Journal Pre-proof

Ichthyoliths of the Corumbataí Formation: New occurrences and interpretations for São Paulo state, Brazil (northeastern Paraná basin)

Isabela Jurigan, Fresia Ricardi-Branco, Rafael Delcourt

Please cite this article as: Jurigan, I., Ricardi-Branco, F., Delcourt, R., Ichthyoliths of the Corumbataí Formation: New occurrences and interpretations for São Paulo state, Brazil (northeastern Paraná basin), *Journal of South American Earth Sciences* (2022), doi: https://doi.org/10.1016/j.jsames.2022.103958.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

ICHTHYOLITHS OF THE CORUMBATAÍ FORMATION: NEW OCCURRENCES AND INTERPRETATIONS FOR SÃO PAULO STATE, BRAZIL (NORTHEASTERN PARANÁ BASIN)

Isabela Jurigan [a], Fresia Ricardi-Branco [a] & Rafael Delcourt [b]

[a] Geoscience Institute, University of Campinas, Carlos Gomes, 250 – 13083-855, Campinas, São Paulo, Brazil

[b] Department of Biology, University of São Paulo, Avenida Bandeirantes, 3900 – 14040-901, Ribeirão Preto, São Paulo, Brazil

Corresponding author: isa.jurigan@hotmail.com (I.Jurigan)

E-mail addresses: fresia@unicamp.br (F.R.B.); rafael.delcourt@gmail.com (R.D.)

Abstract

The Permian ichthyofauna of the Passa Dois Group is well known for the ubiquitous presence of disarticulated elements of a variety of fish taxa that remains largely understudied. Lower actinopterygians (Palaeonisciformes) are the most abundant, together with isolated teeth of Xenacanthiformes chondrichthians. This study brings new information on the external micro-ornamentations of actinopterygian teeth and rhomboid scales of the Corumbataí Formation collected for the first time in Santa Rosa de Viterbo region in the State of São Paulo, as well as a new proposition to approach this remains by using cluster analysis. These fossils were found in distal storm deposits (tempestite) and were separated from the rock matrix for analysis. Six distinct actinopterygian tooth morphotypes were identified. Curved forms are dominant in the assemblage, with ornamentations varying from smooth to ribbed shafts and others with grooves and tubercles. The scales are very fragmented showing surface micro-punctuations and longitudinal ridges. The Xenacanthiformes tricuspid teeth were very scarce in the assemblage and no complete specimen was recovered. Nonetheless, it was possible to identify them by their subtriangular shape and drop-shaped basal tubercle. Both ichthyodonts and scales show characteristics similar to at least other 26 occurrences, spread over more than 1000 km, and already described in the literature stratigraphically

positioned above and below the Corumbataí Formation, attesting the wide temporal and spatial distribution of these fossils.

Keywords: fish teeth, rhomboid scales, lower actinopterygians, Xenacanthiformes, Permian

1. INTRODUCTION

Previous studies (e.g., Richter, 1985; Chahud & Fairchild, 2007) have revealed that the paleovertebrate record of the Passa Dois Group of the Paraná Basin is predominantly composed of fish fossils, including rare but well-preserved actinopterygians (e.g., Richter, 2002; Figueiredo & Carvalho, 2004. See Table 2 for a complete list). Isolated remains, ubiquitous to the basin, are represented by teeth, tooth plates, scales, and shark fin spines (e.g., Würdig-Maciel, 1975; Richter, 1985; Maranhão, 1995; Toledo et al., 1997; Toledo & Renó, 2010). Even though fragmentary and isolated, these dermoskeletal elements of the Passa Dois Group attest the presence of a faunal diversity in the paleoenvironment and are of great importance to improve on our knowledge of the Permian paleofauna that remains largely under-studied. So far, specifically for the Corumbataí Formation, the microvertebrate fossils has yielded remains belonging to Petalodontiformes (Toledo et al., 1997), Orodontiformes (Würdig-Maciel, 1975), Xenacanthiformes (e.g., Würdig-Maciel, 1975; Ragonha, 1984), Eugeneodontiformes (Richter, 2007), lower actinopterygian (Palaeonisciformes, e.g.Würdig-Maciel, 1975; Richter et al., 1985), and Dipnoiformes (Toledo & Bertini, 2005), among others. The most recurrent and abundant fossils belong to the ray-finned fishes (Actinopterygii).

Actinopterygii clade emerged at the Silurian period (Friedman, 2015; Lu et al., 2016) and comprise the largest group of fishes living today (Nelson, 2006). The extinct Palaeonisciformes encompasses several lineages of early actinopterygians that share similar features, being currently considered a paraphyletic or 'non-natural' order (Hamel, 2005; Friedman, 2015). The assumption that their typically basal structure remained practically unaltered from Silurian to Cretaceous period (Moy-Thomas, 1971) has been challenged by the discovery of very diverse body morphologies (Hamel, 2005). The poor preservation of fish fossils, especially chondrichthyans, makes them to be ascribed to new species on the basis of isolated scales and dermal bones (Moy-Thomas, 1971; Malabarba,

2

1988). Regarding the Paleozoic of the Paraná Basin, the same scenario is observed, with abundant isolated elements and rarer complete specimens.

Würdig-Maciel (1975) proposed an artificial classification of the lower actinopterygian teeth that occur in the Paraná Basin. Such classification is exclusively based on the external morphology of each specimen, being later complemented by Richter (1983), Richter et al. (1985), and Maranhão (1995). Those authors have shown that such components could potentially be useful in stratigraphic correlations, thanks to their horizontal occurrence not only in the Passa Dois Group (Würdig-Maciel, 1975), but also in other Brazilian Paleozoic basins, such as the Parnaíba (Alves et al., 2020) and the Amazon basin (Figueroa & Machado, 2018). Nevertheless, none of these authors took into account taphonomic features that could modify original aspects of these isolated remains.

Xenacanthid sharks are represented in the Paraná Basin by teeth and fin spines — which thanks to their more distinctive morphological characteristics — are relatively easier to be assigned to a genera and species than scales and teeth of ray-finned fishes (Würdig-Maciel, 1975). Six species based on isolated teeth have been described for the Corumbataí Formation: *Xenacanthus santosi* Würdig-Maciel 1975; *Xenacanthus angatubensis* Ragonha 1984; *Xenacanthus camaquensis* Ragonha 1984*; Xenacanthus ferrazensis* Ragonha 1984; *'Xenacanthus' moorei* Woodward 1889, and *Wurdigneria obliterata* Richter 2005. Although the species described by Ragonha (1984) have not been officially published (*nomina nuda*).

The purpose of this contribution is to describe new 'palaeoniscoid' and xenacanthid occurrences collected from a distal tempestite layer (storm deposit) of the Corumbataí Formation in the Santa Rosa de Viterbo region. The descriptions bring new information regarding the micro-ornamentations present in teeth and dermal scales, but also some considerations about taphonomic and preservation process and how they might have affected some of the ornamentation patterns observed. Moreover, the micro-ornamentations seem to be a good way to efficiently distinguish between different palaeoniscoid teeth morphotypes, which are a very common element in several deposits around the world, but the difficulty in being taxonomic classify prevents them from being of ample used.

3

2. GEOLOGICAL CONTEXT

The Paraná Basin is a major Paleozoic intracratonic syneclise located in the central-southeastern portion of South America, extending for more than 1.5 million km². The sedimentary package can reach 8 km in thickness (Milani et al., 1998). Based on regional unconformities, this package is subdivided by Milani et al. (1998) in six magmatic-sedimentary supersequences: Rio Ivaí (Ordovician-Silurian); Paraná (Devonian); Gondwana I (Carboniferous-Lower Triassic); Gondwana II (Mid to Upper Triassic), Gondwana III (Jurassic-Lower Cretaceous), and Bauru (Upper Cretaceous).

During the deposition of the Gondwana I Supersequence, the Gondwana supercontinent was becoming closer to the south pole (Caputo et al., 2008), so climatic changes led to glaciation episodes and marine incursions caused by deglaciation. These changes are recorded in the Itararé Group, in the Aquidauana Formation, in the Guatá and Passa Dois groups, as well as in the Pirambóia and Sanga do Cabral formations.

In the states of São Paulo, Goiás, and Mato Grosso, Schneider et al. (1974) subdivides the Passa Dois Group, from base to top, in the Irati and Corumbataí formations. In the central and southern portion of the Paraná Basin (Schneider et al., 1974; Meglhioratti, 2006), the Corumbataí Formation is considered correlatable to the Serra Alta and Teresina formations (Figure 1A). The deposition of these units, as well as the Corumbataí Formation, reflects the progressive continentalization of the Paraná Basin (Meglhioratti, 2006). The deposition began as the sea level rose, followed by the transition of a restricted to a less restricted marine environment, resulting in sedimentation in a tidal flat environment (Milani et al. 2007). This changes in deposition environments are represented by argillite, shale, and siltstone sequences, which are sometimes intercalated with layers of limestones and very thin sandstones in the upper portions of the unit (Schneider et al., 1974).

Absolute dating carried out by Rocha-Campos et al. (2019) of layers of probable volcanic origin located in the basal portion of the Corumbataí Formation yielded a mean ID-TIMS ^{206}Pb/^{238}U age of 257.5 ± 2.2 Ma, which corresponds to the Wuchiapingian (Cohen et al., 2013). The fossiliferous content includes bivalves, ostracods, sponge spicules, palynomorphs, lycophytes, glossopterids, conifer branches, gymnosperms, and charophytes (Faria et al., 2009; Holz et al., 2010, Rocha et al., 2020; Carvalho et al., 2021), besides a variety of vertebrate groups (see item 5. Discussion for more details).

3. MATERIAL AND METHODS

The samples analyzed in this study were collected from a distal tempestite layer of the Corumbataí Formation that crops out in Santa Rosa de Viterbo (SRDV), municipality of the northeastern region of the State of São Paulo (Figure 1B). This argillaceous layer is composed of illite, smectite, and kaolinite (Godoy et al., 2017; Montibeller et al., 2020), and contains coprolite bioclasts, scales, and teeth (Figure 2D-H). Thirty samples were randomly collected along the PH1 and PH3 mine fronts (Figure 2A-C) belonging to the pH7 Mineração de Calcário Ltda. mining company.
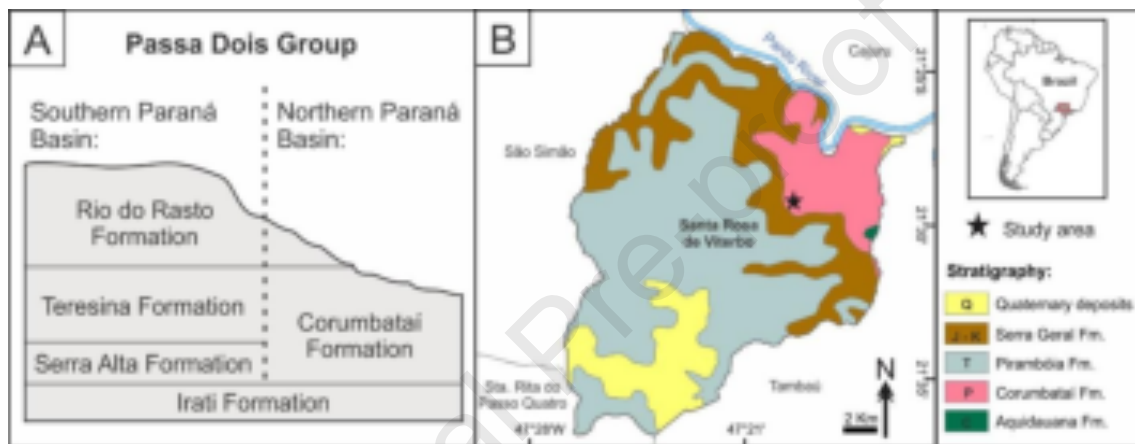

Figure 1 – Subdivision of the Passa Dois Group in the Paraná Basin (Adapted from Meglhioratti, 2006) **(A)**. Geological map and location of the municipality of Santa Rosa de Viterbo **(B)**. C-Carboniferous, P-Permian, T-Triassic, J-K-Jurassic/Cretaceous, Q-Quaternary.

At the laboratory, each sample of 1 kg was soaked in water for 15 days, to disaggregate the rock and separate the bioclasts from the rock matrix. This was the only necessary procedure for the desegregation, as the presence of expansive clays in the matrix (smectites) and the interaction with water were enough to make the rock friable, enabling the separation and preparation of the fossils. Circa 24.5% of the rock soaked in water did not disaggregate and was not used in the study. The disaggregated material was sieved and subdivided in 16-mm, 5-mm, and 0.85-mm (20-mesh sieve) fractions. The scale and tooth morphotypes separated from the rock matrix were classified with the aid of a Zeiss Stemi DV4 stereoscope. The recovered material is stored in the Paleontological Collection of the Geosciences Institute of the University of Campinas (IGe-UNICAMP).
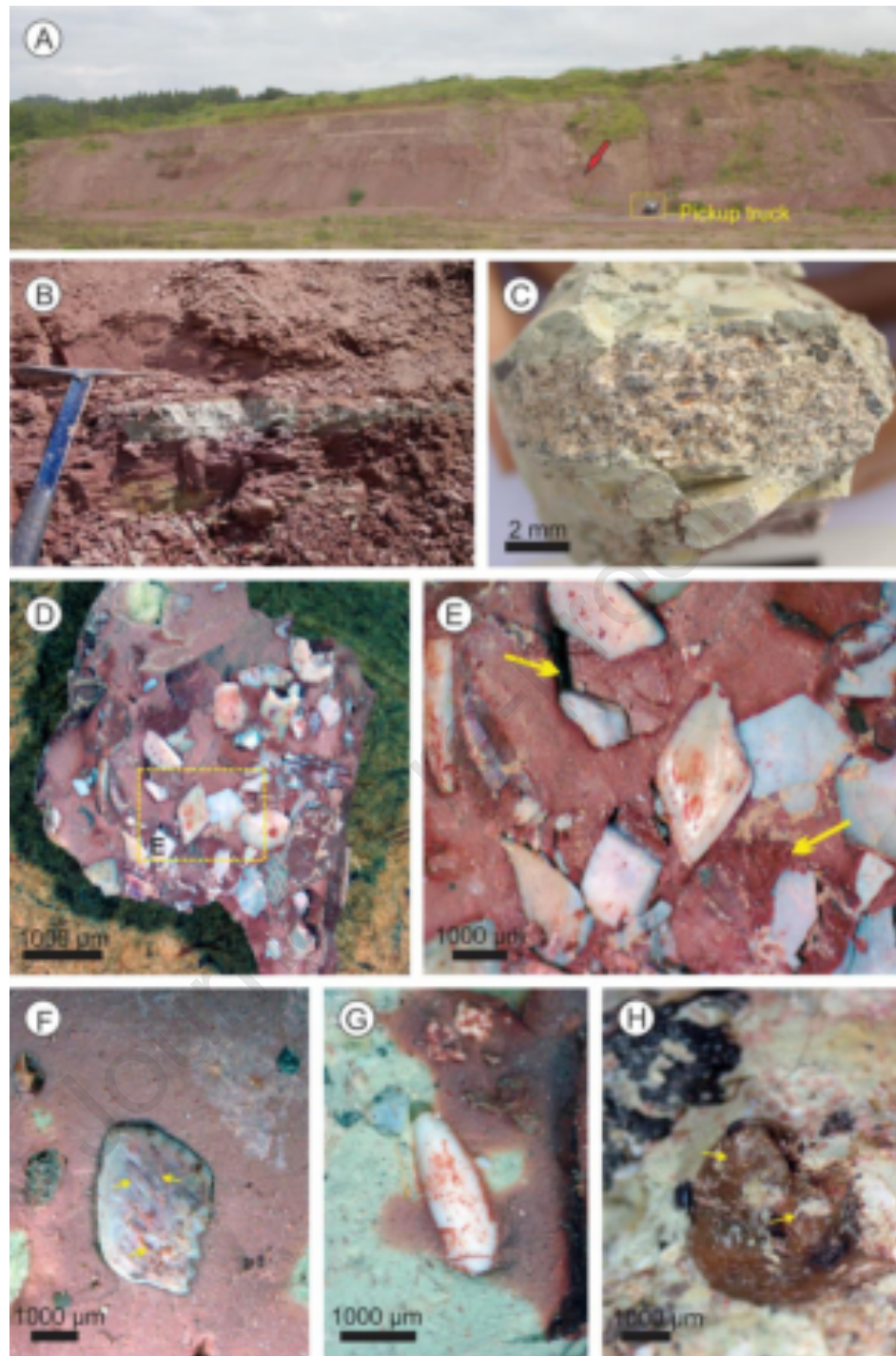
Figure 2 - Collection site and pre-processing hand samples. **A)** PH3 mine front, the arrow indicates the tempestite level where samples came from. The truck in the image is a reference to the size scale. **B)** Tempestite layer, stratigraphic hammer as scale. **C)** Distribution and packing of fossils in the layer, in section. **D)** Distribution of fossils in plant, with several fragments of scales in the sample. **E)** Detailed view of the highlighted region in (D), an entire smooth scale with punctuations on the surface. The arrows also indicate regions with the impression of already deteriorated scales. **F)** Complete ridged scale (indicated by arrows). **G)** Example of a palaeoniscoid tooth. **H)** Example of poorly preserved xenacanthid tooth, arrows indicate main cusps.

