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REVISITING THE CRETACEOUS LUNGFISH *ATLANTOCERATODUS IHERINGI* (AMEGHINO, 1898) FROM THE MATA AMARILLA FORMATION (ARGENTINA) WITH COMMENTS ON TOOTH PLATES HISTOLOGY

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Abstract. *Atlantoceratodus iheringi* (Ameghino, 1898) from Argentine territory is restudied based on its known tooth plates and newly discovered material, which includes previously unknown skull roof bones and vomerine tooth plates. The latter represent the first records of such elements from the Mesozoic era in South America. The comparative morphological analysis reveals its distinctiveness from other dipnoans, and offers valuable data for future systematic and phylogenetic research. The pterygopalatine tooth plates display narrow-based first denticulations and lack anterior wear facets, with the inner angle positioned at the level of the second denticulation. Similarly, the prearticular tooth plates feature straight mediolingual edges, and a wide-based first denticulation without sinuosities at the tip. Histological sections are performed and analyzed in detail for the first time. *A. iheringi* presents in this aspect distinctive features such as: large-lumen denteons tending to cluster together, circumdenteonal dentine arranged in a double band (an inner birefringent and an outer monorefringent), and a disordered interdenteonal dentine, with birefringence surrounding denteons and areas with monorefringence. *A. iheringi* exhibits histological structure closer to Mesozoic and Cenozoic dipnoans than Paleozoic, especially resembling the disposition observed in the Upper Cretaceous Patagonian species *Metaceratodus baibianorum*. The wide distribution of features designated as diagnostic for *Atlantoceratodus* is discussed.

Introduction

Dipnoans are a group of sarcopterygian fish with a fossil record that extends from the Devonian period to the present (Clement 2019). They currently occur in freshwater continental habitats, though they were also present in marine environments in the past. One distinctive characteristic is their unique dentition, which has consisted solely of tooth plates since the Mesozoic era (Smith & Johanson 2010). In the Paleozoic era, other types such as "pseudoteeth" or sheet dentine were also observed (Ahlberg et al. 2006). Only 6 species exist today, which are distributed in Latin America (*Lepidosiren paradoxa* Fitzinger, 1837), Africa (*Protopterus annectens* (Owen, 1839), *P. aethiopicus* Heckel, 1855, *P. amphibius* (Peters, 1844) and *P. dolloi* Boulenger, 1900), and Australia (*Neoceratodus forsteri* (Krefft, 1870)).

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Tooth plates, known for their remarkable durability, are frequently found in Cretaceous sediments of Patagonia, while other cranial and postcranial elements are comparatively rare (Wichmann 1927; Cione 1987; Apesteguía et al. 2007; Panzeri et al. 2022a). In Argentina, the oldest recorded tooth plate belongs to the species *Ptychoceratodus cuyanus* Agnolin, et al. 2016 recovered in the Upper Triassic Potrerillos Formation, Mendoza; while the most recent fossil evidence includes tooth plates assigned to the family Lepidosirenidae, from the Eocene Lumbrera Formation, Jujuy (Fernández et al. 1973). Presently, the recognized valid dipnoan species in Argentina are *Ptychoceratodus cuyanus* (Agnolin et al., 2016), *Atlantoceratodus iheringi* (Ameghino, 1898), *A. patagonicus* Agnolin, 2010, *Chaoceratodus portezuelensis* Apesteguía et al., 2007, *Ceratodus argentinus* Apesteguía et al., 2007, *Metaceratodus kaopen* Apesteguía et al., 2007, *M. wichmanni* Apesteguía et al., 2007, *M. baibianorum* Panzeri et al., 2020, and *Rinconodus salvadori* Panzeri et al., 2022a. The only documented occurrence of an almost fully preserved cranial roof and postcranial remains in Argentina can be attributed to *Rinconodus salvadori*.

In the late 19th century, Carlos Ameghino discovered the first fossil remains of a dipnoan in the 'Piso Sehuense' of the Guaranítica Formation, now recognized as Cretaceous outcrops of the Mata Amarilla Formation. Based on a pterygopalatine tooth plate (originally described as prearticular), the naturalist Florentino Ameghino (1898) named the species *Ceratodus iheringi* due to its resemblance to European species assigned to the same genus. Cione et al. (2007) studied new material recovered from the outcrops of the Mata Amarilla Formation and established a new genus for this species, creating the new combination, *Atlantoceratodus iheringi*.

The current paper presents a morphological reexamination of the tooth plates of *Atlantoceratodus iheringi* including description of new materials, such as skull roof bones and vomerine tooth plates, as well as a histological description of its tooth plates. It follows the recent advancements in the study of the structural and anatomical variations in dipnoan morphology (e.g. Skrzycki 2015; Pawlak et al. 2020; Panzeri et al. 2020, 2022a) and histology (Denison 1974; Smith 1984; Campbell & Barwick 1998; Kemp 2001; Blaauwen et al. 2006; Panzeri et al. 2022b). Finally, the similarity with lungfish from other parts of the world and the taxonomic assignment of other species referred to this genus are discussed.

Geological settings

The Austral Basin exhibits an elongated shape extending in a north-south direction across the Patagonian territories of Argentina and Chile (Varela et al. 2011; Fig. 1A, B). It is bordered to the east by the Río Chico High and to the west by the Patagonian Andes of Tierra del Fuego. The Middle/Late Jurassic to the Neogene sedimentary succession, reaches a maximum thickness of 8.000 meters, overlaying the basement of Tierra del Fuego (Varela et al. 2012).

The Cretaceous sedimentary sequences encompass several formations, including Springhill, Río Meyer, Piedra Clavada, Mata Amarilla, La Anita, Cachorro, and La Irene (Poiré et al. 2017). In southwest Santa Cruz Province, Patagonia, Argentina, the Mata Amarilla Formation crops out (Cenomanian-Santonian; Fig. 1C). This formation overlies the Piedra Clavada Formation and is subsequently overlain by the La Anita Formation. The lower section of the Mata Amarilla Formation is characterized by fine-grained sediments, paleosols, laminated mudstones, and coquinas, indicating a coastal or distal fluvial environment (Varela et al. 2011). The middle section features conglomerates, sandstones, siltstones, and mudstones, suggestive of fluvial environments. The third section exhibits lithological similarities to the first section and its facies association suggests a coastal marine, lagoon, estuarine, and distal fluvial environment (Varela et al. 2012). The materials studied in the present work comes from the upper section of the Mata Amarilla Formation, as described by Cione et al. (2007). This section has yielded remains of plesiosaurs, dinosaurs, turtles, plants, invertebrates, and shark teeth. Specifically, these materials were collected in the locality Estancia Bajada de los Orientales (near the locality of Tres Lagos; Fig. 1C) , while the holotype collected by Carlos Ameghino, comes from Estancia Mata Amarilla (or Ea. La Soriana; Fig. 1C).

Material and Methods

Material

Around 550 tooth plates (complete and fragments) were studied. These include pterygopalatine (upper) and prearticular (lower) tooth plates , associated or not with the corresponding bones, as well as fragments of dermal skull bones and vomerine tooth plates. Some of these materials, corresponding to tooth plates and associated pterygopalatine prearticular bones, were previously studied by Cione

