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A new *Xenacanthiformes* shark (*Chondrichthyes*, *Elasmobranchii*) from the Late Paleozoic Rio do Rasto Formation (Paraná Basin), Southern Brazil

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ABSTRACT

The Brazilian records on *Xenacanthiformes* include teeth and cephalic spines from the Parnaíba, Amazonas and Paraná basins. This work describes a new species of *Xenacanthidae*, collected in an outcrop of Serrinha Member of Rio do Rasto Formation (Wordian to Wuchiapingian), Paraná Basin, municipality of Jacarezinho, State of Paraná. The teeth of the new species are two or three-cuspidated and the aboral surface show a smooth concavity and one rounded basal tubercle. The coronal surface presents one semi-spherical and subcircular coronal button, and also two lateral main cusps and one central (when present) with less than one fifth of the size of the lateral cusps in the labial portion. The lateral cusps are asymmetric or symmetric, rounded in transversal section, lanceolate in longitudinal section, devoid of lateral carinae and lateral serrations, and with few smooth cristae of enameloid. In optical microscope the teeth show a trabecular dentine (osteodentine) base, while the cusps are composed by orthodentine, and the pulp cavities are non-obiterated by trabecular dentine. The fossil assemblage in the same stratigraphical level and in the whole Rio do Rasto Formation indicates another freshwater record for *xenacanthid* sharks.

Key words: Permian, *Xenacanthomorpha*, *Xenacanthidae*, *Xenacanthus*, shark teeth.

INTRODUCTION

The *Xenacanthiformes* (from gr. *xenos* = strange + lat. *acanthos* = spine) are represented by sharks with narrow and fusiform body shapes (Moy-Thomas and Miles 1971), which were common throughout the world in the Middle to Late Paleozoic and Early Mesozoic (Long 2011), ranging from the Lower Carboniferous to the Upper Triassic of shallow-water marine, marginal and freshwater deposits

(Hampe 2003, Turner and Burrow 2011). These sharks are known by their few articulated skeletons and, mainly by cephalic spines and characteristic diplodont teeth with two lateral cusps usually larger than the median one (Ginter 2004).

In Brazil, the *xenacanthiformes* are recorded in the Amazonas, Parnaíba and Paraná basins. In the Amazonas Basin they occur in the Itaituba Formation (Duffin et al. 1996). In the Parnaíba Basin the group occurs in the Pimenteiras (Alves et al. 2008a) and Pedra de Fogo formations (e.g. Silva-Santos 1946,

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Silva-Santos and Salgado 1970, Alves et al. 2008a, b, Souza et al. 2008, Alves 2010). In the Paraná Basin these sharks are found in the transition between Tatuí to Irati formations (Ragonha 1978, Chahud and Petri 2008), Irati Formation (Würdig-Maciel 1975, Chahud and Petri 2009, 2010), Corumbataí Formation (Ragonha 1984a, 1986, 1989a, Toledo et al. 2005, Campanelli and Fernandes 2008), Terezina Formation (Würdig-Maciel 1975, Richter 2005) and Rio do Rasto Formation (Ragonha 1989b, 1990, Dias 1996, Figueiredo et al. 2008, Pauliv et al. 2010). The Corumbataí Formation is currently equivalent to the Serra Alta and Terezina formations (Rohn 2001, Holz et al. 2010) so the records of these formations should be merged. In spite of all these records mentioned above, xenacanthiforms are poorly known in South America and xenacanthid teeth from the Serrinha Member of Rio do Rasto Formation (Paraná State) reported by Pauliv et al. (2010) are detailed in this contribution.

The Rio do Rasto Formation was divided by Gordon Jr. (1947) into two members, the Serrinha Member (inferior) and the Morro Pelado Member (superior) and is considered by Holz et al. (2010) as Wordian to Wuchiapingian (Permian).

Some paleoenvironmental interpretations were proposed for the Rio do Rasto Formation. For the Serrinha Member the majority of these interpretations suggest a shallow lacustrine environment (e.g. Mendes 1967, Ragonha 1989b, Lavina 1991) and for Holz et al. (2010) these shallow lakes were sometimes influenced by storm waves and fluvial incursions. For the Morro Pelado Member, Lavina (1991) and Holz et al. (2010) considered them as sedimentary deposits of smaller lakes, alluvial plains, fluvial meandering streams, delta systems with interdistributary bays, as well as small temporary water bodies. The paleoenvironmental interpretations mentioned above are supported by the floristic and faunistic records, and the presence of conchostraceans indicates a freshwater condition to the whole Rio do Rasto Formation (Holz et al. 2010).