The morphological classification-key proposed by Würdig-Maciel (1975) was chosen to classify the 'palaeoniscoid' teeth. The classification is based on the morphology and external characteristics of the ichthyodonts that are visible to the naked eye and under the stereoscope, referred here as macro-ornamentations (Figure 3 and Table 1), such as: acrodin cap features, shape of the shaft, shaft ornamentation, and base inclination. This classification was further refined using the scanning electron microscope (SEM), which aided the recognition of micro-ornamentations on the tooth and scales surfaces, as in the descriptions of Richter (1983), Richter et al. (1985), and Maranhão (1995). For these observations, seven ichthyodont specimens and one scale were selected and covered with a thin carbon layer. The images were obtained using a JEOL JSM-IT500HR electron microscope, equipped with secondary electron (SE), back-scattered electron (BSE), and dispersive energy (EDS) detectors installed in the IGe-UNICAMP Laboratory for Mineral Quantification.

To validate our teeth classification and verify if the observed features raised in Table 1 — which was used to describe different morphotypes — are justified, we used a statistical hierarchical cluster to check for similarities between the specimens in order to create natural groupings. The analyzes were performed we the aid of the R software, with the package 'cluster' (Maechler et al., 2022), in which the Gower's distance (Gower, 1971) was used for the calculation of the dissimilarity matrix, within the 'daisy' function. Finally, the function 'diana' and 'pltree' were used for the construction of a divisive analysis cluster, which was found to be the most suitable method to group the data presented here. The variables thought to represent the original features of the teeth, and chosen for the similarity analyzes, were the shape of the shaft; macro-ornamentation of the shaft; micro-ornamentations of the shaft and acrodin cap; the length/width ratio, which shows the overall tendency of the tooth being longer rather than wider and vice versa; and the length/acrodin cap length ratio.

The same divise cluster analysis was performed with the data presented in Maranhão (1995), but for the work of Richter et al. (1985) — which complements with SEM analyzes the measurements and descriptions of Würdig-Maciel (1975) — the clustering was not possible, as these authors do not specify the number of specimens or which specimen was examined within each classification. If the SEM information is extrapolated and replicated for several specimens without variations, groups will be formed, but it would be like we are comparing the same specimen over and over again. Therefore, the final cluster will not be reliable. However, the measurements data from

Würdig-Maciel (1975) and Richter et al. (1985), as well as from Maranhão (1995), together we the code and data used for the hierarchical cluster analysis construction is available in the Supplementary Material.
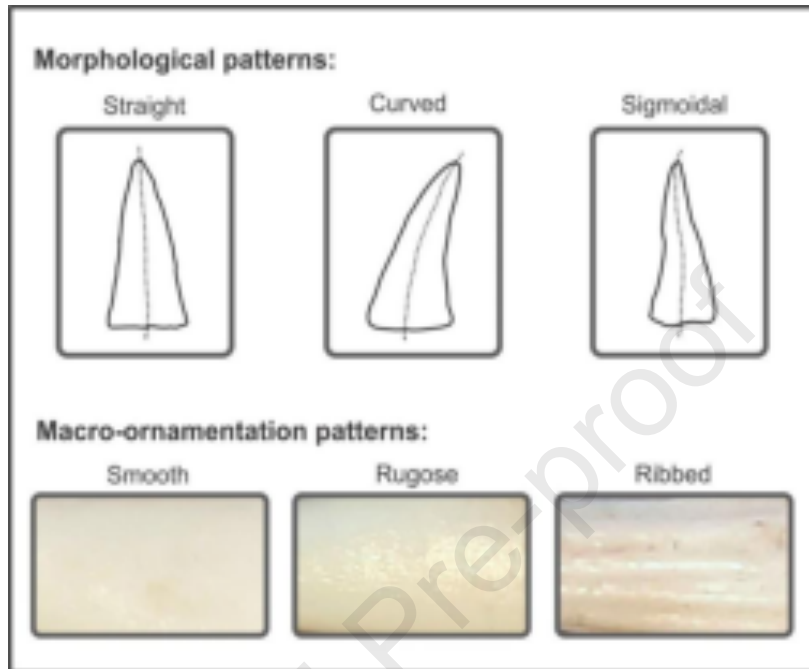

Figure 3 – Classification key adopted here for lower actinopterygian teeth showing the observed morphologies and surface ornamentation under stereoscope (Adapted from Würdig-Maciel, 1975)

Since, at some level, all palaeoniscoid teeth are broken, we found the need to stablish some considerations for the purpose of this work. We considered here as complete teeth, those specimens that probably represent 50-70% of the original tooth length, i.e., presenting the acrodin cap and a considerable part of the shaft. At the broken region the pulp cavity can be observed in cross-section, but the fractured area usually forms a straight, or slightly tilted, surface with serrated-like margins at the proximal portion of the tooth (Figure 6). For the purpose of the descriptions present in this paper this was considered the base of the tooth. In some unusual cases the base was completely rounded, and the pulp cavity is not in display (Figure 6A). In some other specimens, the region of the apex or the region of the base might be absent (with clear evidence of breakage), but since in most cases the shaft is intact, they were regarded as practically complete specimens. What does not fall into complete or practically complete category was considered as a fragment.

Regarding the dermal scales of lower actinopterygians, we preliminarily tried to distinguish smooth from ridged scales, according to Chahud & Petri (2008a). However,

a closer analysis indicated that when part of the enamel layer is removed from the surface, the grooves present in the scales become more evident, making the previously classified as smooth scales more similar to the ridged ones. Thus, instead of classifying and counting the scales in the same way as the ichthyodonts, we simply recorded their shape variations and diagenetically produced features.

4. RESULTS

4.1. Ichthyodonts

The majority of the ichthyodonts showed as main characteristics conical shape and massive acrodin cap in the upper portion, thus being attributed to the Palaeonisciformes Order (Moy-Thomas, 1971; Würdig-Maciel, 1975; Chahud & Petri, 2008a). Another set of teeth was also observed, with characteristics similar to those of Xenacanthiformes, *i.e.,* three non-serrated cusps of different sizes (Hampe, 2003; Ginter et al., 2010). A total of 212 specimens respective to ichthyodonts in the assemblage were analyzed, encompassing fragments and complete teeth , and also considering the fractions 16 mm, 5 mm and 10 samples from the 20-mesh fraction.

All teeth happened to be isolated in the SRDV layer. The majority of the ichthyodonts (71.23%, n=151) came from mine front PH3 and the rest from front PH1 (28.77%, n=61). Besides, the fraction with the largest concentration of ichthyodonts is the 20-mesh, containing 71.23% (n=151) of the total, whereas the 16-mm fraction contained only 3.3% (n=7). Most of the ichthyodont assemblage presented some kind of reworking, polishment and rounding (Figure 4), as usually expected for storm-generated bonebeds, such as:

(i)   cracking of the enamel, which seems the lightest abrasion signal.

(ii)   a slight wear of the surface, where the surface may be locally a little scratchy, but most of the shaft is integer.

(iii)   surface excavation like depressions or little craters on the shaft surface caused by progressive erosion.

(iv)   advanced stages of delamination, in which portions of the enameloid were removed, exposing more fibrous structures of the inner layers of the tooth (Fiorillo, 1988; Irmis & Elliot, 2006).

Only 17,45% (n=37) of all ichthyodont elements were recovered complete or practically complete, and thus being able to receive some taxonomic attribution or

morphological description. While others were too fragmented (58%, n=123) to be described and/or polished to be recognized (24,53%, n=52).

Figure 4 – Continous abrasion process on teeth showing some of the features observed and interpreted as signs of reworking within the assemblage.

4.1.1. Lower actinopterygian

From the total ichthyodont assemblage, only 26 specimens (12.26%) correspond to complete or practically complete palaeoniscoids ichthyodonts. However, at least 68.39% (n=145) of the ichthyodont population can be attributed to 'palaeoniscoids'. In some fragments, it was also possible to identify the general shape and/or the ornamentation of the shaft. However, to avoid misclassification, these fragments were not included in the descriptions.

Morphologies such as straight conical, curved, and sigmoidal teeth were identified in 52 specimens. Among these, the curved types predominate (48.0%, n=25), being 1.91 mm long and 1.1 wide in average, followed by the straight type (44.2%, n=23), 1.95 mm long and 1.19 mm wide in average. The sigmoidal-shaped specimens are rare, representing only 7.7% (n=4) of the assemblage, being 1.51 mm long and 0.78 mm wide in average, mainly concentrated in the 20-mesh fraction. Only one specimen was found in the 5-mm fraction, and none in the 16-mm fraction.

The most common ornamentation type is the smooth (45.9%, n=67), which lack any perceptible ornamentation and can be observed both in complete and incomplete teeth. The second is the rugose ornamentation (17.8%, n=26), being also present in specimens with smooth and rugose faces, totalizing 8.9% of the assemblage (n=16). However, the definition of rugose surface used here differs from the original one proposed by Würdig-Maciel (1975), who describes as rugose ornamentation a surface marked by short, delicate, and discontinuous ribs. For SRDV, we use this denomination to describe a smooth surface that is a little rough under the stereoscope, but not as much as the ribbed ichthyodonts. Under SEM, these ichthyodonts tend to present micro-ornamentations, which are absent on the surface of truly smooth ichthyodonts.

In all, six different morphotypes of palaeoniscoid teeth were recognized, from which two types represent incomplete teeth showing distinct ornamentations under SEM, and therefore they were kept in different categories. An artificial systematics is presented below, including the description of the main characteristics, and a brief discussion on the classifications adopted here. Characteristics for each of the 26 specimens used for the systematics below and for the clustering analyzes (Figure 5) can be individually consulted in Table 1, while Table 2 lists the correspondence between the SRDV ichthyodonts and ichthyodonts with similar features described in the literature.

Table 1 (**AT THE END OF THE MANUSCRIPT**) – General description for each tooth considered in the morphotype grouping.

Class Osteichthyes Huxley (1880)

Subclass Actinopterygii Cope (1887)

Order 'Palaeonisciformes' Hay (1902)

Ichthyodont 1

(Figure 6A and C)

Occurrence: 14PH1/16; 14PH1/20; 31PH1/20; 99PH3/20; 106PH3/20;138PH3/20.

Description: straight shape and smooth surface both under the stereoscope and SEM. Although at least one specimen (99PH3/20) has ribs at the base of the shaft, which acquires a rugose appearance towards the distal margin of the tooth. Two specimens also show faces that vary from smooth to rugose. Yellowish translucent acrodin cap, pointed

tip. The size of the cap varies from 1/3 to 1/5 of the tooth length. Straight base, with average length circa twice the size of the base.

Dimensions (six specimens, 23.08% of the assemblage): 1.18-2.98 mm long, 0.23-1.49 mm wide.

Observation: similar to ichthyodont A of Würdig-Maciel (1975) and I-1 of Richter et al. (1985). The SRDV specimens are smaller, but the length/base ratio is similar to those of the teeth described by Würdig-Maciel (*op. cit.*), the length being up to 2.3 times the width of the base. Whilst for the teeth studied by Maranhão (1995) the length is almost three times the size of the base (2.8x in average). Teeth with similar morphology were also described by Cione et al. (2010) for the El Jarillal Formation in the Calingasta-Uspallata basin (Argentina) as being type I-1, as well as by Piñeiro (2006) in the formations Frayle Muerto e Mangrullo from Uruguay. Nevertheless, the type I-1 described by Richter et al. (*op. cit.*) presented some ribbed structures, and under SEM images some longitudinal to anastomosed ridges (Cione et al., 2010). It is not discarded the possibility that the absence of this ornamentation patterns in SRDV samples are a result of advanced abrasion on the surface of the shaft (see discussion of section 4.1.1.1).

Ichthyodont 2
(Figure 6B and D)

Occurrence: 8PH3/5

Description: curved shape and costate (ribbed) surface, well-marked ribs, straight to slightly concave base. In one specimen, all faces are ribbed, while only the lateral faces of a second specimen show ribs and the labial and lingual faces are smooth. The ribs become incipient towards the apical part and disappear in the acrodin cap. Short, rounded, and massive acrodin cap, size equivalent to circa 1/6 of the length. Length is 1.6 times the base. Under SEM, besides the ribs, the surface of the shaft is smooth, free of micro-ornamentations, as well as the apical apex.

