Dental histology of mosasaurs and a marine crocodylian from the Campanian (Upper Cretaceous) of southern Sweden: incremental growth lines and dentine formation rates

JOHAN A. GREN* & JOHAN LINDGREN

Department of Geology, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden

Abstract – Mosasaurs are an extinct group of secondarily adapted aquatic lizards that became the dominant marine tetrapods in the Late Cretaceous oceans. They continuously shed and replaced their teeth in order to maintain a functional dentition at all times; however, the process of tooth development in mosasaurs is still incompletely known. Based on incremental line width measurements and growth line counts, we assess dentine formation rates in three mosasaur taxa (*Dollosaurus*, cf. *Platecarpus* and *Tylosaurus*) and one genus of marine crocodylian (*Aigialosuchus*), all from the lower Campanian (Upper Cretaceous) of southernmost Sweden. Two sets of periodic dentinal markings characterized by concentric, alternating opaque and transparent laminae are recognized: one set comprising thin bands situated 6–34 µm apart (depending on taxon), which is superimposed onto a second set of coarser bands where spaces vary between 102 and 275 µm. Assuming that the finer striations represent daily increments (i.e. lines of von Ebner), it is estimated that the deposition of dentine at the sectioned level of the tooth-crowns took 342 (cf. *Platecarpus*), 426 (*Dollosaurus*), 487 (*Tylosaurus*) and 259 (*Aigialosuchus*) days, respectively. The coarser bands contain between 11 and 13 thin striations each, and are thus considered to be homologous to similar periodic dentinal markings in extant vertebrates, i.e. Andresen lines. Prolonged tooth development times in large-toothed taxa, such as *Tylosaurus*, presumably increased the risk of long-term incapacity to capture prey after dental trauma, an evolutionary trade-off which may have been compensated for by allometric modifications of the teeth.

Keywords: Andresen, dentine, histology, increments, Mosasauridae, teeth, von Ebner.

1. Introduction

In most living reptiles, teeth are continuously shed and replaced to ensure a regular bite and a lifelong capability to engulf prey (Richman & Handrigan, 2011). However, the process of tooth development in many fossil reptilian groups has only recently become a topic of study (Erickson, 1996*a*; Zaher & Rieppel, 1999; Rieppel & Kearney, 2005; Caldwell, 2007; Chinsamy, Tunoğlu & Thomas, 2010, 2012). Hence, in order to gain a deeper understanding of the odontogenesis in Mosasauridae, a speciose family of secondarily aquatic lizards that became the dominant marine tetrapods in the Late Cretaceous about 98–66 million years ago, we examined periodic dentinal markings in a small number of isolated marginal tooth-crowns collected from the marine Cretaceous of southern Sweden.

Examination of incremental growth lines is an effective method of assessing dentine formation rates and tooth development times in both extant and extinct vertebrates (e.g. Erickson, 1996*a* and references therein). Incremental markings form through periodic alterations in collagen fibre trajectories and/or variations in the mineralization process (Kawasaki, Tanaka & Ishikawa, 1980; Bhaskar, 1991; Erickson, 1996*b*;

Nanci, 2008), thereby providing a continuous and often permanent record of the odontogenesis (Erickson, 1996*a*). Such increments also contribute to our understanding of those mechanisms that underlie morphological change (Dean, 2000), and are thus of importance in the scientific fields of developmental and evolutionary biology.

Despite being illustrated already in the mid-1800s by Richard Owen (1841, 1845; see Erickson, 1996*a*), the importance of dentinal laminations was not recognized until the works of Andresen (1898) and von Ebner (1902, 1906). These latter authors described concentric striations in the teeth of humans and other primates that are now being referred to as incremental lines of von Ebner and Andresen, respectively (e.g. Dean & Scandrett, 1996). Long-period Andresen lines are spaced between 4 and 14 days apart owing to endogenous biorhythms (Kawasaki, Tanaka & Ishikawa, 1980; Dean & Scandrett, 1996; Dean, 2000), and usually contain short-period lines of von Ebner, where the distance between each lamination represents the daily secretion of dentine (Bhaskar, 1991; Dean, 1995, 1998; Dean & Scandrett, 1996; Hillson, 2005).