MATERIALS AND METHODS

The material corresponds to teeth collected from an outcrop of the Serrinha Member of Rio do Rasto Formation in the northeastern region of the State of Paraná, municipality of Jacarezinho, near kilometer 20, west margin of the BR-153 federal highway, coordinates: 23°10'08"S and 49°57'49"W (Figure 1). The studied material are housed in the paleontological collection of the Museu de Ciências Naturais at the Setor de Ciências Biológicas of Universidade Federal do Paraná (MCN-SCB-UFPR) in Curitiba, Paraná, under the numbers MCN.P.453, MCN.P.1088, MCN.P.1089, MCN.P.1090, MCN.P.1091 and thin sections numbers MCN.P.1125, MCN.P.1126a, MCN.P.1126b and MCN.P. 1127. All specimens were collected associated with other fish remains such as actinopterygian scales and teeth. The specimen MCN.P.1088, was associated with a shark fin spine ascribed to a new species of *Sphenacanthus* (Pauliv et al. 2009, 2012).

The type series of *Xenacanthus santosi* and *X. pricei* Würdig-Maciel, 1975 housed in the Micropaleontology collection of the Instituto de Geociências of the Universidade Federal do Rio Grande do Sul (IGeo-UFRGS), Porto Alegre, Brazil; and *Wurdigneria obliterated* Richter, 2005 housed in the Museu de Ciências e Tecnologia of the Pontifícia Universidade Católica do Rio Grande do Sul (MCT-PUCRS), Porto Alegre, Brazil, were analyzed for comparison.

The preparation of the specimens was done under stereomicroscope using mechanical techniques with steel tips. The samples were impregnated with polystyrene dissolved in xylol increasing teeth resistance. The samples were photographed with Olympus SZX9 stereomicroscope of Laboratório de Microtécnica of the Universidade Positivo, Curitiba, Brazil and with Zeiss Discovery.V20 stereomicroscope of Laboratório de Foraminíferos e Micropaleontologia Ambiental (LaFMA-UFPR), Curitiba, Brazil.

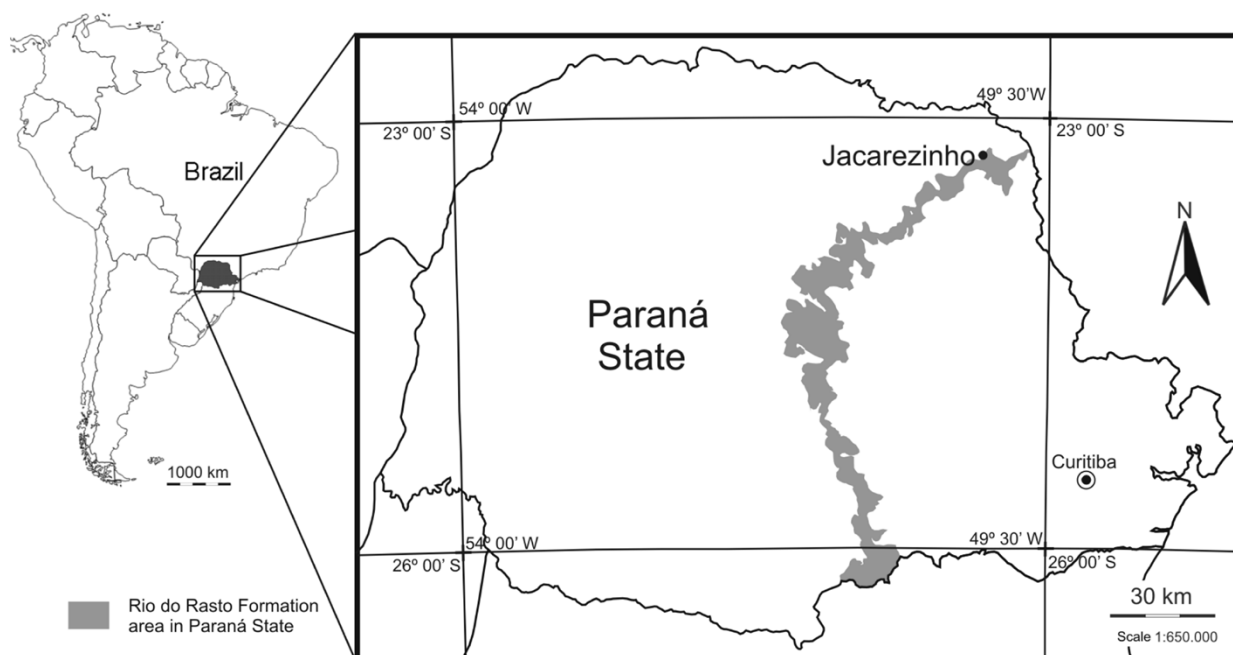


Figure 1 - Distribution of the Rio do Rasto Formation in the State of Paraná with the location of the collecting site in the municipality of Jacarezinho (modified from Mineropar, 2006).

Some of the specimens were thin-sectioned using epoxi 324 resin to include the material and abrasive materials. These sections were photographed in the Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN-FZB-RS) using the Zeiss Axiovert 40 CFL and in the Universidade Estadual do Oeste do Paraná (Unioeste), Cascavel, (Laboratório de Foto Microscopia) using the Olympus BX-60 microscope.

