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Tooth-On-Tooth Interlocking Occlusion Suggests Macrophagy in the Mesozoic Marine Crocodylomorph *Dakosaurus*

MARK T. YOUNG,[1,2]* STEPHEN L. BRUSATTE,[3,4] BRIAN L. BEATTY,[5]
MARCO BRANDALISE DE ANDRADE,[6] AND JULIA B. DESOJO[7]
[1]Institute of Biodiversity, Animal Health and Comparative Medicine,
University of Glasgow, University Avenue, Glasgow, UK
[2]School of Geosciences, University of Edinburgh, Grant Institute, The King's Buildings,
West Mains Road, Edinburgh, UK
[3]Division of Paleontology, American Museum of Natural History,
Central Park West at 79th Street, New York, NY
[4]Department of Earth and Environmental Sciences, Columbia University,
New York, New York
[5]Department of Anatomy, New York College of Osteopathic Medicine, Northern Boulevard,
Old Westbury, New York, New York
[6]Departamento de Paleontologia e Estratigrafia, Instituto de Geociências,
Universidade Federal do Rio Grande do Sul – UFRGS, Av. Bento Gonçalves 9500,
Porto Alegre (RS), Brazil 91501-970, C.P. 15001
[7]Sección Paleontología de Vertebrados, Museo Argentino de Ciencias
Naturales 'Bernardino Rivadavia,' Angel Gallardo 470, C1405DRJ,
Buenos Aires, Argentina

ABSTRACT

Metriorhynchidae was a peculiar but long-lived group of marine Mesozoic crocodylomorphs adapted to a pelagic lifestyle. Recent discoveries show that metriorhynchids evolved a wide range of craniodental morphotypes and inferred feeding strategies. One genus, *Dakosaurus*, is arguably the most aberrant marine crocodylomorph due to its large, robust, ziphodont teeth; very low tooth count; and brevirostrine/oreinirostral snout. We here report an additional unusual feature of *Dakosaurus* that is unique among marine crocodylomorphs: tightly fitting tooth-to-tooth occlusion, whose inference is supported by reception pits along the upper and lower tooth rows, indicative of vertically orientated crowns that were in close contact during occlusion, and three distinct types of dental wear. These include irregular spalled surfaces near the apex (probably caused by tooth-food contact), semi-circular wear near the base, and elongate surfaces extending along the mesial and distal margins of the teeth, obliterating the carinae (including the denticles). Scanning electron micrographs show that these latter surfaces are marked by parallel apicobasal striations, which in extant mammals reflect tooth–tooth contact. As such, we interpret the carinal wear facets in *Dakosaurus* as being formed by repeated tooth–tooth contact

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Abbreviations used: AMNH = American Museum of Natural History, New York, United States; MGGC = Museo Geologico Giovanni Capellini, Bologna, Italy; NHMUK = Natural History Museum, London, United Kingdom; SMNS = Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany).

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*Correspondence to: Mark T. Young, School of Geosciences, University of Edinburgh, Grant Institute, The King's Buildings, West Mains Road, Edinburgh, UK. E-mail: zoologika@gmail.com

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between the mesial and distal margins of the teeth of the upper and lower jaw. We posit that this increased the available shearing surface on their high crowns. Together, these wear patterns suggest that occlusion in *Dakosaurus* was specialized for cutting large and abrasive prey items into portions small enough to swallow, making it a prime example of an aquatic reptile with macrophagous feeding habits. Anat Rec, 295:1147–1158, 2012. © 2012 Wiley-Periodicals, Inc.

Key words: feeding; functional ecology; Metriorhynchidae; occlusion; Thalattosuchia

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INTRODUCTION

Metriorhynchids were a diverse and successful group of pelagic crocodylomorphs that had a near global distribution from the Middle Jurassic to the Early Cretaceous (ca. 168–134 million years ago; Fig. 1; Debelmas, 1952; Hua and Buffetaut, 1997; Young et al., 2010, in press). Within Metriorhynchidae, the genera of the subclade Geosaurini exhibit a wide range of craniodental morphologies and hypothesized feeding strategies (Pierce et al., 2009a,b; Young and Andrade, 2009; Andrade et al., 2010; Young et al., 2010, 2011, in press). Within this subclade, the genus *Dakosaurus* is perhaps the most aberrant, as it possesses several characteristics that are highly unusual for a marine crocodylomorph, such as: large, robust, and ziphodont teeth that resemble the dentition of large theropod dinosaurs; a very low tooth count (13 or less in the maxilla and dentary); a brevirostrine/oreinirostral snout; and a skull that is the strongest of any metriorhynchid (based on biomechanical tests; Fig. 2; Fraas, 1902; Gasparini et al., 2006; Pierce et al., 2009a,b; Pol and Gasparini, 2009; Andrade et al., 2010; Young et al., 2010, in press). These features suggest that *Dakosaurus* was a large-bodied megapredator that was well adapted for feeding on large prey (macrophagy), and as such, was likely an apex predator in many Mesozoic marine ecosystems.

Another unusual feature of *Dakosaurus*, which has been briefly noted and figured by previous authors but largely overlooked (e.g., Mason, 1869), is the common occurrence of elongate macroscopic wear surfaces that obliterate the carinae along the mesial and distal margins of the teeth (Fig. 3; Young et al., in press). Wear surfaces are uncommon in non-mammalian amniotes, but can be caused by a variety of processes such as tooth/tooth contact (attritional wear), tooth/food contact (abrasive wear), or chemical alteration (erosive wear; Pickles, 2006). Aside from wear indicating herbivory in animals with molariform teeth, wear in predators usually comes in two forms: shearing facets that are indicative of tightly fitting occlusion, and apical wear indicative of contact with food items. Excellent examples of tight fitting occlusion of shearing facets can be seen among the carnassial teeth of modern carnivorans (Schubert et al., 2010), on the lateral teeth of large theropod dinosaurs such as *Tyrannosaurus* (Schubert and Ungar, 2005), as well as in the early evolution of whales during the transition from molariform teeth used for herbivory to more conical teeth used for reducing larger prey into smaller pieces (Thewissen et al., 2011). Apical wear, and even complete cusp breakage, is apparent among some modern odontocetes that feed on large and/or abrasive prey items (Werth et al., 2007; Foote et al., 2009; Ford et al., 2010), as well as large theropods that employed strong bite forces to break bone during feeding (Schubert and Ungar, 2005). Tooth wear patterns, therefore, have the potential to reveal critical information about the biology and feeding habits of vertebrates, which is especially important when studying aberrant extinct taxa, such as metriorhynchids, with no obvious modern analogues.

