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ARTICLE

Dental histology of three notosuchians (Crocodylomorpha) from the Bauru Group, Upper Cretaceous, South-eastern Brazil

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ABSTRACT
The Upper Cretaceous Bauru Group deposits furnished several species of Crocodylomorpha, especially notosuchians. However, little is known about the feeding habits of this diverse group of crocodylomorphs. The dental histology is a destructive approach that can provide important information on tooth growth and feeding habits of fossil vertebrates. So far, few studies dealt with crocodylomorph dental histology and the ones available mainly focused on fossil and living neosuchians. In this work, we analyse the dental histology of three notosuchians commonly found in the Upper Cretaceous rocks of the Bauru Group: juvenile and adult Baurusuchidae, a large Sphagesauridae, and *Mariliasuchus amarali*. Our analyses indicate that tooth formation varied in these three taxa. In *Mariliasuchus*, a tooth took less than 2 months to be completely grown. On the other hand, in Sphagesauridae and Baurusuchidae, the tooth formation could take about 6 months to be completed. *Mariliasuchus* and Sphagesauridae have proportionally thicker enamel in comparison to Baurusuchidae. Additionally, the enamel thickness and its substantial development in the chewing area in Sphagesauridae indicate that apical advanced notosuchians are more adapted to process food items than more basal forms like *Mariliasuchus*.

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Notosuchia; dental histology; Bauru Group; Cretaceous; von Ebner lines

Introduction

The dental histology has been used in the study of several aspects of the feeding behaviour (e.g. tooth use and food intake) in different fossil vertebrates like herbivorous dinosaurs, crocodylomorphs, mosasaurids, and mammals (e.g. Dean 1993; D'Emic et al. 2013; Gren and Lindgren 2013). Dental histology data can furnish clues on the palaeobiology of vertebrates that, otherwise, could not be provided by the study of their respective skeletons. During part of the Mesozoic Era, the crocodylomorphs comprised a group that were much more diverse than they are nowadays (e.g. Brochu 2003), with members adapted to different habitats and exhibiting different feeding behaviours (e.g. Thalattosuchia, Notosuchia, Eusuchia). Specifically, in Brazil, several notosuchian crocodylomorphs are mainly known from Upper Cretaceous deposits of the Bauru Group, which crops out in the central/south-eastern portion of Brazil (Fernandes 2004). The most common crocodylomorphs found in Bauru Group deposits are: the Baurusuchidae, that apparently had a limited geographic distribution over the Gondwana, being essentially carnivorous (e.g. Carvalho et al. 2010, 2011); the Sphagesauridae, which are only known for South American deposits and are considered to be either herbivorous or omnivorous (Andrade and Bertini 2008b; Ösi 2013; Pol et al. 2014); and the species *Mariliasuchus amarali*, restricted to the region of Marília, São Paulo State (Carvalho and Bertini 1999; Zaher et al. 2006; Andrade and Bertini 2008a). These three notosuchians are considered to be more adapted to the life on land than the extant semi-aquatic neosuchians due to the presence of several skull and appendicular features such as: narrow and deep skull, nasal opening facing anteriorly, orbits laterally oriented, and relatively less curved femur (e.g. Zaher et al. 2006; Andrade and Bertini 2008b; Nascimento and Zaher 2010, 2011; Carvalho et al. 2011; Godoy et al. 2016).

Recent exceptional findings drew even more attention to these notosuchians such as the report of a new baurusuchid, *Aplestosuchus sordidus*, with Sphagesauridae remains within its abdominal cavity (Godoy et al. 2014), confirming a predator–prey relationship between these two groups. However, although the fossil record of notosuchians is abundant, little is known about the paleoecology of these organisms. These three groups of crocodylomorphs (Baurusuchidae, Sphagesauridae, and *Mariliasuchus*) had heterodont dentition, including evidence that, at least two of these forms (Sphagesauridae and *Mariliasuchus*) processed their food in the oral cavity through propalinal jaw movements (e.g. Pol 2003; Zaher et al. 2006; Andrade and Bertini 2008a, 2008b; Ösi 2013).

These three notosuchians have a relatively close phylogenetic relationship, with *Mariliasuchus* and Sphagesauridae being more related to each other than to Baurusuchidae (Andrade and Bertini 2008a, 2008b; Pol et al. 2014). These first two taxa are nested within a phylogenetic group informally referred to as 'advanced notosuchians' (*sensu* Pol et al. 2014). Baurusuchidae, on the other hand, is more closely related to Sebecidae (*sensu* Pol et al. 2014). In this sense, the

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presence of distinct groups of crocodylomorphs with diverse dental morphology in the same geological unit points to the question of how the niche partition occurred in this environment. As direct evidence of feeding is rare for these crocodylomorphs (see Godoy et al. 2014, for one exception), one of the ways to evaluate different levels of specialisation and feeding habits is the study of their dental histology.

The study of tooth growth lines is an effective way to determine tooth development rates for both extant and extinct animals. Generally, annuli (concentric rings of bone tissue with more organised fibres and less vascularization) or LAGs (lines of arrested growth) seen in long bones of most vertebrates indicate annual growth cycles (e.g. Castanet et al. 1993; Lee et al. 2013). In the dentition, however, the growth lines observed (von Ebner lines) are formed daily (Erickson 1996a, 1996b) in the innermost portion of the dentin as the tooth grows, so that the number of von Ebner lines is equivalent to the number of days needed for tooth formation (Erickson 1996a, 1996b). If the successive replacement tooth is present (for species that have dental replacement), it is also possible to estimate the replacement rate by counting the von Ebner lines of the functional tooth and subtracting the number of lines of the replacement tooth (Erickson 1996a, 1996b). As von Ebner lines are also daily formed in various groups of living vertebrates (e.g. Carlson 1990; Dean 1993; Erickson 1996a, 1996b; Smith et al. 2006), this characteristic is likely to be present in all amniotes and can be inferred for extinct taxa (Erickson 1996a), an interpretation also supported by the use of EPB (= Extant Phylogenetic Bracket) method (Witmer 1995).

The dental histology may also provide clues about the diet of extinct animals. Generally, herbivorous animals (especially those that process food items) tend to have thicker enamel (Hwang 2011) and higher rates of dental replacement when compared to carnivores, probably due to the excessive tooth wear (Erickson 1996a; D'Emic et al. 2013). To date, these studies on fossils are focused mainly on dinosaurs (Erickson 1996a; Hwang 2011; D'Emic et al. 2013; García and Zurriaguz 2016) and mammals (Beynon et al. 1998; Dean et al. 2001), with few ones on extinct crocodylomorphs (Gren and Lindgren 2013) or are mainly focused on living forms (Erickson 1996b). An exception is the recent work of Augusta and Zaher (2019), who studied the enamel structure of *Mariliasuchus* in which they found that this notosuchian bear a complex enamel microstructure with, for instance, modified parallel crystallite enamel with incremental lines and tubules. Therefore, in this work, we describe the dental histological features of three well-known notosuchians (Baurusuchidae, Sphagesauridae, and *Mariliasuchus*) from the Bauru Group and compare them with each other and with living and fossil neosuchians and non-avian dinosaurs.