The anatomical nomenclature was based on Ragonha (1984a), Johnson (1999), Hampe (2003), Richter (2005) and Ginter et al. (2010).

SYSTEMATICS

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Xenacanthiformes (= Xenacanthida) Berg, 1937

Family Xenacanthidae Fritsch, 1889

Genus *Xenacanthus* Beyrich, 1848

Type species: *Xenacanthus decheni* Goldfuss 1847

Xenacanthus ragonhai sp. nov.

Figures 2-4

Etymology. In honor of Evaldo Wehmuth Ragonha, the Brazilian Paleoichthyologist who studied the Xenacanthiformes from the Paraná Basin during the 1970, 1980 and 1990's.

Holotype: MCN.P.1088 a tooth.

Paratype. The isolated teeth MCN.P.453, MCN.P.1089, MCN.P.1090, MCN.P.1091 and thin sections MCN.P.1125, MCN.P.1126a, MCN.P.1126b, MCN.P.1127.

Type locality and horizon. Serrinha Member of the Rio do Rasto Formation (Wordian to Wuchiapingian according to Holz et al. 2010), Passa Dois Group, Paraná Basin, municipality of Jacarezinho, northeastern region of the State of Paraná, South Brazil.

Diagnosis. Chondrichthyans only known by tricuspid or less frequently bicuspid teeth with the following combination of features: teeth with two lateral main cusps and one central (when present) around one fifth (1/5) of the lateral ones; lateral cusps lanceolate without lateral carinae and rounded

in transversal section; thin enameloid present; few smooth cristae of enameloid on the lateral cusps; teeth base composed of trabecular dentine (osteodentine) while the cusps are composed by orthodentine; trabecular dentine overlaps externally the orthodentine on the basal portion of the lateral

cusps; pulp cavity non-obliterated by trabecular dentine; coronal button sub-circular and semi-spherical in shape and sometimes extend among the lateral cusps; coronal button presents a prominent edge and the connection to the base presents a small notch around and by a wide shaft.

