Dental histology and attachment tissues in *Notosuchus terrestris* (Crocodyliformes, Notosuchia): palaeobiological implications

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LETHAIA

Notosuchia represents a highly diverse lineage of Crocodyliformes usually characterized by the presence of a heterodont dentition. Although the dental anatomy has been thoroughly analysed in some taxa, information regarding tooth microstructure and dental attachment tissue are still poorly explored. With the purpose to obtain new data regarding feeding habits, tooth growth rates and nature of the dental attachment in notosuchians, here we describe and interpret the microstructure of the tooth and tooth attachment tissues of *Notosuchus terrestris* from the Late Cretaceous of Argentina (MPCA-PV 250). We found that the relative and absolute enamel thickness of *Notosuchus* is more similar to the one reported for carnivorous notosuchians (e.g. Baurusuchidae). The dentine microstructure allowed us to infer that the tooth growth rates of *Notosuchus* are reduced in comparison with other notosuchians. The tooth attachment of *Notosuchus* corresponds with a typical gomphosis, which involves the presence of cementum, alveolar bone, and periodontal ligamentum. The spatial arrangement of these tissues exhibits the plesiomorphic condition for archosaurs and the new data supports a high degree of conservatism of this feature. The data available on the absolute and relative cementum thickness reveals that *Notosuchus* exhibits the highest values of absolute and relative cementum thickness among the analysed crocodyliforms. Different from other archosaurs, in which alveolar bone is only formed by woven fibred bone, the alveolar bone of our specimen is formed by both woven and parallel fibred bone, which indicates local variations in the rates of the alveolar bone formation. □ *Dental growth rate, dental histology, attachment tissues, Notosuchia, feeding habits.*

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The clade Notosuchia represents a successful lineage of Crocodyliformes that achieved a remarkable diversity during the Cretaceous of Gondwana, especially in South America (Pol & Gasparini 2007; Pol *et al.* 2014; Pol & Leardi 2015). Notosuchians are usually characterized by the presence of a heterodont dentition and a broad range of morphologies has been reported for their posterior teeth (including multicusped crowns), revealing an important diversity of trophic habits and feeding mechanisms (Clark *et al.* 1989; Bonaparte 1991; Wu *et al.* 1995; Buckley *et al.* 2000; Pol 2003). Although the dental anatomy has been thoroughly analysed in some taxa (e.g. Lecuona & Pol 2008; O'Connor *et al.* 2010; Ősi 2014), information regarding tooth microstructure and dental attachment nature in notosuchians are still poorly explored.

To date, the only comprehensive studies on notosuchian tooth histology has been recently published by Ricart *et al.* (2019) and Augusta & Zaher (2019), the first one being the only one that includes analysis based on thin sections. Based on a sample that included teeth from two Baurusuchidae, one Sphagesauridae, and two specimens of *Mariliasuchus amarali* Ricart *et al.* (2019) found interspecific differences regarding the enamel thickness (i.e. *M. amarali* and Sphagesauridae have proportionally thicker enamel in comparison to Baurusuchidae), which were interpreted as indicative of variations in their feeding habits. They also found that the distance between successive von Ebner lines in the dentine (parameter related with the tooth growth rates) exhibited a rather constant average thickness in the three taxa present. Surprisingly, such average thickness is greater than that of other archosaurs.

Given its importance for systematics and palaeobiology, the tooth implantation and the histology

of tooth attachment tissues has started to be deeply explored during the last years (e.g. Zaher & Rieppel 1999; Budney *et al.* 2006; Caldwell 2007; Maxwell *et al.* 2012; LeBlanc & Reisz 2013; García & Zurriaguz 2016; LeBlanc *et al.* 2017; LeBlanc *et al.* 2018; Mestriner *et al.* 2021). Among sauropsids, archosaurs are characterized by a thecodont implantation (i.e. teeth are placed within a socket) (Peyer 1968; Zaher & Rieppel 1999; LeBlanc & Reisz 2013). In this clade, gomphosis (i.e. the teeth are attached at the jaw by a periodontal ligament, LPD) corresponds with most commonly recorded tooth attachment type. Whereas the presence of the tissues involved in the gomphosis (i.e. cementum, periodontal ligamentum and alveolar bone) have been conservatively maintained throughout the evolution of amniotes, and their geometry, microstructure, distribution, and replacement rate exhibit an extraordinary variation among the different clades of non-avian dinosaurs (LeBlanc & Reiz 2013; LeBlanc *et al.* 2017). With the exception of some extant crocodylians, the tooth attachment histology of archosaurs has been mostly analysed for non-avian dinosaurs (e.g. Miller 1968; Zaher & Rieppel 1999; Fong *et al.* 2016; LeBlanc *et al.* 2017; Chen *et al.* 2018), leaving non-ornithodiran archosaurs poorly studied on this regard. Regarding dental attachment microstructure of notosuchians, there are not current data published to date.

Here we describe and interpret the microstructure of the tooth and tooth attachment tissues of *Notosuchus terrestris*, which represents the first notosuchian described worldwide and the most abundant crocodyliform species in Argentina during the Late Cretaceous (Lecuona & Pol, 2008; Barrios *et al.* 2017). Regarding *Notosuchus* feeding habits, the elongated articular facet for the quadrate and the tooth wear facets have been employed to infer fore-aft mandibular movements and omnivorous or even herbivorous feeding habits (e.g. Fiorelli & Calvo 2008; Lecuona & Pol 2008, Ősi 2014). Such inference has been challenged in a recent contribution that proposes a carnivorous habit for this species based on analysis of tooth complexity (Melstrom & Irmis 2019). Taking into account the current knowledge about tooth and tooth attachment histology of archosaurs, the main aims of this work are: (1) to examine and compare the enamel thickness of *N. terrestris* with other pseudosuchians, particularly notosuchians (i.e. *M. amarali*, Sphagesauridae, and Baurusuchidae); (2) to test previous hypotheses about carnivorous versus omnivorous/herbivorous feeding habits of *N. terrestris* based on the enamel thickness; (3) to evaluate the premise that Notosuchia presents a higher dental growth rate (inferred from distance between von Ebner lines) than other archosaurs; and (4) to examine and compare the tooth attachment of *N. terrestris* with other archosaurs, particularly pseudosuchians, evaluating the hypothesis of conservatism in the microstructural and spatial distribution of the involved structures.

