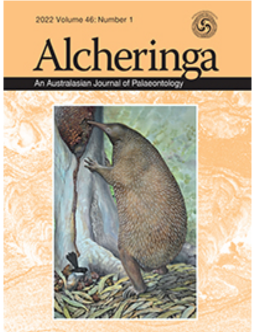

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Metaceratodus baibianorum from the La Colonia Formation: tooth plate anomalies and the possible presence of tertiary dentine

Karen M. Panzeri and Nahuel A. Muñoz

ABSTRACT
The dentition of Mesozoic dipnoans is formed by tooth plates that are not replaced throughout their lives. These can suffer different types of lesions that may be permanent or disappear with wear through action of the jaws. Here, we describe pathologies on the tooth plates of *Metaceratodus baibianorum* from the Late Cretaceous (Maastrichtian) La Colonia Formation of Patagonia in Argentina. Of the total number of analysed tooth plates ($N = 127$), 27.5% show signs of different pathologies including caries, abscesses, hyperplasia, fractures, alterations in growth, and erosion. No tooth plates with parasitic invasions, attrition or osteopenia were observed. Some examples of occlusal caries show pulpal overgrowths on the pulp surface. CT scanning demonstrates that these are similar to tertiary dentine in their coincidence with lesions, higher density relative to the surrounding dentine, and fewer pulp canals resulting in fewer dentinal tubules. Such features may indicate that dipnoans are, or at least were, able to generate some form of reparative or reactionary dentine.

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Cretaceous; Dipnoi; lungfish; pathology; caries; reparative dentine; reactionary dentine

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DIPNOAN tooth plates are frequently recovered fossils in the Cretaceous deposits of Patagonia (e.g., Wichmann 1924, Cione 1987, Apesteguía *et al.* 2007, Cione *et al.* 2007). One of the most productive units is the Maatrichtian to lower Danian La Colonia Formation (Clyde *et al.* 2021), which crops out in the southeast Macizo Somún Curá of Chubut Province (Fig. 1A, B). The middle facies of the La Colonia Formation have faunal associations indicative of an estuarine palaeoenvironment (Pascual *et al.* 2000). The La Colonia Formation dipnoan fossils have been assigned to *Metaceratodus baibianorum* Panzeri, Gouiric-Cavalli, Muñoz, Cione 2020, and are represented by isolated tooth plates or tooth plates with fused jaw bone. In other periods, the documented record of fossil dipnoans from Argentina is scarce but includes a ptychoceratodontid from the Triassic of Mendoza Province (Agnolin *et al.* 2017), a ceratodontid from the Paleocene–Eocene of Chubut Province (Cione *et al.* 2011), and several lepidosirenids from the Eocene of Jujuy Province (Fernández *et al.* 1973).

One of the most distinctive characteristics of both fossil and living dipnoans is their dentition, which has modified into a variety of morphologies throughout their evolutionary history (Campbell & Barwick 1995). Characteristically, all post-Paleozoic dipnoans exhibit a statodont dentition consisting of tooth plates (Jaekel 1901, Smith & Krupina 2001). These are formed by an early fusion of isolated denticles (= primary growth) with the subsequent addition of new dentine from the pulp cavity and new denticles (or cusps) from the labial margin (= secondary growth; Smith & Campbell 1987, Kemp 2002, 2003a, Kemp & Barry 2006).

Dipnoan tooth plates also often show different types of dental anomalies (= abnormal structures with contrasting causes that may not necessarily be immediately fatal: Kemp 2001, 2003a, 2003b), such as trauma, injuries, and diseases or pathologies that remain evident in the fully formed tooth plate (Kemp 2005). Kemp (1990, 2003b) pioneered studies of dental anomalies using extant and fossil dipnoan tooth plates from the Cenozoic, Mesozoic and Palaeozoic strata of Australia, correlating them with possible environmental conditions (Kemp 2005, Kemp & Berrell 2013).

Following Becker *et al.* (2000), dental anomalies are usually classified into two main categories: those caused by vital effects; versus those caused by taphonomic alterations, which are termed ‘pseudopathologies’ (Wells 1967). Post-mortem taphonomic alterations can produce fractures, abrasion, and edge rounding (Becker *et al.* 2000). Anomalies produced during life include caries, abscesses, parasitic lesions, osteopenia, hyperplasia, erosion, fractures, attrition, and alterations in the normal pattern of denticulations (e.g., shortening and duplication). Attempts have been made to classify these pathologies into broader categories (i.e., anomalies produced by genomic variations, environmentally induced malformation, disease and/or trauma; Kemp 2003b, 2003c); however, genomic variations (= developmental anomalies) are difficult to identify in fossils and their formational processes are incompletely understood (Becker *et al.* 2000).

