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The oldest known metriorhynchid super-predator: a new genus and species from the Middle Jurassic of England, with implications for serration and mandibular evolution in predacious clades

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The oldest known metriorhynchid super-predator: a new genus and species from the Middle Jurassic of England, with implications for serration and mandibular evolution in predacious clades

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The Oxford Clay Formation of England has yielded numerous sympatric species of metriorhynchid crocodylomorphs, although disagreement has persisted regarding the number of valid species. For over 140 years teeth reminiscent of the genus *Dakosaurus* have been known from the Oxford Clay Formation but these have never been properly described and their taxonomy and systematic affinity remain contentious. Furthermore, an enigmatic mandible and associated postcranial skeleton discovered by Alfred Leeds in the Fletton brick pits near Peterborough also remains undescribed. We show that this specimen, and several isolated teeth, represents the oldest known remains of a large-bodied predatory metriorhynchid. This material is described herein and referred to *Tyrannoneustes lythrodectikos* gen. et sp. nov. This species has a unique occlusal pattern: the dentition was arranged so that the posterior maxillodentary teeth interlock in the same plane and occlude mesiodistally. It is the first described crocodylomorph with microscopic denticles that are not contiguous along the carinae (forming short series of up to 10 denticles) and do not noticeably alter the height of the keel. Additionally, the dorsally expanded and curved posterior region of the mandible ventrally displaced the dentary tooth row relative to the jaw joint facilitating the enlargement of the dentition and increasing optimum gape. Therefore, *Tyrannoneustes* would have been a large-bodied marine predator that was well-suited to feed on larger prey than other contemporaneous metriorhynchids. A new phylogenetic analysis finds *Tyrannoneustes* to be the sister taxon to the subclade Geosaurini. An isolated tooth, humerus, and well-preserved mandible suggest a second species of metriorhynchid super-predator may also have lived in the Oxford Clay sea. Finally, we revise the diagnoses and descriptions of the other Oxford Clay metriorhynchid species, providing a guide for differentiating the many contemporaneous taxa from this exceptional fossil assemblage.

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Keywords: denticle; Geosaurini; hypercarnivore; Metriorhynchidae; *Tyrannoneustes*

Introduction

Metriorhynchids were small- to large-bodied marine crocodylomorphs that inhabited the epeiric seas of the Middle Jurassic to Early Cretaceous (Fraas 1902; Steel 1973; Pierce *et al*. 2009a, b; Young *et al*. 2010; Young *et al*. 2011a, b). Their bauplan was atypical for crocodylomorphs and was well suited to a pelagic lifestyle. Characteristic features of the group include: lateral orbits, hydrofoil-like forelimbs, a hypocercal tail, loss of osteoderm cover, and well-developed salt glands. The evolutionary relationships within Metriorhynchidae have recently been elucidated by a series of phylogenetic analyses (Mueller-Töwe 2005; Gasparini *et al*. 2006; Young 2007; Wilkinson *et al*.

2008; Jouve 2009; Pol & Gasparini 2009; Young & Andrade 2009; Andrade *et al*. 2010; Cau & Fanti 2011). However, when calibrated against geological time, the most taxonomically complete analysis (Young *et al*. 2011a) implies significant gaps in the metriorhynchid fossil record (Fig. 1). Filling these gaps with new fossil evidence is an outstanding problem of paramount importance for understanding the evolution of Mesozoic marine reptiles.

One of the most frustrating gaps complicates understanding of the evolution of extreme hypercarnivory in Metriorhynchidae. Evidence reviewed by Young *et al*. (2010) indicates that the geosaurine subfamily exhibited a trend towards increasing super-predatory behaviour during the Mesozoic (i.e. predation on animals as large as, or
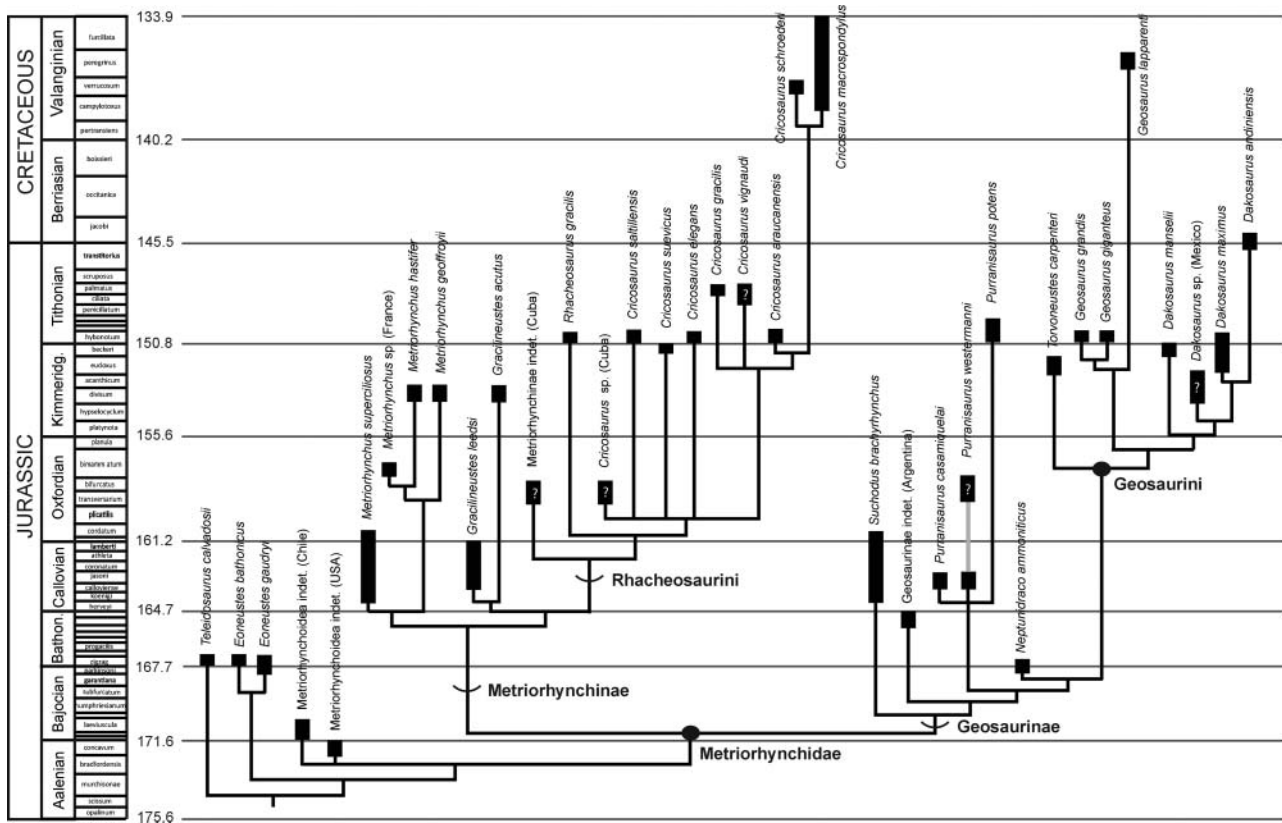
Figure 1. Strict consensus topology of Metriorhynchoidea based on the phylogenetic analysis in Young *et al*. (2011a), calibrated by sub-Mediterranean ammonite zones with the geological timescale based on Ogg *et al*. (2008). Node-based clades are represented by black circles, while stem-based clades are represented by curved lines. The time-spans of taxa with question marks are uncertain.

larger than, the predator itself). In Late Jurassic-Early Cretaceous marine ecosystems geosaurines were either apex-predators or second tier super-predators (Wilkinson *et al*. 2008; Young *et al*. 2010). The most phylogenetically derived geosaurine genera constitute the tribe Geosaurini, defined as the least inclusive clade containing *Dakosaurus maximus*, *Geosaurus giganteus* and *Torvoneustes carpenteri* (see Cau & Fanti 2011). There are currently three genera within Geosaurini - *Dakosaurus*, *Geosaurus* and *Torvoneustes* - all of which are considered super-predators with craniodental adaptations for feeding on large-bodied prey (Andrade *et al*. 2010). However, all three genera are only known from deposits of the Late Oxfordian or younger in age, while their closest known sister taxon, *Neptunidraco ammoniticus*, is from the latest Bajocian or early Bathonian, a gap of approximately 12 million years (Cau & Fanti 2011). There is a morphological and temporal gap between Middle Jurassic mesorostrine, tubular-snouted, opportunistic predators such as *Neptunidraco*, and the clade of Late Jurassic brevirostrine, broad-snouted, super-predators with serrated teeth (Geosaurini). It is frustrating that so little is known about the early evolutionary history of Geosaurini, especially the morphology of older, basal members of the clade and sister groups. This lack of

evidence obscures our understanding of character evolution during the development of super-predatory behaviour.

There are, however, specimens that can fill this gap. Numerous isolated teeth from the Oxford Clay Formation of England, and contemporaneous deposits of northern France, have been referred to *Dakosaurus*. These specimens have been known for more than 140 years (Hulke 1869; Philips 1871), and were recognised as a potential new species (Lydekker 1888). Andrade *et al*. (2010) were the first to include one of these teeth in a phylogenetic analysis (NHMUK PV R486), and as anticipated it did indeed nest with *Dakosaurus*. However, the teeth have received very little attention and have never been properly described. The discovery of more complete metriorhynchid specimens from the Oxford Clay Formation in the collections of the Hunterian Museum (Glasgow) allows some of these teeth to be confidently allied with more diagnostic material, and together this specimen and the teeth can be described as a new genus and species, which is currently the oldest known example of a metriorhynchid super-predator in the fossil record. In this paper we describe the new genus and species, give the first description of NHMUK PV R486, and present a revised phylogenetic analysis of Metriorhynchidae. We also revise the dental description and

update the diagnoses of the other Oxford Clay Formation metriorhynchids, and review the implications these teeth have on our understanding of denticle evolution within Metriorhynchidae.

Historical background

Metriorhynchid teeth from the Callovian-Oxfordian

Isolated teeth referred to *Dakosaurus* have long been known from the Callovian-Oxfordian. Lydekker (1888) mentioned numerous isolated *Dakosaurus* teeth in the NHMUK collection from Oxford, England (Oxford Clay Formation: NHMUK PV R486, NHMUK PV OR47989) and the Falaise des Vaches Noires (situated between Dives-sur-Mer and Villers-sur-Mer), Calvados, France (Tesson Collection: NHMUK PV OR32643, NHMUK PV OR32644, NHMUK PV OR32648). Unfortunately, there is no information as to whether these teeth are upper Callovian or lower Oxfordian in age. Lydekker (1888, p. 94) mentioned that the teeth are smaller and less robust than those from the younger Kimmeridge Clay Formation, and regarded them as possibly belonging to a new species. Steel's (1973, p. 42) review of Crocodylia noted the teeth and reiterated that Lydekker (1888) believed they might represent a separate species.

