First evidence of denticulated dentition in teleosaurid crocodylomorphs

MARK T. YOUNG, BRIAN L. BEATTY, STEPHEN L. BRUSATTE, and LORNA STEEL

Young, M.T., Beatty, B.L., Brusatte, S.L., and Steel, L. 2015. First evidence of denticulated dentition in teleosaurid crocodylomorphs. *Acta Palaeontologica Polonica* 60 (3): 661–671.

Teleosauridae was a group of largely marine Mesozoic crocodylomorphs, typically considered as akin to "marine gavials" due to their elongate, tubular, polydont rostra that are indicative of a piscivorous diet. Here we show that these extinct crocodylomorphs were more anatomically, and perhaps ecologically, varied than previously thought. We report the first evidence of denticles in a teleosaurid tooth, revealed by scanning electron microscopic (SEM) analysis of a tooth from the holotype of "*Steneosaurus*" *obtusidens*. These denticles are cryptic, because they are microscopic, not contiguous along the carinae (instead forming short series), and are detectable only using SEM. This incipient denticle morphology is similar to that recently discovered in a closely related group of marine crocodylomorphs, the Metriorhynchidae. In particular, the denticulation morphology of "*Steneosaurus*" is similar to that of the geosaurin metriorhynchid *Torvoneustes*, indicating that these two taxa may have employed similar feeding styles and that "*S.*"*obtusidens* may have been a nearshore ecological analogue to the more offshore, fast-swimming geosaurins. Previous authors have considered "*S.*" *obtusidens* and *Machimosaurus* to be durophagous, but the discovery of denticulated teeth indicates that they had a more varied diet and feeding style, and included flesh slicing as part of their feeding toolkit. It is currently unknown how extensive denticulate carinae may be in Teleosauridae, and we hypothesise that cryptic denticles may also be present in other marine crocodylomorphs once they are subjected to SEM study.

Key words: Thalattosuchia, Teleosauridae, *Steneosaurus*, denticles, durophagy, functional ecology, Mesozoic, United Kingdom.

Mark T. Young [zoologika@gmail.com], School of Biological Sciences, The King's Buildings, University of Edinburgh, West Mains Road, Edinburgh, EH9 3JW, UK; School of Ocean and Earth Sciences, National Oceanography Centre, University of Southampton, Southampton, SO14 3ZH, UK.
Brian L. Beatty [bbeatty@nyit.edu], Department of Anatomy, NYIT College of Osteopathic Medicine, Northern Boulevard, Old Westbury, NY 11568, USA.
Stephen L. Brusatte [Stephen.Brusatte@ed.ac.uk], School of GeoSciences, Grant Institute, The King's Buildings, University of Edinburgh, West Mains Road, Edinburgh, EH9 3JW, UK.
Lorna Steel [l.steel@nhm.ac.uk], Department of Earth Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK.

Received 25 June 2013, accepted 25 October 2013, available online 28 October 2013.

Introduction

Teleosaurids were a successful group of marine crocodylomorphs that had a global distribution during the Jurassic (Vignaud 1995; Hua and Buffetaut 1997). Teleosaurids are typically known from shallow marine/lagoonal deposits (although some specimens are found in freshwater deposits; see Vignaud 1995), and together with Metriorhynchidae they form the major crocodylomorph clade Thalattosuchia (Buffetaut 1982b; Vignaud 1995; Hua and Buffetaut 1997; Jouve 2009; Young and Andrade 2009). All teleosaurids (*Machimosaurus*, *Peipehsuchus*, *Platysuchus*, *Steneosaurus*, and *Teleosaurus*) share the same basic bauplan, and some of their most distinctive characters include: a tubular snout, a transversely expanded premaxilla and anterior tip of the dentary, oval shaped external nares and surrounding fossae that are transversely aligned, large supratemporal fenestrae, and dorsally inclined orbits (Andrews 1913; Vignaud 1995; Hua and Buffetaut 1997; Hua 1999).

Teleosaurids are often considered as something akin to "marine gavials" due to their elongate, tubular, polydont rostra; presumed primarily piscivorous diet; dorsally directed orbits and a lack of any bone histological adaptations to fully marine life (for discussion see Hua and Buffrénil 1996; Hua and Buffetaut 1997). Recently, however, there has been

a growing realisation that teleosaurids may have been more functionally and ecologically diverse than previously supposed (Hua and Buffetaut 1997; Vignaud 1997; Hua 1999; Pierce et al. 2009b). In particular, the genus *Machimosaurus* is often considered to be durophagous, with teeth well suited for feeding on hard-shelled turtles (chelonophagous; Krebs 1968; Buffetaut 1982a; Vignaud 1997; Hua and Buffetaut 1997; Karl and Tichy 2004; Pierce et al. 2009b; Young and Steel 2014). However, many questions about teleosaurid diet, ecology, and function still remain. Although previous studies have examined the variation in teleosaurid dental morphotypes (Massare 1987; Vignaud 1997), none have examined enamel microstructure or focused on carinal morphology, both of which are often closely related to feeding style and prey choice in extant marine vertebrates (Sasagawa et al. 1984; Frazzetta 1988; Carlson 1990; Francillon-Vieillot et al. 1990; Sato et al. 1990; Motta 2004).

Perhaps unusually, it has long been thought that teleosaurids did not possess teeth with serrations. The possession of serrated (denticulated) teeth, a condition called ziphodonty, is a common feature among carnivores and piscivores. False-serrations, formed by superficial enamel interacting with the carinal keel, have been noted in *Machimosaurus* (Prasad and Broin 2002), but true serrations (discrete, chisel-like denticles arising from the carina) have never been previously observed on a teleosaurid tooth. Currently within Thalattosuchia, only geosaurine metriorhynchids are known to possess ziphodont teeth with true serrations (denticles; see Table 1; e.g., Pol and Gasparini 2009; Andrade et al. 2010; Young et al. 2012, 2013).

Here we modify the definition of a denticle from Legasa et al. (1993) and Prasad and Broin (2002) to mean a discrete morphological unit on, or along, the carinae which is not formed by the surface enamel ornamentation. These units may, or may not, be clearly individualised by an interdenticular groove or notch. In certain cases, either a high carinal keel and/or the denticles being small and poorly developed, results in there being no interdenticular groove. This occurs in the incipient denticle morphology first described by Young et al. (2013).

Recent microscopic examination of metriorhynchid teeth has revealed a great diversity of serration and carinal morphologies which were hitherto unrecognised (Andrade et al. 2010; Young et al. 2013), and it is possible that a similar amount of variation may be present in other marine crocodylomorphs, like teleosaurids. Understanding this variation is important, because dental morphology is related to dietary preference, has functional implications, and may give insight into macroevolutionary patterns over long time scales.