Here, we describe the characteristic wear patterns of *Dakosaurus* in detail and note that three distinctive types of wear are present, including spalled apical facets, semi-circular basal facets, and the previously recognized elongate surfaces along the carinae (Fig. 3). We interpret the apical spalling wear as being formed by repeated contact with abrasive food, such as bone, and interpret the carinal wear as representing the first evidence of attritional wear, and therefore tooth–tooth occlusion, in a marine crocodylomorph. Instrumental to our interpretation of tooth-on-tooth occlusion is evidence from both overall morphology of the tooth bearing bones and scanning electron microscopy (SEM) of the wear facets. First, we report tooth reception pits that are present on both the upper and lower jaws of *Dakosaurus* (Fig. 4), indicating that the teeth were vertically orientated and interlocked in an en-echelon fashion (confirmed *in situ* for *D. andiniensis*; see Pol and Gasparini, 2009). Second, SEM results show that repeated apicobasal striations are present along the carinal wear facets (Fig. 5), similar to striations interpreted as evidence of occlusal contact in crocodylomorphs, mammals, and dinosaurs (e.g., Barrett, 2000; Pol, 2003; Schubert and Ungar, 2005; Andrade and Bertini, 2008a,b,c). In a similar way, microwear has been used to confirm the use of teeth in feeding, or the existence of occlusion, in other vertebrate groups, ranging from anomodonts (Rybczynski and Reisz, 2001) to conodonts (Purnell, 1995).

These observations of overall cranial morphology and tooth wear permit a refined understanding of the paleobiology and dietary habits of *Dakosaurus*, one of the most unusual predators of the Mesozoic seas. We posit that apical spalled wear and breakage in *Dakosaurus* may be indicative of prey items either being large or abrasive (which may include bone), or both. Occlusion in *Dakosaurus* may have been integral in dismembering prey items larger than could be swallowed whole, and as

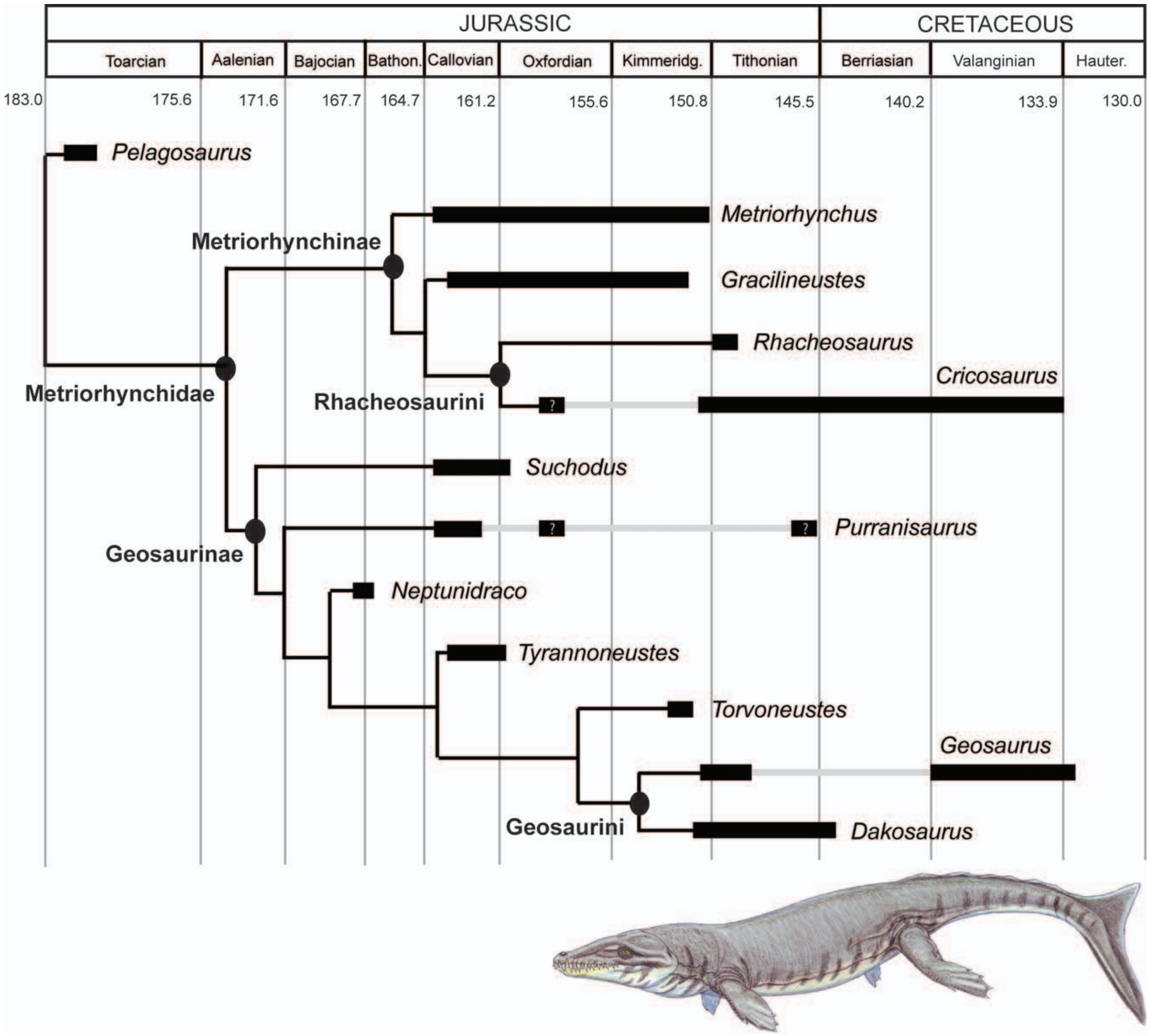

Fig. 1. Genus-level evolutionary relationships of Metriorhynchidae based on the phylogenetic analysis of Young et al. (in press) and calibrated by the geological timescale based on Ogg et al. (2008). *Pelagosaurus* is the closest-known genus of marine crocodyliform that lacks the extensive pelagic adaptations of metriorhynchids (e.g., hydrofoil-like forelimbs, hypocercal tail, and loss of osteoderms). The time-span of genera with question marks is uncertain, and the gray bars are range extensions. Life reconstruction of *Dakosaurus maximus* is by Dmitry Bogdanov.

such, was another feature related to the hyperpredatory lifestyle of this unusual genus.

MATERIALS AND METHODS

We examined numerous *Dakosaurus maximus* teeth, both isolated (~80 from the collections in both NHMUK and SMNS, see Fig. 3) and *in situ* (SMNS 8203, SMNS 10819, and SMNS 82043, see Figs. 2 and 4). One representative tooth crown was chosen for investigation of wear patterns through scanning electron microscopy (SEM). This tooth (NHMUK-PV OR20283) is one of many isolated crowns from the Late Jurassic (late Kimmeridgian) type locality of *Dakosaurus maximus* (Schnaitheim, Baden-Württemberg, Germany). Previously, the serration morphology of one such tooth (NHMUK-PV OR35766) was investigated using SEM (Andrade et al., 2010). For the current project, NHMUK-PV OR20283 was analyzed by means of SEM, producing backscatter electron (BSE) images. The SEM analyses were conducted at the Microscopy and Imaging Facility at the American Museum of Natural History (New York).