Geological setting

The rocks of the Upper Cretaceous Bauru Group, Southeastern Brazil (Figure 1), crop out in the states of São Paulo, Minas Gerais, Mato Grosso do Sul, Mato Grosso, and Goiás, occupying an area of about 230,000 km^2 (Fulfaro 1974). The Bauru Group is divided into the Araçatuba, Adamantina, São José do Rio Preto, Uberaba, and Marília formations which, together with the Caiuá Group, form the Bauru Basin (Batezelli 2010). The limits of the Bauru Basin are characterised by erosive and/or tectonic processes (Batezelli 2010) and the climate at the time of deposition is essentially considered as arid/semi-arid (Batezelli et al. 2005). The rocks of the Adamantina Formation are regarded as braided river deposits (Fernandes and Coimbra 2000; Batezelli et al. 2003). According to Batezelli (2010), it is characterised by reddish, muddy sandstones and, subordinately, conglomerates and mudstone intercalations.

Specifically, for the Adamantina Formation, two age proposals are best known: one considers a Campanian/Maastrichtian age (Gobbo-Rodrigues et al. 2000; Santucci and Bertini 2001; Santucci and Arruda-Campos 2011) and the other, proposed by Dias-Brito et al. (2001), suggests a Turonian-Santonian age. These same authors agree in respect to the age of the overlaying Marília Formation, which is Campanian/Maastrichtian. Moreover, the contact between the top of the Adamantina Formation and the bottom of the Marília Formation, mainly in São Paulo State, is gradational (Fernandes 2004; Batezelli 2010), which weakens the Turonian–Santonian age proposal for the Adamantina Formation. However, it is not possible to conclude that the Adamantina Formation sites that furnished these three taxa studied here are coeval.

The outcrops from which the studied materials (Baurusuchidae and Sphagesauridae) came from are located in Jales and Fernandópolis, State of São Paulo, and are composed mainly of massive, poorly sorted, fine sandstones. The crocodylomorph fossils are generally associated with invertebrate ichnofossils and crocodylomorph coprolites and egg clutches. The remains of *Mariliasuchus* were found in the region of Marília, State of São Paulo. At that site, the Adamantina Formation is comprised by fine/very fine, massive, greenish to reddish sandstones. So far, the fossil evidence suggests that both Baurusuchidae and Sphagesauridae, at least partially, inhabited the same areas since several authors reported the findings of these two groups in the same levels of the Adamantina Formation (e.g. Godoy et al. 2014; Pol et al. 2014) and according to our personal observations in the outcrops near Fernandópolis during this study. Regarding the occurrences of *Mariliasuchus*, however, this taxon is restricted to some Adamantina Formation sites near the city of Marília, where only invertebrate ichnofossils and fish scales have also been found (e.g. Zaher et al. 2006).

Material and methods

The thin sectioned teeth comprise one caniniform and one molariform tooth of *Mariliasuchus* (FUP-Pv 000109 and FUP-Pv 000110, respectively), from Marília; a large molariform tooth of a Sphagesauridae (FUP-Pv 000100, see Cunha et al. Forthcoming for a complete description of this specimen), from Fernandópolis; one tooth of a juvenile Baurusuchid (FUP-Pv 000104), from Fernandópolis, and one mandibular tooth of Baurusuchidae (FUP-Pv 000108), from Jales. These specimens were collected in rocks of the Adamantina Formation (Figure 1).

Most selected teeth came from complete or partially complete skulls of the taxa of interest. We avoided, when possible, the use of isolated teeth to reduce the probability of taxonomic mistakes. There is a varied degree of heterodonty in the three

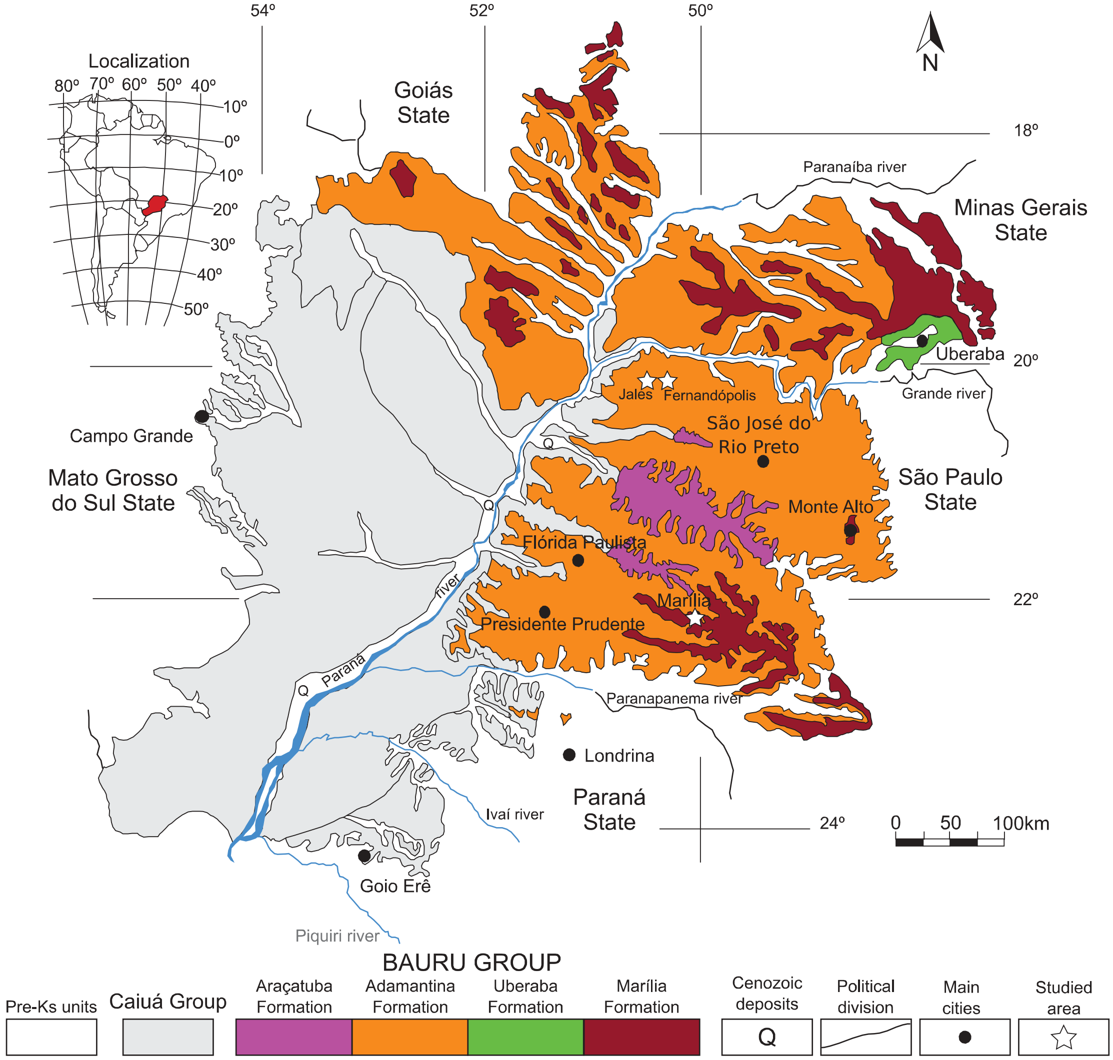

Figure 1. Geological map of the Bauru Group. Redrawn from Fernandes (1998) and Fernandes and Coimbra (1996). The white stars indicate the areas from which the materials came from.

taxa (less evident in Baurusuchidae), where the teeth basically differ from each other by size and cross-section profile (being more labio-lingually compressed in posterior teeth). In Sphagesauridae and *Mariliasuchus*, the dentition is clearly heterodont. In these two taxa, incisiform, caniniform, and molariform teeth are present (e.g. Zaher et al. 2006; Andrade and Bertini 2008a, 2008b; Augusta and Zaher 2019). Given the absence of distinct molariform teeth in Baurusuchidae, a posterior mandibular tooth was sampled instead. FUP-Pv 000109 is the only isolated tooth used in this analysis but corresponds morphologically, in all aspects, to the premaxillary caniniforms seen in other specimens of *Mariliasuchus* (dentary lacks hypertrophied caniniforms; see Zaher et al. 2006; Andrade and Bertini 2008a).