Here we describe the first instance of denticulated ziphodont teeth in Teleosauridae, based on SEM image of a tooth of "*Steneosaurus*" *obtusidens* Andrews, 1909. We show that this teleosaurid had both microscopic true denticles on the carina and false denticles formed from the interaction of enamel ornamentation and the carina. A similar denticulation morphology, as well as many other craniodental characters restricted to the subclade consisting of "*S.*"

Table 1. List of characters accompanied by a description, to elucidate the various carinal/serration morphologies in Thalattosuchia. This table is an updated version of tables 2 and 3 presented in Young et al. (2013), i.e., to include Teleosauridae. All taxa listed have had tooth crowns examined under SEM. In asterisked taxa the superficial enamel ornamentation extends onto the carina, especially in the apical region. In the absence of denticles this constitutes the false-ziphodont condition.

Denticle size	Denticles contiguous	Incipient denticles	Description	Examples
Non-ziphodont	N/A	N/A	Carinae present, but formed solely by a keel (raised ridge). No enamel ornamentation extending onto the carina.	*Metriorhynchus superciliosus* *Gracilineustes leedsi*
Macro-ziphodont	yes	no, well developed	Carinae homogenous, with a long, contiguous series of repetitive isolated and isomorphic true denticles that are visible macroscopically. Dimensions typically exceed 300 μm.	*Dakosaurus andiniensis* *Dakosaurus maximus*
Micro-ziphodont	yes	no, well developed	Carinae homogenous, with a long, contiguous series of repetitive isolated and isomorphic true denticles that are microscopic; whose dimensions typically do not exceed 300 μm.	*Plesiosuchus manselii* *Geosaurus giganteus* *Geosaurus grandis* *Geosaurinae* indet. (NHMUK PV R486)
	yes	yes, poorly developed	Carinae homogenous, with a long, contiguous series of repetitive isolated and isomorphic true denticles that are microscopic; whose dimensions typically do not exceed 300 μm. The denticles themselves are poorly defined and difficult to distinguish even under SEM (although this could be due to the enamel ornamentation extends onto the carina, especially in the apical region).	*Torvoneustes carpenteri**
	no	yes, poorly developed	Carinae heterogeneous, with a series of non-contiguous repetitive isolated and isomorphic true denticles that are microscopic. Series can be short (2) or moderate (~10), but are widely separate from one another, i.e. no contiguous series along the carina. Dimensions typically do not exceed 300 μm. In labial or lingual view, the height of the denticles rarely influences the height of the keel (i.e., little or no serrated edge). The denticles themselves are poorly defined and difficult to distinguish even under SEM.	***"Steneosaurus" obtusidens**** "*Metriorhynchus*" *brachyrhynchus* *Tyrannoneustes lythrodectikos*

obtusidens and *Machimosaurus*, are seen in the distantly related geosaurin metriorhynchid *Torvoneustes*, suggesting these teleosaurids may have been a more nearshore ecological analogue to the open ocean geosaurins. Although previous studies have largely concluded that *Machimosaurus* and close relatives were durophagous predators with teeth adapted for crushing hard prey, the discovery of denticulated teeth indicates that these large, nearshore predators may have had a more varied feeding strategy that also included slicing flesh, and were probably high-order predators in their environment.

Institutional abbreviations.—NHMUK, Natural History Museum, London, United Kingdom.

Other abbreviations.—DEJ, dentine enamel junction.

Taxonomic overview

NHMUK PV R3168 is the holotype of "*Steneosaurus*" *obtusidens*, which is the largest known species of crocodylomorph from the Peterborough Member of the Oxford Clay Formation (Middle Callovian, ca. 165 million years old). Furthermore, with the holotype having a basicranial length of 116 cm, it had the longest skull of any known Early-to-Middle Jurassic crocodylomorph taxon. Assuming the ratio of basicranial-to-body length scaled the same as the skull previously referred to *Machimosaurus mosae* (Hua et al. 1994; Hua 1999; see also Martin and Vincent 2013), then NHMUK PV R3168 would have reached 6.01 m in total body length. Note that like metriorhynchids (see Young et al. 2011), *Machimosaurus* had a head proportionally much larger relative to total body length than extant crocodylians (Hua 1999).

Although NHMUK PV R3168 was originally described as a member of the genus *Steneosaurus* (Andrews 1909), as the holotype of *Steneosaurus obtusidens*, the similarities between "*Steneosaurus*" *obtusidens* and *Machimosaurus* have long been noted (e.g., see Krebs 1968; Buffetaut 1982b). There have unfortunately been numerous competing taxonomic opinions on the validity of "*S.*" *obtusidens* as a species, and even differences on what species it may be a subjective junior synonym of (see Adams-Tresman 1987; Hua et al. 1994; Hua 1996, 1999; Pierce et al. 2009a; Young et al. 2012; Martin and Vincent 2013).

Adams-Tresman (1987) proposed that "*Steneosaurus*" *obtusidens,* along with *S. edwardsi*, *S. hulkei*, and *S. depressus*, were subjective junior synonyms of *S. durobrivensis*. Unfortunately, few of the anatomical comparisons made by Adams-Tresman (1987) regarding "*S.*" *obtusidens* were done by using the holotype (NHMUK PV R3168), but instead using specimens previously referred to this species without justification. In particular, NHMUK PV R3169 was used. Unfortunately, this specimen was only tentatively referred to "*S.*" *obtusidens* by Andrews (1913), and then only based on its large size (as NHMUK PV R3898 was). As such, Adams-Tresman's (1987) rejection of the characteristic dorsal osteoderm ornamentation of "*S.*" *obtusidens* is questionable. This is reinforced by *Machimosaurus mosae* dorsal osteoderms sharing the same ornamentation pattern as "*S.*" *obtusidens* (Hua 1999). Moreover, Adams-Tresman (1987) ignored the presence of three sacral vertebrae as a possible diagnostic characteristic, possibly because Andrews (1913) considered it likely to be an individual peculiarity. However, the *M. mosae* skeleton also shows evidence for three sacral vertebrae (Hua 1999). Nevertheless, we still need to confirm Andrews' (1913) opinion on the sacralisation of the first caudal vertebrae.

Subsequently, "*Steneosaurus*" *obtusidens* was considered a subjective junior synonym of the Kimmeridgian taxon *Machimosaurus hugii* (Hua et al. 1994; Hua 1996, 1999). However, they did note further study was necessary to untangle the taxonomy of blunt-toothed teleosaurids. Pierce et al. (2009a) went further, and synonymised "*S.*" *obtusidens*, *S. hulkei,* and *S. durobrivensis* (all Callovian teleosaurids) with *M. hugii*. However, this synonymy and the accompanying species diagnosis was criticised and rejected by Martin and Vincent (2013).