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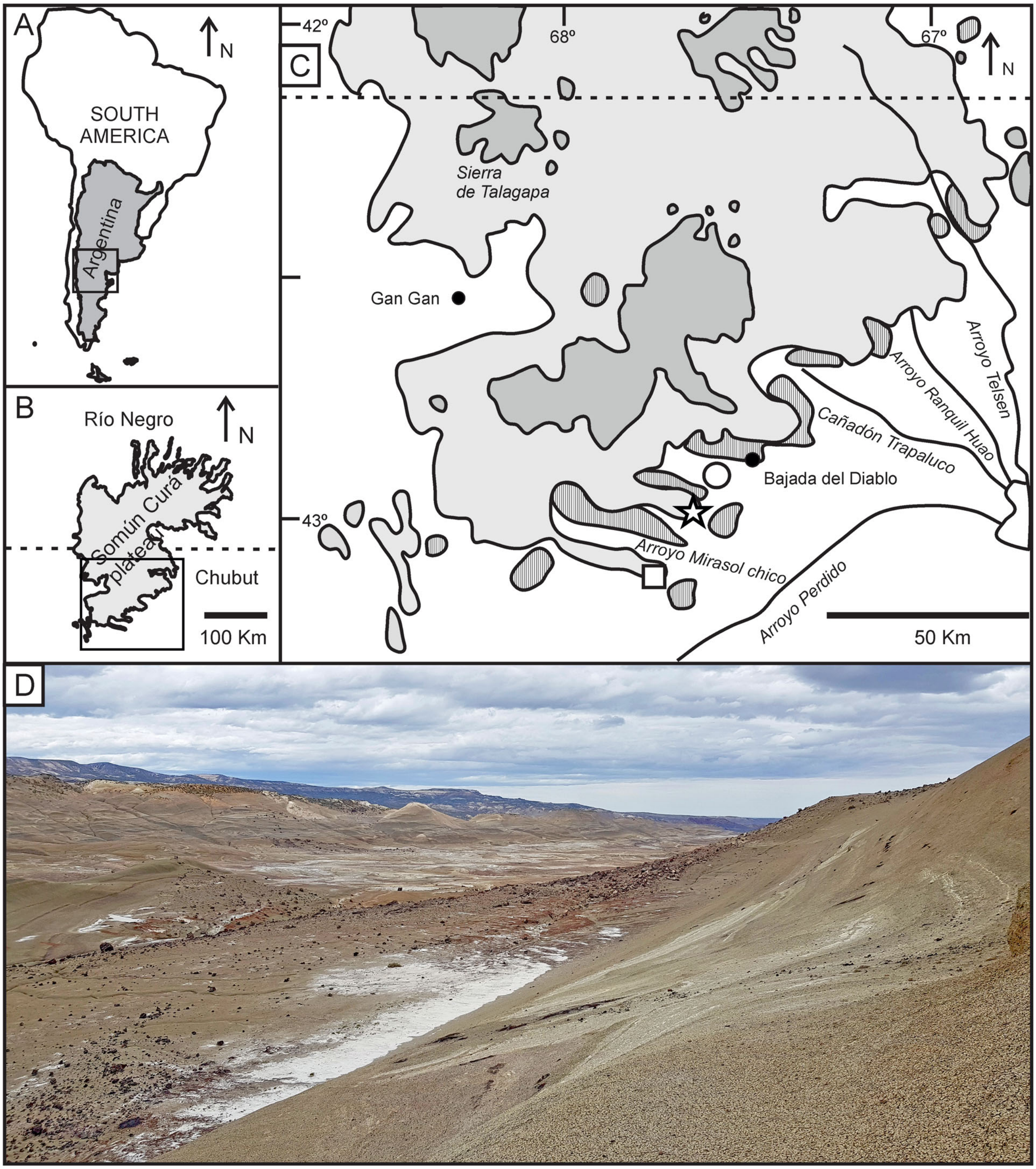

Figure 1. Map of the La Colonia Formation modified from Gasparini *et al.* (2015) and Panzeri *et al.* (2022). **A**, South America, showing Argentina in grey. **B**, Rio Negro and Chubut Provinces, showing the Macizo Somún Curá in grey. **C**, detail of B showing the localities of the La Colonia Formation. **D**, field photography showing the outcrops of the La Colonia Formation. Symbols: circle, Abra de la Tortuga; star, Cerro Bosta; square, Hoyada del Irupé.

Comparable dental anomalies have been recorded elsewhere in pinnipeds (Drehmer *et al.* 2015), sloths (McAfee 2015), marsupials (Martin & Chemisquy 2018), humans (Linnett & Seow 2001, Trinkaus 2018), equines (Dixon & Dacre 2005, Marshall *et al.* 2012), sharks (Gudger 1937, Becker *et al.* 2000) and rays (Gudger 1933, Delpiani *et al.* 2012). Reparative or reactionary dentine (= tertiary dentine: Smith 2000) has been reported in several of these groups (Lund *et al.* 1992, Smith & Sansom 2000), yet it is still unclear whether dipnoans can generate comparable tissues (Smith 1977, Smith & Chang 1990, Smith & Sansom 2000, Kemp 2001). Here, we therefore describe dental anomalies in tooth plates of *M. baibianorum* from multiple localities within the La Colonia Formation (Fig. 1C, D), and identify the presence of possible tertiary dentine.

Institutional abbreviations

MLP, Museo de La Plata, Buenos Aires, Argentina. MPEF, Museo Paleontológico Egidio Feruglio, Chubut, Argentina.