To investigate the reception pits of *D. maximus* and to better understand its occlusion pattern, we examined specimens with dentigerous bones that preserved the crowns *in situ* (Figs. 2 and 4). These specimens come

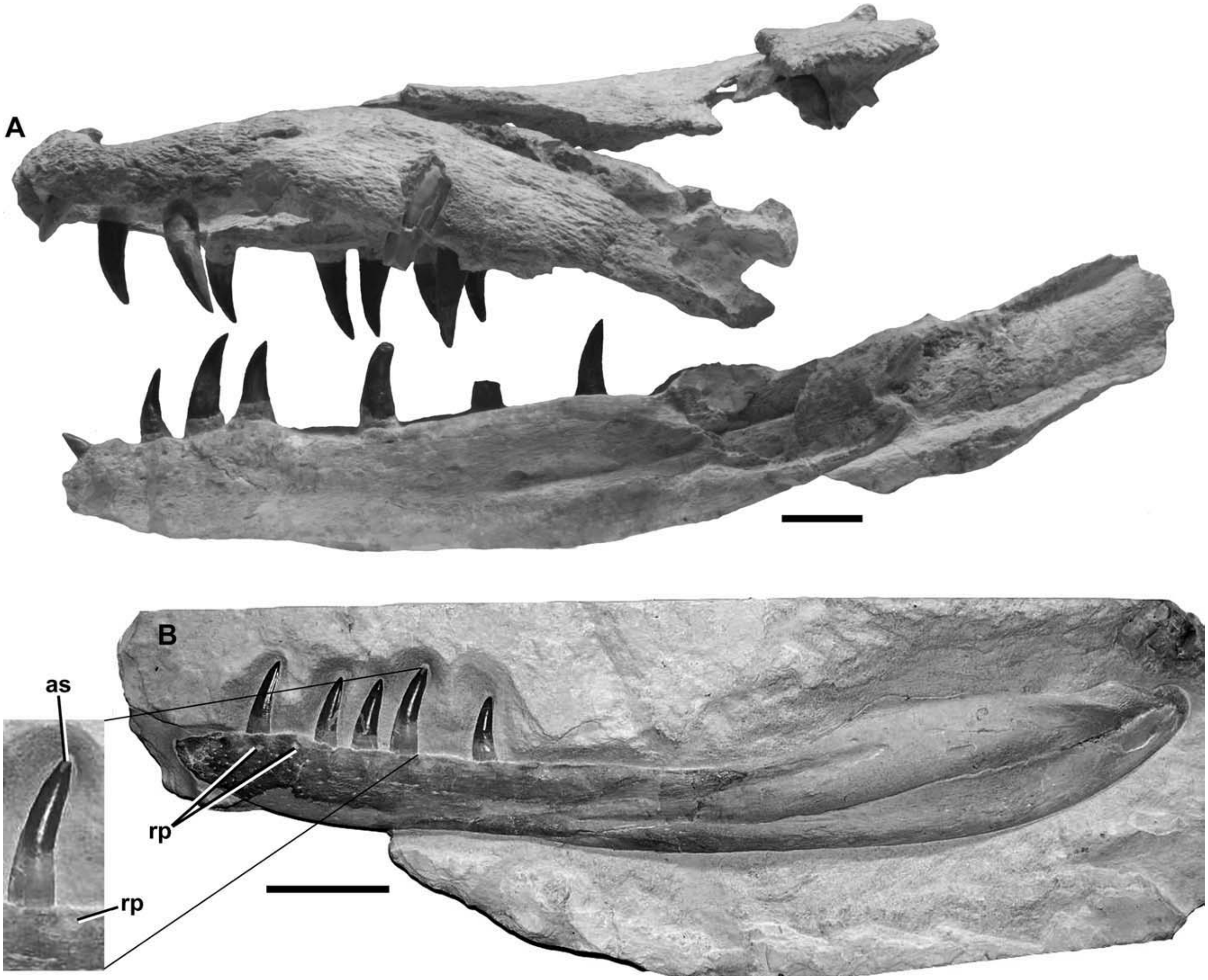

Fig. 2. *Dakosaurus maximus* skull and mandible. **A**: General view of the skull and dentition, in the neotype SMNS 8203. **B**: General view and close-up of an isolated mandible SMNS 82043. Abbreviations: as, apical spalling; rp, reception pits. Scale bars equal 5 cm.

from multiple late Kimmeridgian localities in Germany, with the neotype (SMNS 8203) from Staufen bei Giengen, Baden-Württemberg; a poorly preserved snout (SMNS 10819) from Sontheim an der Brenz, Baden-Württemberg; and a left mandibular ramus preserved in lithographic limestone (SMNS 82043) from Painten, Bavaria.

Overall, dental wear patterns were observed visually and dental microwear was observed using SEM. Dental microwear involves the study of complex patterns of microstriations and pits on a tooth surface, usually the result of complex masticatory events. As most non-mammalian amniotes use their teeth simply to grasp prey and have simple orthal mastication capabilities, the type of dental microwear analysis commonly used to study ungulates and primates (which are capable of more complex jaw movements) is not appropriate. Most microwear studies of non-mammalian amniotes recognize this limitation, and have focused primarily on identifying the presence/absence and form of occlusion and the direction(s) of jaw motion (e.g., Fiorillo, 1998; Rybczynski and Reisz, 2001; Williams et al., 2009; Varriale, 2011; Whitlock, 2011).

Although many microwear methods now exist, SEM and most light microscopy techniques utilize micrographs in which microstriations and pits are identified and marked by a human observer. Although most observers appear able to discriminate distinct microwear patterns associated with specific ecological patterns, observer error in the recognition of these microwear features makes it important for the same observer(s) to do the analyses (Mihlbachler et al., in press). Microwear in this study was limited to a small number of specimens, but all were done by the same observers working together (BLB and SLB) using SEM. Microwear here is limited to qualitative descriptions, as comparative samples of living archosaurs were not available at this time. Even if available, these comparisons would have limited utility because one major clade of living archosaurs has no teeth (birds), whereas the other does not include any