A recent phylogenetic analysis of Thalattosuchia found that "*Steneosaurus*" *obtusidens* is a separate, diagnosable species-level taxon basal to both *M. hugii* and *M. mosae* (Young et al. 2012), but forming a restricted clade with these two species of *Machimosaurus*. However, Martin and Vincent (2013) contend that there is no basis to separate the specimen referred to *M. mosae* (the holotype of which was destroyed during World War One) from *M. hugii*. They conclude that all known *Machimosaurus* specimens from the Kimmeridgian of Europe can be referred to *M. hugii* (although they did not discount the presence of a second Kimmeridgian taxon; see Young et al. 2014a, 2015 for a revision of *Machimosaurus* and the species within). They also argued that "*S.*" *obtusidens*, although the sister taxon to *M. hugii*, should not be referred to *M. hugii* or the genus *Machimosaurus*.

The sister taxon relationship of "*Steneosaurus*" *obtusidens* and *Machimosaurus* is supported by numerous synapomorphies in the phylogeny of Young et al. (2012) and the modified version used by Martin and Vincent (2013). These include: (i), blunt tooth apices; and (ii), a characteristic superficial enamel ornamentation (basal-middle regions have apicobasally aligned ridges while the apical region has an anastomosed pattern). The two following characteristics are shared between "*S.*" *obtusidens* and the *M. mosae* specimen of Hua (1999): (i), three (?) sacral vertebrae and (ii), dorsal osteoderm ornamentation that has: small (for a teleosaurid), irregularly shaped pits arranged in an anastomosed pattern, that can fuse and become elongate grooves that radiate from the keel (Andrews 1913; Hua 1999). The number of sacral vertebrae is unknown for other *Machimosaurus* specimens. Martin and Vincent (2013) note that, other than the *M. mosae* specimen of Hua (1999), other *M. hugii* specimens have a dorsal osteoderm ornamentation pattern consisting of large sub-circular and widely spaced pits. As such, it is unclear if

"*S.*" *obtusidens* and *M. mosae* are more closely related to one another than to *M. hugii*. That is an issue that is beyond the scope of this paper, and will be the focus of a future paper.

However, "*S.*" *obtusidens* differs from *Machimosaurus hugii* and *M. mosae* in: (i) retaining antorbital fenestrae, which are absent in *Machimosaurus* (Martin and Vincent 2013); (ii) in retaining four premaxillary alveoli, whereas in *Machimosaurus* there are only three (Table 2); (iii) having a higher maxillary and dentary tooth count than any known *Machimosaurus* specimen (Table 2); (iv) a proportionally longer rostrum (Table 2); (v) a proportionally narrower posterior skull (Table 2); (vi) proportionally shorter supratemporal fenestrae (Table 2); and (vii) well-developed mesiodistal tooth carinae, whereas in *Machimosaurus* the carinae are generally low, restricted to the apex or completely absent (Krebs 1968; Hua 1999; Martin and Vincent 2013; Young and Steel 2014; Young et al. 2014a).

As such, we consider "*S.*" *obtusidens* to be a valid species-level taxon, and thus it should not be referred to the genus *Machimosaurus*, or treated as a subjective junior synonym of *S. durobrivensis*. Establishing a new genus is outside the bounds of this current paper, and will be handled in our future work re-describing the fully-prepared holotype.

Material and methods

An isolated tooth from the holotype of "*Steneosaurus*" *obtusidens* (NHMUK PV R3168) was analysed by means SEM, producing backscatter electron images. The SEM analyses were conducted at the Microscopy and Imaging Facility at the American Museum of Natural History (New York), using the Zeiss Evo 60 EP-SEM. We used the Zeiss Evo 60 EP-SEM because it does not require coating the specimens in gold or palladium, making these enamel surfaces available for future isotopic analyses or other similar sampling. Both the whole tooth (external surface) and various histological cross sections were imaged in the SEM at 10 to 8 kV.

After the whole tooth was initially subjected to SEM analysis to assess surface details, it was embedded in clear epoxy resin (Epokwik, Buehler Inc.) so that histological and additional surface details could be inspected after sections were made. After embedding, two sections were made (see below) using a Buehler Isomet slow speed saw. After polishing with an Extec twin wheel polisher/grinder with 600 and 1200 grit silicon carbide paper, they were etched with 1 mol l^{-1} HCl ranged from 10 to 60 s. Specimens were then rinsed under tap water for 10 seconds to ensure that acid activity was halted, and then washed in an ultrasonic bath for

Table 2. Comparison of biometric variation between the different species of *Machimosaurus*-lineage teleosaurids. [A] estimated tooth counts from Buffetaut (1982a). However, Martin and Vincent (2013) noted that the state of preservation makes these uncertain. [B] estimated to be 17 by Hua (1999). However, Martin and Vincent (2013) consider this likely to be an underestimate. This specimen does have a lower pre-palatine maxillary count than the *M. hugii* specimen described by Martin and Vincent (2013) (= *M. buffetauti* sensu Young et al. 2014a, 2015). And, as the maxillary tooth row in *Machimosaurus* terminates level to the anterior margin of the suborbital fenestrae (Martin and Vincent 2013), a maxillary tooth count of under 20 is not unreasonable (18 or 19). [C] Estimated to have 16 alveoli per maxilla and 16 alveoli per dentary by Sauvage and Liénard (1879). [D] Posterior surface is made of plaster (Buffetaut 1982a). [E] Sauvage and Liénard (1879) estimate the mandible to have been 132.5 cm long, and the symphysis to have been 62 cm long. This would have given a symphyseal to total mandible length of 46.8%.

