CURRENT STATE OF KNOWLEDGE ON XENACANTHIFORMES (CHONDRICHTHYES, ELASMOBRANCHII) FROM THE TAQUARAL MEMBER, IRATI FORMATION, PERMIAN OF THE PARANÁ BASIN

Artur Chahud[1]
[1]Department of Genetics and Evolutionary Biology, Institute of Biosciences, University of São Paulo, Rua do Matão, 277, Butantã, CEP 05508-090, São Paulo, SP, Brazil.

E-mail: arturchahud@yahoo.com,
ORCID: https://orcid.org/0000-0001-7690-3132

Abstract

The Irati Formation, a Permian geological formation in the Paraná Basin, stands out for its remarkable geological and paleontological characteristics. Two members are currently recognized: the lower Taquaral Member and the upper Assistência Member. The lower portion, corresponding to the Taquaral Member, is predominantly composed of shales facies. At the base of this member, conglomeratic sandstones occur, characterized by a high concentration of vertebrate fossils. The sandy facies of the Taquaral Member is particularly well known for its abundance of Chondrichthyes remains. Xenacanthiformes constitute an extinct order of Chondrichthyes, with a fossil record ranging from the Carboniferous to the Late Triassic. Two families are currently recognized: Diplodoselachidae and Xenacanthidae, both present in the Irati Formation and represented by endemic genera and species. Diplodoselachidae is the most frequent family in the Taquaral Member, represented mainly by isolated teeth of *Taquaralodus albuquerquei*. This species, endemic to the Paraná and Parnaíba basins, is characterized by a well-developed principal cusp occupying a significant portion of the central and lateral regions of the tooth. Small teeth attributed to Xenacanthidae have also been recovered from the sandy facies of the Taquaral Member. Two distinct forms were identified: one belonging to the genus *Xenacanthus* and another assigned to an indeterminate Xenacanthidae.

Keywords: Diplodoselachidae, Xenacanthidae, *Xenacanthus*, Kungurian, endemism.

ESTADO ATUAL DO CONHECIMENTO SOBRE XENACANTHIFORMES (CHONDRICHTHYES, ELASMOBRANCHII) DO MEMBRO TAQUARAL, FORMAÇÃO IRATI, PERMIANO DA BACIA DO PARANÁ

Resumo

A Formação Irati, uma formação geológica permiana na Bacia do Paraná, destaca-se por suas características geológicas e paleontológicas. Dois membros são atualmente reconhecidos: o Membro Taquaral inferior e o Membro Assistência superior. A porção inferior, correspondente ao Membro Taquaral, é composta predominantemente por folhelhos. Na base deste membro, ocorrem arenitos conglomeráticos, caracterizados por uma alta concentração de fósseis de vertebrados. A fácies arenosa do Membro Taquaral é particularmente conhecida por sua abundância de restos de Chondrichthyes. Os Xenacanthiformes constituem uma ordem extinta de Chondrichthyes, com registro fóssil que abrange do Carbonífero ao Triássico Superior. Duas famílias são atualmente reconhecidas: Diplodoselachidae e Xenacanthidae, ambas presentes na Formação Irati e representadas por gêneros e espécies endêmicas. A família Diplodoselachidae é a mais

frequente no Membro Taquaral, representada principalmente por dentes isolados de *Taquaralodus albuquerquei*. Esta espécie, endêmica das bacias do Paraná e do Parnaíba, caracteriza-se por uma cúspide principal bem desenvolvida, que ocupa uma porção significativa das regiões central e lateral do dente. Pequenos dentes atribuídos a Xenacanthidae também foram recuperados das fácies arenosas do Membro Taquaral. Duas formas distintas foram identificadas: uma pertencente ao gênero *Xenacanthus* e outra a um Xenacanthidae indeterminado.

Palavras-chave: Diplodoselachidae, Xenacanthidae, Xenacanthus, Kunguriano, endemismo.

INTRODUCTION

During the Paleozoic and early Mesozoic, rivers and coastal regions were inhabited by several species of Chondrichthyes, among which xenacanth sharks were particularly prominent. The first fossils of this group were discovered in Europe during the 1830s, primarily in England and Germany, and later, in the 1850s, in the United States.

Xenacanth sharks were medium-sized fishes (approximately 3.5 m in length), with slender, elongated bodies, and can be readily distinguished from other elasmobranch groups (GINTER et al., 2010). Most species inhabited freshwater rivers and lakes; however, some forms, particularly during the Early Carboniferous, preferred environments with higher salinity, such as estuaries and coastal zones (BAIRD, 1978; PARRISH, 1978; JANVIER, 1996; JOHNSON, 2005a,b; GINTER et al., 2010). It is not uncommon to find teeth and spines of freshwater species reworked into high-energy coastal marine deposits or deltaic sediments (MOY-THOMAS & MILES, 1971; LONG, 1995; NELSON, 2006).

The Irati Formation is one of the most widely recognized geological units of the Paraná Basin due to its abundant and diverse fossil record. It is currently subdivided into two members: Taquaral and Assistência (BARBOSA & GOMES, 1958; MILANI et al., 2007; HOLZ et al., 2010). The Taquaral Member comprises two main facies: (i) a sandy facies, predominantly restricted to the base of the unit (CHAHUD & PETRI, 2010a; 2016), and (ii) a silty shale facies (CHAHUD & PETRI, 2013a, 2013b).

Radiometric dating performed by SANTOS et al. (2006) and ROCHA-CAMPOS et al. (2007) indicates a Kungurian age for the Irati Formation (279–276 Ma), based on analyses of rocks from the Assistência Member.

The Taquaral Member consists of two facies: an upper shale facies (CHAHUD & PETRI, 2013a, 2013b; CHAHUD, 2017), and a lower facies composed of poorly sorted sediments rich in ichthyoliths (CHAHUD, 2018; CHAHUD & PETRI, 2008a, 2008b) and records of primitive tetrapods (CHAHUD & PETRI, 2010a; 2010b; 2012b).

The Taquaral Member has been the focus of several paleontological and sedimentological studies, including facies analyses, vertebrates, arthropods, ichnofossils, palynology, and taphonomy (LAGES, 2004; HOLZ et al., 2010; CHAHUD et al., 2010a; CHAHUD & PETRI, 2015).

The Paleozoic record of the Paraná Basin includes a rich diversity of fossil teeth from various groups of Chondrichthyes, including Eugeneodontiformes (RICHTER, 2007), Ctenacanthiformes (SILVA SANTOS, 1947; BARCELLOS, 1975; WÜRDIG-MACIEL, 1975; CHAHUD & PETRI, 2012a; 2014; PAULIV et al., 2012; 2014), Petalodontiformes

(TOLEDO, 2001; CHAHUD, 2023), Orodontiformes (CHAHUD et al., 2010b), and Xenacanthiformes (WÜRDIG-MACIEL, 1975; RAGONHA, 1984; RICHTER, 2005; CHAHUD & PETRI, 2009a; 2010c; PAULIV et al., 2014; 2017).