Dimensions (two specimens, 7.69% of the assemblage): 2.06-2.39 mm long, 1.18-1.75 mm wide.

Observation: this description seems equivalent to ichthyodont D of Würdig-Maciel (1975) and I-4 of Richter et al. (1985), despite SRDV specimens having a smaller length/base ratio and being less elongated than those of Würdig-Maciel (*op. cit.*), which present teeth 2.3 times longer than the base, whereas in the teeth presented by Maranhão (1995) the length/base ratio is 2.6 in average. Type I-4 teeth also were reported by Piñeiro

(2006) for the Frayle Muerto and Mangrullo formations in Uruguay, but no description was presented by this author for a better comparison.

Ichthyodont 3
(Figure 6E and F)

Occurrence: 20PH1/5; 31PH1/20

Description: curved to slightly sigmoidal shape, rugose surface, straight and narrow base, massive acrodin cap and pointed tip. Length of the shaft is twice the width of the base, and the acrodin cap equals 1/7 of this length. Under SEM, the acrodin cap is smooth and the shaft presents incipient, 8.87- to 38.24 µm long, fusiform tubercles.

Dimensions (two specimens, 7.69% of the assemblage): 1.98-2.45 mm long, 1.06-1.17 mm wide.

Observation: similar to morphotype I of Richter (1983) and I-9 of Richter et al. (1985).

Ichthyodont 4
(Figure 6G and H)

Occurrence: 14PH1/20; 106PH3/20;150PH3/20

Description: sigmoidal shape and rugose surface, straight tooth base and 2.2 times shorter than the length of the shaft in average. Translucent acrodin cap, pointed tip, 1/9 of the length of the shaft. Under SEM, the surface of the acrodin cap is smooth and the shaft is ornamented with longitudinal, short, slightly sinuous, and discontinuous tubercles on the lateral faces. Tubercles are 48.9-170.6 µm long and 3.9-12 µm wide and spacing from 7.4 to 37.3 µm.

Dimensions (three specimens, 11.54% of the assemblage): 1.63-1.81 mm long, 0.68-0.95 mm wide.

Observation: it seems to correspond to ichthyodont F of Würdig-Maciel (1975) and I-6 of Richter et al. (1985), although the micro-ornamentation patterns look more like type I-9 of Richter et al. (*op. cit.*). Type F is a sigmoidal ichthyodont having a smooth cap but with grooves on the shaft surface (I-6), whereas type I-9 is a curve ichthyodont having a smooth cap and surface covered with tubercles. In turn, the tubercles of the ornamentation of the SRDV ichthyodonts are not as well developed as those of Richter (1983), being more spaced from each other and more sinuous rather than fusiform. This lack of definition in the ornamentation is probably a result from erosion of the tooth surface, which partially deteriorated the original characteristics. Nonetheless, Ichthyodont 4

13

resembles subtype F-1 of Maranhão (1995). The subytype F-1, however, seems to present shorter tubercles than the ones observed for SRDV, ranging from 14 to 22 µm long. But in average these teeth are longer than those from SRDV, showing in average a base three times smaller than the length. This same length/base value was also observed for the type F teeth of Würdig-Maciel (1975).

Ichthyodont lacking an acrodin cap 5A

(Figure 6I and K)

Occurrence: 8PH3/5; C.C.PH3-5; 7PH1/20; 8PH3/20; 138PH3/20; 150PH3/20

Description: curved shape and predominantly rugose surface, presenting variations. Labial view reveals surface varying from smooth to rugose, sometimes in the same specimen. In the lingual view, ornamentation can also vary from smooth to rugose, but three specimens present ribbed surface with well-marked ribs. The acrodin cap is lacking, exposing the protruding round mount at the tip of the tooth shaft from where it was detached. Tilted to straight base, the total length of the shaft being 1.8 times that of the base. Under SEM, the shaft presents sinuous grooves longitudinally distributed along all faces.

Dimensions (nine specimens, 34.62% of the assemblage): 1.77-2.76 mm long, 0.87-1.44 mm wide.

Observation: It is possible that, as ichthyodonts 3 and 4, these ichthyodonts originally presented tubercles as ornamentation and the grooves resulted from erosion and diagenesis. For this reason, some faces are smoother than others. In this case, these ichthyodonts would resemble type I of Richter (1983) and I-9 of Richter et al. (1985).

Ichthyodont lacking the acrodin cap 5B

(Figure 6J and L)

Occurrence: 138PH3/5; 99PH3/20; 153PH3/20; 7PH1/20

Description: Under the stereoscope, straight to slightly curved shape and smooth to rugose surface, straight base, acrodin cap is lacking with protruding ring at the base. Similar to 5A, however, under SEM it is possible to distinguish well-pronounced tubercles of 14.2-34.9 µm in length, spacing varying from 1.16 to 3.37 µm, and width from 1.4 to 2.8 µm. The total length is 1.8 times the base.

Dimensions (four specimens, 15.38% of the assemblage): 1.32-2.06 mm long, 0.72-1.13 mm wide.

<u>Observation:</u> the characteristics of these ichthyodonts resemble the variations of type A of Würdig-Maciel (1975) found by Maranhão (1995), who describes subtypes A-1 and A-2 as straight conical teeth with fusiform tubercles. The main difference between both types is the cap ornamentation, with A-1 gently exhibiting the same tubercles present in the shaft and A-2 being smooth. According to Maranhão (1995), these ornamentations are comparable to those of type I-9 of Richter et al. (1985), who mention curved forms, so that the former author concludes that these variations in type A are probably new morphological types. Subtype A-1 presents tubercles varying from 14 to 30 µm long, similarly to the range observed for SRDV, while Maranhão (1995) does not inform the size variation of the tubercles for subtype A-2. In addition, both subtypes of Maranhão (1995) are circa three times longer than the base width, thus it seems that SRDV could be a shorter version of either of these subtypes, since no acrodin cap was found to differentiate between them.

Table 2- Correspondence between Palaeonisciformes ichthyodonts found and described for SRDV and ichthyodonts with similar features described in the literature.

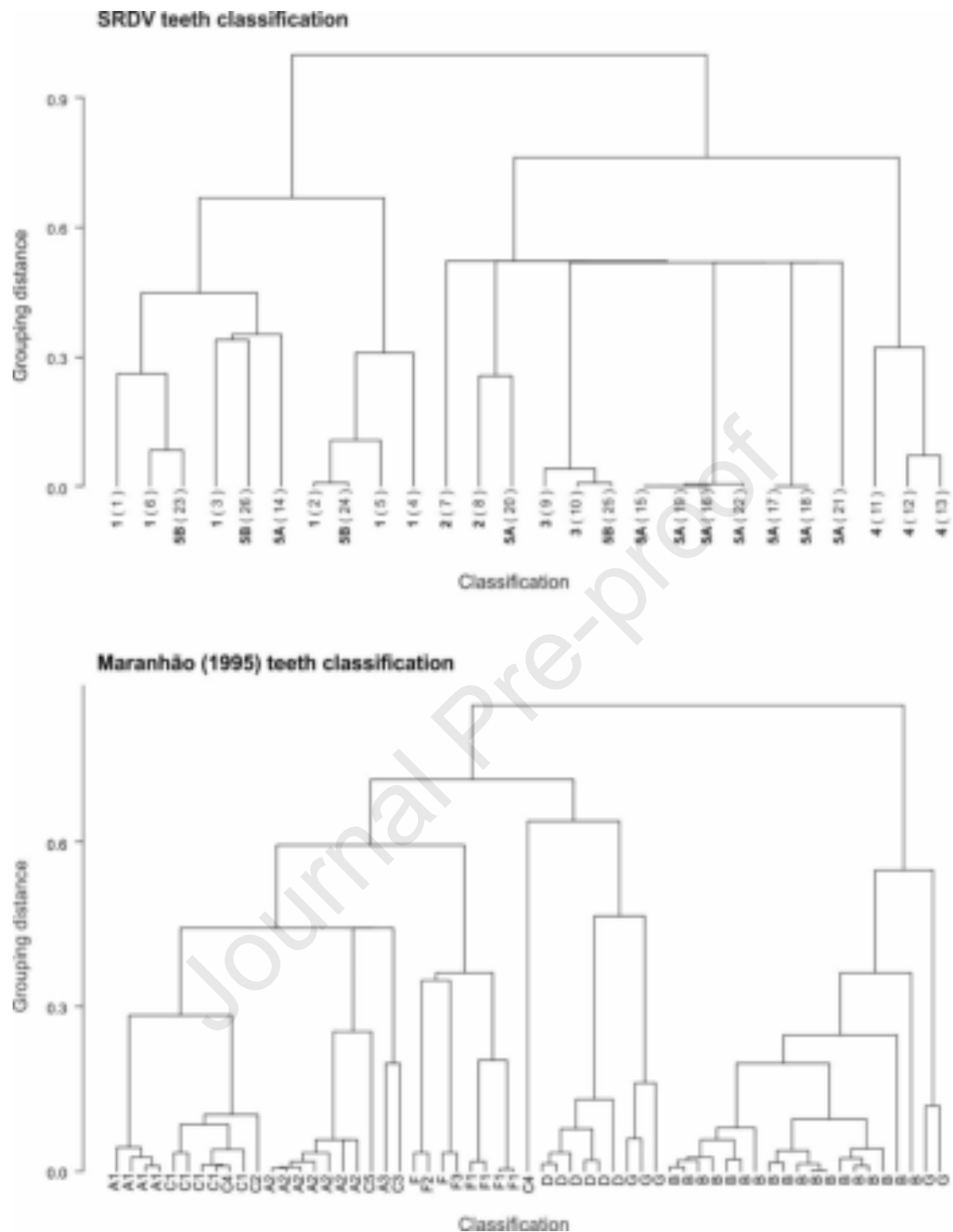| CLASSIFICATION				
This work	**Würdig-Maciel (1975)**	**Richter (1983)**	**Richter et al. (1985)**	**Maranhão (1995)**
Ichthyodont 1	A	A	I-1	A
Ichthyodont 2	D	D	I-4	D
Ichthyodont 3		I	I-9	
Ichthyodont 4	F		I-6/I-9	F-1
Ichthyodont 5A		I?	I-9?	
Ichthyodont 5B	A?		I-9?	A-1/A-2?

Figure 5 – Dendrogram resulted from the hierarchical cluster for the teeth population from SRDV and from Maranhão (1995). The numbers within parenthesis correspond to the observations numbers in Table 1.
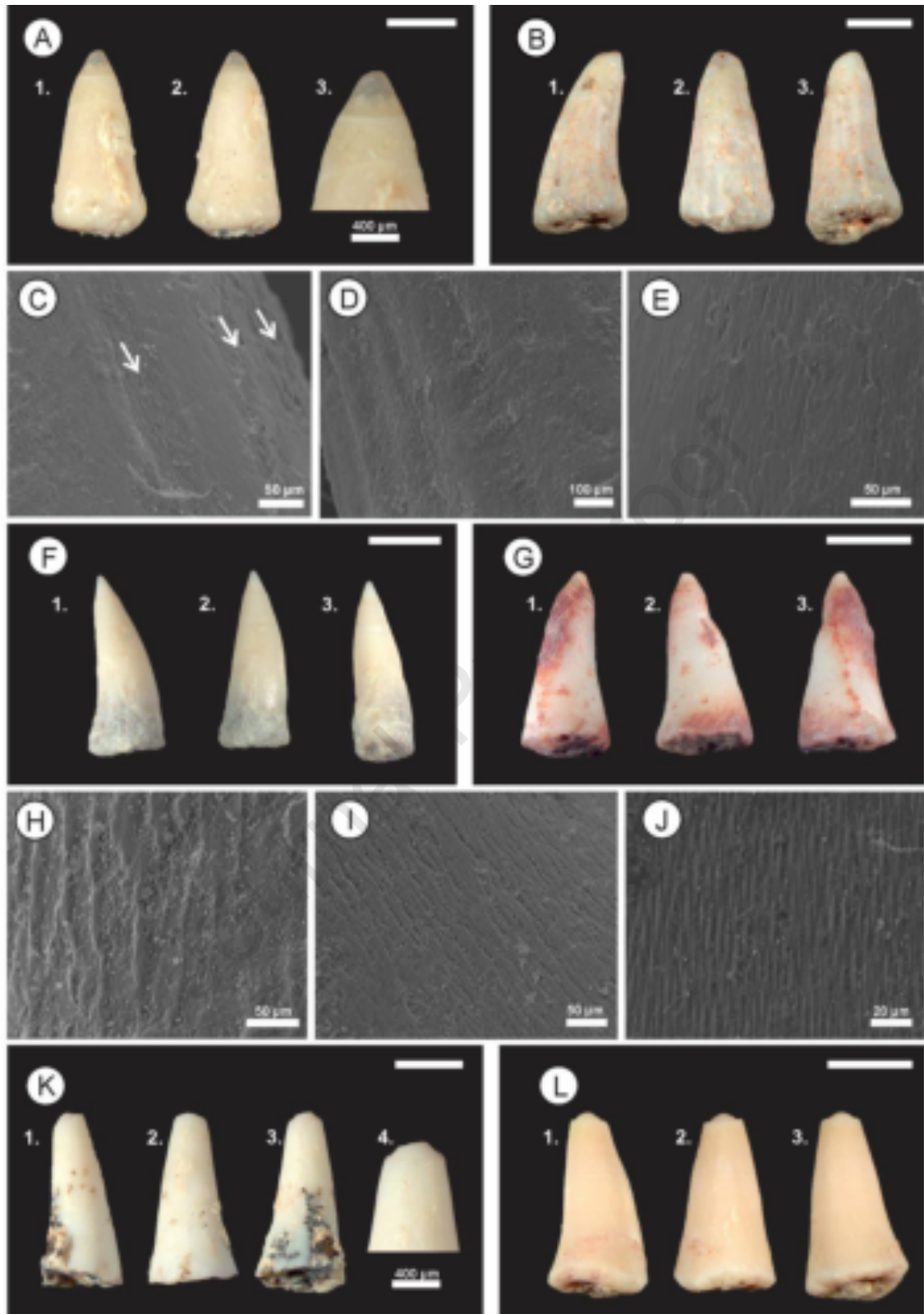
16

Figure 6 - Different palaeoniscoid ichthyodonts found in the layer. Images A-B, F-G and K-L are stereoscopic images and C-E, and H-J are SEM images. **A)** Ichthyodont 1, 14PH1/16 [1. Labial view, 2. Lingual view, 3. Detail of the translucent apical cap]; **B)** Ichthyodont 2, 8PH3/5 [1. Lateral view, 2. Labial view, 3. Lingual view]; **C)** Detail of A, micro-ornaments of Ichthyodont 1. Arrows indicate regions of delamination of the surface caused by abrasion; **D)** Detail of B, micro-ornaments of Ichthyodont 2; **E)** Detail of F, Ichthyodont 3; **F)** Ichthyodont 3, 20PH1/5 [1. Lateral view, 2. Labial view, 3. Lingual view]; **G)** Ichthyodont 4, 106PH3/20 [1. Lateral view, 2.