Using periodic chemical (i.e. fluorochrome) labelling, Erickson (1996*b*) was able to determine the rate and duration of dentine secretion in the modern crocodylians *Alligator mississippiensis* and *Caiman crocodilus*. Moreover, by counting and measuring
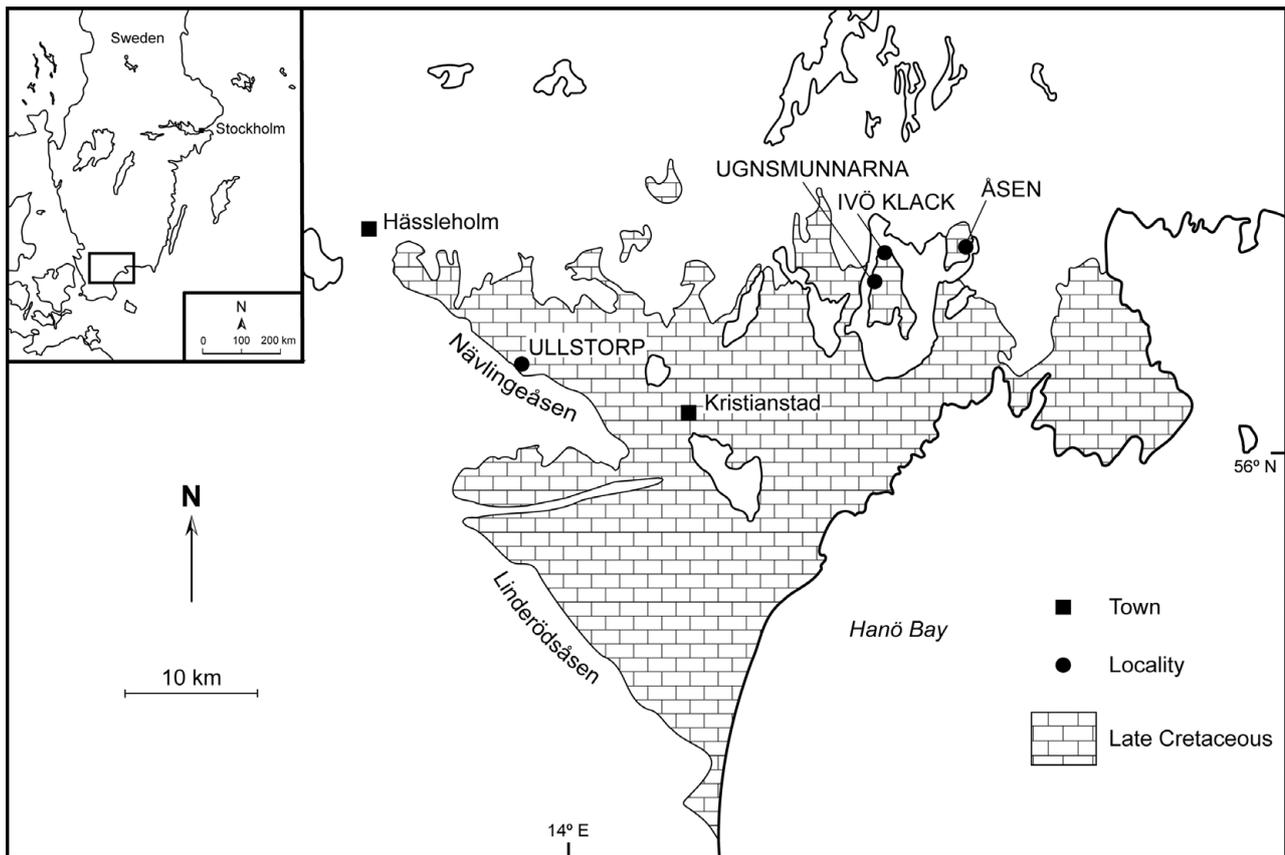
*E-mail: johan.gren@geol.lu.se

Figure 1. Geological map of southernmost Sweden showing the location of the Kristianstad Basin in the northeastern corner of the province of Skåne and the localities from which the analyzed teeth were collected (modified from Lindgren & Siverson, 2002, fig. 1).

the increments laid down between the fluorochrome injections, he (Erickson, 1996*b*) demonstrated that these laminations form on a daily basis (as they do in most amniotes; e.g. Erickson, 1996*a*, *b*; Kamiya *et al*. 2006; Nanci, 2008; Kierdorf *et al*. 2009). Subsequently, Erickson (1996*a*) broadened his investigation to also include Mesozoic crocodylians and nonavian dinosaurs. Comparable markings were found in the fossilized teeth of both groups, to suggest homology given their close phylogenetic relationship (Erickson, 1996*a*). More recently, Chinsamy, Tunoğlu & Thomas (2010, 2012) demonstrated the presence of periodic dentinal increments in a tooth-crown of the derived mosasaur *Mosasaurus hoffmanni*, and building on Erickson's (1996*a*, *b*) model, they estimated that it took 511 days to deposit the dentine at the level of sectioning.

In the present contribution, concentric laminations observed in histological sections of three isolated mosasaur teeth (assigned to *Dollosaurus* sp., cf. *Platecarpus* and *Tylosaurus ivoensis*, respectively) from the Kristianstad Basin, southernmost Sweden, are compared to morphologically similar markings in a tooth-crown of the marine crocodylian *Aigialosuchus* sp. collected from the same area. We begin with a description of various microstructural features that have previously been used to determine crocodylian and mosasaur dentine secretion rates (see Erickson 1996*a*, *b*; Chinsamy, Tunoğlu & Thomas, 2010, 2012). We then estimate the time it took to develop the dentine at the level of

sectioning. Finally, we conclude with a brief discussion on tooth development times and replacement rates in mosasaurs.

2. Geological setting

The Cretaceous deposits of the Kristianstad Basin *sensu* Erlström & Gabrielson (1992) are bordered to the southwest by the Linderödsåsen and Nävlingeåsen horst ridges, whereas the northern demarcation is more diffuse with several outliers of marine strata of Campanian–Maastrichtian age (Fig. 1). The Cretaceous sediments comprise primarily shallow marine calcarenites, calcisilitites and calcareous sandstones, although terrigenous material in conglomerates and boulder beds indicates that nearby land served as important source areas (Christensen, 1975). For more comprehensive descriptions of the geology, development and depositional environments of the Kristianstad Basin, see Christensen (1975), Bergström & Sundquist (1978), Lidmar-Bergström (1982) and Erlström & Gabrielson (1986, 1992).