Species	"*Steneosaurus*" *obtusidens*	*Machimosaurus buffetauti*		*Machimosaurus mosae*	
Reference/specimen	NHMUK PV R3168	Martin and Vincent 2013	Buffetaut 1982a	Hua 1999	Sauvage and Liénard 1879
Age	Middle Callovian	Early Kimmeridgian	Early Kimmeridgian	Late Kimmeridgian	Late Kimmeridgian
Premaxillary alveoli	4	3	3	3	3
Maxillary alveoli	At least 29	22	21? [A]	? [B]	14 preserved [C]
Maxillary alveoli anterior to palatines	?	?16–17	?	14?	7
Dentary alveoli	At least 27	21/22	24/25? [A]	19	? [C]
Dentary alveoli adjacent to mandibular symphysis	22–24	20	19/20? [A]	15–16	?
Dentary alveoli posterior to mandibular symphysis	6	2	4/5? [A]	3–4	3–4
Basicranial length (cm)	116	93.5	100	96.5	~130
Rostrum length (cm)	71	54.7	58	56.2	72
Ratio of rostrum length to basicranial length	61.2%	58.5%	58%	58.2%	55%
Maximum width of the skull	32.3	39.7	33 [D]	43	58
Ratio of maximum skull width to basicranial length	27.8%	42.5%	33%	44.6%	44.6%
Maximum supratemporal fenestra length (cm)	29.9	26	27.5	32.2	~40
Ratio of maximum supratemporal fossa length to basicranial length	25.8%	27.8%	27.5%	33.4%	30.8%
Length of mandible (cm)	137	95.4	?	112	? [E]
Length of mandibular symphysis (cm)	58	48.6	?	47.5	? [E]
Ratio of symphysis length to mandible length	42.3%	50.9%	?	42.4%	? [E]

30 seconds to remove remaining loose particles. Each cross section was then viewed and imaged in the SEM. To manage the conductivity problems that the surrounding epoxy can cause in imaging, two small triangles of copper tape were applied near the regions of interest to aid in clear imaging. We followed the same tooth histological technique (embedding, cutting, etching, and polishing) as Hwang (2005, 2010), with the sole exception of making two cross-sections.

Cross sections were taken near the apex and the base (Fig. 1). Because the apex is a point and the base is not a flat plane, these exact regions are unattainable or would mean very little in interpreting the change in enamel throughout the tooth. To ensure repeatability, the crown was measured prior to embedding, then once embedded it was cross sectioned at locations 1/3 of the crown height from the apex and 2/3 from the crown apex. This divides the crown into thirds, allowing inspection of 2 planes of section, one representing the enamel near the apex, another near the base. Anticipating that future studies may want to compare these results with other teeth that may be too small to be readily sectioned into a greater number of units, we settled on two planes as a standard. These two planes sample sections that are most commonly retrievable despite common damage to the crown apex, and ensure that a sampling of the tooth in at least two regions along the crown height are seen so that trends along the tooth can be seen (Fig. 1).

Because the enamel sides of a conical tooth are not vertically oriented, but tilted so that they meet at the apex, none of these sections can be considered to be perfectly perpendicular to the dentine enamel junction (DEJ), making each of these slightly obliquely cut. Therefore, one cannot compare the absolute values of the thicknesses at different lengths of the crown from apex to base without considering there is some inherent error due to the potential difference in the plane of section. If the section is angled 45° from the perpendicular, then simple geometry dictates that the actual thickness will be $1/\sqrt{2}(0.707x)$ of the measured observation (the hypotenuse of the right isosceles triangle). If the difference between the measures of maximum and minimum thickness differ between the apex by more than this much, then we can assume that they are either actually different or lay at angles that differ >45°.

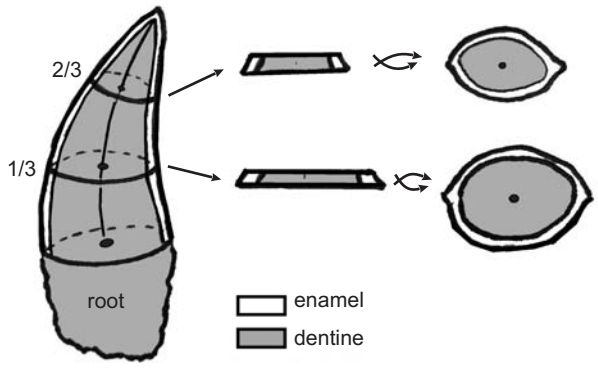

Fig. 1. Diagrammatic reconstruction of the tooth crown showing the cross sections taken.

Description

The holotype of "*Steneosaurus*" *obtusidens* (NHMUK PV R3168) is an almost complete skeleton from a large individual. The skull is robust and mesorostrine, and the mandibular symphysis is short for a teleosaurid (Fig. 2, Table 2). Currently the skull and mandible are undergoing conservation work at the NHMUK and, along with the postcranium, will be the subject of future descriptive work by the authors. In this paper we restrict our anatomical descriptions and comparative comments to the dental morphology, which is the specific focus of our SEM-based study.

The dentition of NHMUK PV R3168 is preserved as a mixture of in situ teeth and isolated teeth found associated with the skeleton. In the skull, the left premaxillary alveoli one and three hold the bases of tooth crowns in situ. All right premaxillary alveoli and the left premaxillary alveoli are empty. Most of the maxillary alveoli are lacking tooth crowns. It looks as if most of the maxillary teeth became disassociated from the skull after death. However, the dentary retains most of the tooth crowns in situ. There are noticeable reception pits on the lateral margins on the maxillae and dentaries. This shows that the dentition was orientated vertically, rather than being procumbent.

Thirty isolated teeth are known, including complete tooth crowns, broken crowns and small tooth crowns (most likely replacement teeth, with one preserved inside a fully erupted crown). Despite being small overall, the replacement teeth retain the robust and blunt morphology of the larger teeth. These isolated tooth crowns have an identical tooth morphology to those in situ.

The teeth of NHMUK PV R3168 are single cusped and conical, with little to no labiolingual compression (Fig. 3). The dentition exhibits heterodonty, with difference in tooth size and dimensions along the tooth row (although the state of preservation precludes a detailed examination). All teeth are robust, and have a ratio of apicobasal height to basal labiolingual width of less than 3. However, the distal (posterior) teeth have a ratio less than 1.8, and are smaller in overall size. Isolated teeth referred to *Machimosaurus hugii* from the Kimmeridgian of Germany also show this difference in tooth size/dimensions (Karl and Tichy 2004; Young and Steel 2014; Young et al. 2014a). The apices are blunt and rounded. No apicobasal facets are evident on either the labial or lingual faces (such as those in the metriorhynchid genus *Geosaurus*; Young and Andrade 2009; Andrade et al. 2010). The crowns are bicarinate with mesial and distal carinae, without any sign of split or supernumerary carinae (a carina that is split into multiple forks or multiple carinae located near each other, sensu Beatty and Heckert 2009). Cingula and accessory cusps/denticles are absent, as in all thalattosuchians (e.g., Vignaud 1997; Pol and Gasparini 2009; Andrade et al. 2010).

As shown by the SEM analysis, the denticles in "*S.*" *obtusidens* are what Young et al. (2013) refer to as "incipient denticles". This morphology consists of poorly defined, microscopic true denticles that are difficult to observe even

Fig. 2. Teleosaurid crocodylomorph "*Steneosaurus*" *obtusidens* holotype NHMUK PV R3168 from Peterborough, UK (Callovian, Middle Jurassic), skull and mandible; in lateral (**A**) and ventral (**B**) view.