Lingual view, 3. Labial view]; **H)** Detail of G, micro-ornaments of Ichthyodont 4; **I)** Detail of K, micro-ornaments of Ichthyodont 5A, 7PH1/20; **J)** Detail of L, micro-ornaments of Ichthyodont 5B, 138PH3/5; **K)** Ichthyodont 5A [1. Lateral view, 2. Labial view, 3. Lingual view, 4. Detail of absent apical apex]; **L)** Ichthyodont 5B [1. Lateral view, 2. Labial view, 3. Lingual view]. Scale bar = 1 mm.

4.1.1.1.<u>Discussion about the specimens</u>

Although one of the main criteria for grouping the teeth into morphotypes is the shape of the shaft, it is worth noting that this feature could be misinterpreted and not actually reveal the true shape of the original teeth. Considering that usually all palaeoniscoid teeth have a broken base — since they generally broke off from the fish mouth — depending on the region of breakage the fossil remain could appear straight, curved, or sigmoidal. The sigmoidal-shaped teeth from SRDV, in particular, could be a configuration produced by abrasion as two out of three specimens show clear signs of a worn surface from the middle to their distal or proximal portion.

Is also important to carefully interpret some acrodin cap features, as the fact that the acrodin cap is short and rounded or elongated and acute, given that this is probably related to natural wear of the tooth still in life. Likewise, the inclination of the base, because it might not be a valid distinguishable feature between morphotypes, since it only represents how the tooth broke off, not reflecting any biological characteristic. It is clear that, in order to better understand the disarticulated remains fidelity to their original features, more complete fossils are needed, as well as reevaluation of species already described. According with the suitability, the use of techniques, like X-ray micro-computed tomography (µCT), on those samples, which probably was not widespread or available at the time some of the species were described, would help to give them a detailed examination of internal skeletal features (Figueroa et al., 2019). Thus, allowing the investigation of shape and macro-ornamentation variability within an individual.

As far as the micro-ornamentations are concerned, despite having classified SRDV teeth into six different morphotypes, the characteristics described here seem to be enough to distinguish, with some certainty, only three true morphotypes, referring to Ichthyodont 1, 2 and 4. Each of these classes has unique shapes and ornamentations within the assemblage, unlike Ichthyodont 3, 5A and 5B, which present similarities, and may or may not be variations of the same morphotype affected by a progressive process of abrasion and diagenesis. Although the specimen analyzed for Ichthyodont 1 under SEM (Figure 6A) shows signs of longitudinal flacking and delamination that could be

misinterpreted as similar to the ribbed surface of Ichthyodont 2. In Ichthyodont 2 the ribs are much more pronounced than the features produced by erosion in 1, and the spaces between the ribs are always smooth, whilst in Ichthyodont 1 they show a fibrous and irregular pattern. However, the delamination process is also evidence of advanced abrasion, therefore the smooth shaft with no micro-ornamentation pattern could be the result of continuous polishment of the shaft.

The Ichthyodont 5B presents well preserved micro-ornaments, with tubercles being readily distinguished and individualized, probably due to less abrasion on the surface of the shaft. In Ichthyodont 3, the tubercles are less pronounced, but have a remarkably similar shape to 5B and could easily be a polished and abraded version of these one. On the other hand, Ichthyodont 5A presents grooves on the surface of the shaft, instead of some more pronounced ornamentation, as in the tubercles of Ichthyodont 5B or 4. This could result from intense abrasion that polished the original tooth textures to a more '2D' version observable in Figure 6I, or it could be a texture created by abrasion itself in originally smooth specimens, for example, generating a pattern of cracking and flaking parallel to the fibrous structure of the tooth (Behrensmeyer, 1978; Fiorillo, 1988; Irmis & Elliot, 2006).

That been said, the fossils recovered for the tempestites from SRDV are a good example that despite reworking and transport micro-ornamentation still can be recognize on the shaft. Considering that the isolated teeth of 'palaeoniscoid' fishes cannot be taxonomic classify, as is impossible to say if they represent only one or several species, it seems that micro-ornamentations observations are a good criterion to categorize them (Richter, 1983). However, any interpretation should also take into account the taphonomic history of each stratum, in order to correctly interpret the features observed on the specimens.

We can note the importance of such micro-ornamentation at the clustering analysis (Figure 5) performed with the data reunited from Maranhão (1995), in which the subtypes A1, C1, C2, and at least one C4 were grouped together. This is due to their smooth macro-ornamentation and presence of fusiform tubercles at the shaft and acrodin cap under SEM, despite A1 being a straight type of teeth and the C type curved. For the SRDV cluster analysis (Figure 5) the lack of SEM information for the majority of the specimens, consequently, assigns a greater weight to the macro-ornamentation and shaft shape features, as well as the length/width ratio, in the final grouping at the cluster. As we can see for the similarity obtain between Ichthyodont 5B and other morphotypes,

especially Ichthyodont 1, but also, for example, for the greater dissimilarity between specimen 4(11) and the others Ichthyodont 4, specimen 1(4) and the rest of Ichthyodont 1, and for specimen 2(7) and 5A(21). Although, for the Ichthyodonts 5A the cluster analysis put them all very close at the dendrogram, suggesting that they actually belong to a separate group of the rest of the ichthyodonts. Whereas the 5B group specimens could belong to other morphotypes described.

4.1.2. *Xenacanthiformes*

Teeth with xenacanthid characteristics represent 5.20% (n=11) of the assemblage. No complete specimen was found, all of them with broken and isolated cusps (45.45%, n=5) or with only the base, without the cusps (36.36%, n=4). The bases and the corresponding broken cusps were found for two specimens (18.18%), being the closest occurrence to a complete Xenacanthiformes tooth. The systematic description of these elements is presented below.

Chondrichthyes Huxley, 1880

Elasmobranchii Bonaparte, 1838

Xenacanthiformes Berg, 1937

Xenacanthidae Fritsch, 1889

Ichthyodont 6

(Figure 7A)

Occurrence: 8PH3/5

Description: tricuspid crown divided in three units: the base and two more fragments of the main cusps. Oval base, more elongated along the labial-lingual direction, rounded margins. Slightly protuberant coronal button. Rhomboid shape, major axis in the labial-lingual direction, extending close to the region between the main cusps, area equivalent to 1/3 of the base area. The right main cusp (lingual view) presents a bigger base when compared to that of the left cusp; both are elongated in the labial-lingual direction, but more accentuated in the right cusp. Right cusp slightly tilts outwards. Both main cusps are smooth in the basal region. The intermediate cusp presents narrower base when compared to those of the main ones and is located slightly ahead of the other two, right to the extremity of the labial margin. Pronounced basal tubercle (lateral view), concave

oval shape in inferior-aboral view. In aboral view at least seven nutritive foramina were recognized surrounding the tubercle.

Dimensions (one specimen, coronal view): base (2.69 mm x 2.13 mm), coronal button (1.29 mm x 0.91 mm), base of the left cusp (0.90 mm x 0.76 mm), base of the right cusp (1.14 mm x 0.79 mm), base of the intermediate cusp (0.65 mm x 0.46 mm), basal tubercle in lateral view (0.44-mm high x 0.87-mm long), width of the basal tubercle in aboral view (1.05 mm).

Ichthyodont 7
(Figure 7B)

Occurrence: 150PH3/20, 153PH3/20

Description: tricuspid crown divided in four units (isolated base and cusps). Subtriangular base, narrowing in the lingual margin direction, originating a "V" shape. Rhomboid to almost rounded coronal button, slightly prominent, area equals half of the area of the base in specimen 150PH3/20 and more than half in 153PH3/20. Oval basal tubercle, slightly concave and pronounced. In lateral view, slightly flattened tooth base. In aboral view at least seven nutritive foramina were recognized surrounding the tubercle in the specimen 150PH3/20, whilst in specimen 153PH3/20 at least five were recognized in aboral view, but also in coronal view, behind the coronal button and close to the lingual margin. Main left cusp with short rib in the upper portion of the labial view and a slight compression in the lingual face. The intermediate cusp presents smaller base when compared to those of the main ones and is located exactly between them, right at the extreme of the labial margin. Cusps slightly curving backwards.

Dimensions (two specimens, coronal view): **150:** base (3.07 mm x 2.39 mm), coronal button (1.19 mm x 1.16 mm), base of the right cusp (1.38 mm x 0.87 mm), base of the left cusp (1.15 mm x 0.94 mm), base of the intermediate cusp (0.43 mm x 0.4 mm), height of the main left cusp (1.20 mm), width of the basal tubercle in aboral view (1.07 mm). **153:** base (2.26 mm x 1.72 mm), coronal button (1.05 mm x 0.91 mm), base of the right cusp (0.85 mm x 0.51 mm), base of the left cusp (0.76 mm x 0.72 mm), base of the intermediate cusp (0.28 mm x 0.38 mm).

Ichthyodont 8
(Figure 7C)

Occurrence: 150PH3/20

Description: Tricuspid crown with broken cusps. Rounded base, slightly narrowing towards the lingual margin. Main cusps with narrow bases, intermediate cusp with base of the same size as those of the main cusps and located slightly ahead of the other cusps, close to the labial extremity. Coronal button, despite covered with sediment, slightly prominent. The cusps seem to be convergent and tilt outwards. Basal tubercle is more prominent and slightly concave.

Dimensions (one specimen, coronal view): base (1.52 mm x 1.49 mm), base of the right cusp (0.35 mm x 0.45 mm), base of the left cusp (0.30 mm x 0.4 mm), base of the intermediate cusp (0.37 mm x 0.36 mm), width of the basal tubercle in aboral view (0.54 mm).
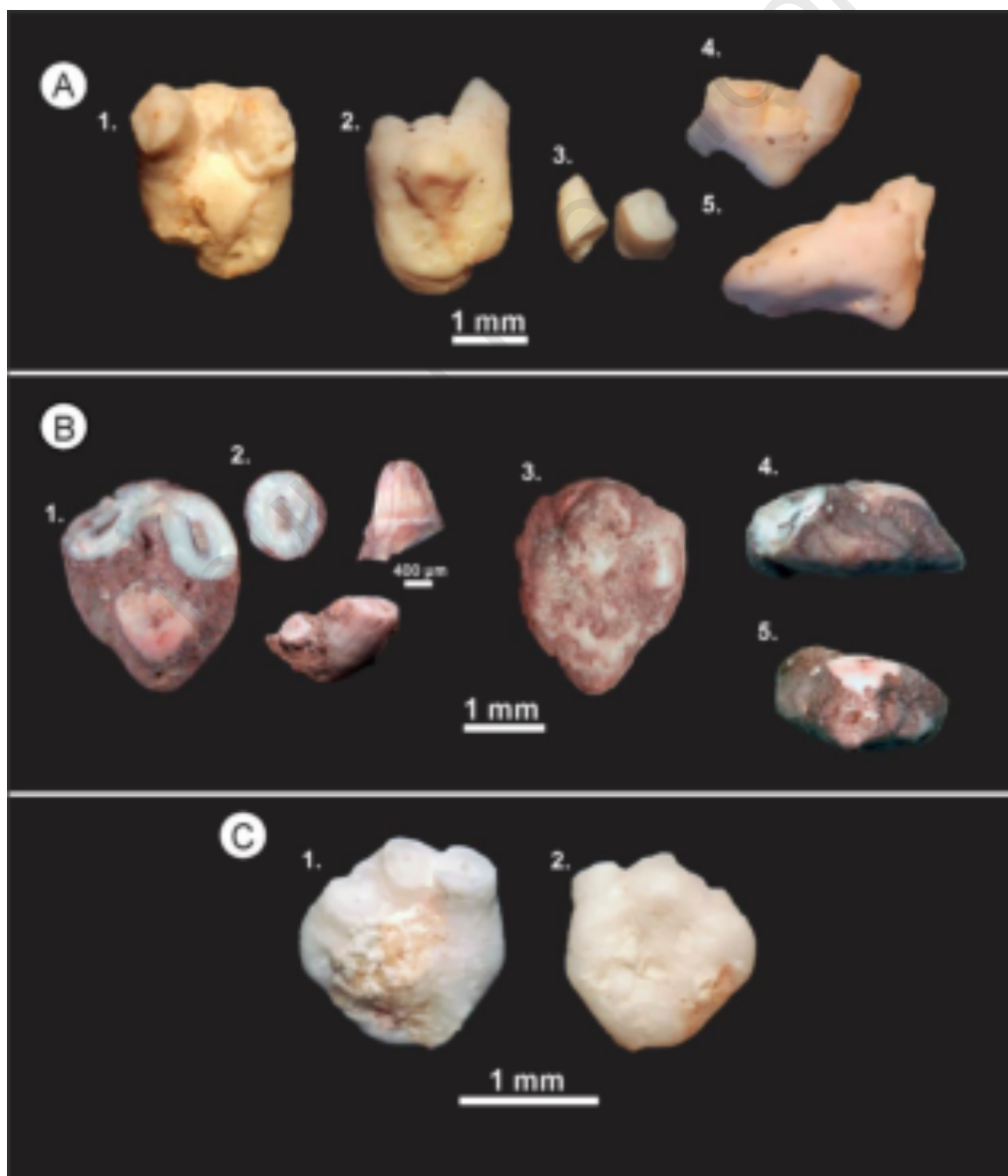

Figure 7 - Xenacanthiformes teeth. **A)** Ichthyodont 6 of rhomboid coronal button, 8PH3/5 [1. Lingual occlusal view, 2. Inferior view, 3. Fragments of the main cusps, 4. Labial view, 5. Lateral view]; **B)** Ichthyodont 7, 150PH3/20 [1. Lingual occlusal view, 2. Fragments of the main cusps,

3. Inferior view. 4. Lateral view, 5. Lingual view]; **C)** Ichthyodont 8, 150Ph3/20 [1. Lingual occlusal view, 2. Inferior view].

4.1.2.1.<u>Discussion about the specimens</u>

Despite some differences in the sizes of the bases of the main cusps in comparison to those of the intermediate cusp's bases in Ichthyodont 8, or the rhomboid shape of the coronal button in Ichthyodont 6, these ichthyodonts share similar characteristics. The bases in all these specimens seem to tend to a subtriangular shape, thanks to the narrowing towards the lingual margin. The coronal button is in general a little prominent and the basal tubercle is drop-shaped and concave. These characteristics suggest that the differences observed in the specimens are all related to Xenacanthidae. In accordance with Ginter et al. (2010) the Xenacanthiformes sharks can be grouped into two families: Diplodoselachidae, the most primitive within the order, and Xenacanthidae.