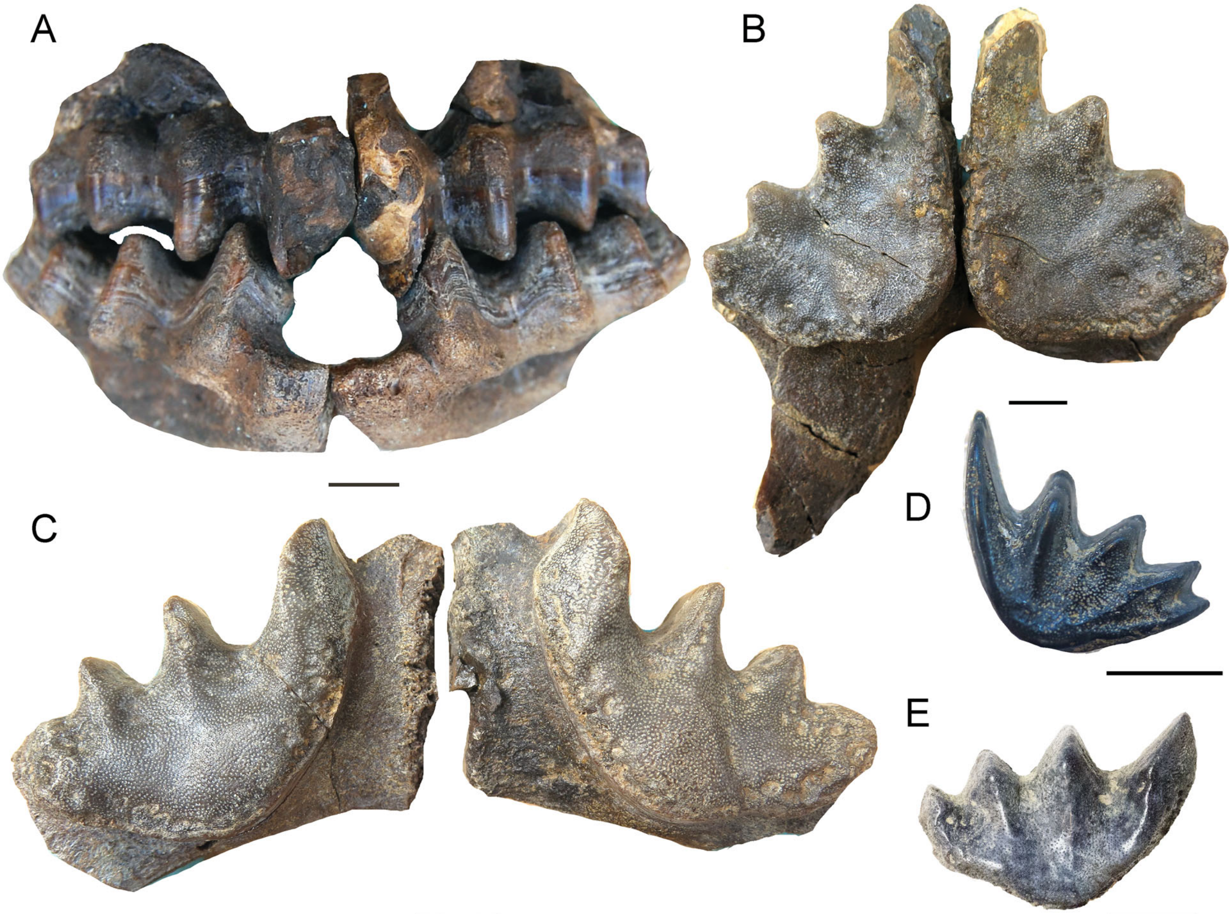

Figure 2. *Metaceratodus baibianorum* from the La Colonia Formation: morphology of tooth plates without pathologies, modified from Panzeri *et al.* 2020. **A–C**, MPEF-PV 11422: **A**, occluding tooth plates in anterior view; **B**, pterygopalatine tooth plates in occlusal view with attached bone; **C**, prearticular tooth plates in occlusal view with attached bone. **D**, MPEF-PV 11417, isolated pterygopalatine tooth plate in occlusal view. **E**, MPEF-PV 11419, isolated prearticular tooth plate in occlusal view. Scale bar = 1 cm.

Materials and methods

A sample of 127 tooth plates, some previously reported in Panzeri *et al.* (2020), were studied from three distinct localities within the La Colonia Formation: 97 from Abra de la Tortuga; 26 from Cerro Bosta; and 2 from Hoyada del Irupé. Institutional accession numbers for these specimens are as follows: MLP 06-VII-1-1-1 (prearticular tooth plate); MLP 06-VII-1-1-2 (prearticular tooth plate); MLP 06-VII-1-1-4 (prearticular tooth plate); MLP 06-VII-1-1-5 (prearticular bone); MLP 06-VII-1-1-3 (pterygopalatine tooth plate); MLP 06-VII-1-1-6 (pterygopalatine tooth plate); MLP 06-VII-1-1-7 (pterygopalatine tooth plate); MPEF-PV 11416 (five tooth plates); MPEF-PV 11417 (eight tooth plates); MPEF-PV 11418 (11 tooth plates); MPEF-PV 11419 (13 tooth plates); MPEF-PV 11420 (15 tooth plates); MPEF-PV 11421 (15 tooth plates); MPEF-PV 11423 (two tooth plates); MPEF-PV 11424 (12 tooth plates); MPEF-PV 11425 (15 tooth plates); MPEF-PV 11426 (five tooth plates); MPEF-PV 11427 (seven tooth plates); MPEF-PV 11428 (isolated tooth plate); MEPF-PV 6785 (prearticular tooth plate). Most of these specimens are fragmentary, but some were found fused to remnants of the jaw bones (Fig. 2A–C), or in isolation (Fig. 2D, E).

The tooth plates were inspected under a Zeiss Stemi 2000-C binocular stereo-microscope, Germany with measurements taken using a Neiko digital calliper, China. Overgrowths associated with caries on MPEF-PV 11425 were examined using a Kodak Cone Beam scanner, USA at the Centro Integral de Radiología Dental (Rayodent) in La Plata, Argentina. Scan settings included a voltage of 70 kV, current of 10 mA, pixel size of 200 µm, and a slice thickness of 0.2 mm. To obtain increased resolution, we also undertook additional scans of MPEF-PV 11425 on a SkyScan1272 Micro-CT, USA at the Facultad de Odontología de la Universidad de Buenos Aires (FOUBA), Argentina. Settings included 100 mA, a voltage of 100 kV, pixel size of 26.40 µm, and a rotation Step (°) of 0.600 resulting in 1455 slices. The dataset was segmented with *Slicer 3D* (http://www.slicer.org: Fedorov *et al.* 2012). We selected the tooth plate MPEF-PV 11425 as it had the anomaly to be analysed and the dimensions allowed by the scanner.