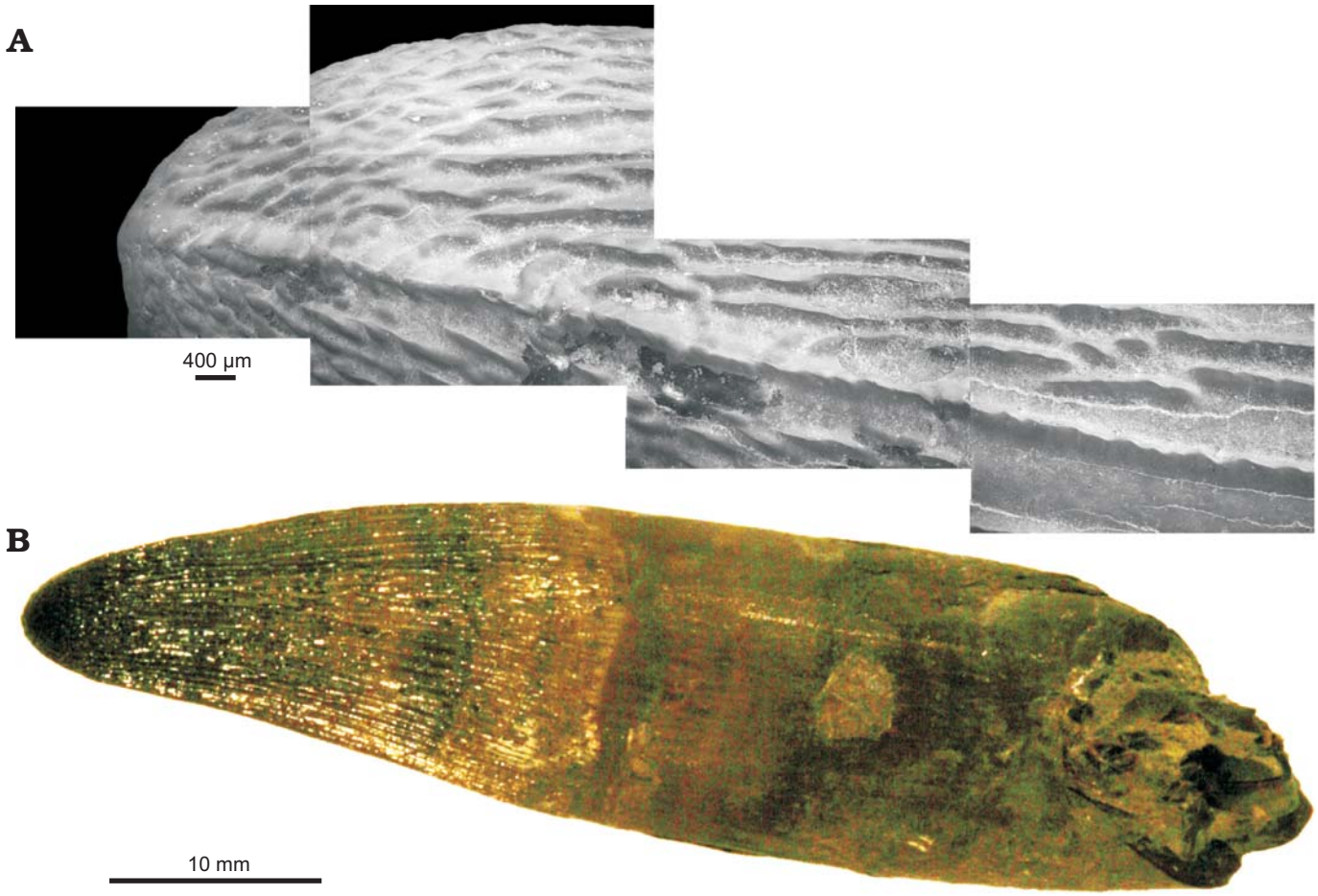

Fig. 3. Teleosaurid crocodylomorph "*Steneosaurus*" *obtusidens* holotype NHMUK PV R3168 from Peterborough, UK (Callovian, Middle Jurassic). **A**. Composite of various SEM micrographs focusing on the carina of an isolated tooth (AMNH SEM settings 20kV, WD = 13 mm). **B**. Photograph of the same tooth in lingual view.

under SEM (Figs. 3, 4; Table 1). They are present on both mesial and distal carinae, but they do not proceed along the entire carina (heterogeneous), but rather appear in small groups. The basal geosaurine metriorhynchids "*Metriorhynchus*" *brachyrhynchus* and *Tyrannoneustes lythrodectikos* share this denticle morphology (Young et al. 2013). These cryptic denticles are less than 300 μm in all dimensions (height, width, and length) and rounded in labial/lingual view. Estimating denticle densities for these taxa is difficult due to both the poorly defined nature of the denticles and the fact that they do not form a contiguous row.

We interpret "*S.*" *obtusidens* as exhibiting both true-ziphodonty (discrete serrations limited to the carina) and extensive enamel ornamentation that contributes to the keel (which in the absence of true-denticles determines the false-ziphodont condition) (Figs. 3, 4). Interestingly, this is the second thalattosuchian species with this morphology. Young et al. (2013) reported that the metriorhynchid *Torvoneustes carpenteri* also has microscopic denticles (microziphodont), and "false serrations" created by superficial enamel in the apical region. In both "*Steneosaurus*" *obstusidens* and *Torvoneustes* identification of the denticles becomes progressively more difficult towards the apex. This is due to the change in enamel ornamentation, which transitions from being composed of numerous apicobasally aligned ridges (near the base and over much of the tooth) to a general anastomosed pattern (near the apex). In the anastomosed region the enamel ridges extend onto the carinal keel, creating "false serrations" (Figs. 3, 4).

When the other isolated teeth are examined under light microscopy the serrations in the apical region are clearly visible. However, without the use of SEM the presence of true denticles cannot always be ascertained.

Prasad and Broin (2002) reported that *Machimosaurus mosae* (specimen referred to *M. hugii* by Martin and Vincent 2013) had false-ziphodont dentition. This was based on examining the photographs of the skull published by Hua (1999) (see Prasad and Broin 2002: 52). However, as the true denticles of "*S.*" *obtusidens* are cryptic and require SEM to identify, we cannot rule out the possibility that *Machimosaurus* also had true serrations like those of "*S.*" *obtusidens*.