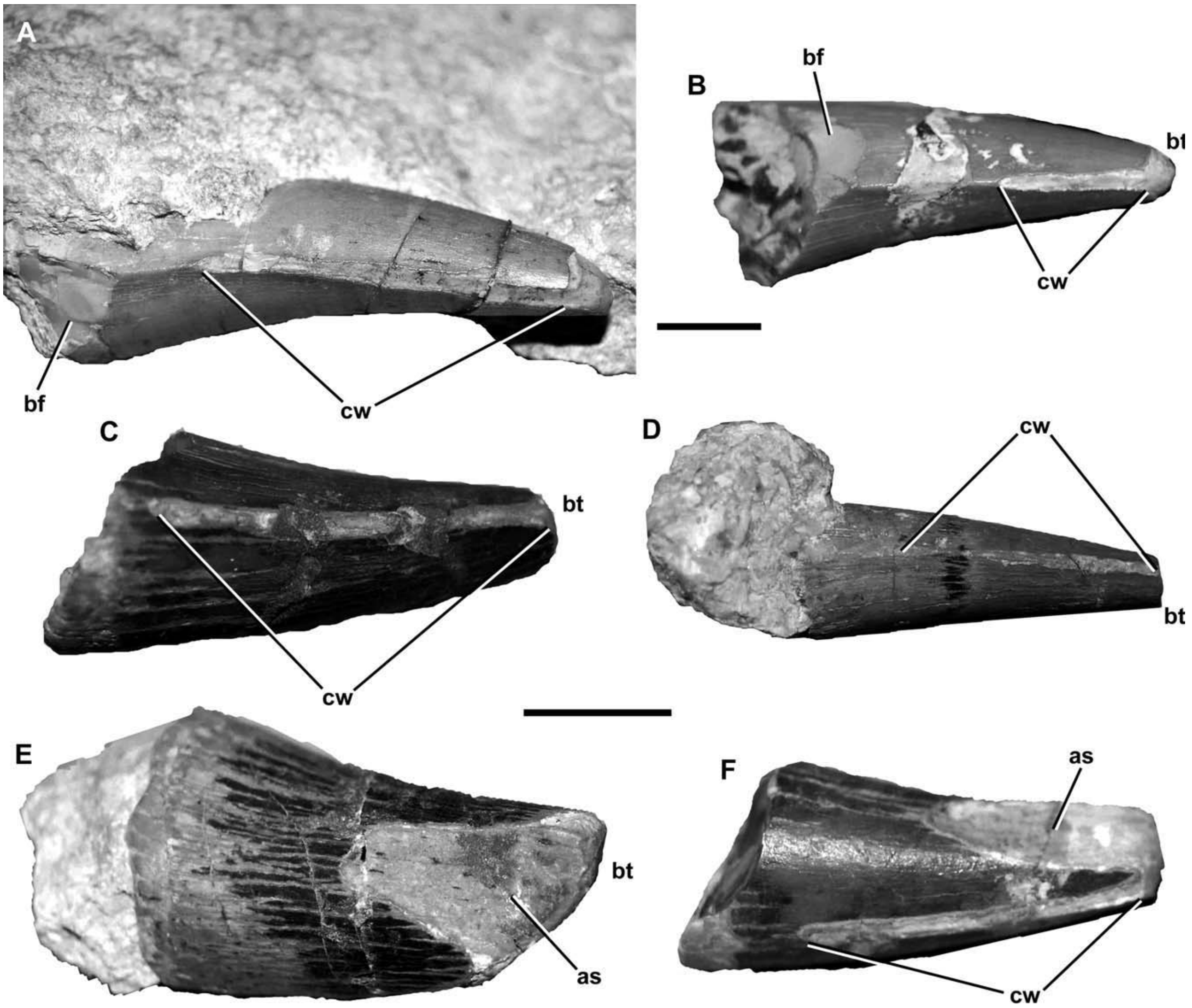

Fig. 3. Isolated teeth of *Dakosaurus* from the SMNS collection showing wear patterns and apical breakage. Abbreviations: as, apical spalling; bf, basal facet; bt, broken tip; cw, carinal wear. Scale bars equal 1 cm. Top scale bar for images **A**–**B**; bottom scale bar for images **C**–**F**. A: SMNS 9808; B–F: SMNS 91425.

extant taxa with occlusion patterns similar to those hypothesized for *Dakosaurus* (living crocodylians: e.g., Schubert and Ungar, 2005).

RESULTS

Macroscopic Wear/Spalling Patterns

Examination of numerous *Dakosaurus* teeth, both isolated (NHMUK and SMNS specimens) and *in situ* (SMNS 8203, SMNS 10819, and SMNS 82043), and of different size and position, shows that three distinct types of macroscopic wear features are often present: spalled enamel near the apex (Fig. 3, as, bt), occlusal wear along the mesial and distal margins (i.e., along the carinae; Fig. 3, cw) and a second wear facet at the base of the crown which is semi-circular (Fig. 3, bf).

Enamel spalling is present on either the labial or lingual surface of numerous isolated teeth, as well as some *in situ* teeth (Figs. 2 and 4), and can be extensive (SMNS 9808; Fig. 3, as). The spalled surfaces are usually a discrete ovoid or triangular facet, which begins at the crown apex and proceeds basally. Previous work has shown that enamel spalling is likely created by impact between the tooth and a prey item, in the same axis in which the jaws close (see Schubert and Ungar, 2005). The teeth of tyrannosaurid dinosaurs, which are similar in size and shape to those of *Dakosaurus*, also exhibit enamel spalling that is interpreted as tooth–food abrasion (Schubert and Ungar, 2005). Tyrannosaurids are unusual among theropod dinosaurs in exhibiting repeated instances of such spalling, which is likely tied to their aberrant feeding style in which they used strong bite forces to break the bones of their prey items—an