Philips (1871, p. 306) also listed *Dakosaurus* teeth from the Oxford Clay Formation, from an unspecified layer at St Clements, Oxford. Hulke (1869, p. 401) quoted a discussion by Seeley, stating: "Mr. Seeley remarked that in the base of the Oxford Clay, there was what he regarded as a peculiar form of *Dakosaurus*, with two serrated ridges close together on one side of the tooth, and one on the other." We have not been able to locate any such *Dakosaurus* teeth with three carinae, but the tooth Seeley referred to could have had a supernumerary carina (a carina that is split into multiple forks or multiple carinae located near each other, *sensu* Beatty & Heckert 2009).

Seeley (1869, p. 109) mentioned a worn *Dakosaurus* tooth from the Corallian Oolite of North Grimston (near Malton, North Yorkshire), thus giving this tooth a definitive lower Oxfordian age. In parenthesis after *Dakosaurus*, Seeley stated "new sp.". Later, Woodward (1885, p. 504) stated that the *Dakosaurus* material noted by Seeley was still undescribed. Regarding the isolated Oxfordian tooth, Woodward raised the question in footnote six (p. 504): "Can this be the same as certain Corallian teeth in the British Museum, bearing the MS. name of *Pliosaurus teretidens*, Owen?". Fraas (1902, pp. 7–8), however, referred this tooth to *D. maximus*.

Recently, an isolated and broken metriorhynchid tooth of Callovian-Oxfordian age was described from a quarry near Ogrodzieniec in the Polish Jura Chain (Zatoń 2007). Like the Callovian-Oxfordian metriorhynchid teeth from

England and France mentioned above, it lacks conspicuous enamel ornamentation at the mid-crown, lacks faceting on labial and lingual surfaces, possesses strongly developed mesial and distal carinae, and has a crown that is oval in cross section (strongly mediolaterally compressed) with the lingual surface more strongly convex and thicker than the labial surface. However, under light microscopy there are no obvious serrations (Zatoń 2007, pers. comm. 2010). Microscopic denticulation along the carinae is known in the genus *Geosaurus* and the Oxford Clay '*Dakosaurus*' tooth NHMUK PV R486 (see Andrade *et al*. 2010). Prasad & Broin (2002) stressed that scanning electron microscopy (SEM) is necessary to properly assess denticle morphology. Andrade *et al*. (2010) further found that the use of SEM was necessary to identify what they termed microziphodonty (denticles on the carinae that are microscopic and whose dimensions (length, width, height) typically do not exceed 300 μm). As such, we used SEM to differentiate between a true lack of serrations and the possession of microscopic serrations on the Polish tooth, other teeth referred to *Dakosaurus*, and the previously described metriorhynchid species from the Oxford Clay Formation (see below).

Additional *Dakosaurus* teeth have been identified from a quarry near Wapienno, north-central Poland (Jentzsch 1884; Gallinek 1895, 1896; Radwañska & Radwañska 2003). The Wapienno teeth come from the Late Oxfordian (Radwañska & Radwañska 2003; Zatoń 2007), and are similar in form to those from Ogrodzieniec (Zatoń 2007, pers. comm. 2010). As with the English teeth discovered in the nineteenth century, these have not been described in detail (Zatoń pers. comm. 2010).

The enigmatic Leeds specimen

Amongst the more than 600 remains of marine reptiles from Alfred Leeds' collection (Peterborough Member, Oxford Clay Formation; Middle Callovian) in the Hunterian Museum, University of Glasgow, 116 are identified as metriorhynchids, of which 15 are selections of isolated teeth. Specimen GLAHM V972 consists of a series of skull elements, most importantly the right mandibular ramus, along with pelvic, vertebral and rib elements. Of particular interest is that Alfred Leeds, the original collector, appears to have specifically highlighted the taxonomic identity of this specimen as an issue worth pursuing. In Alfred Leeds' Eyebury Catalogue (Leeds & Leeds 1919), he listed the specimen as number 167, and itemized the bones present. Alfred Leeds acquired over forty years of experience in identifying the fossil vertebrate bones from the brick pits in and around Peterborough, and became extremely adept at understanding morphology (even on one occasion dismissing in correspondence a new genus - *Apractocleidus* - as an old and diseased individual of *Cryptoclidus*; see Leeds 1956, pp. 51–52), although he modestly refused to write or be a co-author on any publications himself. He was also comfortable in leaving an identification at generic level if

he felt there was not enough information to identify which species it belonged to. However, his entry for crocodilian 167 tellingly (and uniquely, for his catalogue) notes after *Metriorhynchus* sp. an addendum of '?species'. This seems to indicate that he felt the anatomy of the specimen was irreconcilable with the published metriorhynchid species from the Oxford Clay. Charles Andrews (1913) named, diagnosed and described seven metriorhynchid species using the Leeds Collection specimens held in the NHMUK. The morphology of the mandible, dentition, ilium and ischium in GLAHM V972 does not correspond with any of those seven putative species. In addition to GLAHM V972, numerous isolated teeth that share their morphology have been discovered in the Peterborough Member of the Oxford Clay Formation (GLAHM V1399/9, GLAHM V1402/5, GLAHM V1430 and GLAHM V1436).

In Leeds' Eyebury Catalogue (Leeds & Leeds 1919), it is noted that GLAHM V972 was discovered in Pit '1', and it appears to have been excavated between July 1907 and 1909 (inclusive). Although Alfred Leeds collected from a variety of Oxford Clay pits around Peterborough, the numbered pits (1–19) are reserved for a concentrated group of pits in the Fletton area immediately south of what was then referred to as 'Peterborough Within'. The numbers do not reflect any numbers relating to the individual brick companies of the time, but appear to have been adopted by Leeds to counter the frequent change of ownership in the vanguard of the 1880s 'clay rush', and retain an identity for the source that was independent of a potentially ephemeral company name. By 1929 all of these Fletton pits had fallen under the ownership of the London Brick Company.

Hudson & Martill (1994) regarded Bed 10 of the Peterborough Member as the most prolific source of vertebrate fossils. As noted by Noè *et al*. (2003), for the industrial era, this is an artefact generated by the mechanised extraction process: shale planers, used from around the First World War onwards, removed all of the clay immediately above Bed 10, thus destroying the vast majority of specimens higher in the succession. Bed 10 contains many concretionary nodules, and therefore traditionally was not deemed viable for mechanical clay extraction (whether by shale planer or dragline) because of the damage to machinery from the nodules and the poor quality of the clay below; thus, industrial excavation ceases immediately above this level (Hillier 1981; D. M. Martill pers. comm. 20 August 2011). This means that the surface of Bed 10 is the predominant area visible to discover fossils on when any collector enters a clay pit. In contrast, the Leeds' Eyebury Catalogue (Leeds & Leeds 1919), which records specimens collected from the earlier era of manual clay extraction, shows that key specimens came from a wide range of levels within the clay pits. Although manual extraction proceeded by crow bar through the nodule bed, the workable clay below was of a modest depth compared to the height of worked clay above, and of a poorer quality due to the quantity of

shell layers within it. As such, the likelihood of any of Leeds' specimens coming from Bed 10 or below is vanishingly small. This probability is corroborated by significant contemporary finds from above Bed 10 (e.g. Liston 2006). It is therefore with some confidence that GLAHM V972 can be inferred to have been extracted from above Bed 10 of the Peterborough Member.

Abbreviations

Institutional. BRSMG, Bristol City Museum and Art Gallery, Bristol, England; **BSPG**, Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany; **CAMSM**, Sedgwick Museum, Cambridge, England; **GLAHM**, Hunterian Museum, Glasgow, Scotland; **GIUS**, catalogue number for Wydziale Nauk o Ziemi, Uniwersytetu Śląskiego, Poland; **NHMUK**, Natural History Museum, London, England; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Germany.

Anatomical. al, alveolus; **acapc**, laminar crest linking the acetabulum to ischium anterior process; **acet**, acetabulum; **An**, angular; **cen**, vertebral centrum; **cf**, coracoid foramen; **co**, coronoid; **cp**, coronoid process; **den**, dentary; **di**, diapopphyseal process; **dpc**, deltopectoral crest; **ensp**, enamel spalling; **ilap**, ilium anterior process; **isap**, ischium anterior process; **np**, vertebral neural spine; **pa**, parapophyseal process; **poz**, postzygapophysis; **prz**, prezygapophysis; **s1a**, articulation surface for sacral rib one on the ilium; **s2a**, articulation surface for sacral rib two on the ilium; **San**, surangular; **sca**, scapula articulation surface on the coracoid; **Sp**, splenial; **sym**, mandibular symphysis; **rp**, reception pit; **tc**, tooth crown; **tp**, transverse process.

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Superorder **Crocodylomorpha** Hay, 1930
(*sensu* Walker, 1970)
Infraorder **Thalattosuchia** Fraas, 1901
(*sensu* Young & Andrade, 2009)
Family **Metriorhynchidae** Fitzinger, 1843
(*sensu* Young & Andrade, 2009)
Subfamily **Geosaurinae** Lydekker, 1889
(*sensu* Young & Andrade, 2009)

Geosaurinae indeterminate
(Fig. 2)

Material. NHMUK PV R486, incomplete isolated crown.

Locality and horizon. Oxford, England. Oxford Clay Formation. It is unknown whether the specimen is Callovian or Oxfordian in age.