Due to the limited number of samples available, we opted to focus our analysis in posterior teeth because they are more likely to be involved in food processing. Therefore, one molariform tooth of a sphagesaurid (FUP-Pv 000100) and one of *Mariliasuchus* (FUP-Pv 000110) were used for histological analysis. Since baurusuchids lack molariform teeth, a tooth of the mandible from the equivalent position was sampled instead (FUP-Pv 000108). Additionally, we also analysed a caniniform tooth from *Mariliasuchus* (FUP-Pv 000109; isolated) and an anterior maxillary tooth from a juvenile baurusuchid specimen (FUP-Pv 000104). The sampling of more anterior teeth provides comparative data and allows the identification of relevant intraspecific variation between the anterior and posterior teeth of *Mariliasuchus* and baurusuchids. Unfortunately, no anterior sphagesaurid tooth was available for histological analysis.

It was not possible to properly evaluate the ontogenetic stage of most specimens through the fusion of neurocentral sutures (Brochu 1996) due to the incompleteness of the material. Therefore, ontogenetic stage was only tentatively categorised as juvenile, subadult, and adult according to size and tooth volume, compared to other known specimens. The sphagesaurid molariform (FUP-Pv 000100) was sampled from a relatively large individual, comparable to other adults with fused parietals and frontals (e.g. RCL-100) which is presumably an adult specimen. Baurusuchid teeth were taken from a larger (FUP-Pv 000108) and a smaller individual (FUP-Pv 000104), the later about half the size of the former. Given the size difference, FUP-Pv 000104 is interpreted as a juvenile (but possibly not an immature youngling). *Mariliasuchus* teeth were taken from two different individuals, FUP-Pv 000110 (molariform) and FUP-Pv 000109 (caniniform). *Mariliasuchus* FUP-Pv 000110 (molariform) is slightly larger than FUP-Pv 000109 (caniniform), indicating that the former is at a more advanced ontogenetic stage than the later. Nonetheless, both correspond in size to specimens with fused parietals and frontals (such as URC R•67; see Andrade and Bertini 2008a) and are evidently larger than the holotype (UFRJ-DG-50; see Carvalho and Bertini 1999), an immature specimen with paired frontals. As seen in fairly complete specimens of *Mariliasuchus*, the caniniform is larger than any given molariform in a single individual (e.g. see Fig 7C in Andrade and Bertini 2008a). Therefore, given the subtle difference in size between FUP-Pv 000110 and FUP-Pv 000109 (Table 1), the former is considered as a fully grown adult and FUP-Pv 000109 as a putative subadult.

The volume of each tooth was measured by immersion in water in a volumetric flask before thin section procedures. The teeth were vacuum impregnated with transparent epoxy resin before the preparation of thin sections in the laboratories of the University of Brasília and the University of São Paulo, following the procedures described in Padian and Lamm (2013). The thin sections were made transversely at the middle portion of the crown of the teeth. The growth lines (von Ebner lines) were counted manually when possible. In some instances, they were calculated based on the mean size of each von Ebner line previously measured for the tooth. The number of lines was then extrapolated to the dentin radius to obtain the estimated value of daily growth lines for the entire dentin. The thin sections were analysed under the petrographic microscope.

Comparative data regarding number and thickness of von Ebner lines and enamel thickness on other archosaurs were collected from the literature (e.g. Erickson 1996a, 1996b; Hwang 2005; D'Emic et al. 2013; Gren and Lindgren 2013; Augusta and Zaher 2019).

Results

General measurements and other data from sampled teeth are available in Table 1. The Sphagesauridae tooth has a volume of 0.918 cm^3 and the dentin radius is 4.35 mm, not considering the pulp cavity and the enamel. The average enamel thickness is 0.30 mm, varying from 0.26 mm, on the valleys, to 0.36 mm, on the enamel crests. The enamel thickness also varies according to its position on the tooth. On the opposite side to the wear facet, the enamel is thinner, varying from 0.26 mm to 0.30 mm, whereas in the wear facet region (carina), the enamel varies from 0.28 mm to 0.36 mm (Figure 2(a)). In this material, 116 von Ebner lines were identified, with an average thickness of 24 μm. There are several portions where the von Ebner lines are not clear and, therefore, the number of lines for the entire dentin was calculated taking into account the mean thickness of von Ebner lines and the radius of the dentin. The total number of daily growth lines in this tooth is 181. It is also observed that the von Ebner lines are slightly thinner in the outermost portion of the dentin (Figure 2(a)).

The caniniform tooth of *Mariliasuchus* (FUP-Pv 000109) has a volume of 0.031 cm^3 and the dentin radius measures 1.26 mm, not considering the pulp cavity and the enamel. The enamel average thickness is 0.08 mm, varying from 0.06 to 0.09 mm. The enamel thickness varies little, with no difference between the lingual and the labial sides. In this taxon, the tooth ornamentation does not affect the enamel thickness as it does in the Sphagesauridae tooth (Figure 2(b)). Only 20 von Ebner lines could be counted and their average thickness is 25 μm. The most visible region for counting the lines is the outermost portion of the dentin. The region close to the pulp cavity has no clear daily growth lines, showing a pattern of radial thin lines. The calculated total number of daily growth lines in this tooth is about 50 (Figure 2(b)). The molariform tooth (FUP-Pv 000110) has a volume of 0,039 cm^3, which must be considered as a minimum value because the tooth has a well-developed wear facet. The dentin radius varies from 1,65 mm (labio-lingually) to 2,70 mm (mesiodistally). The enamel thickness varies from 0,10 to 0,15 mm, being thicker on both labial and lingual sides. Unfortunately, no von Ebner lines were seen in this sample, but an incipient pattern of radial thin lines is present like in FUP-Pv 000109 (Figure 2(c)).

The juvenile baurusuchid (anterior caniniform) tooth (FUP-Pv 000104) has a volume of 0.055 cm^3 and shows a more elliptical section, with the dentin radius varying from 1.45 mm (on the minor axis, labial–lingual) to 2.30 mm (on the major axis, mesial–distal). The enamel thickness is uniform along the entire circumference of the tooth and measures 0.06 mm (Figure 2(c)). Only 20 von Ebner lines could be counted and they have an average thickness of 25 μm. The tooth is quite brittle in the outermost portion and the area near the pulp cavity has darker spots and radial lines. The calculated total number of von Ebner

Table 1. Data extracted for three different notosuchians from the Bauru Group, including crown measurements (medial–distal x labial–lingual), number of von Ebner lines (vEl) and mean vEl thickness (vElT). Note that mean vEl remains stable regardless of crown dimensions. Also, both the sphagesaurid and *Mariliasuchus* specimens have a proportionally coarser enamel layer relative to the size of tooth than baurusuchids. (*); minimum value, since the tooth has a well-developed wear facet.