With the exception of a single *Aigialosuchus* sp. tooth (LO 11621 *t*) from the lowermost Campanian (*Gonioteuthis granulataquadrata* belemnite Zone, Ullstorp site; see Erlström & Gabrielson, 1986 and Siverson, 1993 for locality information), all fossils examined herein were collected from strata representing a narrow stratigraphic interval (i.e. the informal

Table 1. Measurements and section locations of sampled tooth-crowns

Taxon	Crown height (mm)	Crown width (mm)	Crown length (mm)	Section locations (mm from base, mid-crown; apical section)
Aigialosuchus sp. (LO 11621 *t*)	9	8	6	5; 8
Dollosaurus sp. (LO 11622 *t*)	23	16	14	8; 19
cf. *Platecarpus* sp. (LO 11623 *t*)	33	17	13	10; 23
Tylosaurus ivoensis (LO 11624 *t*)	45	31	25	21; 35

Belemnellocamax mammillatus zone) corresponding to the highest belemnite zone in the lower part of the European two-fold division of the Campanian Stage (see Christensen, 1975). Three localities exposing sediments of latest early Campanian age (Åsen, Ivö Klack and Ugnsmunnarna; Fig. 1) produced the teeth described below. For locality information, see Lindgren & Siverson (2002), Lindgren *et al*. (2007) and Eriksson *et al*. (2011, fig. 2).

3. Methodology

The material selected for histological analysis comprises four isolated, presumably shed marginal tooth-crowns (LO 11621 *t* – LO 11624 *t*) representing three genera of mosasaurs (*Dollosaurus*, cf. *Platecarpus* and *Tylosaurus*) and one genus of crocodylian (*Aigialosuchus*). Comparisons with more complete dentitions in mosasaur and crocodylian skeletons from North America and west-central Europe (see Lindgren & Siverson, 2002, 2004, 2005; Lindgren, 2005*a*, *b*) suggest that all teeth originate from the mid-section of the dental ramus in sub-adult to adult individuals.

Prior to sampling, all tooth-crowns were measured (Table 1), photographed (the crowns were covered with ammonium chloride prior to being photographed) and moulded. Thereafter, the teeth were vacuum-embedded in a clear polyester resin, and millimetre-thick transverse sections were produced using a slow-speed diamond saw (the precise location of each section is listed in Table 1). Additionally, a partial longitudinal section was produced from LO 11621 *t* (*Aigialosuchus* sp.) because previous studies (e.g. Erickson, 1996*b*) have indicated that longitudinal sections may provide additional histological details. The thin-sections were mounted on petrographic slides using polyester resin, ground to optical translucency (i.e. to about 50–100 μm thickness), polished on a felt pad with aluminium oxide powder, and imaged (at × 5–40 magnification) using a Nikon DS-Fi1 camera attached to a binocular microscope. Histological features were documented with particular focus on incremental growth line distribution, spacing and counts. Notes were made also on other potential endogenous markings, as well as on enamel thickness, state of the osteocyte lacunocanalicular system, and possible taphonomic/diagenetic artefacts. In accordance with the published methodology of, for example, Dean (1998), Erickson (1996*a*, *b*) and Nanci (2008), the different types of incremental laminations were identified based on their widths and morphology. In each section examined, the most complete sequences of short- and (if present) long-period lines were measured using an image analysis software (NIS-Elements BR 3.10) from digital micrographs, and the average distance between the individual lines was calculated. These numbers were then extrapolated to include the entire thickness of the dentine (measured using the multipoint circle tool in NIS-Elements BR 3.10) in order to obtain values of the total dentine accumulation at the level of sectioning.

Depository acronym. LO – Department of Geology, Lund University, Lund, Sweden.

4. Histological analyses

The dental morphology of the mosasaur and crocodylian taxa dealt with in this work has been described in detail by, for example, Persson (1959, 1963), Lindgren (2005*a*, *b*) and Lindgren & Siverson (2002, 2004, 2005); here we provide additional microstructural data obtained from recent histological analyses. Basic measurements, such as tooth-crown height, width and length (as preserved), are presented in Table 1.

4.a. LO 11622 *t* (*Dollosaurus* sp.)

Two transverse histological sections were made from LO 11622 *t* (Fig. 2); one near the apex and one at approximately mid-crown height. The apical section preserves closely spaced dentinal tubules that radiate from the margin of the pulp cavity and outward. Numerous odontocyte lacunae are also visible, and these are oriented with their long axis parallel to the tubules. A small number of laminations run parallel to the pulp circumference. The lines are faint, irregularly spaced and too few to allow a confident quantitative analysis. Numerous taphonomically induced micro-cracks are also present, and these have served as loci for bacterial or fungal activity (cf. Underwood, Mitchell & Veltkamp, 1999), resulting in the partial loss of endogenous microstructures.