In cross sections near the apex and base, it is clear that the apicobasally aligned ridges that ornament the surface of the crown are composed of enamel that is not uniformly thick. The DEJ can be seen to be smooth, conforming to the contours of the tooth and consistently perpendicular to the tooth's long axis. The surface texture is formed not at all by the shape of the underlying dentine, but by only the modifications of the enamel's thickness. From the regions imaged using SEM, this enamel varies in thickness from 286 μm to 227 μm (Fig. 5) at the apex, and 212 μm to 87 μm (Fig. 6) at the base of the crown. The difference of maximums between apex and base is 74 μm, and the difference between minimums of the apex and base is 140 μm. The differences in in thickness between the apex and base must be interpreted with caution because of the reasons outlined above (see Material and Methods), but it appears that these

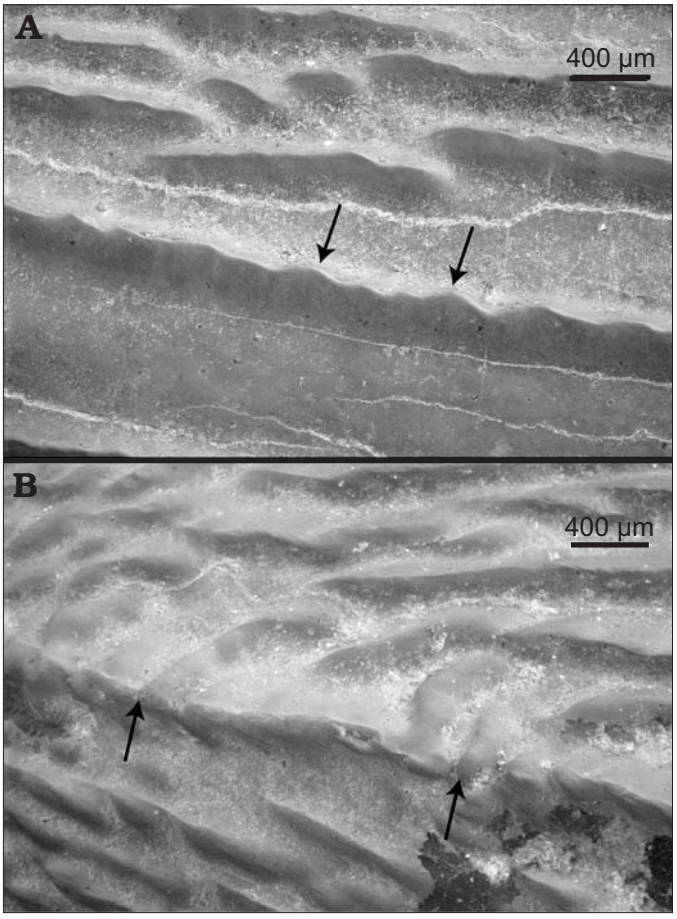

Fig. 4. Teleosaurid crocodylomorph "*Steneosaurus*" *obtusidens* holotype NHMUK PV R3168 from Peterborough, UK (Callovian, Middle Jurassic). SEM micrographs of the carina of an isolated tooth (AMNH SEM settings 20kV, WD = 13 mm), depicting denticles (arrows) formed by true-ziphodonty (**A**) and false-ziphodonty (**B**).

two are substantially greater from what one would expect if they were the same but sectioned at planes angled 45° from each other. If the minimum thickness of the apex was measured at 45° to the correct plane, then it would be 161 μm thick (>>87 μm). If the minimum thickness of the base were measured at 45° to the correct plane, then it would be 123 μm thick (<<227 μm).

The minimum thickness is a measure of the thickness of enamel in between ornamental ridges, possibly representing the morphology that the tooth would have if it lacked the ornamentation. These differences are substantial, and similar to the way in which enamel thickness has been observed to change from thin at the base to thicker near the apex in some archosauromorphs (Beatty and Heckert 2009) and squamates (Pellegrini and Beatty 2011) that lack surface ornamentation. Interestingly, a Kimmeridgian *Machimosaurus* tooth from England also shows this substantial difference in enamel thickness (Young and Steel 2014).

Maximum thickness, on the other hand, is a measure of the portion of the enamel contributing to the apicobasal ridges that ornament the crown surface. If the maximum thickness of the base was measured at 45° to the correct

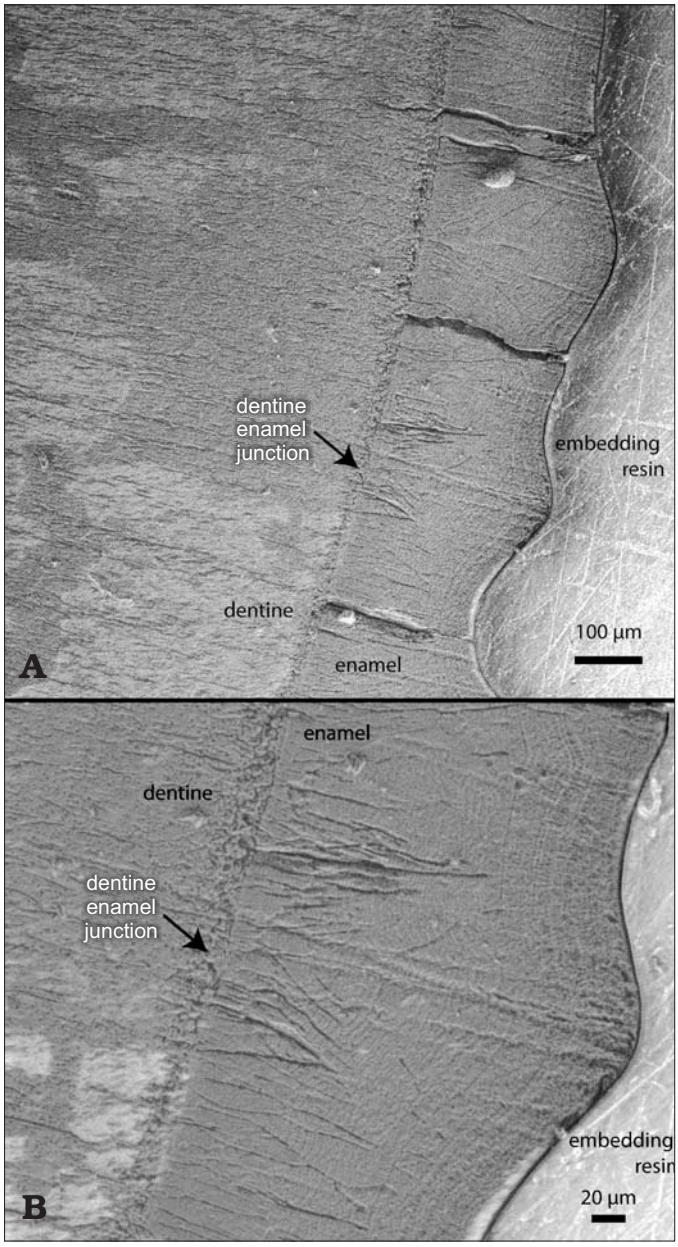

Fig. 5. "*Steneosaurus*" *obtusidens* holotype NHMUK PV R3168 from Peterborough, UK (Callovian, Middle Jurassic). SEM micrographs of cross section near the apex of an isolated tooth (AMNH SEM settings 8kV, WD = 11.5 mm), showing multiple apicobasal ridges (**A**) and one apicobasal ridge in close-up (**B**).