Dental terminology

Dentine is typically classified into primary, secondary, and tertiary depending on when and under what conditions it is secreted (Arana-Chavez & Massa 2004, Cooper *et al.* 2019).

Primary and secondary dentine are associated with normal tooth growth, while tertiary dentine (reparative or reactionary, Smith 2000) is usually associated with lesions (e.g., caries or fractures) and surfaces suffering attrition due to functional wear (Smith & Sansom 2000, Johanson *et al.* 2013, Cooper *et al.* 2019). In dipnoans, the term pleromin or pleromic dentine has been used to describe the dentine that is generated under these conditions (Smith 1977, Lund *et al.* 1992, Smith & Sansom 2000). However, the term pleromic dentine was also used as a synonym for interdenteonal dentine (= vascular pleromic dentine: Ørvig 1976a), petrodentine (= compact pleromic dentine: Ørvig, 1976a) or dentine infilling bony vascular canals (Denison 1974). Like Johanson *et al.* (2013), here we use the term 'tertiary dentine' (instead of pleromic or pleromin dentine) to specifically refer to dentine generated as a result of lesions or attrition. In fossil dipnoans, discerning whether tertiary dentine is reparative or reactionary is problematic because original formation of the tissue by odontoblasts or differentiated cells of the pulp cavity is unknown (Smith & Sansom 2000). We therefore refer only to tertiary dentine, which includes that produced through both mechanisms. General dipnoan tooth plate morphological terminology follows Panzeri *et al.* (2020, 2022) and Kemp (2003b, 2003c).

Description of the dental anomalies

Caries

Caries are injuries caused by acids secreted from bacterial colonies that lead to the demineralization of dental tissues (Pitts *et al.* 2017). Of all the *Metaceratodus baibianorum* tooth plates with anomalies (35), we recognized 45.5% with this type of injury. In some tooth plates, the position and shape of the caries lesions resemble wear patterns produced by jaw actions. These caries are situated on the mediolingual edge, as well as on furrows and areas close to the plateau. The former are located above the junction between enamel and dentine or over the enamel (Fig. 3A, B). The inner surfaces of the caries lesions are rough and have rounded edges (Fig. 3B). Caries on the plateau and on the furrows are also rounded or elongated with rough inner surfaces (Fig. 3C–O). Inside the cavity, some caries have a central dentine column (Fig 3J, L), while this is absent in others. Over the pulpar surface, overgrowths (here interpreted as tertiary dentine) are associated with the occlusal caries (Fig. 3F, H, I, K, N, O). In one pterygopalatine tooth plate (MPEF-PV 1142), the caries on the plateau area are arranged over a larger (10 mm diameter) concavity (Fig. 3M–O); dentine overgrowth on the pulpar surface of this specimen is substantial. Our CT scans (Fig. 4A–E) further reveal that the dentine overgrowths are formed by a denser tissue than the adjacent dentine (Fig. 4C–E), and has fewer pulp canals than in surrounding areas (Fig. 4E). Between the overgrowth and the injury on the occlusal surface, there is a diffuse area that we interpret as demineralized dentine (Fig. 4C–E).

Abscesses

In some tooth plates, caries located at the mediolingual edge involve the underlying bone and form abscesses (Kemp 2005). This pathology is observed in MPEF-PV 11426, a tooth plate with fused bone (Fig. 4F, G). The abscess involves a large portion of the lingual edge and plateau area, together with retraction of the dentine and enamel. The injury surface is rough and has areas of dentine tissue arranged in bands. Two additional isolated tooth plates, MPEF-PV 11419 (Fig. 4H–K) and MPEF-PV 11425 (Fig. 4L, M), have deeper caries that we interpret as abscesses. Although these specimens do not preserve underlying bone, caries are found on the lingual edge in association with both dental tissue retraction and surface banding (Fig. 4J, K, M). Overgrowths delimit these injuries on the pulpar surface (Fig. 4I, K, M). Another tooth plate with a possible abscess (MPEF-PV 11419: Fig. 3C–E) has a deep caries over the plateau area with corresponding reaction over the pulp cavity (Fig. 3F). There is thinning and retraction of the dental tissue medial to the caries, but the causes cannot be determined because of breakage (Fig. 3D, E).

Fractures

MPEF-PV 11427 exhibits a fracture at the level of the first denticulation (Fig. 5A–C). It is most clearly visible close to the occlusal surface, and the entire first denticulation is subsequently thicker than the rest of the tooth plate (Fig. 5B). Another tooth plate, MLP 06-VII-1-1-1, also has a fracture of the first denticulation (Fig. 5D, E); however, it does not show areas of overgrowth as in MPEF-PV 11427.

Alterations in growth

Alterations to normal of the generative area may be caused by genetic variations, fractures or caries (Kemp 2003b, 2003c). These alterations form new dental tissues that vary in position and permanently deform the tooth plate. MEPF-PV 678, has a duplicated third denticulation (Fig. 5F) resulting in five rather than four denticulations as would be typical for a prearticular tooth plate. Another tooth plate, MPEF-PV 11419, has one denticulation with the generative zone of new cusps being labially displaced (Fig. 5G, H) and affected by both caries and erosion.