Description. Tooth NHMUK PV R486 is a poorly preserved crown, with very little of the basal section of the
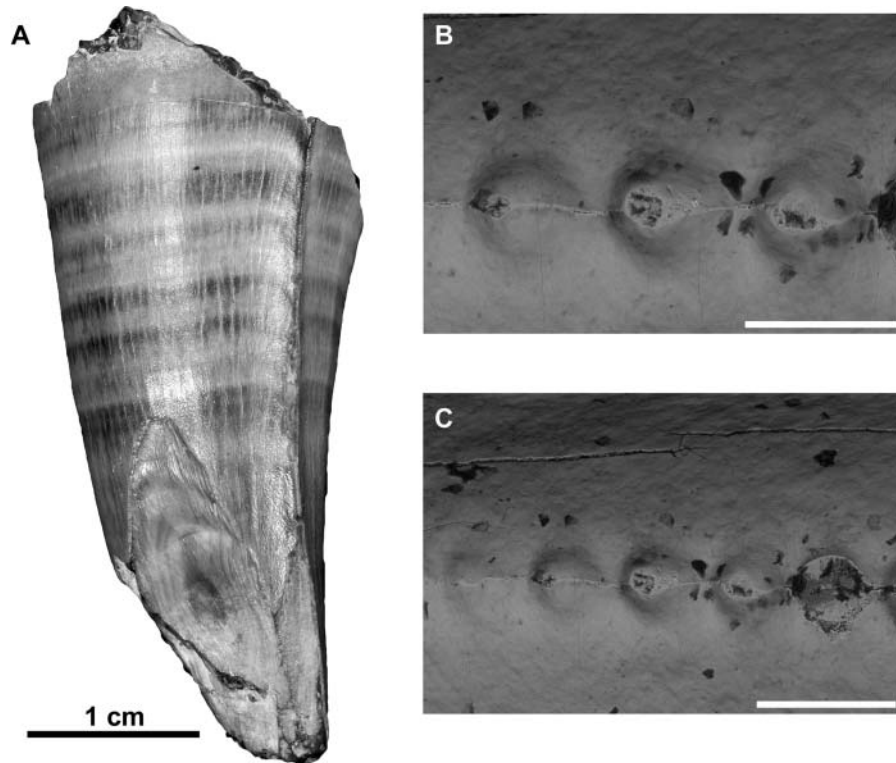
Figure 2. Geosaurinae indeterminate from the Oxford Clay Formation (NHMUK PV R486). **A**, oblique view of the crown; **B**, close-up of carinae and denticles in backscatter scanning electron microscopy (BSEM), scale bar = 200 μm; **C**, carinae under BSEM, scale bar = 300 μm.

root present (Fig. 2). The crown itself is relatively large in comparison to the teeth of most other thalattosuchians (e.g. *Rhacheosaurus gracilis*, NHMUK PV R3948; *Cricosaurus elegans*, NHMUK PV OR37006). Although heavily worn it is greater than 40 mm long apicobasally and its base is greater than 20 mm wide mesiodistally (longer axis). The tooth is single cusped with slight mediolateral compression. No constriction is present at the crown/root junction, but the boundary is evident through colour and texture, due to termination of enamel. The crown is robust and curved lingually. The crown lacks the apicobasal faceting observed on the labial face of *Geosaurus* teeth (see Young & Andrade 2009; Andrade *et al*. 2010).

The apex is damaged: the outer layer of enamel and dentine has been removed but it is unclear if this is a fracture resulting from predatory behaviour (feeding wear) or damage related to taphonomy or preparation. The crown is serrated but the serrations are difficult to observe with the naked eye. Unfortunately, as the position of this tooth in the dental series is unknown, it is not possible to determine if the carinae are mesial or distal. Generally, there is little difference between the denticle densities of mesial/distal carinae in Geosaurini teeth (see Andrade *et al*. 2010); however, an isolated *Dakosaurus* crown from Spain has two carinae with markedly different denticle densities (Ruiz-Omeñaca *et al*. 2010).

In NHMUK PV R486 carinae are comprised of both denticles and a keel, as in true ziphodont teeth (Andrade & Bertini 2008). Contiguous true denticles are present along the mesial and distal borders (24.9–28.5 denticles/5 mm), creating well-defined carinae. Compared to other ziphodont metriorhynchids NHMUK PV R486 had a similar number of denticles per unit length as *Geosaurus*, whereas described species of *Dakosaurus* have fewer (see Andrade *et al*. 2010, table 2). In NHMUK PV R486 the carinae extend from the base to the apex of the crown. Denticles run the entire length of the preserved carinae. Overall, denticles have a fairly consistent height (isometric), but their shape varies substantially (poorly isomorphic). There are only carinae on the mesial and distal edges of the tooth, with no split or supernumerary carinae, or accessory ridges.

The individual denticles of NHMUK PV R486 are small, with maximum measurements of 160 μm × 270 μm (apicobasal length and transverse width, respectively); these dimensions are reasonably similar to those of *Geosaurus* (see Andrade *et al*. 2010, table 2). 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. This morphology (rounded denticles bearing sharp cutting edges) is also observed in *Geosaurus grandis*, *Dakosaurus maximus* and *D. andiniensis* (see Pol & Gasparini 2009; Andrade *et al*. 2010).

The labial and lingual surfaces of NHMUK PV R486 are largely smooth, although there are long, well-spaced apicobasally aligned ridges of low relief on both surfaces. However, they are restricted to the basal half of the crown. The faint enamel ornamentation observed on the rest of the crown is only visible under SEM, and is identical to that observed in *Geosaurus* and *Dakosaurus* (Andrade *et al*. 2010). Cingula and accessory cusps/denticles are absent, as in all thalattosuchians (e.g. Vignaud 1997; Pol & Gasparini 2009; Andrade *et al*. 2010). Enamel wrinkles and bands (*sensu* Brusatte *et al*. 2007) are not present on the crown; as such it is not one of the posterior-most maxillary teeth (Andrade *et al*. 2010).

Remarks. Tooth NHMUK PV R486 (Fig. 2) is a significant specimen because of its geological age and carinal morphology. It was presented to the British Museum (Natural History, now NHMUK) by Sir Richard Owen in 1884. The old registers held in the NHMUK show that the specimen was received from H. G. Day Esq. of St John's College (whether Cambridge University or Oxford University was not recorded). The specimen is from the Oxford Clay Formation and was discovered in or near Oxford, England. Unfortunately, more detailed information has not been recorded.

This specimen has been referred to as *Dakosaurus* sp. indet. (e.g. Lydekker 1888; Andrade *et al*. 2010). The crown morphology is similar to that observed in *Dakosaurus* but there are important distinctions. *Dakosaurus* (*D. maximus* and *D. andiniensis*) teeth have macroscopic denticles along the carinae (>300 μm; macroziphodont) and lack conspicuous enamel ornamentation (apicobasally aligned ridges) (Pol & Gasparini 2009; Andrade *et al*. 2010). However, NHMUK PV R486 has microscopic denticles (<300 μm; microziphodont) and there are apicobasally aligned ridges at the base of the crown. Therefore, this tooth does not correspond to the current diagnosis of *Dakosaurus*.

As geosaurines are very poorly known in the Oxfordian, there is both a morphological and temporal gap in our understanding of the dentition of this subclade. However, due to its age, NHMUK PV R486 could potentially be the oldest known specimen referable to the tribe Geosaurini. Based on the evolution of dental characteristics (see description and phylogenetic analysis below), NHMUK PV R486 shares with Geosaurini: (1) contiguous series of denticles along both the mesial and distal carinae, and (2) denticles which are readily identifiable under SEM. Although NHMUK PV R486 does share these characteristics with Geosaurini, we cannot confidently refer the specimen to this clade until more of this species is discovered, and the evolution of these characteristics are better understood (especially in regards to *Torvoneustes carpenteri*, see below). Therefore, we conservatively refer it to Geosaurinae indeterminate.

A large mandible figured by Lepage *et al*. (2008, pp. 99–101) could belong to the same species/genus as this tooth. It was found at Bénerville-sur-Mer, Calvados, France, in the Marnes de Dives Formation, *Lamberti* Sub-Boreal ammonite-zone (upper Callovian, Middle Jurassic). Lepage *et al*. (2008) referred it to *Metriorhynchus brachyrhynchus* (which Young *et al*. 2010 transferred to the genus *Suchodus*). However, the mandible cannot be referred to either *Suchodus* or *Metriorhynchus* (*sensu* Young *et al*. 2010) as it possesses the mandibular synapomorphies observed in Geosaurini and GLAHM V972 (see description below). These include the low number of dentary teeth (14 or less), 10 teeth adjacent to the mandibular symphysis, and ventral displacement of the dentary tooth row and coronoid process relative to the jaw joint (see description below). Finally, the dentary crowns are mediolaterally compressed and exceed three (possibly four) cm in apicobasal length. The crowns are neither facetted and laminar (like Jurassic *Geosaurus* teeth), nor have intense enamel ornamentation (like *Torvoneustes* teeth). They are more similar to those of NHMUK PV R486 and *Dakosaurus* (i.e. robust). The shape of the mandible in lateral aspect is markedly different from GLAHM V972 (see description below), while the teeth are noticeably larger and more robust. However, until this mandible is studied in detail its taxonomic affinities must remain uncertain.

Tyrannoneustes gen. nov.

Type species. *Tyrannoneustes lythrodectikos* sp. nov.

Etymology. Meaning 'tyrant swimmer': *Tyrannos* is Ancient Greek for an illegitimate ruler, while –*neustes* is Ancient Greek for swimmer.

Geological range. Middle Callovian to Early Oxfordian (possibly Late Oxfordian).

Geographical range. European endemic (England). Isolated Callovian-Oxfordian teeth from France and Poland are referred to this genus (see below).

Diagnosis. As for the only known species.