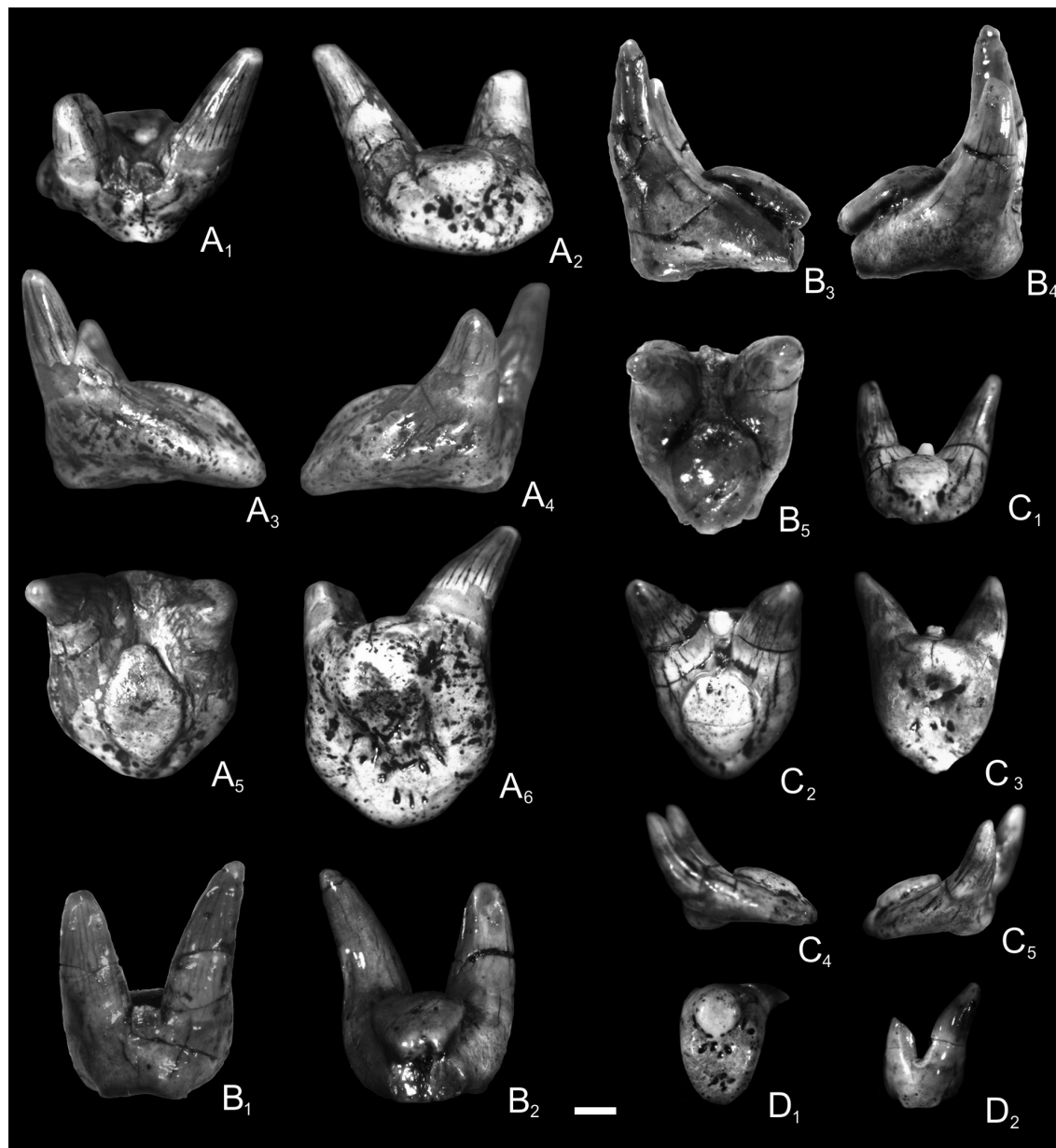


Figure 2 - *Xenacanthus ragonhai* sp. nov. from the Rio do Rasto Formation, Wordian to Wuchiapingian, Brazil. **A:** specimen MCN.P.1088 (holotype), labial (A₁), lingual (A₂), laterals (A₃ and A₄), aboral (A₅) and coronal (A₆) views respectively; **B:** specimen MCN.P.453 (paratype), labial (B₁), lingual (B₂), laterals (B₃ and B₄) and aboral (B₅) views; **C:** specimen MCN.P.1089 (paratype), lingual (C₁), laterals (C₂ and C₃), aboral (C₄) and coronal (C₅) views respectively; **D:** specimen MCN.P.1091 (paratype), lingual (D₁) and aboral (D₂) views respectively. Scale bar = 1mm.

DESCRIPTION

Xenacanthus ragonhai sp. nov. presents teeth with three cusps (MCN.P.453, MCN.P.1089, MCN.P.1125 and MCN.P.1127) or rarely two cusps (MCN.P.1091), in which the two main cusps are lateral and bigger than the third central one, which is typically reduced or absent for xenacanthid teeth (Figure 2). In *X. ragonhai* sp. nov. some teeth have reductions of the central cusp due to a taphonomical process that breaks it or to occlusal wearing, that makes these teeth secondarily bicusps (MCN.P.1088, MCN.P.1089, MCN.P.1090). When present, the central cusp is less than one fifth of the lateral ones. The teeth vary in size between 3mm to 5.5mm in length, 2.5 to 5mm in width and 3 to 6.5mm in height.

In aboral view, the teeth base is slightly concave and almost rounded (Figure 2A₅) or oval shaped (Figure 2D₁), with several foramina predominantly arranged around the basal tubercle. The basal tubercle is also rounded and well developed occupying about one third of this surface and is located close to the labial edge. In coronal view the base presents a coronal button, also known as apical button. In *X. ragonhai* sp. nov. this structure is subcircular, semi-spherical and sometimes, almost flat at the top. The coronal button presents a notch around the connection with the base (Figures 2B₂-B₄), except in the lingual portion, in which there is a wide shaft (Figures A₃-A₄, C₄-C₅). Small foramina on the coronal button surface are present, as well as around the notch, and bigger foramina are present along the lingual edge of the base.

The crown can be tricuspid or bicuspid as already mentioned, with two major lateral cusps, the mesial and distal ones, while the smaller is the central cusp, between the two lateral ones. The lateral cusps are devoid of carinae, rounded proximally, and present a lanceolate longitudinal cross-section. These cusps possess similar or unequal sizes, and this inequality is interpreted as different anatomic positions or, in some cases, as

a result of the cusps wearing stage. This wearing could be related to the taphonomical abrasion or due to the contact with the opposite teeth during feeding, causing an occlusal wearing, as observed in the specimens MCN.P.1088 and MCN.P.1090. The occlusal wearing of MCN.P.1088 is indicated by chamfers on the lateral distal portion of the base (Figure 2A₄-A₅, Figure 3A₁-3A₃) and on the labial surface of the mesial cusp (Figures 2A₂, 2A₆; Figure 3A₄) in addition to the wearing of the central cusp. In the specimen MCN.P.1090, the occlusal wearing evident in the internal surface of the mesial cusp forming a chamfer, and totally consumed the central cusp and reaching the base of the distal cusp internally, making a concavity between the two main cusps (Figures 3B₁-3B₂).