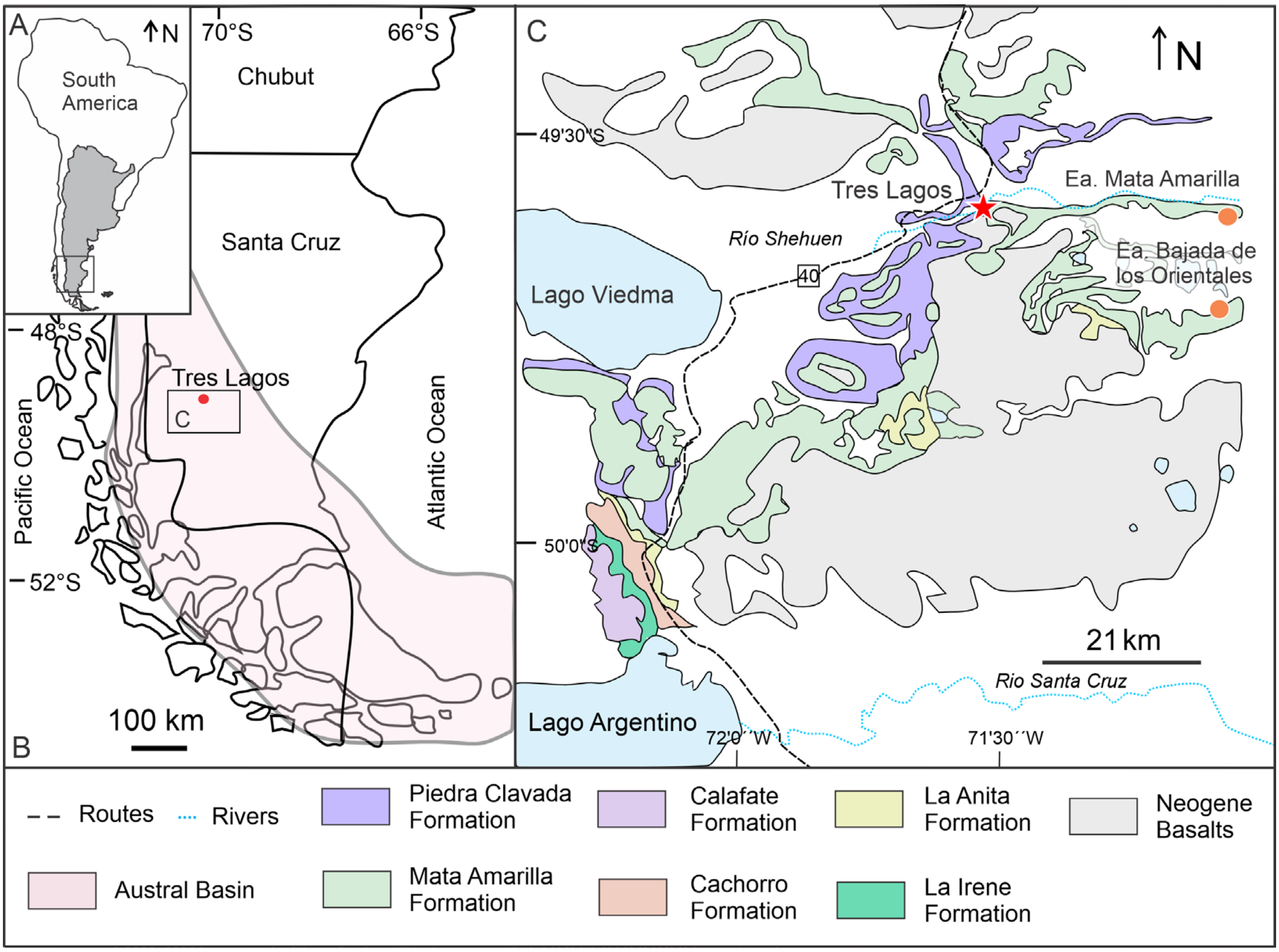

Fig. 1 - Map illustrating the locality where the fossils were extracted (modified from Varela et al. 2012): A, Map of South America; B, Map of the southernmost region of Argentina, with the Austral Basin highlighted in pink; C, Area B (square) near the Tres Lagos locality (star in red), and the fossil sites (circles in orange).

et al. 2007 (MPM-PV-1160.5, MPM-PV-1162.10, MPM-PV-1163.5, MPM-PV-1164.5, MPM-PV-1166.2, MPM-PV-1167, MPM-PV-1169.2, MPM-PV-1171.3, MPM-PV-1172.2, MPM-PV-1173, MPM-PV-1176.4, MPM-PV-1194.4). In the present study, new material is also examined: MPM-PV-1158.15, MPM-PV-1159.27, MPM-PV-1161.48, MPM-PV-1165.3, MPM-PV-1170.3, MPM-PV-1175.28, MPM-PV-1872.11, MPM-PV-1873.173, MPM-PV-1874.22, MPM-PV-1875.36, MPM-PV-1876.29, MPM-PV-1877.111; including the following histological sections: MPM-PV-1878, MPM-PV-1879, MPM-PV-1880, MPM-PV-1881, MPM-PV-1882, MPM-PV-23367, and MPM-PV-23368. The majority of the materials come from Estancia Bajada de los Orientales, except for the holotype of the species and the tooth plates designated as MPM-PV-1176, which come from Estancia Mata Amarilla.

Methods

Morphological descriptions were conducted using the set of terms implemented in Panzeri et al. 2020, and originally defined by Kemp (1977), Churcher & De Iullis (2001), and Smith & Campbell (1987). Each tooth plate consists of a medial, lingual, and labial edge (Fig. 2A). The labial edge presents denticulations (positive features) and clefts (negative features). On the occlusal surface, ridges (coincident with the denticulations) and furrows (coincident with the clefts) can be observed (Fig. 2A). Since the nomenclature of the cranial roof is controversial, here the nomenclatural scheme proposed by Cavin et al. 2007 is followed (for justification of the use of this criterion, see Panzeri et al. 2022a). Measurements of tooth plates were directly taken on the material using a digital caliper and photographs with the ImageJ software (Schneider et al. 2012). The materials were examined under a binocular stereo-microscope (ZEISS Stemi 2000-C).

Histological sections were performed following three main cutting planes (Fig. 2B) referred as horizontal, vertical, and transverse vertical. A total of seven histological cuts were made. Due to the tooth plates being mostly incomplete, only specimens with missing denticulations were sectioned. Additionally, due to their small size and relative thinness, only one horizontal section per tooth plate was obtained, resulting in four horizontal sections: two from prearticular tooth plates (MPM-PV-1882 and MPM-PV-23367) and two from pterygopalatine tooth plates (MPM-PV-1882 and MPM-PV-23368). One vertical cut was obtained from a pterygopalatine tooth plate (MPM-PV-1878), and two transverse vertical sections were obtained from another pterygopalatine tooth plate (MPM-PV-1879, MPM-PV-1880).

The histological sections were performed at CIG, while the analysis was carried out in the INREMI. All sections were observed under a petrographic microscope (Nikon Optiphot - Pol 255884) using transmitted light, with a cross-polarizer (530 nm) and a 1/4 lambda filter, at magnifications of 2x, 5x, 10x, and 20x. All images were captured with a digital camera (Xiaomi RedmiNote 10). Glycerin was

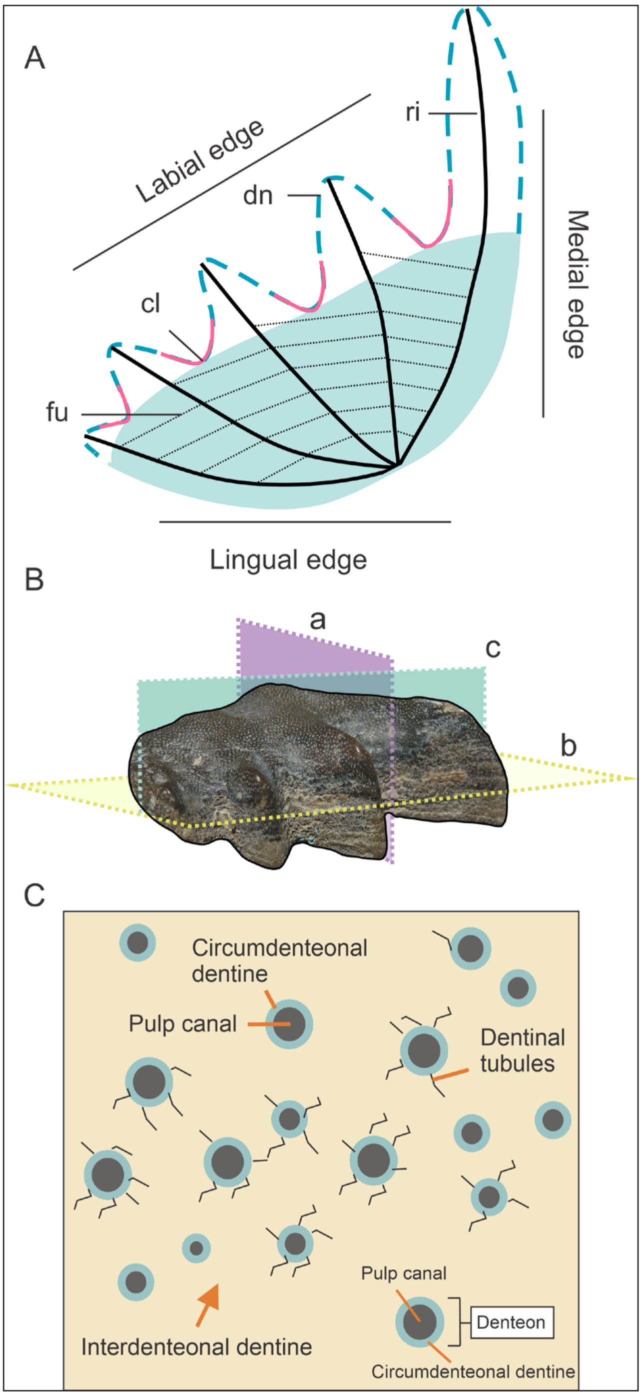

Fig. 2 - Morphological and histological terminology: A, Schematic drawing of a tooth plate in occlusal view showing morphological traits (modified from Panzeri et al. 2020). On the labial edge, the denticulations (discontinuous line) and clefts (continuous line); over the occlusal surface, the plateau area (in light green), ridges (continued line), and furrows (dotted line); B, planes of sections (modified from Panzeri et al. 2022b) named here as vertical plane (a), horizontal plane (b), and vertical transversal plane (c); C, Diagram illustrating the main features in a section of a tooth plate along the horizontal plane. Abbreviations: cl, cleft; dn, denticulation fu, furrow; ri, ridge.

used to enhance the clarity of the sections, and water was used if glycerin did not spread properly. No coverslips were used in any of the sections.

The histological description follows a combination of terms previously implemented in Panzeri et al. 2022b (see references cited there). Briefly, in a horizontal histological section, pulp canals surrounded by circumdenteonal dentine can be identified, collectively forming a denteon (Fig. 2C). The denteons are embedded in interdenteonal dentine. The outermost layer of the tooth plate consists of enamel, and beneath it lies the mantle dentine. In the vertical sections, pulp canals in an occluso-pulpal arrangement surrounded by circumdenteonal dentine can be observed, embedded in interdenteonal dentine.

Morphological abbreviations: af, anterior facet; ap, ascending process; aof, anterior overlapping facet; bfi, birefringent interdenteonal dentine; cd, circumdenteonal dentine; cl, cleft; dn, denticulation; dt, dentinal tubules; dep, descending process; en, enamel; fu, furrow; id, interdenteonal dentine; icb, inner circumdenteonal band; md, mantle dentine; map, medial articular process; mfi, monorefringent interdenteonal dentine; ocb, outer circumdenteonal band; ol, osteocyte lacunae; orp, orbital process; pca, pulp cavity; pf, posterior facet; pof, posterior overlapping facet; prb, prearticular bone; pas, parasphenoid groove; ri, ridge; td, transitional denteons.