Tyrannoneustes lythrodectikos sp. nov.
(Figs 3–9, 12–18)

Holotype. GLAHM V972, right ramus of mandible (angular, dentary, splenial, surangular, eight teeth), fragment of jugal bar (R), quadratojugal (R, fragment), vertebrae: cervical (4), dorsal (9), caudal (20), numerous dorsal vertebrae transverse processes fragments; ribs: axis (R), middle cervical (1R, 2L), anterior dorsal (proximal half of 1R, 1L), middle dorsal (10L, 6L); ilium (R), ischium (L); numerous broken, unplaced fragments.
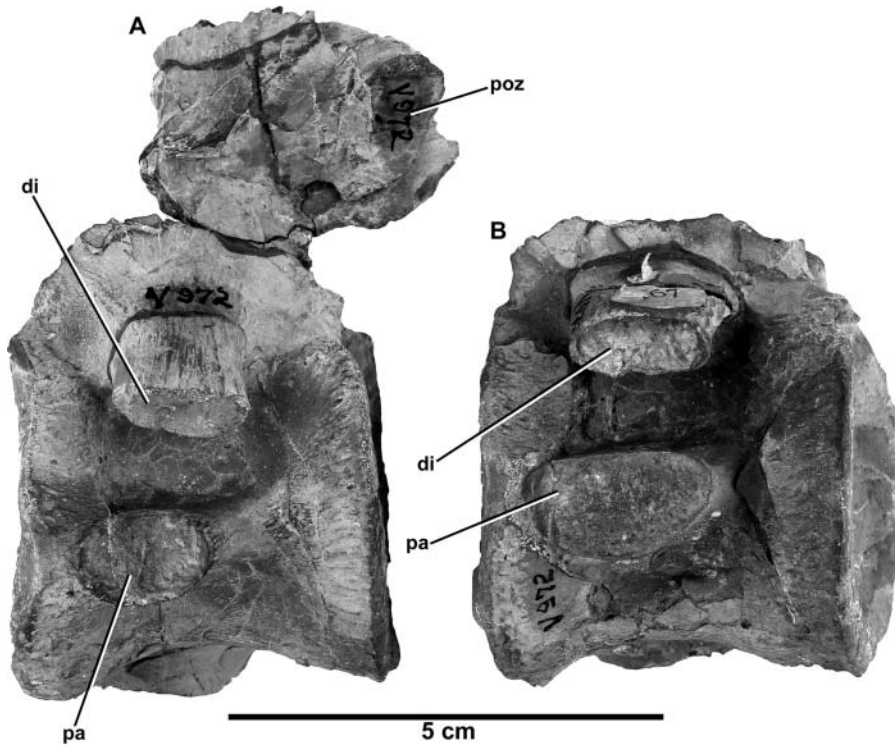
Figure 3. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Two cervical vertebrae in lateral view.
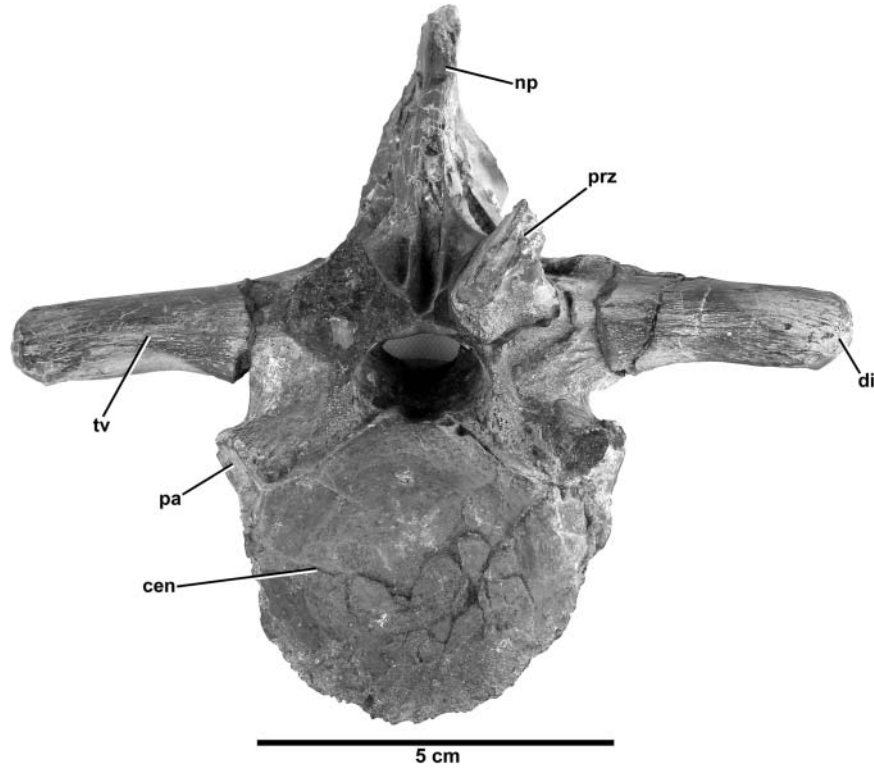
Figure 4. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Lumbar vertebra in anterior view.
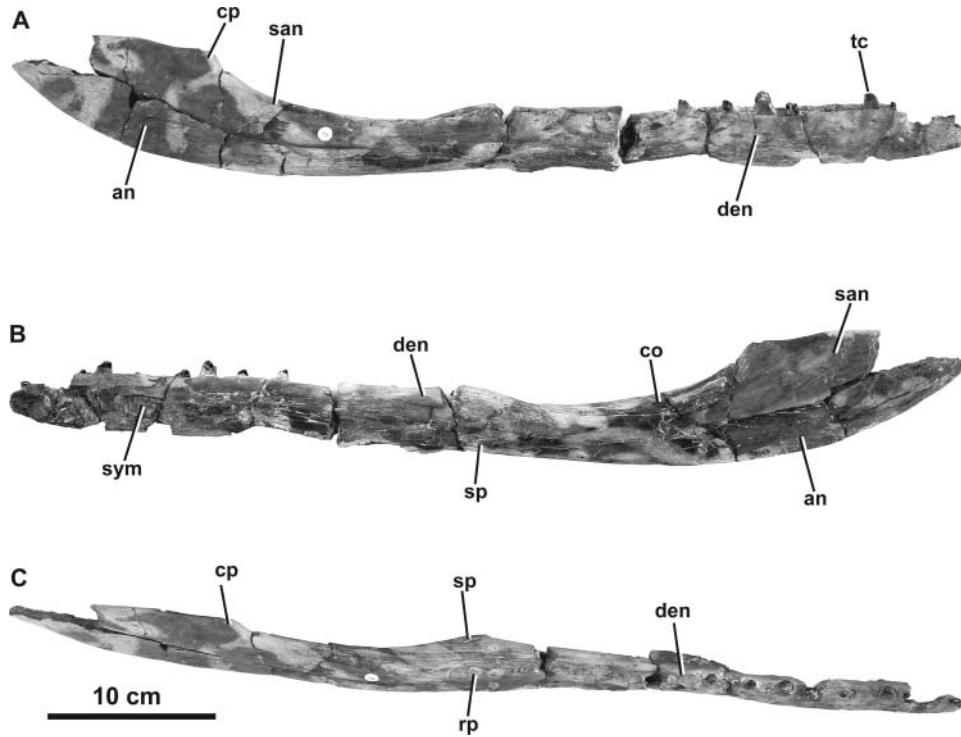
Figure 5. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Right mandibular ramus in: **A**, lateral view; **B**, medial view; and **C**, dorsal view.

Etymology. 'Blood-biting tyrant swimmer'. *Lythros* meaning blood, and *dectikos* meaning biting, both from Ancient Greek; named for its super-predatory nature.

Type locality and horizon. Fletton, Cambridgeshire, England. Peterborough Member, Oxford Clay Forma-

tion. *Jasoni* Sub-Boreal ammonite-zone, Middle Callovian, Middle Jurassic (Cox *et al*. 1992).

Referred specimens. GLAHM V1145: numerous isolated teeth, left humerus, coracoids, femur, ilium; GLAHM V1399/9: isolated tooth; GLAHM V1402/5: isolated tooth;

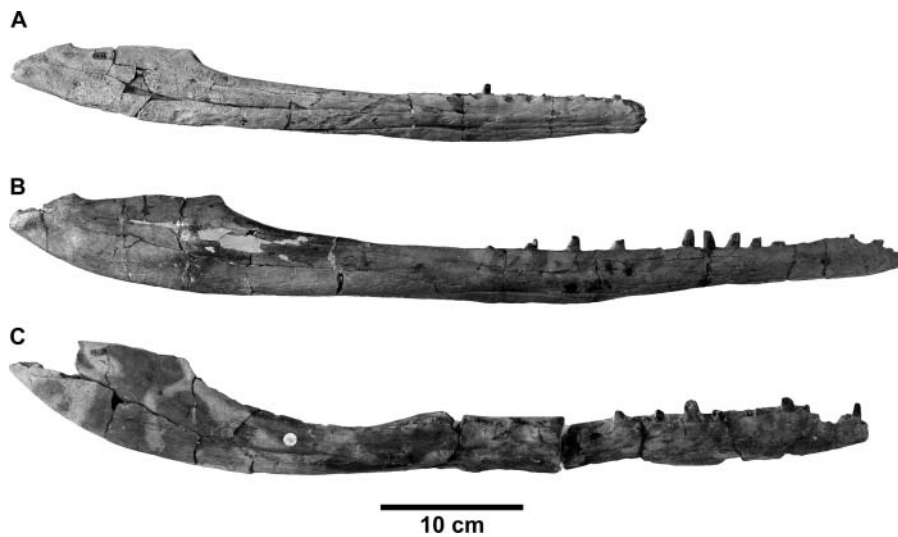**Figure 6.** Comparison of the mandibles from different metriorhynchid species of the Oxford Clay Formation. Note the reception pits extending beyond the dentary tooth row. **A**, *Suchodus brachyrhynchus* (Eudes-Deslongchamps), GLAHM V995; **B**, *Metriorhynchus superciliosus* (Blainville), GLAHM V1141; **C**, *Tyrannoneustes lythrodectikos* sp. nov., GLAHM V972. Note the reception pits on the lateral margin of *S. brachyrhynchus*.
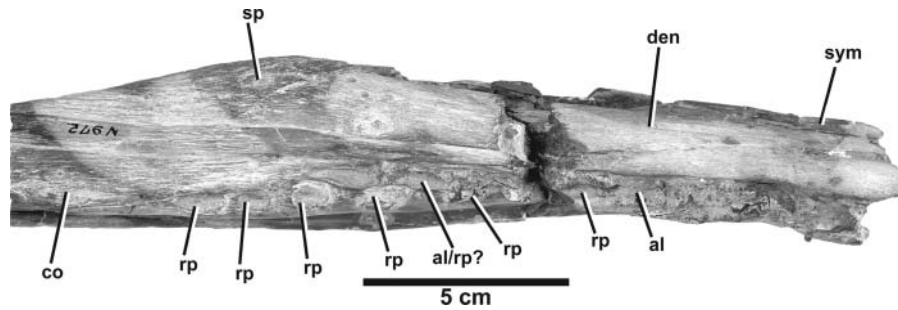
Figure 7. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Close-up of the right mandibular ramus in dorsal view. Note the reception pits extending beyond the dentary tooth row.

GLAHM V1430: isolated tooth; GLAHM V1436: numerous isolated teeth. All from near Peterborough, England (Peterborough Member, Oxford Clay Formation; Middle Callovian).