plane, then it would be 300 µm thick (>286 µm). If the maximum thickness of the apex was but measured at 45° to the correct plane, then it would be 202 µm thick (<212 µm). This suggests that the thickness of enamel at the ornamental ridges is not necessarily different between apex and base. The measured differences could simply be a difference of them being sectioned at different planes with respect to the DEJ, possibly up to 45° to each other. It is noticeable when observed at higher magnification (Figs. 5, 6B) that the enamel grows in layers, and that the layers closest to the DEJ are thicker than those closer to the crown's outer surface. Perhaps these differences in thickness reflect rates of growth that permit the development of these denticles during tooth development.

Discussion

Denticulation and the false-ziphodont condition.—The presence of both true ziphodonty (denticles) and false ziphodonty (superficial enamel interacting with the carinal keel) on the carinae of the same tooth is an intriguing discovery. There is currently no evidence that these morphologies are developmentally linked or homologous, and indeed, such a proposition would be difficult to test without developmental or genetic data. Instead, we suspect the simultaneous presence of both morphologies may in fact be linked to functional ecology and diet (i.e., durophagy plus a more generalist diet, see below). Both "*Steneosaurus*" *obtusidens* and the metriorhynchid *Torvoneustes* (see Young et al. 2013) have robust conical teeth, crowns with blunt apices, and intense enamel ornamentation which at the apical region transitions from being apicobasally aligned to an anastomosed pattern. It is in this anastomosed region that the enamel ridges begin to significantly interact with the keel and form false serrations. Note, however, that the posterior-most teeth of "*Steneosaurus*" *obtusidens* are far more "peg-like" in shape than those of *Torvoneustes*.

We posit that false-ziphodonty in these two taxa is a by-product of this change in enamel ridge alignment. Schmidt (1948) suggested that the apicobasal ridges seen in the metriorhynchid *Metriorhynchus superciliosus* (which are far less numerous and less pronounced than those in either "*S.*" *obtusidens* or *Torvoneustes*; see Young et al. 2013) is a way of mechanically strengthening the teeth against transverse breakage. This hypothesis has yet to be tested using experimental biomechanical methods, but if true, may indicate that false ziphodonty is an epiphenomenon of changes in enamel ornamentation that are driven by biomechanical constraints.

We also reiterate here that, at this time, we cannot discount the possibility that true ziphodonty (as well as false ziphodonty) may be more prevalent among teleosaurids, as is the case in the closely-related metriorhynchids. Only further SEM work and other detailed anatomical study can elucidate the microscopic dental morphologies of other thalattosuchian taxa.

Tooth histology and enamel structures.—Enamel ridges can be found in durophagous squamates, and sauropterygians that are also presumably durophagous, like placodonts (Sander 1999). But these dentitions also have crown shapes that are bulbous. Among possible modern ecological analogues, cetaceans have similarly thin enamel (Beatty et al. 2009; Loch et al. 2013) and possibly have similar feeding modes. The roughtooth dolphin, *Steno*, has apicobasal ridges covering its tooth, yet its diet appears no different than its sister taxon, *Tursiops*, that has smooth enamel surfaces (Nowak

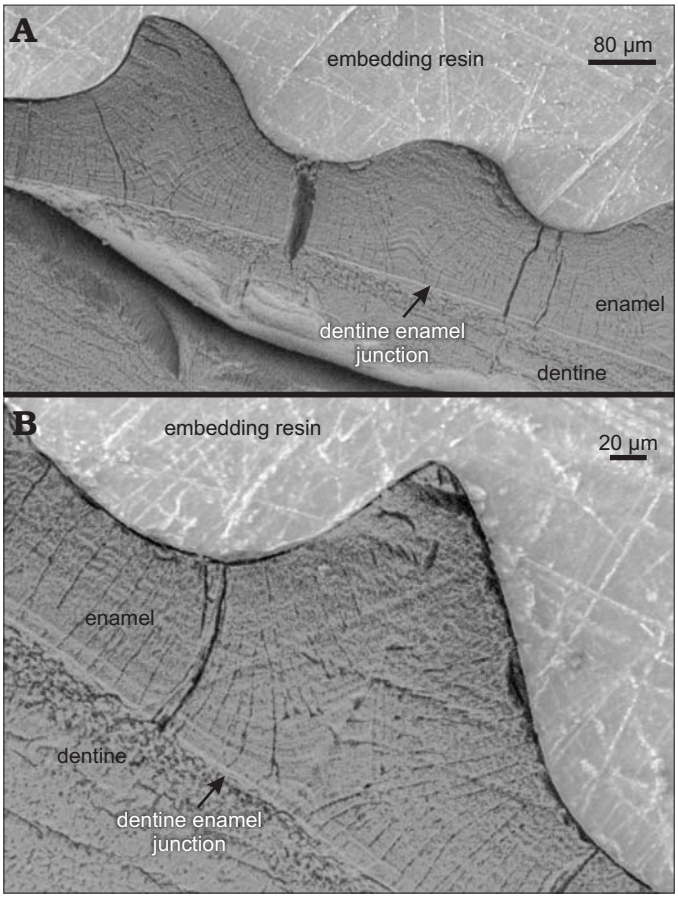

Fig. 6. Teleosaurid crocodylomorph "*Steneosaurus*" *obtusidens* holotype NHMUK PV R3168 from Peterborough, UK (Callovian, Middle Jurassic). SEM micrographs of cross section near the base of an isolated tooth (AMNH SEM settings 8kV, WD = 11.5 mm), showing multiple apicobasal ridges (**A**) and one apicobasal ridge in close-up (**B**).

2003). But recent work on the killer whale, *Orcinus*, suggests that cusp breakage patterns may reflect diet better than small amounts of wear (Foote et al. 2009; Ford et al. 2011), which makes sense considering how thin enamel is in most odontocetes. Unfortunately, data on cusp breakage frequency and how that relates to enamel structure and durophagy in crocodylomorphs or cetaceans is sorely lacking. Recent work has identified patterns of wear in some cetaceans (Loch and Simões-Lopes 2013), and perhaps further study of this topic may permit resolution of this issue.