The base of the Taquaral Member contains a high concentration of Chondrichthyes teeth belonging to species endemic to the Paraná and Parnaíba basins (CHAHUD & PETRI, 2016). Other groups are also represented by spines and isolated teeth (CHAHUD, 2011).

Two families of Xenacanthiformes are currently recognized: Diplodoselachidae and Xenacanthidae (HAMPE, 2003; GINTER et al. 2010), both recorded in the Paraná Basin and represented by endemic genera and species (RAGONHA, 1978; 1984; RICHTER, 2005).

The earliest reference to Xenacanthiformes in the Paraná Basin is *Taquaralodus albuquerquei*, initially identified as *Xenacanthus albuquerquei*, also recorded in the Pedra do Fogo Formation (SILVA SANTOS, 1946; CHAHUD & PETRI, 2008a; 2010c). This species, endemic to the Paleozoic basins of Brazil, was later assigned to Diplodoselachidae (CHAHUD & PETRI, 2010c).

However, this is not the only Xenacanthiformes species present at the base of the Taquaral Member: specimens attributed to Xenacanthidae had already been identified by

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CHAHUD & PETRI (2009a). The purpose of this contribution is to reintroduce those specimens described by CHAHUD & PETRI (2009a; 2010c) e CHAHUD et al. (2012), complement them with additional indeterminate materials from the base of the Taquaral Member.

MATERIAL AND METHODS

The fossil specimens were collected at two localities in the region of the municipality of Rio Claro (Figure 1): Santa Maria Homestead (CHAHUD et al., 2010a; 2010b; CHAHUD & PETRI, 2008a; 2008b; 2009b) and Ponte Nova Farm (CHAHUD, 2011; 2021; CHAHUD et al., 2012). The material is preserved as bioclasts embedded in light-gray to gray conglomeratic sandstone (Figure 2), characterized by upward-fining (granodecrescent) sequences, cross-lamination, and abundant angular to subrounded granules, along with rare quartz and chert pebbles. These clasts are dispersed in a sandy matrix of very fine to coarse grain size, with cementation that firmly integrates the bioclasts into the sedimentary framework.

The specimens were subjected to mechanical cleaning and, when feasible, matrix removal. All material is properly curated and housed in the Vertebrate Collection of the Laboratory of Systematic Paleontology (LPS), Institute of Geosciences, University of São Paulo (IGc-USP)



Figure 1. Outcrop belt of the Irati Formation (adapted from HACHIRO, 1996; CALÇA & FAIRCHILD, 2012).

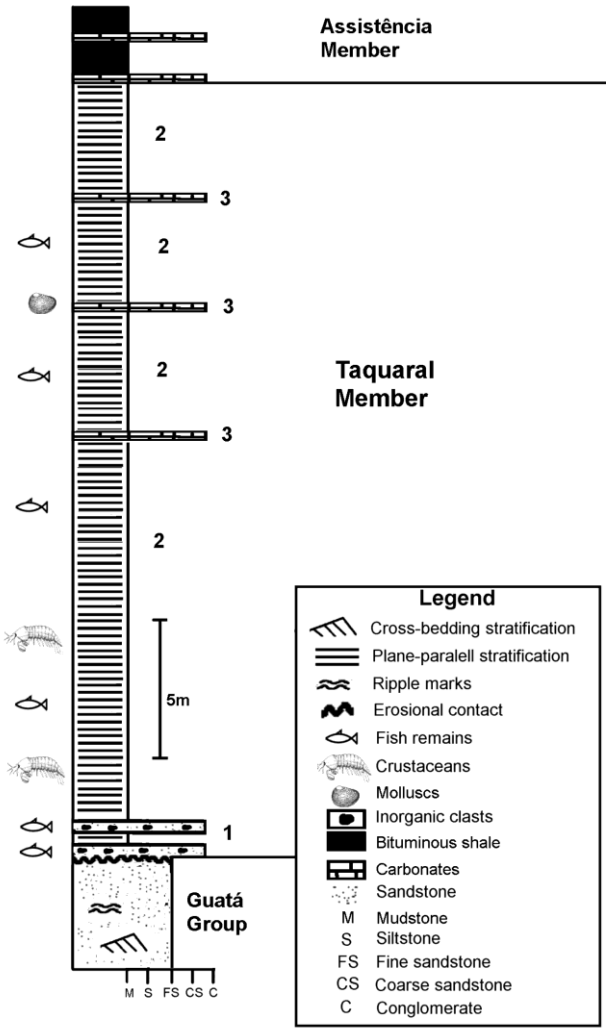

Figure 2. Sketched columnar section of the Taquaral Member, Irati Formation, as exposed in the states of São Paulo and Paraná. 1) Sandy facies; 2) Silty-shale facies; 3) Carbonate layers.

SYSTEMATIC PALEONTOLOGY

Subclass ELASMOBRANCHII Bonaparte, 1838
Order XENACANTHIFORMES Berg, 1940
Family DIPLODOSELACHIDAE Dick, 1981
Genus *Taquaralodus* Chahud & Petri, 2010
Taquaralodus albuquerquei (Silva Santos, 1946)

Synonymies
Pleuracanthus albuquerquei Silva Santos, 1946
Taquaranthus albuquerquei Ragonha, 1978 (nomen nudum)
Xenacanthus albuquerquei Richter, 1985

Geographic and Stratigraphic Distribution: Pedra do Fogo Formation (Permian), State of Maranhão; Base of the Taquaral Member, Irati Formation (Permian), State of São Paulo, Brazil.

Holotype: DGM–DNPM 442-P, incomplete tooth from the Pedra do Fogo Formation, approximately 6 km south of Pastos Bons, Maranhão, Brazil.

Etymology of the genus: "Tooth from the Taquaral," referring to the Taquaral Member, the stratigraphic unit in which the specimens are most abundant.

Diagnosis (Revised from Silva Santos, 1946; Ragonha, 1978): Tooth with a tricuspid crown displaying two unequal main lateral cusps and a very reduced or absent intermediate cusp. Cusps lie approximately in the same plane as the labial margin of the base, inclined toward the lingual face. The primary cusp occupies about half the labial margin and rises perpendicularly from the base; the secondary cusp is positioned laterally; the intermediate cusp, when present, is smaller than the secondary and obliquely situated between the two. Cusps have an oval cross-section, lack serrations, and may bear irregular ridges. The base may be elongated or circular in outline, with the lingual face directed downward and a small elliptical apical button in the upper region. The labial face bears an elongated basal tubercle situated immediately below the main cusp. The lower surface of the base is flat.

Material: Isolated teeth in various states of preservation; GP/2T-210 (Fig. 88A–88D), GP/2T-211 (Fig. 84–86A–D), GP/2T-212 (Fig. 86E–H), GP/2T-213 (Fig. 88E–88F), GP/2T-214 (Fig. 89), GP/2E-6580 (Fig. 87G–87L), GP/2E-6581 (Fig. 87A–87F).