Diagnosis (asterisks denote autapomorphies among metriorhynchids). Metriorhynchid thalattosuchian with moderately enlarged teeth showing strong mediolateral compression, and have a continuous keel at mesial and distal edges. Very poorly defined microscopic true denticles present on both keels, although the denticles do not proceed along the entire carina. In labial or lingual view the height of the denticles does not influence the height of the keel (i.e. no evident/conspicuous serrated edge). Enamel on the labial and lingual surfaces lack conspicuous ornamentation except at the base of the crown where there are accessory ridges orientated to the apicobasal axis of the crown*; these ridges are low, well spaced and very short*. Humerus shaft contributes more than 50% of total humeral length, proximal articular margin not in close contact with the deltopectoral crest, caudal margin of the humerus in lateral view distinctly concave. The deltopectoral crest is well developed with: the width of the humerus distal articular head is subequal to the width that the deltopectoral crest projects out from the humerus shaft. In medial view, the ilium articulation facet for the ischium is orientated horizontally*, and a well-defined crest on the medial margin of the ilium between the articulation facet on the anterior process and the acetabulum*, the dorsal border of the ilium is short, in medial view it terminates prior to the ischium articulation facet*. Reception pits for the maxillary teeth present posterior to the seventh dentary alveolus and continue posteriorly even after the dentary tooth row; these reception pits are in the same plane as the dentary alveoli creating an in-line interlocking dentition for the posterior-half of the tooth rows*.

<div align="center">

cf. *Tyrannoneustes*
(Figs 9, 10)

</div>

Material. NHMUK PV OR47989: isolated tooth; Oxford, England (Oxford Clay Formation). NHMUK PV OR32643:
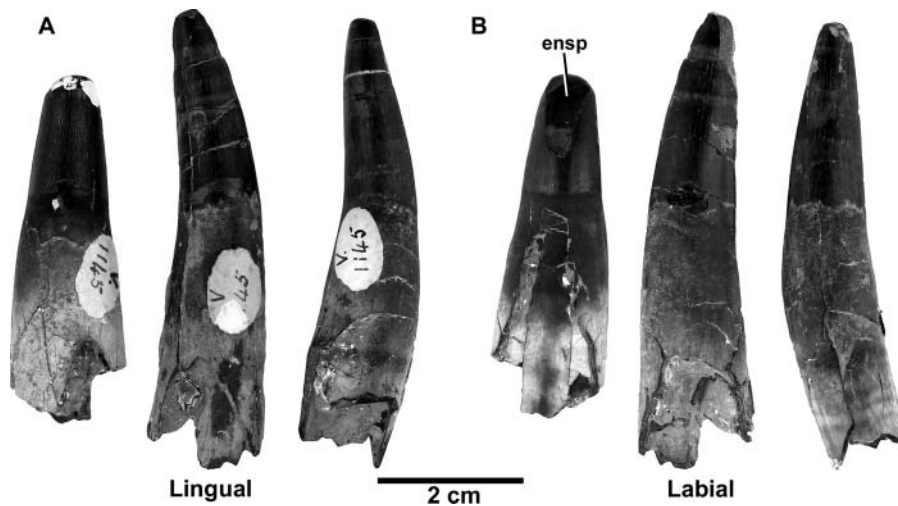

Figure 8. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Three tooth crowns in labial and lingual view. Note the extensive enamel spalling on one of the teeth.
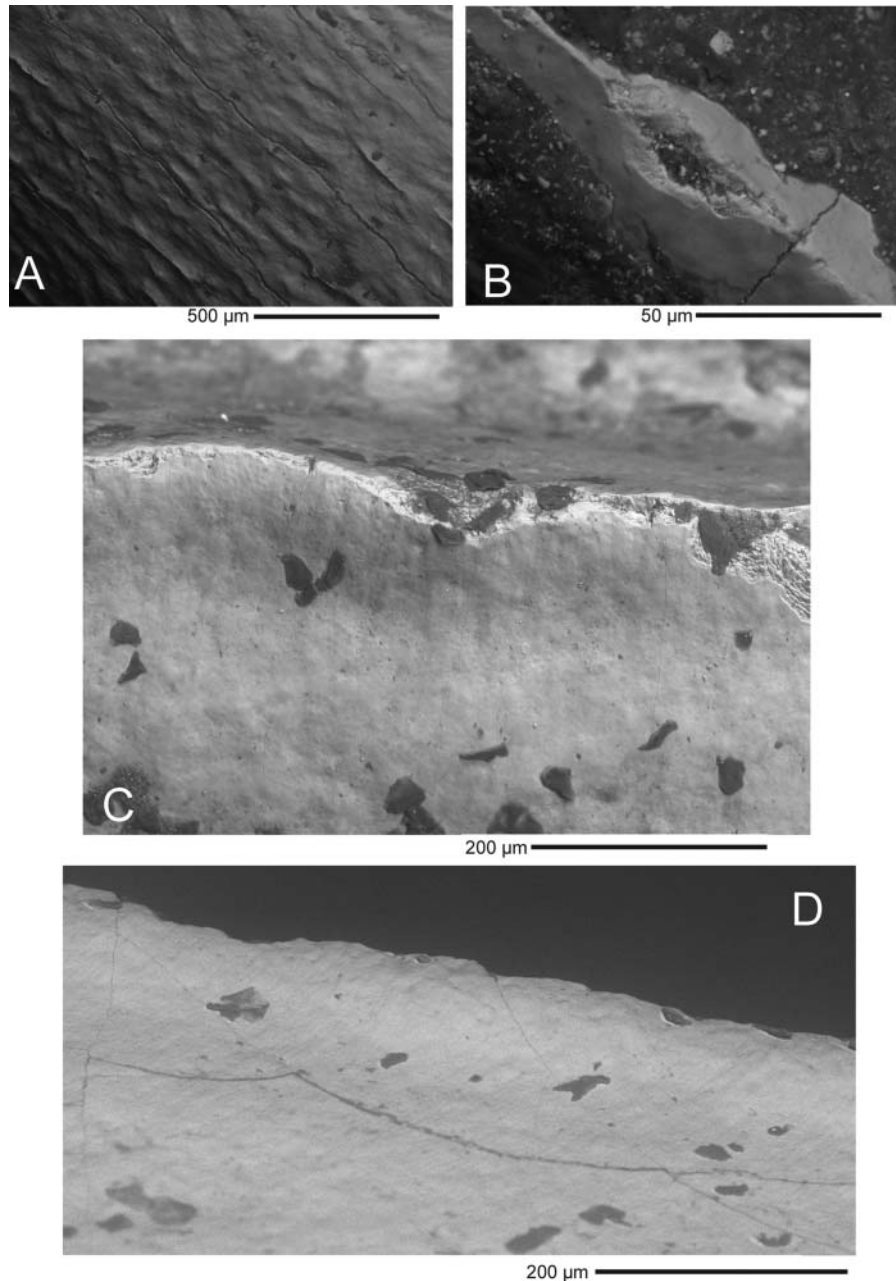
Figure 9. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972 tooth. Backscattered SEM micrographs. **A**, enamel ornamentation at base; **B**, isolated and worn denticle; **C**, close-up of a carina; **D**, carina in lateral view.

isolated tooth; NHMUK PV OR32644: isolated tooth; NHMUK PV OR32648: isolated tooth; Vaches Noires cliffs, Calvados, France. GIUS 8–3044: incomplete isolated tooth; Ogrodzieniec, Poland (uppermost Callovian or lowermost Oxfordian).

Description
Ontogenetic stage. Among fossil crocodylomorphs open sutural contacts between the vertebral centrum and the neural arch are often used as an indicator of juvenile status (Mook 1933). Not only has this been confirmed in extant crocodylians, but the sequence of the neurocentral suture closure in the crocodylian vertebral column follows a consistent pattern: caudal to cranial, with fusion of the cervical neurocentral sutures occurring in morphologically mature specimens (see Brochu 1996 and references therein). Although within Archosauria there is variation in sequence of the neurocentral suture closure (see Irmis 2007), the caudal-cranial pattern has been observed

Figure 10. *Tyrannoneustes* sp., GIUS 8–3044. Incomplete isolated tooth crown from a quarry near Ogrodzieniec in Poland (Callovian or Oxfordian in age). Backscattered SEM micrographs; both **A** and **B** are close-ups of a carina.
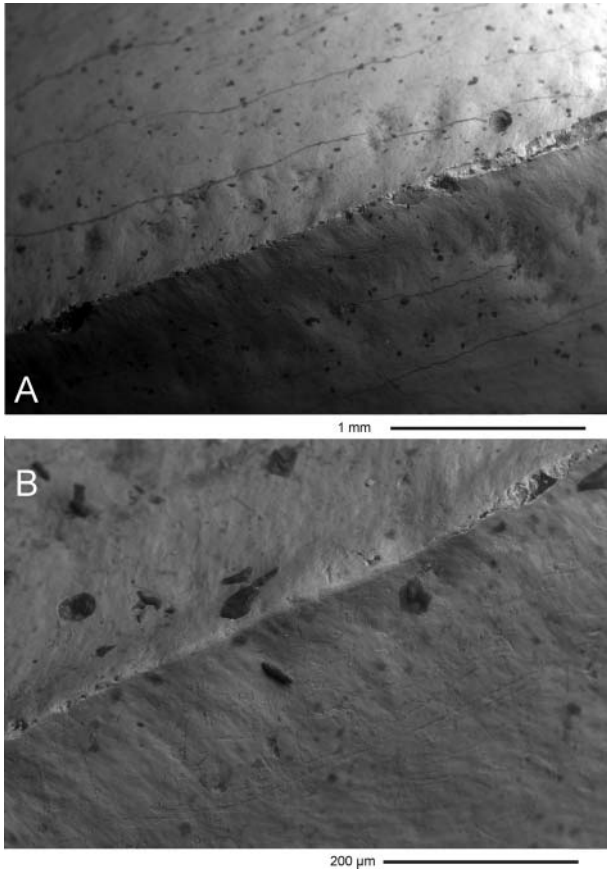
in Early Jurassic thalattosuchians (Delfino & Dal Sasso 2006).

The neurocentral sutures on the cervical and dorsal vertebrae are not fused in GLAHM V972 (Figs 3, 4), but all caudal vertebrae have fused sutures (Fig. 13). As such, this individual is considered a sub-adult. With an approximate length of 670 mm for the incomplete mandible, this makes GLAHM V972 larger than any known specimen of *Gracilineustes leedsi* (see Andrews 1913), and comparable in size to the lower range of adult specimens of *Metriorhynchus superciliosus* (Andrews 1913; MTY pers. obs.). While we cannot make an exact estimate of the total body length of GLAHM V972, we can determine that it was greater than 3.27 m in length. This was done by comparing Oxford Clay specimens with known cranial and mandibular lengths (Andrews 1913) to body length estimates of the same specimens (Young *et al*. 2011a). In particular, NHMUK PV R2044 (*Metriorhynchus superciliosus*) has an approximate mandibular length of 635 mm and a body length of 3.27 m.

