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Holocephali from the Irati Formation (Paraná Basin), Brazil: Origin, paleogeographical and paleoenvironmental considerations

Holocephali de la Formación Irati (Cuenca del Paraná), Brasil: Origen, Consideraciones Paleogeográficas y Paleoambientales

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ABSTRACT

The Irati Formation (Permian, Cisuralian) has several types of aquatic vertebrates, including species of Chondrichthyes. Two members of the Irati Formation are recognized, Assistência (upper) and Taquaral (lower). A sandy facies, at the base of the Taquaral Member, is noteworthy by the richness of the Chondrichthyes. The Holocephali are the most abundant and the species *Itapyrodus punctatus* is the most common. Recent studies with several specimens revealed that some morphotypes must belong to different species of the genus *Itapyrodus*. This genus is endemic to the two Brazilian Basins, Parnaíba and Paraná and is not related to any other known genus, justifying the proposition of the family Itapyrodidae. A new genus and species of this family was identified, *Fairchildodus rioclarensis*. The presence of this endemic family is an argument, among others, for a proposed isolation during the time of deposition of the Irati.

Keywords: Chondrichthyes; Permian; Paraná Basin; Paleozoic; Petalodontiformes.

RESUMEN

La Formación Irati (Pérmico, Cisuraliano) tiene varios tipos de vertebrados acuáticos, incluyendo especies de Chondrichthyes. Se reconocen dos miembros de Irati, Assistência (superior) y Taquaral (inferior). Una facies arenosa, en la base del Miembro Taquaral, destaca por la riqueza de Chondrichthyes. Los Holocephali son los condrictios más abundantes y la especie *Itapyrodus punctatus* es la más común. Estudios recientes de varios especímenes revelaron que algunos morfotipos debían pertenecer a diferentes especies del género *Itapyrodus*. Este género es endémico de las dos cuencas brasileñas, Parnaíba y Paraná, y no está relacionado con ningún otro género conocido, lo que justifica la propuesta de la familia Itapyrodidae. Se ha identificado un nuevo género y especie de esta familia, *Fairchildodus rioclarensis*. La presencia de esta familia endémica es un argumento, entre otros, para una propuesta de aislamiento, durante la época de la deposición de Irati.

Palabras clave: Chondrichthyes; Pérmico; Cuenca del Paraná; Paleozoico; Petalodontiformes.

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Introduction

The Brazilian Paraná Basin Late Paleozoic lithostratigraphic units, present in the State of São Paulo, begin with the Latest Carboniferous – Earliest Permian Itararé Group, followed by Tatuí Formation and Passa Dois Group. The earliest unit of this group is the Irati Formation (Cisuralian). This formation is distinguished by its characteristic important fossil content and diversified paleoenvironments of deposition. The members Taquaral and Assistência (Barbosa & Gomes, 1958; Milani et al., 2007; Holz et al., 2010; Chahud, 2011; 2017; Chahud & Petri, 2015; 2016) make up this formation.

Two lithofacies are recognized in the Taquaral: a sandy facies at the base of this member and a silty one, thicker and lithologically more homogeneous. The sandy facies, even though thinner and not always present, consists of a laterally variable sandstone, fine to conglomeratic, with abundant isolated pieces of vertebrates, both taxonomical and in terms of number of specimens (Assine et al., 2003; Chahud & Petri, 2010).

The Holocephali were much diversified in the Paleozoic and still have living species (Long, 2011). Three orders are known in the Paraná Basin: Eugeneodontiformes, Petalodontiformes and Orodontiformes (Würdig-Maciel, 1975; Toledo et al., 1997; Chahud et al., 2010; Chahud, 2021).

New Holocephali specimens were recently gathered from the State of São Paulo Taquaral sandy facies, resulting in a larger and diversified fossil assemblage. The objective of this contribution is to describe the new forms and to propose a hypotheses on their origin and paleoenvironment.

Materials and Methods

The fossils were collected from a bedding-plane exposure along an area of approximately 7 m × 20 m at the base of the Taquaral Member, SW margin of the Cabeça river, about 850 m NNW from the entrance to the Santa Maria homestead, Municipality of Rio Claro, São Paulo, Brazil (UTM: 23K 0227055/7517325) (Fig. 1).

They are preserved as bioclasts in a 9.5 cm-thick bed of light-gray to gray (Fig. 2), fining-upward, cross-laminated conglomeratic sandstone, with abundant angular to rounded granules and rare pebbles of quartz and chert, dispersed in a very fine to coarse sandy matrix. Bioclasts are firmly cemented within the sandy matrix.