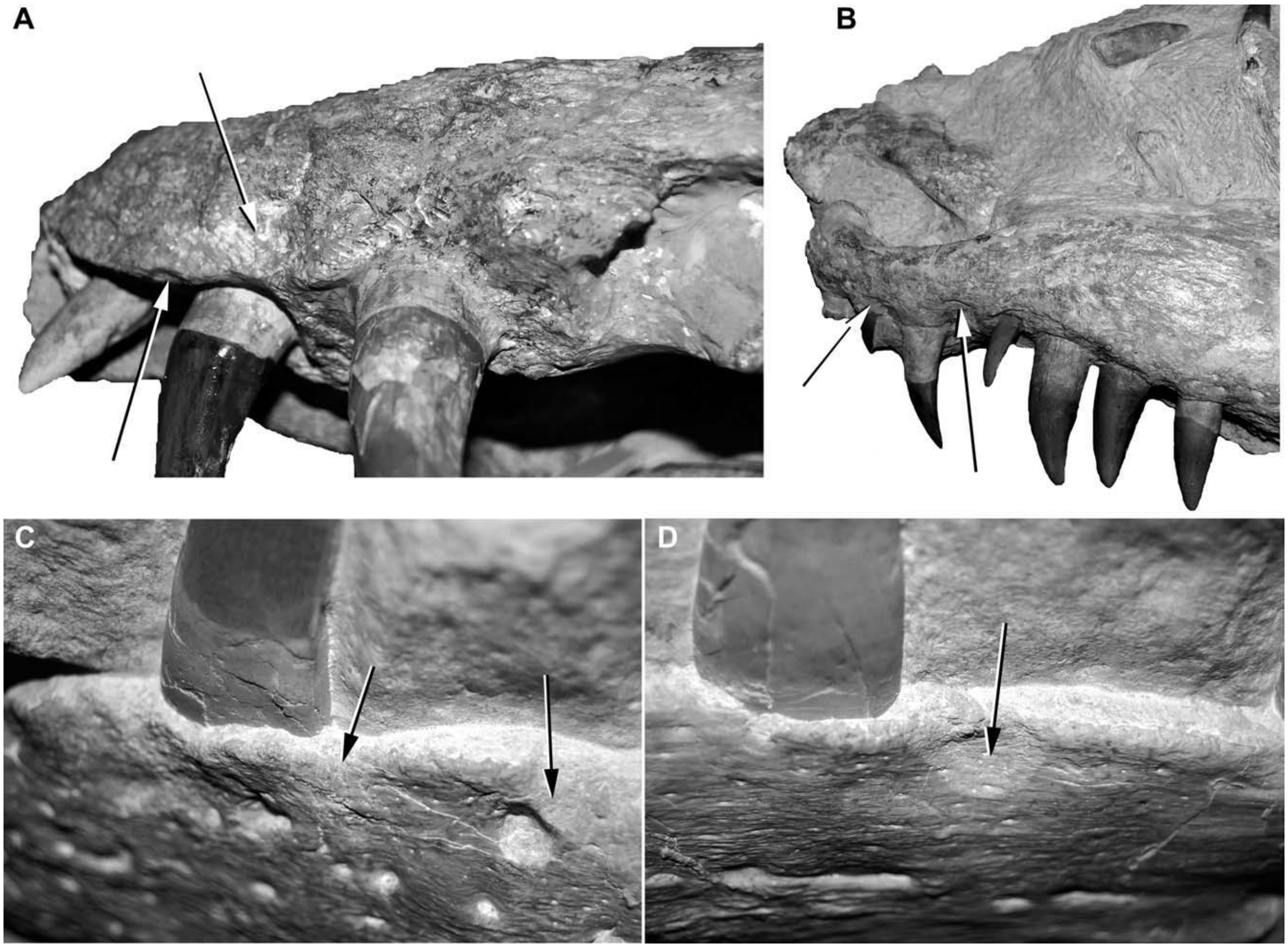

Fig. 4. Reception pits on the dentigerous bones of *Dakosaurus maximus* (indicated by arrows). **A**: Upper jaw reception pits on the neotype, SMNS 8203; **B**: upper jaw reception pits on SMNS 10819; **C** and **D**: lower jaw reception pits on SMNS 82043. For scale, refer to Fig. 2.

unusually hard substance—during feeding (e.g., Erickson et al., 1996; Chin et al., 1998; Rayfield, 2004; Schubert and Ungar, 2005). Extreme spalling and complete tooth breakage patterns have been observed in aquatic amniotes such as the extant killer whale *Orcinus orca* (Foote et al., 2009; Ford et al., 2011), the fossil killer whale *Orcinus citoniensis* (Fig. 6a) and the false killer whale *Pseudorca crassidens* (Nowak, 2003; Fig. 6b). Although studies of larger samples of these teeth are needed to confirm the ecological association of this wear, it appears that for some populations of killer whales this wear pattern is associated with macrophagy, specifically a specialization in preying on sharks (Ford et al., 2011).

The second type of macroscopic wear takes the form of long worn edges along the mesial and distal surfaces of the teeth (Fig. 3, cw). The mesial/distal macrowear extends from the apex and terminates at a variable distance towards the base, and in some isolated crowns the wear can extend along the entire length of the carinae (SMNS 9808). In all examples, this type of wear obliterates the carina (keel and denticles). Similar wear facets, which as in *Dakosaurus* are elongated, elliptical, and follow the long axis of the tooth, have been observed in tyrannosaurid dinosaurs and interpreted as representing tooth-on-tooth attritional wear (Schubert and Ungar, 2005). Additionally, somewhat similar mesial/distal macroscopic wear observed in basal sauropod and eusauropod dinosaurs is considered to be formed by tooth–tooth contact via the margins of opposing crowns shearing one another during jaw closure (Upchurch and Barrett, 2000; Carballido and Pol, 2010; Saegusa and Tomida, 2011). However, in a comparative survey of extant archosaurs (crocodiles) and other reptiles, Schubert and Ungar (2005) found no examples of this type of wear, suggesting that it is not a usual occurrence. We hypothesize that these facets in *D. maximus* were formed in the same way as hypothesized in theropod and sauropod dinosaurs: as a result of tooth-on-tooth occlusion. This suggests that during occlusion the upper and lower jaw teeth would have met each other mesiodistally with carinae-to-carinae contact (i.e., the teeth would have fit in between each other when the jaws closed). The extant false killer whale also exhibits extensive wear along the mesial and distal tooth margins (Fig. 6b). This validates the hypothesis that mesial/distal tooth wear is created by repeated tooth–tooth contact (Fig. 6).

