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MARCO BRANDALISE DE ANDRADE^a; MARK T. YOUNG^{ab}; JULIA B. DESOJO^c; STEPHEN L. BRUSATTE^{de}

^a Department of Earth Sciences, Faculty of Sciences, University of Bristol, Bristol, England, United Kingdom ^b Department of Palaeontology, Natural History Museum, London, United Kingdom ^c Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina ^d Division of Paleontology, American Museum of Natural History, New York, New York, U.S.A. ^e Department of Earth and Environmental Sciences, Columbia University, New York, New York, U.S.A.

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THE EVOLUTION OF EXTREME HYPERCARNIVORY IN METRIORHYNCHIDAE (MESOEUCROCODYLIA: THALATTOSUCHIA) BASED ON EVIDENCE FROM MICROSCOPIC DENTICLE MORPHOLOGY

MARCO BRANDALISE DE ANDRADE,^{*1} MARK T. YOUNG,^{1,2} JULIA B. DESOJO,³
and STEPHEN L. BRUSATTE^{4,5}

¹Department of Earth Sciences, Faculty of Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, England, BS8 1RJ, United Kingdom, marcobranda@yahoo.com.br; Marco.B.Andrade@bristol.ac.uk;

²Department of Palaeontology, Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom, zoologika@gmail.com;

³Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Angel Gallardo 470, C1405DRJ, Buenos Aires, Argentina, CONICET, julideso@maen.gov.ar;

⁴Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, U.S.A., sbrusatte@amnh.org;

⁵Department of Earth and Environmental Sciences, Columbia University, New York, New York 10025, U.S.A.

ABSTRACT—Metriorhynchids were a peculiar group of fully marine Mesozoic crocodylomorphs. The derived genera *Dakosaurus* and *Geosaurus* exhibit a macroevolutionary trend towards extreme hypercarnivory, underpinned by a diverse array of craniodental adaptations, including denticulate serrated (ziphodont) dentition. A comparative analysis of serrations in Metriorhynchidae shows that known *Dakosaurus* species had conspicuous denticles, in contrast to the microscopic denticles of *Geosaurus*. A new tooth from the Nusplingen Plattenkalk of Germany provides evidence for a previously unknown large species of *Geosaurus*. Metriorhynchid specimens from the upper Kimmeridgian–lower Tithonian of Southern Germany show that ziphodont species of *Dakosaurus* and *Geosaurus* co-occurred in the Nusplingen and Solnhofen Seas. Although these genera are similarly denticulate, they diverge in overall crown morphology. Therefore, resource/niche partitioning via craniodental differentiation is posited as maintaining two contemporaneous genera of highly predatory metriorhynchids. Additionally, the new generic name *Torvoneustes* is proposed for “*Geosaurus*” *carpenteri*, the only known metriorhynchid with false-ziphodont dentition. A cladistic analysis shows that ziphodont dentition may have evolved independently in *Dakosaurus* and *Geosaurus*, or been acquired earlier by their common ancestor and secondarily lost in *Torvoneustes* and related taxa.

INTRODUCTION

During the Mesozoic numerous clades of reptiles secondarily returned to the oceans and evolved a fully pelagic lifestyle. One such clade is the Metriorhynchidae, a peculiar group of extinct marine crocodylians that lived from the Middle Jurassic to the Early Cretaceous (~171–136 Ma). Although metriorhynchids were some of the first fossil reptiles to be discovered, investigation of large-scale evolutionary patterns within the group began only recently (see Young et al., 2010; also Pierce et al. 2009a, 2009b). Metriorhynchids, particularly *Geosaurus* and *Dakosaurus*, are recognized as fierce pelagic predators (e.g., Gasparini et al., 2006; Young and Andrade, 2009), and the only marine crocodylomorphs to possess true ziphodont (i.e., serrated) teeth. This morphology, also present in other crurotarsans and theropod dinosaurs, offers important biologic and phylogenetic signals, because it can be functionally related to food selection/acquisition and diet.

Here we use several lines of evidence to study the evolution of extreme strategies of carnivory within metriorhynchids. We describe a distinctive new metriorhynchid tooth from the Late Jurassic of Germany, and use this specimen as a springboard for detailed description and comparison of metriorhynchid dentitions. We focus on microscopic features of metriorhynchid teeth, having analyzed several specimens with scanning electron mi-

croscopy (SEM). This allows for careful description of the size and form of denticles among different taxa, and the identification of possible subtle differences between taxa that are often lumped together as ‘ziphodont.’ With detailed information on tooth and denticle morphology available, a more integrated comprehension of high-order predation in marine crocodylomorphs is possible. In particular, we use this new information to explore (a) prevalence of ziphodonty in metriorhynchids; (b) whether ziphodonty evolved multiple times in the group; (c) the stratigraphic distribution of ziphodont forms; and (d) possible ecological niche partitioning in co-existing, hyperpredatory metriorhynchid taxa due to different tooth morphologies.

Institutional Abbreviations—**BMM**, Bürgermeister-Müller-Museum, Solnhofen, Germany; **BRSMG**, Bristol City Museum and Art Gallery, Bristol, England; **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; **JME**, Jura Museum, Eichstätt, Germany; **MOZ**, Museo “Professor J. Olsacher”, Zapala Argentina; **NHM**, Natural History Museum, London, England; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Germany.

Metriorhynchids and Ziphodonty in Context

Metriorhynchids arguably represent the greatest divergence from the ‘classic’ crocodylian bauplan (taxonomy sensu Martin and Benton, 2008), and exhibit greater marine specializations than any other archosaur clade. Such adaptations include hydrofoil-like forelimbs, a hypocercal tail, and loss of

*Corresponding author.

osteoderm cover (e.g., Fraas, 1902; Young et al., 2010). As in most semi-aquatic/aquatic crocodylians, the majority of metriorhynchids were mainly piscivorous (e.g., Massare, 1987; Andrade and Young, 2008; Young and Andrade, 2009; Pierce et al., 2009b). In these taxa, teeth are essentially conical and lack any type of carinae or keel, although the enamel surface may be intensely ornamented (e.g., *Cricosaurus*). However, in both *Geosaurus* and *Dakosaurus* (Geosaurinae), tooth crowns are ziphodont, a condition that contrasts with all other thalattosuchians, as well as most other pelagic predators (e.g., Gasparini et al., 2006; Pol and Gasparini, 2009; Young and Andrade, 2009).

Ziphodont (or true-ziphodont) dentitions—defined as dentitions where all teeth possess denticulated carinae, comprised of true denticles (see Langston, 1975; Prasad and Broin, 2002; Andrade and Bertini, 2008a)—are fairly common in terrestrial crocodylian groups (e.g., Baurusuchidae, Sebecia, Pristichampsidae). They provide important clues on ecology, because they can be readily linked to diet and feeding behavior. The serrated carinae are related to more efficient processing of mechanically hard prey items, by acting as cutting edges that reduce the energy required to propagate cracks in hard food (Purslow, 1991; Freeman and Weins, 1997; Evans and Sanson, 1998). Teeth with denticulate carinae (true-ziphodonty) facilitate slicing and cutting (Frazzetta, 1988; Abler, 1992). Furthermore, Abler (1992) demonstrated that, at least for the predatory dinosaur *Tyrannosaurus*, denticles aided puncture and grip. Overall, teeth equipped with denticulated carinae require less energy to penetrate food, making larger and tougher organisms more energetically feasible prey items, expanding the range of potential prey in a particular environment. Ziphodonty therefore represents an evident adaptation to high-order carnivory, allowing equipped taxa to maximize their efficiency as predators. Therefore, it is not surprising to recognize that many high-order carnivores possess denticulated carinae (e.g., Massare, 1987).

Among marine tetrapods, serrated carinae was only reported for mosasaurs and a few ichthyosaurs (*Temnodontosaurus*, *Lep-topterygius*), although it remains unclear if these structures are composed of keels (false-ziphodonty) or true denticles.

Terrestrial crocodylians are generally believed to have evolved the ziphodont condition many times (e.g., Langston, 1975; Prasad and Broin, 2002), but less is known about the development of serrated teeth in marine forms. Currently, teeth with denticulated carinae have been reported for three species of *Geosaurus* (Tithonian–early Valanginian) and two species of *Dakosaurus* (late Kimmeridgian–early Berriasian). These include *Geosaurus giganteus* (Von Sömmerring, 1816), *G. grandis* (Wagner, 1852), *G. lapparenti* (Debelmas and Strannoloubsky, 1957), *Dakosaurus maximus* (Plieninger, 1846), and *D. andiniensis* Vignaud and Gasparini, 1996, (see Gasparini et al., 2006; Pol and Gasparini, 2009; Young and Andrade, 2009). The new German tooth described here (SMNS 81834), preliminarily placed in *Geosaurus* by Young and Andrade (2009), also possess finely serrated ziphodont carinae. Further examples include other isolated teeth (e.g., NHM R.486, NHM 47989), currently assigned to *Dakosaurus* (Table 1).

The rise of ziphodont metriorhynchids represented a major event in the evolutionary history of the group, and provides valuable clues on the rise of high-order carnivory within archosaurs and in marine ecosystems. Unfortunately, the form, distribution, and evolution of dental characters associated with high-order carnivory in metriorhynchids have only been explored in a cursory manner (Gasparini et al., 2006; Pol and Gasparini, 2009; Young and Andrade, 2009; Young et al., 2010).

MATERIALS AND METHODS

A number of specimens were analyzed by means of scanning electron microscopy (SEM), producing either secondary electron

TABLE 1. Stratigraphy of metriorhynchids from the upper Kimmeridgian–lower Tithonian of southern Germany.