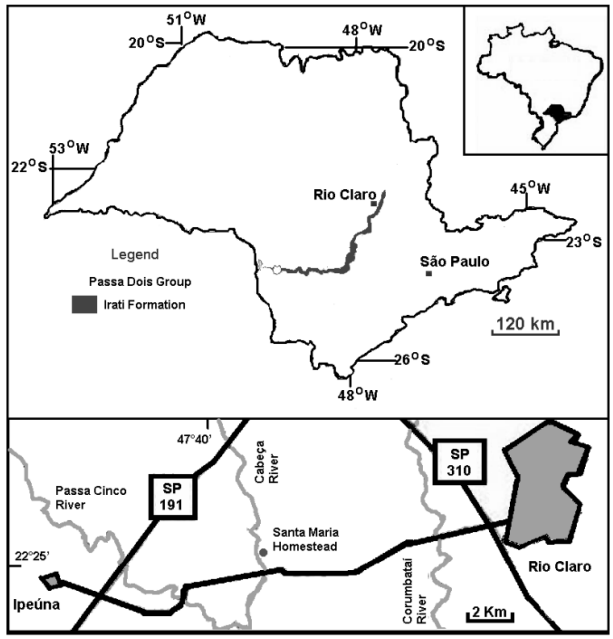

Figure 1.— Outcrop belt of the Irati Formation in the State of São Paulo (above) and access to the fossil locality of the Santa Maria homestead (below).

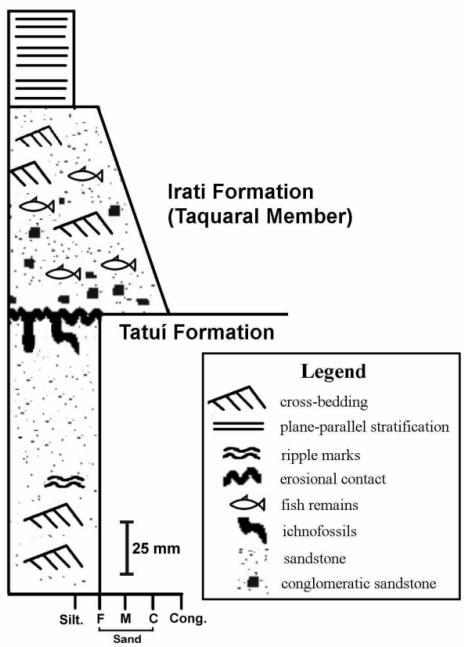

Figure 2.— Schematic cross-section of the fossiliferous bed, Santa Maria Homestead, Rio Claro, São Paulo, Brazil.

The specimens were cleaned or removed from the rock and are deposited in the Vertebrate Collection of the Laboratory of Systematic Paleontology (LPS) of the Institute of Geoscience of the University of São Paulo (IGc-USP).

Systematic Paleontology

Class Chondrichthyes Huxley, 1880
Subclass Holocephali Bonaparte, 1832-41
Genus *Itapyrodus* Silva Santos, 1990
Figures 3 – 5

Material: GP/2E-6290; GP/2E-6258; GP/2E-6304a; GP/2E-6304b; GP/2E-6307; GP/2E-6308. Isolated teeth.

Locality: Flat-lying outcrop on the SE side of the Cabeça river (UTM: 23K 0227055/7517325), about 850 m NNW from the entrance to the Santa Maria Homestead, at the limit between the municipalities of Rio Claro and Ipeúna, São Paulo, Brazil.

Stratigraphy: Type material collected by L. I. Price in the Pedra de Fogo Formation (Permian), Parnaiba Basin, 6 km south of Pastos Bons, Maranhão, Northeast Brazil. New materials from the base of the Irati Formation (Cisuralian, Early Permian), Paraná**.**

Generic diagnosis (Silva Santos, 1990): Elasmobranchs known only from teeth, showing heterodontya with distinctive symphyseal and posterior–lateral teeth. Teeth close-fitting but not fused into a dental plate. Each tooth bears a smooth crown. Symphyseal teeth bear a high crown and are labio-lingually compressed, elongate, and slightly inclined toward the lingual face; the upper margin of the crown has distinct extremities, anteriorly rounded and pointed and laterally sloping slightly downward. Posterior–lateral teeth with low, convex to nearly flat crowns. Base smooth, closed and concave. Lateral borders of the base exhibit grooves and bulges.

Description of GP/2E-6290 (Figs. 3A-D): Labial and lingual faces of the crown are arranged in a 90° angle, just below a cutting ridge turned to the lingual face. The labial face of the tooth is trapezium-shaped (Fig. 3A), but with a lateral greater than the other.

The labial face is plane, with some undulations on the surface (Fig. 3C) smaller in height and greater in length, rather worn out. The lingual face is smaller than the labial one, exhibiting a small central concavity and an extension at one of the laterals (Fig. 3B).

A tip extends anteriorly, along the upper anterior lateral face, whereas a smaller extension is seen on the posterior lateral face. Small center cavities are seen on both sides.

The base articulation is plane near the lingual portion, where a small cavity is seen. Crenulations can be observed on the base surface (Fig. 3D).

The tooth is maximally 13.7 mm long, with 5 mm high and 12 mm width. The labial face is 8 mm in labial-lingual direction and 12 mm long between the laterals. The lingual face is 12 mm long and 5 mm high.

Description of GP/2E-6258 (Fig. 3E-I): angle between the labial and lingual faces is 90º. The labial face is flat, extended at one of the laterals, which could be a sign of pathology (Figs. 3H-I).

The lingual face (8 mm high) is smaller than the labial (11 mm) exhibiting a central cavity separating the whole tooth base. The tooth is an open curved triangle in lateral view (Fig. 3H-I).