Hyperplasia

Hyperplasia is caused by an overgrowth of dental tissue and commonly produces corresponding anomalies in the opposing tooth plate (Kemp 2005). This was observed in four specimens, including a lower tooth plate (MPEF-PV 11419) with an extremely elevated mediolingual edge near the inner angle (Fig. 5I, J). The overgrowth is 13.03 mm high and 14 mm wide. MPEF-PV 11419 further exhibits caries associated with overgrowths in the pulp cavity, while others lack reaction.

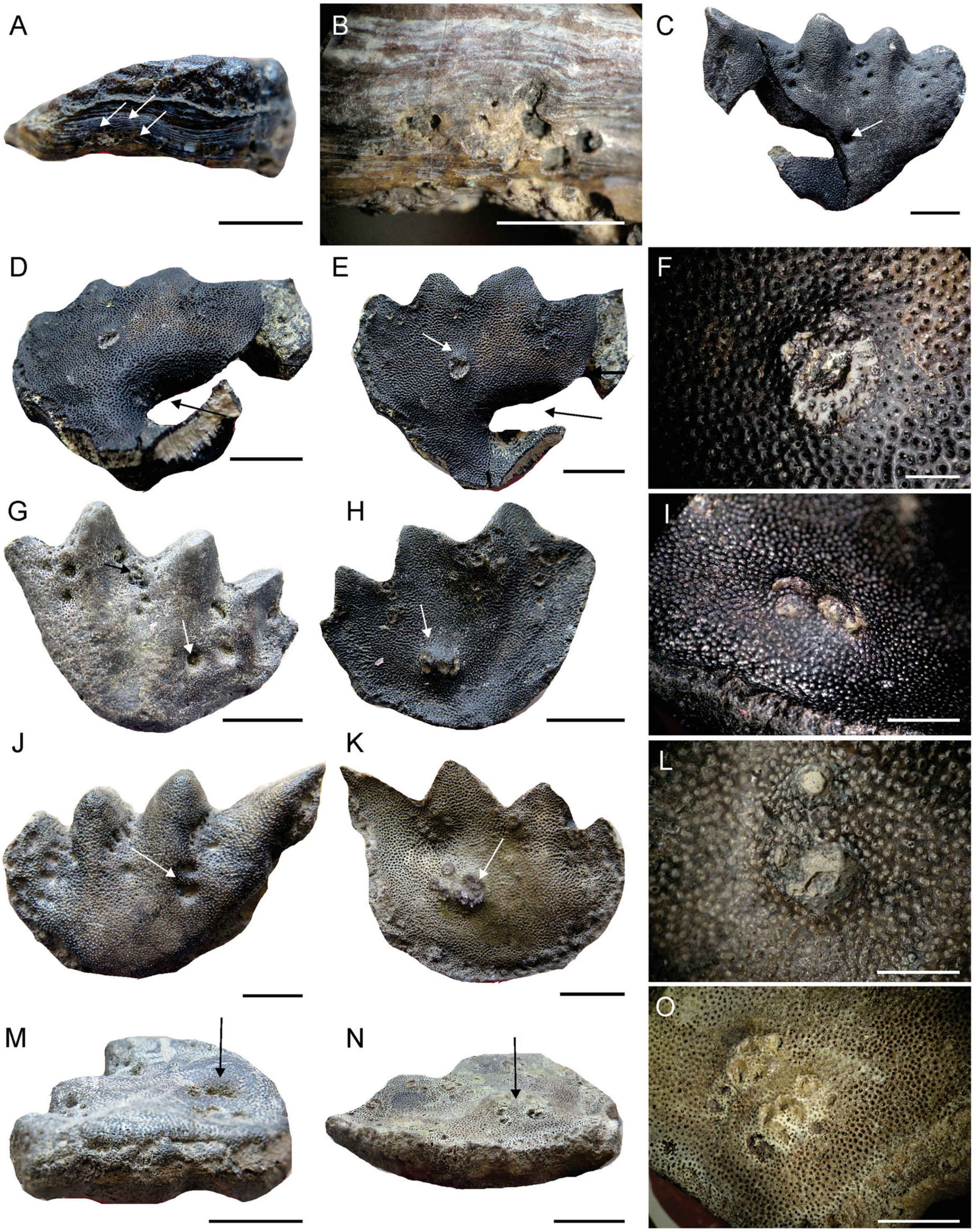

Figure 3. Tooth plates of *Metaceratodus baibianorum* with caries injuries. **A**, MPEF-PV 11417 (from Abra de La Tortuga), caries over the mediolingual edge. **B**, Magnification of A. **C–F**, MPEF-PV 11419 (from Hoyada del Irupé), **C, F**, caries lesion on the occlusal surface; and **D, E**, a coincident overgrowth (arrow) on the pulpar surface; note the retraction of tissue (black arrow). **G–O**, MPEF-PV 11425 (G–I, from Cerro Bosta) and MPEF-PV 1142 (J–O, from Abra de la Tortuga), tooth plates with caries lesion, details on occlusal surface (G, J, L, M) and magnification of J (L), overgrowth on the pulpar surface (H, K, N) and magnifications of H and N (I, O). Scale bar = A, C–E, G, H, J, K, M, N, 1 cm; B, F, I, O, 0.25 mm; L, 0.5 mm.

Erosion

Erosion is produced by environmental pH increases and, unlike caries, is evidenced by non-localized lesions over a large surface area (Linnett & Seow 2001, Kemp 2005). Only 20% of our recovered tooth plates show evidence of erosion that corrodes both the dentine and enamel (Fig. 5K, L). Dentine erosion produces a rough surface texture on the pulp canals (Fig. 5K–M). The lingual edges and areas surrounding the last denticulation are most often affected.