Locality: Santa Maria Homestead outcrop (GP/2T-210, GP/2T-211, GP/2T-212, GP/2T-213, GP/2T-214), municipality of Rio Claro, and Ponte Nova Farm outcrop (GP/2E-6580 and GP/2E-6581), municipality of Ipeúna.

Geographic and Stratigraphic Distribution: Same as the genus.

Specific Diagnosis: Monospecific genus.

Description: Specimens of Taquaralodus may exhibit three, two, or a single cusp. In specimen GP/2T-211, breakage preserved only the lower portions of the cusps. The crown displays two divergent main cusps and one intermediate cusp, arranged along the labial margin of the base. In cross-section, the larger cusps are oval, and the smaller one is circular.

Based on the preserved cusp portions, the size differentiation among the cusps is evident. The primary cusp occupies more than half of the labial margin and appears to rise vertically. The secondary cusp measures 1/3 the maximum diameter of the main cusp

and is located laterally. The intermediate cusp, positioned labially to the others, has a diameter of 1/9 that of the primary cusp (Figs. 3, 4A–B; 5A–D).

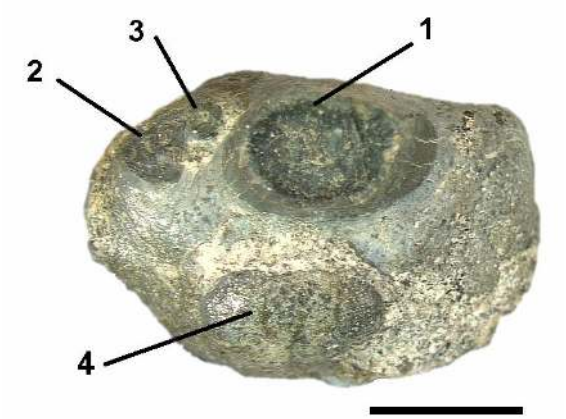

Figure 3. Tooth GP/2T-211 of *Taquaralodus* showing morphological features; 1) Primary cusp; 2) Secondary cusp; 3) Intermediate cusp; 4) Apical button. Scale: 4 mm.

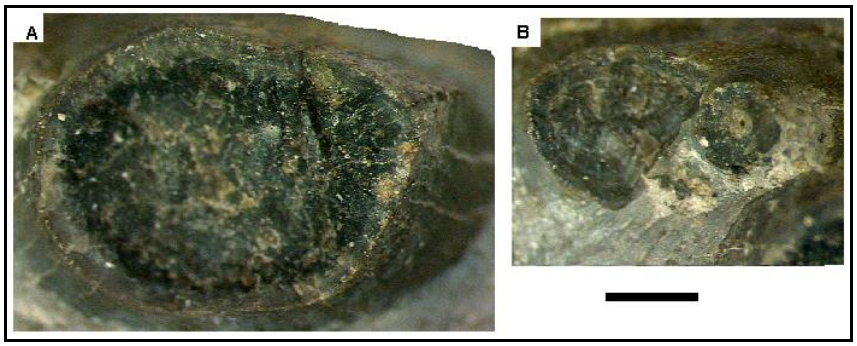

Figure 4. Details of the cusps of the tricuspid specimen of *Taquaralodus albuquerquei* (GP/2T-211). A) Larger primary cusp; B) Lateral secondary cusp and smaller intermediate cusp. Scale: 1 mm.

The second tricuspid specimen, GP/2E-6581, retained part of the principal cusp and both smaller cusps. As in GP/2T-211, the two larger cusps are aligned along the labial margin; the main cusp occupies more than half of this margin, and a small cusp occurs between them. The secondary cusp is inclined toward the lateral side of the tooth and is slightly larger than 1/3 the diameter of the primary cusp; the intermediate cusp has 1/5 the diameter of the main cusp.

In the preserved portion of the principal cusp in GP/2T-211 and GP/2E-6581, the labial face is smooth whereas the lingual face displays fine ridges, similar to those described by SILVA SANTOS (1946) and RAGONHA (1978). The ridges are parallel and originate at the base of the cusp, but vary irregularly in shape, length, and orientation. Ridge spacing is also variable.

The base is elongated and irregular, with a slightly concave lower surface. The labial border exhibits a protrusion, the basal tubercle, while the lingual region shows a downward extension. On the lingual edge of the upper part there is an elliptical prominence, the apical button, separated from the cusps.

The bicuspid specimen (GP/2T-212) is similar to the tricuspid forms but lacks the intermediate cusp (Figs. 5E–5F). The crown bears two cusps of different sizes arranged in the same plane along the labial margin. As in previous specimens, the smaller cusp is slightly more than 1/3 the diameter of the main one.

Specimen GP/2E-6580 represents a unicuspid tooth with only the primary cusp preserved, although small protrusions occur on the labial border at the position where the secondary cusp would have been (Fig. 6G–6H).

The cusp occupies the central-lateral region of the labial border, with very thin ridges that extend parallel to the base and become irregular as they move towards the top of the cusp, both on the labial and lingual surfaces, although on the labial surface they are almost imperceptible.

The base is elongated with a lateral extension to one of the sides, and almost flat, with the lower surface slightly concave near the basal tubercle. The apical bud region preserved the elongated apical bud, and foramina occur on the lower and upper surfaces of the base.

Specimen GP/2T-210 also represents a unicuspid tooth (Fig. 7A–7D). Fine irregular ridges are present on the entire cusp surface, both lingual and labial. The base is subcircular, with a lateral extension relative to the crown. As in GP/2T-211, the lower labial border bears an elongated basal tubercle, while on the lower lingual face there is a downward projection. The upper part displays a small elliptical apical button. Small foramina occur on both the upper and lower surfaces of the base.

The cusp of specimen GP/2T-210 occupies the central region of the labial border, with very thin ridges that extend parallel to the base and become irregular as they move towards the top of the cusp, both on the labial and lingual surfaces. The base is circular and almost flat with the lower surface slightly concave near the basal tubercle. The apical bud region is broken, but still preserves fragments of the apical bud. Foramina occur on the inferior and superior surfaces of the base.