The articulation base is irregular with very large crenulations at the labial-lingual direction. The specimen is heavily worn out, resulting in a clear dotted surface on every face.

Description of GP/2E-6304a (Fig. 4A-D): the outline of both labial and lingual faces show an acute angle smaller than 45°, resulting in a ridge turned toward a lingual face (Fig. 4D).

The base is straight with irregularities and crenulations (Fig. 4B). The labial face is irregular parallelogram-shaped, with one side larger than the other side, strongly curved, exhibiting a projection toward the posterior part of the tooth (Fig. 4A).

The labial face is characterized by a strong concavity near the ridge and by a slight convexity at the distal extremity, whereas a small concavity is present on the center part of the lingual face. The labial face is much larger, 4.5 mm high, than the lingual face, 2.3 mm high.

Description of GP/2E-6304b (Fig. 4E-H): the labial and lingual faces are disposed at an angle slightly smaller than 90°, with a ridge turned toward the lingual face.

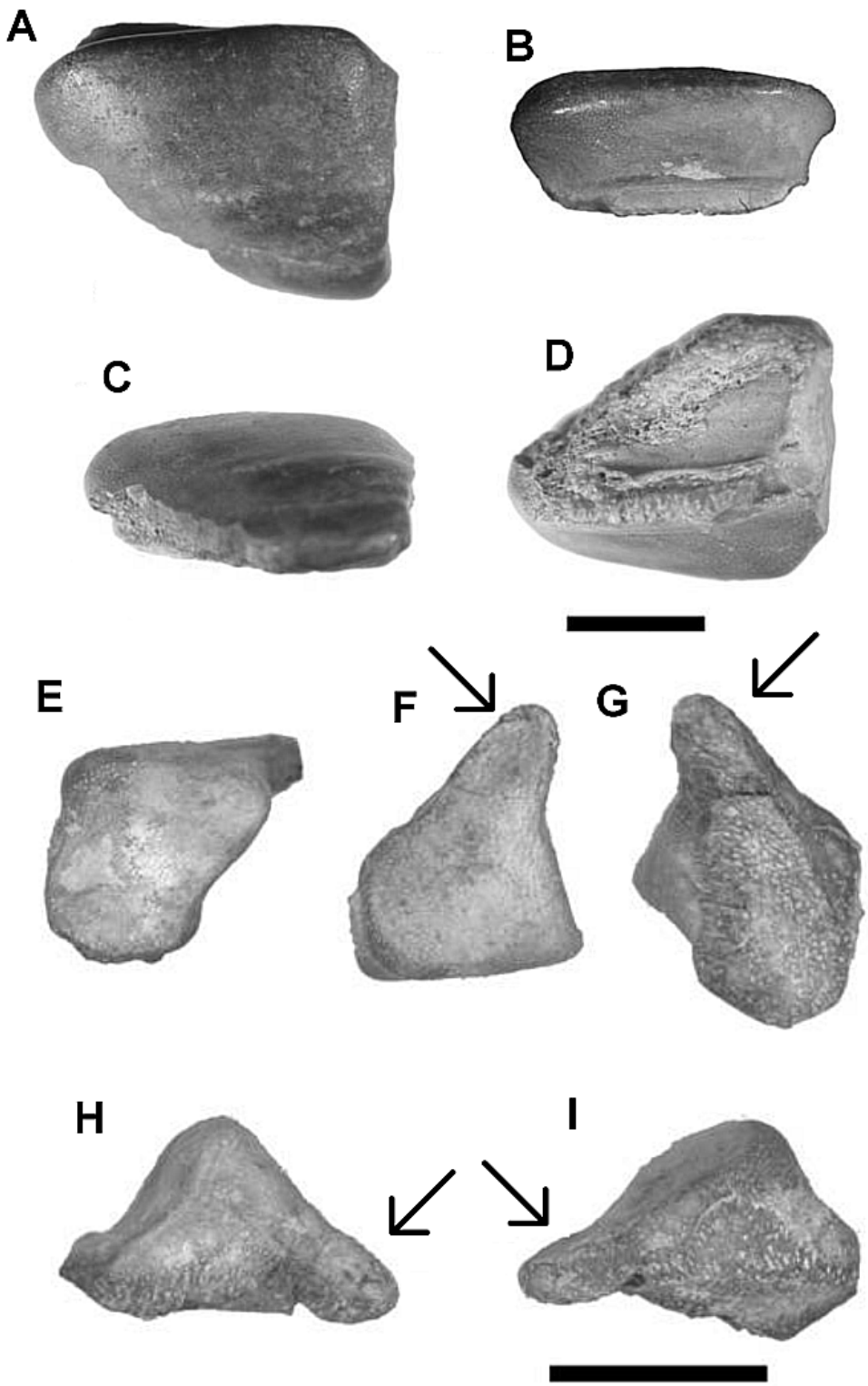

Figure 3.— *Itapyrodus* sp. A-D) Posterior-lateral tooth (GP/2E-6290). A) labial-occlusal view; B) lingual view; C) labial view; D) inferior view. Bar scale = 5 mm. E-I) Intermediate tooth (GP/2E-6258). E) lingual view; F) labial-occlusal view; G) inferior view; H) e I) laterals view. Bar scale = 10 mm. Arrows at F-I; indicate pathological extension of the labial face.