The transverse section taken at mid-crown height is similar to the apical one in that it contains multiple radially oriented dentinal tubules and elongated
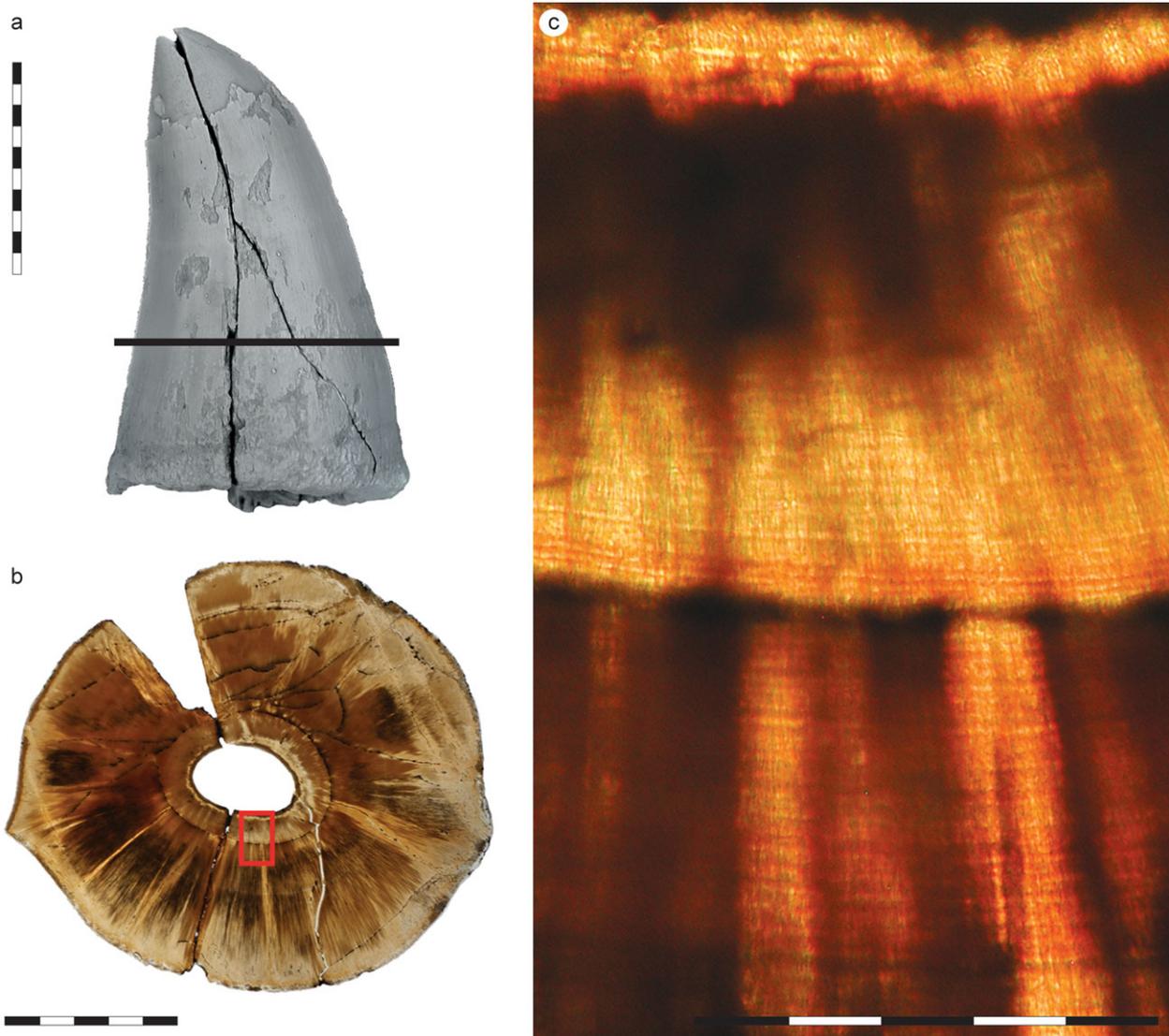
Figure 2. (Colour online) *Dollosaurus* sp., LO 11622 *t*, isolated marginal tooth-crown. (a) Specimen photographed in labial view prior to histological analysis. Level of sectioning is marked with a horizontal bar. (b) Transverse mid-crown section of LO 11622 *t* (labial side faces downwards). (c) Demarcated area in (b) showing periodic incremental markings here interpreted as lines of von Ebner. Scale bars represent 10 mm (a), 5 mm (b) and 500 μm (c).

odontocyte lacunae (Fig. 2b). However, those areas affected by microorganisms are considerably smaller, and consequently the dentine is rich in preserved increments (some of which are accentuated by secondarily deposited minerals). These laminations run perpendicularly to the tubules and are most pronounced in the peri-pulpal part of the dentine, where 105 consecutive lines with a size range of 8–23 μm and an average width of 12.2 μm were documented (Fig. 2c). By extrapolation (mean thickness of dentine = 5194 μm), the sectioned part of the tooth-crown holds a total of 426 periodic dentinal markings.

4.b. LO 11623 *t* (cf. *Platecarpus*)

Two transverse histological sections were made from LO 11623 *t* (Fig. 3): one close to the apex and one at approximately mid-crown height. In the apical section, the enamel displays one distinct and one faint lam-

ination. No increments were observed in the dentine; however, closely spaced dentinal tubules could be seen radiating from the vicinity of the pulp cavity and outward. The dentine is also rich in dark odontocyte lacunae with stubby canaliculi. As in LO 11622 *t*, the lacunae are elongate and oriented with their long axis parallel to the tubules. Diverging channels, joined in discrete networks and probably made by bone-boring bacteria and/or fungal hyphae, surround a number of taphonomically induced micro-cracks.