Material and methods

An incomplete mandible of *Notosuchus terrestris* (MPCA-PV 250) was examined (Fig. 1). The specimen was found in the 'Paso Cordoba (or Paso Cordova)' locality (near General Roca city, Río Negro Province, Argentina), in sediments of Bajo de la Carpa Formation (Río Colorado Subgroup, Neuquén Group). This unit has been considered as Santonian in age (86–83 Ma) (see Garrido 2010 and references therein). The specimen corresponds to an individual
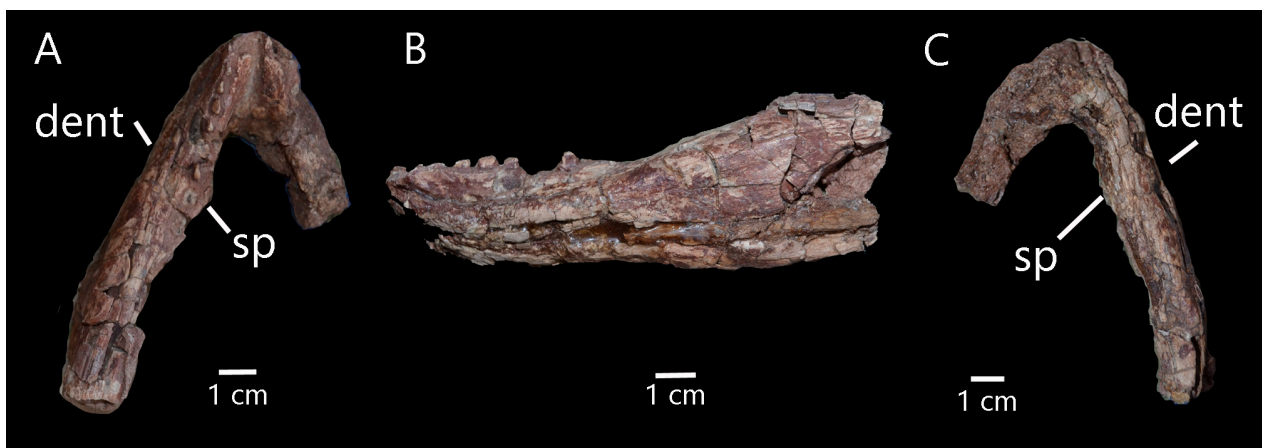

Fig. 1. Incomplete lower jaw of *Notosuchus terrestris* MPCA-PV 250 sampled for histological analysis. Anterior is toward the left the image. A, oclusal view. B, left lateral view. C, ventral view. Sp: splenial bone; dent: dentary bone.

that preserved an almost complete skull and incomplete postcranium, which has been previously studied by Pol (2005) and Barrios *et al.* (2018). It must be noted that the specimen has been incorrectly labelled with the collection number 237 in Barrios *et al.* (2018). Five thin sections were obtained from the left mandible; two transversal (i.e. vertical sections) and three parallel (i.e. longitudinal or occlusal section) to the mandible main axis (Fig. 2). The transversal sections cuts the 6th molariform and the longitudinal sections include the 5th-1st molariform teeth (Fig. 2).
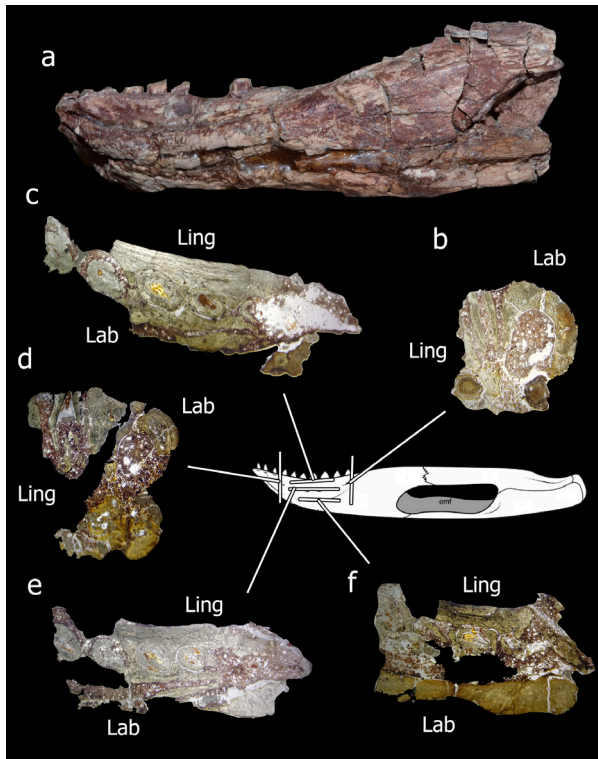

Fig. 2. General view and relative position of the studied sections of *Notosuchus terrestris* MPCA-PV 250 lower jaw. A-E, general view of the complete sections. The schematic representation of the lower jaw indicates the sites and orientation of each section. The sections include sixth molariform: (A,C,D) 1st to 5th molars and 6th (B,E). A,C,D anterior is toward the left and B,E ventral is toward the down image. Schematic figure of the *N. terrestris* lower jaw modified from Barrios *et al.* 2018. Ling, lingual side; Lab, labial side; mec, Meckelian canal.

Slices were prepared following standard procedures (Cerda *et al.* 2020). Thin sections were prepared at the palaeohistological laboratory of Museo Provincial 'Carlos Ameghino (Cipolletti city, Río Negro Province, Argentina). The samples were examined with a petrographic polarizing microscope (BestScope and Leica DM750P). The histological nomenclature and definitions applied in the present study are based on Francillon-Vieillot *et al.* (1990), de Ricqlès *et al.* (1991) and LeBlanc *et al.* (2017).

Measurements of particular histological parameters (e.g. enamel thickness) were made with ImageJ software (Schneider *et al.* 2012). The values were standardized to facilitate comparison with the bibliography. For this we calculated the percentage that enamel and the cementum thickness represent relative to the tooth crown and root radius, respectively. For the crown radius calculation, we divided the average between the longest and the minor axis of the crown in transverse section by two. The tooth root radius was obtained from a different manner. For this, we considered half of the labiolingual root diameter. We chose this diameter for comparative purposes (published data on cementum thickness and root diameter in crocodiles is derived from labiolingual sections of tooth bearing bones (Fong *et al.* 2016, LeBlanc *et al.* 2017, Bramble *et al.* 2017).

Dental attachment tissues nomenclature and definitions

Alveolar bone

The alveolar bone ('attachment bone') surrounds the socketed tooth and it is separated from the jawbone by the reversal line. The matrix can be formed by different bone tissues (e.g. woven fibred bone) depending on its growth rate (Budney *et al.* 2006). In Crocodyliformes, this tissue is poorly vascularized and formed by woven fibred bone (LeBlanc *et al.* 2017). During the tooth replacement, the alveolar bone is partially or completely reabsorbed, leaving remains of one or more generations that are separated by reversal lines. The bone between the teeth is called interdental bone and in the case of Crocodyliformes is formed by alveolar bone and its microstructure can vary during the ontogeny (Miller 1968).