Taxa	Crown measurements (mm)	Volume (cm^3)	Enamel thickness (mm)	# vEl	vEl thickness (μm)
Sphagesaurid FUP-Pv 000100 adult, molariform	15.5 x 11.9	0.918	0.26–0.36	181	24
***Mariliasuchus* FUP-Pv 000109** subadult, caniniform	2.8 x 2.8	0.031	0.06–0.09	50	25
***Mariliasuchus* FUP-Pv 000110** adult, molariform	5.6 x 3.3	0.039*	0.10–0.15	-	-
Baurusuchid FUP-Pv 000104 juvenile, anterior caniniform	5.1 x 3.2	0.055	0.06	58	25
Baurusuchid FUP-Pv 000108 adult, posterior caniniform	7.5 x 7.5	0.554	0.08	146	25

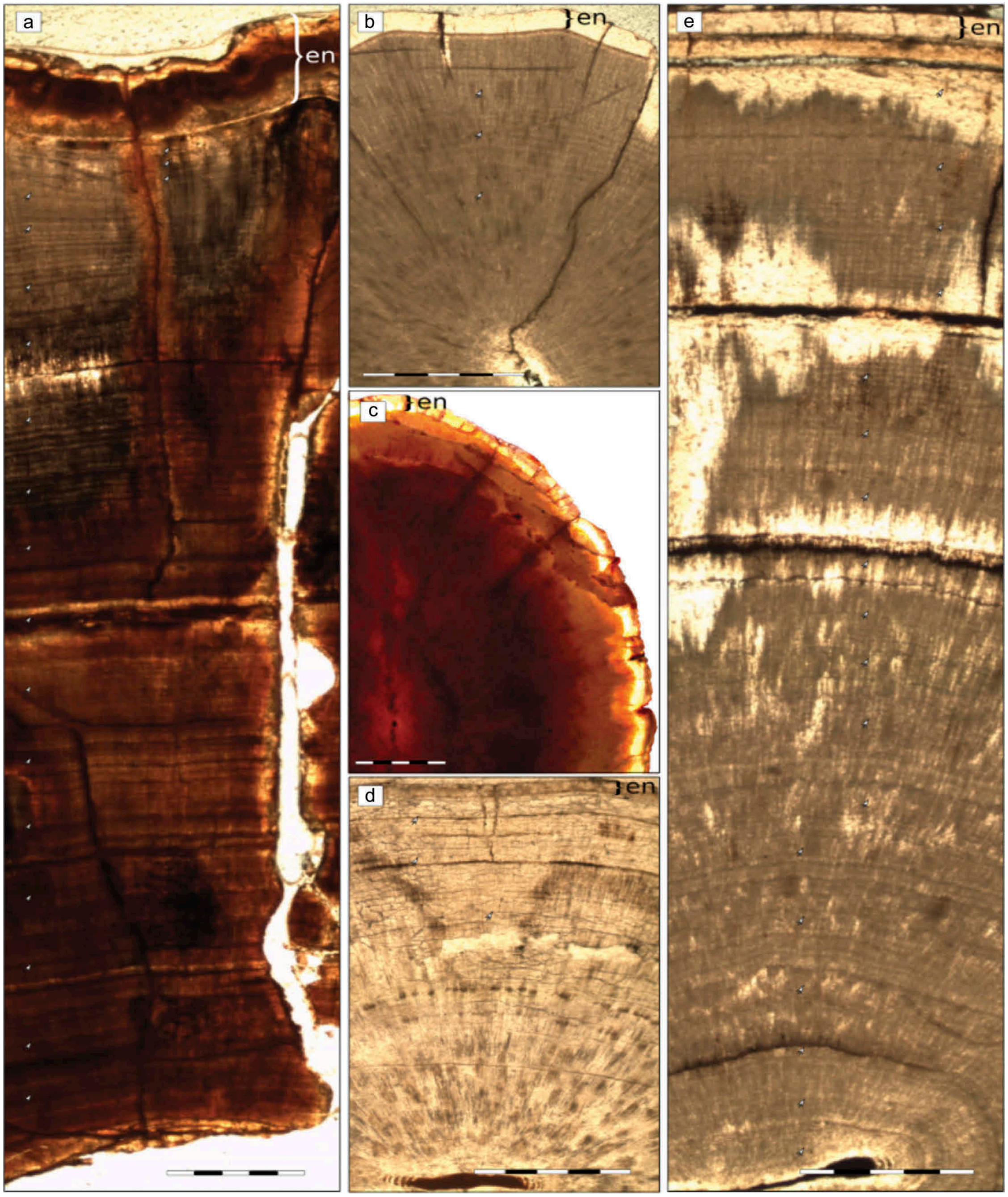

Figure 2. Thin sections of the selected notosuchians teeth from the Adamantina Formation, Bauru Group. (a), Sphagesauridae (FUP-Pv 000100), a molariform tooth; (b), *Mariliasuchus* (FUP-Pv 000109), a premaxillary caniniform tooth; (c), *Mariliasuchus* (FUP-Pv 000110), a posterior molariform tooth; (d), juvenile Baurusuchidae (FUP-Pv 000104), an anterior caniniform; and E, adult Baurusuchidae (FUP-Pv 000108), a posterior dentary caniniform. In all images, the enamel is at the top portion and the pulp cavity at the bottom. The white arrows mark a set of 10 von Ebner lines interval. Note the thicker enamel layer (en) in Sphagesauridae and *Mariliasuchus* teeth. Scale bar equals 0,5 mm.

lines is about 58 (Figure 2(c)). The adult baurusuchid (posterior caniniform) tooth (FUP-Pv 000108) has a volume of 0.554 cm^3 and the dentin radius is 3.65 mm, not considering the pulp cavity and the enamel. The enamel average thickness is 0.08 mm and, as in the juvenile Baurusuchidae tooth, it does not vary along its entire circumference (Figure 2(d)). One hundred and eight von Ebner lines were counted and they have an average thickness of 25 μm. The calculated number of daily growth lines for the entire dentin is 146 (Figure 2(d)).

The tooth replacement rates could not be evaluated because no reposition teeth were found.

Discussion

Enamel thickness

The enamel thickness is commonly related to the animal feeding habits and, generally, the presence of thicker tooth enamel is associated with herbivory and ingestion of more abrasive food items and/or incorporation of grains of sand (e.g. Hwang 2005; D'Emic et al. 2013). The same can be said about asymmetric enamel deposition in a single tooth, with carnivores tending to have homogenous thickness and herbivores showing asymmetric deposition (Hwang 2005; D'Emic et al. 2013).