German zone	Formation	Ammonite zone	Localities	Taxa (using the revised taxonomy of Young and Andrade, 2009)
Malm Zeta 3	Mörnsheim Formation	Uppermost <i>hybonotum</i> -zone	Daiting	<i>Cricosaurus elegans</i> ^a (BSPG AS I 504) <i>Rhacheosaurus gracilis</i> (Lost holotype, lost holotype of <i>C. medius</i>) <i>Geosaurus giganteus</i> ^b (NHM R.1229 , NHM R.1230) <i>Geosaurus grandis</i> ² (BSPG AS I VI 1)
Malm Zeta 2b	Solnhofen Formation	Upper <i>hybonotum</i> -zone Lower <i>hybonotum</i> -zone	Solnhofen	<i>Cricosaurus elegans</i> ^a (NHM 43005) <i>Geosaurus giganteus</i> ^b (NHM 37016–37020)
			Eichstätt	<i>Rhacheosaurus gracilis</i> (NHM R.3948) <i>Cricosaurus elegans</i> ^a (NHM 37006)
			Schernfeld Zandt	<i>Dakosaurus maximus</i> (JME-SOS4577, JME-SOS2535) <i>Rhacheosaurus gracilis</i> (Broili, 1932)
Malm Zeta 1	Painten Formation	<i>beckeri</i> -zone, <i>ulmense</i> -subzone	Painten	<i>Cricosaurus</i> sp. (BMM uncategorized)
	Mergelstätten Formation	<i>beckeri</i> -zone, <i>ulmense</i> -subzone	Schnaitheim	<i>Dakosaurus maximus</i> (Lost holotype, NHM 33186, NHM 35766, NHM 35835–7) Cf. <i>Geosaurus</i> (SMNS 51494) <i>Dakosaurus maximus</i> (SMNS 8203) <i>Dakosaurus maximus</i> (SMNS 81793)
	Nusplingen Plattenkalk	<i>beckeri</i> -zone, <i>ulmense</i> -subzone	Staufen Nusplingen	<i>Cricosaurus suevicus</i> ^a (SMNS 3808, SMNS 90513) <i>Geosaurus</i> sp. ^b (SMNS 81834)
	Rögling Formation	<i>beckeri</i> -zone, <i>setatum</i> -subzone	Schamhaupten	<i>Dakosaurus maximus</i> (JME uncategorized—M. Kölbl-Ebert, pers. comm., 2008)

For data on the geological subdivision of southern Germany see Fürsich et al. (2007) and Schweigert and Garassino (2003) and references therein. Malm Zeta 1 is the uppermost Kimmeridgian, whereas Malm Zeta 2–3 are the lowermost Tithonian. Type specimens in bold.

^aThere is a potential synonymy between *Cricosaurus elegans* and *C. suevicus*. Note that currently all specimens attributed to *C. suevicus* are restricted to Malm Zeta 1, whereas those of *C. elegans* are known from Malm Zeta 2–3.

^bThere is a potential synonymy between *Geosaurus giganteus* and *G. grandis*. *Geosaurus grandis* is known from only the Mörnsheim Formation, whereas *G. giganteus* is known from Malm Zeta 2–3. The Nusplingen species, which is a posterior maxillary tooth, is very similar in form (but bigger) to *Geosaurus* specimens in Malm Zeta 2–3.

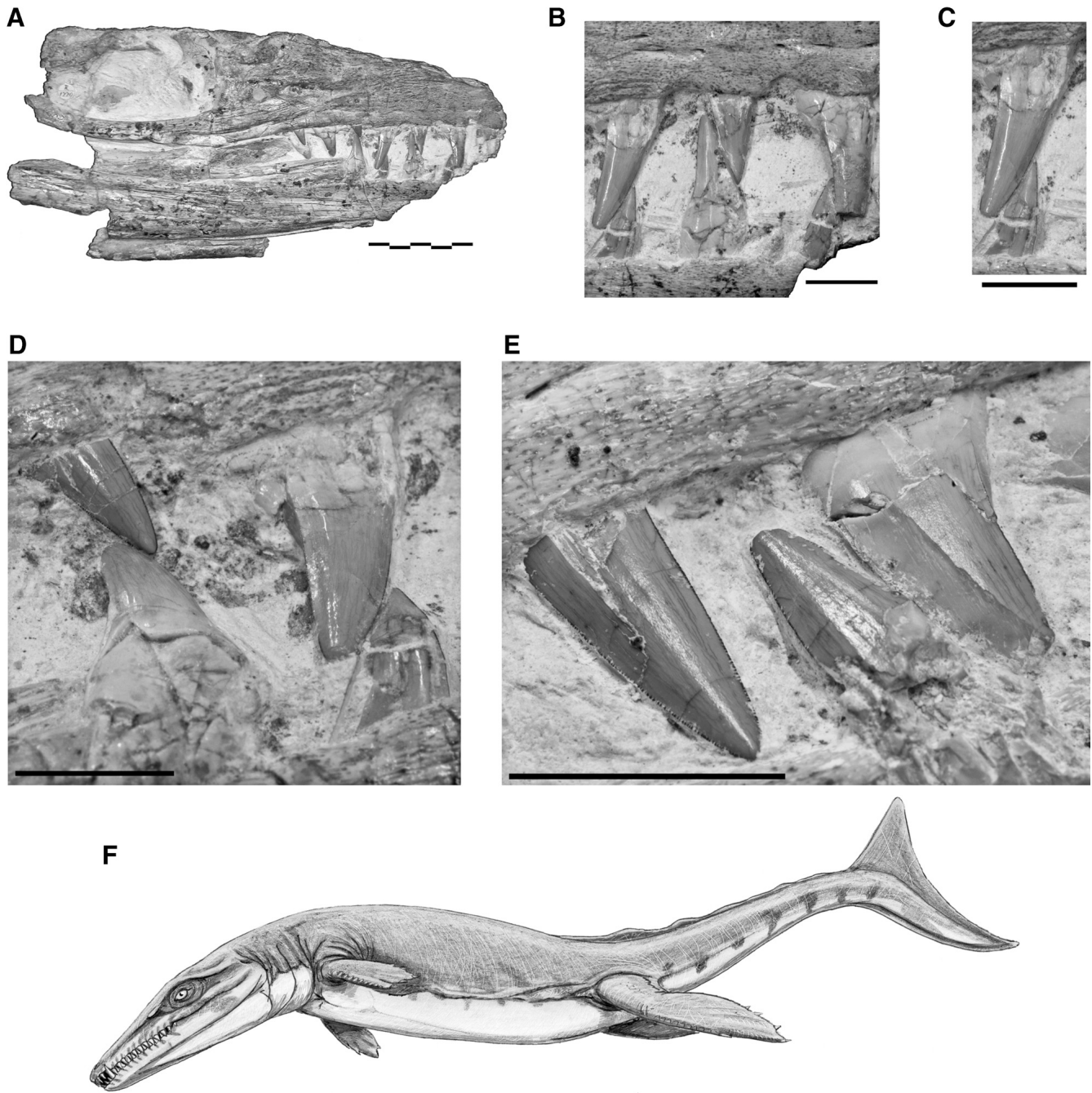


FIGURE 1. Dentition in *Geosaurus giganteus*, as seen in NHM R.1229, type specimen. **A**, General aspect of skull. **B–C**, Detail of teeth at mid-dentition, at the right side, showing the occlusion pattern and general crown morphology. **D**, Oblique view of crowns at the right side, where it is possible to note the facets and carinae. **E**, Oblique close up of teeth at the left side, where serrations in the carinae are barely perceptible. **F**, Life reconstruction of *Geosaurus*. Solid bar equals 10 mm. Life reconstruction in **F** by Dmitry Bogdanov.

(SE-SEM) or backscatter electron (BSE) images, as well as common optical microscopic techniques. All SEM analyses were conducted at the Electron Microbeam Facility (University of Bristol), under the advice of S. Kearns.

The use of SE-SEM provides images of better quality, but require gold-coating the specimen, whereas BSE-SEM avoids such damage to the fossil. As a result, BSE-SEM was applied to the majority of the specimens, whereas an isolated tooth from *Geosaurus grandis* was analyzed through SE-SEM. The dentition

of *Geosaurus giganteus*, solely represented by in situ teeth in the two known skulls (NHM R.1229 and NHM 37020), could only be imaged by light microscopy, and were registered by means of macrophotography (Fig. 1).

The new tooth, SMNS 81834 (Fig. 2), is a critical specimen due to its fine preservation and size. It is part of a larger sample of teeth collected by G. Schweigert during an SMNS excavation (May 9, 2000) in the Hoelderer Horizon (uppermost Kimmeridgian) of the Nusplingen Plattenkalk, Southwestern Germany.

TABLE 2. Measurements (minimum/maximum) for selected teeth of *Dakosaurus* and *Geosaurus*, as plotted in Figure 7.

Species	Denticle measurements			Denticle density (denticles/5 mm)	Denticle size difference index	Type
	Length	Height	Width			
<i>Dakosaurus maximus</i> (NHM 35766)	300/425	300/330	600/675	16/17	1.06	Macroziphodont
<i>Dakosaurus andiniensis</i> (MOZ 6146P)	330/500	150/200	700/800	9.5/13	—	Macroziphodont
<i>Dakosaurus</i> indet. (NHM R.486)	100/160	—	200/270	24.9/28.5	1.14	Microziphodont
<i>Geosaurus grandis</i> (BSPG AS-VI-1)	150/270	150/165	210/270	28.1	1.00	Microziphodont
<i>Geosaurus</i> indet. (SMNS 81834)	100/200	100/135	200/320	33.3/41.7	1.25	Microziphodont
<i>Batrachotomus kupferzellensis</i> (SMNS 91050)	240/345	210/450	490/700	20.8/21.4	1.03	Macroziphodont
<i>Erythrosuchus africanus</i> (NHM R.3592)	334/449	862/987	—	11.6	—	Macroziphodont
<i>Nicrosaurus kapffi</i> (NHM 38068)	231/435	430/693	295/374	14.1/18.6	1.32	Macroziphodont
<i>Phytosaurus</i> sp. (NHM R.5950)	332/457	669/902	492/701	11.9/12.3	1.03	Macroziphodont

Note that various non-metriorhynchid taxa, with typical true ziphodont teeth, are used for comparison. Microziphodont dentition will typically have carinae with denticles not exceeding 300 μm , in most or all its dimensions. Denticle density (denticles/5 mm) in selected ziphodont crocodylian tooth-crowns (measurements taken at the middle of the crown). Denticle size difference index is the ratio of the number of denticles per given length unit of the mesial and distal carina, taken from the same tooth. Data for *D. andiniensis* from Pol and Gasparini (2009). All measurements in μm . Type specimens in bold.

This tooth displays a highly characteristic crown morphology (e.g., ‘tri-faceted’ labial surface), which is otherwise only seen in *Geosaurus giganteus* and *G. grandis* (see Young and Andrade, 2009). Other teeth from the same sample include SMNS 9808, SMNS 51494, SMNS 80148, and SMNS 80480. These, however, lack any macroscopic characteristics that can be used to relate them to *Geosaurus* (see below), but also exhibit ziphodonty. Because they are comparatively robust and weakly compressed, they are preliminarily identified as cf. *Dakosaurus*, and otherwise excluded from the present study.