The enamel of the mid-crown section holds three weak and incomplete increments consisting of alternating dark and light bands. The section is rich in both endogenous microstructures and diagenetic artefacts, such as micro-fractures filled with brownish matter. Towards the circumference the dentine is largely deteriorated by microorganisms (Fig. 3b, c). Micro-borings are also present in the region of the pulp cavity, although some original structures, including darkly
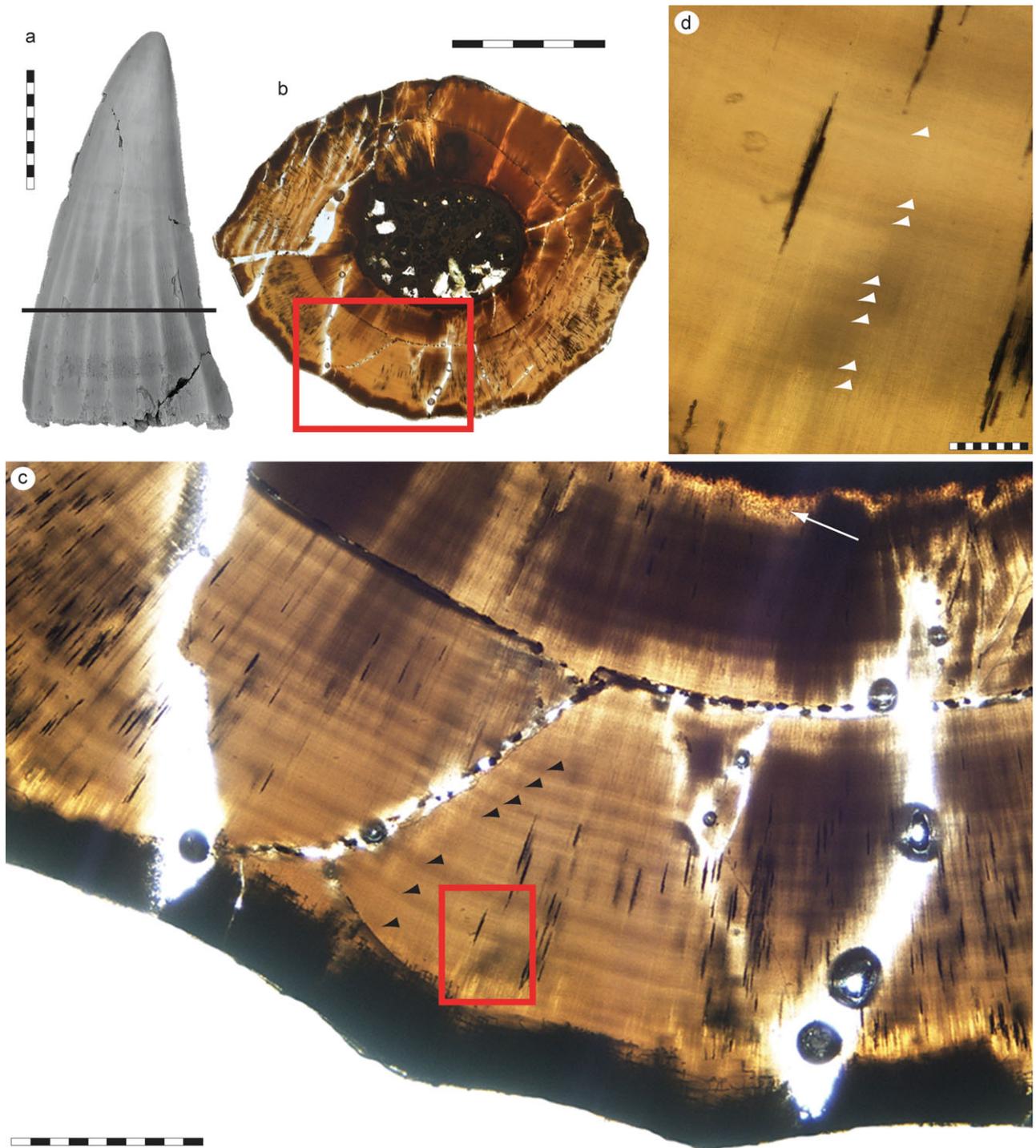
Figure 3. (Colour online) cf. *Platecarpus*, LO 11623 *t*, isolated marginal tooth-crown. (a) LO 11623 *t* in labial view prior to histological analysis. Level of sectioning is marked with a horizontal bar. (b) Transverse mid-crown section of LO 11623 *t* (labial side faces downwards). (c) Demarcated area in (b) showing long-period incremental markings (here interpreted as Andresen lines – black arrowheads), radially oriented dentinal tubules, possible calcospherites (arrow), and elongate osteocyte lacunae. (d) Demarcated area in (c) showing a second set of finer concentric laminations here interpreted as lines of von Ebner (better preserved striae are marked with white arrowheads). Scale bars represent 10 mm (a), 5 mm (b), 1 mm (c) and 100 μm (d).