Notosuchians show evident variation of enamel thickness between the studied taxa (Table 1, Figure 3). The teeth of sampled baurusuchids have much thinner enamel layers (2,1–4,0% of crown radius) when compared to the tooth values observed in Sphagesauridae (6,5%). *Mariliasuchus* does show somewhat intermediate values (~5,8% of the crown radius), but since this is a smaller taxon with smaller teeth (probably feeding on smaller food items), the enamel layer can be considered relatively thick. Unfortunately, the relative enamel thickness could not be calculated for the *Mariliasuchus* teeth studied by Augusta and Zaher (2019) because the dentin radius was not provided. However, since they found some variation in the enamel thickness in the *Mariliasuchus* teeth, it is possible that enamel represents a different proportion in different teeth of the same individual.

Regarding enamel distribution, uniform enamel thickness (i.e. it does not vary around the tooth circumference) is found in baurusuchid teeth and the premaxillary caniniform of *Mariliasuchus*. Enamel thickness variation in *Mariliasuchus* caniniform relates only to the valleys and ridges formed by the ornamentation and not to differential distribution between the labial and lingual crown facets. True asymmetric enamel distribution is found in molariform teeth, both of the sphagesaurid and *Mariliasuchus*. It seems clear that baurusuchids have uniform enamel distribution from the anterior to the posterior dentition, while *Mariliasuchus* in contrast have

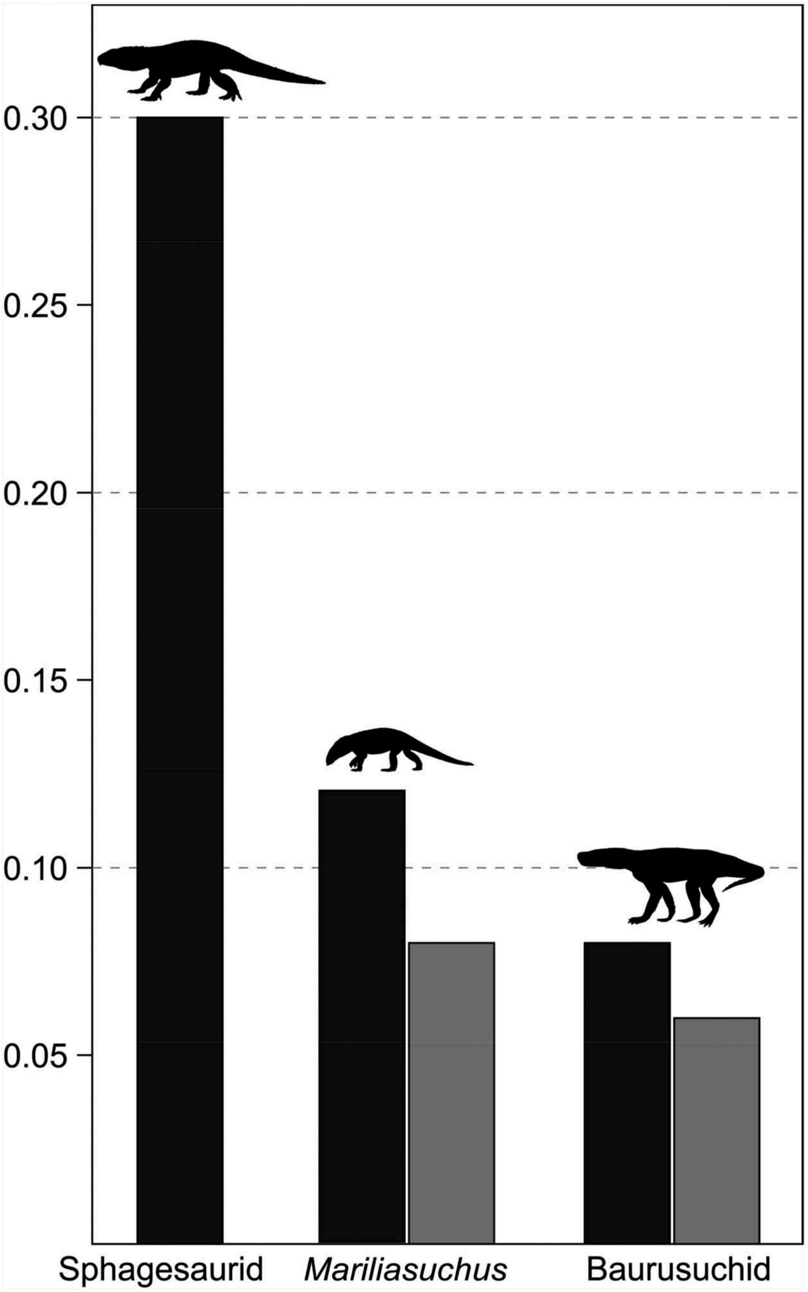

Figure 3. Absolute enamel thickness in sampled notosuchian specimens. Enamel thickness values plotted correspond to median values for the specimen, whenever enamel thickness is variable in the tooth. Note that even though *Mariliasuchus* is the smallest taxon (with smaller tooth volume values; Table 1), it has slightly higher average enamel thickness values than the equivalent baurusuchid specimens. Adults in dark grey bars; relatively younger specimens in light grey; values according to Table 1.

symmetric enamel thickness confined to the anterior dentition. Regarding the molariform teeth, the sphagesaurid conforms with the condition found in *Mariliasuchus*, showing a certain degree of asymmetry in the enamel thickness. Unfortunately, no sphagesaurid caniniform was available for histologic analysis, and it remains unclear if this group has asymmetric enamel distribution throughout the entire dentition or if it shows the same pattern of enamel distribution as *Mariliasuchus*.

In non-avian dinosaurs, herbivores species generally have a ticker and less uniform enamel than carnivores, a characteristic that seems to be more related to feeding habits than to size (Table 2; Figure 4). Even large-sized theropods, such as *Albertosaurus*, show thinner enamel layers than modest-sized herbivores, such as *Psittacosaurus*. Indeed, theropods stand out as having the thinnest known enamel layers. *Ankylosaurus* stands alone among herbivores, with proportionally thin layers, considering its size (Table 2; Figure 4).

Overall data on enamel thickness of dinosaurs and notosuchians show that enamel thickness seems to achieve relatively high values in crocodylomorphs than in theropods. Obviously, notosuchians are surpassed in terms of enamel thickness by large-sized herbivorous dinosaurs. However, sampled baurusuchids and *Mariliasuchus* show higher enamel thickness values even when compared to *Ankylosaurus* and *Psittacosaurus*, while the sphagesaurid tooth has about the same enamel thickness of *Triceratops*, a much larger taxon (see Table 1–2; Figure 4). It seems clear that notosuchian crocodylomorphs show thicker tooth enamel than dinosaurs of equivalent size. However, within each taxonomic group (dinosaurs X notosuchians), the thicker enamel coupled with its asymmetric distribution seems to support the interpretation that sphagesaurid, and perhaps *Mariliasuchus*, were capable of ingesting plant material as part of their diets.

The relationship between tooth enamel thickness and diet also seems to affect the rate of dental replacement, but in the case of the teeth analysed here, their respective successive replacement teeth were not available.

Average thickness of von Ebner lines

The average von Ebner line thickness is found to be constant for the three notosuchian taxa (Table 1). Because of that, the difference in the number of lines is proportional to the total size of the tooth. The values shown by notosuchians differ substantially from previously studied archosaurs (Table 3, Figure 5). In non-avian dinosaurs, the von Ebner thickness varies (14.0–19.8 μm), the same occurring with neosuchian crocodylomorphs (12.7–19.0 μm). In opposition, the average thickness of von Ebner lines found in the studied notosuchians is clearly higher and also show a much narrower range of values (24.0–25.0 μm).