Cementum

The cementum is a mineralized tissue similar to the bone (Francillon-Viellot *et al.* 1990; Budney *et al.* 2006) and is located around the dentine at the tooth root. Based on the presence of cells, cementum can be characterized as cellular or acellular. Whereas the acellular cementum forms a layer located adjacent to the dentine, cellular cementum (particularly thick) is located further away from the dentine (Budney *et al.* 2006; LeBlanc & Reisz 2013; LeBlanc *et al.* 2017). The cementocytes, the cells that secrete the cementum, are trapped in the calcification process resulting in a granular appearance and giving this layer its name. In Crocodylomorpha, both layers

are present in the location mentioned above, being the cellular cementum thicker towards the root apex (LeBlanc *et al.* 2017).

Periodontal ligament (PDL)

The collagen fibre bundles of the periodontal ligament extend between the cementum and alveolar bone and become incorporated into both tissues, and being identified as Sharpey's fibres are composed of collagen fibre bundles (Miller 1968; Nanci 2013). The difference between ankylosis and gomphosis attachment is mainly based on the degree of mineralization of the periodontal ligament. While in ankylosis the ligament is entirely mineralized, a very important portion of the same remains unmineralized in the gomphosis (Peyer 1968; Zaher & Rieppel 1999; LeBlanc & Reisz).

Results

The teeth of *N. terrestris* are not ankylosed to the jawbones. Instead, they are implanted in distinct alveoli in typical thecodont fashion. It is worth noting that, before sectioning and in occlusal view (Fig. 1), the posterior teeth are located within a single alveolar groove enclosed between the splenial and the dentary, which suggest that the boundaries between successive alveoli does not reach to the dorsal margin of the jaw. Only two replacement teeth are recorded. These are being formed inside the pulp cavity of the functional tooth. The tooth root and the alveolar surface are separated by a periodontal space that is filled with sediment. The sectioned portion of the jaw includes part of the dentary and, in a smaller proportion, the splenial. Despite that the sample has been altered by diagenesis and exhibits abundant fractures in several areas, the main histological features are still discernible.

Tooth histology

Since the obtained sections mostly correspond to the root of the teeth, enamel is absent in most of our samples. A very thin layer (0.01 mm = 10 micrometres) of birefringent tissue observed in the remains of a replacement tooth (i.e. molariform) appears to be the only remains of enamel (Fig. 3A). This layer represents 0.37% of the total radius of the dental crown. A more detailed characterization of this tissue cannot be performed beyond its optical properties. The dentine (i.e. orthodentine) forms the bulk of each tooth and exhibits a homogeneous appearance in all thin sections (Fig. 3A, B). Its thickness varies according to its position on the tooth. The dentine is an avascular tissue, which exhibits abundant micro-canals (i.e. dentinal tubules) that extend perpendicular to the pulp cavity toward the outer surface of the tooth. The dentine exhibits numerous concentric faint bands, which are spaced approximately 0.017 ± 0.001 mm apart (Fig. 3B). The shape and spacing between successive bands is consistent with daily lines of von Ebner (i.e. incremental lines). The spacing between successive lines of von Ebner can only be measure in some areas because the diagenetic alteration of the sample.

Tooth attachment tissues

The dentine of the roots is lined by cementum, which can be divided into two distinct layers: acellular and cellular cementum in MPCA-PV 250 (3C-F). Whereas the thickness of the acellular cementum is rather invariable, the thickness of the layer of cellular cementum exhibits variation, even within a single tooth. Both layers occupy between 18 and 22% of the total radius of the tooth root. We must note that these values were not taken in the sites, in which the cementum has the greatest thickness, which implies that can be higher. The acelullar cementum lies adjacent to the dentine of the root and consists of a thin (0.034 mm) band of birefringent tissue (Fig. 3C-F). There are no particular variations in terms of the acellular cementum thickness. The acellular cementum band is covered by a layer of cellular cementum, which is avascular and possess abundant cementocyte lacunae (Fig. 3D-F). The surface of the cellular cementum is irregular, possibly due to postmortem alterations. The cellular cementum is comparatively much thicker than the acellular one, reaching a maximum thickness of 0.66 mm. The thickness of the cellular cementum is not homogeneous around the tooth root, being thicker toward the root apex. Longitudinal sections reveal that the cellular cementum extends beyond the root crown boundary of functional teeth. Cementocyte lacunae are mostly ovoid shaped and tend to be more abundant in the vicinity of the acellular cementum (Fig. 3D-F). The cellular cementum contains Sharpey's fibres, which represent the mineralized portions of the periodontal ligament. Longitudinal sections of the teeth (i.e. transverse section of the jaw) reveal that Sharpey's fibres penetrate obliquely the cementum surface (Fig. 3G). In this regard, these fibres ascend from the inner portion of the cellular cementum (i.e. adjacent to the acellular cementum layer) to the cellular cementum surface. Sharpey's fibre density is not homogenous, being more abundant in some areas than others.
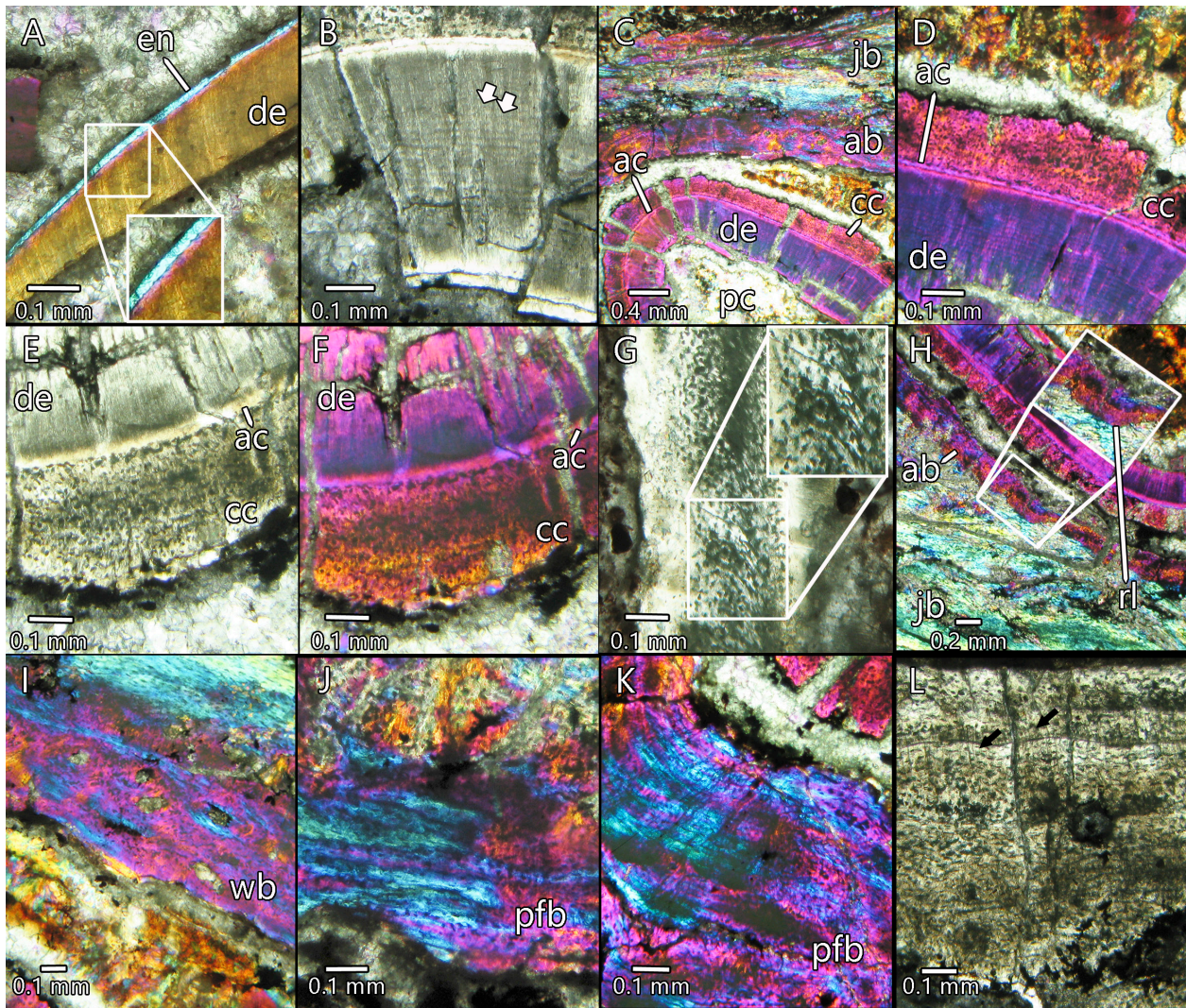
Fig. 3. Histology of tooth and tooth attachment tissues in *Notosuchus terrestris* (MPCA-250). A, general and detailed view of the crown section showing enamel and dentine. Note the strong birefringence of the enamel. B, detailed view of dentine. Von Ebner lines are signed with arrowheads. C, general view showing a tooth root, alveolar bone and jawbone in transversal section. D, detail of the tooth root (square inset in C) showing dentine and cementum (acellular and cellular). E,F, detail of acellular and cellular cementum. Note the high density of cementocyte lacunae toward the dentine. G, general and detailed view of Sharpey's fibres in the cementum. H, general and detailed view of the jawbone and the alveolar bone which are bounded by a distinct reversal line. I, J, K detail of alveolar bone, which is formed by woven fibred bone (I) and parallel fibred bone (J and K). L, Sharpey's fibres in alveolar bone marked with black arrowheads. A,C,D, F,H,I,J,K: cross polarized light with lambda filter; B,E,G,L: normal transmitted light. Abbreviations: ab, alveolar bone; ac, acellular cementum; cc, cellular cementum; de, dentine; jb, jawbone; pc, pulp cavity; rl, reversal line.