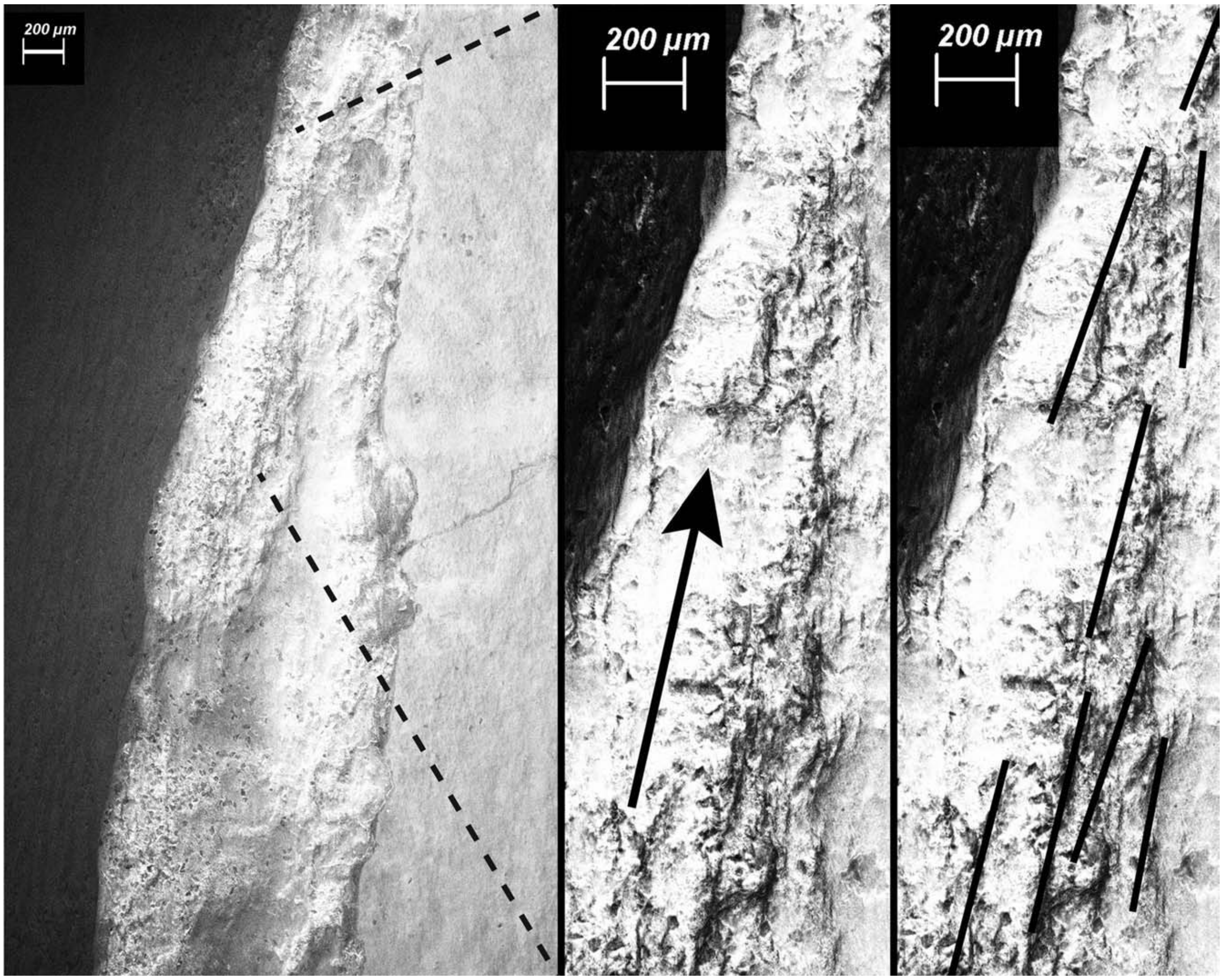

Fig. 5. Left, SEM of worn carina of *Dakosaurus maximus* (NHMUK PV-OR-20283) from the Kimmeridge Clay Formation, Cambridgeshire, UK (AMNH SEM settings 20 kV, WD = 15 mm). Middle, close-up view of scratches oriented along carina longitudinal axis, with arrow showing average scratch orientation (AMNH SEM settings 20 kV, WD = 14 mm). Right, same close-up view, with scratches marked.

The third type of macroscopic wear is present at the base of the tooth crown, and is semi-circular (Fig. 3, bf). We hypothesize that this macroscopic wear is formed during the final phase of occlusion, when the apex from the opposing tooth comes into contact with the base of the crown. These wear facets are a by-product of the tightly packed, and apicobasally elongated, dentition (see occlusion patterns below).

Two other lines of evidence support the hypothesis that tooth-to-tooth occlusion formed these latter two wear facets in *Dakosaurus*, and argue against the possibility that these surfaces represent taphonomic or preservational damage.

Microwear Patterns

Enamel thickness in observed specimens shows that, like many other archosauromorphs (Sander, 1999; Beatty and Heckert, 2009), *Dakosaurus* enamel remained thin despite the large size of the teeth. This restricts microwear studies largely to the dentine surface. Recent studies have shown that microwear studies of dentine can be informative (Green, 2009). In the *Dakosaurus* tooth analyzed with SEM, the most salient feature of the apicobasal mesial/distal wear facet is a regular pattern of apicobasally oriented striations (Fig. 5). This suggests that the events creating the macroscopic and microwear patterns were regular in their direction. Taphonomic abrasion, on the other hand, is more likely to result in randomly oriented microstriations, as teeth are worked and transported in the environment. It is possible that these apparent striations are the result of dentine fracture that has a microstructure predisposing it to fracture along its longitudinal axis. However, as these striations are not observed everywhere dentine is exposed (and presumably would also be fractured), this would be a more complex and unlikely interpretation.

The regularity of these striations along the longitudinal axis of the tooth indicates that they were formed by

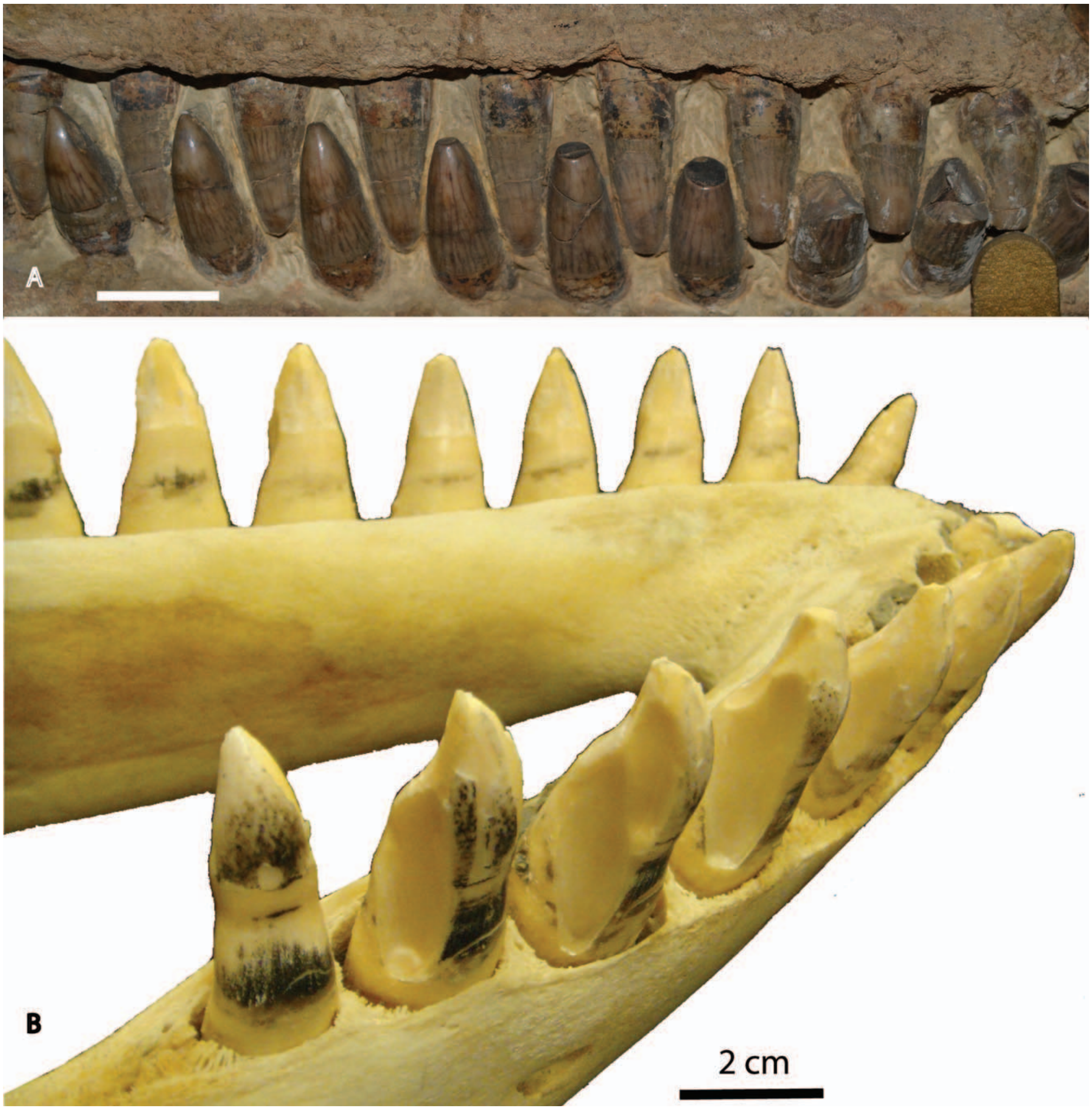

Fig. 6. Close-up on the dentition of two odontocete species. **A**: The Pliocene-aged killer whale, *Orcinus citoniensis* (MGGC-1COC17); note the extensive apical wear of the teeth crowns and the interdigitating occlusion. **B**: The extant false killer whale, *Pseudorca crassidens* (AMNH 169488); note the extensive wear on the mesial and distal margins of the tooth crowns, and the enamel spalling on the labial surface near the apex. Scale bar is the same for A and B.

vertical forces, most likely occlusal events. Extremely similar patterns of microscopic wear, in which the striations are regularly oriented, large, and restricted to the wear facet itself, have been noted in extant taxa with repeated tooth-on-tooth shearing occlusion such as lions (e.g., Schubert et al., 2010), as well as tyrannosaurid theropods (Schubert and Ungar, 2005). Additionally, similar patterns of interdigitating wear can be seen in living odontocetes (Beatty, personal observation; Fig. 6), mammals that have an orthal occlusion pattern in which the teeth of the upper and lower jaws make extensive contact when the jaws close.