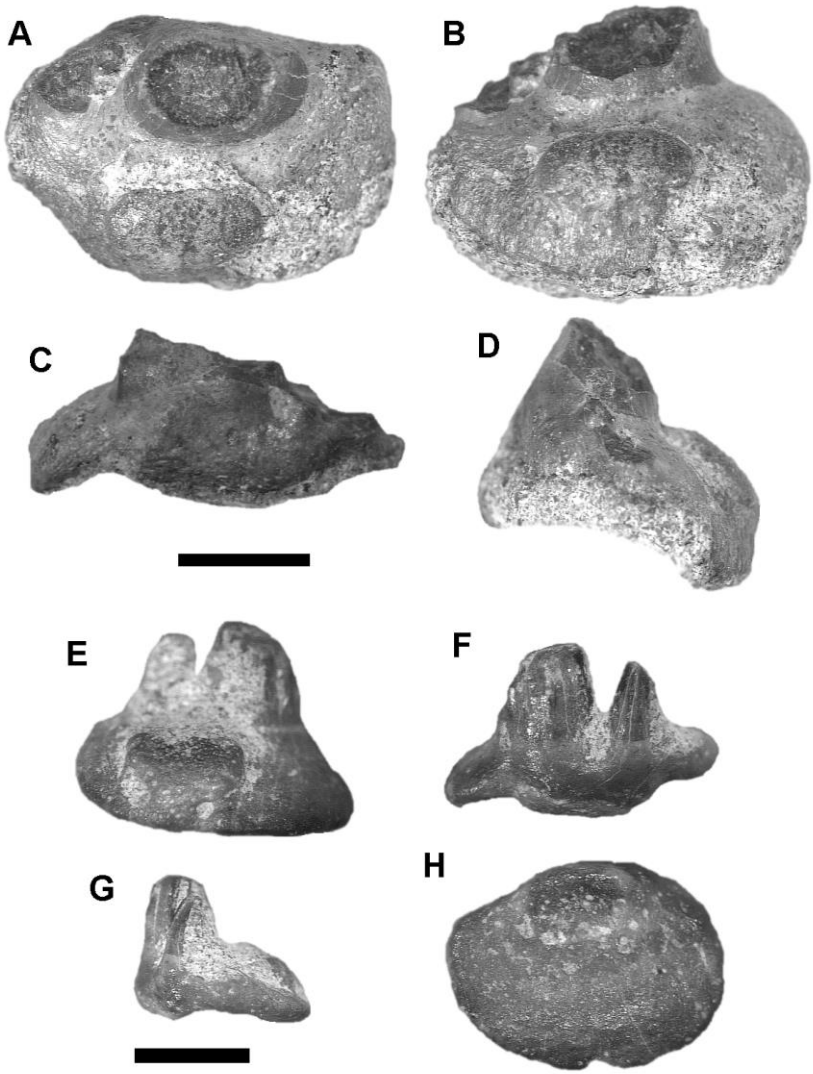

Figure 5. *Taquaralodus albuquerquei* teeth from the Santa Maria Homestead outcrop. Tricuspid tooth (GP/2T-211), A) Dorsal view; B) Lingual view; C) Labial view; D) Lateral view. Scale: 4 mm. Bicuspid tooth (GP/2T-212), E) Lingual view; F) Labial view; G) Lateral view; H) Basal view. Scale: 2 mm.

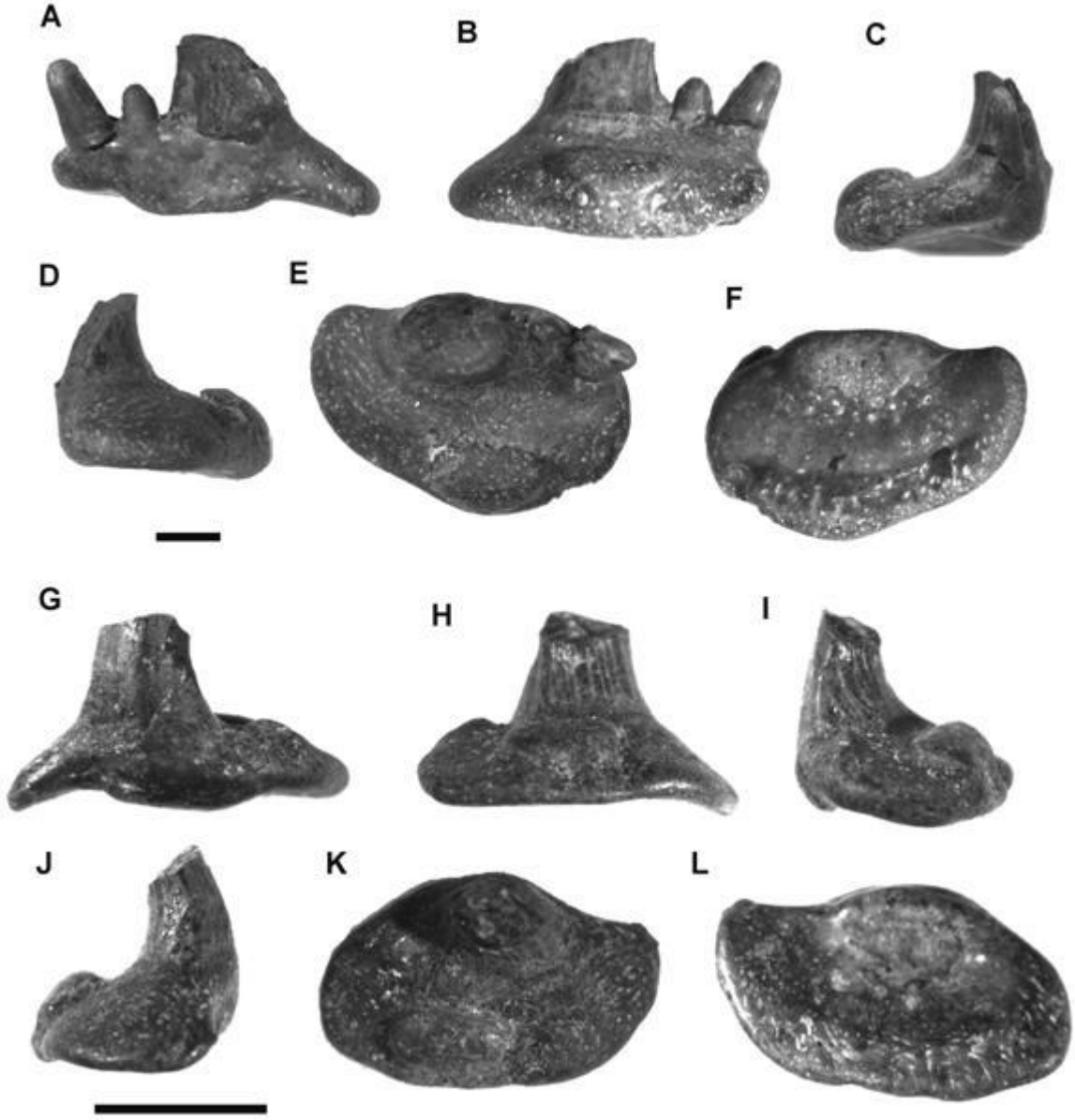

Figure 6. *Taquaralodus albuquerquei* teeth from the Ponte Nova Farm outcrop. GP/2E-6581: A) Labial view; B) Lingual view; C–D) Lateral views; E) Occlusal view; F) Basal view. Scale: 2 mm. GP/2E-6580: G) Labial view; H) Lingual view; I–J) Lateral views; K) Occlusal view; L) Basal view. Scale: 5 mm.

The maximum length of the base of the tricuspid specimen GP/2T-211 is 10.3 mm, and the width is 7.1 mm. The apical button is 4.2 mm long and 2.4 mm wide. In cross-section, the primary cusp is oval (4.7 × 3.1 mm), the secondary cusp measures 1.6 × 1.0 mm, and the intermediate cusp 0.5 × 0.4 mm.