Feeding ecology.—Studies examining *Machimosaurus* dentition suggest their crowns were adapted for seizing and crushing hard prey, especially turtles (e.g., Krebs 1968; Buffetaut 1982a; Vignaud 1997; Karl and Tichy 2004). Furthermore, direct evidence for chelonophagy among teleosaurids does exist. Marine turtle shells (Plesiochelyidae) from the "Solothurn Turtle Limestone" (Reuchenette Formation) of Switzerland have bite marks matching *Machimosaurus* teeth, and in some instances still have *Machimosaurus* teeth embedded within them (Meyer 1991). As previously noted, there is a strong similarity in dental morphology between *Machimosaurus* and "*Steneosaurus*" *obtusidens* (although the carinae are more prominent in "*S.*" *obtusidens*; Martin and Vincent 2013). However, the question of why a putatively durophagous/chelonophagous teleosaurid would have denticulated teeth is curious, as serrations are generally thought to perform cutting and slicing functions, such as the procurement of flesh (e.g., Abler 1992).

The presence of incipient, non-contiguous denticles (see Table 1) suggests that perhaps the unusual dental features in "*Steneosaurus*" *obtusidens* were not solely adaptations for durophagy, but for a more generalist diet (compared to most teleosaurids which are considered to be "marine gavials" which predated upon small, fast-moving fish/cephalopods; e.g., Hua and Buffetaut 1997).

In basal geosaurine metriorhynchids the incipient, non-contiguous denticle morphology was considered intriguing (see Young et al. 2013). There, the heterogenic nature of the denticles and their microscopic size meant they probably did not create a functional saw (little to no variation in the height of the carinal keel). However "*Steneosaurus*" *obtusidens* differs from this morphology, as the apical region has false serrations (created by the superficial enamel ornamentation) in addition to true incipient, non-contiguous denticles. This creates a more noticeable serrated edge, that most likely acted like a functional saw (i.e., the carinal keel is variable in height; see Figs. 3A, 4B). Until detailed study of more teleosaurid teeth is completed, we cannot be comment about the evolution and variation of tooth serrations among Teleosauridae.

Interestingly, the suite of craniodental adaptations observed in *Machimosaurus*-lineage teleosaurids is shared with a contemporaneous subclade of metriorhynchids, Geosaurini, a group of macrophagous predators that could have fed on larger-bodied prey than other metriorhynchids (see Young et al. 2012, 2013). (Note that we use term macrophagy as defined by Young et al. 2014b: the capability of feeding on larger bodied prey items than their phylogenetic sister taxon.) During their evolution across the Middle–Late Jurassic, these two clades of thalattosuchians convergently evolved: shortened tooth-rows (upper and lower tooth-rows with 20 or fewer teeth), foreshortened snouts (antorbital length contributing less than 60% of basicranial length), increased size of the supratemporal fenestrae/fossae, robust jaws and denticulated (serrated) dentition. It is therefore likely that *Machimosaurus*-lineage teleosaurids and geosaurins (especially *Torvoneustes*, see comparative description above) may have employed similar feeding styles and/or fed on similar prey types. These similarities also hint at a larger macroevolutionary phenomenon of iterative evolution in Mesozoic marine crocodylomorphs.

Competition between *Machimosaurus*-lineage teleosaurids and contemporaneous geosaurins would likely have been minimal due to differing habitat preference. Teleosaurids are almost exclusively known from nearshore/lagoonal environments and are believed to be shallow water ambush predators, unlike metriorhynchids which are found in deeper water deposits and have more extreme skeletal modifica-

tions for fast swimming and a fully-marine lifestyle (e.g., Buffetaut 1982b; Massare 1988; Hua and Buffrénil 1996; Hua and Buffetaut 1997; Hua 1999; Pierce et al. 2009a; Benson and Butler 2011; Young and Steel 2014). Moreover, it has even been suggested that *Machimosaurus* was well suited for turbulent environments (Hua 1999), a palaeoenvironment that has never been postulated for geosaurins. We suggest, therefore, that *Machimosaurus*-lineage teleosaurids may have been a nearshore analogue to the more open marine geosaurin metriorhynchids.

Conclusions

Thalattosuchian dentition seems to be incredibly plastic. These unusual marine crocodylomorphs exhibit variation in both macroscopic (crown morphology and enamel ornamentation) and microscopic (denticle size, density, and morphology) features. The range of dental variability can, however, be very subtle. One prime example is incipient microscopic denticles, which are usually too small to be seen with the naked eye. Only recently have these features have been discovered, and only with the use of SEM. This explains why the presence of denticles in Teleosauridae has never been previously reported.

Scanning electron microscopy of an isolated tooth from the "*Steneosaurus*" *obtusidens* holotype provides the first evidence of denticulated carinae in Teleosauridae. Furthermore, this provides the second recorded co-occurrence of true- and false-ziphodonty on the same tooth within Thalattosuchia (also seen in the geosaurin metriorhynchid *Torvoneustes*). The discovery of serrated dentition in *Machimosaurus*-lineage teleosaurids provides yet another craniodental character convergently shared with the geosaurin metriorhynchids, and suggests that both groups had similar feeding ecology, although they were able to minimize competition by inhabiting different portions of the nearshore-offshore gradient.

Recent phylogenetic analyses place "*S.*" *obtusidens* as the sister taxon to the genus *Machimosaurus*, forming a clade of durophagous/generalist teleosaurids. The discovery of serrated teeth within an otherwise durophagous crocodylomorph lineage indicates that these species had a more varied diet than originally thought. It suggests that both hard object crushing and flesh slicing were important components of the feeding repertoire of "*Steneosaurus*" *obtusidens*. Due to their large size and dietary range, "*Steneosaurus*" *obtusidens* and *Machimosaurus* would have been an important component of Mesozoic marine ecosystems, being high-order predators in coastal/lagoonal environments at the same time that some metriorhynchids were inhabiting similar niches more offshore.

The microscopic serrations reported here on the holotype of "*Steneosaurus*" *obtusidens* are too small to be seen with the naked eye and were only discovered when a tooth was subjected to SEM analysis. We anticipate that future SEM studies will help elucidate dental morphology, functional utility, and evolution in marine crocodylomorphs.

Acknowledgements

We thank James Thostenson and Morgan Hill (both American Museum of Natural History, New York, USA) for access to, and assistance with, the SEM. We also thank Jeremy Martin (University of Bristol, UK) for discussion on *Machimosaurus*. We would also like to thank Marco Brandalise de Andrade (Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil) and Angela Buscalioni (Universidad Autónoma de Madrid, Madrid, Spain) for their constructive comments that helped improve the quality of the manuscript. SLB was funded by a National Science Foundation Graduate Research Fellowship.

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