Occlusion Pattern

If the macro- and micro-wear described earlier (other than the spalled surfaces) was created by tooth-on-tooth attrition, then the teeth of *Dakosaurus* must have been

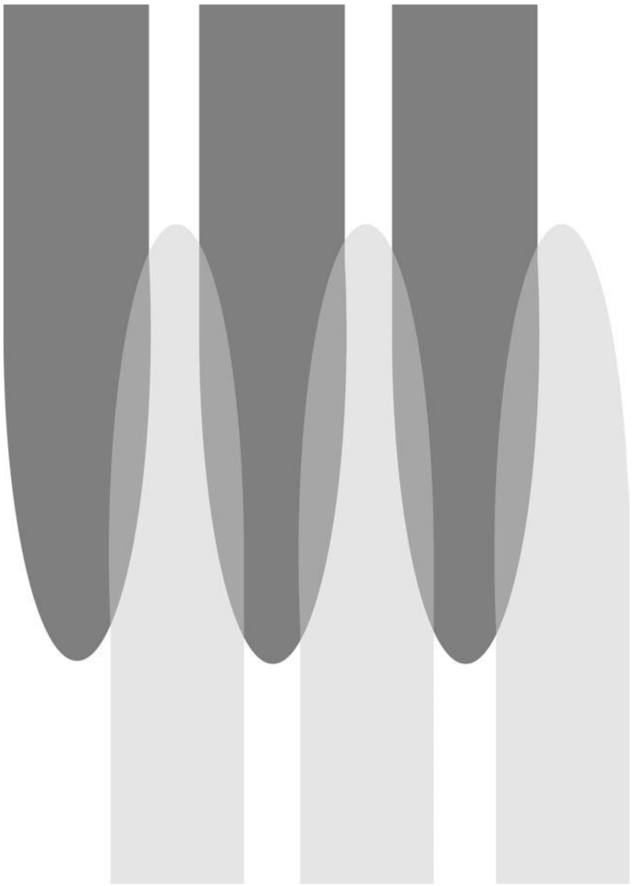

Fig. 7. Diagrammatic reconstruction of the inter-locking shearing occlusion of *Dakosaurus*.

tightly packed and vertically oriented. This would enable the teeth of the upper and lower jaws to contact one another mesiodistally along their carinae during occlusion (Fig. 7). Overall, morphological examination of the skull of *Dakosaurus* shows that this is indeed the case.

First, the complete and articulated skull and mandible of *Dakosaurus andiniensis* exhibits *in situ* vertical orientation of the tooth crowns, which are so closely packed that they touch (or nearly touch) when the jaws are in occlusion (see Pol and Gasparini, 2009). Second, three *D. maximus* specimens with dentigerous bones (SMNS 8203, SMNS 10819, and SMNS 82043) exhibit tooth reception pits on both the upper and lower jaws (Figs. 2 and 4). The presence of reception pits, formed by impressions from the apex of tooth crowns in the opposing tooth row, is a common trait in crocodylomorphs. However, their occurrence on both upper and lower jaws is unusual. For example, the closely related species *Geosaurus giganteus* has reception pits only on the lateral margin of the dentary, due to a maxillary overbite in which the laminar and triangular-shaped dentition creates a scissor-like occlusion pattern (Young and Andrade, 2009; Andrade et al., 2010). Therefore, the unusual presence of reception pits on both jaws in *D. maximus* indicates that this species had vertically orientated crowns, which would have repeatedly contacted the opposing jaw bone during occlusion. It is interesting to note that a subtle re-alignment of tooth crown position and rostrum shape (narrower in *Geosaurus* than in *Dakosaurus*) can lead to functionally different types of bite. While in *Geosaurus* the teeth slide pass each other without direct contact (due to the partial maxillary overbite), which is useful in slicing prey, in *Dakosaurus* the tighter arrangement of teeth allows serrations to contact one another and effectively chop meat (and maybe crush bones, if the similarities in tooth size, form, and wear with the bone-crushing *Tyrannosaurus* are indicative of a similar feeding style: see below).

In summary, although fossil tooth-bearing bones of *Dakosaurus* are rare, there is currently an example (*D. andiniensis*) showing that *in situ* teeth of both jaws were oriented vertically in life and extremely closely packed, as well as examples (late Kimmeridgian *D. maximus*) with upper and lower reception pits showing that the teeth were vertically oriented and had apices that could reach the opposing dentigerous bone during occlusion (Figs. 2 and 4). All of these features are necessary for tooth–tooth contact in manner we hypothesize.

DISCUSSION

Biting Performance at Wide-Gape

Dakosaurus is a member of the metriorhynchid subclade *Tyrannoneustes* + Geosaurini, which are characterized by the ventral displacement of the dentary tooth row relative to the jaw joint and an increase in tooth crown apicobasal length. These adaptations are considered indicative of wide-gape, or greater optimum gape, feeders (i.e., feeding on larger-bodied prey than other metriorhynchids; see Young et al., in press). Biting performance is known to decrease as gape increases (see Herring and Herring, 1974; Dumont and Herrel, 2003; Bourke et al., 2008), and therefore predatory taxa tend to exhibit adaptations for higher biting performances at wider gapes (Herring and Herring, 1974). A wider gape is also necessary for consuming larger prey items. The *Tyrannoneustes* + Geosaurini subclade exhibits three notable adaptations that would increase performance during wide gape biting (see Young et al., in press). First, muscle force transmission is increased by increasing mechanical advantage of the adductors (by foreshortening the rostrum: the brevirostrine condition). Second, the adductor muscle force magnitude is increased by enlarging muscle cross-sectional area (increased supratemporal fenestra diameter) and increasing the adductor muscle attachment site area (increased supratemporal fossa size). Finally, as we show in this article, shearing surface area is increased by the development of high tooth crowns (large apicobasal length) and sophisticated occlusal patterns. The occlusal patterns differ greatly among different genera in this clade. *Tyrannoneustes* has an in-line locking mechanism (Young et al., in press), *Geosaurus* has a maxillary overbite and dentition that would have created a scissor-like double-bladed occlusion (Young and Andrade, 2009; Andrade et al., 2010), and *Dakosaurus* had the precise tooth-to-tooth occlusion pattern that we describe here.