Xenacanthid sharks were a global widespread group from Lower Carboniferous to Upper Triassic (Hampe, 2003), being very common in Europe and North America, but Gondwanan species are rarer. Based on teeth record, some of the occurrences were reported from the Lower Carboniferous of Australia, where the genus *Reginaselache* is designated by Turner & Burrow (2011) to the Diplodoselachidae family. This same family was also documented in the Irati Formation, Permian unit that underlies the Corumbataí Formation, in which Chahud & Petri (2008b) reported the species '*Xenacanthus*' *albuquerquei* Silva Santos 1946, the oldest occurrence of Xenacanthiformes in the Paraná Basin.

This taxon was first known for the Lower Permian of the Parnaíba Basin, in the Pedra do Fogo Formation, where the original description of the species was made, and evidence the similarity between faunas of the Paleozoic Brazilian basins (Figueroa & Machado, 2018). Later the species was reassigned by Chahud & Petri (2010) to the new genus *Taquaralodus* by virtue of its cusps morphology. One the main characteristic of this specie is that one of the lateral cusps is always bigger than the other, both are always tilted towards the lingual margin, and rise perpendicularly from the base. Even though one of the lateral cusps of Ichthyodont 6 is larger than the other, the remaining part of the cusp is tilted since the base of the tooth towards the labial margin. In addition, none of the other specimens of SRDV show great size difference in the base of lateral cusps.

Concerning the Xenacanthidae family, there are records for Gondwanaland for the Middle Triassic from Australia (Ginter et al., 2010), and Upper Triassic from India

(Bhat et al., 2018) — linked to the genus *Mooreodontus*, a taxon limited to the Triassic — and Permian occurrences only known for South America from sediments of Brazil (Cione et al., 2010). According to Ginter et al. (2010) the Xencanthidae family encompasses the genera: *Xenacanthus*, *Triodus*, *Plicatodus*, *Wurdigneria*, and *Mooreodontus*. Except for *Plicatodus* — a Carboniferous-Permian genus known from Czech Republic, Austria, and Germany (Ginter et al., 2010) — the other four genera were recorded for the Paraná Basin within the Passa Dois Group. Many attributes that are very characteristic of *Plicatodus*, such as distally sigmoidal lateral cusps and pattern of cristae distribution, could not be compared to the specimens presented here since they occur in the cusps of the tooth, which in SRDV are broken or missing. Nonetheless, the samples from SRDV diverge from the genus *Plicatodus* because the latter has an elliptical base due to a mesio-distal elongation not seen in SRDV specimens, thus they cannot be ascribed to this genus.

The genus *Triodus* was designated by Pauliv et al. (2017) for teeth found in the Rio do Rasto Formation, Late Permian unit that overlies the Corumbataí Formation, which comprises the youngest, and first record of this taxon in Western Gondwana. Several aspects that characterize *Triodus richterae* Pauliv et al. 2017 can be found in Ichthyodont 7, such as: vertical cristae on the labial face of the cusp, though more details of the distribution and ornamentation pattern could not be observed; coronal button with a rhomboid shape; presence in oral view of one foramen at the lingual margin of the coronal button; rounded or horseshoe shaped basal tubercle. However, the average size described by Pauliv et al. (2017) to *T. richteae* is smaller than the measures obtained for the teeth presented here, and the base of SRDV specimen is not oval, but more like a triangular base.

Besides, *T. richteae* displays at most two large and two minor nutrient foramina in aboral view surrounding the tubercle, whereas in Ichthyodont 7 at least seven foramina were recognized, despite the base have been abraded in aboral view. The erosion process transformed these structures into shallow depressions, but might also had erase some of them, precluding the right count of nutritive foramina. Additionally for the Rio do Rasto Formation, Pauliv et al. (2014) described as well the species *Xenacanthus ragonhai.* This differs from SRDV teeth because its coronal button is more prominent and inflated than in the SRDV specimens, and because it also presents a sub-circular and semi-spherical shape. Moreover, the basal tubercle is rounded in aboral view, while SRDV is more drop shaped.

For the Corumbataí Formation, was reported by Ragonha (1984) the occurrence of '*Xenacnathus' moorei* Woodward 1889, which is now recognize as *Mooreodontus moorei* Woodward 1889 after the species has been revised by Hampe & Schneider (2010). What would imply that this is the youngest occurrence of this genus and the only known occurrence before the Triassic period, since this genus is currently considered to be strictly post-Paleozoic (Ginter et al., 2010) and the Corumbataí Formation Late Permian in age (Rocha-Campos et al., 2019). Consequently, the findings of Ragonha (1984) should be carefully interpreted until detailed revaluation. In accordance with the description of the specimens found by Ragonha (1984) and the characterization of this genus stated by Hampe and Schneider (2010) this taxon differs from the teeth of SRDV by: the large size and oval shape of the coronal button, although it can sometimes assume a diamond shape similarly to the one of Ichthyodont 6; basal tubercle poorly developed and with a discrete depression. Nevertheless, the base of *M. moorei*, a triangular shape base pointed lingually, resembles the base of Ichthyodont 7.

Despite never formally published, Ragonha (1984) also described in his doctoral thesis the occurrence, in the Corumbataí Formation, of three new *Xenacanthus* species based only on teeth: *Xenacanthus angatubensis*, *Xenacanthus camaquensis*, and *Xenacanthus ferrazensis*. In *X. angatubensis*, the width of base tends to be greater than the length; one of the striking features of *X. camaquensis*, besides the smooth cusps, is the aboral face of the base completely concave and circular; and in *X. ferrazensis*, the base is characteristically rhomboid, and the cusps are smooth. Only one almost complete cusp was found in SRDV, but it contained at least one rib, which would discard the possibility to be *Xenacanthus camaquensis* or *Xenacanthus ferrazensis*.

In the correlatable Estrada Nova and Teresina Formation in the State of Rio Grande do Sul, Würdig-Maciel (1975) and Richter (2005) also reported new xenacanthid species. Würdig-Maciel (1975) described the species *Xenacanthus santosi* in the Teresina Formation, and *Xenacanthus pricei* in the Irati Formation. While Richter (2005) reported a new genus and species, named *Wurdigneria obliterata*, and considered that *X. santosi* external morphologies are practically those of *Wurdigneria obliterata*, being the main differences the presence or lack of cristae on the cusps and the histology of the cusp of each species. Thereby, Ginter et al. (2010) suggests merging both species in ?*Wurdigneria santosi*, within the Xenacanthidae family, and not Diplodoselachidae as originally attributed by Richter (2005). Which means that the Corumbataí paleoichthyofauna would have had only representatives of the Xenacanthidae family.

Although, for Pauliv et al. (2014), the taxa should be kept separate because the obliteration by osteodentine of the pulp cavity seen in *W. obliterata* is not present in *X. santosi*.

Analyzing the characteristics of these three species, it is possible to say that the SRDV specimens differs from *X. pricei* by presenting greater width for the coronal button, and for the basal tubercle when in comparison to the size of the main cusps base. In *X. pricei* the basal tubercle shape tends to be more round and narrower, whilst in *X. santosi* this structure tends to a rhomboid shape and its width is greater than in *X. pricei*, being usually broader than the base of the main cusps. Though, it is worth noting that this width variation of the basal tubercle may be due to position of the teeth in the shark arcade (Richter, 2005) and not a true diagnose feature, in SRDV, the width of the tubercle does not exceed the size of the base of the main cusps in some specimens. Even so, the shape of the tubercle shows a better similarity with *X. santosi*. In addition, one of the diagnostic characteristics of *W. obliterata* is the intermediate cusp with a small base, less than 1/3 of the width of the main cusps, characteristic that was not observed in the SRDV fossils.

Nonetheless, in SRDV's teeth the basal tubercle is more prominent than in *X. santosi*, showing a round inferior margin especially in lateral and labial view (Figure 7A$_{4-5}$), resembling in that manner *X. pricei*, whereas the inferior margin of the tubercle of *X. santosi* is straight. Both species can also be distinguished from one another by its cusps inclinations (Würdig-Maciel, 1975). The same way, the cristae pattern is also useful and essential to discriminate between xenacanthid species. Unfortunately, as only one almost complete cusp was recovered from SRDV a better distinction, between the genera and the species aforementioned, is not possible. We can only rely on the morphological characteristics of the base, and that seems not to be sufficient to confidently taxonomic identified the specimens. Especially because some of the observed features can be presented by more than one taxon, as the rhomboid/diamond-like coronal button (*T. richteae* and *M. moorei*) or the drop/horseshoe-shaped basal tubercle (*X. santosi* and *T. richteae*). Therefore, more complete specimens, as well as histological work, are necessary.

4.2. Dermal Scales

As the teeth, all the fish scales occurred isolated and disarticulated. Complete or partially complete scales are rare, fragments being more frequent. They can be recognized because in several specimens the caramel-colored enamel layer covering the

surface is still distinguishable. Besides, many are broken transversally, making it possible to recognize under the stereoscope two layers that compose the scales: the bright enamel layer on the surface, and the massive white isopedine layer. In some fragments, the presence of thin black layers, composed of Mn oxides, are observed intercalated with the isopedine layers (Figure 8P).

In general, the more complete units show rounded, smooth edged margins and rhomboid shape, even when the edges are more rounded or when are more elongated and angular. Most of the scales seem to be "smooth"; however, below the enamel layer striated ornamentations distributed longitudinally and concentrically are observed, being more evident close to the margins (Figure 8B). Imbrication zones were possible to be identified both in fragments and in more complete specimens, represented by zones close to the margins without enamel or ornamentation (Figure 8A). Besides, articulation processes of the peg-and-socket type were also identified, which, depending on the scale shape, could be more or less pronounced, more elongated or rounded.

A greater variety of shapes was observed in hand specimens, before proceeding with the disaggregation of the samples. Besides the rhomboid shape, more rectangular ones with a narrower and rounded extremity were identified (Figure 8N). Some impressions left in hand specimens (Figure 2E) can be attributed to scales of other shapes, such as more elongated ones (Figure 8M), or shapes with rounded edges and a slight constriction in the middle (Figure 8O), which demonstrate a greater diversity of scales and distinct preservation potentials.

Several scales underwent advanced diagenesis, but it was still possible to observe parts of the isopedine; in others, most of the enamel is absent or lost all its shine. Sometimes the scales were covered by gray layers produced by secondary calcium phosphate precipitation during diagenesis (Figure 8Q-R), giving it a "precipitated material" look to the scale and a rough surface. A third, very frequent change, was the loss of hydroxyapatite on the scale, and only a mold of clay assuming the rhomboid-like shape of the scales (Figure 8S); in these cases, no ornamentation features were preserved.
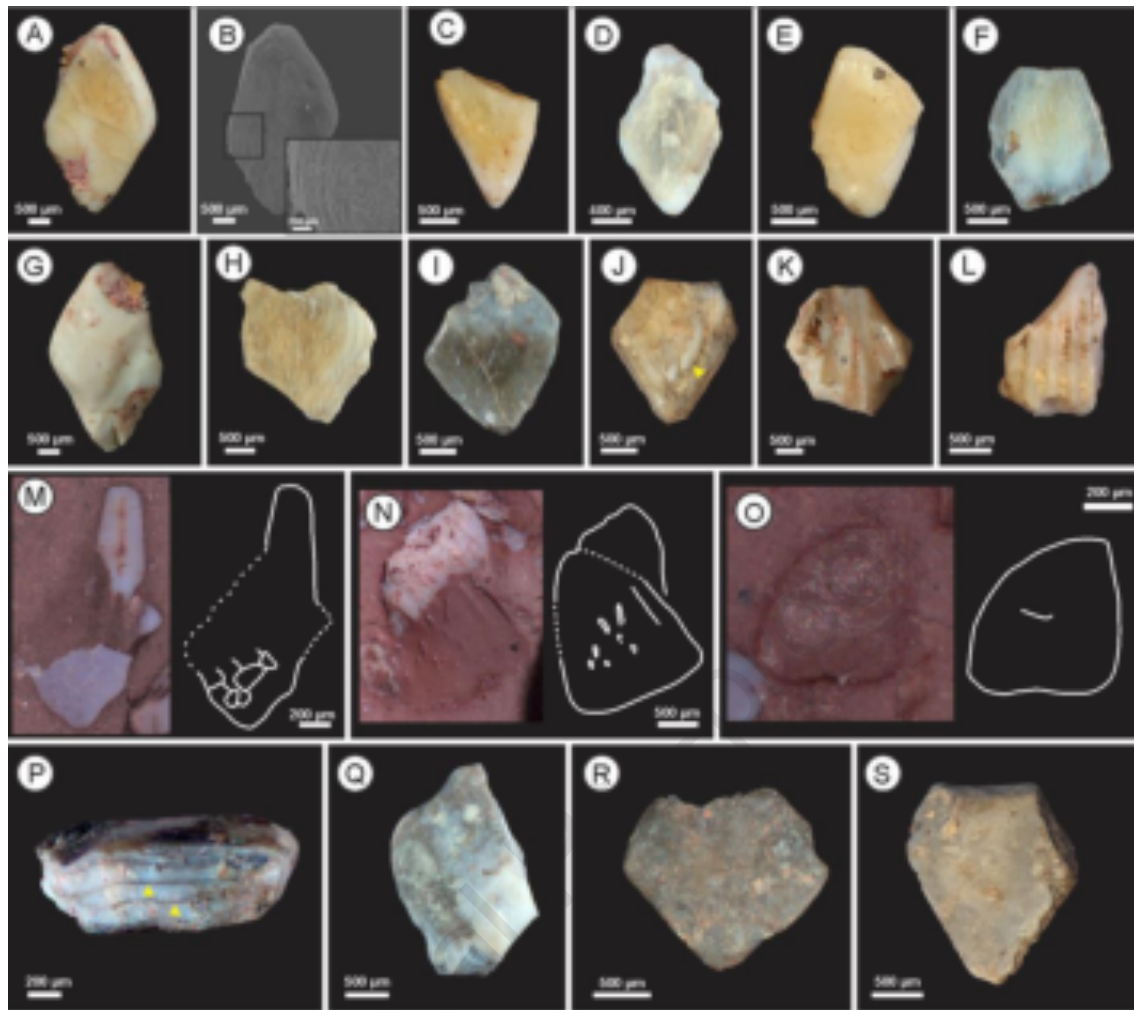
Figure 8 - Rhomboid scales observed in stereomicroscope and their variations. **A)** Complete rhomboid scale, with region of overlap without enamel and very discreet articulation process, 83PH3/16. **B)** SEM image of (A), showing the ridges ornamentation at margin of the scale. **C)** Scale fragment that suggests a more elongated than wide shape, 8PH3/20. **D)** Scale with a more rounded shape and with slightly more pronounced articulation process, 31PH1/20. E-F, H-I) Increasingly rounded shapes with almost imperceptible articulation processes. **E)** 8PH3/20. **F)** 31PH1/20. **G)** Bottom view of (A). **H)** Fragment with punctuations on the surface and ornamentation similar to (F), 31PH1/20. **I)** 31PH1/20. **J)** Fragment that lost part of the enamel exposing the ornamentation below (yellow arrow), 8PH3/20. K-L) Fragments of ridged scales. **K)** 8PH3/5. **L)** 8PH3/20. M-O) Impressions and remains of scales on rock samples. **M)** Scale more elongated and rectangular. **N)** More quadrangular format. **O)** A more rounded shape. P-S) Diagenesis altered scales. **P)** Black colored layers (arrows) intercalated with isopedine, 8PH3/5. **Q)** Initial process of secondary mineral deposition on the surface, 31PH1/20. **R)** More advanced stage than in (Q), the scale looks opaque and recrystallized, 8PH3/20. **S)** Scale-shaped mold of clay, 8PH3/20.