Discussion

Dipnoan tooth plates are prone to injuries that manifest changes in their shape and external surface structures

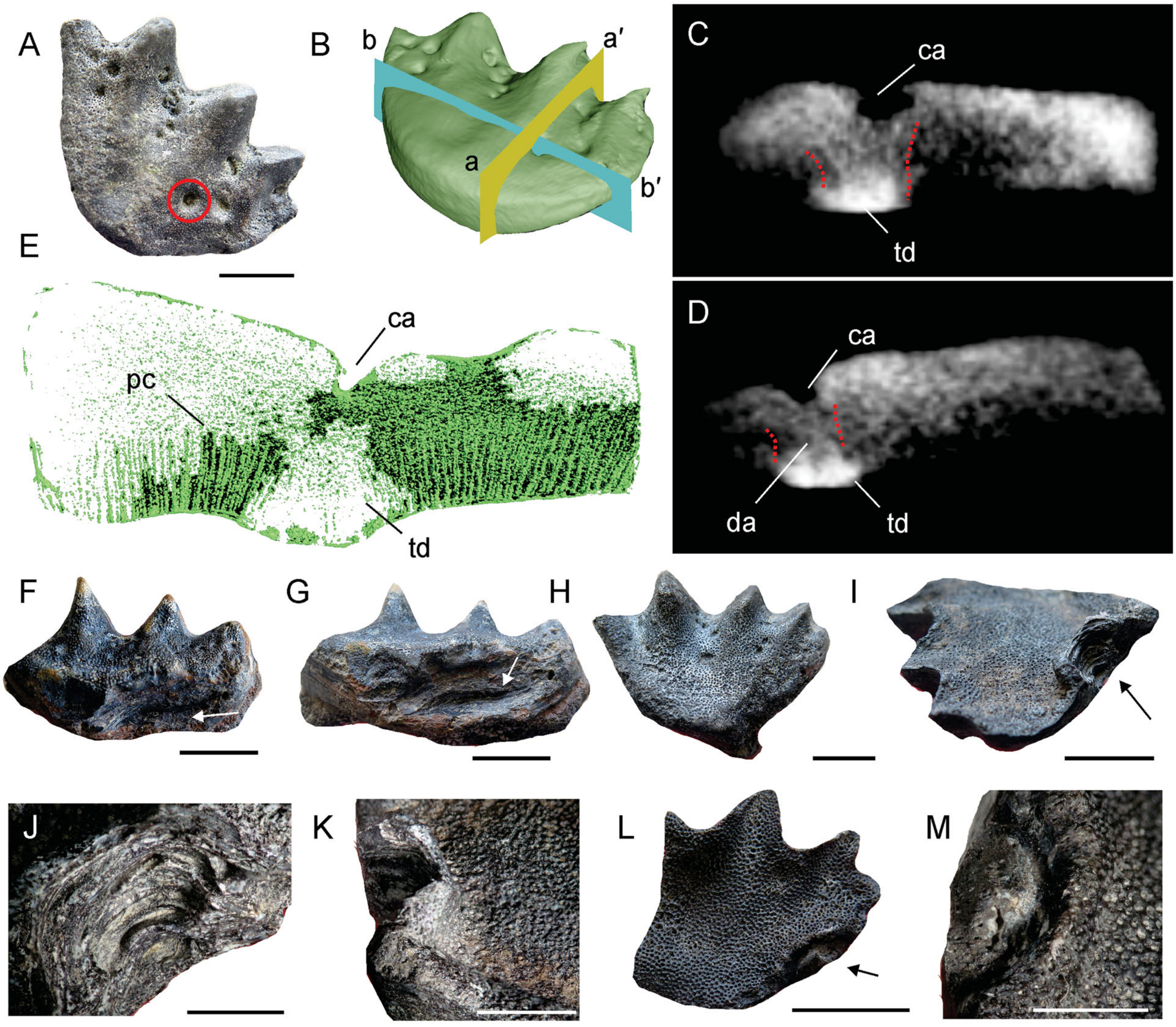

Figure 4. Tooth plates of *Metaceratodus baibianorum* with caries and abscesses injuries. **A**, MPEF-PV 11425 (from Cerro Bosta), scanned pterygopalatine tooth plate. **B**, render of A, with planes of tomograms a–a′ and b–b′. **C**, tomogram in plane a–a′. **D**, tomogram in plane b–b′, showing the caries and overgrowth of dentine, the dotted line indicates the limits of the injury. **E**, MPEF-PV 11425, render at level of the injury, showing the spaces of pulp canals in green. **F, G**, MPEF-PV 11426 (from Cerro Bosta), prearticular tooth plate with an abscess, the arrow indicates the banded tissue (G). **H, I**, MPEF-PV 11419 (from Hoyada del Irupé), pterygopalatine tooth plate with an abscess (arrows). **J, K**, magnifications of H–J with banded tissue. **L**, MPEF-PV 11425 (from Cerro Bosta), pterygopalatine tooth plate with a small abscess (arrow). **M**, Magnification of the injury in L. Scale bar = A–I, L, 1 cm; J, K, M, 0.5 mm. Abbreviations: ca, caries; da, demineralized area; pc, pulp canals; td, tertiary dentine.

(Kemp 2003b, 2005, Kemp & Berrell 2013). To date, studies of fossil dipnoans from southern South America have focused on their taxonomy rather than dental pathologies (Wichmann 1924, Cione 1987, Apesteguía *et al.* 2007, Cione *et al.* 2007, Panzeri *et al.* 2020). Nonetheless, studies of tooth plate anomalies in the extant ceratodont lungfish *Neoceratodus forsteri* (Krefft, 1870) and other fossils (Kemp 2001) provide a comparative basis for our primary assessment of the South American fossil material.