The lateral cusps are relatively asymmetric in labial view (MCN.P.453, MCN.P.1088, MCN.P.1090, MCN.P.1091) or almost symmetric (MCN.P.1089, MCN.P.1125, MCN.P.1127) indicating heterodont condition in *Xenacanthus ragonhai* sp. nov. similar with the specimens described by Hampe (1988). Thus the asymmetric specimens mentioned above are interpreted here as lateral teeth since the lateral main cusps are slightly inclined, while the almost symmetric specimens are interpreted as mesial teeth. The specimen MCN.P.1091 is interpreted as posterior due to being a small tooth and due to the absence of the central cusp.

HISTOLOGICAL ASPECTS

The *Xenacanthus ragonhai* sp. nov. teeth base are composed by trabecular dentine (= osteodentine) while the cusps are made up of an orthodentine (Figure 4A₁). In longitudinal cross-section the cusps are composed by concentric orthodentine layers with a central pulpar cavity (Figures 4 A₁, B₁, C, D). The pulpar cavity is non-obliterated by trabecular dentine, extending from the cusp base until its apical portion and could present a small projection of trabecular dentine as seen

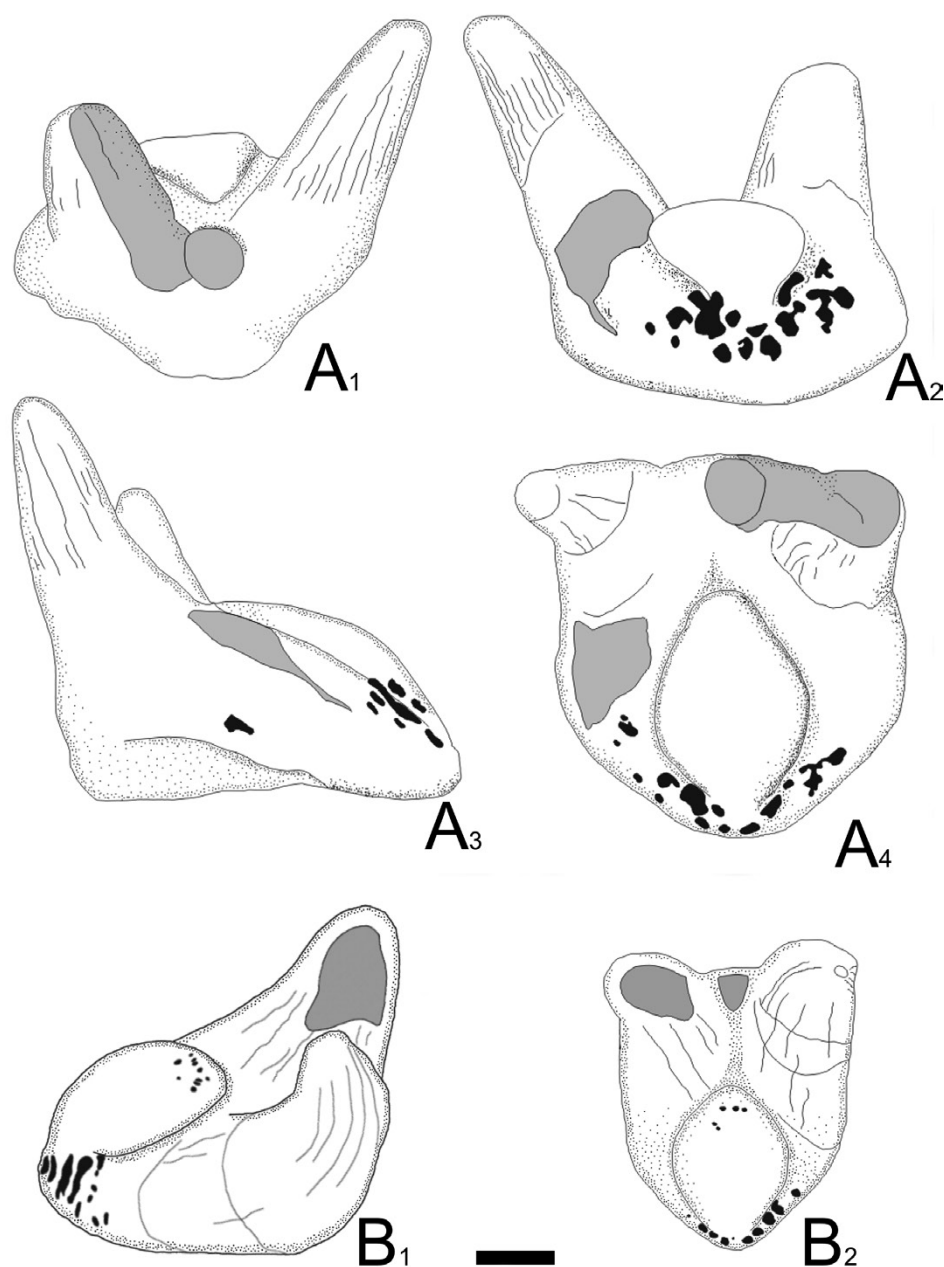


Figure 3 - *Xenacanthus ragonhai* sp. nov. from the Rio do Rasto Formation, Wordian to Wuchiapingian, Brazil. **A:** MCN.P.1088 (holotype), labial (A_1), lingual, (A_2), lateral (A_3) and coronal (A_4) views respectively; **B:** MCN.P.1090 (paratype) latero-occlusal (B_1) and occlusal (B_2) views respectively. Gray areas represent occlusal wearing on the lateral distal portion of the base, on the labial surface of the mesial cusp (MCN.P.1088), on the lateral medial portion of the mesial cusp and on the central cusp (MCN.P.1090). Scale bar = 1 mm.