Each alveolus is lined by a distinct layer of alveolar bone, which is separated of the jawbone by a reversal line (Fig. 3H). The alveolar bone reveals an important variation regarding its microstructural features. The bone matrix of the alveolar bone varies from well-vascularized woven fibred bone to poorly vascularized or even avascular parallel fibred bone or crossed parallel fibred bone (*sensu* Cerda *et al.* 2018) (Fig. 3I-K). Although crossed parallel fibred bone was first described for osteoderms, this tissue has been also recognized in other elements as appendicular bones

(Pereyra *et al.* 2020). The less vascularized alveolar bone is mostly located toward the alveolus surface. Several generations of alveolar bone are separated by reversal lines representing accumulations of previous generations of tissues caused by various episodes of resorption. Sharpey's fibres are recorded in the alveolar bone (Figs. 3K, L, 4A, B). In this regard, Sharpey's fibres in the alveolar bone are commonly more abundant in those areas in which these extrinsic fibres are also abundant in the cellular cementum of the adjacent tooth root. Consistently with the observations in

the cellular cementum, the Sharpey's fibres penetrate obliquely the alveolar bone surface, descending from the inner portion of the alveolar bone (i.e. near the jawbone) toward the alveolar surface. Sharpey's fibres maintain their continuity even in those areas of the alveolar bone that exhibits resorption lines. It is worth to note that alveolar bone and cellular cementum exhibit similar appearance in some areas.

Jawbone histology

The sectioned portion of the jaw is formed by both dentary and splenial bones. The best-preserved portions reveal that both elements are formed by a compact cortex encircling a reduced core of cancellous bone tissue. The Meckelian canal, when preserved, is lined by a layer of compact bone formed by parallel fibred and crossed parallel fibred bone (Fig. 4 C, D). In the general terms, the jawbones are formed by parallel fibred bone, crossed parallel fibred bone and lamellar bone (Fig. 4D-F). Vascularization is relatively low and consists of longitudinally oriented simple vascular canals. Sharpey's fibres are observed in the sampled elements. However, their location and density strongly vary in the different regions of the jaw. In this regard, whereas Sharpey's fibres are absent of poorly developed in some areas, in others they are profuse, blurring the structure of the primary bone matrix and even reaching the dental alveoli (Fig. 4F-H). Sharpey's fibres are particularly abundant at the ornamented portions of the dentary. The outer cortical region of these areas exhibits an undulated surface, with distinct valleys and crest. Dense bundles of Sharpey's fibres penetrate perpendicularly to the jaw main axis and are more abundant at the crests (Fig. 4H). Distinct structures, interpreted as large vascular spaced entirely obliterated by lamellar bone tissue (i.e. the vascular space appear to be completely filled by lamellar bone), are recorded in the dentary. The same are oriented roughly perpendicular to the jaw main axis and they are delimited by a resorption line. Lines of arrested growth (LAGs) are recorded in both dentary and splenial bones (Fig. 4H). Cancellous bone, when preserved, consists of short trabeculae formed by secondarily deposited lamellar bone tissue. Remains of coarsely compacted cancellous bone are recorded in the ventral portion of the jaw (Fig. 4I).

Discussion

Enamel thickness

There is no current consensus about the feeding habits of *Notosuchus terrestris*. In this regard, Fiorelli & Calvo (2008) suggested, based on anatomical characters of the skull, an herbivorous diet for this notosuchian. On the other hand, based on the degree of morphological complexity of the crown surface, Melstrom & Irmis (2019) inferred carnivorous feeding habits for *N. terrestris*.

