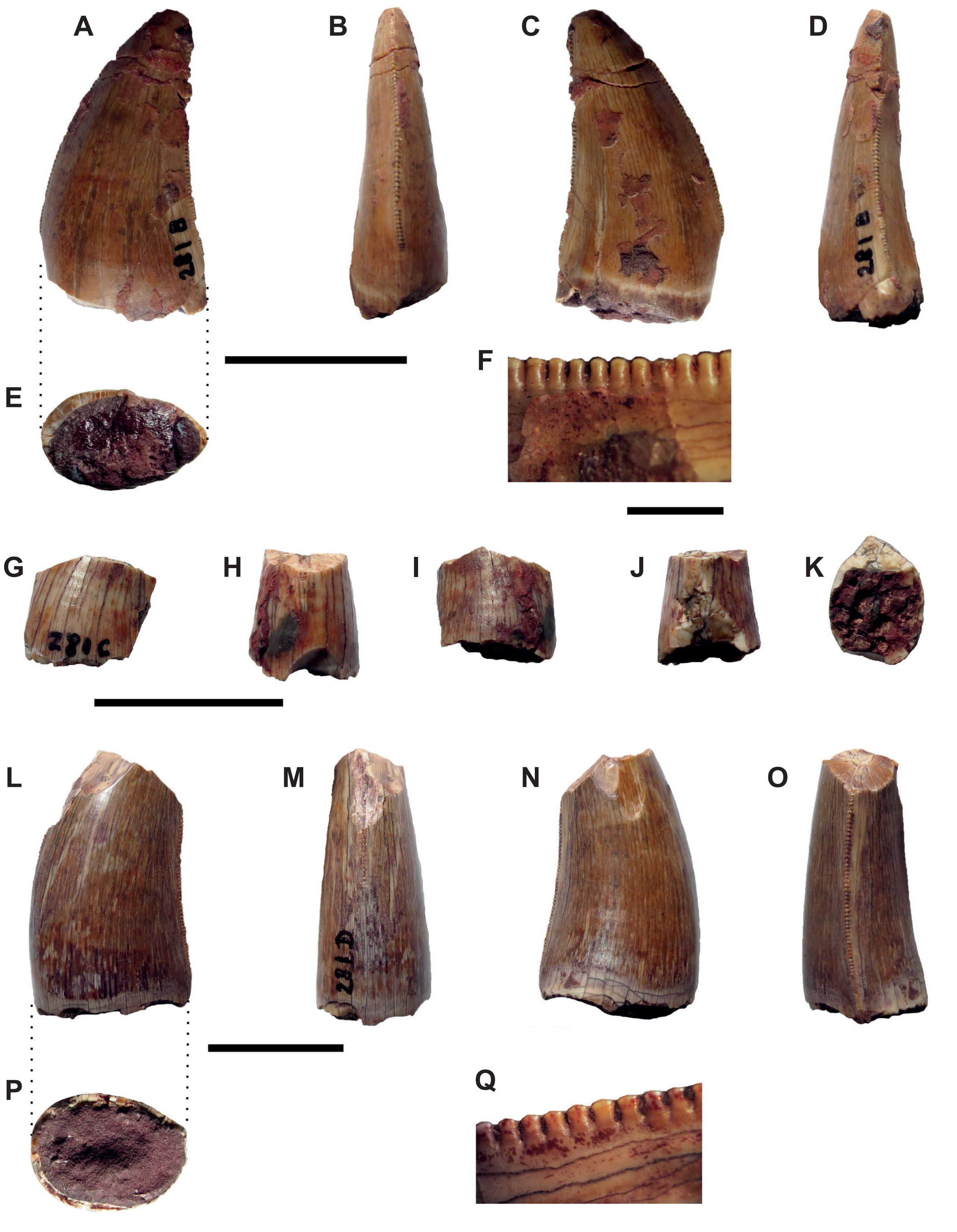

Figure 3. Teeth belonging to morphotype II. **A–F**, specimen 281-B in **A**, labial; **B**, mesial; **C**, lingual; **D**, distal and **E**, basal views. **F**, distal serrations of 281-B. **G–K**, specimen 281-C in **G**, labial; **H**, mesial; **I**, lingual; **J**, distal and **K**, basal views. **L–P**, specimen 281-D in **L**, labial; **M**, mesial; **N**, lingual; **O**, distal and **P**, basal views. **Q**, distal serrations of 281-D. A–E, G–P = 20 mm; F, Q = 2 mm.

denticles decrease in size in basal direction, while the distal denticles are well developed throughout the specimen. The base is asymmetric, with a flat lingual face and a round labial one (CBL/CBW = 1.36). The extension in which the denticles are absent corresponds to 7 mm of the total length. This specimen shows demarcated enamel wrinkles on both lingual and labial surfaces.