in Figure 4C. On the tooth base, the trabecular dentine overlaps externally the orthodentine on the basal portion of lateral cusps (similar to that seen in *Lebachacanthus senkenbergianus* Hampe

1991). In *X. ragonhai* sp. nov. the lateral cusps are covered with a thin enameloid layer (Figure 4B₂), and this layer forms a few smooth cristae of enameloid on the lateral cusps (Figure 4B₂).

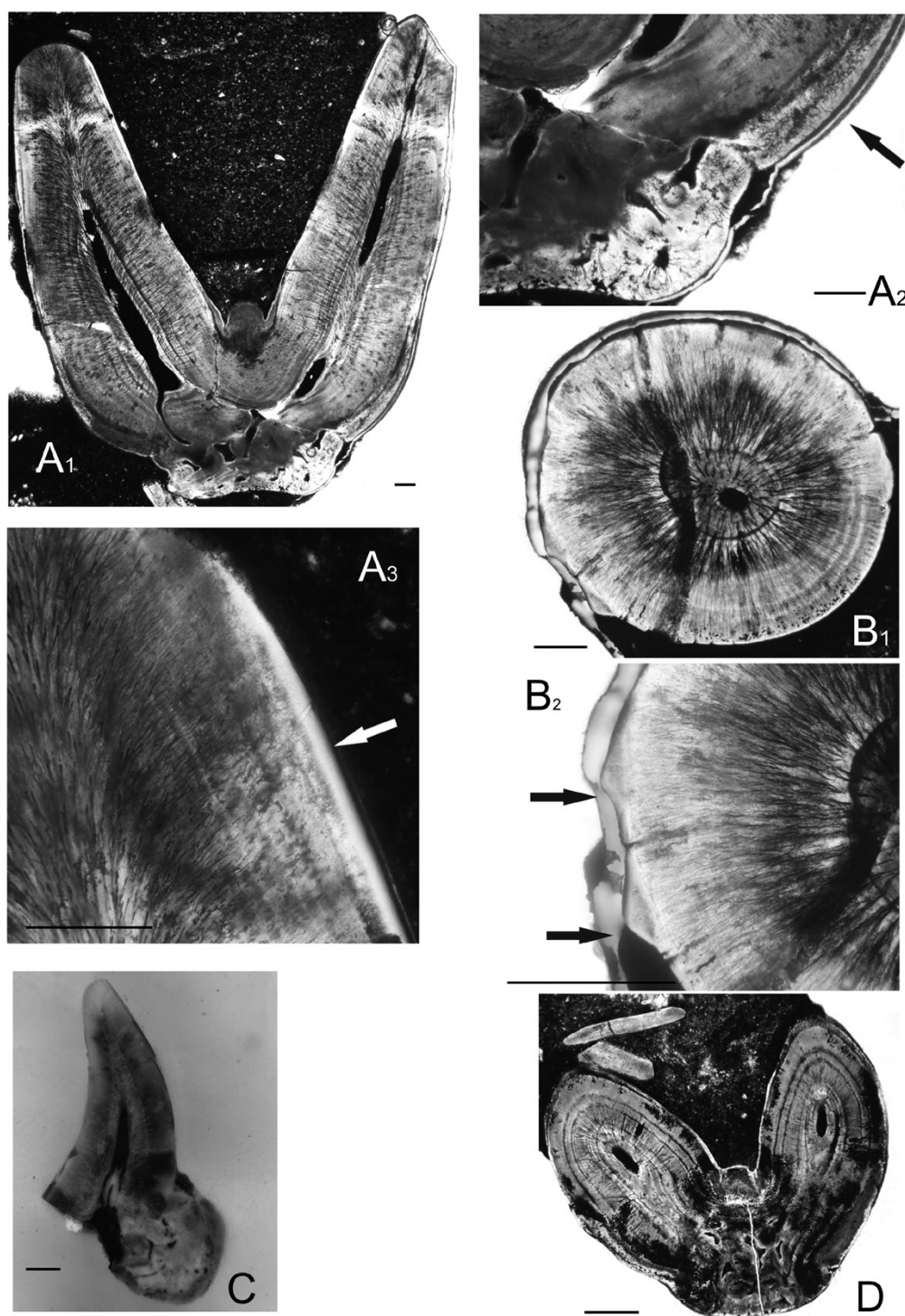


Figure 4 - *Xenacanthus ragonhai* sp. nov. from the Rio do Rasto Formation, Wordian to Wuchiapingian, Brazil teeth histology. **A**, MCN.P.1125, **A**₁: longitudinal section through the lateral cusps, **A**₂: arrow points to the trabecular dentine overlapping externally to the orthodentine on the basal portion of lateral cusps, **A**₃: arrow points to a detail of the thin enameloid layer; **B**, MCN.P.1126a, transversal section through a lateral cusp (**B**₁) and the arrow points to the few smooth cristae of enameloid (**B**₂), **C**, MCN.P.1126b, polished section through a lateral cusp showing a small projection of trabecular dentine; **D**, MCN.P.1127, oblique longitudinal section through a teeth Scale bars A-B = 200 µm C-D = 500 µm.

DISCUSSION AND CONCLUSIONS

According to Zangerl (1981) the Order Xenacanthiformes is represented by sharks with a fusiform body shape, one dorsal spine and teeth modified from the cladodont design, in which the lateral cusps are enhanced and the central cusp is slender, small or even absent. These features are present in the studied teeth indicating that they belong to this order. Following Hampe (2003) and Ginter et al. (2010), this order is divided into two families: Diplodoselachidae and Xenacanthidae. These authors mentioned that Xenacanthidae teeth show non-serrated lateral edges on the cusps, cusps often equipped with vertical cristae and basal tubercle always with a concave depression. The studied specimens present all these features, so they are attributed to the Family Xenacanthidae.

Ginter et al. (2010) mentioned that five genera are included in the Xenacanthidae: *Plicatodus* Hampe 1995, *Triodus* Jordan 1849, *Mooreodontus* Ginter et al. 2010 *Wurdigneria*, Richter 2005 and *Xenacanthus* Beyrich 1848.

Based on the summary of *Plicatodus* presented by Ginter et al. (2010), *Xenacanthus ragonhai* differs from this genus. *Plicatodus* have cusps with elliptical cross-section near the base; lateral cusps curved sigmoidally throughout their apical portion; surface of the cusps exhibiting a pattern of generally strong, wavy or curved vertical cristae; elliptical shaped base; small coronal button; base and crown consisting almost entirely of orthodentine and by the absence of enameloid.