Both the enamel thickness and the degree of symmetry regarding its distribution in the tooth crown have been related with feeding habits (Hwang 2005; D'Emic *et al.* 2013). Whereas herbivorous vertebrates have usually thick enamel asymmetrically distributed, carnivorous forms have an enamel that is comparatively thinner and symmetrically distributed (Hwang 2005; D'Emic *et al.* 2013). To our knowledge, information regarding these parameters in omnivorous animals is unknown. The relative enamel thickness of *N. terrestris* (0.37% as mentioned above) is noticeably reduced in comparison with the reported for Sphagesauridae (3.8–5.2%); *Mariliasuchus* (4.3–6.8%) and Baurusuchidae (2.1/2.9%) (Augusta & Zaher 2019; Ricart *et al.* 2019). Regarding absolute values, the enamel of *N. terrestris* is also reduced (0.010 mm thick) in comparison with other notosuchians (Sphagesauridae 0.26–0.36 mm; *Mariliasuchus* 0.06–0.15 mm; Baurusuchidae 0.06–0.08 mm). Therefore, the enamel thickness recorded in *N. terrestris* is relatively and absolutely smaller than other notosuchians, even those than have been proposed as essentially carnivorous (i.e. Baurusuchidae, Carvalho *et al.* 2010, 2011). Our results regarding enamel thickness (enamel distribution cannot be assessed with confidence) are compatible with the enamel thickness found in carnivorous notosuchians. Nevertheless, since the enamel thickness of *N. terrestris* was obtained from a single tooth sectioned in the basal area of crown, the values might not be representative and this inference must be taken with caution.

Dental growth rates

Based on the distance between successive von Ebner lines in the dentine, Ricart *et al.* (2019) propose that notosuchians exhibited higher tooth growth rates than other archosaurs, including other crocodyliforms (such as neosuchians). Specifically, they found that this parameter in non-avian dinosaurs and neosuchian crocodyliforms were lower (between 0.014–0.019 and 0.012–0.019 mm respectively) than those reported for notosuchians (0.024–0.025 mm). Based on these results, Ricart *et al.* (2019) suggest that at least part of the notosuchian lineage (i.e. Sphagesauridae, *M. amarali* and Baurusuchidae) may be characterised by a high rate of daily deposition of dentine throughout most of their lives. The average recorded for *N. terrestris* (0.017 mm), however,
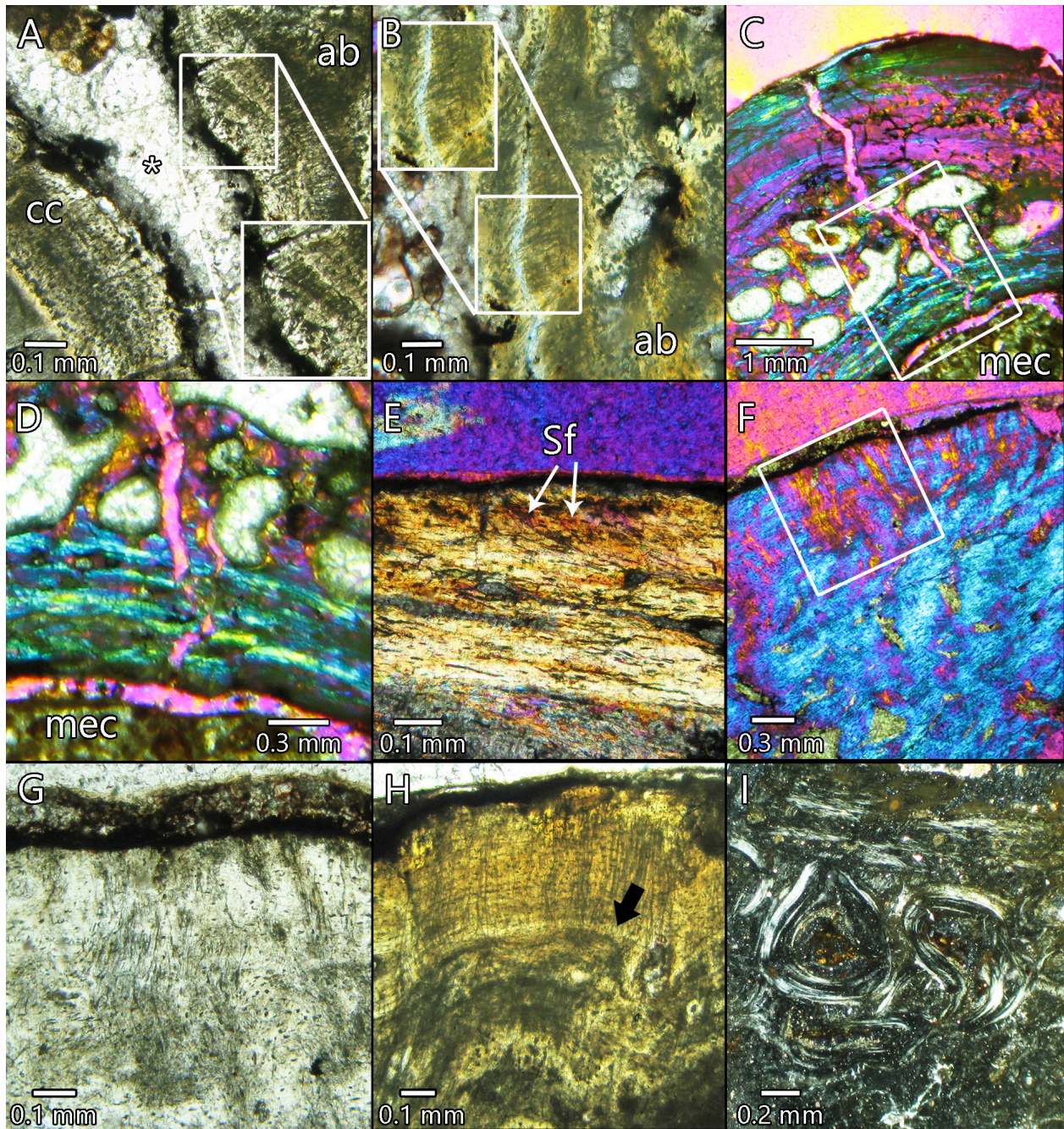
Fig. 4. Tooth attachment and jawbone histology in *Notosuchus terrestris* (MPCA-250). A, general and detailed view showing cellular cementum and alveolar bone. Sharpey's fibres are present in both cementum and alveolar bone. The asterisk indicates the space formerly occupied by periodontal ligament in life. B, general and detailed view of Sharpey's fibres in alveolar bone. C, D, general (C) and detailed (D) view of the jawbone in transversal section. E–H, general (E, F) and detailed (G, H) views of jawbone in longitudinal section. The image showed in G corresponds with the box inset in F. Sharpey's fibres are detailed in F and G. In H, a black arrow highlighted a line of arrested growth (LAG). I, coarsely compacted cancellous bone. A, B,H, normal transmitted light; C–F, cross polarized light with lambda filter and G cross polarized light. Abbreviations: ab, alveolar bone; cc, cellular cementum; mec, Meckelian canal; Sf, Sharpey's fibres.