The base is irregular, straight and with crenulations. It is smaller than the crown width, measured at the anterior-posterior direction, with 4 mm at the base and 5 mm at the crown, here marked by the ridge length (Fig. 4G-H).

The labial face is trapezium-shaped, with one of the sides greater, one of the tips rounded and the other sharp, exhibits a strong concavity near the ridge and a small convexity at the distal extremity. The lingual face exhibits a small center concavity.

The lateral borders are different at both sides, convex at the greater portion and almost straight at the smaller portion, where it exhibits a small curvature near the lingual extremity. The lingual face is 4 mm high, while the labial measure 9 mm.

Description of GP/2E-6307 (Figs. 5A-D): the lingual face is larger (4mm) than the labial (2mm). The crown is massive, turned toward the lingual face, rounded at the top, with a ridge disposed on the anterior-posterior lingual face. The labial face is flat and inclined toward the lingual face. The lingual face exhibits concavity, starting on the central crown, getting stronger near the lingual border.

The inferior portion of the base is flat and smooth, only with some irregularities, more clear at the lingual border. The length is 7.5 mm diagonally measured. The labial border is 5.5 mm long and the lingual 4 mm.

The crown, 4 mm high, is askew toward one of the laterals, top rounded, strongly convex on its center. The ridge is a little over 5 mm long.

Both the anterior and posterior faces are smooth and straight. The posterior one is more inclined than the labial margin.

Description of GP/2E-6308 (Figs. 5E-H): Tooth with a depressed elongate ridge, disposed along the anterior-posterior direction. The labial face is an inclined plane. The lingual face exhibits a strong concavity on the central crown.

The lingual face is 5 mm wide and the labial measures only 3 mm, measured along the labial-lingual direction.

The smooth and flat base is shaped like a parallelogram. It bears crenulations on the lingual region. The maximum length, 8 mm, was measured diagonally. Both the labial and lingual borders are 4 mm long.

The crown, 4 mm high, is askew toward the posterior lateral. Its top is convex, increasing the convexity at the posterior portion. The ridge is 5 mm long.

Both lateral faces (anterior and posterior), are straight and flat, keeping the same inclination.

Discussion: The first *Itapyrodus* fossil came from an outcrop in Permian Pedra de Fogo Formation at State of Maranhão, Brazil, collected by Llewellyn Ivor Price in 1948. Ragonha (1978) informally attributed it to a petalodont new genus and species, *Itapyrodus punctatus.* Silva Santos (1990) described and formalized this taxon, based only on Pedra de Fogo specimens.

Although none of the teeth reported here were found in physical contact to each other, their positions within the fish mouth may be inferred from features of their lateral faces and ridges. For example, the sharp ridge likely used for nipping or cutting must be located at the front of the mouth. The lateral posterior margins teeth could easily have accommodated to the anterior bulges of the adjacent tooth, forming a continuous and close-fitting surface for crushing food.

The crown of the specimen GP/2E-6258 (Fig. 3E-I) is higher than a conventional postero-lateral tooth, even though unlike typical symphysian teeth. The worn out ridge top separates the lingual from the labial face, disposing diagonally between the laterals. This specimen seems to be an intermediary tooth between the symphysian teeth and the posterior-laterals, suggesting a gradual change of dentition.

The tooth GP/2E-6290 (Fig. 3A-D) should be placed in the *Itapyrodus punctatus* posterior–lateral teeth sequence according to Silva Santos (1990).

The *Itapyrodus* teeth GP/2E-6304a and GP/2E-6304b (Fig. 4) stand out compared with other material of this genus. The GP/2E-6304a is a posterior-lateral tooth, with well-developed labial face; however, its lingual face bears a strong salient ridge. GP/2E-6304b bears an extended labial face larger than other *Itapyrodus* teeth with similar positions in the mouth. This odd anatomy may be a result of a different feeding strategy.

The dotted aspect of the specimens GP/2E-6307 and GP/2E-6308 (Fig. 5) and the high crown disposition, are typical of symphysian teeth of *Itapyrodus*. However, different from *I. punctatus*, the labial face is much smaller than the lingual face. Therefore, these teeth must not be included in the *I. punctatus*. The teeth are slenderer than those of *I. punctatus,*