Institutional abbreviations*:* CIG, Centro de Investigaciones Geológicas; INREMI, Instituto de Recursos Minerales; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia; MLP, Museo de La Plata; MML, Museo Paleontológico "Héctor Cabaza", Lamarque; MPM, Museo Regional Padre Jesús Molina.

Results - Systematic Paleontology

Class **SARCOPTERYGII** Romer, 1955
Order **Dipnoi** Müller, 1845
Genus *Atlantoceratodus* Cione et al., 2007

Diagnosis (slightly modified from Cione et al. 2007): Tooth plates with sharp, slender and acute ridges that originate posteromedially; five ridges in the upper tooth plates and four ridges in the lower tooth plates; restricted pulp cavity; limited mantle dentine visible on occlusal surface; punctations simple (petrodentine sensu Kemp, 2001 absent) and not arranged with a particular pattern. Tooth plates most resemble those of *Ptychoceratodus* and *Ferganoceratodus* but differ from them in that the inner apex it is not so well defined, it is rounded, a larger angle is usually formed by first and last ridges, and the ridges are more slender and acute.

Atlantoceratodus iheringi (Ameghino, 1898)

Holotype: MLP 21-967, partially preserved pterygopalatine tooth plate without an attached bone.

Type locality: Estancia Mata Amarilla (loc. 3LAG2)

Referred Material: Approximately 500 tooth plates, mostly fragmented. Additionally, there are vomerine tooth plates and bone fragments identified as parts of the skull roof, parasphenoids, pterygopalatine, and prearticular bones. Each collection number represents a set of tooth plates and bones: MPM-PV-1160.5, MPM-PV-1162.10, MPM-PV-1163.5, MPM-PV-1164.5, MPM-PV-1166.2, MPM-PV-1167, MPM-PV-1169.2, MPM-PV-1171.3, MPM-PV-1172.2, MPM-PV-1173, MPM-PV-1176.4, MPM-PV-1194.4, MPM-PV-1158, MPM-PV-1159, MPM-PV-1161, MPM-PV-1165, MPM-PV-1170, MPM-PV-1175.28, MPM-PV-1872.11, MPM-PV-1873.173, MPM-PV-1874.22, MPM-PV-1875.36, MPM-

PV-1876.29, MPM-PV-1877.111, and the following histological sections: MPM-PV-1878, MPM-PV-1879, MPM-PV-1880, MPM-PV-1881 (Fig.S1), MPM-PV-1882 (Fig.S2), MPM-PV-23367 (Fig. S3), MPM-PV-23368 (Fig. S4).

Diagnosis: Tooth plates reaching a small to medium size (1.61 cm on the medial edge and 1.35 cm on the lingual edge) with a reduced plateau area. A minimal wear pattern is observed on the furrow and the medial-lingual edge. The medial edge is longer than the lingual edge and equally curved in pterygopalatine tooth plates, while tending to be straight in prearticular tooth plates. The lingual edge of pterygopalatine tooth plates forms a slightly obtuse angle with the sagittal plane. The inner angle is located at the level of the second denticulation in the pterygopalatine tooth plates and at the level of the first cleft in prearticular tooth plates. The first denticulation of pterygopalatine tooth plates is narrow-based, anterolabially directed, without an anterior wear facet, and slightly curved posteriorly. The first denticulation of prearticular tooth plates is straight, thin and narrow-based. The fifth and fourth denticulations have similar length and width in pterygopalatine tooth plates, both anteriorly directed. The fifth ridge in the pterygopalatine tooth plates is involved in the formation of the step, while the fourth ridge in the prearticular tooth plates forms the spur. The pterygopalatine symphysis is longer than wide, displaying consistent thickness, a dorsal convex and a ventral flat contour. The ascending process of the pterygopalatine bone is at level of the second denticulation. In some areas, the circumdenteonal dentine is arranged in a double band.

Description

Morphological Description

The tooth plates of *Atlantoceratodus iheringi* exhibit small to medium sizes: the larger tooth plates measure up to 1.61 cm in length along the medial edge and 1.35 cm along the lingual edge. The furrows are shallow, and the denticulations have rounded ridges with rounded or pointed crests. In the pterygopalatine tooth plates, the inner angle (R1-RN) measures approximately 92.706°, while in the prearticular tooth plates, it measures around 98.082°.

Pterygopalatine tooth plates and fused bones: The pterygopalatine tooth plates are fused to the pterygopalatine bones (Fig. 3A-C). The symphysis of the bone is located close to the first denticulation of the tooth plates and appears homogenous (without anterior widening), with a curved dorsal and a straight ventral contour (Fig. 3B). The pterygopalatine bone exhibits slender crests that delimit small negative areas. Dorsally, the pterygopalatine bone features the ascending process at the level of the second denticulation, and its base is circular (Fig. 3C).

The pterygopalatine tooth plates have five denticulations, and their occlusal surface is covered with punctuations without a defined pattern (Fig. 3D). The inner angle of the pterygopalatine tooth plates is located at the level of the second denticulation or slightly behind it (Fig. 3A, D, E). The inner angle is not prominently marked due to the curvature of the mediolingual edge. The plateau area near this zone is poorly developed, and ridges and furrows can be observed reaching the inner angle.

The first denticulation is the longest, while the following ones decrease in length posteriorly (Fig. 3A, D). The first denticulation curves slightly backward. It is narrow while maintaining its thickness towards the tip and lacking an anterior wear facet. The posterior denticulations have similar shapes and lengths to each other, with wider bases, while the last three denticulations remain close to each other. The fourth and fifth ridges curve anteriorly, and the last ridge forms an incipient step when prolonged wear occurs (Fig. 3D). The enamel covers the entire edge and exhibits distinct banding (Fig. 3B, F-H). In some specimens, it can also be observed on the occlusal surface.

In-life wear is evident on the plateau area, the posterior facets of the denticulations, the depth of the furrows, and the last denticulation. The plateau area shows a concave surface due to wear, with a slightly elevated mediolingual edge (Fig. 3E, H). Typically, the first and second furrows exhibit the greatest depth, while the remaining are shallower. The posterior facets of the denticulations lose enamel due to contact with the prearticular tooth plates (Fig. 3F, G). Towards the posterior area, a wear pattern in the form of small circles can be observed (Fig. 3D).

Smaller specimens have cusps positioned along the midline of the crest or ridges (Fig. 3H). In a profile view, the crest of the denticulations appears smooth with gentle slopes in smaller individuals, whereas in bigger ones, they become more pronounced (Fig. 3H).

The vomerine tooth plates (Fig. 3I-L) are curved, with the concave side positioned lingually (Fig. 3J) and the convex side positioned labially (Fig. 3I). Towards the anterior end, they curve ventrally and end in a pointed shape, while the posterior end is rounded. The occlusal portion features a convex ridge with denticles lining its edge (Fig. 3L). The pulp cavity is concave, has an oblong shape, and widens towards the anterior end (Fig. 3K). Bands of enamel can be observed on both the labial and lingual surfaces.

Parasphenoid and Skull Roof Bones: These elements are preserved as fragmented pieces. The fragments identified as parts of the parasphenoid only conserve the central portion. The anterior section appears widened (Fig. 3M), while the posterior section is narrow and has a groove delimited by two crests (Fig. 3N). Among the bones comprising the skull roof, one bone from the medial series (with some uncertainty) and one from the mediolateral series have been identified. Both are incomplete, with only the right lateral side preserved. The bone from the medial series displays a V-shaped commissure on its external and medial surfaces, with an overlapping suture for the anterior bone of the same series (Fig. 3O). On its right lateral side, a facet is evident, possibly for articulation with one of the bones from the mediolateral series. On the ventral surface, a bony projection can be observed, which may come in contact with the endocranium (Fig. 3P).

The anterior bone of the mediolateral series bear marks of the supraorbital canal of the lateral line system on their dorsal surface associated with pores. The dorsal margin of the orbit is concave and delimited posteriorly by the lateral process and anteriorly by the anterolateral edge of the mediolateral bone (Fig. 3Q). Posterior to the lateral process, there is an overlapping articulation facet for another bone (from the same or different series). Ventrally, part of the descending process can be identified, which would articulate with the ascending process of the pterygopalatine bone (Fig. 3R).

Prearticular tooth plates and fused bones: The prearticular tooth plates are fused to the prearticular bones (Fig. 4A). The symphyseal surface of the bone is linear, narrow, and located at a certain distance from the first denticulations, resulting in the separate positioning of the tooth plates (Fig. 4A, B). The bone has a ventral and labial sulcus (Ruge's canal) divided by a ridge (Fig. 4C, D). The anterior groove is smaller than the posterior groove. It also has a surface texture equal to that of the pterygopalatine bone (Fig. 3A-C).

The prearticular tooth plates have four denticulations, and their occlusal surface is covered with randomly arranged punctuations (Fig. 4E, F). The medial edge is longer than the lingual edge (Fig. 4E). The lingual edge curves backward, forming a vertex (Fig. 4E-G). The first denticulation is the longest, with a narrow base that tapers towards the tip. It is straight and without sinuosity (Fig. 4E). The length of the subsequent denticulations decreases posteriorly, and the third and fourth denticulations curve anteriorly. The base of the first denticulation is higher than the lingual edge (Fig. 4H).