stained mineral globules (possibly calcospherites) remain (Fig. 3c, white arrow). Radially oriented dentinal tubules and odontocyte lacunae are dispersed throughout the dentine (Fig. 3b, c, d). The blackish lacunae are elliptical, and remains of the canalicular system occur as thread-like extensions from the surfaces of the secondarily filled cavities (Fig. 3d). Two sets of incre-

mental growth lines were measured: one set of ten consecutive long-period lines, characterized by alternating opaque and transparent bands, with a size range of 102–201 μm and an average width of 141 μm (Fig. 3c), and one set of 128 short-period lines with a size range of 6–19 μm and an average width of 11.3 μm (Fig. 3d). By extrapolation, at the level of sectioning the tooth
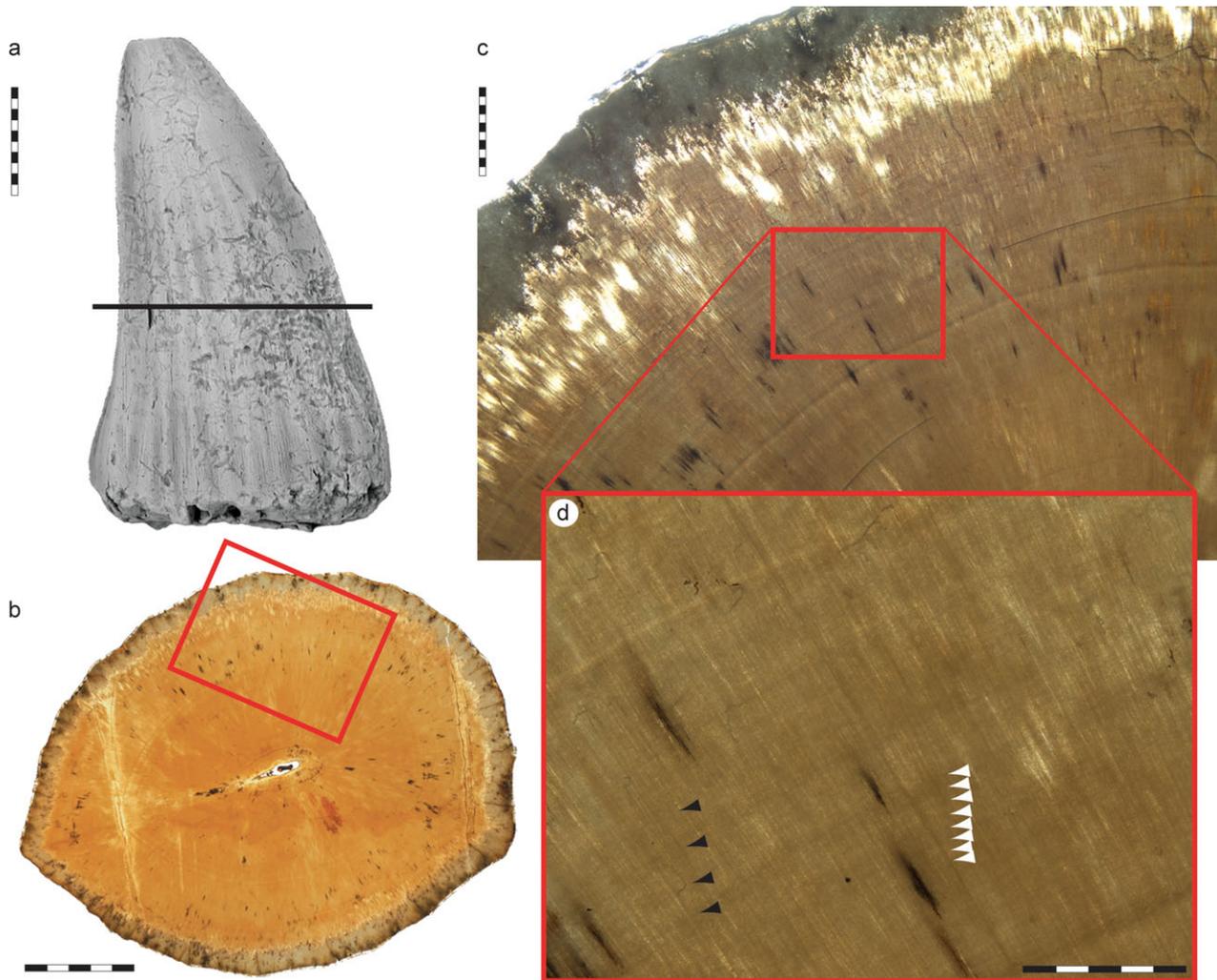
Figure 4. (Colour online) *Tylosaurus ivoensis*, LO 11624 *t*, isolated marginal tooth-crown. (a) Specimen photographed in labial view prior to histological analysis. Level of sectioning is marked with a horizontal bar. (b) Transverse mid-crown section of LO 11624 *t* (labial side faces downwards). (c) Demarcated area in (b) showing long-period incremental markings (here interpreted as Andresen lines), radially oriented dentinal tubules and elongate osteocyte lacunae. (d) Demarcated area in (c) showing presumed Andresen lines (black arrowheads) and a second set of finer concentric laminations here interpreted as lines of von Ebner (better preserved striae are marked with white arrowheads). Scale bars represent 10 mm (a), 5 mm (b), 1 mm (c) and 500 μm (d).

holds a total of 342 short-period lines with one long-period line for every twelfth or thirteenth short-period line (mean thickness of dentine = 3860 μm).