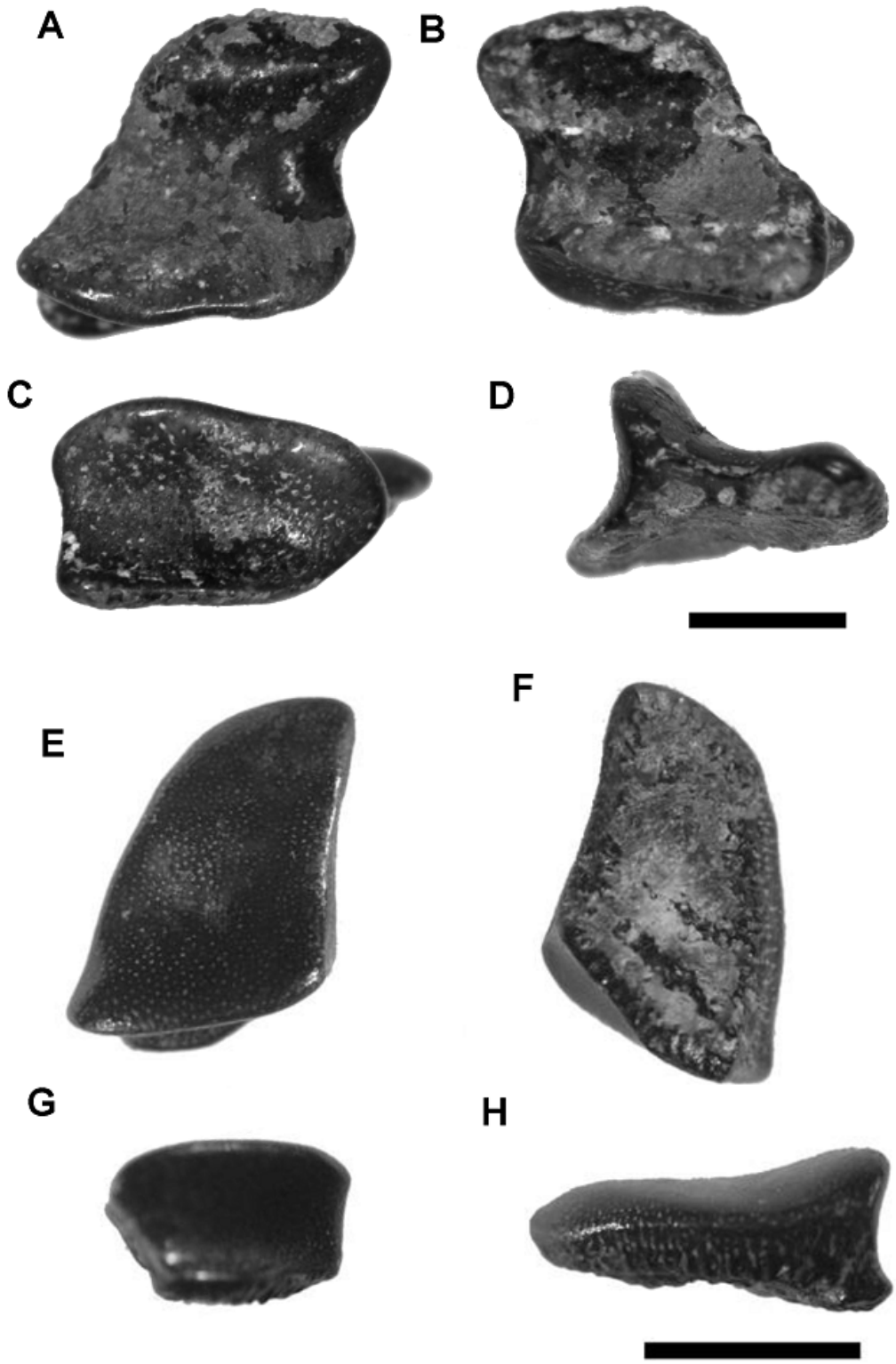

Figure 4.— *Itapyrodus* sp. A-D) Tooth GP/2E-6304a. A) Labial – occlusal view; B) inferior view; C) lingual view; D) lateral view. Bar scale: 2 mm. E-H) Tooth GP/2E-6304b. E) labial – occlusal view; F) inferior view; G) lingual view; H) lateral view. Bar scale: 2 mm.