For specimen GP/2E-6580, the base is 10.0 mm long and 6.1 mm wide. The apical button measures 3.7 × 2.5 mm. In cross-section, the primary cusp is 3.8 × 2.3 mm, the secondary 1.5 × 1.0 mm, and the intermediate 0.8 × 0.4 mm.

For the bicuspid specimen GP/2T-212, the base length is 4.4 mm, the width 3.2 mm. The larger cusp (incomplete) has 1.6 mm height and 1.9 mm diameter. The smaller cusp has approximately 0.9 mm diameter and 1.0 mm height. The apical button has a maximum length of 1 mm.

The unicuspid specimen GP/2T-210 is the second largest, with a base length of 7.7 mm and width of 7.4 mm. The cusp measures 3.7 mm maximum diameter and 2.8 mm minimum.

The unicuspid specimen GP/2E-6580 (Fig. 6G–L) has a base length of 9.5 mm and width of 5.5 mm. The cusp has 3 mm maximum diameter and 2.8 mm minimum.

Other incomplete fossils helped in the description of the species. In specimen GP/2T-213 (Fig. 7E–F), no ridges or fine longitudinal striations occur on the base. The basal tubercle is flattened and elongated (Fig. 7E), and the apical button is reduced compared to other Xenacanthiformes, and has a trapezoidal shape (Fig. 7F). This incomplete specimen has an elongated base, similar to those of the tricuspid (GP/2T-211) and bicuspid (GP/2T-212) specimens, and preserves part of the secondary cusp. Foramina occur in the lingual region in direct contact with the apical button.

Specimen GP/2E-6314 (Fig. 8A–F) displays morphological features resembling a unicuspid form, such as a subcircular base and a centrally positioned cusp. However, it is uncertain if it possessed a single cusp, because one side of the crown is broken. The basal tubercle (Fig. 8D) is more prominent than in the multicuspid specimens, and the apical button is hexagonal, whereas other specimens have trapezoidal or elliptical shapes.

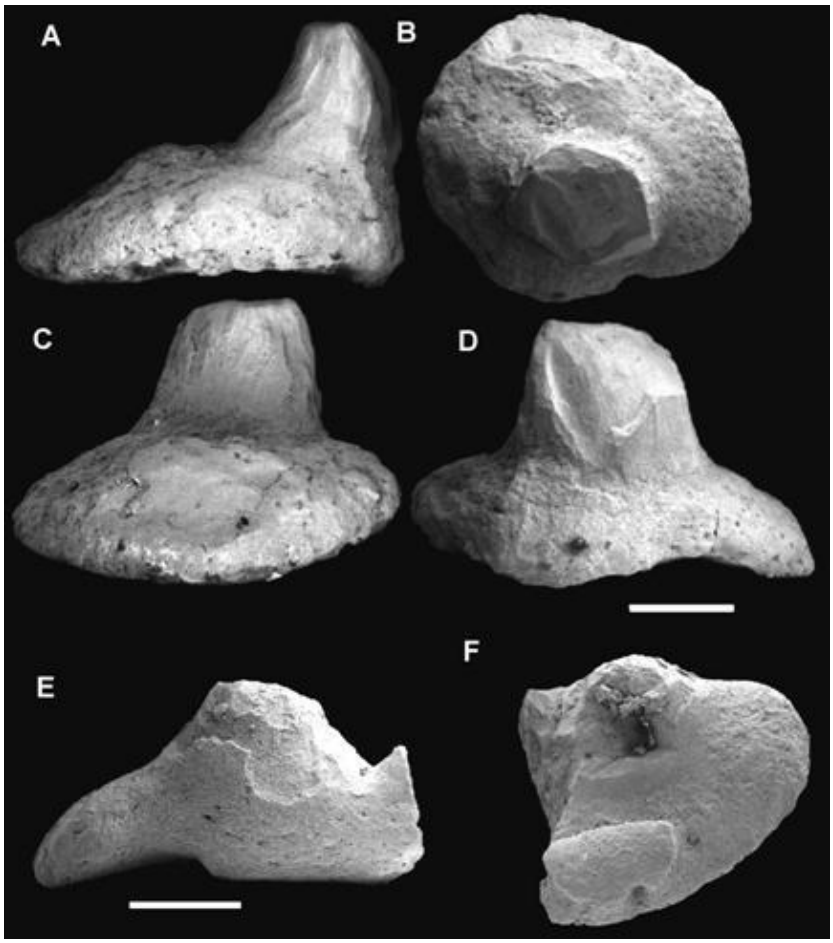

Figure 7. SEM photographic montage of *Taquaralodus albuquerquei*. Unicuspid specimen GP/2T-210: A) Lateral view; B) Dorsal view; C) Lingual view; D) Labial view. Specimen GP/2T-213: E) Incomplete labial face showing fragment of the larger cusp; F) Occlusal view with apical button highlighted. Scale: 2 mm.

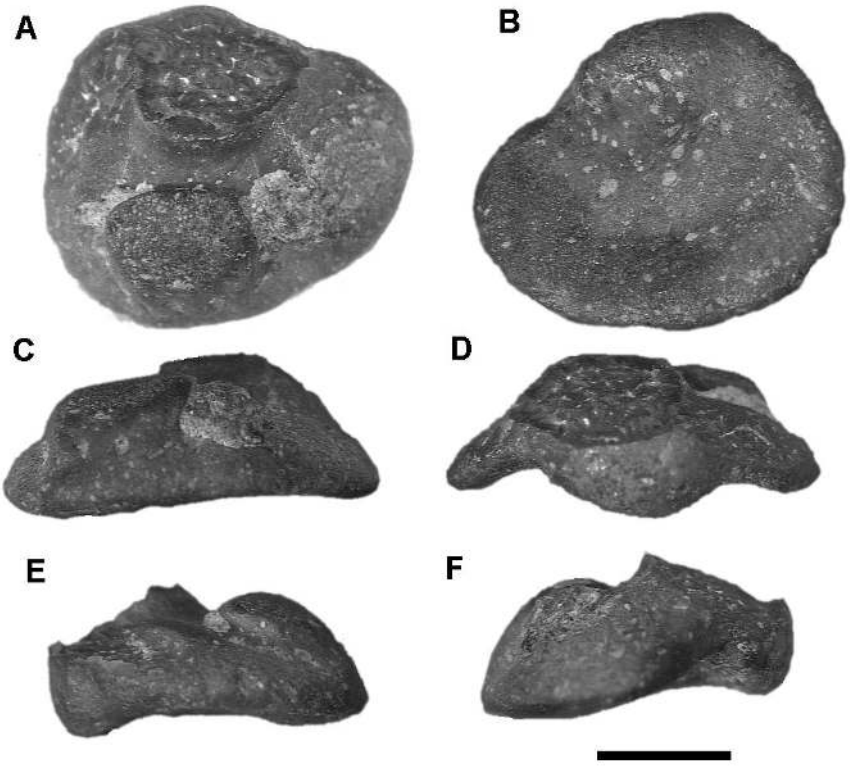

Figure 8. *Taquaralodus albuquerquei* specimen GP/2E-6314. A) Dorsal view; B) Basal view; C) Lingual–lateral view; D) Labial view; E–F) Lateral views. Scale: 2 mm.