departs from the above mentioned notosuchians, being more similar to the ones recorded for other archosaurs (Fig. 5). These results do not support existence of a uniform pattern regarding tooth growth rates in notosuchians and suggest, instead, that some degree of variation actually occur in this diverse lineage. Interpreting this data within the phylogenetic affinities of *N. terrestris* (Pol *et al.* 2014) indicates that the low tooth growth rates recorded for this taxon correspond with the plesiomorphic condition of other

crocodyliform clades. This could indicate that higher rates are a derived feature independently acquired by the clades of *Mariliasuchus*+Sphagesauridae and by Baurusuchidae. Alternatively, an equally parsimonious scenario is that higher rates appeared in the common ancestor of all these forms and the condition of *N. terrestris* represents a reversal to the plesiomorphic condition (Fig. 5). Data on other notosuchians is required to test these two alternative hypotheses. The functional significance of the derived condition is difficult to establish based on the current data, since there is not an apparent correlation between this feature with feeding habits or another possible factor.
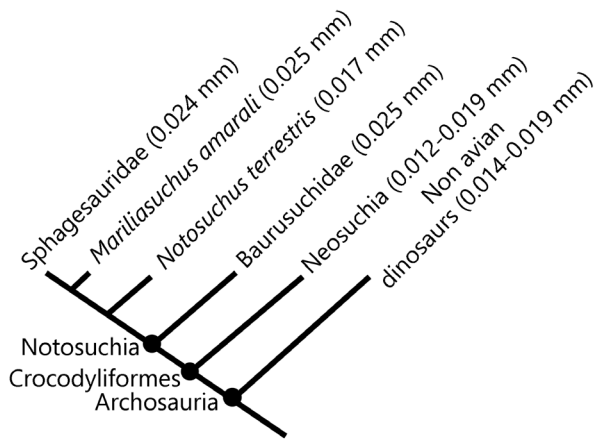

Fig. 5. Simplified phylogeny of Archosauria showing values of distance between successive von Ebner lines in different taxa. The phylogenetic relationships are based on Pol *et al.* (2014).

Dental attachment tissues

As in other Crocodyliformes, the dental attachment of *Notosuchus terrestris* is a gomphosis, characterized by the presence of three attachment tissues: cementum, alveolar bone and PDL (Miller 1968; Berkovitz & Sloan 1979; McIntosh *et al.* 2002; Enax *et al.* 2013; Mestriner *et al.* 2021). The identification of these attachment tissues presented here are the first for a notosuchian crocodyliform and allows comparisons with other toothed archosaurs, including non-avian dinosaurs and other pseudosuchians. The cementum distribution (i.e. roughly homogenously around the tooth root) resembles the condition reported for other pseudosuchians (LeBlanc *et al.* 2017) and non-avian dinosaurs, including saurischians (García & Cerda 2010, García & Zurriaguz 2016), ceratopsians (Erickson *et al.* 2015; LeBlanc *et al.* 2017) and basal ornithopods (Chen *et al.* 2018). This distribution of the cementum likely represents the plesiomorphic condition for archosaurs, and differs from the apomorphic arrangement reported for hadrosaurid dinosaurs (Bramble *et al.* 2017, LeBlanc *et al.* 2017). The acellular cementum histology of *N. terrestris* does not exhibit particular differences with the condition reported for other archosaurs. The cellular cementum, on the other hand, exhibits some degree of variation among archosaurs regarding its thickness. The relative thickness of *N. terrestris* is higher (18–22% of the root radius) than that recorded in *Alligator missisipiensis* (4%, from LeBlanc *et al.* 2017 fig. 7) but resembles that of *Caiman sclerops* (23% from Bramble *et al.* 2017 fig. 3) and therefore this may represent an apomorphic condition of mesoeucrocodylians or a more inclusive clade. Although there is no much data available for dinosaurs on this regard, both the relative and absolute cementum thickness in this group appears to be lower than the recorded one for *N. terrestris*. For example, theropods and sauropod dinosaurs exhibit values of 6 and 9–10% respectively (from Fong *et al.* 2016, fig. 2 and García & Cerda 2010, fig. 2). The increased cementum thickness in these mesoeucrocodylians (*N. terrestris* and *C. sclerops*) possibly provides a reinforced attachment of the tooth to the alveolus in comparison with other archosaurs in which the cementum is less developed. An increased attachment could be a response to diverse factors, but one possible explanation is that mesoeucrocodylians have a strong sutural integration of the skull bones that has been related to the development of large bite forces (Erickson *et al.* 2003; Pol *et al.* 2013; Gignac & Erickson 2016). Irrespective of its possible functional implications, the cementum thickness does not appear to be a conservative feature among archosaurs, nor even within crocodyliforms.

The histology of the alveolar bone in *N. terrestris* presents some differences in comparison with other archosaurs. In extant crocodyliforms (LeBlanc *et al.* 2017) and in non-avian dinosaurs, including ceratopsians (Erickson *et al.* 2015; LeBlanc *et al.* 2017), basal ornithopods (Chen *et al.* 2018) and saurischians (García & Cerda 2010, García & Zurriaguz 2016, Fong *et al.* 2016), the alveolar bone is formed by regularly distributed woven fibred bone. The alveolar bone in *N. terrestris* is formed either by woven and parallel-fibred bone. Woven fibred and parallel fibred bone are characterized by different rates of formation, which are higher in the first. The variability recorded in *N. terrestris* indicates local variations in the rates of the alveolar bone formation. Such variability has not been recorded in other archosaurs and could be related to eruption patterns and/or dental replacement in the jaw.

Conclusions

A detailed study of the dental histology and attachment tissues of *Notosuchus terrestris* was presented. Although a direct correlation between enamel thickness and feeding habits is still controversial, we found that the relative and absolute enamel thickness of *N. terrestris* is more similar to the reported for carnivorous notosuchians such as Baurusuchidae. The dentine microstructure allowed us to infer (from the distance between successive von Ebner lines) that the tooth growth rates of *N. terrestris* are reduced in comparison with other notosuchians. This result does not support the existence of a particular, clade specific tooth growth rate for notosuchians. Concerning the tooth attachment in *N. terrestris*, the same corresponds with a typical gomphosis, which involves the presence of cementum, alveolar bone, and periodontal ligamentum. However, the spatial arrangement of these tissues exhibits the plesiomorphic condition for archosaurs and the new data support a high degree of conservatism of this feature. The limited data available on the absolute and relative cementum thickness indicates mesoeucrocodylian crocodyliforms have an increased thickness relative to other archosaurs. In this sense, *N. terrestris* exhibits the highest values of absolute and relative cementum thickness among the analysed crocodyliforms. Different from other archosaurs, in which alveolar bone is only formed by woven fibred bone, the alveolar bone of our specimen is formed by both woven and parallel fibred bone, which indicates local variations in the rates of the alveolar bone formation.