The inner angle is located at the first furrow, and is well-defined (Fig. 4F, G). The enamel is positioned on the mediolingual edge and on the bases of the clefts and denticulations. In some cases, it is observed on the occlusal surface.

Wear on the prearticular tooth plates is evident on the area of the plateau, the anterior facet of the denticulations, the furrows, and the formation of the spur. The area of the plateau is convex and, in some cases, it may appear flat. The anterior facets of the denticulations lose enamel. The fourth ridge forms the spur that occludes against the step of the pterygopalatine tooth plates. The wear pattern due to occlusion is in the form of circular depressions positioned towards the posterior part of the tooth plate (Fig. 4I). Cusps are often distributed along the midline of the crests and ridges (Fig. 4J).

Fig. 3 - Palatal region and cranial roof bones of *Atlantoceratodus iheringi*: A) MPM-PV-1872.11.1, pterygopalatine tooth plate with a fused bone. The solid line indicates the decreasing depth of the clefts backward, and the dashed line indicates the position of the inner angle; B) MPM-PV-1872.11.1, the shape of the pterygopalatine symphysis with the dashed line indicating the contour; C) MPM-PV-1872.11.2, the position of the base of the pterygopalatine ascending process; D) MPM-PV-1872.11.3, the position of the inner angle (dashed line) and the posterior area with wear pattern (arrows); E) MLP 21-967, concave plateau area with the elevated mediolingual edge (arrow); F) MPM-PV-1877.111.1, posterior wear facet of a first denticulation without enamel; G) MPM-PV-1877.111.1, anterior surface of the same denticulation with enamel; H) MPM-PV-1872.11.4, concave plateau area with elevated mediolingual border. The white arrow points to enamel banding, and the black arrows point to cusps on the crests; I-L) MPM-PV-1876.29.1 vomerine tooth plates in labial (I), lingual (J), pulpal (K), and occlusal (L) views; M, N) MPM-PV-1877.111.2, and .3, incomplete parasphenoid bones; note the enlarged anterior portion and the posterior groove; O, P) MPM-PV-1876.29.2, bone (identified with doubts) of the medial series in dorsal (O) and ventral (P) views; Q, R) MPM-PV-1876.29.3, anterior bone of the mediolaterial series in dorsal (Q) and ventral (R) views. Abbreviations: ap, ascending process; aof, anterior overlapping facet; dep, descending process; map, medial articular process; pf, posterior facet; pof, posterior overlapping facet; pas, parasphenoid groove orp, orbital process. All scale bars represent: 1 cm.