Specimen 281-C. Specimen 281-C (Figures 3G–K) presents a labiolingual width of 9 mm and length of basal cross section measuring 10 mm. Most of its distal portion is broken, and the mesial and distal carinae are fragmented. The absence of the apical extremity hinders the proper evaluation of features such as the serration density. There are no serrations in the preserved basal part of the tooth, but it is probable that they were present in the broken apical extension. CBL / CBW = 1.53. This specimen shows well-demarcated enamel wrinkles distally.

Specimen 281-D. Although also broken, this specimen (Figures 3L–Q) has better preservation when compared to specimen 281-C, since its apical extremity is only partially fragmented. Specimen 281-D has a total length of 33 mm, with the lingual face slightly flattened in relation to labial one. The crown base is 20 mm in length (CBL), while the labiolingual width measures 13 mm (CBW). Both anterior and posterior carinae have about 3 denticles per millimetre (serration density), while the area without denticles equals to 15 mm. CBL / CBW = 1.54. The size of denticles decreases in basal direction on the mesial margin of the tooth. On the distal margin, however, the denticles remain subequal in size throughout the whole extension of the carina. This specimen does not show well-demarcated enamel wrinkles.

Morphotype III
"Rauisuchia" indet.
(Figure 4)

Specimen 281-E. The last specimen (Figure 4) presents total size of 25 mm, crown base length of 10 mm (CBL) and labiolingual width corresponding to 7 mm. This specimen shows greater inclination of the distal carina when compared to what is seem in morphotype II. In morphotype II the distal and mesial margins are recurved posteriorly starting on the basal region, so that the tooth narrows in apical direction. In morphotype III, the mesial and distal margins are almost parallel to each other at the base, and the tooth is posteriorly curved only in the apical portion. Also, morphotype III shows a more rounded cross-section than what is seem in morphotype II. The anterior and posterior carinae have about four denticles per millimetre (serration density), and 15 mm of the distal face lack serrations. CBL/CBW = 1.43. This specimen does not present pronounced inequality in denticle size throughout the whole extension of both mesial and distal carinae.