Table 2. Enamel thickness in carnivorous and herbivorous dinosaurs, as taken from the bibliography. Note that most herbivorous dinosaurs have coarser enamel layers relative to carnivorous taxa. K = Cretaceous; J = Jurassic; Tr = Triassic.

Taxa		Age	Enamel thickness	Author
Theropoda	*Coelophysis*	Late Tr	0.01 mm	Hwang (2005)
Theropoda	*Albertosaurus*	Late K	0.015–0.018 mm	Hwang (2005)
Theropoda	*Velociraptor*	Late K	0.024 mm	Hwang (2005)
Sauropoda	*Camarasaurus*	Late J	1.0 mm (no variation between labial and lingual sides)	D'Emic et al. (2013)
Sauropoda	*Diplodocus*	Late J	0,5 mm (varying up to 125–150% labio-lingually)	D'Emic et al. (2013)
Thyreophora	*Ankylosaurus*	Late K	0.05 mm	Hwang (2005)
Marginocephalia	*Psittacosaurus*	Early K	0.06 mm (lingual side) and 0.002–3 mm (labial side)	Hwang (2005)
Marginocephalia	*Triceratops*	Late K	0.300–0.325 mm	Hwang (2005)
Ornitopoda	*Corythosaurus*	Late K	0.180 mm	Hwang (2005)

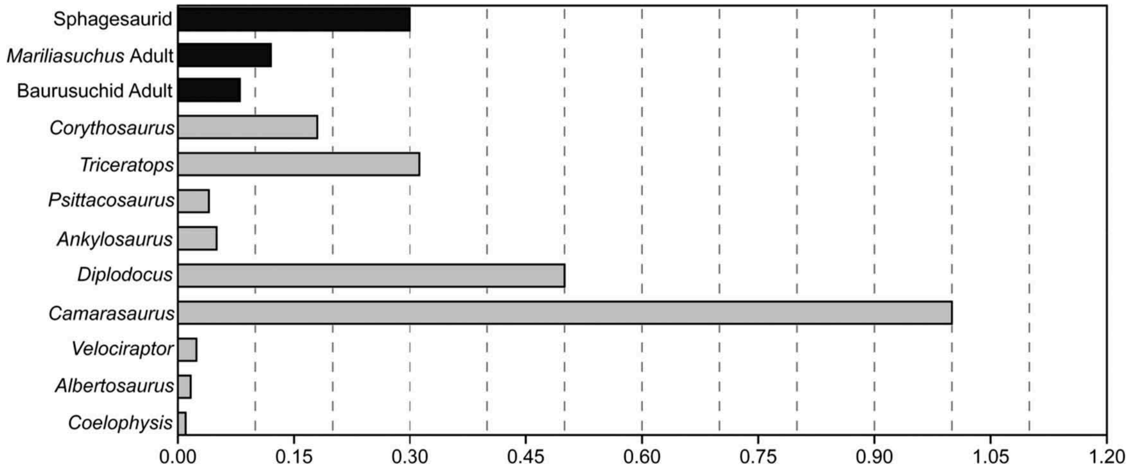

Figure 4. Absolute enamel thickness of sampled notosuchians compared to non-avian dinosaurs. Enamel thickness values plotted correspond to median values. Note that carnivorous theropods display the lowest values, while the highest values are dominated by large-sized herbivores. Note also that notosuchian values are noticeably high when compared to theropods. Finally, within each taxonomic group (Dinosauria, Notosuchia), putative herbivores display higher enamel values than known carnivores. Notosuchians in dark grey bars; non-avian dinosaurs in light grey; values according to Table 1–2.

Table 3. Number of von Ebner lines (vEl), thickness of von Ebner lines, and tooth crown volume in selected archosaurs, as taken from the literature. Note that a higher number of von Ebner lines are found in larger teeth, but von Ebner line thickness maintains a relatively narrow range of values (10,1–19,8 μm) regardless of the size. Also, vEl thickness values showed here are noticeably lower than vEl thickness of notosuchian teeth (see Table 1).

Taxa		Age	Mean crown volume (cm^3)	# vEl	vEl thickness (μm)	Author
Neosuchia	crocodile	Recent	0.90	246	13.0	Erickson (1996b)
Neosuchia	*Leidyosuchus*	Late K	1.20	283	19.0	Erickson (1996b)
Neosuchia	*Aigialosuchus*	Late K	-	259	12.7	Gren and Lindgren (2013)
Dinosauria	*Edmontosaurs* (juvenile)	Late K	0.43	225	14.0	Erickson (1996b)
Dinosauria	*Edmontosaurus* (adult)	Late K	2.0	339	19.8	Erickson (1996b)
Dinosauria	*Deinonychus*	Early K	0.2	413	10.1	Erickson (1996b)
Dinosauria	*Tyrannosaurus* (juvenile)	Late K	1.8	264	14.0	Erickson (1996b)
Dinosauria	*Tyrannosaurus* (adult)	Late K	138.0	933	17.0	Erickson (1996b)
Dinosauria	*Camarasaurus*	Late J	26.5	315	-	D'Emic et al. (2013)
Dinosauria	*Diplodocus*	Late J	1.7	185	-	D'Emic et al. (2013)

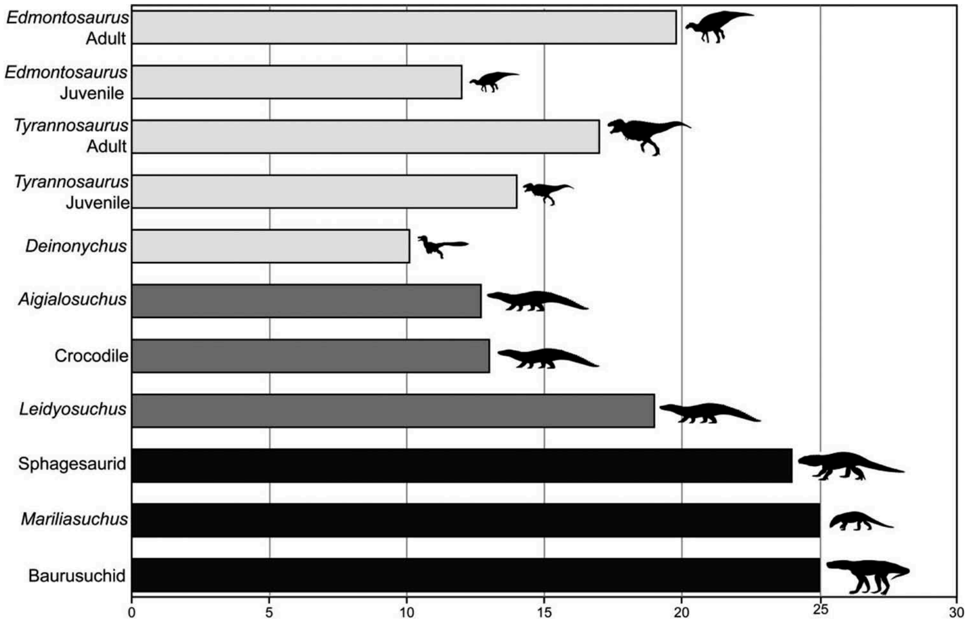

Figure 5. Average values for von Ebner line thickness of sampled notosuchians compared to other crocodylomorphs and non-avian dinosaurs. Note that notosuchians display the highest values, surpassing even large-sized dinosaurs. Note also that von Ebner line thickness appears to increase through ontogeny in non-avian dinosaurs (*Edmontosaurus, Tyrannosaurus*), but remain stable in Baurusuchidae. Notosuchians in black bars; neosuchians in dark grey, non-avian dinosaurs in light grey; values according to tables 1 and 3.