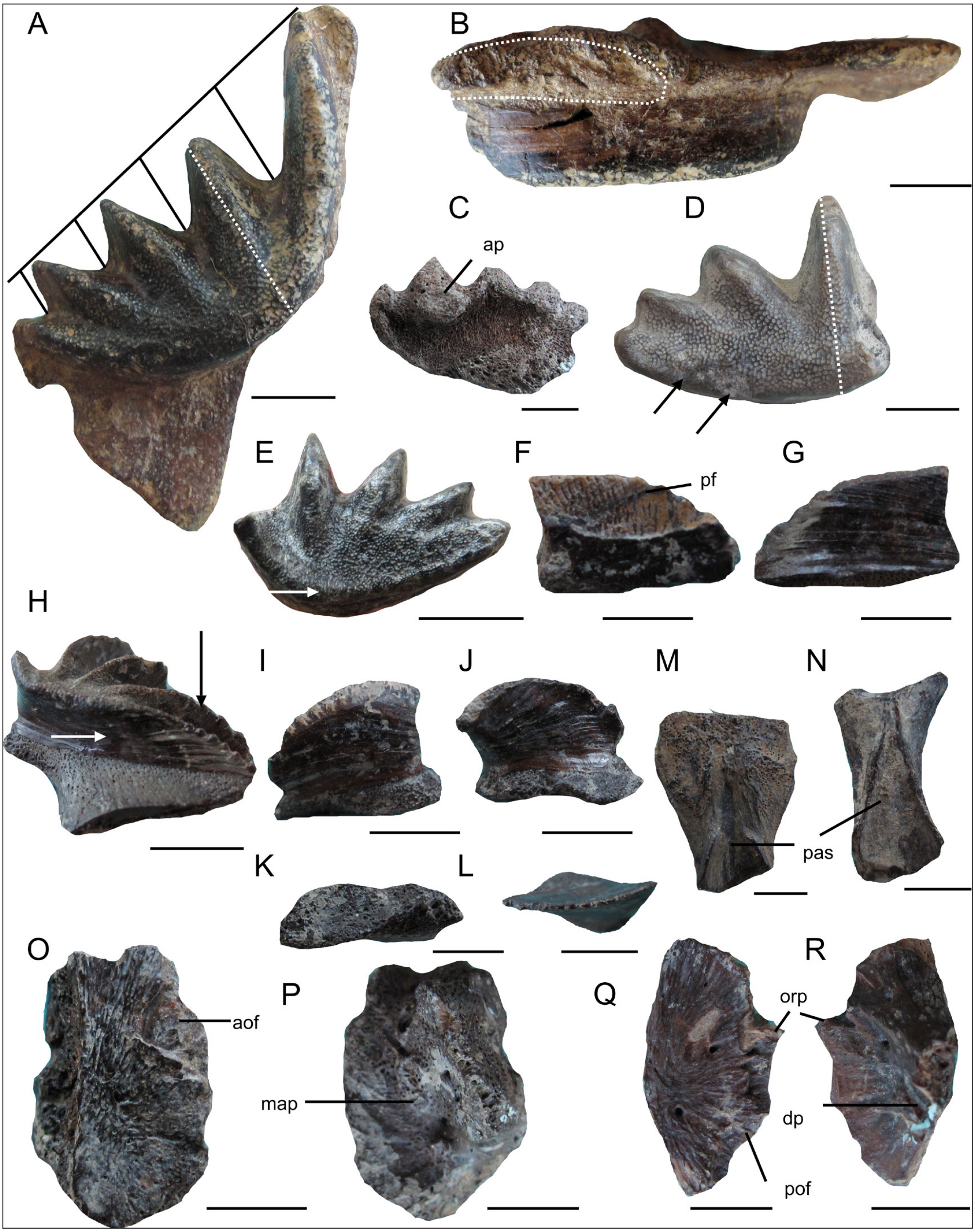

FIGURE 3

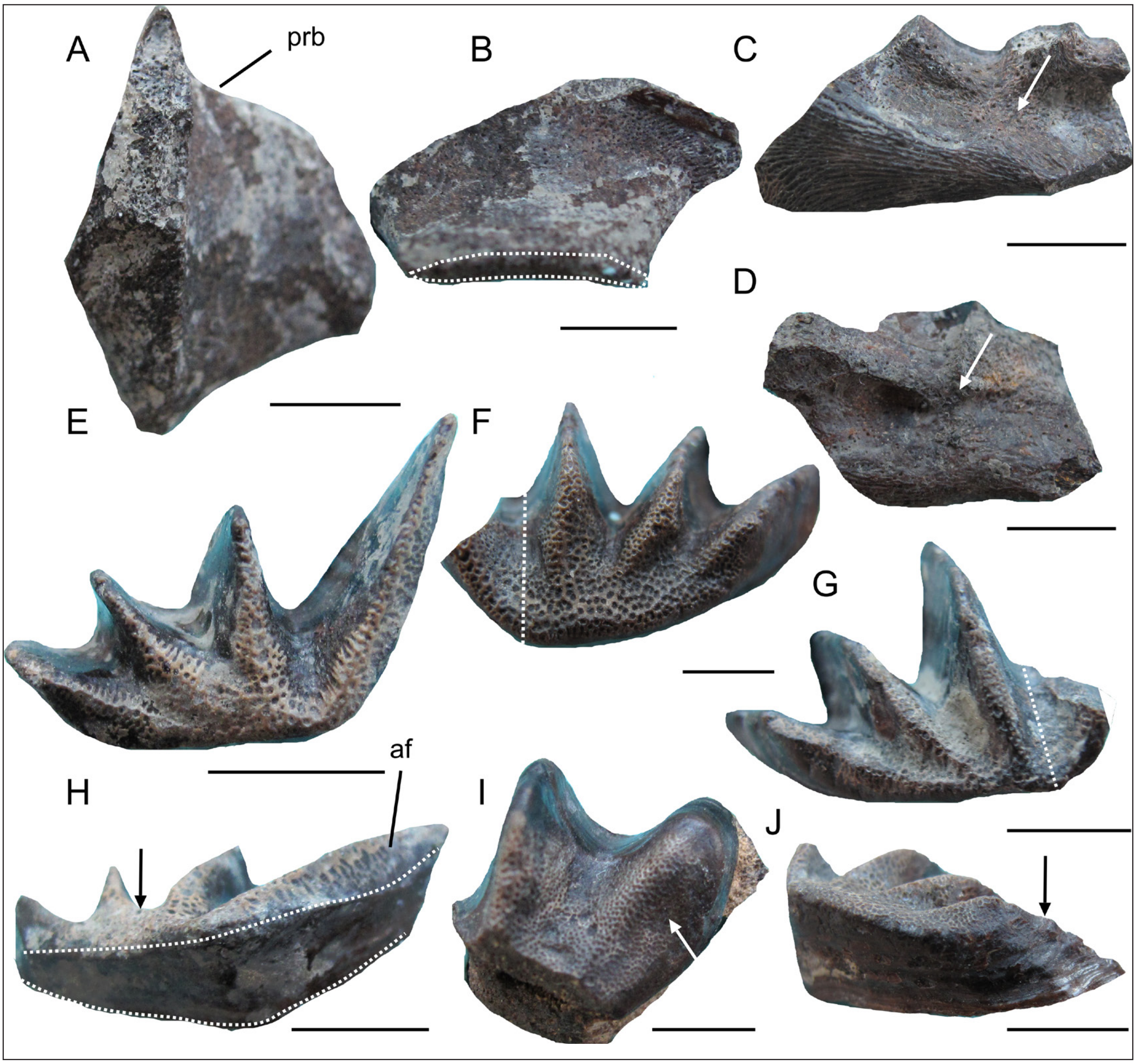

Fig. 4 - Prearticular tooth plates and fused bones of *Atlantoceratodus iheringi* (Mata Amarilla Formation): A, B) MPM-PV-1877.111.4, prearticular bone illustrating the distance of the symphysis from the first denticulation (A) and the contour of the symphysis (B); C, D) MPM-PV-1877.111.5 (C) and .6 (D), prearticular bones illustrating the Ruge's canal divided by a ridge (arrow); E) MPM-PV-1874.22.1, complete prearticular tooth plate; F, G) MPM-PV-1874.22.3 (F) and .4 (G), tooth plates illustrating the position of the inner angle; H) MPM-PV-1874.22.1, tooth plate with the medial edge higher than the lingual edge; I) MPM-PV-1874.22.2, prearticular tooth plate with the last ridge worn; J) MPM-PV-1874.22.3, tooth plate illustrating cusps on the crest. Abbreviations: prb, prearticular bone; af, anterior facet. All scale bars represent: 1 cm.

Histological description: Horizontal sections (Fig. 5A)

Plateau area: The denteons are embedded in interdenteonal dentine, which contains hydroxyapatite crystals oriented in two patterns: one birefringent and parallel to the occlusal surface, and another monorefringent with randomly arranged fibers (Fig. 5B, C). The birefringent interdenteonal dentine surrounds the clusters of denteons and rarely forming a cross-like pattern. Monorefringent interdenteonal dentine patches are positioned between the denteons and the birefringent interdenteonal dentine.

Each pulp canal is surrounded by two bands of circumdenteonal dentine: an outer and an inner band (Fig. 5D, E). In the sections with greater polishing (MPM-PV-1882), the inner band of circumdenteonal dentine appears amber-colored under polarized light, while the outer one appears dark under polarized light. Implementing a lambda filter, the inner band appears birefringent and its fibers surround the pulp canals in concentric lamellae. The outer band appears monorefringent and may correspond to an outer layer of circumdenteonal dentine where the fibers are randomly or parallelly arranged concerning the ray of light (Fig. 5D, E). In the other sections MPM-PV-1881, this arrangement is not as evident, the outer layer is reduced, and the inner layer appears darker (Fig. 5F). In all sections, dentinal tubules are sparsely distributed and uniformly encircle the denteons (Fig. 5E, F). The denteons appear clustered and are larger compared to those found at the edges.

Mediolingual area: Towards the inner angle, the mantle dentine differs from the central interdenteonal dentine (Fig. 5G, I). This area exhibits an amber coloration (Fig. 5G; birefringent under polarized light) with darker patches (Fig. 5H, I; monorefringent areas under polarized light). Osteocyte lacunae and bone fibers are observed (Fig. 5H). Transitional denteons arise from the mantle dentine, with a great amount of circumdenteonal dentine surrounding the canals. Externally, a thin layer of birefringent enamel is visible (Fig. 5I). Dentinal tubules interconnect with each other forming tangles, and granules are observed at their bases (Fig. 5J). The granules are present throughout the section, but they are mainly gathered at the mediolingual border.

Labial area: At the labial edge, the denteons originate from the margin of the denticulations and converge towards the ridge (Fig. 5K). Along the margins, the denteons are smaller and exhibit a slight curvature towards the center of the denticulation, where they merge with others and increase in size (Fig. 5K). The arrangement of the mantle dentine is similar to that in the mediolingual edge, predominantly monorefringent when viewed under polarized light. Towards the furrow, an amber-colored mass containing a significant number of denteons and bone with osteocyte lacunae is evident (Fig. 5L).

Vertical and transverse vertical sections

The pulp canals are arranged occluso-pulpally, originating from a specific point and typically not continuous (Fig. 6A-C). They are surrounded by a band of monorefringent circumdenteonal dentine (Fig. 6A, C), while an outer band encloses this structure and some adjacent pulp canals. Between the pulp canals, the interdenteonal dentine is organized into two birefringent rows (Fig. 6B), defining a central row of monorefringent interdenteonal dentine (Fig. 6D).

Dentinal tubules of adjacent pulp canals intertwine, resembling incremental lines (Fig. 6E). Towards the ends, especially in the lingual edge, a large number of osteocyte lacunae can be observed (Fig. 6F).

In the transverse vertical slices, some denteons are sectioned longitudinally and others transversely. In certain areas, the interdenteonal dentine is arranged in bands while, in others, it forms clusters (Fig. 6G, H). Between denticulations and over the furrows, there is a significant amount of amber-colored mantle dentine and osteocyte lacunae (Fig. 6I). Beneath the pulp cavity, a substantial amount of bone tissue is observed (Fig. 6I). Below each ridge, the pulp cavity exhibits greater width compared to the furrows. In the latter situation, the bone tissue comes into contact with the tooth plate (see Fig. 6H, I).

Fig. 5 - Horizontal sections of tooth plates of *Atlantoceratodus iheringi*, MPM-PV-1881 and MPM-PV-1882: A) sections under binocular magnifier, MPM-PV-1881 (left), and MPM-PV-1882 (right); B) MPM-PV-1881 denteons embedded in birefringent and monorefringent interdenteonal dentine, arrows indicate circumdenteonal dentine; C) MPM-PV-1882, same traits as in B; D) MPM-PV-1882, clustered denteons surrounded by the outer circumdenteonal band (monorefringent); E) MPM-PV-1882, same image as F but with a lambda filter, showing the outer (monorefringent) and the inner (birefringent) circumdenteonal bands; F) MPM-PV-1881, detail of pulp canals surrounded by double band of circumdenteonal dentine; G) MPM-PV-1882, mantle dentine towards the edges (arrow); H) MPM-PV-1882, mantle dentine with birefringent zones and osteocyte lacunae; I) MPM-PV-1881, outer mantle dentine with birefringent zones and transitional denteons, externally a thin layer of enamel; J) MPM-PV-1881, denteons surrounded by long and tangled dentinal tubules; K) MPM-PV-1882, denticulation with clustered denteons towards the ridge and transitional denteons towards the edges; L) MPM-PV-1882, furrow area with a large amount of mantle dentine. Sections under a petrographic microscope (B-L), polarized light (C, D, G, K, L), polarized light with lambda filter (B, E, H, I, J). Abbreviations: bfi, birefringent interdenteonal dentine; dt, dentinal tubules; en, enamel; icb, inner circumdenteonal band; md, mantle dentine; mfi, monorefringent interdenteonal dentine; ocb, outer circumdenteonal band; ol, osteocyte lacunae; td, transitional denteons. Scale bars represent: 0.5 cm (A); 1 mm (B, C, G, K, L, F, I); 500 μm (H); 250 μm (D, E, J).

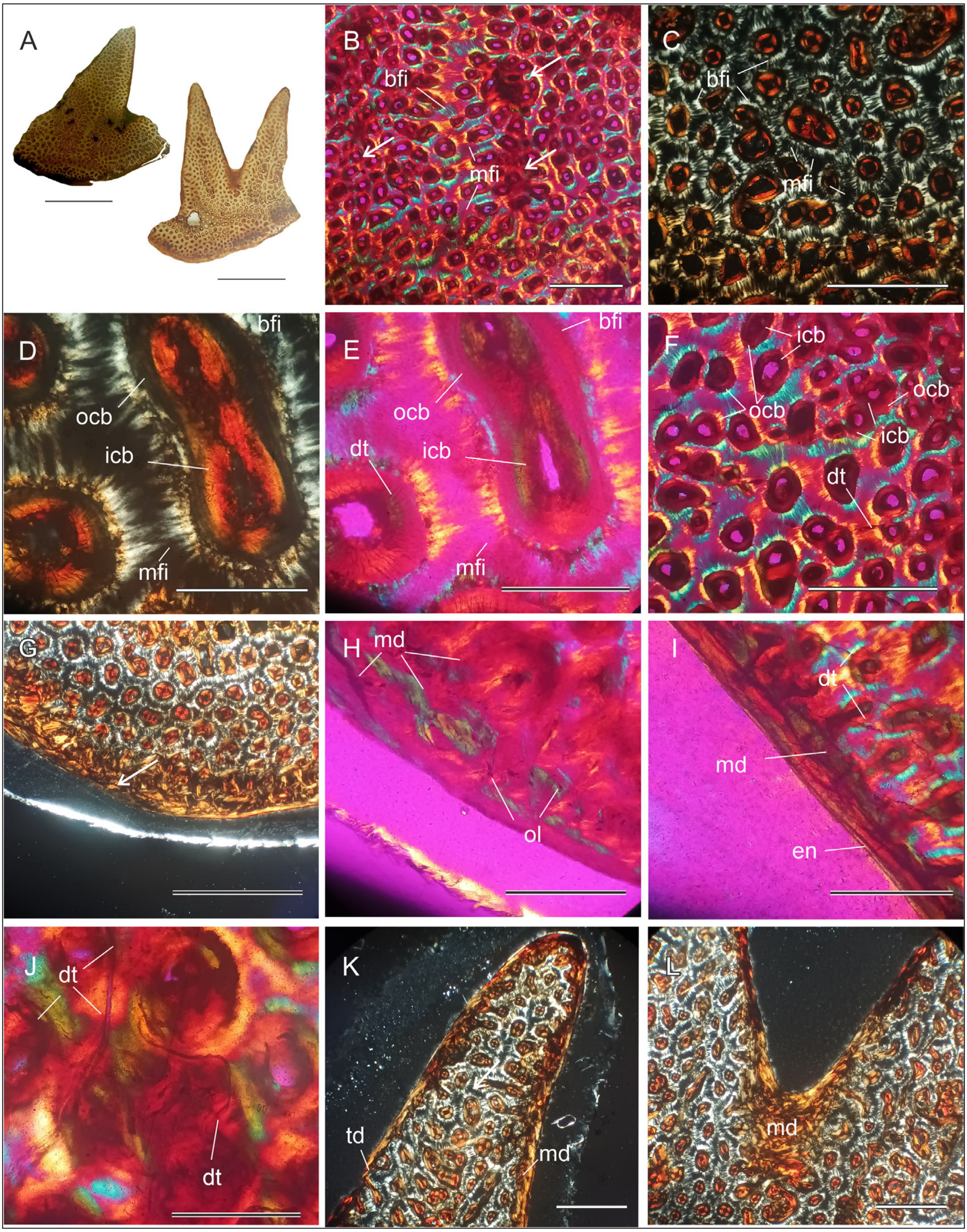
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Figure 5