4.c. LO 11624 *t* (*Tylosaurus ivoensis*)

Two transverse histological sections were made from LO 11624 *t* (Fig. 4): one close to the apex and one at approximately mid-crown height. In the apical section, the enamel contains four incomplete increments. Evidence of bacterial or fungal activity is apparent towards the periphery of the dentine, thus limiting the amount of observable primary features in this part of the section. Odontocyte lacunae and dentinal tubules appear scattered throughout the dentine, the latter of these microstructures being intersected by a continuous set of 77 incremental laminations ranging in size from 10 to 26 μm and with an average width of 15.7 μm. Given that the thickness of the dentine is 6441 μm, there are

410 daily increments at the level of sectioning. Additionally, a few coarser markings occur among the short-period lines, roughly 100–200 μm apart.

In the mid-crown section, only one incremental line can be traced over some distance in the enamel. Although the perimeter of the dentine is remodelled by bone-boring bacteria and/or fungal hyphae, its inner parts are well preserved with abundant dentinal tubules and elongate odontocyte lacunae. One set comprising 16 consecutive long-period lines, with a size range of 122–275 μm and an average width of 219 μm, is present in the peri-pulpal dentine (Fig. 4d, black arrowheads). Additionally, there is one set of 82 short-period lines with a size range of 9–34 μm and an average width of 19.4 μm (Fig. 4d, white arrowheads). Thus, at the level of sectioning the tooth-crown holds a total of 487 short-period lines (mean thickness of dentine = 9440 μm) with one long-period line for every eleventh or twelfth short-period line.
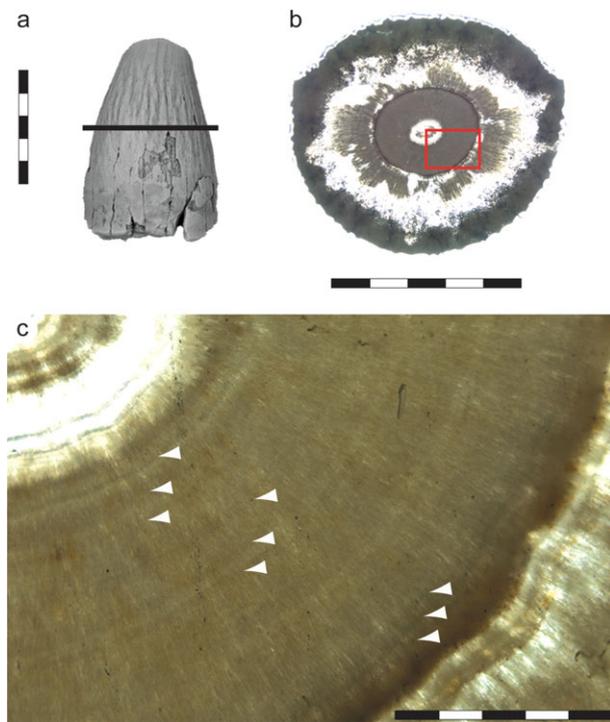
Figure 5. (Colour online) *Aigialosuchus* sp., LO 11621 *t*, isolated tooth-crown. (a) LO 11621 *t* as it appeared (in labial view) prior to histological analysis. Level of sectioning is marked with a horizontal bar. (b) Transverse mid-crown section of LO 11621 *t* (labial side faces downwards). (c) Demarcated area in (b) showing periodic incremental markings (arrowheads) here interpreted as lines of von Ebner. Scale bars represent 5 mm (a, b) and 500 μm (c).

4.d. LO 11621 *t* (*Aigialosuchus* sp.)

Three histological sections were made from LO 11621 *t* (Fig. 5): one transverse section close to the apex, one transverse section at approximately mid-crown height, and one longitudinal section near the base of the crown. In the apical section, the enamel holds three incomplete increments preserved as alternating opaque and transparent laminae. Most primary features of the dentine are obscured by an interconnected lattice of thread-like channels that was probably made by bone-boring bacteria and/or fungal hyphae, although densely spaced, radially oriented dentinal tubules and a few faint, concentric laminations are visible in some areas.

The section taken at mid-crown height is also partially affected by microorganisms, particularly in the peripheral parts of the dentine (Fig. 5b). Close to the pulp cavity, fine dentinal tubules extend radially from the crown centre and outward (Fig. 5c). These tubules are intersected perpendicularly by a number of concentric and gently undulating incremental growth lines (consisting of alternating dark and light bands) of somewhat varying widths (6–19 μm) and thickness (Fig. 5c, arrowheads). A strong band at about 1200 μm from the centre of the pulp cavity is surrounded by a micro-crack, about 1 μm wide. This crack indicates a weakening zone in the dentine, which may have been exploited by bacteria and/or fungi (Fig. 5c).

Proximal to the pulp cavity, increments are regular and well preserved, whereas distally, the laminations are more irregular and diffuse. Fifty-one consecutive short-period growth lines were measured, rendering an average width of 12.7 μm. By extrapolation (mean thickness of dentine = 3287 μm), the tooth-crown contains a total of 259 dentinal increments over the sectioned surface. The longitudinal section did not yield any additional information.

5. Discussion

Lines of von Ebner form through a circadian rhythm involving alternating accumulation and mineralization of dentine (Nanci, 2008), and the daily increments seen in extant crocodylian teeth are presumably deposited in a similar manner (Erickson, 1996*b*). The short-period markings observed in *Aigialosuchus* sp. have a morphology and size range consistent with the periodic increments documented by Erickson (1996*b*), and homologous increments are also found in *Dollosaurus* sp., cf. *Platecarpus* and *Tylosaurus ivoensis*, thus corroborating the presence of von Ebner's lines in Mesozoic crocodylian and mosasaur dentine (cf. Erickson, 1996*a*; Chinsamy, Tunoğlu & Thomas, 2010, 2012).