Discussion: In general, xenacanthiform teeth exhibit the following characteristics: an elongated or circular base projecting lingually; when more than one cusp is present, two are main lateral cusps situated along the labial border, with slight curvature toward the lingual face; an intermediate cusp may occur between the lateral cusps, always smaller; an apical button is present on the lingual margin of the base; a basal tubercle occurs on the labial margin of the base (DAVIS, 1892; RAGONHA, 1984; LONG, 1995; JANVIER, 1996; HAMPE, 2003; GINTER et al., 2010).

Dentitions identical to those described herein were previously reported by SILVA SANTOS (1946) from the Pedra do Fogo Formation in Maranhão, originally assigned to "*Pleuracanthus albuquerquei*." RAGONHA (1978) observed that the very large lateral cusp, evident in all bicuspid and tricuspid specimens, was unusual among known Xenacanthiformes, prompting him to propose the new genus *Taquaranthus* (*nomen nudum*), never formally published. The meaning of *Taquaranthus*, "spine from Taquaral", relates to spines, which have never been found, making the name inappropriate.

RICHTER (1985) later considered "*Pleuracanthus*" a synonym of *Xenacanthus*. The "*Pleuracanthus*" refers to a coleopteran genus and is no longer used for xenacanthiforms, and *Expleuracanthus* is considered a synonym of *Xenacanthus* or Triodus (HAMPE, 2003).

The species described here shares several features with Xenacanthidae, such as cusps lacking cutting or serrated edges and bearing fine ridges. A small apical button isolated from the cusps is known in some Devonian xenacanthiforms, but is rare among Permo-Carboniferous genera such as *Wurdigneria*, *Orthacanthus*, *Triodus*, *Reginoselache*,

and the Xenacanthimorpha *Bransonella* (RAGONHA, 1978; 1984; HAMPE, 2003; JOHNSON, 2005a,b; RICHTER, 2005; GINTER et al., 2010; TURNER & BURROW, 2011).

Variability in cusp size is not uncommon in xenacanthiforms (WÜRDIG-MACIEL, 1975; JOHNSON, 1980; HAMPE, 2003; GINTER et al., 2010), but the degree of disparity observed in *Taquaralodus* is unusual.

Other Brazilian Xenacanthiformes are younger (Late Permian) and occur in the Corumbataí Formation, state of São Paulo (RAGONHA, 1984) and Teresina Formation state of Rio Grande do Sul (WÜRDIG-MACIEL, 1975; RICHTER, 2005). Their dentitions are quite similar to one another, differing only in minor characters. Some southern Paraná Basin species, such as *Wurdigneria obliterata* (Teresina Formation) and *Xenacanthus pricei* (Irati Formation, Assistência Member), possess lateral cusps of unequal size, but the disparity is far smaller than in *Taquaralodus*. Another striking difference is the very large apical button of these taxa, often in direct contact with the cusps, whereas *Taquaralodus* shows a small button, resembling that of *Dicentrodus*.

Small apical buttons and tricuspid dentitions also occur in Devonian and Mississippian sharks, including cladodont teeth and Phoebodontidae (HAMPE, 2003; GINTER et al., 2005). These groups, however, differ in having a centrally located main cusp and lacking the xenacanthiform basal tubercle.

Among all xenacanthiform taxa examined, *Dicentrodus* (Diplodoselachidae) is the most morphologically similar to *Taquaralodus*. HAMPE et al. (2006) were the first to compare "*Pleuracanthus albuquerquei*" with *Dicentrodus*, noting the unusually prominent lateral cusp, a feature otherwise known only in *Dicentrodus*. Another similarity is the small apical button, although in *Dicentrodus* it is rounded or triangular rather than elongated, and a third cusp is uncommon in *Dicentrodus*, unlike *Taquaralodus*.

HAMPE (2003) and HAMPE et al. (2006) suggested affinities with *Triodus*, based on cusp ridges and apical button morphology, but in *Taquaralodus* the button is elongated rather than rounded, and the irregularly fine ornamentation (Fig. 5A) differs from that genus.

Thus, the establishment of the genus *Taquaralodus*, as originally implied by RAGONHA (1978) and proposed by CHAHUD & PETRI (2010c), is justified due to the distinctive external morphology of the apical button, the size and ornamentation of the cusps, and overall differences from all other xenacanthiform genera.

The absence of the intermediate cusp, and sometimes also the secondary cusp, may be related to tooth position within the jaw and/or ontogenetic stage, as originally suggested by SILVA SANTOS (1946) for the Pedra do Fogo material. If ontogenetic, the tricuspid teeth would represent the most mature forms, whereas unicuspid teeth would be the youngest, consistent with patterns observed in *Orodus* (CHAHUD, 2007; CHAHUD et al. 2010b) and other xenacanthiforms (HAMPE, 2003; HAMPE et al., 2006; GINTER et al., 2010). This hypothesis is supported by the unicuspid specimen GP/2E-6580, which bears an elongated base and a small protrusion where a secondary cusp would develop.

Ridge ornamentation on both labial and lingual faces of bicuspid and unicuspid teeth, but only lingual ornamentation on tricuspid teeth, may reflect wear, further supporting

ontogenetic interpretation, since the unicuspid and bicuspid teeth would be younger and less worn.

Cusp breakage likely occurred during transport or functional use. If breakage occurred during transport, it was probably brief, because the tooth bases exhibit little abrasion.

Family XENACANTHIDAE Fritsch, 1889
Genus *Xenacanthus* Beyrich, 1848
Xenacanthus sp.

Material: GP/2T-215. Isolated tooth fixed in matrix (Fig. 9).

Locality: Santa Maria Homestead outcrop.

Description: The tooth exhibits extensive abrasion marks over its entire surface, but in a homogeneous manner, with all lateral edges and cusps rounded. It possesses two lateral cusps that stand out, developing parallel to each other and directed toward the labial face of the base.

The base is triangular and thin, with a large apical button occupying the entire space between the cusps and the centro-labial region. Small nutritive foramina occur between the apical button and the base margin. The height of the larger cusp is 1.6 mm, and the smaller cusp measures 1.5 mm. The base is 1.3 mm wide. The apical button measures 0.6 mm in width and 0.9 mm in the labiolingual dimension. The cusps originate from roughly the same region of the labial face, with no median cusp; they are slightly rounded in cross-section, with mild labiolingual compression. Despite abrasion, they are originally smooth, with the smaller cusp bearing some fractures. The lateral angle between the crown and the base exceeds 130°.



Figure 9. Tooth of *Xenacanthus* sp. (GP/2T-215). Scale: 1 mm.