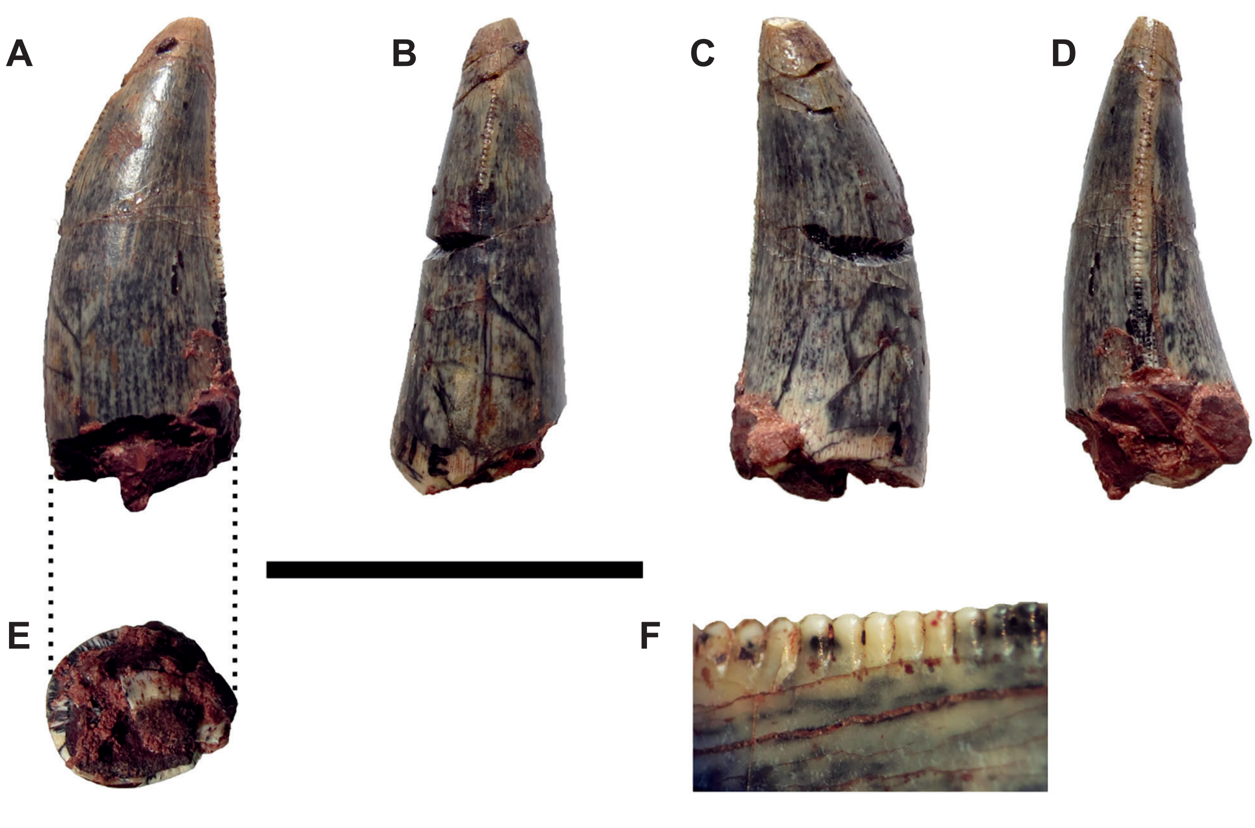

Figure 4. Tooth belonging to morphotype III. Specimen 281-E in **A**, labial; **B**, mesial; **C**, lingual; **D**, distal and **E**, basal views. **F**, distal serrations of 281-E. A–E = 20 mm; F = 1 mm.

DISCUSSION

Tooth morphology is intimately related to feeding habits, and the ziphodont pattern, characterized by labiolingually narrow crown, distal curvature and typically serrated carinae (as observed in the teeth described here), is consistent with a carnivorous diet (*e.g.* Hendrickx *et al.,* 2015). Ray & Chinsamy (2002) emphasize that ziphodont teeth collected in Upper Triassic rocks should be regarded with caution, because the conservative morphology observed in the dentition of Triassic carnivores difficult the taxonomic attribution of isolated elements.

During the Carnian, three main groups of archosauriforms presented ziphodont dentition: phytosaurs, "rauisuchids" and basal dinosaurs (Renesto *et al*., 2003). In addition, other carnian taxa such as Gracilisuchidae and Ornitosuchidae also had ziphodont dentition. Tooth 281-A (morphotype I) presents a consistent morphology with Phytosauria, and is here classified as cf. Phytosauria. This attribution is mainly grounded on its rounded base, absence of labiolingual compression and the typical wear pattern. The presence and morphology of serrations are difficult to access due to intense wear, particularly concentred in the apical portion of the tooth. A similar wear pattern was reported by Hungerbühler (2000) for phytosaur lower jaw teeth. This same author reports evidences that the serration density varies strongly according to the tooth position. For example, phytosaur middle teeth can be distinguished by their circular cross-section and unserrated carinae.

Phytosaur dentition resembles sphenosuchids and crocodylomorphs, mostly concentrated in the Late Triassic. In contrast to the teeth presented here, crocodyliforms usually have well-marked grooves along the carinae and serrated edges, configuring a false ziphodont tooth type (Tavares, 2011). In addition, the classification must take into consideration the most representative fauna**,** and at least one confirmed specimen of phytosaur has been recovered in the Upper Triassic of Rio Grande do Sul (Kischlat & Lucas, 2003), whereas the Brazilian Triassic record still lacks crocodyliforms. The phytosaur specimen reported by Kischlat & Lucas (2003) was collected from the Norian *Riograndia* AZ, making our (albeit tentative) taxonomic attribution of morphotype I a relevant contribution to the record of this group in South America. According to Hungerbühler (2000), the wear pattern described here to morphotype I is a typical of phytosaur premaxillary teeth. A single adult phytosaur can often possess heterodont dentition that encompasses several tooth morphotypes (Godefroit & Cuny, 1997; Hungerbühler, 2000). Heckert (2004) described a tooth-bearing fragment from the anterior portion of a premaxilla or dentary of a mid-sized phytosaur. The sole tooth preserved in this specimen is a conical, slightly recurved, unerupted replacement tooth with approximately 11 mm high. This same author attributed a number of isolated teeth to Phytosauria based on their recurved, moderately tall morphology, circular in occlusal view and lacking serrations**.** The presence of phytosaurs in Brazilian Carnian may have deep paleoecological and biostratigraphic implications. We, thus, emphasize that, in the absence of more representative specimens, the identification of UNIPAMPA 281-A as a phytosaur is highly tentative. This identification may be tested by the recovery of additional specimens showing the peculiar morphology described here.