References

Augusta, B.G. & Zaher, H. 2019: Enamel dentition microstructure of *Mariliasuchus amarali* (Crocodyliformes, Notosuchia), from the Upper Cretaceous (Turoniane Santonian) of the Bauru Basin, Brazil. *Cretaceous Research 99*, 255–268.

Barrios, F., Bona, P., Paulina-Carabajal, A. & Gasparini, Z. 2017: Re-description of the cranio-mandibular anatomy of *Notosuchus terrestris* (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Patagonia. *Cretaceous Research 83*, 1–37. http://dx.doi.org/10.1016/j.cretres.2017.08.016

Bramble, K., LeBlanc A.R.H., Lamoureux D.O., Wosik M. & Currier P.J. 2017: Histological evidence for a dynamic dental battery in hadrosaurid dinosaurs. *Scientific Reports 7*, 1–13, https://doi.org/10.1038/s41598-017-16056-3

Berkovitz, B.K.B. & Sloan, P. 1979: Attachment tissues of the teeth in *Caiman sclerops* (Crocodilia). *The Zoological Society of London 187*, 179–194.

Bonaparte, J.F. 1991: Los vertebrados fósiles de la Formación Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico superior, Argentina. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' e Instituto Nacional de Investigación de las Ciencias Naturales, sección Paleontología 4*, 17–123.

Buckley, G.A., Brochu, C.A., Krause, D.W. & Pol, D. 2000: A pugnosed crocodyliform from the Late Cretaceous of Madagascar. *Nature 405*, 941–944.

Budney, L.A., Caldwell, M.W. & Albino A. 2006: Tooth socket histology in the cretaceous snake *Dinilysia*, with a review of amniote dental attachment tissues. *Journal of Vertebrate Paleontology 26*, 138–145.

Cadwell, M.W. 2007: Ontogeny, anatomy and attachment of the dentition in mosasaurs (Mosasauridae: Squamata). *Zoological Journal of the Linnean Society 149*, 687–700.

Carvalho, I.S., Gasparini, Z.B., Salgado L., Vasconcellos, F.M. & Marinho, T.S. 2010: Climate's role in the distribution of the Cretaceous terrestrial crocodyliformes throughout Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology 297*, 252–262.

Carvalho, I.S., Teixeira, V.P.A., Ferraz, M.L.F., Ribeiro, L.C.B., Martinelli, A.G., Neto, F.M., Sertich, J.J.W., Cunha, G.C., Cunha, I.C.& Ferraz, P.F. 2011: *Campinasuchus dinizi* gen. et sp. nov., a new Late Cretaceous baurusuchid (Crocodyliformes) from the Bauru Basin, Brazil. *Zootoxa 42*, 19–42.

Cerda I.A., Pereyra M. E., Garrone, M., Ponce, D., Navarro, T.G., González, R., Militello, M., Luna, C. A. & Jannello, J.M. 2020: A basic guide for sampling and preparation of extant and fossil bones for histological studies. *Publicación Electrónica de la Asociación Paleontológica Argentina 20*, 15–28.

Cerda, I.A., Desojo, J.B. & Scheyer, T.M. 2018: Novel data on aetosaur (Archosauria, Pseudosuchia) osteoderm microanatomy and histology: palaeobiological implications. *Palaeontology 61*, 721–745.

Chen, J., LeBlanc, A.R.H., Jin, L., Huang, T. & Reisz, R. R. 2018: Tooth development, histology, and enamel microstructure in *Changchunsaurus parvus*: Implications for dental evolution in ornithopod dinosaurs. *PLoS One 13*, 1–18. https://doi.org/10.1371/journal.pone.0205206

Clark, J.M., Jacobs, L.L. & Downs, W.R. 1989: Mammal-like dentition in a Mesozoic crocodilian. *Science 244*, 1064–1065.

D'Emic, M.D., Whitlock, J., Smith, K.M., Fisher, D.C.& Wilson, J. 2013: Evolution of high tooth replacement rates in sauropod dinosaurs. *PloS One 8*, e69235. https://doi.org/10.1371/journal.pone.0069235

De Ricqlès, A., Meunier, F.J., Castanet, J.& Francillon-Vieillot, H. 1991: Comparative microstructure of bone. *In*: Hall, B.K (Ed.): *Bone Matrix and Bone Specific Products, 1–78. Bone, vol. 3. CRC Press*, Boca Raton, Florida, USA.

Enax, J., Fabritius, H. O., Rack, A., Prymak, O., Raabe, D. & Epple, M. 2013: Characterization of crocodile teeth: correlation of composition, microstructure, and hardness. *Journal of Structural Biology 184*, 155e163.

Erickson, G. M., Lappin, A. K. & Vliet, K. A. 2003: The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *Journal of Zoology 260*, 317–327. https://doi.org/10.1017/s0952836903003819

Erickson, G. M., Sidebottom, M. A., Kay, D. I., Turner, K. T., Ip, N., Norell, M. A., Sawyer, W. G. & Krick, B.A. 2015: Wear biomechanics in the slicing dentition of the giant horned dinosaur Triceratops. *Science Advances 1*, e1500055. https://doi.org/10.1126/sciadv.1500055 PMID: 26601198

Fiorelli, L. & Calvo, J.O. 2008: New remains of *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes: Mesoeucrocodylia) from Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional, Rio de Janeiro 66*, 83–124.

Fong, R.K.M., LeBlanc, A.R.H, Berman. D.S.& Reisz, R.R. 2016: Dental histology of *Coelophysis bauri* and the evolution of tooth attachment tissues in early dinosaurs: dinosaur dental

histology. *Journal of Morphology 277*, 916–924. https://doi.org/10.1002/jmor.20545 PMID: 27087142

Francillon Vieillot, H., Buffrénil, V. de, Castanet, J., Géraudie, J., Meunier, F.J., Sire, J.Y., Zylberberg, L.& De Ricqlès, A. 1990: Microstructure and mineralization of vertebrate skeletal tissues. *In*: J.G. Carter (ed.), *Skeletal biomineralization: Patterns, Processes and Evolutionary Trends,* 471–548. Volume 1. Van Nostrand Reinhold, New York.

García, R.A.& Zurriaguz, V. 2016: Histology of teeth and tooth attachment in titanosaurs (Dinosauria; Sauropoda). *Cretaceous Research 57*, 248–256. https://doi.org/10.1016/j.cretres.2015.09.006

García, R.A. & Cerda, I.A. 2010: Dentición de titanosaurios (Dinosauria, Sauropoda) del Cretácico Superior de la provincia de Río Negro, Argentina: morfología, inserción y reemplazo. *Ameghiniana 47*, 45–60.