Discussion: Smooth cusps, approximately circular in cross-section, together with a large apical button and nutritive foramina near the base, represent diagnostic features of the genus *Xenacanthus* (HAMPE, 2003). Because only a single specimen with these features was recovered, identification cannot be refined to the species level.

Parallel cusps forming a large labial angle (>120°) occur in three Northern Hemisphere species of *Xenacanthus*: *X. laevissimus, X. elegans, X. tenuis*. However, the specimen studied here differs in lacking a median cusp and the curvature of the main cusps, typical of these European–North American species.

Among Brazilian species, it most closely resembles *Xenacanthus* pricei (WÜRDIG-MACIEL, 1975) from the uppermost Irati Formation in Rio Grande do Sul.

The differences lie in: the greater size disparity between the main cusps in *X. pricei*; the presence of very fine ridges in *X. pricei*, which occur on the upper face of that species but are absent here.

Genus *incertae sedis*

Material: GP/2T-216 (Fig. 10), GP/2E-6456 (Fig. 11), and GP/2T-217 (Fig. 12) Fragmented teeth.

Locality: Santa Maria Homestead outcrop (two localities).

Description of GP/2T-216 (Figure 10): The crown consists of two divergent cusps, one of them strongly inclined, both similar in size (approximately 1 mm wide at their thickest point). There is no evidence of

an intermediate cusp. Despite fragmentation, the cusps can be inferred to have been elongated. Striations (likely worn ridges) are present on one cusp, with no serrations observed.

The base is thin, with the lingual face directed downward. Despite the preservation, nutritive foramina are visible, one of them very close to the apical button. The apical button, also broken, is small, completely separate from the cusps, and positioned on the lingual face.

Measurements: Base: 3.4 mm anteroposterior length; 4.3 mm height; Larger cusp: 2.1 mm height × 0.9 mm diameter; Smaller cusp: 1.9 mm height × 0.9 mm diameter; Apical button: 1 mm maximum length.



Figure 10. Specimen GP/2T-216 of Xenacanthidae attached to a rock matrix. Scale 1mm.

Description of GP/2E-6456 (Figure 11): Tooth composed of two main lateral cusps and remains of an intermediate cusp, all in direct contact. The main cusps are fragmented but rounded in cross-section. The intermediate cusp, smaller in diameter, is likewise broken and measures approximately half the diameter of the main cusps. All cusps are positioned on the labial face.

The base shows minor breakage but has a rounded or quadrangular outline. Nutritive foramina occur on the upper lingual surface near the apical button, on the lateral areas, and on the lower surface. No significant concavity was observed on the inferior face of the base. The basal tubercle is heavily worn and encrustations hinder its assessment.

The apical button is circular and does not contact the cusps; it is positioned on the lingual face of the base.

Measurements: Base: 1.0 mm anteroposterior × 1.0 mm labiolingual; Larger cusp: 0.8 mm height; Apical button: approx. 0.5 mm length.

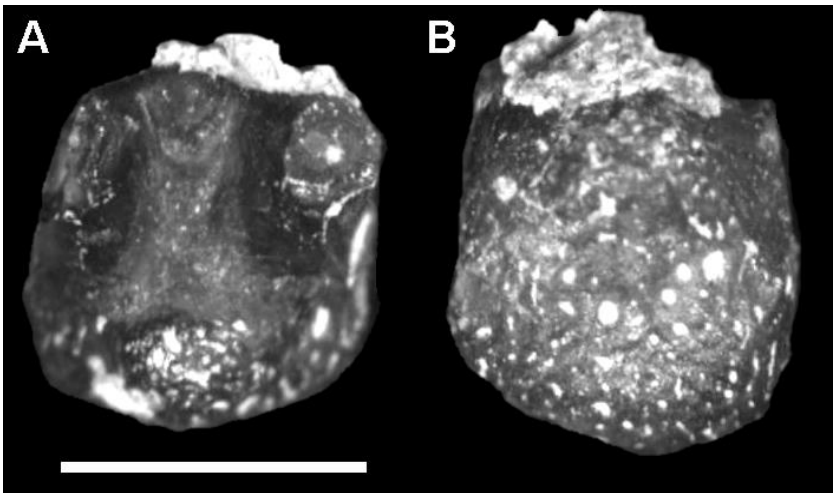

Figure 11. Specimen GP/2E-6456 of indeterminate Xenacanthidae. A) Occlusal view; B) Basal view. Scale: 1 mm.

Description of GP/2T-217 (Figure 12): The tooth is composed of two lateral cusps of slightly different sizes, the larger measuring 0.9 mm in diameter and the smaller 0.7 mm. An intermediate cusp, situated between the lateral cusps, has less than half the diameter of the largest one, is in direct contact with the larger cusps, and is positioned obliquely on the labial face.

One lateral portion of the base is preserved, indicating a rounded base outline. Nutritive foramina occur on the upper lingual surface near the apical button, and centrally on the lower face, where a small depression is present. The absence of a basal tubercle may be due to breakage along the labial margin.

The apical button contacts the cusps but does not extend to the labial face; it is restricted to the central and lingual regions of the base.

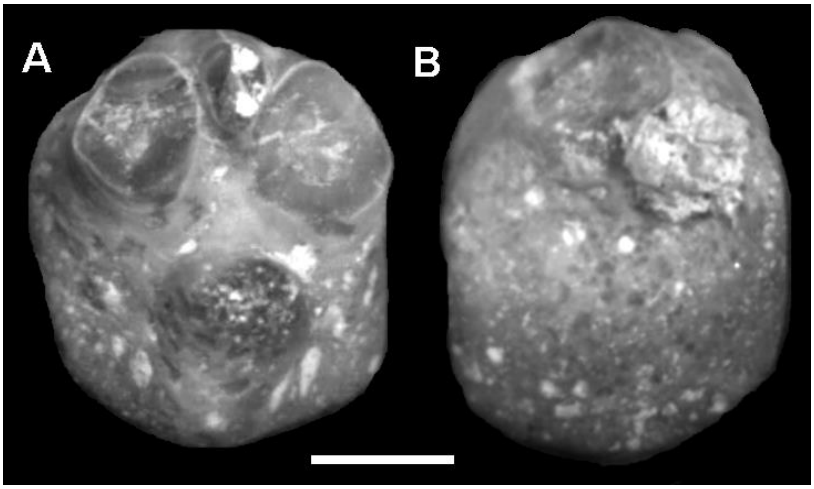

Figure 12. Specimen GP/2T-217 of indeterminate Xenacanthidae. A) Occlusal view; B) Basal view. Scale: 1 mm.

Discussion: The two specimens (GP/2T-216 and GP/2T-217) appear to belong to the same species, given the similarity in base morphology and apical button structure. The absence of the intermediate cusp in GP/2T-216 may reflect heterodonty.

Although preservation is poor and the sample is small, several taxonomic inferences can be made.