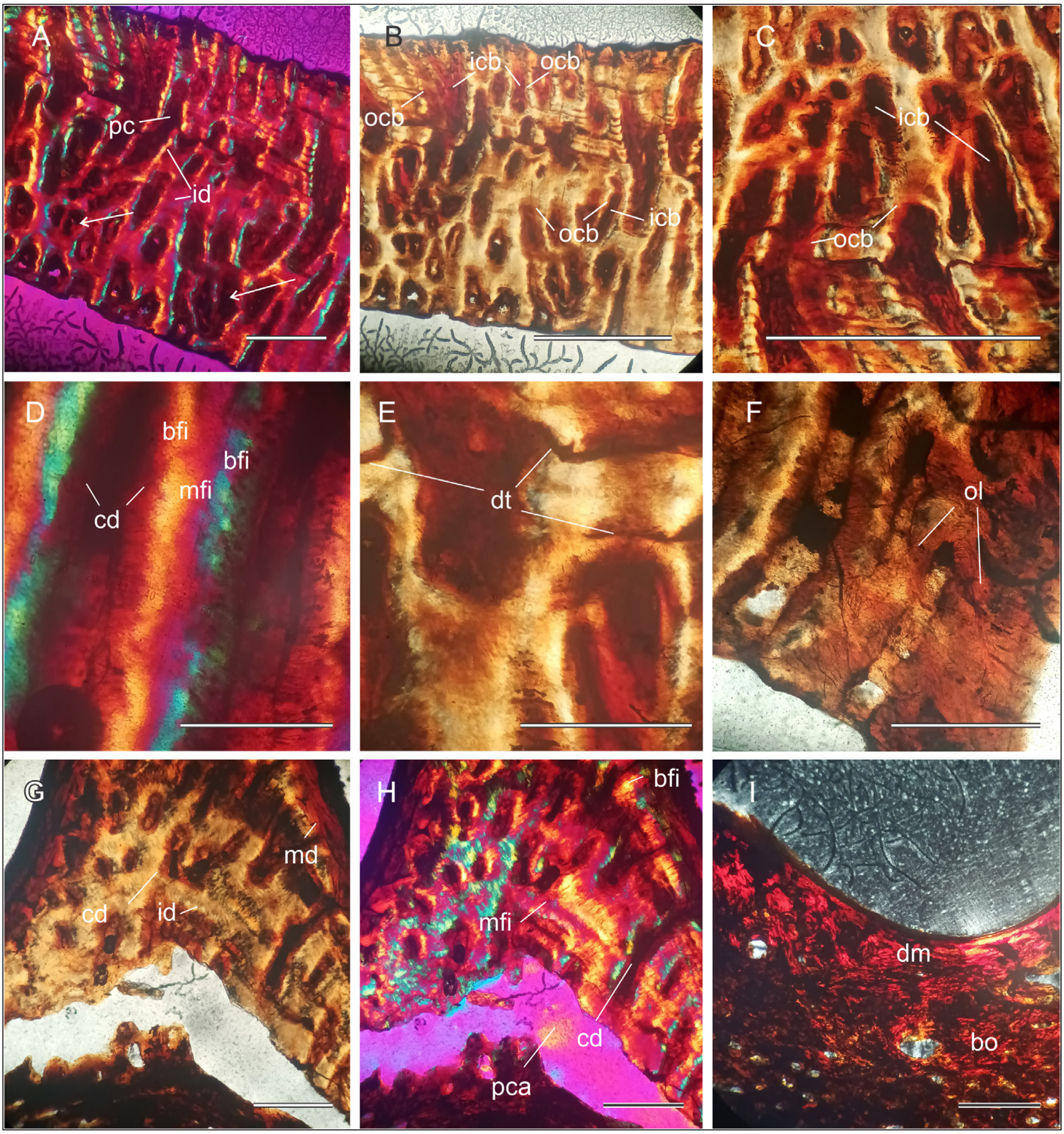

Fig. 6 - Vertical MPM-PV-1878 (A-F) and transverse vertical sections MPM-PV-1879 (G, H), MPM-PV-1880 (I) of the tooth plates of *Atlantoceratodus iheringi*. A) discontinuous pulp canals: linear and ramified in an occluso-pulpal direction; B) same section under normal light; C) pulp canals surrounded by two bands of circumdenteonal dentine; D) rows of interdenteonal dentine with opposite birefringence between pulp canals; E) pulp canals laterally connected through dentinal tubules and circumdenteonal dentine; F) osteocyte lacunae on the lingual edge near the inner angle; G) transverse vertical section with outer mantle dentine and central interdenteonal dentine; H) same as F under lambda filter to visualize the orientation of interdenteonal dentine crystals, the pulp cavity is positioned between the bone and the tooth plate; I) furrow area where the plate contacts the bone. Sections under a petrographic microscope (A-I), with polarized light (B, D, E, F), polarized light with lambda filter (A, C, G-I). Abbreviations: bfi, birefringent interdenteonal dentine; cd, circumdenteonal dentine; dt, dentinal tubules; icb, inner circumdenteonal band; id, interdenteonal dentine; md, mantle dentine; mfi, monorefringent interdenteonal dentine; ol, osteocyte lacuna; ocb, outer circumdenteonal band; pca, pulp cavity. Scale bars represent: 1 mm (B); 500 µm (A, C, F-I); D, E: 250 µm.

Discussion

Historical background and taxonomy of *Atlantoceratodus iheringi*

The study of fossil lungfish in Argentina began in the late 19th century when Ameghino (1898) reported the first fossil material of lungfish found in the Patagonian territory, specifically a tooth plate. Due to its resemblance to the tooth plates of *Ceratodus runcinatus* Plieninger, 1844, Ameghino classified it under the genus *Ceratodus*, naming the species *Ceratodus iheringi* (Ameghino, 1898). He also provided a brief description of the material in a section of supplements and corrections (Ameghino 1899). Therein, the size, shape, and position of the tooth plate within the jaws are described as follows: 'Very small in size, the lower tooth is not triangular but elongated with five branches or horns on the outer side separated by deep notches (…)' (Ameghino 1899: 10). However, it is important to clarify that this tooth plate is detached from the bony base thus its identity as upper or lower was not clear. Nevertheless, it appears to represent a pterygopalatine tooth plate since among all tooth plates associated with basal bones collected from the Mesozoic of Argentina, only upper ones exhibit five denticulations (Panzeri et al. 2020; Fig. S5). Additionally, Ameghino proposed a closer relationship between the Patagonian dipnoans and the Jurassic and Cretaceous species of Europe rather than with today living *Neoceratodus forsteri* from Australia ('*Epiceratodus*' in Ameghino 1906).

The holotype of '*Ceratodus*' *iheringi* was reexamined by Cione et al. (2007) together with additional specimens. In their study, they proposed the genus *Atlantoceratodus* and established the new combination *Atlantoceratodus iheringi*. Within this genus, they also incorporated the Malagasy species *Atlantoceratodus madagascariensis* (Priem, 1924), previously assigned to *Ferganoceratodus*, as it exhibits similar characteristics to *A. iheringi* such as: 'tooth plates of medium size, high crowned and with sharp, slender, and acute ridges that originate anteriorly; five ridges in the upper plates and four ridges in the lower plates; inner angle not so well-defined and rounded, relatively large angle formed by the first and last ridges; occlusal tubercles absent; limited mantle dentine visible on the occlusal surface; simple punctuations (petrodentine sensu Kemp 2001 absent) and not arranged with a particular pattern.' Cione et al. (2007: 8). Prior to the work of Cione et al. (2007), other authors suggested a close relationship between the Patagonian species and *A. madagascariensis*. Martin et al. (1999) established this similarity based on several features, including the presence of fewer than 7 denticulations, a long first denticulation, an invisible apex of the inner angle, a pattern of radiating denticulations with sharp ridges, and a continuous curvature formed by the medial and lingual edges. However, while a possible close phylogenetic relationship between these two species is not ruled out, the characteristics they share are widely distributed among other Mesozoic lungfish. Unlike *A. madagascariensis*, *A. iheringi* has longer first denticulations with narrower bases, remaining denticulations with wider bases, the inner angle at the level of the second denticulation, and less developed plateau areas. The prearticular tooth plates have more obtuse inner angles (positioned at the level of the first cleft) and straighter lingual edges.