It is not possible to fully relate the average thickness of von Ebner lines to size, niche or phylogeny, though, as the sample size is far too small. Taking the archosaur dataset as reference, it seems that adult herbivorous taxa have thicker von Ebner lines, while small-sized carnivores tend to have thinner lines. Among the dinosaurs known from the literature, the adult *Edmontosaurus* did show the highest value for von Ebner line thickness (Table 3, Figure 5–6).

Notosuchians do not seem to follow the dinosaurian pattern. They stand out among archosaurs as having the thickest von Ebner lines, with almost no variation within the group. This points to a daily dentin deposition rate that is much higher than neosuchian crocodylomorphs and surpass even large-sized herbivore dinosaurs. This indicates that a particularly high deposition of daily dentin is possibly a characteristic of this evolutionary group of crocodylomorphs.

Number of growth lines

There is a large variation in the number of growth lines and, consequently, in the number of days of tooth formation among notosuchians, neosuchians, and non-avian dinosaurs (Tables 1 and 3; Figure 6). Considering the notosuchians studied here, the number of von Ebner lines varied from 50 to 181.

The sphagesaurid tooth has the highest number of lines, with an estimated total number of 181 for the entire dentin. The baurusuchid teeth presented 58 and 146 lines for the juvenile and the adult specimens, respectively. The caniniform tooth of *Mariliasuchus* has 50 growth lines for the entire dentin. Therefore, it took almost 5 months for the adult baurusuchid posterior caniniform tooth FUP-Pv 000108 to reach a fully erupted stage, and slightly more than 6 months for the sphagesaurid molariform FUP-Pv 000100 be completely formed. In contrast, both the *Mariliasuchus* premaxillary caniniform FUP-Pv 000109 and the juvenile baurusuchid caniniform FUP-Pv

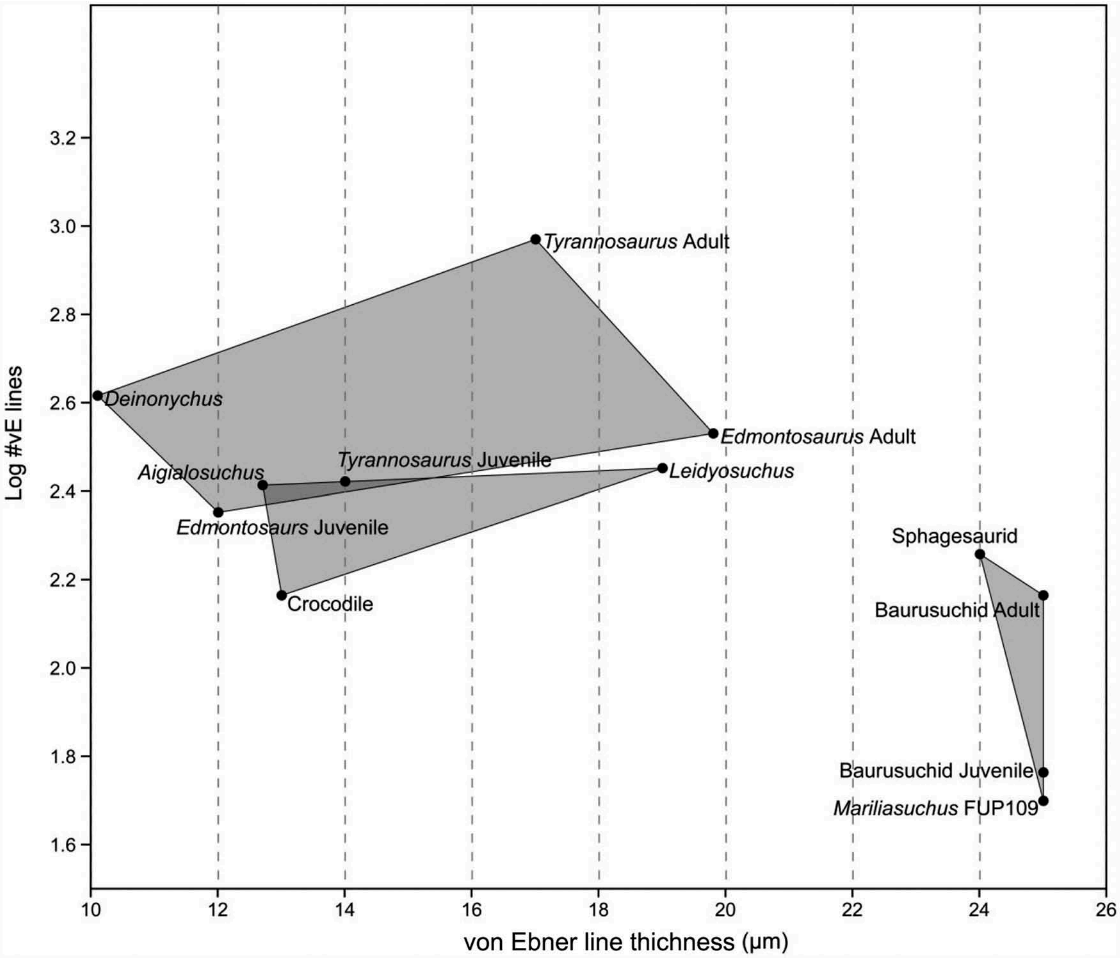

Figure 6. Bivariate plot displaying the number of von Ebner lines (#vEl) against von Ebner line thickness (vElT), to summarise tooth growth strategies in notosuchians, neosuchians, and non-avian dinosaurs. Note that neosuchian crocodylomorphs cluster near dinosaurs but show lower values in general, while notosuchians are set well apart from both groups. Note also that young individuals of *Edmontosaurus, Tyrannosaurus*, and Baurusuchidae plot closer to the X-axis than their adults, showing substantial differences in #vEL values through life. #vEl plotted as log scale to avoid the flattening of data due to extreme values of *Tyrannosaurus*. Source values according to tables 1 and 3.

000104 needed slightly less than 2 months to reach the same fully erupted stage.

Values observed for FUP-Pv 000108 and FUP-Pv 000100 are not surprising, as crocodylomorphs (crocodile, *Aigialosuchus*, and *Leidyosuchus*; see Table 3, Figure 6) show growth time of 5 to 9 months, approximately. However, FUP-Pv 000104 and FUP-Pv 000109 did seem to have produced fully erupted teeth in a relatively short time (<2 months). Unfortunately, no histological data is available in the literature for immature–subadult extant neosuchians, precluding further comparison on tooth growth strategies.