Specimen SMNS 81834 and other isolated ziphodont metriorhynchid teeth were analyzed with the aid of scanning electron microscopy (SEM), including the following specimens: (1) *Geosaurus grandis* (BSPG AS-VI-1 [Fig. 3]; Daiting, Germany; lower Tithonian); (2) *Dakosaurus maximus* (NHM 35766 [Fig. 4]; Schnaitheim, Germany; upper Kimmeridgian); (3) *Dakosaurus* indet. (NHM R.486 [Fig. 5]; Oxford, England; upper Callovian to lower Oxfordian). Additionally, the false-ziphodont “*Geosaurus*” *carpenteri* (BRSMG Ce17365 [Fig. 6]; Westbury, England; upper Kimmeridgian) yielded a comparative view of the tooth morphology of a non-ziphodont metriorhynchid. Finally, the Lower/Middle Triassic archosauriform *Erythrosuchus*, upper Middle Triassic ziphodont ‘rauisuchian’ *Batrachotomus*, and Late Triassic phytosaurs (*Nicrosaurus* and *Phytosaurus*) provided comparative data on terrestrial and semi-aquatic non-crocodylian taxa (see Table 2).

In order to quantify denticle size, parameters such as length, width, and height were measured (Table 2) from SEM images, following Sankey et al. (2002). Microscopic images from carinae (SEM) were mostly taken at mid-section, where denticles were best defined and preserved. Due to the small number of specimens and reduced sampling available, only maximum, minimum, and median values were calculated. Height measurements of denticles must be treated with particular caution, because (a) the identification of the base of each denticle is subjective, due to the gradual transition with the crown surface, presence of a keel and proximity to other denticles; and (b) wear and/or breaks affect height measurements with greater impact than the width or length of the denticles (see Figs. 1–4). It must be noted that ex-

treme measurements were not necessarily taken from the same denticle; therefore the denticle with the smallest length in a taxon is not necessarily the same with the smallest height or width. For the purposes of this study, the full range of size for each particular taxon is considered relevant to differentiate microscopic from macroscopic serrations, not the average values. Serration density (sensu Farlow and Brinkman, 1987) was measured as close to the mid-crown point on the carinae as possible (as recommended by Farlow and Brinkman, 1987; Farlow et al., 1991; Smith et al., 2005). The final denticle size metric used is denticle size difference index (DSDI sensu Rauhut and Werner, 1995). This metric is the ratio of the number of denticles per given length unit of the mesial and distal carinae. Total body length for metriorhynchids either follows data known from specimens (e.g., Fraas, 1901) or estimated length, as in Young (2009).

COMPARATIVE DESCRIPTION

The tooth SMNS 81834 is a well-preserved crown, with the basal section of the root present (Fig. 2B). The crown itself is relatively large in comparison to the teeth of most other thalattosuchians (e.g., *Pelagosaurus*, *Cricosaurus*); it is 31.7 mm long apicobasally and its base is 16.0 mm wide mesiodistally (longer axis). Based on comparison to complete dentitions of *G. giganteus* (NHM R.1229, NHM 37020) and *G. grandis* (BSPG AS-VI-1), SMNS 81834 appears to be a posterior tooth of either the maxillary or dentary series, and clearly is not a premaxillary or an anterior dentary tooth. In *G. giganteus*, anterior teeth tend to be slender (height/base = 2.77–2.33:1), whereas proportionally lower crowns (height/base < 2:1) are located at the mid-posterior region of the tooth row. SMNS 81834 has a height/base ratio of 1.98:1, consistent with our interpretation as a posterior tooth. In absolute size, SMNS 81834 is larger than most crowns found in *G. giganteus* (the largest crown is 35 by 16 mm, a dentary crown occluding against the premaxillary-maxillary notch of NHM 37020), and certainly much larger than all crowns of posterior teeth. Although it is difficult to produce a proper size estimate of the individual to which SMNS 81834 belonged, it seems fair to consider

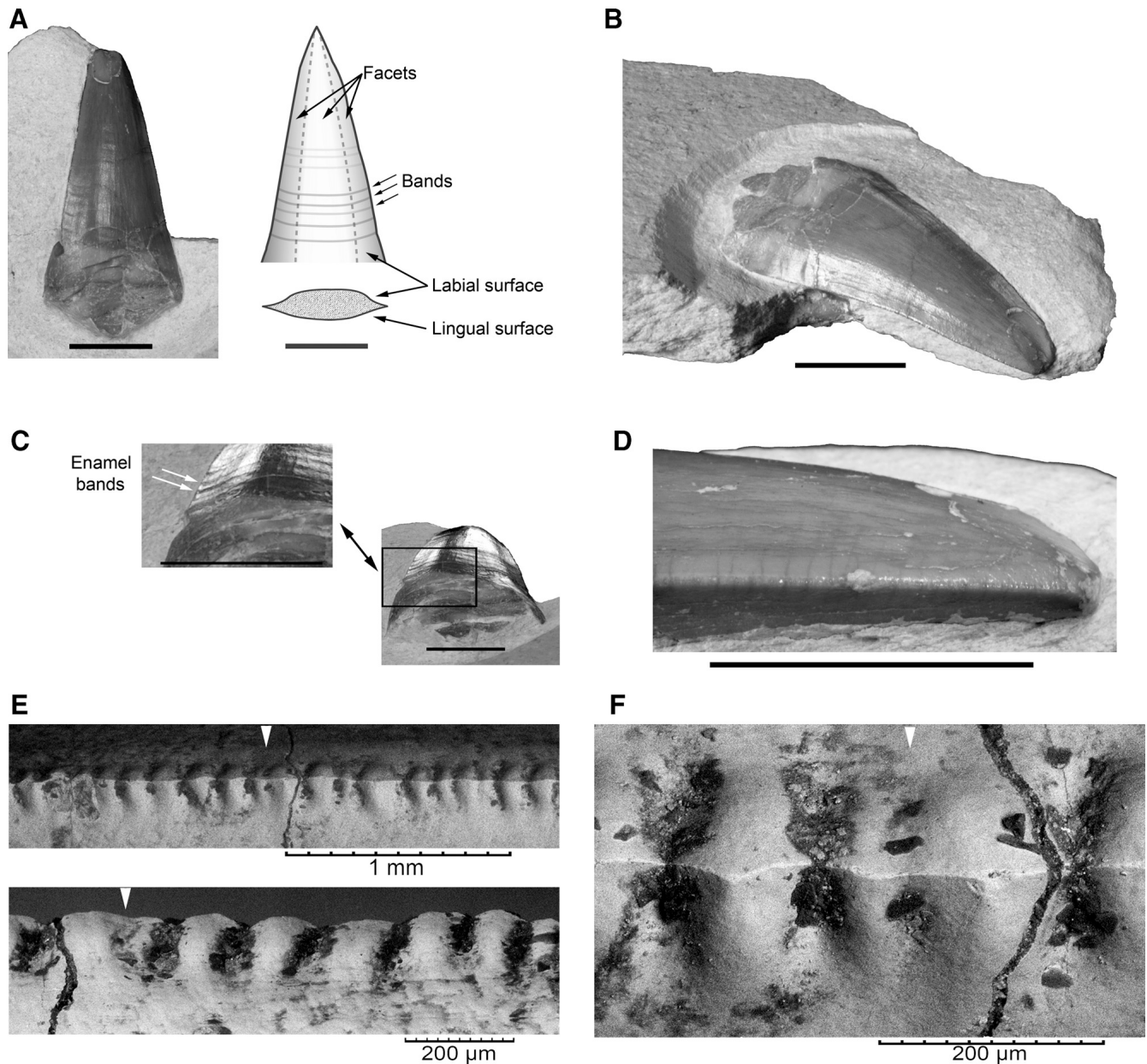


FIGURE 2. *Geosaurus* sp. SMNS 81834, from the Nusplingen Plattenkalk (upper Kimmeridgian), Late Jurassic of Germany, a single tri-faceted crown exposed at the labial surface. **A**, General view of the specimen, with main structures and cross-section made evident in schematic drawing (right). **B**, Oblique view of the crown, where the typical facets of German *Geosaurus* are evident. **C**, Low angle images of the crown, taken from the base of the tooth, showing that enamel wrinkles that cross the crown from mesial to distal edges, forming bands. **D**, Macrophotograph of crown in oblique (mesial?) view showing the carina, where denticles are barely perceptible. **E**, Microscopy images of the carina in different views, showing that the serrations are composed by microscopic true denticles. **F**, Denticles in close view, where the presence of a keel is evident. White pointers indicate a double denticle. Electron microscopy obtained through the use of backscatter secondary image (BSE). Note that it is not possible to establish whether the carina analyzed is mesial or distal, because SMNS 81834 is partially embedded in matrix and only one carina is fully exposed. Solid bar in **A–D** equals 10 mm.

this animal approximately twice the size of the largest known specimens of *G. giganteus*.

The tooth is strongly mediolaterally compressed, single cusped, and the preserved section of the root is undivided. No constriction is present at the crown/root junction, but the boundary is evident through color and texture, due to termination of enamel. The crown is laminar and curved lingually. In labial view, the crown widens constantly, assuming a triangular profile, somewhat reminiscent of *Carcharodon* teeth, rather than the teeth of

dinosaurs or other ziphodont crocodylians. On the labial face, three facets (planar surfaces) on the crown surface are clearly identifiable, progressing from base to apex. The central facet is widest at the base of the crown, and wider than the lateral facets; its mesiodistal width diminishes towards the apex and becomes more convex along the last quarter of its length. The lateral facets are symmetrical and have the same width along the entire crown. The entire lingual surface is slightly more convex than the labial surface, due to the presence of facets on the later.

The apex is damaged: the outer layer of enamel and dentine has been removed, but it is currently unclear if this is a fracture resulting from predatory behavior or damage related to taphonomy or preparation.

The crown is serrated, but serrations are microscopic. As the specimen is partially embedded in matrix, only one carina is exposed. Unfortunately, as the position of this tooth in the dental series is unknown, it is not possible to determine if the carina is mesial or distal. However, observation of *Geosaurus* teeth suggests that there are no significant differences in the morphology of mesial/distal carinae in the group (BSPG AS-VI-1, NHM R.1229, and NHM 37020).