Recently, Agnolin (2010) described the new species *Atlantoceratodus patagonicus* Agnolin, 2010, from the Allen Formation. The holotype of this species (MML 197) is identified as a right pterygopalatine tooth plate fragmented at the level of the first denticulation (Fig. 7A). Moreover, as additional material, Agnolin (2010) mentions two tooth plates from the Los Alamitos Formation (MACN PV RN 1080, Fig. 7B and MACN PV RN 157C, Fig. 7C) and one from the Allen Formation (MML157, Fig. 7D, E). When compared to these specimens, the tooth plates of *Atlantoceratodus iheringi* are smaller in size and exhibit a reduced plateau area in relation to the denticulations. It is noteworthy that the holotype of *A. patagonicus* differs from *A. iheringi* in the deep second cleft, the second denticulation having a wide base, and in bigger plateau development, resembling the characteristics observed in *M. wichmanni* (Apesteguía et al. 2007, Fig. 7F, G). Conversely, the paratypes assigned to *A. patagonicus* consist of either juvenile individuals (Fig. 7C), a specimen displaying anomalies (Fig. 7B), or transported fragments (Fig. 7D, E), acquiring many of the characteristics listed in the diagnosis of the species. For example, in MML157 (Fig. 7E), the first denticulation is not short but rather fractured, as evidenced by the pulp canals.

In Agnolin et al. (2023), tooth plates from the Cerro Fortaleza Formation (Campanian) were also attributed to the species *Atlantoceratodus iherin-*

Fig. 7 - Tooth plates from Patagonia, Argentina, some previously attributed to the genus *Atlantoceratodus*: A) MML 197, holotype of *Atlantoceratodus patagonicus*, right pterygopalatine tooth plate with the first denticulation broken (arrow); B) MACN PV RN 1080, left pterygopalatine tooth plate with an anomaly in the first denticulation (arrow); C) MACN PV RN 157C, right prearticular tooth plate of a juvenile stage; D, E) MML157, right prearticular tooth plate transported and fragmented at the base of the first denticulation (arrows); F) MML 198, left pterygopalatine tooth plate referred to *Metaceratodus wichmanni* from the Allen Formation; G) MML 202, right prearticular tooth plate from the Allen Formation assigned to *Metaceratodus wichmanni*; H, I) MPM-PV 23339, right pterygopalatine tooth plate with a wear facet (arrow in H) from the Cerro Fortaleza Formation; J, K) MPM-PV 23338, right prearticular tooth plate with fused bone illustrating the divided sulcus (arrow in J) from Cerro Fortaleza Formation; L) MPM-PV-1166 prearticular bone of *Atlantoceratodus iheringi* with a divided sulcus M, N) MPM-PV 23338, right pterygopalatine tooth plate in occlusal view and illustrating part of the ascending process (arrow in N) from Cerro Fortaleza Formation. All scale bars represent: 1 cm.

gi. However, the pterygopalatine tooth plates from this unit differ from *A. iheringi* in the slightly larger plateau area, having denticles despite their medium size, a reduced fifth denticulation, and a wear facet anterior to the first denticulation (Fig. 7H, I). Compared to *A. iheringi*, the prearticular tooth plates of Cerro Fortaleza Formation exhibit a sinuosity at the level of the first denticulation, mediolingual edges tending to be curved, and a wider and more extensive anteroposterior prearticular symphysis (Fig. 7J, K). Consequently, obtaining more comprehensive material is crucial for a more precise taxonomic assignment and to rule out potential dental anomalies and intra-specific variation.

Finally, Agnolin et al. (2023) claimed to be making the first reference to a prearticular bone within the species *A. iheringi*, emphasizing its undivided prearticular groove. However, more careful observations show that preservation of this region is poor in specimens described by Agnolin et al. (2023), and the groove appears to be originally divided (Fig. 7J, K). Nevertheless, it is important to note that Cione et al. (2007) documented two prearticular bones, one of which is illustrated but exhibits sediment or precipitate within the prearticular groove, while the other displays clear division (Fig. 7L). The tooth plates of Cerro Fortaleza Formation consist of six pterygopalatine tooth plates (including MPM-PV 23338, Agnolin et al. 2023, fig. 3O; Fig. M, N), three prearticular tooth plates, and a fragment of prearticular bone.

Comments on *Atlantoceratodus*

In the present study, the decision has been made to maintain the generic diagnosis formulated by Cione et al. (2007) with minor modifications, due to the absence of a clearer phylogenetic and systematic framework currently available. However, it is important to note that many of the characteristics mentioned in the diagnosis vary during the ontogeny of the organism, and some are observed only in one type of tooth plate (prearticular or pterygopalatine). For example, the ridges and denticulations in *A. iheringi* exhibit varying degrees of roundness depending on the size, appearing sharper and longer in smaller individuals. In the prearticular tooth plates of the species, the inner angle is prominent, particularly in smaller individuals, while in pterygopalatine tooth plates, it is slightly diffused. Other characteristics present in the diagnosis are widely distributed among lungfish species from different parts of the world, and therefore, it is important to consider that they are not diagnostic on their own. For example, the number of denticulations, with five present in pterygopalatine plates and four in prearticular plates, is found in certain North American species (e.g. *Potamoceratodus guentheri* (Marsh, 1878); Kirkland 1987, Pardo et al. 2010; Frederickson & Cifelli 2017; Harrel & Ehret 2019; Pawlak et al. 2020), as well as in other species from Patagonia (e.g. *Rinconodus salvadori*; Apesteguía et al. 2007; Panzeri et al. 2020, 2022a), Asia (e.g. *Ferganoceratodus martini* Cavin, Suteethorn Buffetaut & Tong 2007; Liu & Yeh 1960; Wang et al. 2022), and Europe (e.g. *Ptychoceratodus roemeri* Skrzycki, 2015*;* Krupina 1995; Martin 1999; Hagdorn & Mutter 2013; Czepiński et al. 2021).

Regarding the taxonomic assignment at the family level, Cione et al. (2007) have decided to retain the genus within an undetermined family. Previously, Martin (1981, 1982) proposed that the Patagonian species belonged to the family Ptychoceratodontidae, where the species *A. madagascariensis* (Priem, 1924) is also placed. However, the adult tooth plates of *A. iheringi* and the other Patagonian species correspond to both the diagnoses provided by Martin (1981) at the family level of Ceratodontidae (due to having four to five denticulations, crushing ridges, and an enlarged central parietal) and Ptychoceratodontidae (four to six denticulations, cutting ridges that can become crushing, and a constricted central parietal in the orbital region). Recent phylogenetic analyses have shown that the family-level groupings proposed by Martin (1981, 1982) are not recovered as monophyletic (Kemp et al. 2017). These difficulties in the family-level assignment have been previously raised in studies of lungfish tooth plates from other parts of the world, due to the overlap in the provided diagnoses (see Skrzycki 2015). Moreover, these challenges also extend to certain traditional genera, which might not form cohesive natural groupings (Cavin et al. 2007; Pardo et al. 2010; Frederickson & Cifelli 2017). Therefore, taking these considerations into account, the generic diagnosis of *Atlantoceratodus* is retained, albeit with slight modifications derived from observations made in this study. One of the adjustments to the generic diagnosis involves the posteromedial position of the inner angle, as the medial edge is longer the lingual edge. The second alteration is the presence of a wear pattern on the occlusal surface (described as tubercles in Cione et al. 2007). The classification within an undetermined family is retained.

Morphological Comparisons

Atlantoceratodus iheringi is the oldest species documented from the Cretaceous period in Argentina. Its adult tooth plates are smaller in size compared to other Patagonian species. Moreover, it stands out as the only species with a substantial representation of juveniles. In addition to pterygopalatine and prearticular tooth plates, cranial roof bones and vomerine tooth plates are also well-known. Notably, vomerine tooth plates are not known for other southern South American dipnoan species.

Compared to other Mesozoic Argentinean species, the pterygopalatine tooth plates of *Atlantoceratodus iheringi* exhibit distinctive characteristics. These include a less developed plateau area, a narrow base of the first denticulation, the last three denticulations anteriorly curved, a curved mediolingual edge, the inner angle at the level of the second denticulation, and a symphysis of the pterygopalatine bone that is consistently uniform without anterior widening. Additionally, the prearticular tooth plates feature straight or nearly straight medial and lingual edges, a first denticulation that does not end sinuously, the inner angle positioned at the level of the first cleft, and anteriorly curved ridges.

On the contrary, the majority of Cretaceous Patagonian species of *Metaceratodus* (*M. baibianorum* and *M. wichmanni*, Apesteguía et al. 2007; Panzeri et al. 2020) exhibit pterygopalatine tooth plates with a more pronounced development of the plateau area, denticulations directed towards the labial side, the inner angle positioned at the level of the second furrow, and a heterogeneous symphysis of the pterygopalatine bone (broader anteriorly). The prearticular tooth plates often display a sinuosity at the end of the first denticulation, the inner angle positioned at the level of the second denticulation (or slightly posterior to it), and curved mediolinguinal edges.