4.2.1. Discussion about the specimens:

The majority of the SRDV scales seems to correspond to scales P-1 and P-2 of Richter et al. (1985). They present, respectively, either short grooves and punctuations on the enamel or longitudinal ribs. The authors define scales of the P-3, P-4, and P-5 type,

which seem to be similar to some ribbed fragments found in SRDV, but since not a single complete or almost complete specimen was recovered, it is difficult to classify them, as these fragments can refer either to a single or to too many scale types. Scales of other fish groups reported elsewhere in rocks of the Passa Dois Group, such acanthodians (Mutter & Richter, 2007) and petalodontiformes (Toledo et al., 1997), have not been identified in the studied samples. However, the more rounded and elongated rhomboid shapes that were observed in more complete specimens, as well as the variety of scale shapes found in hand specimens, seem to have a closer relationship with the position they occupied in the fish body (Alves et al., 2020) than with taxonomic diversity.

According to Burrow (1994), in more rounded, rhomboid-shaped palaeoniscoid scales the peg-and-socket structure is lacking or is poorly developed, because they are scales from more flexible regions of the body, such as the posterior half of the flank and the base of the fins. Towards the caudal fin, however, the scales tend to be more elongated and lenticular, whereas the scales of regions more anterior to the flank — and posterior to the shoulder girdle — are more rectangular and contain well-developed joint structures, because they occupy regions of less movement (Burrow, 1994). Knowing the pattern and morphology of the scales that cover each position of the body of more complete and articulated specimens, it is possible to make an attempt to classify isolated scales (Trinajstic, 1999).

In the Passa Dois Group, for example, as the scales of types P-1 and P-2 and the ichthyodonts I-1 to I-10 occur together in the same strata, Richter et al. (1985) consider the possibility that they compose the same taxonomic group. Besides, the authors also observe that the ornamentations of scales P-1 and P-2 are comparable to those of African specimens, such as *Elonichthys punctatus* Aldinger 1937. Specifically, for the Corumbataí Formation, only the species *Tholonotus braziliensis* Dunkle and Schaeffer 1956 and *Angatubichthys mendesi* Figueiredo and Carvalho 2004 have been described up to now, and one of the main differences between these two species is the ornamentation pattern in the scales. Whereas Figueiredo & Carvalho (2004) report *A. mendesi* as having the body covered by scales of smooth surface, the scales of *T. braziliensis* are ornamented with well-defined striations in the anterior, dorsal, and ventral regions. However, the ornamentation progressively disappears from the central region of the flank towards the caudal fin, becoming smooth in the posterior-ventral area (Dunkle & Schaeffer, 1956). Therefore, the 'paleoniscoid' scales vary a lot according to the region of the body in which it occupies, and within the same individual, so that they do not have enough

29

morphological differences to properly allow taxonomic classification of isolated elements (Cione et al., 2010).

5. DISCUSSION

When analyzing the components present in the SRDV layer, we can attest that its ichthyofossilliferous record expresses a low diversity, concentrated in two orders: Xenacanthiformes and Palaeonisciformes, being the latter the dominant in the assemblage. The Palaeonisciformes occurrences in the Paraná Basin were listed in Table 2 and plotted in Figure 9. They are reported in the literature from the top of the Itararé Group (Rio do Sul Formation, Malabarba, 1988; Hamel, 2005) to the upper portion of the Rio do Rasto Formation of the Passa Dois Group (Vega-Dias et al., 2000; Richter, 2002). As observed in Figure 9, palaeoniscoids occur for more than 1300 km in the Paraná Basin alone. But there are also reports of these fishes in the Parnaíba (Alves et al., 2020) and Amazonas (Figueroa & Machado, 2018) basins in Brazil, and in Uruguay (Piñeiro, 2006), Argentina (Cione et al., 2010), Africa (Gardiner, 1969), and Australia (Burrow, 1994; Trinajstic, 1999), which attests the importance of this fossil group in the composition of the Paleozoic ichthyofaunas of Western Gondwana.
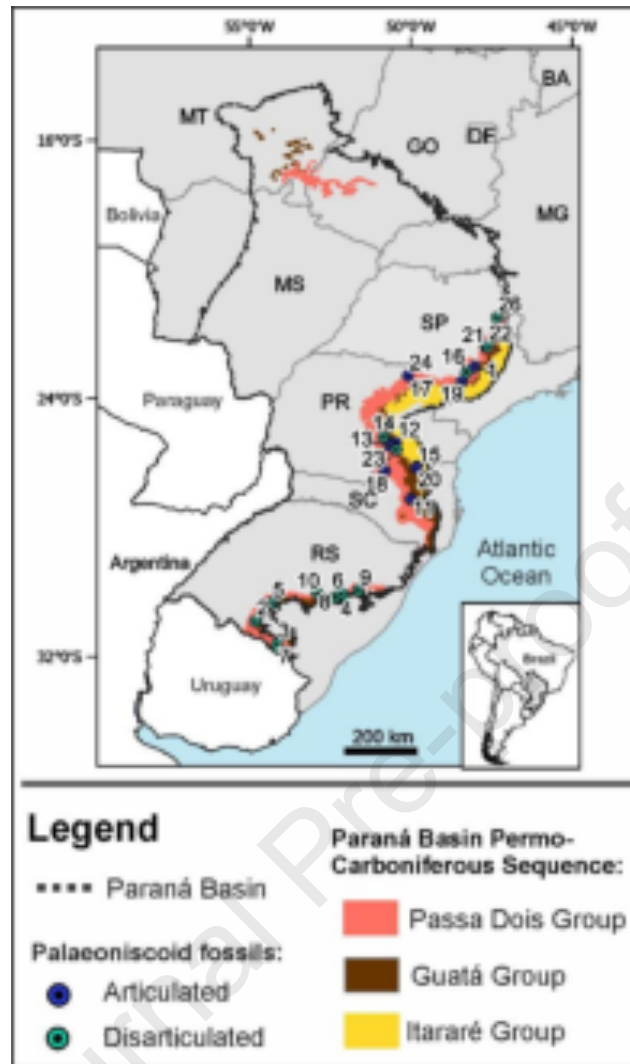
Figure 9 - Map of the Permo-Carboniferous sequence of the Paraná Basin showing the distribution of palaeoniscoids remains in the basin. The map occurrences numbers are in accordance with Table 3, where the complete or semi-complete specimens correspond to Articulated on the map and the isolated elements to Disarticulated.

Table 3 **(AT THE END OF MANUSCRIPT)** - Distribution map of palaeoniscoids occurrences in the Paraná Basin according to the literature.

Regarding the scales, the types identified in SRDV seem to be more akin to scales P-1 and P-2 of Richter et al. (1985), as well as to scales of *T. braziliensis*, when taking into consideration complete specimens of the Corumbataí Formation. However, a taxonomic classification of disjointed elements based on these complete specimens is a little complicated, because, once they are rare, they tend to obscure perceptions of possible interspecific variations. Therefore, this fact prevents a better understanding of

31

the vertical distribution of Palaeonisciformes families and species that lived in the Paraná Basin.

Despite the low diversity observed in SRDV, when it comes to vertebrate paleofauna, the Corumbataí/Teresina Formation is still under-exploited, but it encompasses abundance and diversity of environments and taxa. Besides Palaeonisciformes and Xenacanthiformes, the following groups have been recorded in the literature up to now for the Corumbataí/Teresina Formation:

Chondrichthyes

• Ctenacanthiformes. Despite being considered a marine group (Chahud, 2007; Benton, 2008), some ctenacanth species were reported in non-marine deposits, suggesting that they could live in freshwater or low-salinity environments (Chahud, 2007). The record of ctenacanths is rare in the Paraná Basin. So far, spines are the only record for the group in the Corumbataí Formation (Würding-Maciel, 1975; Richter, 1985). Richter (1985) have presented spines of *Ctenacanthus* sp. from the Corumbataí Formation, nevertheless without any further description neither illustration.

• Hybodontiformes. The Brazilian record of the group is quite rare in the Corumbataí Formation. It is associated with xenacanthiform sharks (Ragonha, 1984) from a spine impression of the dorsal fin, classified as *Hybodus florencei* (Ragonha and Silva Santos, 1987).

• Acanthodii. The only record of this group in the Basin occurs within the Teresina Formation. Mutter and Richter (2007) described acanthodian fragmentary scales and fin spines associated with shark teeth, osteichthyan remains and possibly amphibians; all retrieved from tempestites levels in a continental sequence.

• Petalodontiformes. The record of petalodontiformes in the Corumbataí Formation comes from several isolated dental plates in a bone-bed (Toledo et al., 1997).

• Eugeneodontiformes. The record for the group is restricted to an isolated tooth described by Richter (2007) and named after *Tiaraju tenuis* in the Teresina Formation. The material came from hummocky deposits in the state of Rio Grande do Sul.

Osteichtyes

• Dipnoi. The dipnoi (lungfishes) record for the Corumbataí Formation is still scarce studied (Chahud and Fairchild, 2007), despite being well represented in places (Toledo, 2001; Toledo and Bertini, 2005) with different families in the fossil record:

32

Ceratodontidae, Neoceratodontidae and Gnarthorizidae (Toledo, 2001). The dipnoi fishes have been interpreted as freshwater forms due to the association with xenacanthiforms (Ragonha, 1991). Although Xenacanthiformes being recorded in marine strata elsewhere (Hampe, 2003; Turner and Burrow, 2011; Pauliv et al., 2017). Dipnoans are sarcopterygian fishes, a group that includes several extinct tetrapodomorph, coelacanthids and tetrapods. Only indetermined dermal scales of Coelacanthidae have been recorded in the Corumbataí Formation by Würdig-Maciel (1975).

Tetrapods

• The tetrapod record from Teresina/Corumbataí Formation is diverse with amphibian teeth registered for the geological unit (Toledo, 2001), and footprints (Andreis and Carvalho, 2001). Several of the last ones were firstly interpreted as belonging to tridactyl reptiles (Andreis and Carvalho, 2001). Nevertheless, Silva et al. (2012) reinterpreted them as the ichnogenus *Chelichnus* probably belonging to an animal with semi-erect posture and raised tail, suggesting a Synapsida (Pelycosauria?) as their producers.

6. CONCLUSIONS

The dynamics and palaeogeographical disposition of the Paraná Basin, during the Passa Dois Group deposition, would provide a wide range of paleoenvironments conditions, supporting a variety of fish assemblages configurations (Richter, 2005), and could as well reflect in an endemic fish fauna (Mutter and Richter, 2007). Based on its fossil record, the Corumbataí Formation paleovertebrates tend to indicate freshwater continental environments, mostly because of the absence of strictly marine groups (Holz et al., 2010), and by the presence of xenacanthids elements. Supporting this interpretation, an oxygen isotope study performed by Vennemann & Richter (2000 *apud* Richter, 2005) using ichthyodonts of several taxonomic groups of the Teresina Formation showed that all of them underwent strong continental influence

Ragonha (1984) suggested that Xenacanthiformes sharks lived at the bottom of freshwater bodies, consuming smaller fishes. Kriwet et al (2007) also reported predation by *Triodus* xenacanth sharks on two different species of temnospondyl, and one of these amphibians had preyed an acanthodian fish, which is an important evidence of a continental aquatic food web. Pauliv et al. (2017) also interpret the occurrence of the

species *Triodus* of the Rio do Rasto Formation as a freshwater shark, but also presents a revision about the possibility of this fish group being euryhaline organisms. Thus, there is also record of xenacanthid sharks in marginal marine environments (Hampe, 2003; Ginter et al., 2010; Turner and Burrow, 2011).

The complete Palaeonisciformes specimens described by Dunkle & Schaeffer (1956) and Figueiredo & Carvalho (2004) were found associated with marine strata (Richter, 1985). Isolated ichthyodont elements and scales of these fish can be found both in marine and continental deposits (Maranhão, 1995). In the Pedra de Fogo Formation of the Parnaíba Basin, for example, the species *Brazilichthys macrognathus* Cox & Hutchinson 1991, identified via cranial portions and isolated scales and teeth, is attributed to sediments totally of continental origin, associated with fluvial and lacustrine systems (Cox & Hutchinson, 1991; Iannuzzi et al., 2018; Alves et al., 2020). In addition, Palaeonisciformes elements can also be associated with continental vertebrates, such as temnospondyls (Cox & Hutchinson, 1991; Toledo & Renó, 2010). Therefore, there is the possibility of existing freshwater and marine species (Trinajstic, 1999; Piñeiro, 2006).

It is also worth noting that in the Paraná Basin the majority of the ichthyofossils are found and described from layers interpreted as resulting from storm events (e.g., Toledo et al., 1997; Toledo & Bertini, 2001), and were reworked by waves (Rohn, 1994; Klein et al., 1997). Thus, it is more probable that they are, to a certain extent, allochthonous in the final depositional setting. Accordingly, it can be said that in general none of the SRDV ichthyofauna components can be safely used as paleoenvironmental indicators (Richter, 1985; Maranhão & Petri, 1996). In the other hand, it is known that during the deposition of the Corumbataí/Teresina formations great salinity variability occur, presenting from time to time freshwater and hypersalinity conditions (Holz et al., 2010; Kern et al., 2021). So, considering that both palaeoniscoid and xenacanthid shark are recorded along all the Passa Dois Group, even in the deposits above the Corumbataí/Teresina formations, we can affirm that this fish groups attest the presence of a diverse fauna adapted to survive stressed environments.