The exposed carina of SMNS 81834 differs markedly from the false-ziphodont (sensu Prasad and Broin, 2002) dentition of “*Geosaurus*” *carpenteri* (Fig. 6), in which serrations (but not true denticles) are created on the surface of the carinal keel by the conspicuous superficial ornamentation of enamel. In SMNS 81834, carinae are comprised of both denticles and a keel, as in true ziphodont teeth (Andrade and Bertini, 2008a). Several true denticles are present at the mesial and distal borders (6.66–8.35 denticles/mm), creating well-defined carinae. In comparison with other ziphodont metriorhynchids, *Geosaurus grandis* (see Table 2) possesses a smaller number of denticles per unit length (5.62 denticles/mm), whereas species of *Dakosaurus* have even fewer (1.9–3.4 denticles/mm). In SMNS 81834, the carinae extend from the base to apex of the crown. Overall, denticles have a similar height (isometric), but shape varies substantially (poorly isomorphic). Furthermore, the size and shape of the interdenticular spaces are also variable. In a few cases, denticles are positioned extremely close together and are fused, creating larger ‘double’ denticles (Fig. 2), a condition fairly common in other ziphodont crocodylians (e.g., *Geosaurus grandis*; Fig. 3). However, some of the size differences observed in the denticles of SMNS 81834 can be recognized as the result of wear or breaks. There are only carinae on the mesial and distal edges of the tooth, with no split or supernumerary carinae (sensu Beatty and Heckert, 2009), or accessory ridges.

The individual denticles of SMNS 81834 are small, with maximum measurements of 200 μm \times 320 μm \times 135 μm (length, width, and height, respectively), with dimensions reasonably similar to those of *Geosaurus grandis* (see Table 2). The ‘rauisuchian’ *Batrachotomus*, in comparison, has much larger denticles, as do Kimmeridgian-Berriasian species of *Dakosaurus* (see Table 2). However, the Oxfordian *Dakosaurus* indet. has a maximum denticle length (160 μm) and width (270 μm) similar to the ones found in *Geosaurus* (height not sampled). The DSDI for SMNS 81834 is 1.25, which is high, when compared to other Kimmeridgian-Tithonian geosaurines (which have a DSDI around 1.0; see Table 2). In all *Geosaurus* teeth, denticles never reach 350 μm in width, and will typically have a length/height below 250 μm . Therefore, SMNS 81834 is the largest *Geosaurus* crown known to date, and is the only with denticle widths marginally surpassing 300 μm . The profile of the denticles is rounded in lingual view, but the serrations bear a sharp cutting edge (the keel) on the distal and mesial margins (Fig. 2C). This morphology is also observed in *Geosaurus grandis* (Fig. 3C–D), *Dakosaurus maximus* (Fig. 4), *Dakosaurus* indet. (Fig. 5), and *Dakosaurus andiniensis* (see Pol and Gasparini, 2009). The false-ziphodont “*Geosaurus*” *carpenteri* also has a keel, but because it lacks true denticles, its morphology can only be considered as analogous (Fig. 6).

Although both the labial and lingual surfaces of the crown of SMNS 81834 are smooth, faint ornamentation is present on both surfaces, which is only visible under SEM. The ornamentation is comprised of low hills and valleys, subcircular to elliptical in shape, formed by low and poorly marked enamel foldings. Most elongated foldings are apicobasal in orientation, and resemble the enamel foldings present in *G. grandis* (Fig. 3) and *G. gigan-*

teus. None of these foldings form the accessory ridges/keels, common in teleosaurids, goniopholidids, or pholidosaurids (M.B.A., pers. observ.), as well as some theropod dinosaurs that have teeth that superficially resemble those of crocodylians (e.g., spinosaurids: Charig and Milner, 1997; *Ceratosaurus*: Madsen and Welles, 2000). Cingula and accessory cusps/denticles are absent, as in all thalattosuchians.

Enamel wrinkles (sensu Brusatte et al., 2007) are present at least on the labial surface of the crown, extending perpendicular to the apicobasal axis of the crown. They flank the denticles and curve towards the root as they continue across the labial surface. The wrinkles are more evident on the two smaller lateral facets, but are also present across the medial facet, forming even fainter enamel bands (sensu Brusatte et al., 2007). It is not possible to verify that these bands completely encircle the crown, due to the presence of matrix. These wrinkles/bands are fewer in number and not as conspicuous as those seen in some theropod dinosaurs (see Brusatte et al., 2007). Enamel bands are also known to be present on the posterior-most maxillary teeth of *Dakosaurus andiniensis* (Pol and Gasparini, 2009) and *Geosaurus giganteus* (NHM 37020). As discussed by Brusatte et al. (2007), enamel wrinkles and bands may be remnants of tooth growth and/or a mechanical adaptation for tooth strengthening.

Characterization of Macro- and Microziphodont Dentitions

Small to large serrations in the teeth of crocodylomorphs are often reported, particularly in fully terrestrial lineages (e.g., Baurusuchidae, Peirosauridae, Sebecidae, Sphagesauridae, Trematochampsidae, *Pristichampsus*, *Araripesuchus*, “Sphenosuchia”). In all documented cases, the denticles are macroscopic and their presence can be recognized without the aid of special equipment (although proper recognition of morphology and differentiation from non-ziphodont serrations demand the use of SEM; see Prasad and Broin, 2002; Andrade and Bertini, 2008a). *Geosaurus* is the only crocodylian taxon previously reported to have a true ziphodont carina with microscopic denticles (see Young and Andrade, 2009). Before the present study, other crurotarsans with serrated teeth (e.g., *Batrachotomus*, *Baurusuchus*, *Mariliasuchus*) generally have denticles with much greater dimensions than 300 μm (Riff and Kellner, 2001; Prasad and Broin, 2002; Andrade and Bertini, 2008a; Pinheiro et al., 2008), and serrated carinae can be promptly identified.

The SEM analysis presented here show that SMNS 81834, *Geosaurus giganteus*, *G. grandis*, and the Oxfordian “*Dakosaurus*” teeth (NHM R.486, NHM 47989) have denticles of microscopic dimensions. In all such cases, these dimensions rarely surpass 300 μm (see Fig. 7; Table 2). Therefore, specimens having microscopic denticles can be easily misidentified as non-ziphodont upon simple macroscopic examination. This raises the possibility that microscopic examination of teeth in collections worldwide may reveal further examples of such microscopic serrations in taxa previously thought to be non-ziphodont. Despite size being a continuous variable, it is therefore of practical use to characterize the microscopic serrations as ‘microziphodont,’ which are currently known in SMNS 81834, *Geosaurus giganteus* (Young and Andrade, 2009), *Geosaurus grandis* (BSPG AS-VI-1), and the Oxfordian “*Dakosaurus*” (NHM R.486).

Microziphodont teeth are here defined as teeth with denticles in the carinae that are microscopic, and whose dimensions (length, width, height) typically do not exceed 300 μm . Microziphodont dentitions are those with all teeth corresponding to these parameters. Macroziphodont teeth and dentitions, on the other hand, are characterized by the presence of conspicuous serrations, clearly visible microscopy, where true denticles are present and typically exceeding 300 μm in most dimensions; this is the most common morphology among crocodylians and,

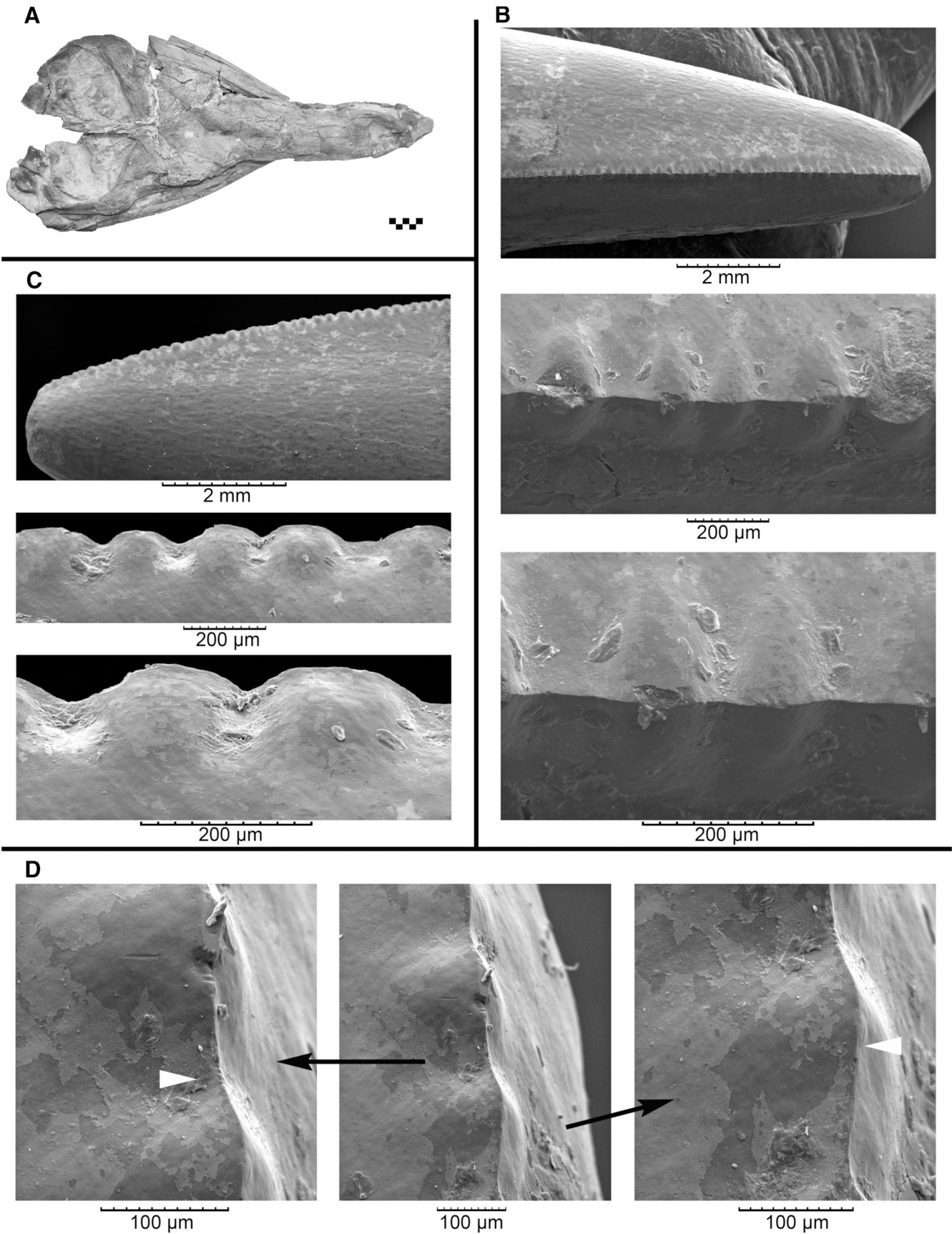


FIGURE 3. Dentition in *Geosaurus grandis* BSPG AS-VI-1, holotype, as shown in SEM. **A**, Skull in dorsal view. **B**, Carinae and denticles in occlusal view. **C**, Carinae and denticles in lateral view. **D**, Denticles in oblique view, with close details showing the presence of a conspicuous continuous keel running along the carina, both between denticles (left) and on top of each denticle (right), as indicated by white pointers. Solid bar in **A** equals 10 mm.