The specimens can be confidently assigned to Xenacanthidae based on: circular cusps, lack of cutting edges or serrations, features that distinguish them from Diplodoselache, *Dicentrodus, Lebachacanthus, Orthacanthus*, and *Hagenoselache* (HAMPE, 2003; JOHNSON, 1999; 2003; HAMPE et al., 2006).

Whether they represent a known genus or a new one is uncertain, as better-preserved specimens are needed.

The divergence of the cusps is common in *Orthacanthus* and *Wurdigneria*, but GP/2T-216 differs from those genera in cusp ornamentation, apical button morphology, and base shape.

Longitudinal irregular ridges over the cusp surface, clear in GP/2T-216 and faintly present in GP/2E-6456 and GP/2T-217, exclude the possibility of *Xenacanthus* affinity and resemble *Plicatodus* and *Triodus* (HAMPE, 2003; GINTER et al., 2010).

The Xenacanthimorpha *Barbclabornia* (JOHNSON, 2003), a bicuspid genus, resembles specimen GP/2T-216, but differs in having a thicker base and larger apical button.

The presence of two robust, similarly sized cusps distinguishes these specimens from *Taquaralodus albuquerquei*, the most common xenacanthiform in the unit; cusp and apical button morphologies differ substantially. They also differ markedly from *Xenacanthus* sp. described above, in apical button shape, base outline, and cusp arrangement.

PALEOENVIRONMENTAL AND PALEOGEOGRAPHIC DISCUSSION

Taquaralodus and the other xenacanthiforms occurring at the base of the Taquaral Member were recovered from high-energy deposits, and many specimens are heavily worn or fragmented. Such depositional settings hinder precise paleoenvironmental interpretations; however, some hypotheses can be proposed.

The basal sandy facies of the Taquaral Member has been interpreted as reflecting variable salinity, either predominantly fresh (MUSSA et al., 1980) or with some degree of salinity and continental influence (CHAHUD, 2007).

Taquaralodus is far more abundant than any other xenacanthiform in the Irati Formation. RAGONHA (1978) recorded it in sandy deposits of Itapetininga and Assistência; CHAHUD (2021) and CHAHUD et al. (2012) documented its presence in deposits between Rio Claro and Ipeúna, all in the state of São Paulo. The only known occurrence outside São Paulo is in the Pedra do Fogo Formation of Maranhão, described by SILVA SANTOS (1946), also from high-energy deposits.

The material includes teeth of various degrees of preservation (Figs. 13 and 14), size, and ontogenetic stage.

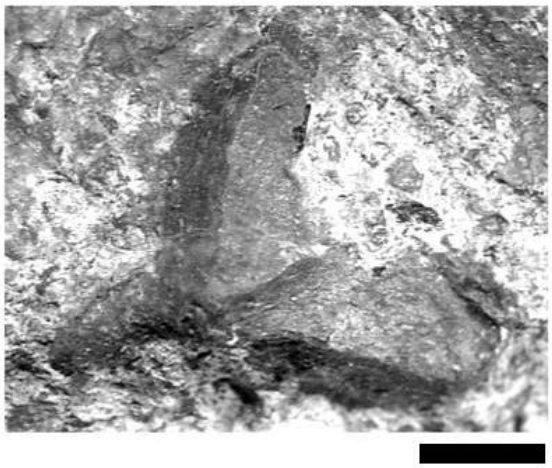

Figure 13. *Taquaralodus* tooth with cusp preserved in rock. GP/2E-3753. Scale: 2 mm.

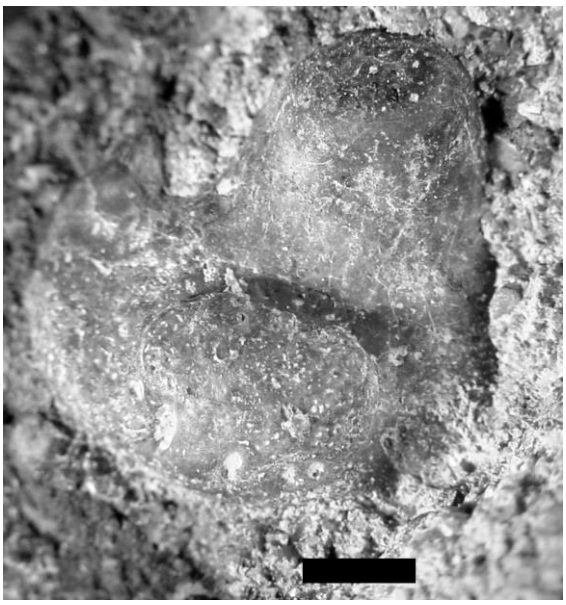

Figure 14. Heavily worn *Taquaralodus* tooth fixed in matrix. GP/2E-6251. Scale: 2 mm.

Other xenacanthiforms are exceedingly rare, observed only in the Santa Maria Homestead outcrops. In the thickest outcrop at this locality, *Taquaralodus* is absent, and the specimen GP/2E-6456 (Xenacanthidae indet.) was found, along with two additional highly fragmented specimens preserved only as cusp impressions and apical button remnants.

It is possible that Xenacanthidae specimens are allochthonous, transported from fluvial systems. This interpretation is supported by their high degree of abrasion, fragmentation, and rarity. In contrast, *Taquaralodus albuquerquei* was likely autochthonous or parautochthonous, inferred from its abundance and morphological variability.

A plausible paleoenvironmental interpretation for these deposits is that they were fed by a fluvial system discharging into a larger water body, with additional sediment reworking by waves.

CONCLUSIONS

The Taquaral Member is interpreted as representing a paleoenvironment with variable salinity, sometimes fresher (MUSSA et al.,

1980), other times with salinity but under continental river influence (CHAHUD, 2007; 2011; CHAHUD & PETRI, 2016).

The basal sandy facies was deposited under high-energy conditions, which explains the strong abrasion and fragmentation of the fossils. Because of this, a precise paleoenvironmental interpretation is not possible, though some hypotheses are reasonable.

Xenacanthiforms represent the second most abundant Chondrichthyes in the basal Taquaral Member, surpassed only by the petalodont Itapyrodus punctatus. Their preservation varies widely, with specimens ranging from well-preserved to extremely worn, suggesting time-averaging.

The family Diplodoselachidae is the most common in the Taquaral Member and is represented by isolated teeth of *Taquaralodus albuquerquei*. This species is endemic to the Paraná and Parnaíba basins and is characterized by its large cusp occupying much of the central and lateral areas of the tooth. It is a heterodont species, with tricuspid, bicuspid, and unicuspid teeth.

Teeth of Xenacanthidae from the Taquaral Member represent at least two species. One may belong to the genus *Xenacanthus* and is similar to X. pricei from the top of the Irati Formation in Rio Grande do Sul, although more specimens are needed to confirm this. The second species is of uncertain classification due to strong abrasion of the available material.

In general, xenacanthid fossils are rare and heavily worn, suggesting an allochthonous origin, in contrast with *Taquaralodus albuquerquei*, which appears autochthonous or parautochthonous due to its abundance.

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