Garrido, A.C. 2010: Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): nueva propuesta de ordenamiento litoestratigráfico. *Revista del Museo Argentino de Ciencias Naturales 12*, 121–177.

Gignac, P. M. & Erickson, G. M. 2016: Ontogenetic bite-force modeling of *Alligator mississippiensis*: implications for dietary transitions in a large-bodied vertebrate and the evolution of crocodylian feeding. *Journal of Zoology 299*, 229–238.

Hwang, S. 2005: Phylogenetic patterns of enamel microstructure in dinosaur teeth. Journal of Morphology 266, 208–240.

LeBlanc, A.R.H., Brink, K.S., Whitney, M., Abdala, F.& Reisz, R.R. 2018: Dental ontogeny in extinct synapsids reveals a complex evolutionary history of the mammalian tooth attachment system. *Proceedings of the Royal Society B: Biological Sciences 285*, 20181792. http://dx.doi.org/10.1098/rspb.2018.1792

LeBlanc, A. R. H., Brink, K. S., Cullen, T. M., & Reisz, R. R. 2017: Evolutionary implications of tooth attachment versus tooth implantation: a case study using dinosaur, crocodilian, and mammal teeth. *Journal of Vertebrate Paleontology 37*, e1354006. https://doi.org/10.1080/02724634.2017.1354006.

LeBlanc, A.R.H.& Reisz, R.R. 2013: Periodontal Ligament, Cementum, and Alveolar Bone in the Oldest Herbivorous Tetrapods, and Their Evolutionary Significance. *PLoS One 8*, e74697. https://doi.org/10.1371/journal.pone.0074697

Lecuona, A. & Pol. D. 2008: Tooth morphology of *Notosuchus terrestris* (Notosuchia: Mesoeucrocodylia): New evidence and implications. *Comptes Rendus Palevol 7*, 407–417.

Maxwell, E.E., Caldwell, M.W.& Lamoureux, D.O. 2012: Tooth histology, attachment, and replacement in the Ichthyopterygia reviewed in an evolutionary context. *Palöntologische Zeitschrift 86*, 1–14, https://doi.org/10.1007/s12542-011-0115-z

McIntosh, J.E., Anderton, X., Flores De Jacoby, L., Carlson, D.S., Shuler, C.F. & Diekwisch, T.G. 2002: Caiman periodontium as an intermediate between basal vertebrate ankylosis-type attachment and mammalian 'true' periodontium. *Microscopy Research and Technique 59*, 449–459.

Melstrom, K.M. & Irmis, R.B. 2019: Repeated Evolution of Herbivorous Crocodyliforms during the Age of Dinosaurs. *Current Biology 29*, 2389 –2395.

Mestriner, G., LeBlanc, A., Nesbitt, S.J., Marsola, J.C.A., Irmis, R.B., Stock Da-Rosa, A.A., Ribeiro, A.M., Ferigolo, J. & Langer, M. 2021: Histological analysis of ankylothecodonty in Silesauridae (Archosauria: Dinosauriformes) and its implications for the evolution of dinosaur tooth attachment. *The Anatomical Record.* 1–31, https://doi.org/10.1002/ar.24679

Miller, W. A. 1968: Periodontal attachment apparatus in the young *Caiman sclerops*. *Archives of Oral Biology 13*, 735–743, https://doi.org/10.1016/0003-9969(68)90091-5

Nanci, A. 2013: *Ten Cate's Oral Histology: Development, Structure, and Function*. Amsterdam: Elsevier. 379 p

O'Connor, P. M., Sertich, J. J. W., Stevens, N. J., Roberts, E. M., Gottfried, M. D., Hieronymus, T. L., Jinnah, Z.A., Ridgely, R., Ngasala, S. & Temba, J.2010: The evolution of mammal-like crocodyliforms in the Cretaceous period of Gondwana. *Nature 466*, 748–751.

Ősi, A. 2014: The evolution of jaw mechanism and dental function in heterodont crocodyliforms. *Historical Biology 26*, 279–414, https://doi.org/10.1080/08912963.2013.777533

Pereyra, M.E., Bona, P., Cerda, I.A., Jannello, J.M., De la Fuente, M.S. & Desántolo, B. 2020: Growth dynamics and body size evolution of South American long-necked chelid turtles: a bone histology approach. *Acta Palaeontologica Polonica 65*, 535–545.

Peyer, B. 1968: *Comparative Odontology*. The University of Chicago Press, Chicago, 347 pp.

Pol, D. & Leardi, J.M. 2015: Diversity patterns of Notosuchia (Crocodyliformes, Mesoeucrocodylia) during the Cretaceous of Gondwana. *In*: M. Fernández y Y. Herrera (Eds) Reptiles Extintos – Volumen en Homenaje a Zulma Gasparini. *Publicación Electrónica de la Asociación Paleontológica Argentina 15*, 172–186.

Pol, D., Nascimento, P.M., Carvalho, A.B., Riccomini, C., Pires-Domingues, R.A. & Zaher, H. 2014: A New Notosuchian from the Late Cretaceous of Brazil and the Phylogeny of Advanced Notosuchians. *PLoS One 9*, e93105. https://doi.org/10.1371/journal.pone.0093105

Pol, D. & Gasparini, Z.B. 2007: Crocodyliformes. *In*: Gasparini, Z.B., Salgado, L., Coria, R.A. (Eds), Patagonian Mesozoic Reptiles. Indiana University Press, Bloomington, pp. 116–142.

Pol, D. 2003: New remains of *Sphagesaurus huenei* (Crocodylomorpha: Mesoeucrocodylia) from the Late Cretaceous of Brazil. Journal of *Vertebrate Paleontology 23*, 817–831.

Ricart, R. S. D., Santucci, R. M., Andrade, M. B., Oliveira, C. E. M., Nava, W. R. & Degrazia, G. F. 2019: Dental histology of three notosuchians (Crocodylomorpha) from the Bauru Group, Upper Cretaceous, South-eastern Brazil. *Historical Biology* 1–12, https://doi.org/10.1080/08912963.2019.1675057

Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. 2012: NIH Image to ImageJ: 25 years of image analysis'. *Nature methods 9*, 671–675. PMID 22930834 (on Google Scholar).

Wu, X.C., Sues, H.D.& Sun, A. 1995: A plant-eating crocodyliform reptile from the Cretaceous of China. *Nature 376*, 678–680.

Zaher, H. & Rieppel, O. 1999: Tooth implantation and replacement in squamates, with special reference to mosasaur lizards and snakes. *American Museum Novitates 3271*, 1–19.