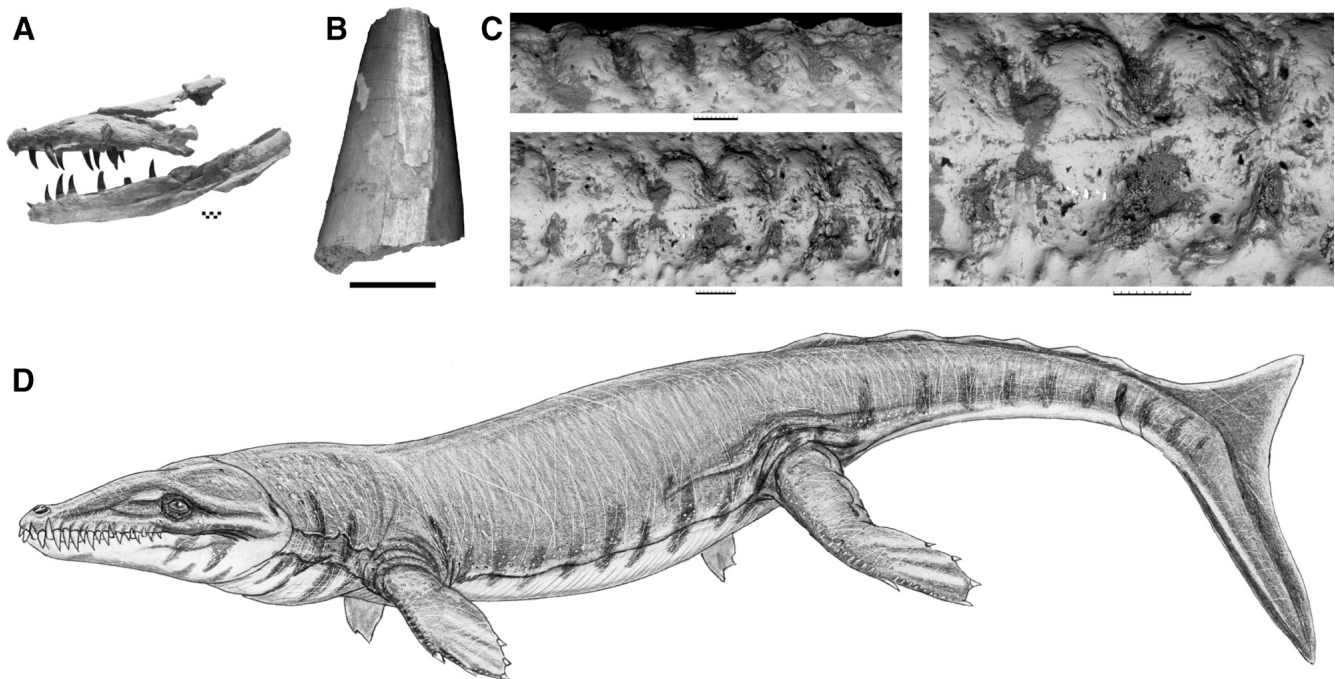


FIGURE 4. Ziphodont dentition in *Dakosaurus maximus*. **A**, General view of the skull and dentition, as seen in SMNS 8203, neotype. **B**, Close view of NHM 35766, a typical *D. maximus* crown, used in this study to access carinal morphology. **C**, BSE microscopy of NHM 35766, showing morphology of carina, in lateral (top) and occlusal (bottom) views, with detail of denticles in occlusal view (right). **D**, Life reconstruction of *Dakosaurus maximus*. Note the robustness of denticles. Solid bar in **A–B** equals 10 mm; graduated bar in **C** equals 200 μm . Life reconstruction in **D** by Dmitry Bogdanov.

possibly, in Crurotarsi. Currently, no crurotarsan species has been observed with a dentition, including both macro- and microziphodont teeth. Nonetheless, it is not necessary to create a new nomenclature to refer to this combination, because the identification of the ziphodont condition is immediate. Therefore such pattern will be consistent with the concept of macroziphodont dentition.

Microscopic denticles may pack closely in the carinae, resulting in high denticle density, which occurs in all known microziphodont taxa. However, high density alone does not imply in microscopic denticles, and can occur in macroziphodont taxa (e.g., *Batrachotomus* has denticle density $>20/5$ mm, but denticle width >400 μm ; Table 2).

PHYLOGENETIC ANALYSIS

Until recently, the evolutionary relationships within Metriorhynchidae were understudied (Mueller-Töwe, 2005; Gasparini et al., 2006; Young, 2007; Wilkinson et al., 2008; Jouve, 2009;

Pol and Gasparini, 2009). Currently, the most complete analysis includes all known valid metriorhynchid taxa (Young and Andrade, 2009). With a global phylogeny now available, it is possible to investigate the character evolution and morphological change associated with extreme marine hypercarnivory, especially concerning the microscopic and macroscopic dental features discussed in this paper.

The phylogenetic analysis herein follows Young and Andrade (2009), with the addition of SMNS 81834, and the lower Oxfordian *Geosaurus* (NHM 36336, NHM 36339) and *Dakosaurus* (NHM R.486, NHM 47989) teeth mentioned by Young and Andrade (2009) (see Appendix 1). However, as only metriorhynchids are of interest here, *Teleidosaurus calvadosii*, *Cricosaurus suevicus*, and *Rhacheosaurus gracilis* were used as outgroups and no non-metriorhynchoid crocodylians are included. The phylogenetic analysis was run in using TNT v1.1 (Willi Hennig Society Edition) (Goloboff et al., 2008). Tree space was searched using a heuristic search algorithm with TBR branch swapping and 1000 random addition replicates. The analysis was

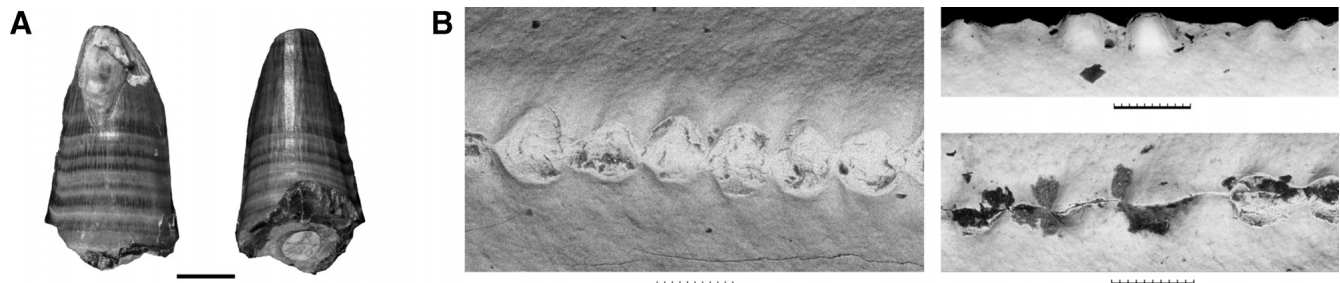


FIGURE 5. Ziphodont dentition in *Dakosaurus* indet. from the Oxford Clay Formation (NHM R.486). **A**, Close view of the crown in labial (left) and lingual (right) views. **B**, Details of carinae and denticles in BSE microscopy. Solid bar equals 10 mm; graduated bar equals 200 μm .

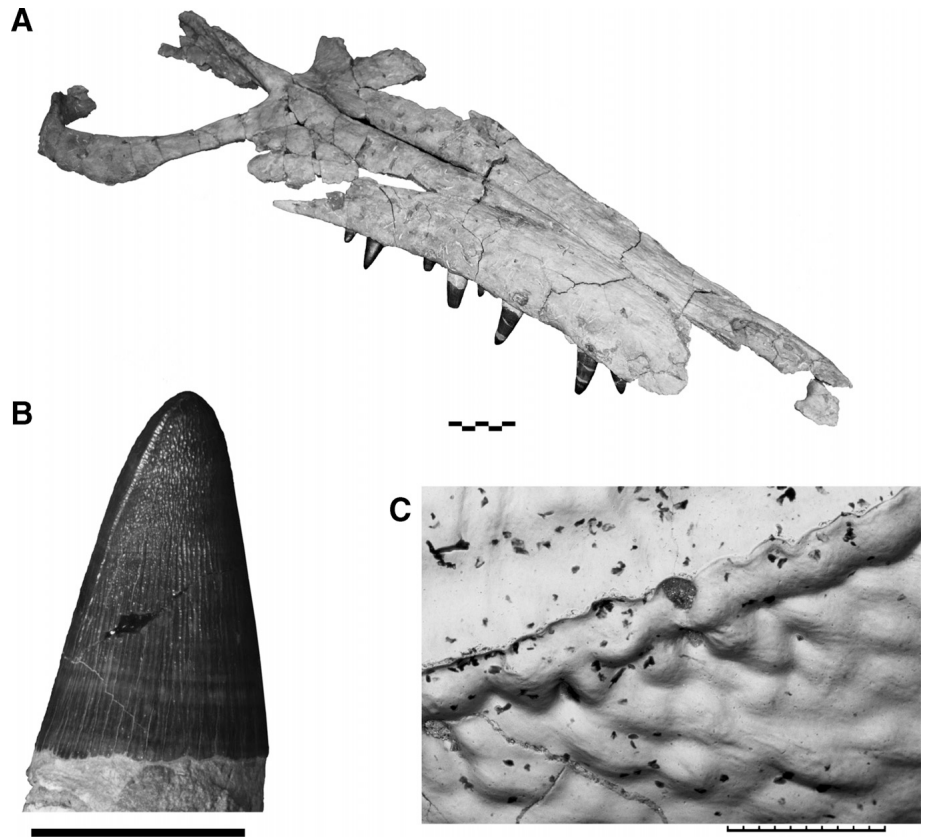


FIGURE 6. Dentition in *Torvoneustes carpenteri* (Wilkinson et al., 2008), comb. nov. **A**, Oblique view skull of BRSMG Ce17365, holotype, where the robust dentition with proportionally large teeth is evident. **B**, Crown BRSMG Cd7203, in close view. **C**, BSE microscopy of BRSMG Cd7203, where it is possible to see the false-zipodont serrations at the carina, in occlusal view. Solid bar equals 10 mm; graduated bar equals 500 μ m.

then subjected to the advanced methods in TNT, namely, sectorial search, tree fusion, ratchet, and drift. Nodal support was evaluated using two methods. Firstly, non-parametric bootstrapping (Felsenstein, 1985) with 500 replicates, each with 100 random addition sequences, was conducted using heuristic searching with TBR branch swapping. In addition, double-decay anal-

ysis (Wilkinson et al., 2000) was calculated using RadCon v.1.1.6 (Thorely and Page, 2000). Ten replicates using heuristic searching with TBR branch swapping was employed.