ACKNOWLEDGEMENTS

REFERENCES

Alves, Y.M.; Gama Junior, J.M.; Cupello, C. 2020. Palaeoniscoid remains from the lower Permian Pedra de Fogo Formation (Parnaíba Basin): Insights from general morphology and histology. Historical Biology. https://doi.org/10.1080/08912963.2020.1754815

Andreis, R. R. & Carvalho, I. de S. 2001. A Formação Corumbataí (Permiano Superior-Triássico Inferior, Bacia do Paraná) na Pedreira Pau Preto, Município de Taguaí, São Paulo, Brasil: Análise paleoambiental e das pegadas fósseis. Revista Brasileira de Paleontologia, 2: 33–46.

Behrensmeyer, A.K. 1978. Taphonomic and ecologic information from bone weathering. Paleobiology, 4(2): 150–162. https://doi.org/10.1017/S0094837300005820

Benton, M. 2014. Vertebrate palaeontology. John Wiley & Sons, London, 480 p.

Bhat, M.S.; Ray, S.; Datta, P.M. 2018. A new assemblage of freshwater sharks (Chondrichthyes: Elasmobranchii) from the Upper Triassic of India. Geobios, 51(4), 269–283. https://doi.org/10.1016/j.geobios.2018.06.004

Burrow, C. 1994. Form and function in scales of Ligulalepis Toombsi Schultze, a palaeoniscoid from the Early Devonian of Australia. Records of the South Australian Museum, 27: 175–185.

Caputo, M.V.; de Melo, J.G.; Streel, M.; Isbell, J.L.; Fielding, C.R. 2008. Late Devonian and early Carboniferous glacial records of South America. Geological Society of America Special Papers, 441: 161-173. https://doi.org/10.1130/2008.2441(11)

Carvalho, T.S.; Fernandes, M.A.; Ricardi-Branco, F.; Ghilardi, A.M.; Peixoto, B. C.P.M.; Buck, P.V.; Aureliano, T. 2021. A plant fossil assemblage of Lycopodiopsis cf. derbyi from the Corumbataí Formation, Paraná Basin, São Paulo State, Brazil. Palaeobiodiversity and Palaeoenvironments, v. 3, p. 1-15. https://doi.org/10.1007/s12549-020-00477-6

Chahud, A. & Fairchild, T.R. 2007. Vertebrados paleozóicos do estado de São Paulo. In: Carvalho, I. de S.; Cassab, R. de C.T.; Schwanke, C.; Carvalho, M.A.; Fernandes, A.C.S.; Rodrigues, M.A. de C.; Carvalho, M.S.S. de C.; Arai, M.; Oliveira, M.E.Q. (eds.), Paleontologia: Cenários de vida: Vol.1, Editora Interciência, Rio de Janeiro, 1° ed., p.: 101–110.

Chahud, A. & Petri, S. 2008a. Registro de Paleoniscóides na Base do Membro Taquaral, Formação Irati, Permiano da Bacia do Paraná. Revista Do Instituto Geológico, 29(1/2): 33–40. http://dx.doi.org/10.5935/0100-929X.20080003

Chahud, A. & Petri, S. 2008b. Chondrichthyes no Membro Taquaral, base da Formação Irati, no centro leste do Estado de São Paulo, Brasil. Revista de Geologia, 21 (2).

Chahud, A. & Petri, S. 2010. O tubarão Taquaralodus albuquerquei (SILVA SANTOS, 1946) do Membro Taquaral (Permiano, Formação Irati) no Estado de São Paulo. Acta Biol.Par., 39(1–2): 1–17.

Chahud, A. 2007. Paleontologia de vertebrados da transição entre os Grupos Tubarão e Passa Dois (Neopaleozóico) no centro-leste do estado de São Paulo. Dissertação de mestrado, Instituto de Geociências, Universidade de São Paulo, 184 p. https://doi.org/10.11606/D.44.2007.tde-31072007-111405

Cione, A.L.; Gouiric-Cavalli, S.; Mennucci, J.A.; Cabrera, D.A.; Freije, R.H. 2010. First vertebrate body remains from the Permian of Argentina (Elasmobranchii and Actinopterygii). Proceedings of the Geologists' Association, 121(3): 301–312. https://doi.org/10.1016/j.pgeola.2010.04.003

Cohen, K.M.; Finney, S.C.; Gibbard, P.L.; Fan, J.-X. 2013. The ICS International Chronostratigraphic Chart. Episodes, 36: 199-204.

Cox, C. B. & Hutchinson, P. 1991. Fishes and Amphibians from the Late Permian Pedra de Fogo Formation of northern Brazil. Palaeontology, 34(3): 561–573.

Dunkle, D.H. & Schaeffer, B. 1956. Preliminary description of a Paleoniscoid Fish from the Late Paleozoic of Brazil. 13: 5–22. https://doi.org/http://dx.doi.org/10.11606/issn.2526-3862.bffcluspgeologia.1956.121775

Faria, R.S.; Ricardi-Branco, F.; Giannini, P.C.F.; Sawakuchi, A.O.; Del Ben, L.E.V. 2009. *Lycopodiopsis derbyi* Renault from the Corumbataí Formation in the state of São Paulo (Guadalupian of Paraná Basin, Southern Brazil): New data from compressed silicified stems. Review of Palaeobotany and Palynology, v. 158, p. 180-192. https://doi.org/10.1016/j.revpalbo.2009.08.005

Figueiredo, F.J. de & Carvalho, B.C.M.C. 2004. A New Actinopterygian Fish from The Late Permian of the Paraná Basin, Southern Brazil. Arquivos Do Museu Nacional, 62(4): 531–547.

Figueroa, R.T.; Friedman, M.; Gallo, V. 2019. Cranial anatomy of the predatory actinopterygian Brazilichthys macrognathus from the Permian (Cisuralian) Pedra de Fogo Formation, Parnaíba Basin, Brazil. Journal of Vertebrate Paleontology, 39(3). https://doi.org/10.1080/02724634.2019.1639722

Figueroa, R.T. & Machado, D.M. da C. 2018. The Paleozoic ichthyofauna of the Amazonas and Parnaíba basins, Brazil. Journal of South American Earth Sciences, 82: 122–132. https://doi.org/10.1016/j.jsames.2018.01.001

Fiorillo, A.R. 1988. Taphonomy of Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska. Rocky Mountain Geology, 26(2): 57–97.

Friedman, M. 2015. The early evolution of ray-finned fishes. Palaeontology, 58(2): 213–228. https://doi.org/10.1111/pala.12150

Gardiner, B.G. 1969. New palaeoniscoid fish from the Witteberg series of South Africa. Zoological Journal of the Linnean Society, 48: 423–452. https://doi.org/https://doi.org/10.1111/j.1096-3642.1969.tb00722.x

Ginter, M.; Hampe, O.; Duffin, C. 2010. Chondrichthyes Paleozoic Elasmobranchii Teeth. In: Schultze, P.H. (Ed), Handbook of Paleoichthyology, 3D. München: Verlag Dr. Friedrich Pfeil, 168 p.

Godoy, L.H.; Sardinha, D. de S.; Moreno, M.M.T. 2017. Major and trace elements redistribution in weathered claystones from the Corumbataí Formation, Paraná Sedimentary Basin, São Paulo, Brazil. Brazilian Journal of Geology, 47(4): 615–632. https://doi.org/10.1590/2317-4889201720170086

Gower, J.C. 1971. A General Coefficient of Similarity and Some of Its Properties. Biometrics, 27(4): 857–871. https://doi.org/10.2307/2528823

Hamel, M.H. 2005. A new lower actinopterygian from the early permian of the paraná basin, Brazil. Journal of Vertebrate Paleontology, 25(1): 19–26. https://doi.org/10.1671/0272-4634(2005)025[0019:ANLAFT]2.0.CO;2

Hampe, O. 2003. Revision of the Xenacanthida (Chondrichthyes: Elasmobranchii) from the Carboniferous of the British Isles. Transactions of the Royal Society of Edinburgh: Earth Sciences, 93: 191–237. https://doi.org/10.1017/S0263593300000419

Hampe, O. & Schneider, J.W. 2010. Mooreodontus Hampe & Schneider gen. nov. In: Ginter, M.; Hampe, O.; Duffin, C.J. (Eds.), Chondrichthyes. Paleozoic Elasmobranchii: teeth. Verlag Dr. Friedrich Pfeil, München, p. 168

Holz, M.; França, A.B.; Souza, P.A.; Iannuzzi, R.; Rohn, R. 2010. A stratigraphic chart of the Late Carboniferous/Permian succession of the eastern border of the Paraná Basin, Brazil, South America. Journal of South American Earth Sciences, 29(2): 381–399. https://doi.org/10.1016/j.jsames.2009.04.004

Iannuzzi, R.; Neregato, R.; Cisneros, J.C.; Angielczyk, K.D.; Rößler, R.; Rohn, R.; Marsicano, C.; Fröbisch, J.; Fairchild, T.; Smith, R.M.H.; Kurzawe, F.; Richter, M.; Langer, M.C.; Tavares, T.M.V.; Kammerer, C.F.; Conceição, D.M.; Pardo, J.D.; Roesler, G.A. 2018. Re-evaluation of the Permian macrofossils from the Parnaíba Basin: Biostratigraphic, palaeoenvironmental and palaeogeographical implications. *In*: Daly, M. C.; Fuck, R.A.; Julià, J.; Macdonald, D.I.M. & Watts, A.B. (Eds.), Cratonic Basin Formation: a case study of the Parnaíba Basin of Brazil, Geological Society, 472(1): 223–249. https://doi.org/10.1144/SP472.14

Irmis, R.B. & Elliott, D.K. 2006. Taphonomy of a Middle Pennsylvanian marine vertebrate assemblage and an actualistic model for marine abrasion of teeth. PALAIOS, 21(5): 466–479. https://doi.org/10.2110/palo.2005.P05-105R

Klein, C.; Simões, M.G.; Leipnitz, I.I.; Richter, M. 1997. Interpretação dos dados tafonômicos na deposição de peixes e pelecípodes da Formação Teresina (Grupo Passa

Dois), na região de Tiaraju, RS, Brasil. In: 15° Congresso Brasileiro de Paleontologia, São Pedro, Boletim de Resumos, Unesp, p.166.

Kriwet, J.; Witzmann, F.; Klug, S.; Heidtke, U.H.J. 2008. First direct evidence of a vertebrate three-level trophic chain in the fossil record. Proceedings of the Royal Society B: Biological Sciences, 275(1631): 181–186. https://doi.org/10.1098/rspb.2007.1170

Lu, J.; Giles, S.; Friedman, M.; den Blaauwen, J.L.; Zhu, M. 2016. The Oldest Actinopterygian Highlights the Cryptic Early History of the Hyperdiverse Ray-Finned Fishes. Current Biology, 26(12): 1602–1608. https://doi.org/10.1016/j.cub.2016.04.045

Maechler, M.; Rousseeuw, P.; Struyf, A.; Hubert, M.; Hornik, K. 2022. *cluster:* Cluster Analysis Basics and Extensions. R package version 2.1.3. https://CRAN.R-project.org/package=cluster.

Malabarba, M.C.L. 1988. A new genus and species of stem group actinopteran fish from the Lower Permian of Santa Catarina State, Brazil. Zoological Journal of the Linnean Society, 94: 287–299. https://doi.org/10.1111/j.1096-3642.1988.tb01197.x

Maranhão, M. da S.A.S. & Petri, S. 1996. Novas ocorrências de fósseis nas formações Corumbataí e Estrada Nova do estado de São Paulo e considerações preliminares sobre seus significados paleontológico e bioestratigráfico. Revista IG São Paulo, 17(2): 33–54.

Maranhão, M. da S.A.S. 1995. Fósseis das Formações Corumbataí e Estrada Nova do Estado de São Paulo: Subsídios ao conhecimento Paleontológico e Bioestratigráfico. Doctoral thesis, Instituto de Geociências, Universidade de São Paulo, 576 p. https://doi.org/10.11606/T.44.1995.tde-18092015-182742

Meglhioratti, T. 2006. Estratigrafia de seqüências das formações Serra Alta, Teresina e Rio do Rasto (Permiano, Bacia Do Paraná) na porção nordeste do Paraná e centro-sul de São Paulo. Master dissertation, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, 147 p.

Milani, E.J. & Ramos, V.A. 1998. Orogenias Paleozóicas no Domínio Sul-Ocidental do Gondwana e os Ciclos de Subsidência da Bacia do Paraná. Revista Brasileira de Geociências, 28(4): 473–484.

Milani, E.J.; Melo, J.H.G. de; Souza, P.A.; Fernandes, L.A.; França, A.B. 2007. Bacia do Paraná. Boletim de Geociências da Petrobrás, 15(2): 265–287.

Montibeller, C.C.; Navarro, G.R.B.; Zanardo, A.; Rohn, R.; del Roveri, C.; Rocha, R.R. da; Conceição, F.T. da. 2020. Geochemistry of siltstones from the Permian Corumbataí Formation from the Paraná Basin (State of São Paulo, Brazil): Insights of provenance, tectonic and climatic settings. Journal of South American Earth Sciences, 102: 102582. https://doi.org/10.1016/j.jsames.2020.102582

Moy-Thomas, J.A. 1971. Palaeozoic Fishes. Springer US, 260 p. https://doi.org/10.1007/978-1-4684-6465-8

Mutter, R.J. & Richter, M. 2007. Acanthodian remains from the Middle-Late Permian of Brazil. Geological Journal, 42(2): 213–224. https://doi.org/10.1002/gj.1081

Nelson, J.S. 2006. Fishes of the World. Wiley, 4th ed., United States of America, 620 p.

Pauliv, V.E.; Dias, E.V.; Sedor, F.A.; Ribeiro, A.M. 2014. A new xenacanthiformes shark (Chondrichthyes, Elasmobranchii) from the Late Paleozoic Rio Do Rasto Formation (Paraná Basin), Southern Brazil. Anais Da Academia Brasileira de Ciencias, 86(1): 135–145. https://doi.org/10.1590/0001-37652014107612

Pauliv, V.E.; Martinelli, A.G.; Francischini, H.; Dentzien-Dias, P.; Soares, M.B.; Schultz, C.L.; Ribeiro, A.M. 2017. The first Western Gondwanan species of Triodus Jordan 1849: A new Xenacanthiformes (Chondrichthyes) from the late Paleozoic of Southern Brazil. Journal of South American Earth Sciences, 80: 482–493. https://doi.org/10.1016/j.jsames.2017.09.007

Piñeiro, G. 2006. Nuevos aportes a la paleontología del Pérmico de Uruguay. In: Veroslavsky, G.; Ubilla, M. & Martínez, S. (Eds.), CUENCAS SEDIMENTARIAS DE URUGUAY: Geología, paleontología y recursos naturales. PALEOZOICO. D.I.R.A.C., p.: 257-279.

Ragonha, E.W. & Santos, R.S. 1987. Nova classificação de Dentalium florencei Moraes Rego, 1936 (Mollusca, Scaphopoda) para Hybodus (Chondrichthyes, Elasmobranchii). In: Anais of the X Congresso Brasileiro de Paleontologia, Rio de Janeiro.