Daily dentine formation rates (and incremental line widths) in modern amniotes are between 1 and 30 μm regardless of the size of the tooth (and animal), something that led Erickson (1996*a*) to conclude that there are important structural or physiological constraints that limit the amount of dentine that can form on a daily basis. The consequences of these restraints are interesting, particularly when considering animals that attain gigantic proportions. During the evolution of obligatory marine mosasaurs, body size increased and so did tooth size (Russell, 1967; Lingham-Soliar, 1995). However, the time required to develop the teeth seemingly increased as well, as indicated by the growth line counts in *T. ivoensis* (410 and 487 days at the apex and mid-crown section, respectively) and *Mosasaurus hoffmanni* (511 days; see Chinsamy, Tunoğlu & Thomas, 2010, 2012) – two enormous species with massive marginal tooth-crowns – compared to cf. *Platecarpus* (342 days at mid-crown height) (the moderately robust crown of *Dollosaurus* sp. takes an intermediate position with 426 daily increments at mid-crown height). Although both *T. ivoensis* and *M. hoffmanni* undoubtedly were capable of eating almost anything that they encountered, including sea turtles and other mosasaurs (e.g. Massare, 1987 and references therein), the risk of long-term incapacity to overwhelm prey following breakage or other severe dental injuries may have been high (assuming that tooth replacement rates declined in conjunction with prolonged tooth development times, as they do in extant animals; cf. Kline & Cullum, 1984; Erickson, 1996*a*). Nonetheless, in similarity with the giant tyrannosaurid dinosaurs (see Erickson, 1996*a*), this evolutionary trade-off presumably was compensated for by allometric modifications of the teeth, including, for example, the

development of more robust crowns and broader tooth bases (Massare, 1987; Lingham-Soliar, 1995; Lindgren & Siverson, 2002). Not only did these adaptations enable the capture of larger prey items, but they also increased the resistance of the teeth to mechanical damage, thereby extending their functional longevity (Lingham-Soliar, 1995).

In addition to lines of von Ebner, coarser and more widely spaced incremental markings were observed in LO 11623 *t* (cf. *Platecarpus*) and LO 11624 *t* (*T. ivoensis*) (Figs. 3, 4). These long-period lines contain between 11 and 13 short-period lines each, to suggest formation periodicities similar to those of Andresen lines in extant animals (Dean & Scandrett, 1996). However, unlike typical Andresen lines, which are spaced on average between 15 and 30 µm apart (Dean & Scandrett, 1996), the long-period lines documented in this study have a mean width of 141 µm (cf. *Platecarpus*) and 219 µm (*T. ivoensis*), respectively. Assuming depository rhythms similar to those of Andresen lines, this would imply that the amount of dentine secreted at any given time was between 4 and 15 times higher in mosasaurs relative to modern mammals (cf. Dean & Scandrett, 1996). Given that mosasaurs, as opposed to most mammalian taxa, continuously shed and replaced their teeth, significantly higher tooth formation rates are expected (and in line with calculated tooth formation times in other reptilian groups, including *Aigialosuchus*, other crocodylians, and nonavian dinosaurs; Erickson, 1996*a*, *b*; Sereno *et al*. 2007; D'Emic *et al*. 2009). Nonetheless, in a study devoted to Bauer's (1898) collection of ichthyosaur tooth sections, Scheyer & Moser (2011) pointed out that similarly spaced incremental lines are variably assigned to as von Ebner and Andresen lines by different authors (see also Dean, 1998, 2000). Moreover, they (Scheyer & Moser, 2011) documented two sets of incremental markings in ichthyosaur dentine: a first set comprising very fine laminations situated about 2–3 µm apart, and a second set of coarser markings where spaces varied around 15–20 µm. Scheyer & Moser (2011) interpreted the thin, short-period lines as those of von Ebner based on their comparable thickness to the daily increments in human dentine, whereas the coarser, long-period lines were referred to as Andresen lines. If this interpretation is correct, then the short-period lines recorded in mosasaur and nonavian dinosaur dentine would represent Andresen lines, which in turn would result in even shorter tooth development times than those estimated by us and others (cf. Erickson, 1996*a*; Sereno *et al*. 2007; D'Emic *et al*. 2009; Chinsamy, Tunoğlu & Thomas, 2010, 2012). However, increments with a periodicity of less than a day (infradian markings) have been identified in some animals (see Dean & Scandrett, 1996), and it should also be pointed out that Maxwell, Caldwell & Lamoureux (2012) failed to find any regular incremental banding pattern in their sample of sectioned ichthyosaur teeth. Even though we were unable to confirm the presence of laminations spaced less than about 6 µm apart, we cannot rule out the possibility of three different sets of incremental markings in mosasaur dentine because of potential preservational artefacts, such as diagenetic colouration or secondary mineralization, which might obliterate the original ultrastructure of the dentine.

In order to fully understand the process of tooth development and replacement in mosasaurs, more comprehensive studies based on larger sample sizes are required. However, because the incremental growth lines observed in mosasaur marginal teeth are homologous to those in the dentine of extant animals, it is likely that the dentinal deposition rhythms we record herein represent primitive features that can be found in all tooth-bearing vertebrates.

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