The analysis returned a single most parsimonious cladogram (length = 111 steps, CI = 0.903, RI = 0.902, RC = 0.781) (Fig. 8). It is clear that SMNS 81834 is more closely related to *G. giganteus* and *G. grandis* than to any other metriorhynchid species, supporting taxonomic assignment of the tooth to *Geosaurus*. Within Metriorhynchidae, two monophyletic clades of zipodont taxa are recovered: the genus *Geosaurus* (*G. grandis*, *G. giganteus*, *G. lapparenti* and the Nusplingen specimen) and the genus *Dakosaurus*.

“*Geosaurus*” *carpenteri*, the ‘Portomaggiore croc’ (see Leonardi, 1956; Kotsakis and Nicosia, 1980), and a few isolated teeth assigned to *Geosaurus* (NHM 36336, NHM 36339) cluster separately as a putative third lineage, sister taxon to true *Geosaurus*. Most of these specimens differ from *Geosaurus* and *Dakosaurus* in tooth morphology (e.g., false-zipodont and conical dentition in “*G.*” *carpenteri*; Fig. 6), but the fragmentary nature of the remains prevents further assessment of their characteristics, particularly in the case of the ‘Portomaggiore croc,’ where dentition is unknown. This clade exhibits weak nodal support, and its position is poorly corroborated (double decay index = 1; bootstrap <50%) relative to *Geosaurus* and *Dakosaurus*. Furthermore, previous analyses show that there is currently no consensus for the placement of “*G.*” *carpenteri* (formerly *Dakosaurus carpenteri*) into either of these genera (compare Wilkinson et al., 2008; Young and Andrade, 2009).

Unfortunately, character optimization regarding acquisition of zipodont carinae is ambiguous. It remains unclear whether denticulated carinae evolved early at the base of the Geosaurinae clade, and was subsequently lost in “*G.*” *carpenteri*, or if

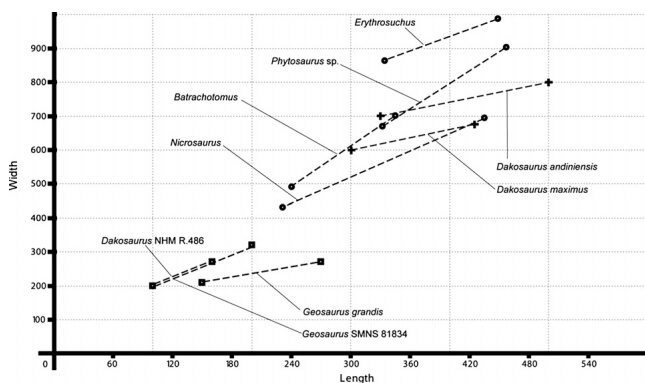


FIGURE 7. Data plot for ranges of minimum and maximum values for denticle length and width in zipodont metriorhynchids, compared against terrestrial crurotarsans (see Table 2). Note that macro- and microzipodont teeth group in different areas of the graph, and the values for *Geosaurus* sp. (SMNS 81834) plot close to *Geosaurus grandis*. Although NHM R.480 also shares microzipodont carinae, crown morphology is clearly the same as in other species of *Dakosaurus*. Ranges in dashed line. Square = marine microzipodont taxa; cross = marine macrozipodont taxa; circle = terrestrial macrozipodont taxa (basal Crurotarsi).

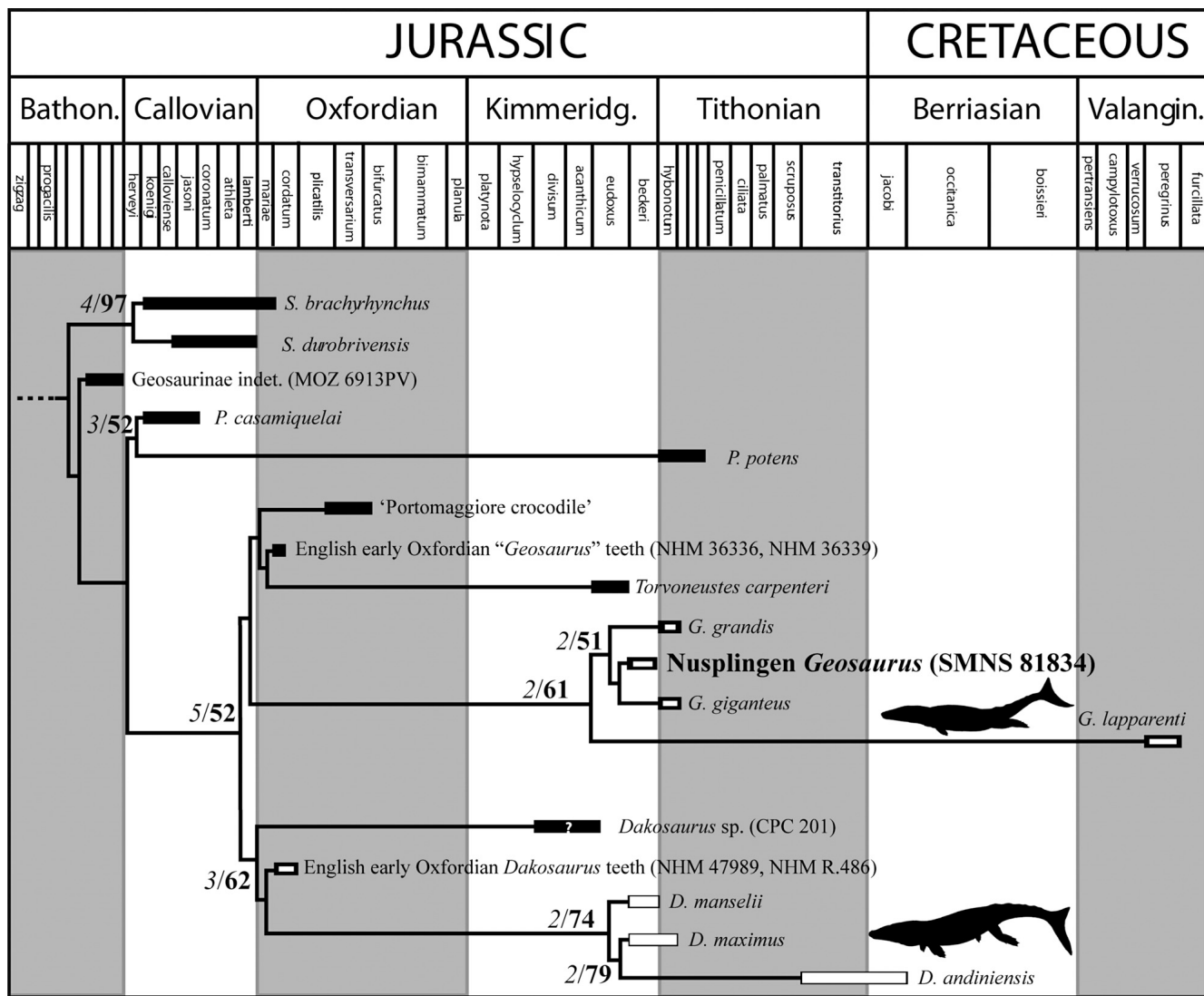


FIGURE 8. Reduced phylogeny based on Young and Andrade (2009), and including new metriorhynchid ziphodont teeth. The phylogeny is calibrated with the stratigraphical record, and firmly places SMNS 818384 within *Geosaurus*. Ziphodont taxa (white squares) may have either microscopic (small squares) or macroscopic (large squares) denticles. Note that ghost lineages extend the range of *Geosaurus* and *Dakosaurus* into the early Oxfordian. Currently, *Geosaurus* is restricted to the Late Jurassic–Early Cretaceous of Europe. Nodal support values as follows: double decay index above 1 (italicized); bootstrap above 50% (bold).

it evolved independently in *Geosaurus* and *Dakosaurus*. However, as *Geosaurus* and *Dakosaurus* exhibit different ziphodont morphologies when examined in detail, multiple acquisition of ziphodonty in metriorhynchids may be a more likely hypothesis.

DISCUSSION

Taxonomic Implications

The detailed description of microscopic and macroscopic morphology of metriorhynchid dentitions and the phylogenetic analysis herein imply some taxonomic amendments. Three major points deserve attention. First, we can show that SMNS 81834 is referable to *Geosaurus*, and represents both the largest known tooth and the oldest material currently assignable to this genus. Second, we provide a modified diagnosis of *Geosaurus*, which excludes all material with false-ziphodont/non-ziphodont dentitions, and/or with well-ornamented teeth. Third, relying on this

new diagnosis, we provide a new generic name for the highly autapomorphic, false-ziphodont “*Geosaurus*” *carpenteri*, a taxon whose phylogenetic relationships have proven controversial (i.e., divergent phylogenetic hypotheses of Wilkinson et al., 2008, and Young and Andrade, 2009).