Other Patagonian species, such as *Chaoceratodus portezuelensis* (represented by a prearticular tooth plate) and *Ceratodus argentinus* (represented by a pterygopalatine tooth plate), exhibit distinctive characteristics (Apesteguía et al. 2007). *Chaoceratodus portezuelensis* has shorter and thicker denticulations and an inner angle with acute values. On the other hand, *Ceratodus argentinus* displays a larger plateau area, with denticulations directed labially instead of anteriorly.

Among the Cretaceous Patagonian species, *Rinconodus salvadori* has pterygopalatine tooth plates, with narrower first denticulations that curve posteriorly at its tip (Panzeri et al. 2022a). Additionally, its prearticular tooth plates have shorter denticulations compared to those found in *A. iheringi*. Another notable Mesozoic species from Argentina, dating back to the Triassic period, is *Ptychoceratodus cuyanus* (Agnolin et al*.,* 2016). This species is distinguished from *A. iheringi* by its concave lingual edge and posteriorly directed last two denticulations. Furthermore, the second and third denticulations are larger compared to the rest.

In relation to tooth plates from other parts of the world (excluding the species *Atlantoceratodus madagascariensis*), *A. iheringi* and the remaining Patagonian species exhibit similarities to the tooth plates of North American species, such as *Potamoceratodus guentheri* (Pardo et al*.,* 2010), *Ceratodus molossus* Frederickson & Cifelli, 2017, or *C. robustus* (Knight, 1898). These similarities include the number of denticulations, the longer medial edge compared to the lingual edge, the curved lingual edge and the well-developed plateau area. The resemblance between North American and Patagonian species has been previously noted by other authors (Martin 1981, 1982; Schultze 1991; Apesteguía et al. 2007; Panzeri et al. 2022b), and they may indicate a shared evolutionary history preceding the Jurassic era when these continents were communicated (Krause et al. 2019). Regarding the tooth plates assigned to the genera *Ptychoceratodus* and *Ferganoceratodus*, the tooth plates of Argentinean species exhibit longer medial edges than lingual edges, with the lingual edges in pterygopalatine tooth plates being distinctly curved.

Lastly, the species *Atlantoceratodus iheringi* preserves vomerine tooth plates, which represent the first known occurrence of such plates in southern South America. Vomerine tooth plates are not commonly found in Mesozoic strata, but there are some known records from around the world. The vomerine tooth plates of *Atlantoceratodus iheringi* show a closer resemblance to those of *Ptychoceratodus roemeri* from the Triassic of Poland (Skrzycki 2015) and *Ptychoceratodus serratus* (Agassiz, 1838) from Germany (Schultze 1981), rather than to those of *Ceratodus parvus* Agassiz, 1838 from the Swiss Trias (Peyer 1959) or *Ferganoceratodus martini* from the Upper Jurassic Phu Kradung Formation in Thailand (Cavin et al. 2007). They also show resemblance to the vomerine tooth plates described by Jain (1968), assigned to the genus *Ceratodus,* and recovered from the Triassic Maleri Formation in India. However, unlike the latter, the vomerine tooth plates of *A. iheringi* exhibit a greater number of denticles. This difference could be attributed to better preservation or a less advanced ontogenetic stage.

The skull roof bones of *A. iheringi* exhibit similarities to those described in the Patagonian species *Rinconodus salvadori* (Panzeri et al*.,* 2022a) and species from other regions of the world. The anterior mediolateral bone has a longer-than-wide morphology, and its lateral edge shows a concave dorsal margin with the orbital process and the overlapping suture for the posterior mediolateral bone. These same structures are also present in other dipnoans, such as *Rinconodus salvadori* (Panzeri et al*.,* 2022b), *Ptychoceratodus serratus* (Schultze, 1981), *Ferganoceratodus martini* (Cavin et al*.,* 2007), and *Arganodus atlantis* Martin, 1979.

Histological Comparisons

Since the Mesozoic era, dipnoans exclusively have tooth plates characterized by a single pulp cavity and tubular dentine (Denison 1974). In contrast, Paleozoic dipnoans exhibit a variety of dental types, typically lacking a single pulp cavity, and their dentine arrangement differs from that observed in Mesozoic dipnoans, primarily consisting of trabecular dentine (e.g. Campbell & Barwick 1998, fig. 30). Previous extensive studies on dental histology have been focused on Devonian species (e.g. *Dipterus valenciennesi* Sedgwick & Murchinson, 1829; *Chirodipterus australis* Miles, 1977; *Scaumenacia curta* Whiteaves, 1881; *Griphognathus whitei* Miles, 1977; *Tarachomylax oepiki* Barwick Campbell & Mark- Kurik, 1997; and *Adololopas moyasmithae* Campbell & Barwick, 1998). In the Paleozoic dipnoan *Dipterus valenciennesi*, a dentine pattern differs from that observed in *Atlantoceratodus iheringi*: the denteon is enclosed by a square of birefringent dentine, with monorefringent dentine surrounding the pulp canal (Blaauwen et al. 2006, fig. 13). Contrary, in the histological sections of *A. iheringi*, show that dentine surrounding the pulp canals is organized into a double band with different crystal arrangement (in MPM-PV-1882 a birefringent inner band and a monorefringent outer band). Furthermore, the thickness of the circumdenteonal dentine surrounding a pulp canal, is lesser than the one present in *D. valenciennesi* and *Tarachomylax oepiki* (Barwick et al. 1997, fig. 15).

The histology of the tooth plates in *Atlantoceratodus iheringi* shares similarities with those described in Mesozoic and Cenozoic species; however, certain differences exist. The observation of the crystal arrangement of hydroxyapatite in the interdenteonal and circumdenteonal dentine requires the use of polarized light, ideally supplemented with a lambda filter. Unfortunately, studies employing these methodologies are scarce.

Comparable studies have been conducted on the tooth plates of *Metaceratodus baibianorum*, employing polarized light and a lambda filter. Unlike the histological arrangement observed in *M. baibianorum*, the tooth plates of *Atlantoceratodus iheringi* exhibit a more disorganized interdenteonal dentine and do not form a continuous cross pattern along the surface. The circumdenteonal dentine is arranged in a double band, with the innermost band exhibiting birefringence under polarized light. Furthermore, *A. iheringi* possesses a higher number of denteons, which tend to cluster together and have larger lumens. Conversely, the tooth plates of *M. baibianorum* exhibit a well-organized cross pattern of interdenteonal dentine, a single layer of circumdenteonal dentine, and a greater number of isolated denteons with a reduced lumen.

The arrangement of the double band of circumdenteonal dentine is also observed in the vertical sections of *A. iheringi*. It encompasses multiple pulp canals, which are generally not continuous. The pulp canals are interconnected partially through the outer circumdenteonal dentine band and partially through elongated dentinal tubules, resulting in lines that resemble incremental lines. In the vertical section of *M. baibianorum*, the pulp canals are surrounded by a single band of circumdenteonal dentine, most of which are continuous, branching at specific points, and incremental lines can be seen on the interdenteonal dentine (Panzeri et al. 2022b).

In the ceratodontid *Retodus tuberculatus* (Tabaste, 1963), while accumulations of smaller-sized denteons are present along the ridges, they are more spaced out between them (Kemp 2001, fig. 16). In the case of another ceratodontid, *Ceratodus parvus* Agassiz, 1838, the denteons converge towards the occlusal surface (Denison 1974, fig. 8). The arrangement of denteons observed in *A. iheringi* is similar to that found in *Atlantoceratodus madagascariensis* (Priem, 1924) and certain sections of *M. baibianorum*, which are parallel and continuous without branching (Smith 1984, figs. 33-38).

The tooth plates of *Atlantoceratodus iheringi* exhibit a more developed interdenteonal dentine compared to species that possess petrodentine, such as *Mioceratodus anemosyrus* Kemp, 1997 (Kemp 2001, fig. 10) or *Mioceratodus gregoryi* Kemp, 1997 (Kemp 2001, fig. 12). The latter species displays islands of interdenteonal dentine with denteons positioned between the columns of petrodentine. Other species that have been reported to have petrodentine and have illustrated histological sections include *Sagenodus* sp. (Smith 1979, fig. 9; Kemp 2001, fig. 19), *Lepidosiren paradoxa* (Bemis 1984, fig. 15), and *Protopterus annectens* (Kemp 2001, fig. 7). In terms of interdenteonal dentine, *Atlantoceratodus iheringi* exhibits a disorganized pattern, while in the Australian species *Neoceratodus forsteri*, it is arranged in a more organized pattern with birefringent fibers radiating from the denteons (Smith 1984, fig. 28). Conversely, in *A. iheringi*, the pattern of interdenteonal dentine is not consistent; in certain areas, a cross pattern can be observed, but in most of the analyzed sections, it appears disorganized, possibly due to the clustering of denteons.

Conclusions

The species *Atlantoceratodus iheringi* differs from other Argentinean species in several aspects. In the provided diagnosis, emphasis is placed on distinguishing the characteristics present in each type of dentition, as they vary between pterygopalatine and prearticular tooth plates. The diagnosis has also been supplemented with histological features observed exclusively in this species.

Histological studies on dipnoan tooth plates are scarce, especially those employing petrographic microscopy with a lambda compensator. It was observed that the dental histology of *A. iheringi* differs more from Paleozoic dipnoans than it does from Mesozoic or Cenozoic ones. In Argentina, only the dental histology of the species *Metaceratodus baibianorum* has been studied, and although similarities exist, certain differences are present. This study provides evidence that the histological diversity of tooth plates in Patagonian dipnoans is greater than previously recognized and, in addition to the detailed morphological description, valuable information is provided for future systematic and phylogenetic studies.

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