We posit that the carina-to-carina contact between the upper and lower jaw dentition was an adaptation for higher biting performance at wide-gape. This is in agreement with other adaptations exhibited by *Dakosaurus*, which include the shortest snout of any known metriorhynchid (highest muscle force transmission) and greatly enlarged supratemporal fenestrae (highest muscle force magntiude; Pol and Gasparini, 2009). Therefore, this genus possessed the most extreme adaptations for increasing biting performance of any metriorhynchid.

Feeding Ecology

In addition to increased biting performance and a wider gape, *Dakosaurus* exhibited adaptations for dismembering large-bodied prey. For an aquatic amniote, this is important because of limitations on the breadth of the path around the larynx for food as it is being swallowed, which limits the size of boluses and increases the risk of asphyxiation or drowning if larger food is consumed (MacLeod et al., 2007; Mignucci-Giannoni et al., 2009). In whales, the larynx is elevated to form a watertight seal with the soft palate, so that air is transmitted directly to the nasopharynx to avoid drowning while swallowing (MacLeod, 2007; Reidenberg and Laitman, 2007). This limits the available breadth of the oropharynx, making large food harder to swallow. Therefore, dental specializations for breaking prey items into smaller pieces are needed if prey is going to be bigger than the size of food the predator is able to swallow whole, and this can be seen to some degree in some cetaceans, such as killer whales (MacLeod et al., 2007) and false killer whales (Nowak, 2003).

It is unknown whether *Dakosaurus* had any of these soft tissue specializations, but its unusual cranial and dental features—analogous to those in killer whales and false killer whales—would have been useful in killing large prey and breaking it into smaller pieces. Biomechanical modelling shows that an oreinirostral snout with a secondary palate (like that in *Dakosaurus*) is more resistant to both torsional and bending stresses than a platyrostral or tubular snout, with oreinirostral taxa having a better overall mechanical performance in orthal and twist feeding bites (McHenry et al., 2006; Rayfield et al., 2007; Rayfield and Milner, 2008). The *Dakosaurus* skull would have been further stabilized against torque through the rostromedial enlargement of the intratemporal flange (shallow basin at the rostromedial portion of the supratemporal fossae; see Pol and Gasparini, 2009), as this would have increased the medial component of the adductor muscle force vectors (see Buchy, 2008). Indeed, explicit biomechanical modelling has shown that the robust skull and wide snout of *Dakosaurus* resulted in it having the strongest skull of any metriorhynchid (Pierce et al., 2009a; Young et al., 2010).

We hypothesize that the dentition of *Dakosaurus* was adapted for dismembering large-bodied prey. The teeth were large and robust, with serrated carinae; in fact, *Dakosaurus* is the only known metriorhynchid to exhibit macroziphodonty (Fig. 3; Andrade et al., 2010; Young et al., 2010). Denticulated teeth are more efficient at slicing and cutting and require less energy to penetrate food, thereby making larger and tougher organisms more energetically feasible prey items (Frazzetta, 1988; Abler, 1992; Andrade et al., 2010). The presence of enamel spalling and crown apex breakage, which we document here (Fig. 3), is another powerful line of evidence supporting the hypothesis that *Dakosaurus* was a predator of large-bodied prey. Recent work on the killer whale suggests that cusp breakage patterns may reflect diet better than small amounts of wear (Foote et al., 2009; Ford et al., 2011). The high incidence of carinal wear and apex breakage in *D. maximus* teeth, and their extensive nature, suggests that this species had a feeding mechanism capable of consuming large prey. When compared to other crocodylomorphs, including modern crocodylians, this is unusual. Most have numerous conical teeth in a long rostrum, ideally suited for raptorial capture of prey items small enough to swallow. Most non-mammalian amniotes do not masticate, forcing them to either eat prey they can swallow whole or to pull off small pieces of large prey. Small, conical teeth are poorly suited for the task of consuming large prey, and all of the evidence presented above suggests that *Dakosaurus* was extremely well-suited for using its teeth for cutting small pieces off of large prey items.

On the basis of these lines of evidence, we interpret *Dakosaurus* as having a food procurement strategy analogous to that of killer whales and false killer whales. Overall, cranial and dental morphology shows that *Dakosaurus* was a hypercarnivore and its large body size would have allowed it to feed on large-bodied prey (macrophagy). Consistent enamel spalling indicates that *Dakosaurus* fed on abrasive prey, perhaps utilizing strong bite forces to break through bone as in tyrannosaurids (see Erickson and Olson, 1996; Erickson et al., 1996; Chin et al., 1998; Meers, 2002; Rayfield, 2004; Bates and Falkingham, 2012), and tooth-on-tooth occlusion would have been useful in breaking down large and/or hard prey items. Biomechanical modelling shows that strong bite forces are indeed plausible in *Dakosaurus* (Pierce et al., 2009a; Young et al., 2010), but this hypothesis, that *Dakosaurus* regularly bit through bone, remains to be supported with bite marked prey bones or bone-filled coprolites, as has been done for tyrannosaurids (Erickson et al., 1996; Chin et al., 1998).

It is possible that some of the characteristic tooth wear patterns of *Dakosaurus*, and a similar vertical interlocking tooth occlusion mechanism, are present in other large-bodied Mesozoic marine reptiles that fed on large or abrasive prey, such as mosasaurs, plesiosaurs, and ichthyosaurs. Our survey of the American Museum of Natural History's mosasaur tooth collection ($N = 100+$ teeth) revealed several instances of apical spalling but no instances of elongate mesial or distal wear facets. This suggests that some mosasaurs likely ate abrasive prey, but that there is currently no evidence for *Dakosaurus*-like tooth-on-tooth interlocking occlusion (although several mosasaurs do exhibit vertical tooth occlusion: Konishi et al., 2011, Leblanc et al., 2012). Given that interlocking vertical occlusion with mesial/distal wear is limited to *Dakosaurus* among metriorhynchids, it may not be surprising that we have yet to notice it in a mosasaur. We encourage researchers working on other Mesozoic marine reptile groups to carefully examine tooth wear and occlusion patterns, as it is possible that the type of occlusion seen in *Dakosaurus*, killer whales, and false killer whales is more widespread among large marine tetrapods.

CONCLUSIONS

On the basis of overall morphological observation of cranial bones and teeth and SEM of tooth wear surfaces, we show that the teeth of the aberrant Mesozoic marine crocodylomorph *Dakosaurus* had an unusual occlusion patterns in which teeth of the upper and lower jaws met each other, and wore against each other, during bites. Furthermore, the presence of extensive enamel spalling and crown breakage suggests that *Dakosaurus* fed on abrasive food, such as sharks (scales) or other large vertebrates (bones) (Schubert and Ungar, 2005; Foote et al., 2009; Ford et al., 2011). These new observations, along with previous biomechanical modelling of the *Dakosaurus* skull and observations of serration morphology, strongly indicate that *Dakosaurus* was an apex predator specialized to feed on large-bodied prey (macrophagy). In essence, *Dakosaurus* may have been a Mesozoic analog of a killer whale/false killer whale, and also shared dental and cranial features with large theropod dinosaurs like *Tyrannosaurus*. By weaving together many disparate lines of evidence, the paleobiological and dietary habits of one of the most unusual Mesozoic tetrapods can be reconstructed in tantalizing detail.

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