The new species also resemble the teeth features presented by Ginter et al. (2010) to the *Triodus* genus. However, the crown and the base of *Triodus* teeth are almost entirely composed by orthodentine (except the coronal button that is made by trabecular dentine), the cusps have a variable number of consistently vertical cristae and, finally, the most remarkable feature of *Triodus* is an elongated median cusp that in some species reach almost the same length of the lateral cusps, which are evidently different from the Rio do Rasto specimens described here.

The dropped shaped to triangular shaped tooth base of *Mooreodontus* differs from *X. ragonhai* tooth base, which is almost rounded or oval shaped and the comparison with *Wurdigneria* will be dealt with latter.

The emended diagnosis of *Xenacanthus* presented by Hampe (2003) and the summary of the genus of Ginter et al. (2010), allowed for the determination that the Rio do Rasto specimens here described belong to this genus, sharing almost all features presented by these authors. These shared features comprise: cusps usually lanceolate in cross-section and with smooth lateral edges; coronal button varying in size but being predominantly circular in shape; shaft developed; constantly large number of nutrient foramina perforating the base; basal tubercle with variable degrees of basal depression; cusps composed by orthodentine surmounting a base of trabecular dentine.

The species *Xenacanthus ragonhai* sp. nov. diverges from the other known species of *Xenacanthus* on the presence of a fine enameloid covering on the teeth, in the presence of a few smooth cristae of enameloid on the lateral cusps and the trabecular dentine overlapping externally the orthodentine on the basal portion of the lateral cusps, which are peculiar features of the new species.

The comparison between *Xenacanthus ragonhai* sp. nov. with other Brazilian xenacanthids that closely resemble this species is presented below.

X. ragonhai sp. nov. differs from *Xenacanthus pricei* Würdig-Maciel 1975 due to the presence, in the latter, of smooth carinae on the entire edge of the cusps, coronal button and basal tubercle proportionally minor, few foramina on the aboral surface of the base, and finally, all known teeth of *X. pricei* are very small. Beyond these features, *X. pricei* is described for the Irati Formation (Late Artinskian according to Holz et al., 2010), so it is at least 8 M.y. older than *X. ragonhai* sp. nov. from the Rio do Rasto Formation (Wordian to Wuchiapingian).