The number of growth lines relates to the size of tooth and therefore with size of the individual (Table 3; Figure 6, *y* axis). Non-avian dinosaurs have the highest values, with teeth that take longer to achieve a fully erupted stage. Neosuchian crocodylomorphs have slightly lower values when compared to adult dinosaurs, so teeth would need less time to achieve the fully erupted stage. Notosuchians have values that overall match neosuchian crocodylomorphs, but younger specimens and perhaps small-sized taxa, such as *Mariliasuchus*, seem to be able to produce fully erupted teeth in substantially less time.

Intraspecific variation

Intraspecific variation is an important element regarding the analysis of enamel thickness, average von Ebner line thickness, and number of von Ebner lines. Variation occurs both in notosuchians (Table 1) and at least two taxa of non-avian dinosaurs (*Edmontosaurus* and *Tyrannosaurus*; see Table 3), which provide useful data for comparison. Intraspecific variation may be the result of two key elements: ontogenetic stage and/or regional specialisation of the dentition. Unfortunately, the current sample does not provide the appropriate information to evaluate intraspecific variation relative to stratigraphy or sexual dimorphism.

Intraspecific enamel thickness variation is observed in baurusuchids and *Mariliasuchus* specimens (Table 1). The smallest specimen of each taxon have thinner enamel layers than the largest ones, but *Mariliasuchus* teeth show more evident differences in enamel thickness than baurusuchids. Baurusuchids have a relatively narrow range of values (Δ = 0,02 mm), despite noticeable size difference between the crown volumes of FUP-Pv 000104 and FUP-Pv 000108 (Δ = 0,499 cm^3). *Mariliasuchus* specimens, on the other hand, show a more evident variation

(Δ = 0,04 mm) for specimens of similar size (Δ = 0,008 cm^3). This suggests that the intraspecific variation seen in *Mariliasuchus* teeth may be better explained via functional regionalization (i.e. heterodonty) than by size differences alone. Indeed, FUP-Pv 000109 is an anterior (premaxillary) caniniform, while FUP-Pv 000110 is a posterior molariform, so a certain degree of morphological variability can be expected. Additionally, the sampled notosuchian that shows the greatest degree of heterodonty and greater tooth volume is the sphagesaurid, which shows an even thicker enamel layer.

Thickness of von Ebner lines seems to vary in specimens of the same taxon, which may result from growth (ontogeny). Comparative data from the literature samples juvenile and adult *Tyrannosaurus* and *Edmontosaurus* (Table 3). In both cases, adults have thicker von Ebner lines than juveniles do. In contrast, ontogeny seems to play no role regarding von Ebner line thickness within Notosuchia, as baurusuchid and *Mariliasuchus* teeth show no variation regarding von Ebner line thickness between adults and ontogenetically younger individuals. Unfortunately, the literature on dental histology of crocodylomorphs is scarce and provide no comparative ontogenetic data on neosuchian tooth histology, so it is impossible to define if this feature is a phylogenetic characteristic of crocodylomorphs or just occurs in Notosuchia. In any case, notosuchians seem to show high and uniform dentin deposition through their entire lives, while non-avian dinosaurs seem to increase daily deposition as they grow.

Intraspecific variation in the number of von Ebner lines is expected in crocodylomorphs and dinosaurs, as tooth eruption is not synchronic in these groups, and it may occur while sampling different teeth from a single individual. The use of functional teeth with fully erupted crowns for histology tends to overcome this problem, so major shifts through ontogeny can be devised. Considering the non-avian dinosaurs available from the literature, intraspecific variation for *Tyrannosaurus* (264–933 lines) and *Edmontosaurus* (225–339) shows what seems to be evident changes through ontogeny, with younger specimens requiring substantially fewer days to produce fully erupted teeth. Baurusuchid teeth FUP-Pv 000104 and FUP-Pv 000108 are in line with this general claim, with a substantial variation between both specimens (58–146 lines).

Wear facets and diet

The teeth of baurusuchids have uneven wear facets, which reach the dentin. These wear facets are longitudinal with respect to crown length (e.g. have an apico-basal orientation), apparently caused by the orthal movement of occlusion. The teeth of *Mariliasuchus* and Sphagesauridae present horizontal wear facets on the lingual side of the maxillary teeth and on the labial side of the mandibular teeth, which have been considered as an evidence of chewing (Pol 2003; Andrade and Bertini 2008a; Augusta and Zaher 2019). These marks would have been caused by the antero-posterior (propalinal) movement of the mandible when processing food (Andrade and Bertini 2008a; Ösi 2013; Augusta and Zaher 2019).

Both Sphagesauridae and *Mariliasuchus* are regarded as crocodylomorphs that could chew their food (Pol 2003; Andrade and Bertini 2008a, 2008b; Ösi 2013; Pol et al. 2014; Augusta and Zaher 2019). So far, there is no conclusive evidence on which food items they feed on. However, the proportionally thicker enamel (see Table 1, Figures 2 and 4) observed in the Sphagesauridae tooth, mainly in the chewing portion, suggest that within advanced notosuchians (*sensu* Pol et al. 2014) the dentition could have been more adapted to heavy food processing of proportionally harder items, which conform either to abrasive plant material and/or the scavenging of large carcases.

It is important to highlight the congruence of histological data towards the interpretation of sphagesaurids as herbivorous crocodylomorphs. The results herein provide data on enamel thickness and von Ebner line thickness that are in agreement with this interpretation. *Mariliasuchus* remains in a somewhat intermediate situation. However, it is clear that *Mariliasuchus* does share morphological and dental histological features with sphagesaurids and this, at least in part, favours its interpretation as a taxon able to process plant material as part of its diet.

Conclusions

Our analyses on dental histological features of three notosuchians from the Adamantina Formation showed that in *Mariliasuchus*, a tooth took less than 2 months to be developed. On the other hand, in Sphagesauridae and Baurusuchidae, the tooth formation could take about 6 months to be completed, conforming to the expected time seen in neosuchian crocodylomorphs.

Sphagesauridae and *Mariliasuchus* have proportionally thicker enamel than Baurusuchidae. They also show strong evidence they could process food to a certain degree (presence of horizontal dental wear facets). The process of mastication implies more dental wear, as is effectively observed in *Mariliasuchus* and Sphagesauridae, and thicker enamel would prevent excessive teeth wear before replacement. However, the enamel thickness and its substantial development in the mid-to-posterior (chewing) teeth in Sphagesauridae confirm that advanced notosuchians are more adapted to process hard/abrasive food items than more basal forms like *Mariliasuchus*. In the same way, this indicates that both genera are clearly more adapted to food processing than baurusuchids.

Although closely related, the three notosuchians studied here show some variation in enamel thickness and number of dental daily growth lines (von Ebner lines), indicating different patterns of tooth growth. However, the thickness of the daily growth lines is virtually constant, varying from 24 to 25 µm, which differs from what is known for recent and fossil Neosuchia and even for dinosaurs, which generally have more and thinner daily growth lines (Table 3). This suggest that at least part of the notosuchian lineage may be characterised by proportionally thicker von Ebner lines and a high rate of daily deposition of dentin throughout most of their lives. Furthermore, tooth growth strategies in notosuchians clearly present important differences when compared to the growth strategies of neosuchian crocodylomorphs and dinosaurs.

Finally, when available for thin sectioning, the study of other types of teeth (e. g. caniniform and incisiform) will furnish more complete information on how this pattern of dentin deposition is restricted only to some types of teeth or present in the entire dental series of these notosuchians.

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