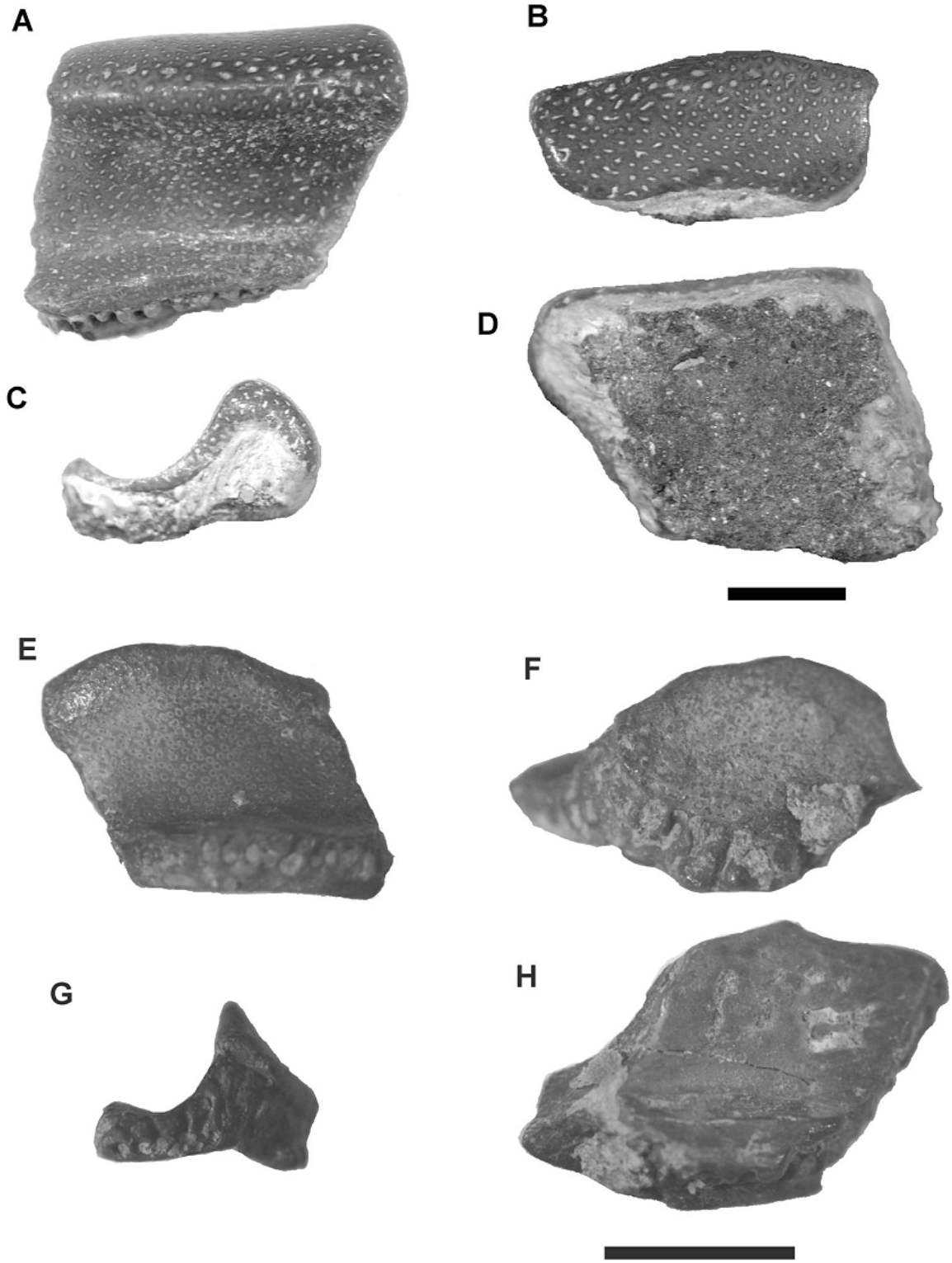

Figure 5.— *Itapyrodus* symphyseals teeth. A-D) Tooth GP/2E-6307. A) lingual view; B) labial view; C) lateral view; D) inferior view. Tooth GP/2E-6308. E) lingual view; F) labial view; G) lateral view; H) inferior view. Bar scales: 2 mm.

suggesting different prey such as small fishes or invertebrates.

The genus *Itapyrodus* has been attributed to Petalodontiformes since its formal description by Silva Santos (1990), based on the following similarities with *Chomatodus, Antliodus* and *Tanaodus/Climaxodus*: the shape of the labial-lingual faces, high crowns on the symphysian teeth and the absence of teeth fusion, like in some species of *Tanaodus/Climaxodus* (Woodward, 1919) and *Chomatodus* (Eastman, 1903).

Silva Santos (1990) considered the taxonomic position within Petalodontidae with caution, due to the smooth base and absence of denticles, as is the case in *Polyrhizodus* and *Petalodus*, both from northern hemisphere.

Lund et al. (2014a, 2014b) suggested "*Chomatodus* Group", sister group of Petalodontiformes for *Chomatodus* and *Tanaodus/Climaxodus,* which represents an important improvement for understanding the Petalodontiformes systematics. So, the genus *Itapyrodus* is questionably included in the Petalodontidae family, as previously classified by Silva Santos (1990).

The smooth and dotted crown observed on *Itapyrodus* teeth are like those of the taxa of the family Janassidae, such as *Janassa*, and Pristodontidae, similar to *Megactenopetalus* (Ossian, 1976; Merino-Rodo & Janvier, 1986).

The specimens dealt with herein differ from other Holocephali like Cochliodontiformes in the absence of teeth surface undulations, as is the case of *Deltodus, Helodus* and *Cochliodus*. They differ also by the absence of plate folds attaching to the mandibular region (Stahl, 1999).

The *Itapyrodus* posterior-lateral teeth have similar external surface shapes to the teeth of *Psammodus* and *Lagarodus* (Lebedev, 2008), but differ from them in the rather higher crown and the sharp cutting borders.

The several differences in the dentition observed when comparing with the holocephalans of the northern hemisphere justify the position of these Brazilian forms in a new family, Itapyrodidae.

The family Itapyrodidae appears suddenly in Paraná and Parnaíba basins in the Early Permian, without any record in older deposits. Originally reported in Pedra de Fogo Formation of the Parnaíba Basin, by Ragonha (1978) and Silva Santos (1990), in a thin but complex lithologic unit consisting of coarse sandstone, breccia and conglomerate with silex, the same lithotypes reported by Chahud et al. (2010) in the Taquaral Member sandy facies.

Examples of endemism during deposition of the sediments of the Taquaral Member deposition were disclosed before. The endemic taxa were recognized by Mezzalira (1952), Chahud & Petri (2013a; 2013b) and Chahud (2017), such as the crustaceans *Clarkecaris* (family Clarkecaridae, Brooks, 1962) and *Platuropodus odysseus* (Pazinato et al*.,* 2021).