Therefore, the acquisition of large body size (e.g. greater than 3.27 metres in length while still subadult) occurred

prior to the subclade Geosaurini. Regardless of whether the large mandible described by Lepage *et al*. (2008, pp. 99–101) belongs to another large-bodied geosaurine species, this specimen would have been the largest metriorhynchid known from the Middle Jurassic. The mandible figured by Lepage *et al*. (2008) is approximately 970 mm in length, which results in a conservative cranial length estimate of 920 mm and total body length of 5 m.

Mandible. Only the right mandibular ramus is present (Fig. 5). It is incomplete, measuring approximately 670 mm in length, and is missing the retroarticular process and articular. The depth of the dentigerous region of the dentary is 34 mm, while the depth of the mandible at the coronoid process is 79 mm. The shape of the mandibular ramus is noticeably different from other Oxford Clay metriorhynchids (except for the Lepage *et al*. 2008 '*brachyrhynchus*' mandible), as there is a strong curvature of the posterior region, resulting in further ventral displacement of the dentary tooth row (Fig. 6). All metriorhynchids from the Oxford Clay Formation exhibit some ventral displacement of the dentary tooth row, such that the coronoid process is located above the plane of the tooth row (*Metriorhynchus superciliosus*: GLAHM V1141; *Gracilineustes leedsi*: NHMUK PV R3014, NHMUK PV R3015; *Suchodus brachyrhynchus*: GLAHM V995, NHMUK PV R3804).

Notwithstanding, in the other Oxford Clay metriorhynchids the coronoid process is on the same plane as both the retroarticular process and the glenoid fossa (Fig. 6). Although the articular, jaw joint and retroarticular process are missing in GLAHM V972, it is clear from what is preserved that the coronoid process has been ventrally displaced as the angular continues to rise dorsally caudal to the coronoid process (Figs 5, 6). The ventral displacement of the coronoid process relative to the jaw joint is observed in *Dakosaurus manselii* (NHMUK PV OR40103), *D. maximus* (SMNS 82043) and the '*M. brachyrhynchus*' mandible of Lepage *et al*. (2008, pp. 99–101). The preservation of *Geosaurus giganteus* (NHMUK PV OR37020) makes it unclear whether it shared this feature, and no described *Torvoneustes* specimen has a complete mandible. Interestingly, the reconstruction of *D. andiniensis* (see Pol & Gasparini 2009, fig. 2) shows a greatly expanded coronoid process.

A lateral mandibular groove (= surangulodentary groove) is present on the surface of the dentary and surangular (Fig. 5). It lacks the large foramen at the dentary end, as observed in *Dakosaurus maximus* (SMNS 8203) and *D. andiniensis* Pol & Gasparini 2009, but this may be the result of poor preservation. The depth and preservation of the surangulodentary groove is more reminiscent of that observed in other Oxford Clay metriorhynchids (e.g. *M. superciliosus*: GLAHM V1141; *S. brachyrhynchus*: GLAHM V995) than the well-delimited and deep groove

observed in *Dakosaurus*. There is, however, a foramen at the surangular end of the groove. As with other metriorhynchids (Fraas 1902; Andrews 1913), no external mandibular fenestra is evident.

Dentary. The right mandibular ramus is broken into two pieces at the position of the tenth dentary alveolus (Figs 5, 7). The anterior section has suffered from post-mortem damage and crushing. This has resulted in the symphyseal sutural contact surface being badly damaged and incomplete. However, in the posterior section the dentary sutures with the surangular and angular can be clearly identified. The external surface of the dentary is slightly convex (although the natural shape of the anterior region has been lost due to compression) and lacks conspicuous ornamentation. Along the dorsal margin of the dentary there is no evidence of festooning, as in all other thalattosuchians (Fig. 6). The dentary has 12 visible alveoli, 10 of which are adjacent to the mandibular symphysis (only visible by the articulation facet on the medial surface). We cannot discount the possibility that there are two more dentary alveoli, as the mandible is broken where the 13th alveoli would be, while posterior to that break the dorsal margin of the dentary is damaged.

Angular and surangular. *Tyrannoneustes lythrodectikos*, as with other metriorhynchids (Fig. 6), has an angular and surangular that are strongly sutured along their entire border, with the angular forming the ventral half of the posterior mandible and the surangular the dorsal half (Fig. 5). The angular ventral margin is gently convex, curving dorsally towards the jaw joint (which is missing due to poor preservation). The angular terminates significantly higher than the dentary tooth row (also observed in *S. brachyrhynchus*: NHMUK PV R3804). As with the angular the surangular gentle curves dorsally, far more so than in contemporary metriorhynchids (see Fig. 6). As with all other metriorhynchids (Fig. 6), there is a well-developed coronoid process. Interestingly, the coronoid process would not have been parallel to the jaw joint in GLAHM V972. As mentioned above, this is due to the dorsally re-orientated posterior end of the mandible.

Splenial. As with other thalattosuchians (e.g. *Steneosaurus leedsi*: NHMUK PV R3806; *Metriorhynchus superciliosus*: GLAHM V1141; *Suchodus brachyrhynchus*: NHMUK PV R3804), the splenial on GLAHM V972 is well developed rostrally but its anterior extent cannot be determined due to post-mortem damage of the anterior region (Figs 5, 6). The splenial shape and sutural contacts match those described and figured for *Suchodus brachyrhynchus* (Andrews 1913, pp. 157–158, text-fig. 60). It certainly contributed to the symphysis, and this contribution was most probably as significant as that in *Suchodus brachyrhynchus*.

Dentition. Unfortunately, the dentition of the new species is too poorly known to characterize it as either homodont or heterodont.

Tooth morphology. The dentition of *Tyrannoneustes* is mediolaterally compressed and lingually recurved. Enamel ornamentation is poorly developed, and composed of apicobasally aligned ridges only at the base of the crown. The teeth are bicarinate (i.e. carinae on mesial and distal edges), with the carinae composed of a keel and denticles. The denticles are microscopic and wider transversely than apicobasally. The overall crown is unfaceted and oval in cross-section, with the labial surface labiolingually thinner than the lingual surface (Figs 8, 9). The isolated Polish and French tooth crowns herein referred to *Tyrannoneustes* share this morphology (Figs 10, 11). As with all other thalattosuchians (e.g. *Steneosaurus leedsi*: NHMUK PV R3806; *Metriorhynchus superciliosus*: GLAHM V1141; *Suchodus brachyrhynchus*: NHMUK PV R3804; *Dakosaurus maximus*: SMNS 8203, SMNS 82043), the teeth are single cusped. The teeth show a non-taphonomic lateral compression, but they are not laminar. There is no constriction present at the crown/root junction, but the boundary is evident due to colour and texture.

Type of occlusion. During occlusion, the posterior maxillary and dentary teeth would have met each other mesiodistally (i.e. along an essentially sagittal plane). Posterior to the seventh dentary alveolus there is a reception pit for the corresponding maxillary crown. From D7 posteriorly, there is a reception pit between each pair of dentary alveoli, followed by three post-dentary alveoli reception pits (Fig. 7). The posterior maxillodentary teeth (D7–12, maxillary tooth row unknown) not only interlock, but do so 'in-line', namely: the dentary alveoli and reception pits for the maxillary crowns are in the same plane as one another. This occlusal pattern is unique to *Tyrannoneustes* (see below) among thalattosuchians. Anterior to D7 there are no reception pits for the maxillary crowns. However, the lateral margins of the dentary do 'undulate' (in dorsal view), indicative of a 'fish-trap' interlocking dentition. This is not the festooning observed in most eusuchians, but protruding alveoli that project laterally in narrow-snouted taxa; these alternate with laterally-opened occluding pits, creating an undulating outline, evident in dorsal/ventral views. This is the typical thalattosuchian occlusal morphology, and is analogous to that seen in the other narrow-snouted forms, including the extant *Gavialis* (NHMUK PV Vert. Pr 3.11, NHMUK PV 61.4.1.2), fossil gavialoids (*Eosuchus* and *Piscogavialis*) and dyrosaurids (see Kraus 1998; Delfino *et al*. 2005; Jouve *et al*. 2006). This morphology is observed along the entire tooth row in the metriorhynchid genera *Metriorhynchus* (GLAHM V1141, NHMUK PV R2030, NHMUK PV R3016), *Gracilineustes* (CAMSM J29475,
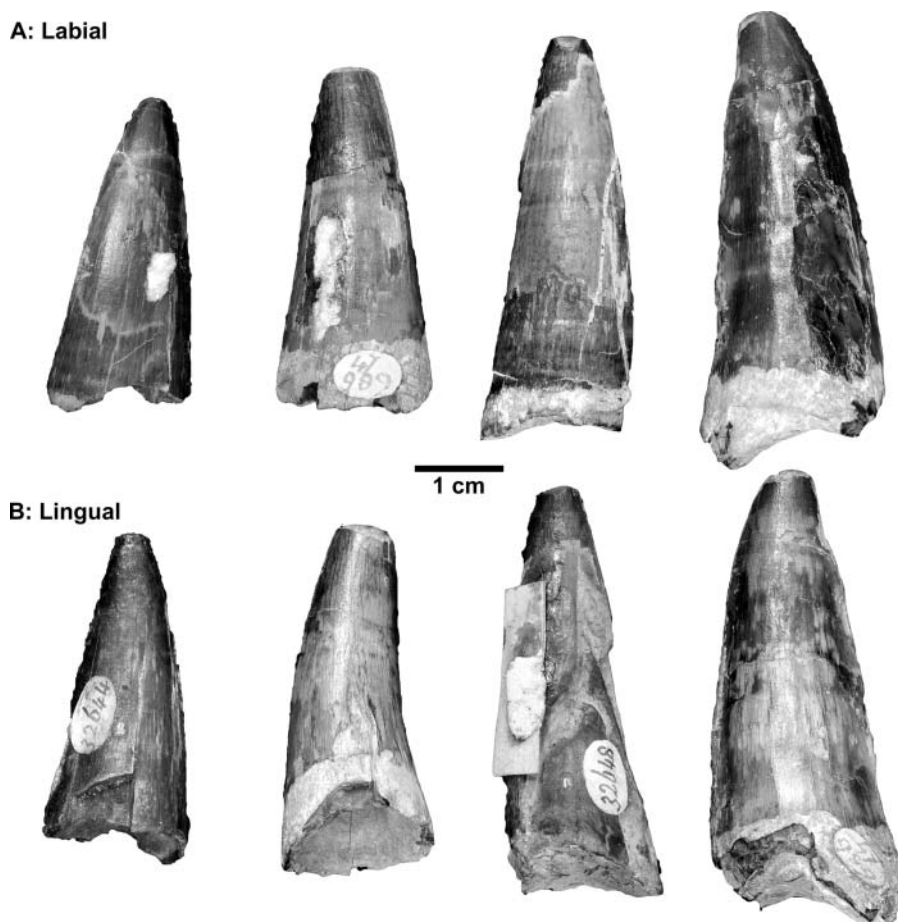
Figure 11. *Tyrannoneustes* sp., NHMUK PV OR47989. Four tooth crowns in: **A**, **B**, labial and lingual view from the Falaises des Vaches Noire, Calvados, France (Callovian or Oxfordian in age).