Ragonha, E.W. 1984. Taxionomia de dentes e espinhos isolados de Xenacanthodii (Chondrichthyes, Elasmobranchii) da Formação Corumbataí: Considerações cronológicas e paleoambientais. Doctoral thesis, Instituto de Geociências, Universidade de São Paulo, 184 p. https://doi.org/10.11606/T.44.1984.tde-03082015-144959

Ragonha, E.W. 1991. Peixes pulmonados triássicos de Rio Claro, Estado de São Paulo. In: Boletim de Resumos of the 12° Congresso Brasileiro de Paleontologia, Universidade de São Paulo.

Richter, M. 1983. Ultra-estrutura de dentes de Palaeoniscoid (Pisces) do Grupo Passa Dois, RS, Brasil. IHERINGIA. Série Geológica, 8: 131–145.

Richter, M. 1985. Situação da pesquisa paleoictiológica no Paleozóico brasileiro. Coletânea de Trabalhos Paleontológicos, 2(27): 105–110.

Richter, M. 2002. A ray-finned fish (Osteichthyes) from the Late Permian of the State of Santa Catarina (Paraná Basin), southern Brazil. Revista Brasileira de Paleontologia, 3: 56–61.

Richter, M. 2005. A new Xenacanthid shark (Chondrichthyes) from the Teresina Formation, Permian of the Paraná Basin, Southern Brazil. Revista Brasileira de Paleontologia, 8(2): 149-158.

Richter, M. 2007. First record of Eugeneodontiformes (Chondrichtyes: Elasmobranchii) from the Paraná Basin, Late Permian of Brazil. In: Carvalho, I. de S.; Cassab, R. de C.T.; Schwanke, C.; Carvalho, M.A.; Fernandes, A.C.S.; Rodrigues, M.A. de C.; Carvalho, M.S.S. de C.; Arai, M.; Oliveira, M.E.Q. (eds.), Paleontologia: Cenários de vida: Vol.1, Editora Interciência, Rio de Janeiro, 1° ed., p.: 150–156.

Richter, M.; Piccoli, A.E.M.; Lima, M.C.F.S. 1985. Variação morfológica de restos de Palaeoniscoid (Pisces) no Permiano da Bacia do Paraná. Coletânea de Trabalhos Paleontológicos, DNPM, 2(27): 111–122.

Rocha, H.V.; Mendes, M.; Rodrigues, C.; Fernandes, P.; Lopes, G.; Sant'Anna, L.G.; Tassinari, C.C.G.; Lemos de Sousa, M.J. 2020. New palynostratigraphic data of the Irati (Assistência member) and the Corumbataí formations, Paraná Basin, Brazil, and correlation with other south American basins. Journal of South American Earth Sciences, 102, 102631. https://doi.org/10.1016/j.jsames.2020.102631

Rocha-Campos, A.C.; Basei, M.A.S.; Nutman, A.P.; Santos, P.R.; Passarelli, C.R.; Canile, F.M.; Rosa, O.C.R.; Fernandes, M.T.; Ana, H.S.; Veroslavsky, G. 2019. U-Pb zircon dating of ash fall deposits from the Paleozoic Paraná Basin of Brazil and Uruguay: A reevaluation of the stratigraphic correlations. Journal of Geology, 127(2): 167–182. https://doi.org/10.1086/701254

Rohn, R. 1994. Evolução ambiental da Bacia do Paraná durante o Neopermiano no leste de Santa Catarina e do Paraná. Tese de doutorado, Instituto de Geociências, Universidade de São Paulo, 418 p. https://doi.org/10.11606/T.44.1995.tde-22062015-145002

Schneider, R.L.; Muhlmann, H.; Tommasi, E.; Medeiros, R.A.; Daemon, R.F.; Nogueira, A.A. 1974. Revisão Estratigráfica da Bacia do Paraná. In: XXVIII Congresso Brasileiro de Geologia, Anais, p.: 41–65

Silva, R.C.; Sedor, F.A.; Fernandes, A.C.S. 2012. Fossil footprints from the Late Permian of Brazil: an example of hidden biodiversity. Journal of South American Earth Sciences 38:31-43. https://doi.org/10.1016/j.jsames.2012.05.001

Toledo, C.E.V. & Bertini, R.J. 2005. Occurrences of the fossil Dipnoiformes in Brazil and its stratigraphic and chronological distributions. Revista Brasileira de Paleontologia, 8(1): 47–56. https://doi.org/10.4072/RBP.2005.1.04

Toledo, C.E.V. & Renó, D.L. de S. 2010. Análises histológicas de Actinopterygii primitivos "Paleonisciformes" da Formação Corumbataí, na região do município de Rio Claro, estado de São Paulo. Brazilian Geographical Journal: Geosciences and Humanities Research Medium, 1(2): 352–361.

Toledo, C.E.V. 2001. Análise paleoictiológica da formação Corumbataí na região de Rio Claro, Estado de São Paulo. Master Dissertation, University of São Paulo State.

Toledo, C.E.V.; Brito, P.M.M.; Bertini, R.J. 1997. Chronologial meaning about the presence of petalodonts (Holocephali incertae sedis) in the Corumbataí Formation of São Paulo state (Brazil). In: 15° Congresso Brasileiro de Paleontologia, São Pedro, Boletim de Resumos, Unesp, p.80.

Trinajstic, K.M. 1999. Scales of palaeoniscoid fishes (Osteichthyes: Actinopterygii) from the Late Devonian of Western Australia. Records of the Western Australian Museum Supplement, 57: 93-106.

Turner, S. & Burrow, C.J. 2011. A Lower Carboniferous xenacanthiform shark from Australia. Journal of Vertebrate Paleontology, 31(2): 241–257. https://doi.org/10.1080/02724634.2011.550359

Vega-Dias, C.; Dias, E.V.; Richter, M. 2000. Actinopterygian Remains from the Rio do Rasto Formation, Upper Permian of the Paraná Basin, Brazil. Acta Geologica Leopoldensia, XXIII (51): 21–31

Vennemann, T. & Richter, M. 2000. Stable isotope composition of phosphatic fossils from the Upper Permian Teresina Formation of the Paraná Basin: Evidence for a freshwater influence. In: 31° International Geological Congress, Abstracts, Rio de Janeiro, SBG.

Würdig-Maciel, N.L. 1975. Ichtodontes e Ichtodorulitos (Pisces) da Formação Estrada Nova e sua aplicação na estratigrafia do Grupo Passa Dois. Pesquisas Em Geociências, 5(1): 7–166. https://doi.org/10.22456/1807-9806.21830

Table 1 – General description for each tooth considered in the morphotype grouping.

Observation	Sample	Mining Front	Fraction	Preservation state of the tooth	Ichthyodont classification	Lenght of the shaft	Acrodin cap lenght	Base width	Acrodin cap features	Shape of the shaft	Shaft ornamentation	Base feature	Enamel fracturing	Fracturing on the shaft
1	14	PH1	16	integer	1	2.98	0.4	1.49	rounded and translucent	straight	smooth to rugose	straight	yes	no
2	138	PH3	20	shaft without the base	1	1.18	0.39	0.58	elongated, acute and translucent	straight	smooth		no	yes
3	99	PH3	20	shaft without the base	1	1.88	0.38	1.17	elongated, acute and translucent	straight	ribbed		yes	yes
4	106	PH3	20	integer	1	1.49	0.49	0.23	elongated, acute and translucent	straight	smooth	straight	no	yes
5	14	PH1	20	shaft without the base	1	1.28	0.22	0.59	elongated, acute and translucent	straight	smooth		no	yes
6	31	PH1	20	shaft without the base	1	2.42	0.38	0.78	elongated, acute and translucent	straight	smooth to rugose		yes	yes
7	8	PH3	5	integer	2	2.39	0.24	1.75	translucent, short, rounded	curved	ribbed	straight	no	no
8	8	PH3	5	integer	2	2.06	0.33	1.18	massive, short and rounded	curved	smooth to ribbed	straight	yes	no
9	20	PH1	5	integer	3	2.45	0.34	1.06	massive, elongated, acute	curved	smooth	straight	yes	no
10	31	PH1	20	shaft with no acrodin cap	3	1.98		1.17	absent	curved	smooth	straight	yes	yes

42

11	106	PH3	20	integer	4	1.63	0.2	0.95	acute, elongated, massive	sigmoidal	rugose	straight	yes	no
12	150	PH3	20	integer	4	1.81	0.25	0.76	average lenght, rounded and massive	sigmoidal	smooth	straight	yes	no
13	14	PH1	20	integer	4	1.65	0.18	0.68	translucent, average lenght, acute	sigmoidal	smooth	straight	yes	no
14	8	PH3	5	shaft with no acrodin cap	5A	1.87		1.4	absent	straight	smooth to ribbed	straight	no	no
15	8	PH3	5	shaft with no acrodin cap	5A	1.89		0.94	absent	curved	smooth to rugose	tilted	no	no
16	0	PH3	5	shaft with no acrodin cap	5A	1.77		0.87	absent	curved	smooth to rugose	tilted	no	yes
17	138	PH3	20	shaft with no acrodin cap	5A	1.79		1.04	absent	curved	rugose	straight	no	no
18	150	PH3	20	shaft with no acrodin cap	5A	2.44		1.44	absent	curved	rugose	straight	no	no
19	150	PH3	20	shaft with no acrodin cap	5A	1.91		0.95	absent	curved	smooth to rugose	tilted	yes	no
20	150	PH3	20	shaft with no acrodin cap	5A	2.43		1.31	absent	curved	smooth to ribbed	straight	no	yes
21	8	PH3	20	shaft with no acrodin cap	5A	1.91		0.97	absent	curved	ribbed to rugose	straight	no	no

22	7	PH1	20	shaft with no acrodin cap	5A	2.76	1.42	absent	curved	smooth to rugose	tilted	yes	no
23	138	PH3	5	shaft with no acrodin cap	5B	2.02	1.13	absent	straight	smooth to rugose	straight	no	no
24	99	PH3	20	shaft with no acrodin cap	5B	2.06	1.07	absent	straight	smooth	tilted	no	yes
25	153	PH3	20	shaft with no acrodin cap	5B	1.32	0.72	absent	curved	smooth	tilted	no	no
26	7	PH1	20	shaft with no acrodin cap	5B	1.38	0.92	absent	straight	rugose	tilted	no	no

Table 3 – Distribution map of palaeoniscoids remains occurrences in the Paraná Basin according to the literature.

Occurrence	Form of occurrence	Fossil	Localization	Geological unit	Reference
1	Articulated element	*Tholonotus braziliensis* Dunkle and Schaeffer 1956	Conchas, SP	Corumbataí Fm., Passa Dois Group	Dunkle & Schaeffer (1956)
2	Isolated element	Scales, teeth	Dom Pedrito, RS	Estrada Nova Fm., Passa Dois Group	Würdig-Maciel (1975)
3	Isolated element	Scales, teeth	Between Bagé and Aceguá, RS	Estrada Nova Fm., Passa Dois Group	Würdig-Maciel (1975)
4	Isolated element	Scales, teeth	Butiá, Minas do Leão, RS	Irati Fm., Passa Dois Group	Würdig-Maciel (1975)
5	Isolated element	Scales, bones	São Gabriel, RS	Irati Fm., Passa Dois Group	Richter et al. (1985)

6	Isolated element	Scales, bones	Between Pantano Grande and Rio Pardo, RS	?	Richter et al. (1985)
7	Isolated element	Scales	Between Bagé and Aceguá, RS	Estrada Nova Fm., Passa Dois Group	Richter et al. (1985)
8	Isolated element	Scales, teeth	Cachoeira do Sul, RS	Irati and Estrada Nova Fm., Passa Dois Group	Richter et al. (1985)
9	Isolated element	Scales	Charqueada, RS	Itararé Group; Palermo Fm. (Guatá Gp.); Irati and Estrada Nova Fm. (Passa Dois Gp.)	Richter et al. (1985)
10	Isolated element	Scales	Rio Pardo, RS	Irati Fm., Passa Dois Group	Richter et al. (1985)
11	Articulated element	*Tholonosteon santacatarinae* Beltan 1978	Taió, SC	Rio Bonito Fm., Guatá Group	Richter et al. (1985)
12	Articulated element	*Elonichthys gondwanus* Hussakof 1930	Teixeira Soares, PR	Rio do Sul Fm., Itararé Group	Richter et al. (1985)
13	Articulated element	Undetermined	Irati, PR	Irati Fm., Passa Dois Group	Richter et al. (1985)
14	Isolated element	Scales	Between Ponta Grossa and Prudentópolis, PR	Irati Fm., Passa Dois Group	Richter et al. (1985)
15	Articulated element	*Santosichthys mafrensis* Malabarba 1988	Mafra, SC	Rio do Sul Fm., Itararé Group	Malabarba (1988)
16	Isolated element	Scales, teeth	SP-280/ 161,5-162 km	Estrada Nova Fm., Passa Dois Group	Maranhão & Petri (1996)
17	Articulated element	Undetermined	Santo Antônio da Platina, PR	Rio do Rasto Fm., Passa Dois Group	Vega-Dias et al. (2000)
18	Articulated element	*Rubidus pascoalensis* Richter 2002	São Pasocal/Irineópolis, SC	Rio do Rasto Fm. Passa Dois Group	Richter (2002)

19	Articulated element	*Angatubichthys mendesi* Figueiredo and Carvalho 2004	Angatuba, SP	Corumbataí Fm., Passa Dois Group	Figueiredo & Carvalho (2004)
20	Articulated element	*Roslerichthys riomafrensis* Hamel 2005	Mafra, SC	Rio do Sul Fm., Itararé Group	Hamel (2005)
21	Isolated element	Scales, teeth	Rio Claro, SP	Irati Fm., Passa Dois Group	Chahud & Petri (2008a)
22	Isolated element	Scales, teeth	Rio Claro, SP	Corumbataí Fm., Passa Dois Group	Toledo & Renó (2010)
23	Isolated element	Scales, bones	São Mateus do Sul, PR,	Irati Fm., Passa Dois Group	Dias et al. (2011)
24	Articulated element	*Paranaichthys longianalis* Dias 2012	Santo Antônio da Platina, PR	Rio do Rasto Fm., Passa Dois Group	Dias (2012)
25	Isolated element	Scales, teeth	Santa Rosa de Viterbo, SP	Corumbataí Fm., Passa Dois Group	This paper

Highlights

- New description of 'palaeoniscoid' and xenacanthid scale and tooth for the Gondwana

- Xenacanthid shark teeth are similar to species described elsewhere in Paraná basin

- Six different morphotypes of actinopterygian teeth were identified

- The actinopterygian tooth shaft present a variety of micro-ornamentations

Declaration of interests

☒ 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.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: