Dental histology of Cretaceous mosasaurs (Reptilia, Squamata): incremental growth lines in dentine and implications for tooth replacement

Johan Gren

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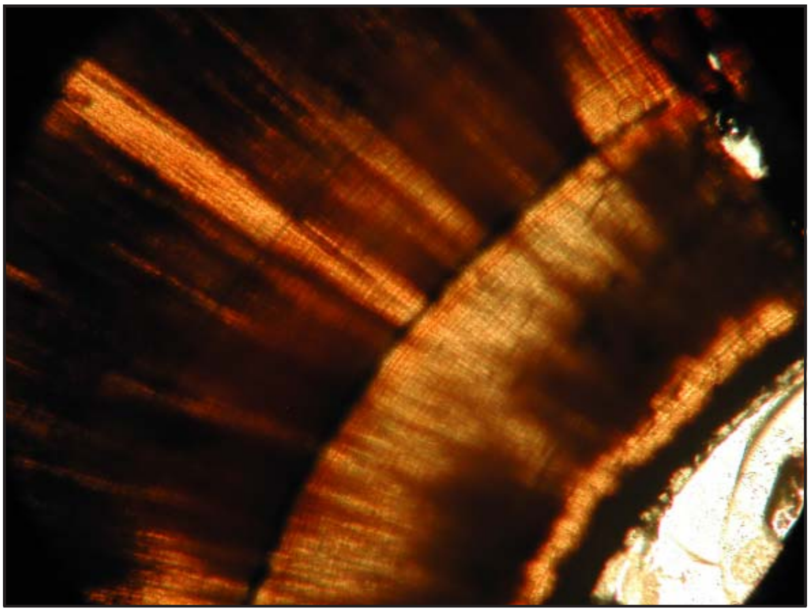

**Department of Earth- and Ecosystem Sciences
Division of Geology
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Contents

Cover picture: Incremental lines of von Ebner in *Dollosaurus* (*Prognathodon*) (JAG 0005 *t*), ×10 magnification. Field width = 2 mm.

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Abstract: The dentine of teeth from five genera of mosasaurs [i.e., *Clidastes, Halisaurus, Dollosaurus* (*Prognathodon*), cf. *Platecarpus*, and *Tylosaurus*] and a Mesozoic crocodylian (*Aigialosuchus*) from the Campanian of the Kristianstad Basin, southernmost Sweden, displays two types of incremental growth lines; i.e., von Ebner's and, for the first time in extinct animals, Andresen's lines. These lines are homologous to incremental growth lines found in the dentine of extant mammals and reptiles, as well as in the teeth of non-avian dinosaurs and extinct mammal-like reptiles, and are probably homologous for the entire Amniota. The incremental lines document different accumulation rates, where the lines of von Ebner are deposited daily and the Andresen's lines are deposited roughly every 7–8 day. Incremental lines were measured and counted to obtain replacement rate values for the teeth being analysed. For mosasaurs, the tooth replacement rates varied between 260 (*Platecarpus*) and 593 days (*Tylosaurus*), whereas the corresponding rate for the contemporaneous crocodylian *Aigialosuchus* was 240 days. The dentine accretion rates were similar to one another independent on phylogenetic relationship and tooth-size, to suggest that the tempo was genetically controlled rather than an effect of diet or habits. A replacement tooth was observed growing inside the functional *Aigialosuchus* tooth, thus providing evidence that tooth replacement was a continuous process where a germ tooth was always ready to replace an older one.

Keywords: Dental histology, mosasaurs, Cretaceous tetrapods, incremental lines, von Ebner, Andresen, tooth replacement

Johan Alfred Gren, Department of Earth and Ecosystem Sciences, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden. E-mail: johan.gren.mail@gmail.com

Tandhistologi hos kretaceiska mosasaurier (Reptilia, Squamata): tillväxtlinjer och implikationer för tandersättningsmönster

JOHAN ALFRED GREN

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Sammanfattning: Dentin i tänder från fem campanska mosasaurier [*Clidastes, Halisaurus, Dollosaurus* (*Prognathodon*), cf. *Platecarpus* och *Tylosaurus*] och en samtida krokodil (*Aigialosuchus*) som samlats in i Kristianstadbassängen, sydligaste Sverige, uppvisar två typer av tillväxtlinjer: von Ebnerlinjer och, för första gången hos utdöda djur, Andresenlinjer. Dessa linjer är homologa med de tillväxtlinjer som förekommer i dentin i tänder hos nutida däggdjur och reptiler, liksom i tänder från dinosaurier och utdöda däggdjursliknande reptiler, och är troligtvis homologa för alla amnioter. Tillväxtlinjerna representerar olika tillväxtrytmer, där en von Ebnerlinje tillkommer varje dygn medan en Andresenlinje bildas ungefär var 7:e till 8:e dag. Tillväxtlinjerna i de fossila tänderna mättes upp och räknades i syfte att beräkna den tid det tar för varje tand att nå funktionell storlek och därefter ersättas av en ny tand. Hos mosasaurierna varierade tändernas tillväxttid från 260 dagar (hos cf. *Platecarpus*) till 593 dagar (hos *Tylosaurus*), medan motsvarande hastighet i den samtida krokodilen *Aigialosuchus* var 240 dagar. Ackumulationshastigheten av dentin är till synes oberoende av såväl släktskap som tandstorlek, och reglerades således troligtvis av genetiska faktorer (istället för födoval eller djurens beteende). I den undersökta krokodiltanden växer en ersättningstand inuti den funktionella tanden, vilket visar att tänderna ersattes kontinuerligt.

Nyckelord: Tandhistologi, mosasaurier, kretaceiska tetrapoder, tillväxtlinjer, von Ebner, Andresen, tandersättning

Johan Alfred Gren, Institutionen för geo- och ekosystemvetenskaper, Lunds universitet, Sölvegatan 12, SE-223 62 Lund, Sverige. E-mail: johan.gren.mail@gmail.com

1 Introduction

The study of incremental growth lines is an effective way of assessing tooth development and replacement rates, even in extinct animals. These lines form through a cyclic accumulation of dentine (i.e., matrix deposition and mineralization occur alternately on a regular basis; see Nanci, 2008), similar to growth rings of trees (although the latter accumulate reversely), thereby providing a continuous record of the developmental stages of the tooth (Erickson, 1996a). Incremental markings also contribute to our understanding of those mechanisms underlying morphological change, and thus may be of importance in the fields of developmental and evolutionary biology (Dean, 2000).

Despite being observed already by Richard Owen in the mid-1800s (Owen, 1841, 1845), the importance of incremental growth lines was not fully appreciated at that time. Through more careful studies, primarily on human teeth (e.g., Andresen, 1898; von Ebner, 1902), two main types of incremental growth lines are now known; i.e., Andresen's and von Ebner lines. The 'long period' Andresen's lines are usually deposited in cycles of 5–8 days; these are usually interlayered by the short period lines of von Ebner, which are deposited on a daily basis (Hillson, 2005; Dean, 1995, 1998). Growth marks may be accentuated if the tooth suffers nutrition deficiencies or if the animal is subject to physiological stress during the time of tooth development, a phenomenon that may result in the so called 'contour lines of Owen' (Bhaskar, 1991; Nanci, 2008).

To study the incremental growth rate in dinosaur teeth, Erickson (1996a, p. 14624) argued that 'if the teeth of the fossil crocodylians (*i*) possessed comparable growth lines to those in dinosaur teeth and (*ii*) these growth lines were morphologically equivalent to those in extant crocodylians, it would suggest that the fossil crocodylian and dinosaur laminations were the result of a biologic process and not a product of diagenesis.' To test this hypothesis, Erickson (1996b) analyzed tooth replacement rates in *Alligator mississippiensis* and *Caiman crocodilus* through fluorochrome markings, and concluded that incremental lines in crocodylian dentine were deposited on a daily basis. The incremental lines were then compared to markings in the teeth of fossil crocodylians and dinosaurs, to demonstrate that they most likely reflect homology. In the present study, a tooth-crown from the Mesozoic crocodylian *Aigialosuchus* is used as a reference in line with the arguments presented above. The data obtained from the tooth are then compared to mosasaur (an extinct group of marine lizards, see below) teeth collected from the same area as the *Aigialosuchus* tooth to ascertain whether or not these incremental lines may be homologous also in mosasaurs. If mosasaur teeth (*i*) display incremental lines of von Ebner and/or Andresen's lines, and (*ii*) if these lines are morphologically similar to those observed in Mesozoic crocodylians (Erickson, 1996a), this would suggest a dentine accumulation process similar to that documented for modern crocodylians (Erickson, 1996b).

The squamate family Mosasauridae is subdivided into the subfamilies Mosasaurinae and Halisaurinae, and the parafamily Russellosaurina (Fig. 1). Most scholars (e.g., Russell, 1967; deBraga & Carroll, 1993; Luan *et al*., 2009) nest mosasaurs with Varanidae (which includes e.g., extant monitor lizards), whereas others (e.g., Lee, 1997) consider Mosasauridae to be more basal within the Squamata, closer to snakes. Mosasaurs first appear in the Cenomanian (Polcyn *et al*., 1999), and the group went through a significant radiation during the first half of the Late Cretaceous (Luan *et al*., 2009), becoming one of the most widespread groups of marine tetrapods of the Cretaceous (Bengtson & Lindgren, 2005). Derived mosasaurs were highly adapted to a marine life with e.g., a streamlined body shape and a two-lobed, hypocercal tail fin (Lindgren *et al*., 2010), and they preyed on fish, sea turtles and, occasionally, even on birds (Massare, 1987; Russell, 1967).

To withstand the stress inflicted on the teeth during feeding, mosasaurs and Mesozoic crocodylians (like most extant and extinct reptiles) continuously shed and replaced their teeth. The mosasaurian tooth replacement pattern is similar to that of modern reptiles, where the germ tooth is developed in a slightly inclined, upright position below the functional tooth, i.e., a thecodont tooth implantation (the teeth grow inside of, and are attached to, bony sockets) (Rieppel & Kearney, 2005). When a functional tooth has served its use, the pulp cavity seals and the tooth is shed. The stress exerted on the teeth while feeding can, however, lead to premature detachment, in which case

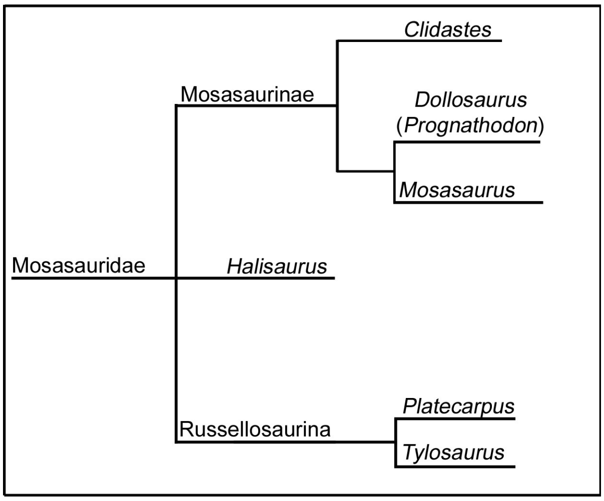

Fig. 1: Simplified cladogram showing the phylogenetic relationship within the family Mosasauridae (modified from Polcyn & Bell, 2005).

the pulp cavity will not be entirely sealed. The mosasaur tooth attachment is reviewed in detail by Lee (1997) and Zaher & Rieppel (1999). The crocodylian tooth attachment is thecodont as in mosasaurs. The replacement tooth-crown develops on the lingual side of the functional tooth, while the root of the latter is resorbed. Eventually, the replacement tooth migrates through the resorption gap into a position directly below the functional tooth, where it can grow laterally to full size. In extant crocodylians, such as the Nile crocodile (*Crocodilus niloticus*), it is not uncommon that two or three replacement crowns grow at the same tooth position simultaneously (Poole, 1961).

This study investigates dental microstructures in isolated, presumably shed marginal tooth-crowns (JAG 0001 *t*–0007 *t*) of five genera of mosasaurs (representing all sub- and parafamilies of Mosasauridae), including *Clidastes*, *Halisaurus*, *Dollosaurus* (*Prognathodon*), cf. *Platecarpus*, and *Tylosaurus*, collected from latest early Campanian (*sensu germanico*) strata of the Kristianstad Basin, southernmost Sweden. Incremental lines of von Ebner and Andresen are documented and quantified in an attempt to determine dentinal growth rates and tooth replacement rates. Possible reasons for differences of these parameters in relation to e.g., tooth-crown (and animal) size, prey preference and phylogeny are discussed.

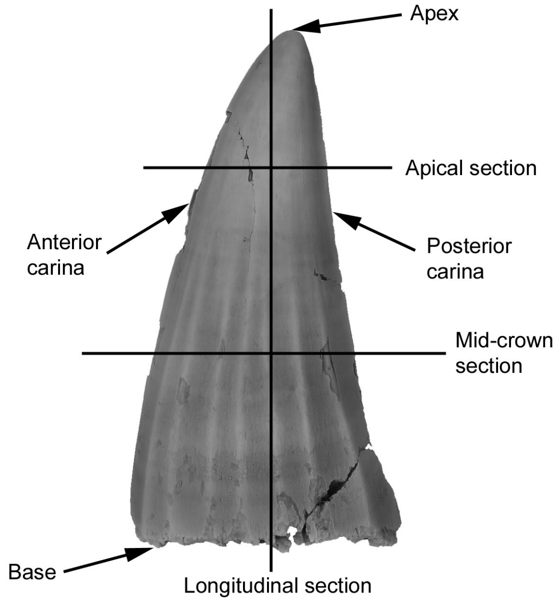

Fig. 2: cf. *Platecarpus* (JAG 0006 *t*) in labial view. Apex, base and carinae are marked, together with lines showing where the sections were taken. Note that a longitudinal section was made only for *Aigialosucus* (JAG 0001 *t*).

2 Materials and methods

The teeth examined herein derive from seven animals; five mosasaurs and two crocodylians. Figure 2 schematically shows the different parts of a mosasaur tooth. The specimens used were collected by Johan Lindgren (Lund University) from four localities; i.e., Ivö Klack (Blaksudden) (JAG 0002 *t*), Ugnsmunnarna (JAG 0007 *t*), Ullstorp (JAG 0001 *t*), and Åsen (JAG 0003 *t*–0006 *t*), all located within the Kristianstad Basin area, north-eastern Skåne, southernmost Sweden (Fig. 3). To the south the basin is confined by the Linderödsåsen and Nävlingeåsen horst ridges while the basin's northern boundary is irregular with several sediment outliers of Cretaceous age. The Cretaceous sediments deposited within the basin are predominantly shallow marine calcarenites and calcisilitites, but some terrigenous conglomerates and boulder beds also occur, particularly in marginal areas. The geological evolution and development of the marine Cretaceous of the Kristianstad Basin have been discussed at length by several authors (e.g., Christensen, 1975; Bergström & Sundquist, 1978; Lidmar-Bergström, 1982; Erlström & Gabrielson, 1986, 1992). Detailed locality information has been provided by e.g., Lindgren & Siverson (2002) and Lindgren *et al*. (2007).

Before being subject to histological analysis, all teeth were measured and photographed in labial ('lip-side') and lingual ('tongue-side') view (Table 1 and Fig. 4). In addition, moulds were made of all teeth using a two-component silicone rubber. Thereafter, the teeth were vacuum-embedded in epoxy resin and millimetre-thick cross sections were produced using a slow speed diamond saw (the specific location for each section is listed in Table 1). Additionally, a longitudinal section was constructed for JAG 0001 *t* (*Aigialosuchus*), because some studies (e.g., Erickson, 1996b) indicate that such sections may enhance the detail of dental microstructures, thereby facilitating estimations of tooth replacement rates. The sections were mounted with epoxy resin onto glass slides and then manually sanded with descending grits (600–1200 grit) to a thickness suitable for transmitted light microscopy (i.e., about 50–100 μm). The sections were then polished on a felt pad with aluminium oxide powder. The sections were studied under transmitted light microscopy at ×5–100 magnification, and photographs were taken at ×5–40 magnification. Histological characteristics were examined with particular focus on incremental line distribution, spacing and counts. Notes were made also on other possible growth marks, as well as on enamel thickness, size, shape, and frequency of odontocyte lacunae, and on the extent of mineral recrystallization and other taphonomic artefacts. Incremental lines in each section were mapped and identified based on spacing and morphology as lines of von Ebner, Andresen's lines and contour lines of Owen, in accordance with previous works (e.g., Bhaskar, 1991; Dean, 1995; 1998; Erickson, 1996a; 1996b; Nanci, 2008).

In each section, the longest sequence of consecutive lines of von Ebner and Andresen, respectively, was measured and a mean distance between the lines was calculated. These numbers were then extrapolated over the entire radius of the dentine to obtain estimated values of total dentine accumulation and thereby replacement time.

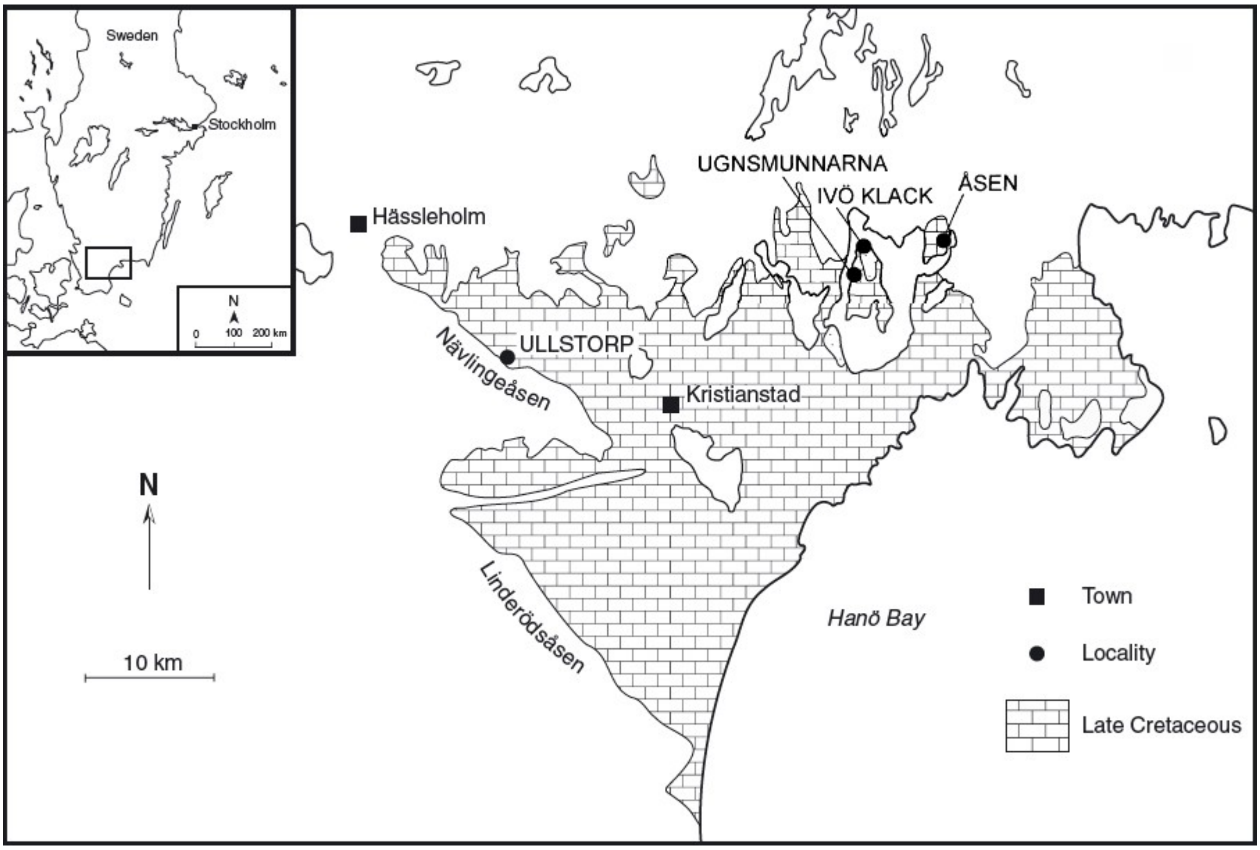

Fig. 3: Simplified geological map of southernmost Sweden, showing the location of the Kristianstad Basin and the localities from which the sampled teeth were collected (modified from Lindgren & Siverson 2002: fig. 1).

Table 1: Measurements of tooth-crowns, incremental line width, and calculated replacement rates of the sampled teeth.

Sample	Crown height (mm)	Crown width (mm)	Crown length (mm)	Cross section locations (mm from base, mid-crown; apical section)	Mean von Ebner increment line width (µm)	Mean Andresen increment line width (µm)	Calculated tooth replacement rate (days)
Aigialosuchus (JAG 0001 *t*)	9	8	6	5; 8	16.86	N/A	240
Aigialosuchus (JAG 0002 *t*)	13	9	8	9; 11	N/A	N/A	N/A
Clidastes (JAG 0003 *t*)	9	6	4	1; 3	N/A	N/A	N/A
Halisaurus (JAG 0004 *t*)	8	6	5	3; 6	N/A	N/A	N/A
Dollosaurus (*Prognathodon*) (JAG 0005 *t*)	23	16	14	8; 19	13.90	N/A	374
cf. *Platecarpus* (JAG 0006 *t*)	33	17	13	10; 23	14.96	111.1	260
Tylosaurus (JAG 0007 *t*)	45	31	25	21; 35	14.67	105.7	593

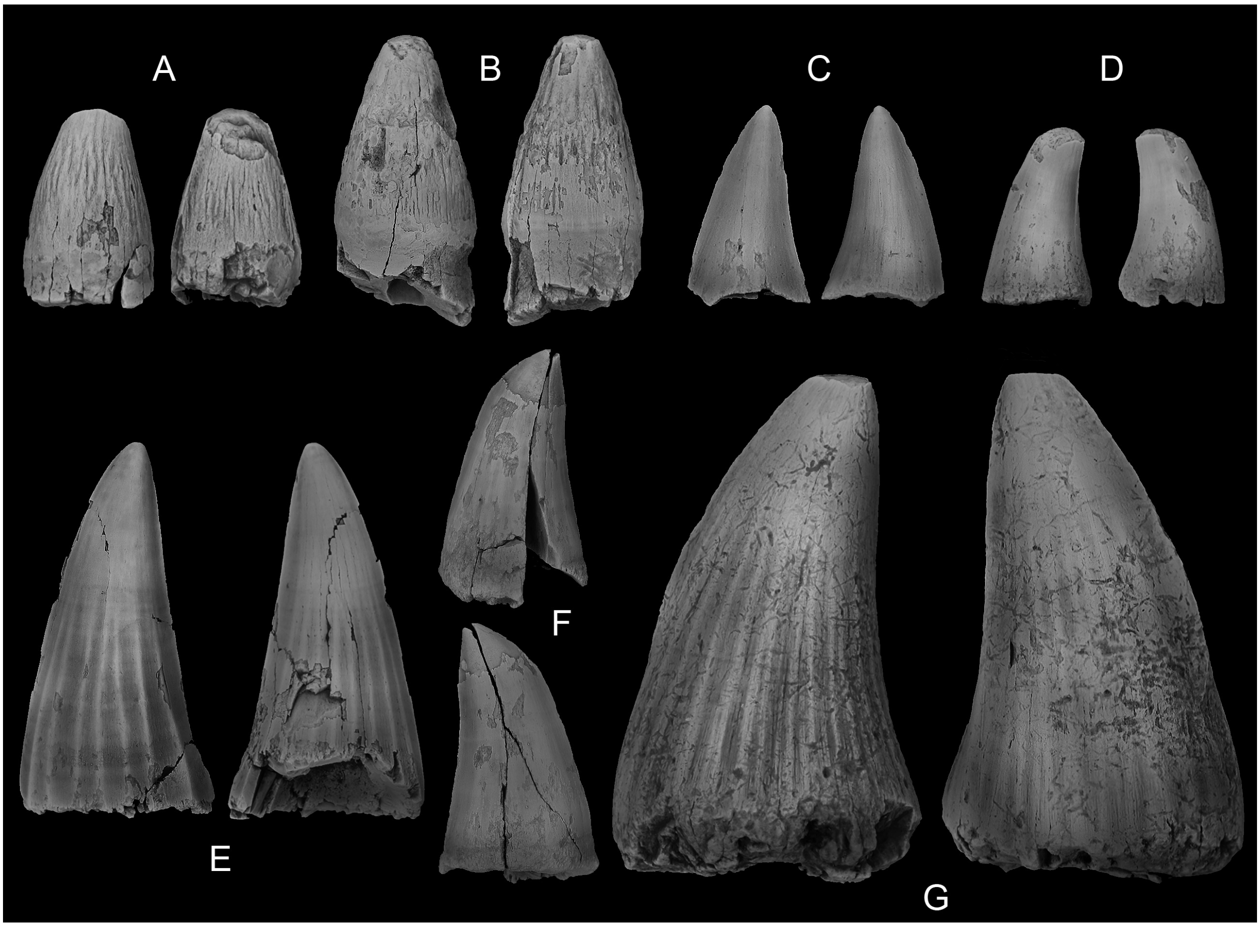

Fig. 4: Plate displaying all teeth included in the study. **A**, *Aigialosuchus* (JAG 0001 *t*), left: labial view, right: lingual view; **B**, *Aigialosuchus* (JAG 0002 *t*), left: labial view, right: lingual view; **C**, *Clidastes* (JAG 0003 *t*), left: labial view, right: lingual view; **D**, *Halisaurus* (JAG 0004 *t*), left: lingual view, right: labial view; **E**, cf. *Platecarpus*, (JAG 0006 *t*), left: labial view, right: lingual view; **F**, *Dollosaurus* (*Prognathodon*) (JAG 0005 *t*), top: lingual view, bottom: labial view; **G**, *Tylosaurus* (JAG 0007 *t*), left: lingual view, right: labial view. **A**–**D** in 300% and **E**–**G** in 150% of actual size.

3 Descriptions and results

3.1 *Aigialosuchus* (JAG 0001 *t*); Fig. 4, A

The tooth-crown is cone-shaped with a blunt, worn apex. It measures 9 mm in height and it is 8 mm wide at the base. The enamel-covered surfaces display distinct undulating and anastomosing striae that extend over the entire height of the crown. The labial face is substantially larger than the lingual one, and the partially sealed pulp cavity is elliptical, measuring about 2 × 1 mm in cross section.

Three histological sections were made; one close to the apex, one approximately at mid-crown height (i.e., about 6 mm from the base of the enamel) and a longitudinal one. In the apical section the enamel is ~200 µm thick and the entire surface measures about 4 mm in diameter. With the exception of some radially oriented fibre bundles and a few lacunae with their canaliculi, no original histological features are preserved in the dentine. Instead, most of the section is dominated by a fine network of thread-like canals which probably were made by bone boring bacteria or fungal hyphae. However, the enamel does not seem to have been affected by bacteria and here three incremental lines are visible.

The section taken at mid-crown height is also affected by bone-boring bacteria, especially in the peripheral parts of the dentine (Fig. 5). This section measures about 6.5 mm in diameter. Close to the pulp cavity dense fibre bundles extend from the centre and outward. These fibre bundles are perpendicularly intersected by a number of incremental lines of somewhat varying thickness and spacing. A strong line at ~1.2 mm (when measured perpendicularly from the pulp cavity) is surrounded by a layer of enamel, to suggest that it is part of a replacement tooth located inside the fully grown crown (Fig. 5; 6). About 50 of the innermost incremental growth lines are readily visible but farther from the pulp cavity the lines are more diffuse. The peripheral part of the section does not display any incremental growth lines, although fibre bundles are visible. 51 consecutive incremental lines of von Ebner were observed, with a mean spacing

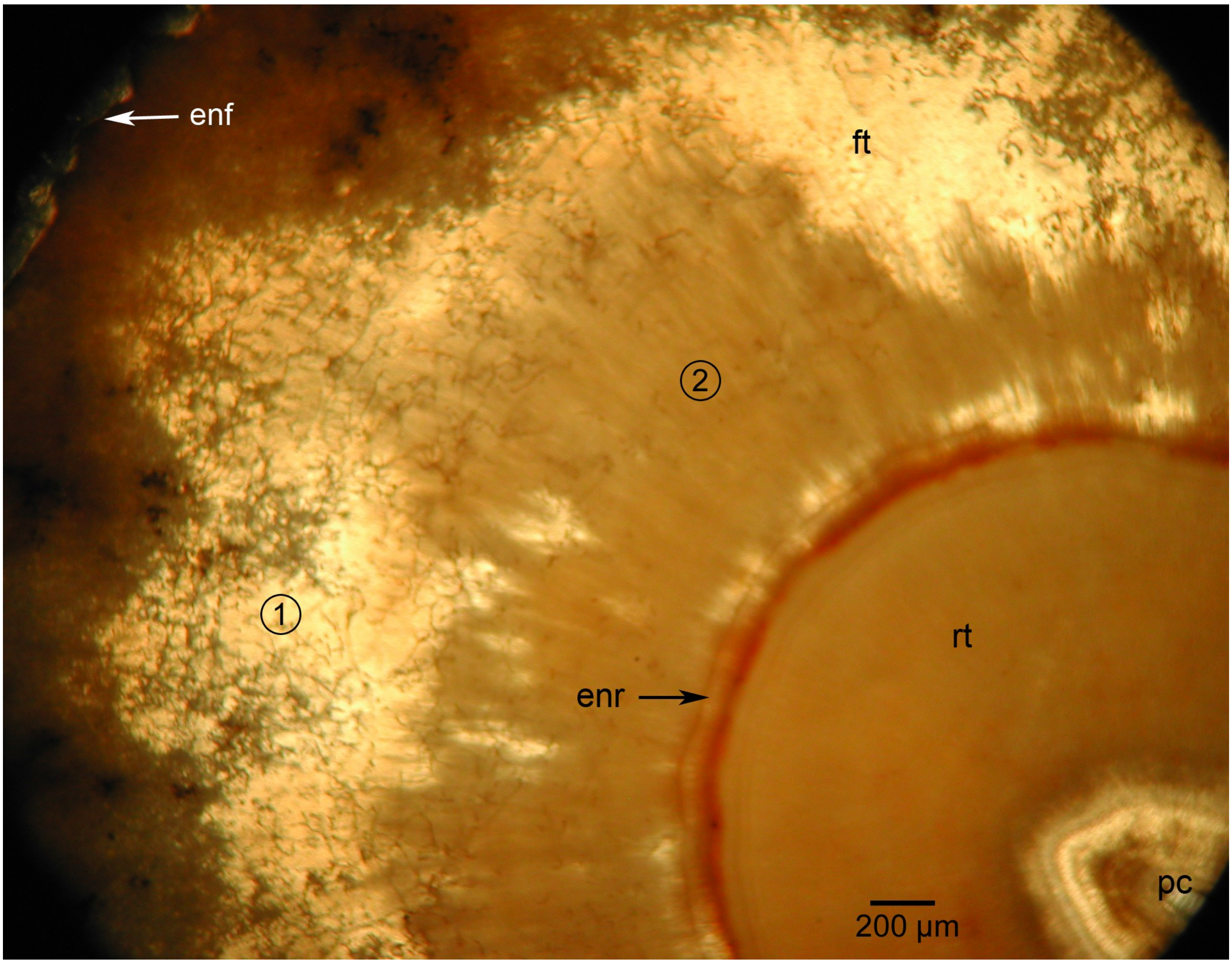

Fig. 5: Mid-crown section of an *Aigialosuchus* tooth-crown (JAG 0001 *t*), ×5 magnification. Bacterial activity obscure most of the original histological features in the functional tooth (area around **1**), although some fibre bundles (darker area, marked **2**) are present, radiating from section centre (ft, functional tooth; rt, replacement tooth; pc, pulp cavity; enf, functional tooth enamel; enr, replacement tooth enamel).

of 16.86 µm. All of these lines lie within the replacement tooth. By extrapolation, the replacement tooth contains a total of 91 lines, whereas the functional tooth contains 149 lines of corresponding spacing, totalling 240 lines of von Ebner in the entire section.

The 5.9 mm high longitudinal section provided no additional information to what is mentioned above, but corroborated the conclusion of a replacement tooth growing inside an older one (see Fig. 6).

3.2 *Aigialosuchus* (JAG 0002 *t*); Fig. 4, B

The tooth-crown is in the shape of a slightly curved cone. It is 13 mm high and 9 mm wide at crown base. Morphologically, the labial face is similar to the lingual one, although it is somewhat more convex. A weak striation extends over the enamelled surfaces from the apex to the base of the crown. The pulp cavity is circular in outline, measuring about 2.5 mm in diameter and it is not entirely closed, to suggest that the tooth was still in development when detached from the jaw.

Two cross sections were made; one close to the apex (measuring approximately 5 mm in diameter) and one approximately at mid-crown height (measuring about 8 mm in diameter).

The dentine is completely recrystallized and displays no original histological features (Fig. 7).

3.3 *Clidastes* (JAG 0003 *t*); Fig. 4, C

In lateral view, the tooth is roughly triangular, measuring 9 mm in height and 6 mm in maximum width. The labial and lingual faces are sub-equally convex and both carinae are sharp. Weak facets are present on the lower half of the crown, and the elliptical pulp cavity measures about 0.9 mm in diameter.

Two cross sections were made; one close to the apex (measuring about 3 mm in diameter) and one approximately at mid-crown height (measuring about 6 mm in diameter). Both sections reveal that the dentine is completely recrystallized and without any original histological features (Fig. 8).

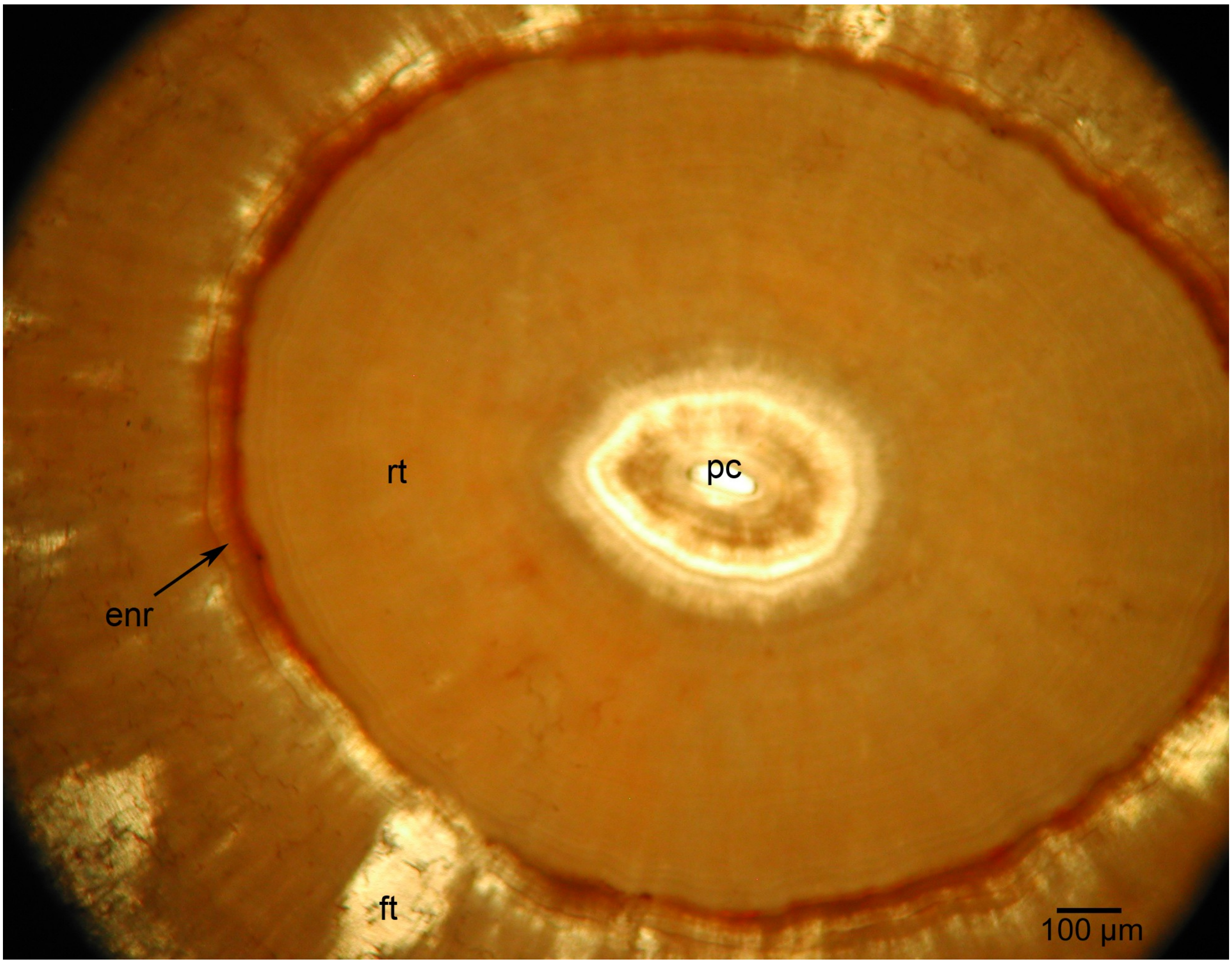

Fig. 6: Mid-crown section of an *Aigialosuchus* tooth-crown (JAG 0001 *t*), ×5 magnification. A layer of enamel separates the functional tooth from an intruding replacement tooth. Note the presence of incremental lines in the replacement tooth, whereas the dentine in the functional tooth is largely reworked through bacterial activity (ft, functional tooth; rt, replacement tooth; enr, replacement tooth enamel; pc, pulp cavity).

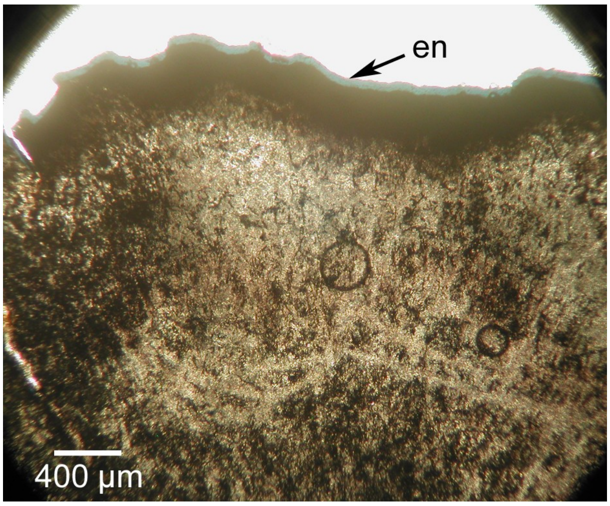

Fig. 7: Mid-crown section of an *Aigialosuchus* tooth-crown (JAG 0002 *t*), ×5 magnification. No original histological features are preserved due to the high recrystallization level of the tooth (en, enamel).

3.4 *Halisaurus* (JAG 0004 *t*); Fig. 4, D

The tooth is 8 mm high, 6 mm wide and is shaped as a blunt, curved cone with a heavily worn apex. The enamel is also partially abraded, particularly on the labial face. Thin, hairline striations run along the entire height of the crown, both on the lingual and the labial faces; however, the striae are more distinct on the basal half of the crown. The lingual and labial faces are roughly equal in convexity with slightly rounded carinae separating them from one another. The pulp cavity is elliptical with a diameter of about 1.5 mm.

Two cross sections were made; one close to the apex (measuring about 3 mm in diameter) and one approximately at mid-crown height (measuring about 5 mm in diameter). The dentine is completely recrystallized and displays no apparent original histological features (Fig. 9).

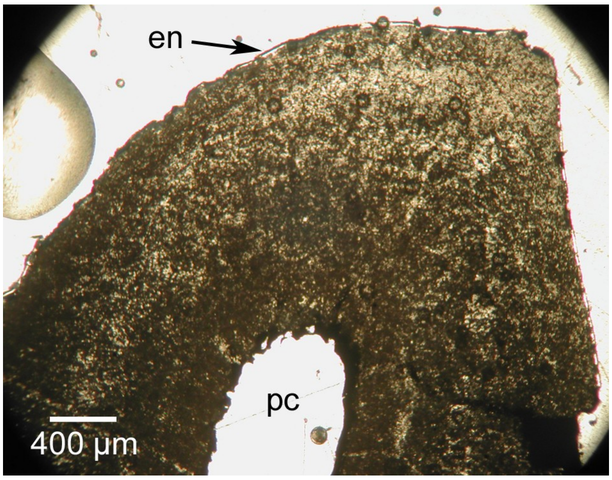

Fig. 8: Mid-crown section of Clidastes (JAG 0003 *t*), ×5 magnification. No original histological features are preserved due to the high recrystallization level of the tooth (en, enamel; pc, pulp cavity).

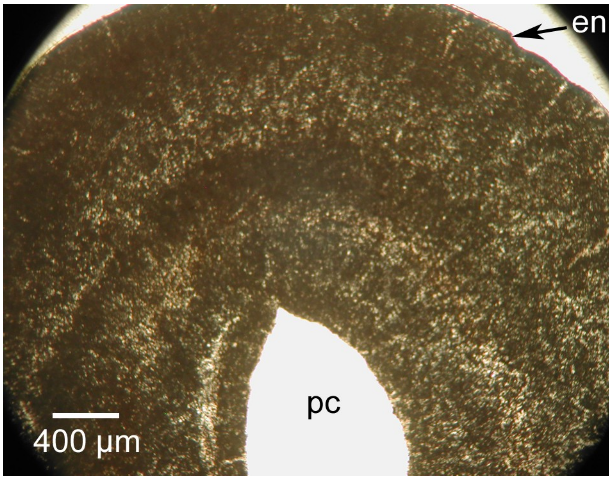

Fig. 9: Mid-crown section of *Halisaurus* (JAG 0004 *t*), ×5 magnification. No original histological features are preserved due to the high recrystallization level of the tooth (en, enamel; pc, pulp cavity).

3.5 *Dollosaurus* (*Prognathodon*) (JAG 0005 *t*); Fig. 4, F

The tooth is shaped as an elliptical, slightly curved cone with a sharp apex. It measures 23 mm in height and 16 mm in maximum width. Parts of the enamel, including the apical 6 mm, are worn off. Weak facets occupy both the lingual and labial faces. The lingual face is substantially larger than the labial one, and the carinae separating the two surfaces from one another are sharp. In some areas weak, wavy striations are visible. The pulp cavity has an elliptical outline with a diameter of about 6.5 mm.

Two cross sections were made; one close to the apex and one approximately at mid-crown height. The apical section is about 9 mm in diameter and preserves bundles of fibres radiating from the pulp cavity and outward. Several odontocyte lacunae are visible. These are elongated parallel to the fibre bundles and are seemingly devoid of canaliculi. Some incremental lines were observed perpendicular to the fibre bundles and lacunae. These growth lines are very faint, irregularly spaced and too few for a quantitative analysis. Several post-depositional cracks were observed, and close to these the dentine has been subject to bacterial activity which has destroyed many of its original features.

The section taken at mid-crown height is about 14 mm in diameter (Fig. 10). It is similar to the apical section; i.e., it displays multiple pronounced fibre bundles and elongated, radially oriented lacunae. However, the areas taphonomically affected by microorganisms are less abundant, and consequently this section is rich in incremental growth lines. These lines run perpendicular to the fibre bundles and are most pronounced in the inner half of the section where 77 consecutive lines of von Ebner with a mean spacing interval of 13.90 μm were observed. One of the lines, at about ~730 μm from the perimeter of the pulp cavity, is a particularly distinct contour line of Owen (Fig. 10). By extrapolation of the lines of von Ebner, the entire section holds a total of 374 growth lines.

3.6 cf. *Platecarpus* (JAG 0006 *t*); Fig. 4,E

The tooth is shaped as a slightly curved cone, and the labial and lingual faces are roughly equal in size with sharp carinae located in between. The tooth is 33 mm high and its maximum width is 17 mm. Both enamelled surfaces are distinctly faceted; eight facets are discernable on the labial face and nine facets are present on the lingual face. The facets are confined to the lower two thirds of the crown. Basally, fine striations run in between the facets, particularly on the lingual face. The elliptical pulp cavity measures about 8 mm in diameter, and is filled by secondary minerals. At least 10 irregularly distributed growth marks can be observed on the enamel surface (see Fig. 4, E).

Two cross sections were made; one close to the apex (measuring about 7 mm in diameter) and one approximately at mid-crown height (measuring about 14 mm in diameter). The apical section displays at least four incremental growth lines in the enamel. In the dentine, dense bundles of fibres radiate from the pulp cavity area. The section is rich in odontocyte lacunae with abundant canaliculi. The lacunae are oriented parallel to the fibre bundles. No incremental lines were observed in the dentine. Networks of channels originating from the activity of bone boring bacteria occur in places, primarily in the vicinity of taphonomically induced cracks.

The mid-crown section is rich in histological features (Fig. 11). The enamel displays three apparent incremental lines. As in the apical section, fibre bundles and lacunae occur frequently. The lacunae are elongated and some canaliculi are preserved. To a

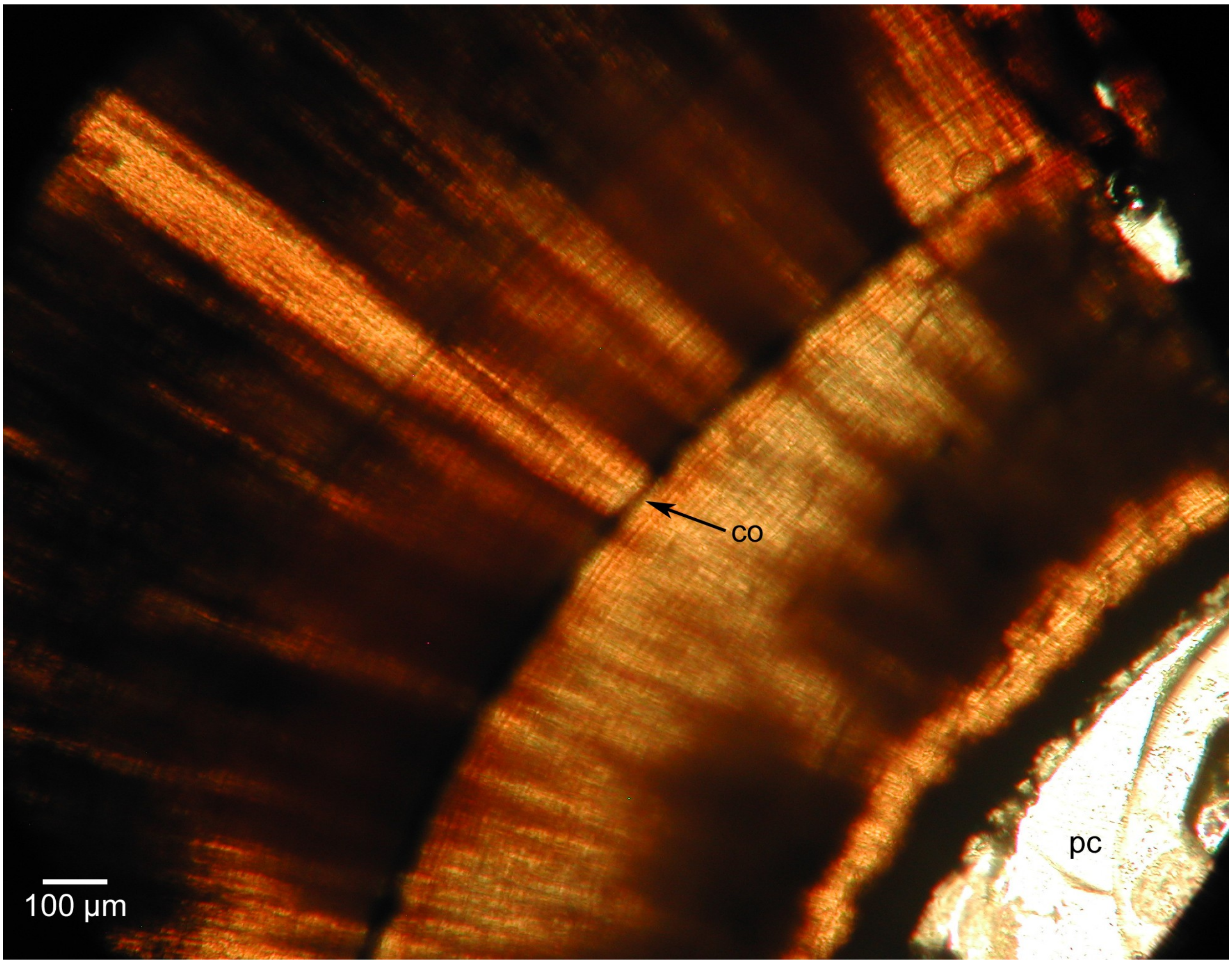

Fig. 10: Mid-crown section of *Dollosaurus* (*Prognathodon*) (JAG 0005 *t*) in ×10 magnification. Incremental lines of von Ebner are readily visible, running from upper right to lower left. About 730 µm from the pulp cavity a particularly distinct contour line of Owen is visible. A large amount of fibre bundles (darker areas) are radiating from the pulpcavity, perpendicularly crossing the incremental lines (co, countour line of Owen; pc, pulp cavity).

large extent the lacunae are concentrated to the peripheral 2 mm of the section, except for the outermost ~500 µm where large amounts of bacterial borings have intruded and destroyed most of the original features. Two different sets of incremental lines are observed in the dentine; one set of 9 Andresen's lines with a mean spacing of 111.1 µm, and a set of 67 lines of von Ebner, with a mean spacing of 14.93 µm (Fig. 11). When extrapolated over the section radius this would give the tooth a total of 260 lines of von Ebner and one Andresen's line for every 7–8 line of von Ebner.

3.7 *Tylosaurus* (JAG 0007 *t*); Fig. 4, G

Substantially larger than the other tooth-crowns examined in this study (45 mm high and 31 mm wide), JAG 0007 *t* is slightly curved with the enamel being damaged in places. Moreover, the apex is blunt due to extensive abrasion. Both enamelled surfaces are faceted and basal striae are present on the lingual face. The carinae are sharp without apparent serrations, although these may have been lost during occlusion and/or abrasion. The lingual face is more convex than the labial one. The apical 13 mm of the crown is slightly darker in colour than the rest of the tooth and has a somewhat smoother surface texture. The partly sealed pulp cavity is strongly elliptical, measuring about 13 × 8 mm.

Two cross sections were made; one close to the apex (measuring about 16 mm in diameter) and one approximately at mid-crown height (measuring about 23 mm in diameter). In the apical section, the enamel contains six distinct incremental growth lines. Numerous lacunae are preserved, and these are elliptical in the peripheral parts of the section and more rounded near its centre. No canaliculi are visible. Scattered bundles of collagen fibres radiate from the pulp cavity. These are perpendicularly intersected by a continuous set of 67 incremental lines with an average spacing of about 20.0 µm (Fig. 12). Additionally, a few wider spaced lines appear scattered over the section, roughly 100–300 µm apart. These are most

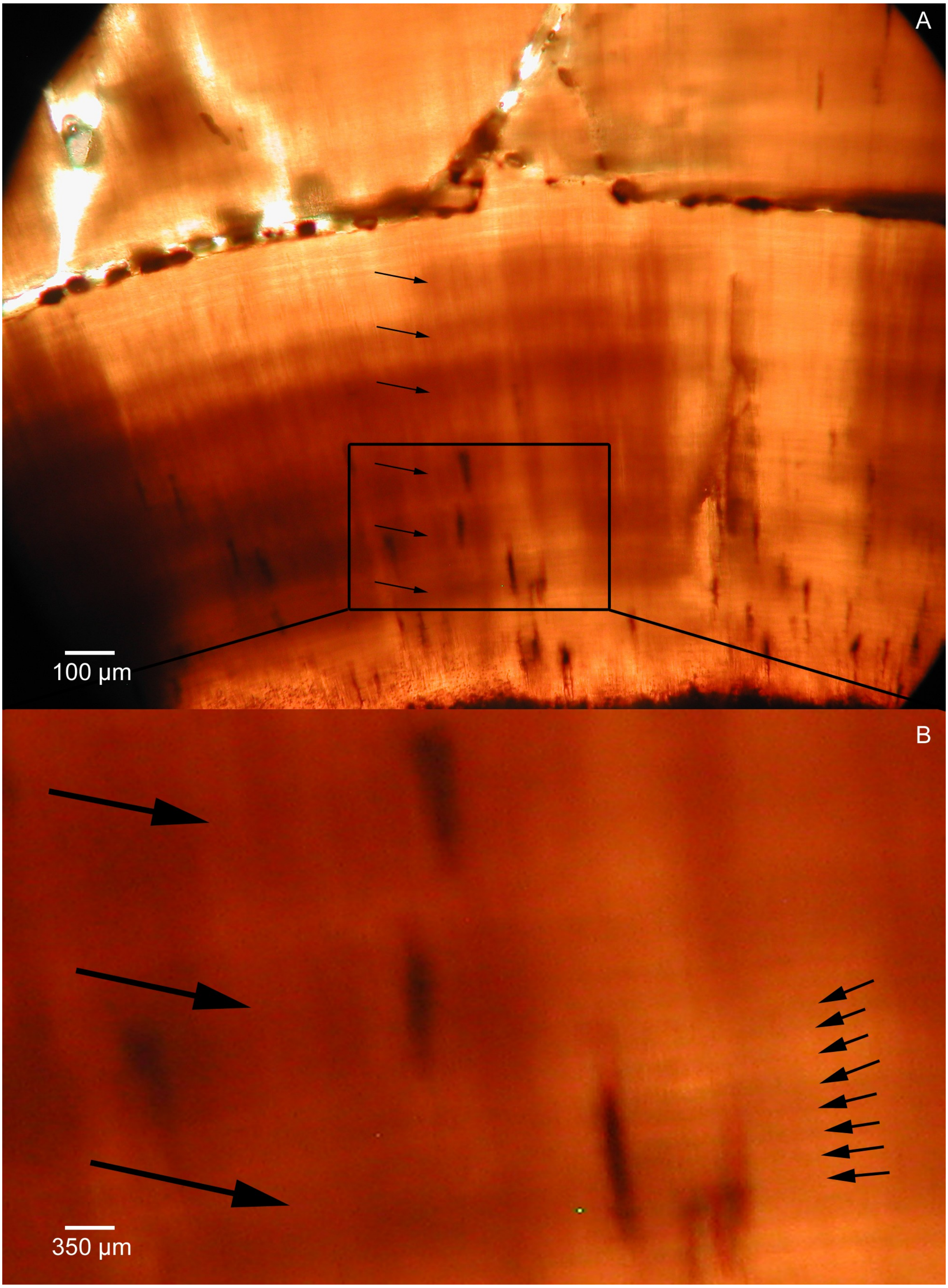

Fig. 11: Mid-crown section of cf. *Platecarpus* (JAG 0006 *t*) in ×10 magnification. **A**, Arrows mark six of the distinct Andresen's lines documented in this section, running from left to right, spaced roughly 100–150 µm apart. Perpendicular to these, fibre bundles are readily visible. **B**, Each pair of Andresen's lines (large arrows) is interlayered by 7–8 lines of von Ebner (small arrows). Elongated odontocyte lacunae are visible as darker, elliptic areas.

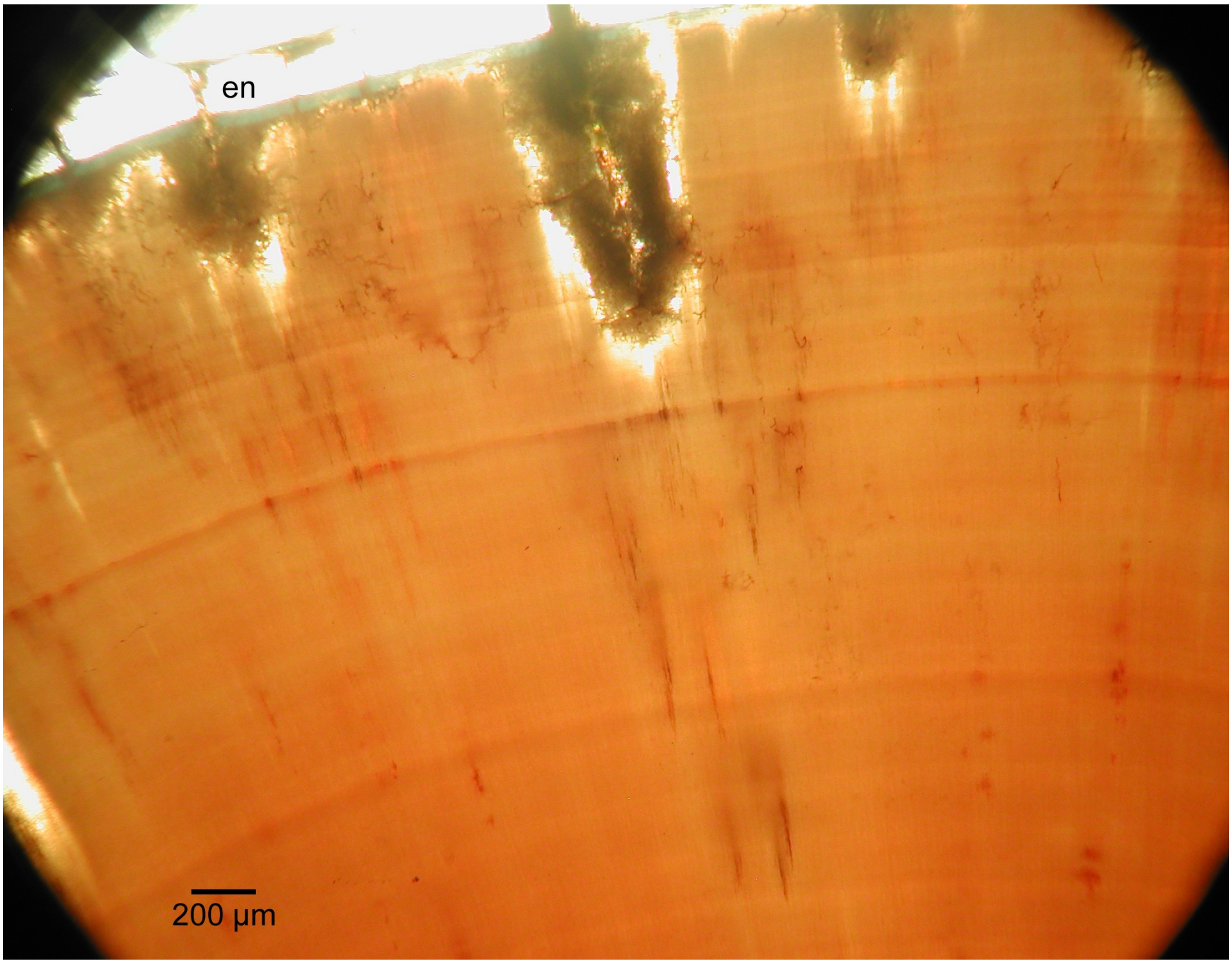

Fig. 12: Apical section of a *Tylosaurus* tooth-crown (JAG 0007 *t*), ×5 magnification. The dentine is rich in von Ebner lines (about 100 are observable in the photograph above), spaced some 20 µm apart, running from the left to the right (en, enamel).

pronounced near the middle of the section. Evidence of bacterial activity occurs in the outermost parts of the crown, limiting the amount of observable original histological features.

In the mid-crown section only one distinct incremental line is visible in the enamel. Instead, bacterial networks fill the peripheral 1.3 mm of the section. The lacunae are more elliptical in the peripheral parts than are those close to the pulp cavity. A number of the lacunae have their canaliculi preserved. In the dentine, a set of at least 7 pronounced Andresen's lines (Fig. 13) with a mean spacing of 105.7 µm are observed close to the pulp cavity. Additionally, there is a set of 45 lines of von Ebner spaced at a mean distance of 14.67 µm. Extrapolating this, the entire section would originally have held 593 lines of von Ebner, with one Andresen's line for every 7–8 line of von Ebner. The lines gradually fade about halfway from the centre of the section but reappear close to the periphery of the crown with the same pattern of coarser lines interspaced by 7–8 narrower ones.

4 Discussion

Most non-mammalian vertebrates continuously replace their teeth as an irregular bite may result in incapability to consume prey (Kline & Cullum, 1984). It is not known what mechanisms underlie the rate of this replacement; however, in a study of the green iguana (*Iguana iguana*), Kline & Cullum (1984) concluded that an increase in size and age of the animal increases the lifespan of the teeth. Erickson (1996b) also points out that for crocodylians, tooth replacement rates tend to slow down during the latter parts of their ontogeny. The deposition of primary dentine takes place close to the pulp cavity and this is also where the dentine formation rate is maximal (Dean, 1998). von Ebner lines in extant mammal (Nanci, 2008) and crocodylian (Erickson, 1996b) teeth form through a circadian rhythm of accumulation and mineralization of dentine, and incremental growth lines of mosasaurs and extinct crocodylians presumably were deposited in a similar way. In humans and primates, Andresen's lines readily appear with a spacing of about 20–30 µm, whereas the lines