The deposits and the fossils are suggestive of a similar paleoenvironment of both basins, probably high energy, shallow water and a strong continental influence, resulting in a low degree salinity.

Genus *Fairchildodus* gen. nov.
Figure 6

Etymology: In honor to Dr. Thomas Rich Fairchild. Paleontologist from the University of São Paulo and collector of the holotype.

Diagnosis: Elasmobranchii known only by the teeth. High crown, without cusps, elongated in lingual-labial direction. Thickness of the base (root) equal to or less than the crown. The sides of the tooth perpendicular to the labial and lingual faces have a triangular-shape with the central region of the triangle being convex on one side and concave on the opposite side. Row teeth touching each other but do not form dental plates. Apex longitudinal ridge separates the labial and lingual faces, which form an acute angle.

Fairchildodus rioclarensis sp. nov.
Figure 6

Etymology: referring to the town of Rio Claro (state of São Paulo, Brazil), , where the specimens were found.

Holotype: GP/2E-5929, a complete isolated tooth.

Syntype*:* GP/2E-6459, a complete isolated tooth.

Type locality: Flat-lying outcrop on SW side of the Rio Cabeça, about 850 m NNW from the entrance to the Santa Maria homestead (UTM: 23K 0227055/7517325) at the limit between the munic-

ipalities of Rio Claro and Ipeúna, São Paulo, Brazil.

Stratigraphy: A conglomeratic sandstone layer at the base of the Taquaral Member, Irati Formation, Lower Permian, Cisuralian, immediately above the Tatuí Formation.

Material: GP/2E-5929 and GP/2E-6459. Only the two type specimens.

Diagnosis: as for the genus

Description: The GP/2E-5929 is a complete triangular tooth, slightly worn by transport, base bilobate and concave with a small straight protrusion in the center base, possibly related to the articulation.

The very high crown, marked at the top by an elongated and curved longitudinal ridge in anterior – posterior direction, inclined a little toward the lingual face and a projection to the tooth posterior face.

The central concavity exposes, at the anterior face, a dentine system, from the base to the top of the crown (Fig. 6A). The tubular dentine, at the posterior face, is not so clearly seen, but still evident by the dotted system.

Both lingual and labial faces are similarly flat, resulting in a rectangle (Fig. 6C), but it is still possible to distinguish the faces by the top ridge inclination toward the lingual side, the angle between the faces is about 40º.

The two common features of the teeth are the triangular-shape outline formed by the laterals (Figs. 6A-B and 6D-E) and the different size of the laterals, though the difference is greater in the GP/2E-6459 (Figs. 6D-E). This specimen also is flattened on the base, exhibiting a greater central concavity at the anterior face, greater than in the specimen GP/2E-5929.

The specimen GP/2E-5929 is 14.5 mm long, 10.5 mm wide at the base; the ridge, 7.0 mm long. And