The morphology of morphotypes II and III is congruent with their attribution to "Rauisuchia", and they are here classified as "Rauisuchia" indet**.** Brusatte *et al*. (2010) use the capitalized taxon name Rauisuchia to refer to the clade comprised by all traditional "rauisuchian" taxa (*e.g. Prestosuchus, Saurosuchus, Decuriasuchus*). However, only some analyses find a monophyletic Rauisuchia, and many authors (*e.g*. Weinbaum & Hungerbühler, 2007; Gauthier *et al*., 2011, Nesbitt, 2011) still use the term "rauisuchians" to refer to these animals in a paraphyletic sense. As described, these specimens are labiolingually compressed and present serration density between three and four denticles per millimetre. Leaf-shaped basal cross sections, such as is observed in morphotype II, are common among "rauisuchians" (*e.g*. Henderson & Weishampel, 2002; Nesbitt *et al*., 2013). The literature is still uninformative with respect to the range of variation in serration density within "Rauisuchia", what makes difficult a more refined taxonomic attribution of isolated dental elements. Among Ornitosuchidae, *Riojasuchus tenuisceps* presents the premaxillary teeth slightly laterally compressed and curved posteriorly. However, no serrations can be recognized on any of the preserved teeth, probably due to over preparation of specimens (Baczko & Desojo, 2016). Lecuona (2013) reanalyzed specimens attributed to *Gracilisuchus stipanicicorum* from the Middle Triassic of Argentina. Better preserved materials present conical and posteriorly recurved teeth with oval to subcircular cross sections. Teeth of this species have semicircular mesial and slightly sharpened distal surfaces (albeit not forming distinct carinae). These specimens are somewhat similar to what is observed in our morphotype I, albeit being considerably smaller.

Teeth belonging to morphotypes II and III have a congruent morphology with specimens previously illustrated in other studies, such as SAM-PK-K1497, described by Ray & Chinsamy (2002) as a possible "rauisuchian". The redescription of *Rauisuchus tiradentes* holotype (also belonging to the Carnian *Hyperodapedon* AZ) by Lautenschlager & Rauhut (2014) reported serration density between four and five denticles per millimetre in the whole tooth. In addition, the teeth of this species are labiolingually compressed and distally curved. Benton (1986) described *Teratosaurus* as a potential "rauisuchid", presenting teeth with three denticles per millimetre and a length of basal cross section of 23 mm.

Carnian carnivorous dinosaurs, such as *Staurikosaurus*, *Eoraptor* and *Herrerasaurus*, present very distinct tooth morphology from what is observed in the morphotypes reported here. In *Staurikosaurus*, the serrations are restricted to distal carina and spaced around two denticles per millimetre (Bittencourt & Kellner, 2009). *Eoraptor* also has lateral teeth in which only the distal edges are serrated, while the anterior ones are slick (Sereno *et al*., 2013). *Herrerasaurus* teeth have sharp posterior margins with serration density of about 6 denticles per millimetre (Sereno & Novas, 1994). These morphologies are quite different from that observed in our morphotypes II and III, which present between three and four denticles per millimetre and have serrations on both mesial and distal margins.

Occasionally, Triassic theropods may also present higher serration density, with up to eight denticles per mm, as in coelophysoids (Upper Triassic–Lower Jurassic) (Rinehart *et al*. 2007). In some other cases, the attribution of isolated teeth to theropods is only based on faunal associations (*e.g.* Ray & Chinsamy, 2002).

The difficulty of attaining unequivocal classifications of isolated archosauriform teeth draws attention to the need of a comprehensive reappraisal of the taxonomic significance of anatomical traits. Achieving this, we would have a clearer picture of the diversity and evolution of Triassic faunas.

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