SYSTEMATIC PALEONTOLOGY

- CROCODYLOMORPHA Walker, 1970
- CROCODYLIA Gmelin, 1789 (sensu Martin and Benton, 2008; = Crocodyliformes Benton and Clark, 1988)
- THALATTOSUCHIA Fraas, 1901 (sensu Young and Andrade, 2009)
- METRIORHYNCHIDAE Fitzinger, 1843 (sensu Young and Andrade, 2009)
- GEOSAURINAE Lydekker, 1889 (sensu Young and Andrade, 2009)
- GEOSAURUS Cuvier, 1824 (sensu Young and Andrade, 2009)

Amended Diagnosis—Metriorhynchid thalattosuchian possessing the following combination of characters: brevirrostrine to short mesorostrine snout; maxillary crowns moderately enlarged; cranial bones smooth, lacking conspicuous ornamentation; prefrontal teardrop-shaped, with the inflexion point directed posteriorly approximately 70° from the anteroposterior axis of the skull; acute angle formed by the lateral and medial processes of the frontal; antorbital fossa present and much longer than higher; lacrimal-prefrontal fossa present, with a crest along the sutural contact (adapted from Young and Andrade, 2009); strongly lateromedially compressed teeth, with crowns that may be trifaceted or not; all teeth possessing denticulate carinae with true microscopic denticles; crowns with a continuous keel at mesial and distal edges; enamel surface at labial/lingual facets lacks conspicuous ornamentation or apicobasal accessory ridges (this paper).

GEOSAURUS sp.

Material—SMNS 81834: isolated tooth partially embedded in matrix (Fig. 2).

Locality and Horizon—Nusplingen, Zollernalbkreis, Baden-Württemberg, Germany. Hoelderi horizon, Nusplingen Plattenkalk—Malm Zeta 1 (German zone), *beckeri* tethys ammonite-zone (upper Kimmeridgian, Upper Jurassic; Grawe-Baumeister et al., 2000).

TORVONEUSTES, gen. nov.

Type Species—*Torvoneustes carpenteri* (Wilkinson et al., 2008) comb. nov.

Etymology—‘Savage swimmer.’ *Torvus*- is Latin for ‘savage,’ whereas *neustes* is Ancient Greek for ‘swimmer.’ The generic named acknowledges the morphology of skull, postcrania, and dentition, which indicate a large and robust marine predator, as indicated in its original description by Wilkinson et al. (2008).

Diagnosis—As for the only known species.

TORVONEUSTES CARPENTERI (Wilkinson et al., 2008)
comb. nov.
(Fig. 6)

Metriorhynchus superciliosus (de Blainville, 1853): Grange and Benton, 1996:497, figs. 3–9.

Dakosaurus carpenteri Wilkinson et al., 2008: Grange and Benton, 1996:1307, figs. 2–10.

Geosaurus carpenteri (Wilkinson et al., 2008): Young and Andrade, 2009; Young et al., 2010.

Holotype—BRSMG Ce17365: incomplete skull (Fig. 6).

Type Locality—Westbury, Wiltshire, England (lower Kimmeridge Clay Formation). *Mutabilis* to *eudoxus* ammonite zones (Upper Kimmeridgian, Upper Jurassic).

Etymology—Carpenter’s savage swimmer.

Referred Specimens—BRSMG Cd 7203: isolated postcranial and mandibular remains (see Wilkinson et al., 2008).

Amended Diagnosis—Metriorhynchid thalattosuchian distinguished from other species of *Dakosaurus*, *Geosaurus*, and *Metriorhynchus*, by the following combination of characters: the supratemporal fossae are enlarged and project further forward than in other species; teeth somewhat smaller than those of other species of *Dakosaurus*, but larger than those of all species of *Metriorhynchus*; robust cranium, lacking ornamentation; prefrontal makes a greater angle with the long axis of the skull than in *Dakosaurus* (50 degrees), but less than in species of *Metriorhynchus* (60–70 degrees); number of teeth in each jaw ramus estimated at 14, similar to *D. maximus* and *D. andinensis* (12–16), and far fewer than in any species of *Metriorhynchus* (typically 22–29) (adapted from Wilkinson et al., 2008); acute angle formed by the lateral and medial processes of the frontal; small antorbital fenestra present, enclosed within an oblique antorbital fossa; lacrimal-prefrontal fossa present (modified from

Young and Andrade, 2009); teeth large, robust, mostly conical, but with little mediolateral compression; intensely ornamented crowns, and carinae formed by a keel with false-serrations (i.e., created by conspicuous superficial ornamentation of the enamel; false-ziphodont); anteromedial process of the frontal triangular, projecting anteriorly, reaching the same relative position as the anterior border of the orbit; mandibular symphysis longer than wide, terminating prior to the antorbital fossa (this paper).

Taxonomic Comment—Unfortunately, our phylogenetic analysis found only feeble nodal support for an expanded clade containing *Torvoneustes carpenteri*, the ‘Portomaggiore croc’ (see Leonardi, 1956; Kotsakis and Nicosia, 1980) and the early Oxfordian “*Geosaurus*” teeth NHM 36336 and NHM 36339 (Fig. 8). Therefore, whether these latter specimens can be referred to *Torvoneustes* remains uncertain. These specimens, however, cannot be considered as part of either *Geosaurus* or *Dakosaurus*.

Updated Dental Description—The teeth of *Torvoneustes carpenteri* are single cusped and conical, with slight mediolaterally compression (although newly erupted crowns can be mediolaterally compressed; BRSMG Cd7203). No constriction is present at the crown/root junctions, but the boundary is evident due to color and texture. No facets are evident on either the labial or lingual faces. Crowns are intensely ornamented. The enamel on the premaxillary, maxillary, and dentary crowns have fine apicobasally aligned ridges that become coarser away from the smooth apex. Grange and Benton (1996:505) considered the highly polished apices of the crowns to have been formed by tooth-to-food abrasion, in particular from hard prey. Furthermore, Young et al. (2010) consider the crowns of *T. carpenteri* to be indicative of Massare’s (1987) ‘general guild,’ supporting the hypothesis of feeding on hard prey items. With an estimated 14 teeth per upper tooth-row (Wilkinson et al., 2008), *Torvoneustes* has one of the shortest tooth-rows of any metriorhynchid. Moreover, along with *Geosaurus* and *Dakosaurus*, the apicobasal length of the premaxillary, maxillary, and dentary crowns in *T. carpenteri* exceed 20 mm (reaching a maximum of 32 mm in BRSMG Ce17365). All other metriorhynchid genera have teeth <20 mm in apicobasal length (M.T.Y., pers. observ.).

The teeth of the holotype bear false serrations (false-ziphodont carinae, sensu Prasad and Broin, 2002), but these are microscopic and could only be identified with the use of SEM. In this type of morphology, the ‘serrations’ are created on the surface of the carinal keel by the conspicuous superficial ornamentation of enamel (Fig. 6). False-ziphodonty is rare in Thalattosuchia: prior to its discovery in *T. carpenteri*, it was only reported in the teleosauroid genus *Machimosaurus* (see Prasad and Broin, 2002). No true denticles are present on the carinae of *Torvoneustes*, and split or supernumerary carinae were not found on any tooth.

Metriorhynchid Ziphodont Morphotypes

The general pattern of shared dental features seen in the different species of ziphodont metriorhynchids is consistent throughout the group (Wagner, 1858; Fraas, 1902; Debelmas and Stranouloubsky, 1957; Pol and Gasparini, 2009; Young and Andrade, 2009). As seen above, the only marine crocodylians possessing ziphodont teeth are *Dakosaurus* and *Geosaurus*, both of which can be diagnosed by tooth morphology alone. Furthermore, by examining crown morphology and denticle size, it is possible to recognize four well-delimited ‘groups’ within these genera, which are here proposed as morphotypes. These morphotypes enable the identification of isolated marine crocodylian teeth—particularly ziphodont teeth—allowing revision of material currently preserved in collections, or new material as it is recovered from the field.

Other metriorhynchid teeth are not included below, because they are not ziphodont, and workers should follow previous nomenclatural proposals when describing or identifying such

teeth (Prasad and Broin, 2002; Andrade and Bertini, 2008a). In most cases, non-ziphodont taxa have conical, curved teeth, with well-ornamented crowns. Unfortunately, this description applies to many taxa, and is of little taxonomic value.

The proposed morphotypes for recognition of ziphodont marine crocodylians are as follows.

Morphotype 1—Crowns poorly compressed mediolaterally, but very robust, without conspicuous ornamentation; carinae with macroscopic denticles ($>300\ \mu\text{m}$; macroziphodont). No faceting on labial or lingual surface of the crowns. Currently includes *Dakosaurus maximus* (Fig. 4) and *D. andiniensis* (Gasparini et al., 2006; Pol and Gasparini, 2009).

Morphotype 2—Crowns poorly compressed mediolaterally, but very robust, without conspicuous ornamentation; carinae with microscopic denticles ($<300\ \mu\text{m}$; microziphodont). No faceting on labial or lingual surface of the crowns. Currently includes *Dakosaurus* indet. NHM R.486 (Oxfordian “*Dakosaurus*”; Fig. 5).

Morphotype 3—Crowns strongly compressed mediolaterally, without conspicuous ornamentation; carinae with microscopic denticles ($<300\ \mu\text{m}$; microziphodont). Labial surface of the crown exhibits strong tri-faceting. Currently includes *Geosaurus giganteus*, *G. grandis* (“Solnhofen *Geosaurus*”), and *Geosaurus* sp. SMNS 81834 (Fig. 2).

Morphotype 4—Crowns strongly compressed mediolaterally, without conspicuous ornamentation; carinae with microscopic denticles ($<300\ \mu\text{m}$; microziphodont). No faceting on labial or lingual surface of the crowns. Currently includes *Geosaurus lapparenti* (Valanginian).

Inferred Diet for *Geosaurus* and *Dakosaurus*

Morphology provides a reasonable proxy for identification of diet, and it is especially important to consider functionally related characters such as type of carina, denticle morphology and density, tooth crown shape, proportional mandible depth, and presence or absence of grinding areas and worn teeth (e.g., Van Valkenburgh and Molnar, 2002; Pol, 2003; Van Valkenburgh et al., 2004; Andrade and Bertini, 2008a).