Another Brazilian species is *Xenacanthus santosi* Würdig-Maciel 1975, collected in the Caveiras Facies of Estrada Nova Formation of Rio Grande do Sul State. These beds are actually included in the Terezina Formation, Late Kungurian to Rodian, thus being a little older than the Rio do Rasto Formation specimens. The new species *X. ragonhai* diverges from *X. santosi* by the presence, in the latter, of laterally compressed cups with smooth carinae on the lateral edges plus some branching cristae. The coronal button in *X. santosi* does not present a prominent edge, and in the connection with the base does not have a notch nor a shaft, which are evident in *X. ragonhai* sp. nov.

Würdig-Maciel (1975) considered in the diagnosis of *X. pricei* and *X. santosi* some unreliable features, such as cusps with different sizes and inclinations, which could be related to distinct positions in the jaw, occlusal wearing and taphonomical abrasion as already mentioned by Ragonha (1984a) and Richter (2005).

Some other Brazilian xenacanthid species were presented for the São Paulo State, *Xenacanthus angatubensis*, *X. camaquensis*, *X. ferrazensis*, *X. santaritensis* and *X. taquaritubensis* all described by Ragonha (1984a) for the Corumbataí Formation (= Serra Alta and Terezina formations *sensu* Holz et al. 2010). These five species were not formally published, remaining as *nomina nuda*. In spite of this, Ginter et al. (2010) indicate that these unpublished species could have affinities with the Middle to Upper Triassic *Mooreodontus* genus based on the fact that Ragonha (1984b) attributed a Carnian age (Triassic) to the Corumbataí Formation and *Mooreodontus* is the only known post-Paleozoic species of Xenacanthidae. However, this seems to be a historical mistake, since it is now well known that Corumbataí Formation has an estimated age between Lower to Middle Permian (Kungurian to Rodian *sensu* Holz et al. 2010).

Richter (2005) describes *Wurdigneria obliterated* also for the Terezina Formation (Rio Grande do Sul State). *Xenacanthus ragonhai* sp. nov. differs

from *W. obliterated* because the latter have cusps laterally compressed distally, smooth carinae on the cusps edge, pulp cavity obliterated by osteodentine, absence of enameloid covering the lateral cusps and also the lack of trabecular dentine overlapping the orthodentine of the basal portion of the lateral cusps.

One of the most remarkable diagnostic feature of *Wurdigneria obliterated* pointed out by Richter (2005) is the obliteration of the pulpar cavity by trabecular dentine which indicates affinities with Diplodoseichidae. Ginter et al. (2010) mentioned that *Xenacanthus santosi* could be merged in a new combination ?*Wurdigneria santosi*. However, this obliteration is not present in *X. santosi* and the other morphological features presented by Würdig-Maciel (1975), fits better with the emended diagnosis of the *Xenacanthus* genus proposed by Hampe (2003) and by Ginter et al. (2010), so this species could not belong to the genus *Wurdigneria*.

Concerning the paleoenvironment, in the type locality and stratigraphical horizon, *X. ragonhai* sp. nov. is associated with fossil plants, conchostraceans and actinopterygian remains. In the Serrinha Member, a short-snouted temnospondil amphibian also occurs (Barberena et al. 1985, Barberena and Dias 1998). This, in addition with the whole paleontological record, indicates continental and freshwater conditions for the entire Rio do Rasto Formation, as already proposed by Holz et al. (2010). Therefore, *Xenacanthus ragonhai* sp. nov. could represent another freshwater record for xenacanthid sharks.

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RESUMO

O registro brasileiro dos Xenacanthiformes inclui dentes e espinhos cefálicos encontrados nas bacias do Parnaíba, Amazonas e Paraná. Este trabalho descreve uma nova espécie de Xenacanthidae, coletada em um afloramento do Membro Serrinha da Formação Rio do Rasto (Wordiano ao Wuchiapingiano), Bacia do Paraná, Município de Jacarezinho, Estado do Paraná. Os dentes da nova espécie são bi ou tricuspídeos e a superfície aboral apresenta uma suave concavidade e um tubérculo basal arredondado. A superfície coronal apresenta um botão coronal semi-esférico e subcircular, além de duas cúspides laterais principais e uma central (quando presente) com menos de um quinto do tamanho das cúspides laterais em sua porção labial. As cúspides laterais são assimétricas ou simétricas, arredondadas em corte transversal, lanceoladas em corte longitudinal, carenas laterais e serrilhas laterais ausentes, e com suaves cristas de enamelóide. Em microscopia óptica os dentes apresentam base composta por dentina trabecular (osteodentina), enquanto que as cúspides são compostas por ortodentina, e os canais pulpares não são obliterados por dentina trabecular. A assembléia fóssil no mesmo nível estratigráfico e na Formação Rio do Rasto como um todo indica mais um registro de água doce para os tubarões xenacantídeos.

Palavras-chave: Permiano, Xenacanthimorpha, Xenacanthidae, *Xenacanthus*, dentes de tubarão.

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