The type and degree of injuries affecting dipnoan tooth plates is known to vary between species and localities (Kemp 1996, 2005, Kemp & Berrell 2013). Moreover, lesions occurring on the occlusal surfaces that do not affect the generative area usually do not modify tooth plate growth and eventually disappear with wear and overgrowth of new dental tissues (Kemp 2001, 2003b). The lesions we observed on our sample of *Metaceratodus baibianorum* tooth plates are mostly located on the mediolingual edge and over the occlusal surface. Only two tooth plates (MEPF-PV 678 and MPEF-PV 11419) preserve lesions on the generative area of the new cusps. Caries, fractures, hyperplasia and erosion are otherwise the most recurrent pathologies (Table 1). Examples of attrition, osteopenia or parasitic invasions were not recorded. Attrition occurs when an individual grinds its tooth plates without food, resulting in deep furrows and depressed or flattened plateau areas (Kemp 2005). The tooth plates of *M. baibianorum* usually have rounded, defined ridges and shallow furrows. The remnant bone tissues fused to the tooth plates are also not porous or weakened, which would otherwise evidence osteopenia. Parasitic lesions are uncommon (Kemp 2005, Kemp & Berrell 2013), and were likewise not observed in our fossils.

The caries evident in our *M. baibianorum* tooth plates have different morphologies accordant with their position.