Dakosaurus and *Geosaurus* possess the proportionally shortest and deepest rostra (Gasparini et al., 2006; Pol and Gasparini, 2009; Young and Andrade, 2009) among thalattosuchians, and also proportionally deep mandibles. They also lack grinding areas on tooth crowns, although broken teeth are common (expected in predators; see Van Valkenburgh, 1988). These factors, along with tooth crown morphology, and presence of true serrations and a keel, are consistent with a hypercarnivorous diet (i.e., composed at least 70% by meat; Van Valkenburgh, 1988, 2007; Holliday and Stepan, 2004). The ziphodont dentition, along with other features of gross morphology (see Young et al., 2010), indicate that *Geosaurus* and *Dakosaurus* were well adapted not only to hypercarnivory, but to extreme strict carnivory, whereas piscivory was probably not their main dietary strategy (although fish could have been an important part of their diet).

Body size is likely to have influenced prey selection in *Geosaurus* and *Dakosaurus*, which were larger (estimated size ≥ 4 m) than their close relatives and most other putative predators in their environment (≤ 4 m), such as *Cricosaurus* (see Young, 2009). In terrestrial ecosystems there is a positive relation between prey and predator size, allowing the inclusion of prey larger than the predator itself (Van Valkenburgh and Molnar, 2002; Van Valkenburgh et al., 2004). Although energetic constraints of marine and terrestrial predators may differ from their terrestrial counterparts, tooth morphology and the larger size of ziphodont metriorhynchids are consistent with selection of proportionally large prey (including both vertebrates and invertebrates). Further, it has been shown that short-snouted metriorhynchids were biomechanically fit to perform the ‘death roll’

(Pierce et al., 2009b; Young et al., 2010), a feeding strategy that increases efficiency with predator size at an exponential rate, being particularly useful in the killing and dismemberment of large prey (see Fish et al., 2007, and references within).

The single non-ziphodont metriorhynchid to reach a comparable size to *Geosaurus* and *Dakosaurus* is *Torvoneustes* (see Wilkinson et al., 2008; Young, 2009), which is convergent on these genera by possessing a false-ziphodont dentition, and was also able to perform the ‘death roll.’ The presence of false serrations in the enamel ornamentation of *Torvoneustes* is a clear convergence towards extreme hypercarnivory, allowing a diet of large prey, although its proportionally shorter and blunter teeth were not as well suited for the penetration or slicing action that its ziphodont relatives were able to inflict (see Young et al., 2010).

Stratigraphic Range of Metriorhynchid Ziphodonty

Isolated *Dakosaurus* tooth crowns have long been known (e.g., Lydekker, 1888), but the confirmation that NHM R.486 is microziphodont extends the range of ziphodonty in metriorhynchids back into the Oxford Clay Formation (upper Callovian–lower Oxfordian). The extension of ziphodont metriorhynchids further back in time makes these crocodylomorphs the earliest known examples of both true- and false-ziphodonty in secondarily pelagic tetrapods. Nonetheless, the range of macroziphodonty in the genus seems to be substantially shorter (upper Kimmeridgian to the lower Berriasian). Unfortunately, there are no reliably known specimens of *Dakosaurus* (sensu Young and Andrade, 2009) from sediments younger than the lower Berriasian, preventing further extension of the ziphodonty range in the genus.

The new tooth, SMNS 81834, is the oldest known true (i.e., ziphodont) *Geosaurus*. The description of SMNS 81834 directly extends the range of ziphodonty in this genus, from the lower Tithonian (*G. giganteus*, *G. grandis*) to the upper Kimmeridgian. *Geosaurus lapparenti* is the youngest known geosaurine (lower Valanginian), and is the last known occurrence of ziphodonty in Metriorhynchidae (although ziphodonty persisted in terrestrial crocodylians through the Upper Cretaceous, Paleogene, and Neogene). When the phylogenetic relationships of Geosaurinae are calibrated against stratigraphy, further extension of lineages occurs through addition of ghost ranges. Considering material unequivocally assigned to *Dakosaurus*, this genus spanned at least 15.7 million years. The fossil record of *Geosaurus* currently spans only ~ 11 million years, but it is substantially increased if ghost ranges are taken into consideration. Combined, the total record of ziphodont metriorhynchids spreads over some 23 million years.

The distribution of ziphodonty in time (early Oxfordian to early Valanginian) implies that two pivotal lineages of ziphodont metriorhynchids co-existed in time for at least 16 million years. This is surprising, as in terrestrial paleoecosystems, apex predators tend to persist for much shorter periods of time (e.g., ~ 6 million years in canids; see Van Valkenburgh et al., 2004; Van Valkenburgh, 2007). Additionally, the distribution of microziphodonty in time (≥ 20 million years) is surprisingly longer than macroziphodonty (currently restricted to the *Dakosaurus* lineage; ≤ 10 million years). Therefore, microziphodonty is revealed to be the most resilient pattern in metriorhynchid history, contrasting with the pattern seen in terrestrial taxa.

Co-occurrence of *Geosaurus* and *Dakosaurus*, and Niche Partitioning in the Nusplingen Sea

Prior to the discovery of SMNS 81834, the only known co-occurrence of *Geosaurus* and *Dakosaurus* was in the Solnhofen Formation (lower Tithonian; Table 1). The new tooth shows that the two genera also co-existed in the Nusplingen Sea (Mergelstätten Formation; lower Tithonian). The co-occurrence of large-sized ziphodont species of *Dakosaurus* and *Geosaurus*

in these two seas is remarkable, especially because they shared features of gross morphology that relate to high-order carnivory (i.e., body size, aquatic adaptations, binocular vision). Dental features, on the other hand, may explain how two large predators were able to co-exist in multiple seas during much of the Late Jurassic.

Although both *Geosaurus* and *Dakosaurus* possess ziphodont teeth, their overall crown morphologies are distinct both microscopically and macroscopically. *Dakosaurus* is the only example of a marine ziphodont crocodylian with robust and recurved crowns, comparable with large theropod dinosaurs such as *Tyrannosaurus*. *Geosaurus* has slender to triangular, blade-like crowns, reminiscent of *Carcharodon*. Mechanical testing by Abler (1992) determined that the primary function of *Tyrannosaurus* denticles is to puncture and grip, and that slicing and cutting roles were secondary, whereas *Carcharodon* teeth are optimized for slicing and cutting. Taking *Tyrannosaurus* and *Carcharodon* as models for, respectively, *Dakosaurus* and *Geosaurus*, different biological functions (and diets) can be deduced for these crocodylian taxa. Furthermore, denticles in *Geosaurus* are rounder, joining smoothly the crown surface, and can be proportionally narrower than the denticles of Solnhofen/Nusplingen *Dakosaurus*, which potentially reduces the drawing force necessary to cut.

The mid-crown denticle density measurements also differ between *Geosaurus* and Kimmeridgian-Berriasian *Dakosaurus*. In the later they are within the range observed in many clades of large theropod dinosaurs (<20 denticles/5 mm, e.g., Smith et al., 2005; Brusatte and Sereno, 2007; Sereno and Brusatte 2008), baurusuchid crocodylians (e.g., Riff and Kellner, 2001; Pinheiro et al., 2008), rauisuchians (e.g., Peyer et al., 2008), phytosaurs, and *Erythrosuchus* (Table 2). In contrast, mid-crown densities of Kimmeridgian-Tithonian *Geosaurus* and the Oxfordian "*Dakosaurus*" are similar to those of small- to medium-sized theropod dinosaurs (>20 denticles/5 mm; e.g., Smith et al., 2005) and terrestrial crocodylians (e.g., Company et al., 2005). Many taxa with coarse denticle density morphology are well suited to deliver high bite forces or endure impact feeding (e.g., Rayfield et al., 2001; Rayfield, 2004), including *Dakosaurus* (Young et al., 2010). On the contrary, it is generally thought that theropod dinosaurs with higher denticle densities possessed proportionally lower bite forces (e.g., Therrien et al., 2005). Therefore, the higher denticle density in *Geosaurus* indicates that this taxon was not as adapted as *Dakosaurus* for high bite force (or impact feeding).

In sum, although *Geosaurus* and *Dakosaurus* were both able to feed on large-bodied prey, differences in their dentitions (denticle size, crown morphology, mid-crown density) indicate specialization towards 'softer' and 'harder' diets, respectively. These differences may have enabled niche partitioning, and thus the co-existence of these two large predators. *Dakosaurus*, equipped with robust and recurved crowns, was biomechanically able to withstand high bite forces, and may have included armored prey in its diet (e.g., teleosaurids, thick-shelled ammonites). *Geosaurus*, on the other hand, would have possessed a lower bite force, but the dentition, arranged as opposing blades, enabled this taxon to slice through fleshy prey more efficiently (Young et al., 2010). By abstaining from a diet of armored/shelled prey, *Geosaurus* would have reduced the hindrances of tooth breakage against heavy bones/shells (Van Valkenburgh, 1988).

CONCLUSIONS

Ziphodont teeth in metriorhynchids exhibit variability in both macroscopic (crown morphology) and microscopic (denticle size and density) features. Many of these features are subtle, and are often overlooked or entirely impossible to identify without the use of SEM or optical resources. However, when identified, these characters are useful in distinguishing isolated material and can

be utilized in broader discussions of phylogeny, macroevolutionary trends, functional morphology, and paleoecology.

Based on its possession of derived characters, the new tooth from the Nusplingen Plattenkalk (SMNS 81834) unequivocally pertains to a large species of the genus *Geosaurus* (sensu Young and Andrade, 2009). It is now evident that *Geosaurus* inhabited the Nusplingen Sea, not only *Dakosaurus* as previously thought. SMNS 81834 is currently the oldest specimen assignable to a ziphodont species of *Geosaurus*, whereas SEM analysis indicates that other ziphodont metriorhynchids were already present by the Oxfordian. Ziphodont metriorhynchid lineages persisted for longer than previously thought and co-existed in individual ecosystems, seemingly enabled by niche partitioning due to differences in craniodental morphology. Unfortunately, it is still unclear whether ziphodonty in *Dakosaurus* and *Geosaurus* is homologous or evolved independently. Further, the false-ziphodont "*Geosaurus*" *carpenteri* diverged in tooth morphology from both these lineages, and is reassigned to a new genus, *Torvoneustes*.

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APPENDIX 1. Phylogenetic analysis after Young and Andrade (2009), with the addition of the following codings for new taxa.

Nusplingen *Geosaurus* indet. (SMNS 81834)

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English (lower Oxfordian) *Geosaurus/Torvoneustes* teeth (NHM 36336, NHM 36339)

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English (upper Callovian–lower Oxfordian) *Dakosaurus* teeth (NHM 47989, NHM R.486)

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