NHMUK PV R3014) and *Cricosaurus* (BSPG AS-I-504, SMNS 9808).

While no other crocodylomorph has an occlusal pattern similar to *Tyrannoneustes*, the Geosaurini genus *Geosaurus* possessed a distinct occlusal pattern. The arrangement of dentition in *Geosaurus* is well suited to maximise efficiency through slicing (Young & Andrade 2009; Young *et al*. 2010; Andrade *et al*. 2010). The dentition of *Geosaurus* does not interlock as observed in the traditional 'fish-trap' occlusal pattern, as the upper tooth row overbites the lower tooth row (with the premaxilla poorly known in *Geosaurus*, we restrict our discussion to the maxillary/posterior tooth row), creating well-developed reception pits on the lateral margins of the dentary (NHMUK PV R1229, NHMUK PV OR37020). These reception pits are created by the apex of the upper jaw teeth when the jaw is closed. As such, the upper-and-lower tooth rows function as a set of opposing blades which could slice prey through point cutting (*sensu* Evans & Sanson 2003; see Young & Andrade 2009; Andrade *et al*. 2010). This is supported by mechanical modelling of the great barracuda, an extant bony-fish species whose posterior tooth rows are arranged as blades that enable it to slice through fish, even severing prey into pieces (Grubich *et al*. 2008). Grubich *et al*. (2008, p. 27) concluded that the 'scissor-like' occlusal pattern in the great barracudas 'enhances their feeding performance as apex predators through the ability to quickly dismember large prey and thereby reduce the effects of gape limitation on prey handling'. We posit the same for *Geosaurus* (see Young & Andrade 2009; Andrade *et al*. 2010). A further analogy between *Geosaurus* and the great barracuda is their comparatively low bite forces (see Habegger *et al*. 2011 for bite force measurements in barracudas; Young *et al*. 2010 for finite element biomechanical analysis for *Geosaurus*). As such, high bite forces are not necessary to evolve super-predatory behaviour and occupy the niche of apex predator, at least in metriorhynchids.

The only Oxford Clay metriorhynchid with reception pits is *Suchodus brachyrhynchus* (GLAHM V995, NHMUK PV R2618, NHMUK PV R3804; see Fig. 6A). As observed in *Geosaurus* the reception pits are labially displaced on the dentary, caused by a maxillary overbite. The reception pits either continue along the entire tooth row or are only prominent on the posterior half of the tooth row. As

both the occlusal morphology and dental morphology of *Geosaurus giganteus* and *S. brachyrhynchus* are comparable, both having crowns that are blade-like and strongly labiolingually compressed (see Young *et al*. 2010, fig. 8), the two species may have had a similar feeding ecology.

Ornamentation, carinae and wear. Ornamentation is light, composed of microscopic ridges arranged in an anastomosing pattern, creating a fabric of poorly defined crests over the surface (Figs 8–11). Given the morphology and small size of these ridges, the overall macroscopic appearance of the tooth surface is reasonably smooth. However, at the base of the crowns, on the labial and lingual surfaces, there are conspicuous accessory ridges orientated to the apicobasal axis of the crown. Unlike the apicobasal ridges of other Oxford Clay metriorhynchids, these are restricted to the base of the crown and are low, well spaced and very short.

Very poorly defined microscopic true denticles are present on both keels (GLAHM V972, GLAHM V1430, GIUS 8–3044; Figs 9, 10). Scanning electron microscopy was necessary to identify the presence of denticles. The denticles are not contiguous along the carinae, but instead form short lines of 2–10 denticles. Interestingly, in both labial and lingual views the height of the denticles weakly influenced the height of the keel, and thereby the denticles created a poorly serrated subtle edge. This morphology has not been identified in crocodylomorphs before (for comparisons with other metriorhynchids, see Andrade *et al*. 2010). Split or supernumerary carinae were not found on any tooth, nor was there any evidence for false-ziphodont serrations.

Spalling of the enamel is present on the labial surface of numerous isolated teeth (GLAHM V1145, GLAHM V1399/9, GLAHM 1402/5 and GLAHM 1430; Fig. 8). However, the spalling is not as extensive as that observed on the labial surface of NHMUK PV R486 (Oxford Clay Geosaurinae indet., see Fig. 2A). Enamel spalling is probably created by impact between the tooth and a prey item, in the same axis that the jaws close (see Schubert & Ungar 2005). No evidence for wear facets (tooth-to-tooth occlusion) was found, but the available material is quite restricted.

Post crania
Cervical vertebrae. Both the first (atlas) and second (axis) vertebrae are missing from GLAHM V972. There should be no more than five post-axial cervical vertebrae in metriorhynchids (see Wilkinson *et al*. 2008 for discussion), with the cervical vertebrae being defined as those vertebrae in which the parapophyses are borne on the centrum and not on the neural arch (Andrews 1913). In GLAHM V972, four out of the five post-axial cervicals are preserved, namely C3 to C6 (Fig. 3). We can rule out C8 (the final post-axial cervical) as this vertebra can be identified because both the diapophysis and parapophysis are borne higher up on the centrum with the parapophysis situated just below the diapophysis

(see Wilkinson *et al*. 2008). As with all other thalattosuchians (e.g. *Steneosaurus leedsi*: NHMUK PV R3806; *Metriorhynchus superciliosus*: NHMUK PV R2032) the cervical vertebrae are amphicoelous, with the articular faces being moderately concave and oval to circular in shape. Unfortunately, none of the cervical vertebrae preserve both the neural spine and an undeformed centrum.

The cervical vertebrae in GLAHM V972 closely resemble those of other metriorhynchids, with an hourglass shape in ventral aspect. The parapophyses are situated anteriorly and towards the base of the centrum, without protruding beyond the bottom of the centra. The parapophyses are short and at their distal (lateral) end they bear an articulation surface for attachment with the capitulum of the corresponding cervical rib. The diapophyses of these vertebrae (only two cervicals possess well-preserved diapophyses) are located on the neural arch, have a smaller articulation facet than parapophysis, and are angled downwards. The zygapophyses of these vertebrae are either missing or distorted. The preserved cervical ribs match those described for other Oxford Clay metriorhynchids (Andrews 1913) and *Torvoneustes carpenteri* (Wilkinson *et al*. 2008) (Fig. 12C).

Thoracic vertebrae. Herein we define the thoracic vertebrae of the metriorhynchid vertebral column as those vertebrae in which the parapophysis is wholly or partly borne on the transverse process. In GLAHM V972 there are eight identifiable thoracic vertebrae. Unfortunately, all nine vertebrae have been compressed anterioposteriorly and/or distorted mediolaterally. In addition, all eight lack complete transverse processes and/or a neural spine, with the neural arch and its processes suffering deformation and damage. The shape of the thoracic centra in anterior/posterior aspect ranges from circular, similar to that of the cervical vertebrae, to more elongate and oval. Whereas the anterior articulation surface of the centra is notably concave, the posterior surface is only faintly concave. The preserved dorsal ribs match those described for other Oxford Clay metriorhynchids (Andrews 1913) and *Torvoneustes carpenteri* (Wilkinson *et al*. 2008) (Fig. 12A, B).

Lumbar vertebrae. Herein we define the lumbar vertebrae of the metriorhynchid vertebral column as those vertebrae in which the parapophyses are no longer borne on the transverse process but are either borne on the neural arch entirely or shared with the centrum (see Fig. 4). In GLAHM V972 there is only one identifiable lumbar vertebra. Interestingly, the lumbar vertebrae of metriorhynchids possess parapophyses that project anteriolaterally from the anterior face of the vertebrae (Fig. 4). This morphology is not only observed in GLAHM V972, but also in *Metriorhynchus superciliosus* (GLAHM V1142) and *Suchodus brachyrhynchus* (GLAHM V995). However, GLAHM V972 is the only known metriorhynchid specimen in which the parapophysis is partially located on the
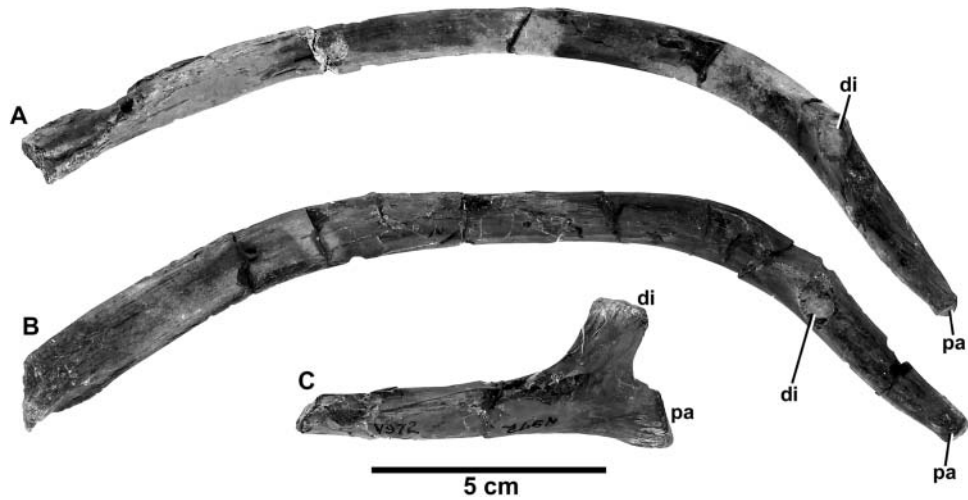
Figure 12. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Selection of ribs: **A**, **B**, two dorsal ribs; **C**, cervical rib.

centrum and the articulation facet is concave. Unfortunately, until the vertebral morphology of Metriorhynchidae is better understood and specimens are described for a range of other species, we cannot confidently determine whether this morphology is an apomorphy for this taxon.