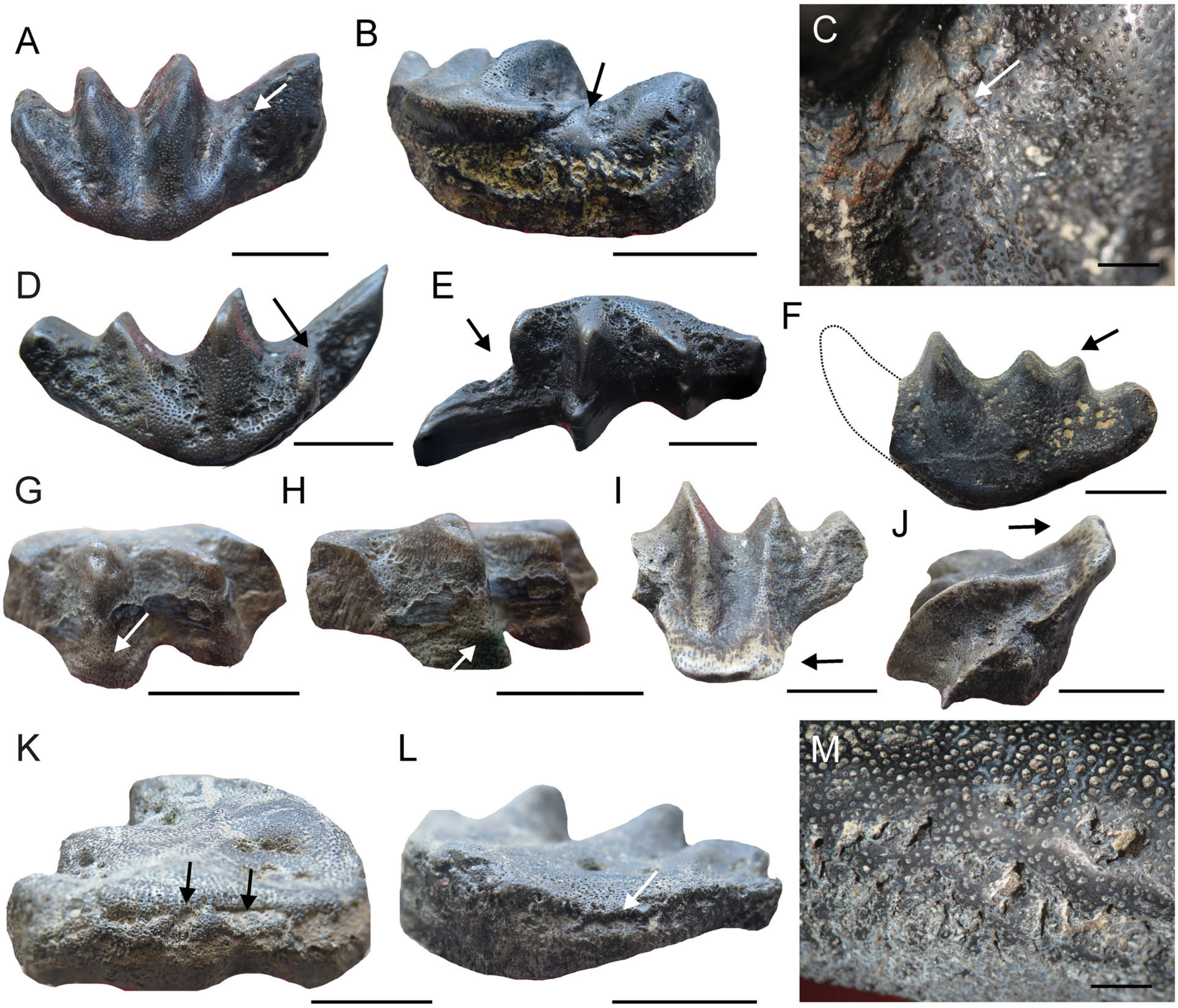

Figure 5. *Metaceratodus baibianorum* tooth plates with fractures, hyperplasia erosion and growth anomalies. **A, B**, MPEF-PV 11427 (from Cerro Bosta), prearticular tooth plate with a fracture at level of the first denticulation. **C**, magnification of A (the arrow points the fracture). **D, E**, MLP 06-VII-1-1-1 (from Cerro Bosta), prearticular tooth plate with fracture at the level of the first denticulation. **F**, MEPEF-PV 6785 (from Abra de la Tortuga), prearticular tooth plate with double denticulation anomaly (arrow), in dotted line the reconstructed first denticulation. **G, H**, MPEF-PV 11419 (from Abra de la Tortuga), prearticular tooth plate with displaced denticles. **I, J**, MPEF-PV 11419 (from Cerro Bosta), prearticular tooth plate with hyperplasia on the mediolingual edge. **K, L**, MPEF-PV 11421 (from Abra de la Tortuga), pterygopalatine tooth plate with erosion on the mediolingual edge. **M**, magnification of L. Scale bar = A, B, D–L, 1 cm; C, M, 0.25 mm.

Table 1. Number of tooth plates with each anomaly.

Anomaly	Number of tooth plates
Caries with reaction	8
Caries without reaction	8
Fracture	2
Hyperplasia	4
Erosion	7
Alteration in growth	2
Abscess	4
Total	35

In many cases, the caries are located on the plateau areas and furrows coincident with overgrowths of dental tissue on the pulp cavity. Although the production of tertiary dentine (reactionary or reparative) is controversial in dipnoans, our micro-CT results show that these dentine overgrowths possess similar properties to the tertiary dentine associated with mammalian caries (Wang *et al.* 2017, Carvalho *et al.* 2018, Eslami *et al.* 2021). Key features include: lesions on the occlusal surface, areas of demineralized dentine, and dense dentine deposits on the pulpal surface. The overgrowth dentine also has fewer pulp canals (and fewer dentinal tubules) than the surrounding dentine, which may reduce porosity of the tooth (Senawongse *et al.* 2008). The formation of tertiary dentine and its grade of permeability depends on the history of the lesion (Bjørndal 2008).

Amongst fishes, the dentitions of chimaerids possess incremental mineralization of the trabecular and hard dentine towards the occlusal surface (Smith *et al.* 2019). Smith *et al.* (2019) proposed that an external stimulus, such as wear on the functional occlusal surface of the chimaerid tooth plates, could cause incremental mineralization resembling tertiary dentine. A similar phenomenon has been observed in the dermal shields of agnathans (Halstead 1969, Ørvig 1976b, Johanson *et al.* 2013). In dipnoans, Kemp (2003b) also recognized evidence of healing, which we likewise observed in the La Colonia Formation fossils. Furthermore, as noted by Kemp (2001), we did not observe tertiary dentine associated with growth remodelling, nor complete infilling of fractures, caries, or lesions.

The ability to generate tertiary dentine has been recorded in several vertebrate groups spanning some 380 million years (Johanson *et al.* 2013, Herbst *et al.* 2019). Without the ability to generate reactionary or reparative dentine, deep caries would lead to infection and loss of non-replacement dentitions. Local reinforcement with tertiary dentine near the pulp cavity is therefore critical to avoid possible necroses.

When caries involves part of the underlying bone, abscesses are formed and can affect the formational arrangement of new dental tissues (Kemp 2005). One of our sampled tooth plates with attached bone (MPEF-PV 11426) has banded dentine and enamel within the lesion. Other isolated specimens (MPEF-PV 11419, MPEF-PV 11425) show similar banding and lesion injuries. Lastly, our identification of abscesses adds to the previously scarce record of such pathologies in Mesozoic dipnoans (Kemp 2003b).

Fractures vary in position relative to the generative area, and may be superficial or severe (Kemp 2001, fig. 6B, 7B), and can affect the underlying bone (Kemp 2001, fig. 9B). The fractures in our sample of *M. baibianorum* tooth plates are relatively superficial and infrequent.

Only one *M. baibianorum* specimen (MPEF-PV 11419) exhibits hyperplasia integrating a large development of dental tissue. However, compared to similar overgrowths reported in *N. forsteri* (Kemp 2001, fig. 13), this condition is less severe and rarely present in the La Colonia Formation dipnoan remains.

Erosion has been documented in the Australian ceratodonts *N. forsteri* and *Mioceratodus gregoryi* (White, 1925), with varying severity dependent upon water acidity in the surrounding habitat (Kemp & Berrell 2013). The examples of erosion in *M. baibianorum* tooth plates from the La Colonia Formation involve both the dentine and enamel in a few specimens; which implicates a non-acidic depositional setting (Kemp & Berrell 2013). Finally, our sample of *M. baibianorum* tooth plates from the Cerro Bosta and Hoyada del Irupé localities, although less abundant, manifest the most severe anomalies. Nonetheless, minimal erosion, caries, abscesses and the absence of parasitic lesions indicates uniformly non-acidic water quality, and a probably stable palaeoenvironmental setting for the assemblage (Kemp & Berrell 2013).

Conclusions

- Dipnoan tooth plates frequently display intraspecific variations in shape (Kemp 1990) that can be attributed to differences in growth, environment, or injury (Kemp 2005). Our sample of 127 tooth plates attributed to *Metaceratodus baibianorum* from late Maastrichtian deposits of the La Colonia Formation in Patagonia accordingly revealed 27.5% evidencing some form of pathological dental tissue modification.
- Hyperplasia, erosion, caries, abscess fractures, and developmental abnormalities were the most common pathologies.
- Some tooth plates also showed overgrowths of the dentine covering the pulp cavity that were coincident with occlusal caries. The close compatibility of these structures with tertiary dentine indicates that dipnoans are likely capable of generating this distinctive healing-associated dental tissue.

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Disclosure statement

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