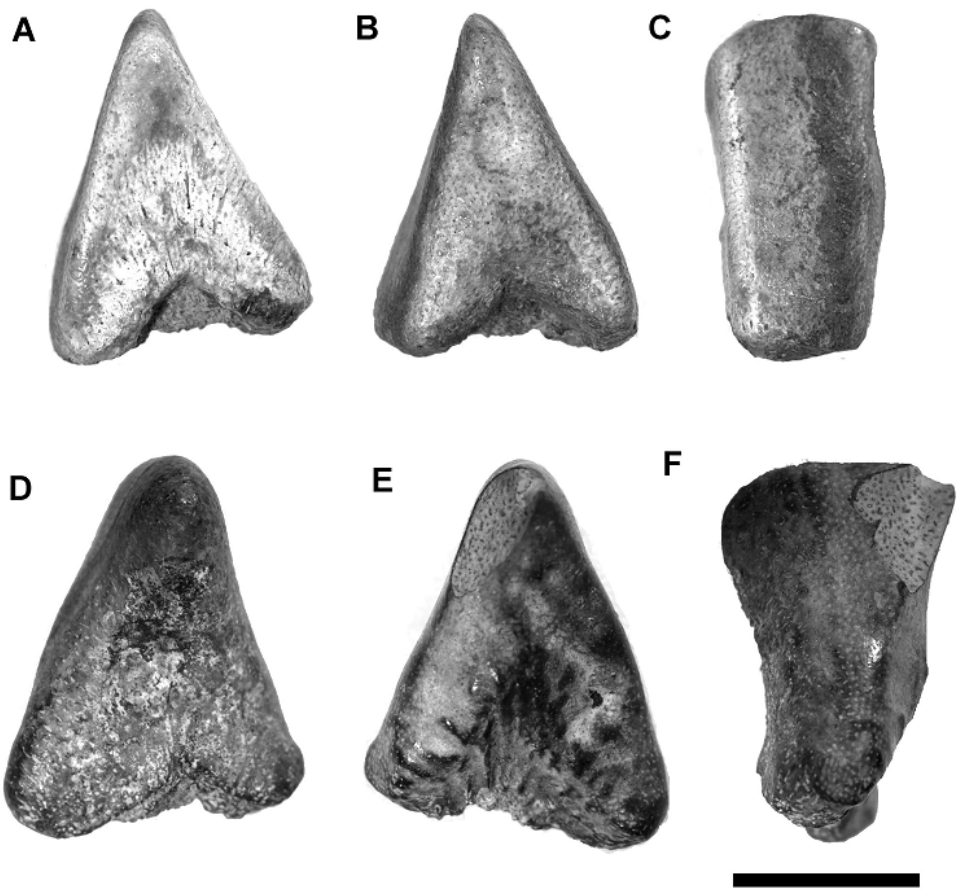

Figure 6.— *Fairchildodus rioclarensis.* A-C) Holotype tooth GP/2E-5929; A-B) lateral views; C) lingual view; D-F) Tooth GP/2E-6459; D and E) lateral views; F) lingual view. Bar scales: 8 mm.

the specimen GP/2E-6459 is 16.3 mm long, 13 mm wide at the base, with a ridge 10.0 mm long.

Discussion: The triangular-shape also is present in species of Helodontiformes, *Helodus coniculus,* United States Mississippian and *H. appendiculatus*, British Mississippian (Stahl, 1999). However, the Brazilian specimens do not have any cusps, denticles, the bulge at the occlusal region, and do not form dental plates, which discard their inclusion in the Helodontiformes.

The Brazilian teeth seem to belong to similar sequences as in the Eugeneodontiformes *Lestrodus, Parahelicoprion, Helicoprion, Sarcoprion, Parahelicampodus* and *Helicampodus*. However, the sequences in these genera are defined by the growth and later substitution by the spiral teeth (Zangerl, 1981), however this characteristic cannot be confirmed and would need other specimens.

The Brazilian specimens, now assigned to *Fairchildodus*, were compared by Chahud (2007) to the Pennsylvanian *Petalodus ohioensis* from Ohio, United States, and from the Italian Alps (Dalla Vecchia, 1988), in view of the teeth triangular shape of laterals teeth of *Fairchildodus* similar to the labial and lingual faces at the base of dental plates. However, the *Petalodus* laterals are thin or tapering to the vertex, distant from the triangle. The same occurs in living and fossil Neoselachii with triangular teeth.

A longitudinal ridge going up to the tooth apex is similar to *Itapyrodus*. However, a bulged point is present on the *Fairchildodus* tooth apex, which suggests a different feeding behavior.

The central lateral faces of *Fairchildodus* teeth are concave at one side and convex at the opposed side. This situation suggests a position in sequence on the jaw, forming two lateral rows, as Silva Santos (1990) suggested for *Itapyrodus*. There would be no internal rows or palatal teeth.

The triangular-shaped lateral faces are similar in both genera. However, the labial and lingual faces are very well developed in *Itapyrodus* and discret in *Fairchildodus*, justifying the proposition of a new genus and species, but both in the family Itapyrodidae.

Itapyrodus is rather common in the sandy Taquaral facies, while *Fairchildodus* is rare. It is believed then that this last genus is derived from *Itapyrodus* inside the Paraná Basin and is endemic in this basin.

Paleoenvironmetal considerations

The sandstones of the Taquaral Member means a high energy deposition. Fining upward from a coarse poorly sorted sandstone with more than 10 mm clasts (conglomerate) to fine sandstone, suggest a transgression with gradual increase of water depth.

The fossils were hardly transported, as inferred by the following observations: A) some teeth are in good state of preservation with no or very small flaws (Chahud & Petri, 2010; Chahud et al., 2012); B) great vertebrates still keeping some kind of articulations and teeth still connected with jaw parts (Chahud & Petri, 2010). This suggests some transport or occasional reworking.

The different state of preservation of the fossils might be due to sudden changes of water energy, taking the deposits to points of better chance of preservation.

Marasco et al. (1993) reported few beds containing acritarchs associated with the fossils studied here. These acritarchs would eventually indicate some salinity, but not so great to allow the presence of exclusively marine organisms.

The occurrence of characteristic fluvial fossils (basal tetrapods) (Chahud & Petri, 2010), the scarce presence of acritarchs (Marasco et al., 1993) and the absence of stenohaline species discard ocean paleoenvironment (Chahud, 2011).

The most convincing hypothesis for the paleoenvironment of deposition of the lowermost sandy Taquaral beds, is a large water body under strong continental influence and low salinity, as are the cases of the Baltic Sea, Black Sea or Caspian Sea.

Conclusions

Detailed research on the Holocephali of the Irati Formation revealed diversified forms of *Itapyrodus*, many of which still demanding more studies, but this genus was not monospecific. It differs from other genera and families, known from the Northern Hemisphere, as a consequence of the Paraná and Parnaíba basins isolation in those times. The time of confinement was sufficient to develop an endemic family, the Itapyrodidae.

A new genus and species based on teeth, endemic to the Paraná basin, is the herein proposed *Fairchil-*

dodus rioclarensis n. gen. et sp.. Some morphologic characteristics are similar to those of *Itapyrodus,* allowing its allocation in the family Itapyrodidae.

No marine stenohaline fossils were recognized in the sandy Taquaral facies. The continental influence is suggestive that these Chondrichthyes thrived at low salinity and high energy paleoenviroments.

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