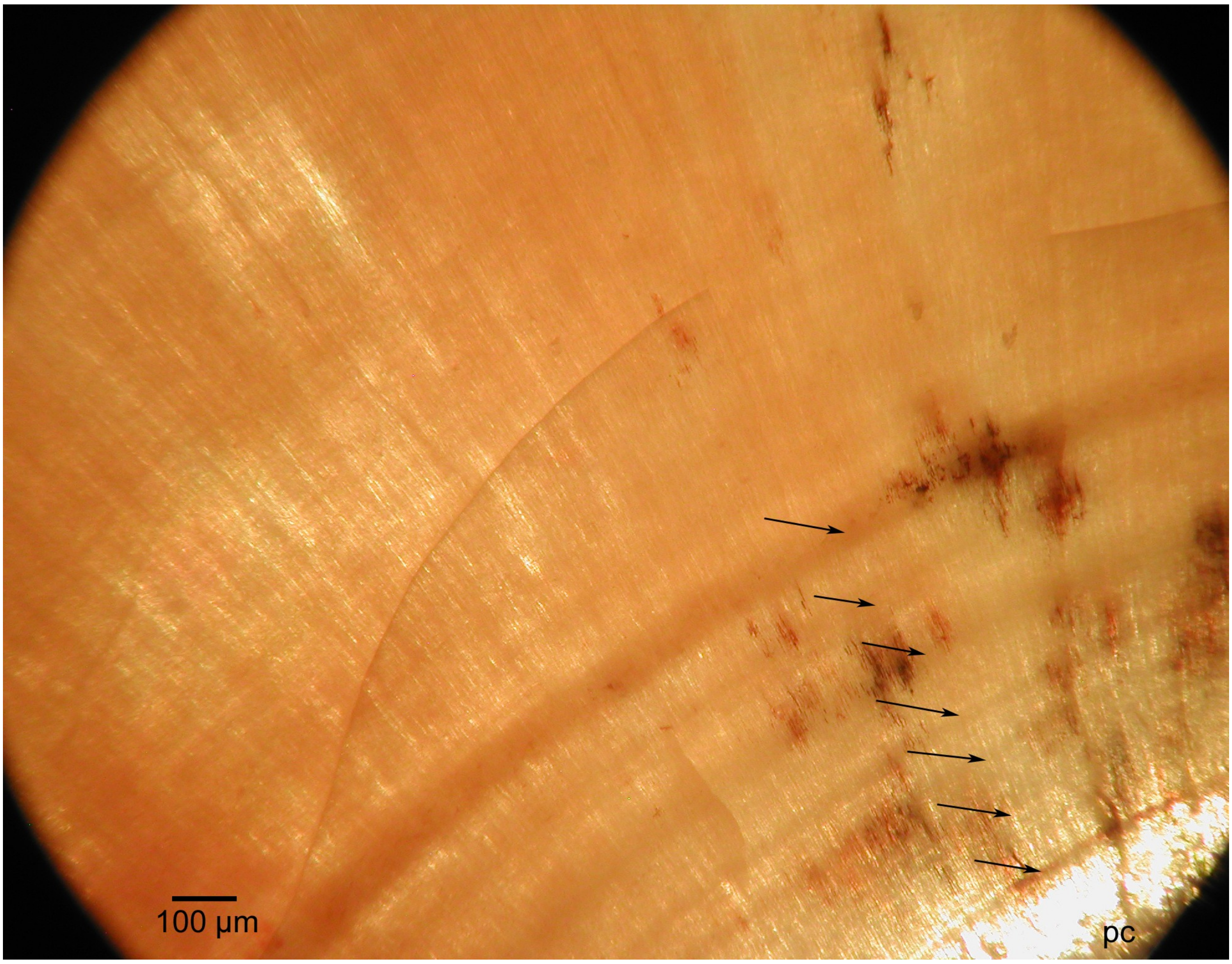

Fig. 13: Mid-crown section of a *Tylosaurus* tooth-crown (JAG 0007 *t*), ×10 magnification. Arrows show seven Andresen's lines about 100 µm apart. Farther from the pulp cavity the Andresen's lines are more diffuse. Between each pair of these lines, 7–8 less distinct lines of von Ebner occur (pc, pulp cavity).

of von Ebner are usually situated about 2–4 µm apart. In fast growing regions of some mammal teeth, however, spacing intervals of up to 16 µm between individual lines of von Ebner have been recorded (Dean, 1995). Erickson (1996a) documented a spacing that ranged from 10 to 20 µm among certain dinosaur taxa. For mosasaurs, the only published data on incremental growth lines are on the teeth of the Late Cretaceous *Mosasaurus hoffmanni* (Chinsamy *et al*., 2010). In that work, the authors conclude that a tooth with a dentinal layer of approximately 5.57 mm grew in 511 days, which corresponds to a daily incremental growth of about 10.9 µm.

The present study documents incremental growth lines of von Ebner and Andresen in marginal teeth of the mosasaur genera *Dollosaurus* (*Prognathodon*), cf. *Platecarpus* and *Tylosaurus*, as well as in the contemporary marine crocodylian *Aigialosuchus* (taphonomic artefacts precluded determination of growth lines in *Halisaurus* and *Clidastes*). Comparable studies of other extinct tetrapods, such as dinosaurs and crocodylians (e.g., Erickson, 1996a), suggest that von Ebner-like incremental markings are the results of physiologic processes and not a product of fossilization or taphonomy. Morphologically, the growth lines observed in the mosasaur tooth-crowns are indistinguishable from those described by Erickson (1996a, 1996b) to suggest homology. This is corroborated by the fact that Kamiya *et al.* (2006) documented incremental lines of von Ebner in the dentine of a mammal-like reptile (Tritylodontidae), which would suggest homology for the entire Amniota (see also Erickson, 1996b).

The observed lines of von Ebner show an average daily growth of 13.90 µm in *Dollosaurus* (*Prognathodon*), 14.67 µm in *Tylosaurus* and 14.93 µm in cf. *Platecarpus*. The daily growth in the dentine of the *Aigialosuchus* tooth was slightly higher, with an average incremental growth of 16.86 µm/day. This number is somewhat below that documented in the crocodylian *Leidyosuchus* by Erickson (1996a), which showed a mean increment width of about 19.0 µm.

The similar spacing of the lines of von Ebner, even in different-sized teeth (Table 1) and between different genera, attests to a genetically controlled rhythm rather than an ecological effect, such as prey selection or habitat. This also speaks against the daily incremental growth rate being dependant on the size of the animal (and of the tooth). The daily incremental growth of the *Dollosaurus* (*Prognathodon*) tooth (present study) and the *Mosasaurus hoffmanni* tooth (Chinsamy *et al*., 2010) is slightly below that recorded for cf. *Platecarpus* and *Tylosaurus*. As *Dollosaurus* (*Prognathodon*) and *Mosasaurus* are more closely related to one another than either are to cf. *Platecarpus* and *Tylosaurus* (Fig. 1; see Polcyn & Bell, 2005), this suggests the possibility of phylogenetic differences between mosasaurine and russellosaurine mosasaurs.

Unfortunately, none of the teeth examined preserved a continuous record of von Ebner's lines because of taphonomy and/or recrystallization. Extrapolation of the measured incremental lines of von Ebner in relation to the total dentinal layer suggests, however, that the teeth grew for 260 days in cf. *Platecarpus*, 374 days in *Dollosaurus* (*Prognathodon*), 593 days in *Tylosaurus*, and for 240 days in *Aigialosuchus* before being replaced. Judging by the size and shape of the pulp cavity, the *Dollosaurus* (*Prognathodon*) and cf. *Platecarpus* teeth were not fully developed when detached from the jaw, and these numbers should thus be treated as minimum values for tooth replacement rates, whereas the *Aigialosuchus* and *Tylosaurus* teeth appear to be shed as fully grown. The tooth-crowns of *Tylosaurus* and *Dollosaurus* (*Prognathodon*) display considerably more abrasion than do that of cf. *Platecarpus*, which had a faster tooth replacement rate based on the incremental line count. This suggests that a slower replacement rate inevitably leads to more abrasion, although the differences in apical wear could also be related to prey choice.

In addition to the incremental lines of von Ebner, Andresen's lines were observed in the tooth-crowns of cf. *Platecarpus* and *Tylosaurus*. Andresen's lines have hitherto not been documented in teeth of extinct animals, but morphologically the mosasaurian incremental lines are remarkably similar to those described in human and other mammalian teeth (e.g., Dean, 1998; Kierdorf *et al*., 2009). Although slight variations occur in the width of the increments of respective teeth, these growth lines appear to be deposited at similar rates throughout tooth development, as the mean line spacing is roughly equal for each tooth independent of distance to the pulp cavity. The Andresen's lines observed in cf. *Platecarpus* (with a mean spacing of 111.1 µm) and *Tylosaurus* (with a mean spacing of 105.7 µm) appear once for every 7th or 8th line of von Ebner, indicating depository rhythms similar to those of humans and primates (Dean, 1998). However, if these numbers can be linked to a genetically inherited rhythm (i.e., daily deposition of lines of von Ebner and roughly weekly deposition of Andresen's lines) homologous for both mammals and reptiles is hard to assess, as the sample size is small and because previously documented data on Andresen's lines derive from very distantly related animal groups (e.g., humans and primates; [Dean 1995, 1998] pigs; [Kierdorf *et al*., 2009]). Notable is that although the depository rhythms are alike, the amount of dentine accumulated every day is between 5–10 times higher in mosasaurs than it is in humans (Dean, 1995), which consequently would suggest that the tooth as a whole grew 5–10 times faster in the former animals. This is a credible number, given that mosasaurs, as opposed to humans, continuously shed their teeth.

Apart from the von Ebner and Andresen rhythms, the sectioned *Dollosaurus* (*Prognathodon*) tooth displays an accentuated incremental line (a 'contour line of Owen', Fig. 10; see Bhaskar, 1991; Nanci, 2008), indicating that the animal may have been subjected to some kind of stress during the time of tooth development.

The sectioned *Aigialosuchus* (Ullstorp) tooth displays a replacement tooth located inside an older one (Figs. 5; 6). Although no lines of von Ebner are preserved in the mature tooth, extrapolation of the incremental growth rate in the replacement tooth shows that the 91-day old replacement tooth started accumulating dentine already when the functional tooth was less than 150 days old. The pulp cavity of this tooth is only partially sealed, suggesting it may have been lost while feeding. The functional tooth was thus not shed until the replacement tooth had reached a sufficient size and was ready to fully replace the old one, providing the animal with a constant set of functional teeth. This is well in agreement with the tooth replacement strategy of both extant and extinct archosaurs (see Erickson, 1996a, 1996b).

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