Sacral vertebrae. No sacral vertebrae are preserved.

Caudal vertebrae. The caudal series is the longest in the vertebral column, which in other Oxford Clay metriorhynchids is composed of between 33 and 36 elements (Andrews 1913). For GLAHM V972 only 20 caudal vertebrae are preserved, and all are incomplete (lacking neural spines and complete neural arches) (Fig. 13). The vertebral dimensions and shape variation along the column closely resemble that observed in *Metriorhynchus*
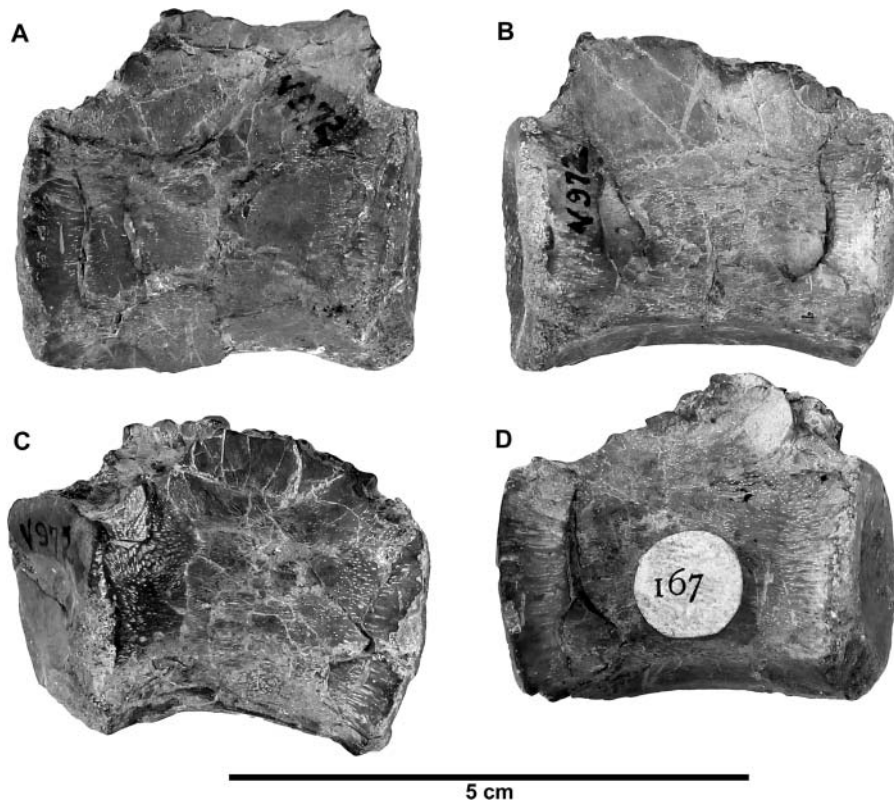

Figure 13. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Four caudal vertebrae in lateral view.

superciliosus (GLAHM V990), *Gracilineustes leedsi* (NHMUK PV R3014) and *Suchodus brachyrhynchus* (NHMUK PV R3804). Most of the vertebrae are hourglass shaped, depressed in the centre with round concave articular faces. Based upon comparison with the other three Oxford Clay metriorhynchids with complete tails, there are three vertebrae which may have formed part of the caudal fluke, or were anterior to the fluke. These three vertebrae have a convex ventral margin with a varying degree of curvature, and are more strongly mediolaterally compressed than other caudals, just as described by Andrews (1913) for the fluke vertebrae of other Oxford Clay species. However, without the neural arch and spines, we cannot be sure whether they formed part of the fluke or were anterior to it.

Humerus. The humerus of GLAHM V1145 (Fig. 14) is very similar in shape to that observed in *M. superciliosus* (GLAHM V1140, NHMUK PV R1530, NHMUK PV R3016), *G. leedsi* (NHMUK PV R3015) and *S. brachyrhynchus* (NHMUK PV R4763). Of these it most closely resembles the morphology observed in *S. brachyrhynchus*. In both species the deltopectoral crest is well developed, as the width of the distal articular region is subequal to the width of the deltopectoral crest projecting

out from the humerus shaft. In both *M. superciliosus* and *G. leedsi* the deltopectoral crest is noticeably smaller. In all Oxford Clay species except *G. leedsi* the deltopectoral crest has a distinctive triangular shape in lateral view (in *G. leedsi* it forms a gentle convex curve). The specimen measures 87 mm in length; the proximal articular head is 23 mm wide, while the distal articular region is 16 mm wide.

The humerus of *Tyrannoneustes lythrodectikos* is unlike the short, stocky humeri of *M. geoffroyii* (OXFUM J.55476–8), *C. suevicus* (SMNS 9808), *C. araucanensis* (Herrera *et al*. 2009), *T. carpenteri* (BRSMG Cd7203) and *D. maximus* (Fraas 1902). In these species the deltopectoral crest either contacts the proximal articular surface or comes very close to it. Furthermore, the shaft contributes 50% or less of total humeral length and is straight, lacking the 'kink' (caudal margin is concave and the proximal head noticeably projects further posteriorly than the distal head) observed in *M. superciliosus*, *G. leedsi*, *S. brachyrhynchus* and GLAHM V1145. It is interesting that GLAHM V1145 had not developed a more flattened humerus with a short shaft and a strongly convex proximal margin, as this suggests that this 'flattened' humeral morphology was independently acquired at least three times by the Kimmeridgian:
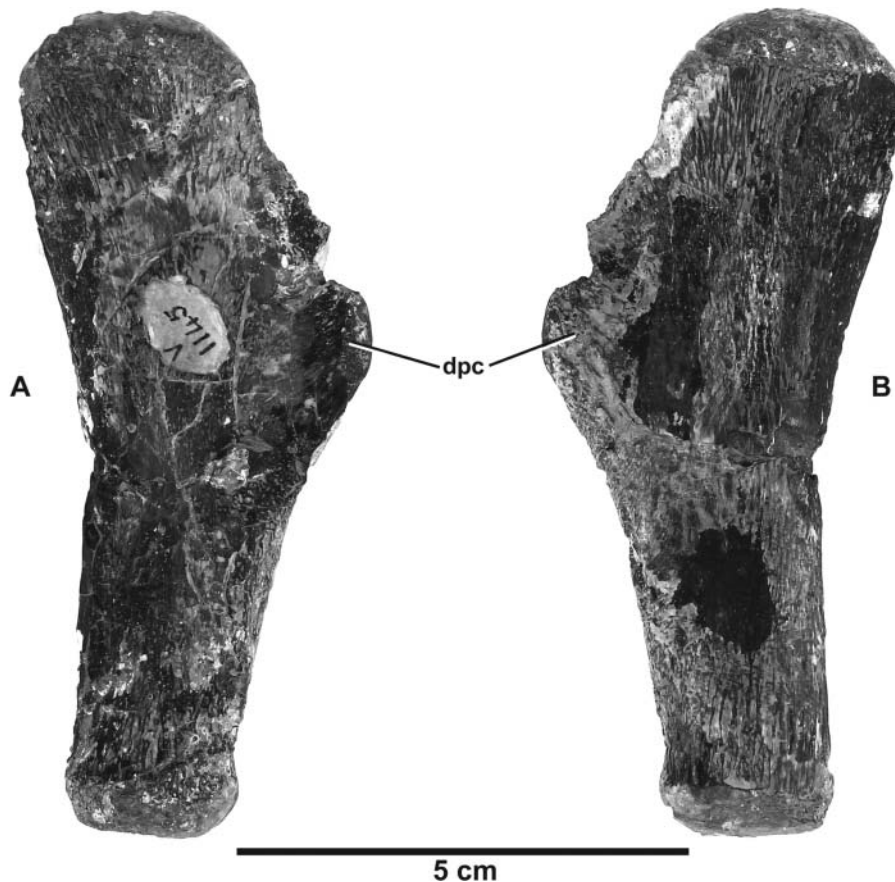

Figure 14. *Tyrannoneustes lythrodectikos* sp. nov., GLAHM V1145. Humerus in: **A**, medial view; **B**, lateral view.

(1) within the genus *Metriorhynchus*; (2) by *Cricosaurus;* and (3) by Geosaurini (based on optimisation of this character onto the phylogenetic tree discussed below).

It is worth noting that there is a humerus morphology intermediate between that observed in the Kimmeridgian taxa and those described for *M. superciliosus*, *G. leedsi*, *S. brachyrhynchus* and GLAHM V1145. The specimen with this intermediate morphology, GLAHM V1146, also from the Middle Callovian (Peterborough Member of the Oxford Clay Formation), has a more convex proximal margin, which reaches more closely to the deltopectoral crest, and a proportionally short shaft but still possesses a slight concave curvature of the posterior margin. This morphology is not seen in any of the currently named Oxford Clay metriorhynchid species. Along with the isolated tooth NHMUK PV R486 and the Lepage *et al*. (2008) mandible, both of which are morphologically distinct from *Tyrannoneustes*, this distinctive humerus specimen suggests there is at least one other large super-predatory metriorhynchid yet to be described from the Oxford Clay.

Coracoid. The coracoids (GLAHM V1145; Fig. 15) are very similar to those described for *M. superciliosus* (NHMUK PV R3016; Andrews 1913). As with *M. superciliosus* the coracoid foramen is developed into a notch on the distal end. Andrews' (1913, text-fig. 70) drawing of the coracoid of NHMUK PV R3016 is virtually identical to the right coracoid of GLAHM V1145. The coracoid blade of *Gracilineustes leedsi* (NHMUK PV R3014) is not as expanded as that observed in *M. superciliosus* or GLAHM V1145 (see Andrews 1913, text-fig. 69). The right (and most complete) coracoid measures 93 mm in length, with a width of 54 mm for the coracoid blade. The articulations for the scapula and humerus differ considerably. The humerus articulation surface forms a smooth and slightly concave basin restricting the humerus to motion in a single plane. Although the scapulae are missing, they too would have possessed a glenoid fossa for the humerus, further restricting the possible range of motion (see Andrews 1913). Correctly reconstructing the exact plane of motion must await discovery of the entire pectoral girdle. The articulation surface for the scapula is complex with troughs and hills, thereby firmly suturing both bones.

Ilium. The shape of the ilia in *Tyrannoneustes lythrodectikos* (GLAHM V972, GLAHM V1145; Fig. 16) is very
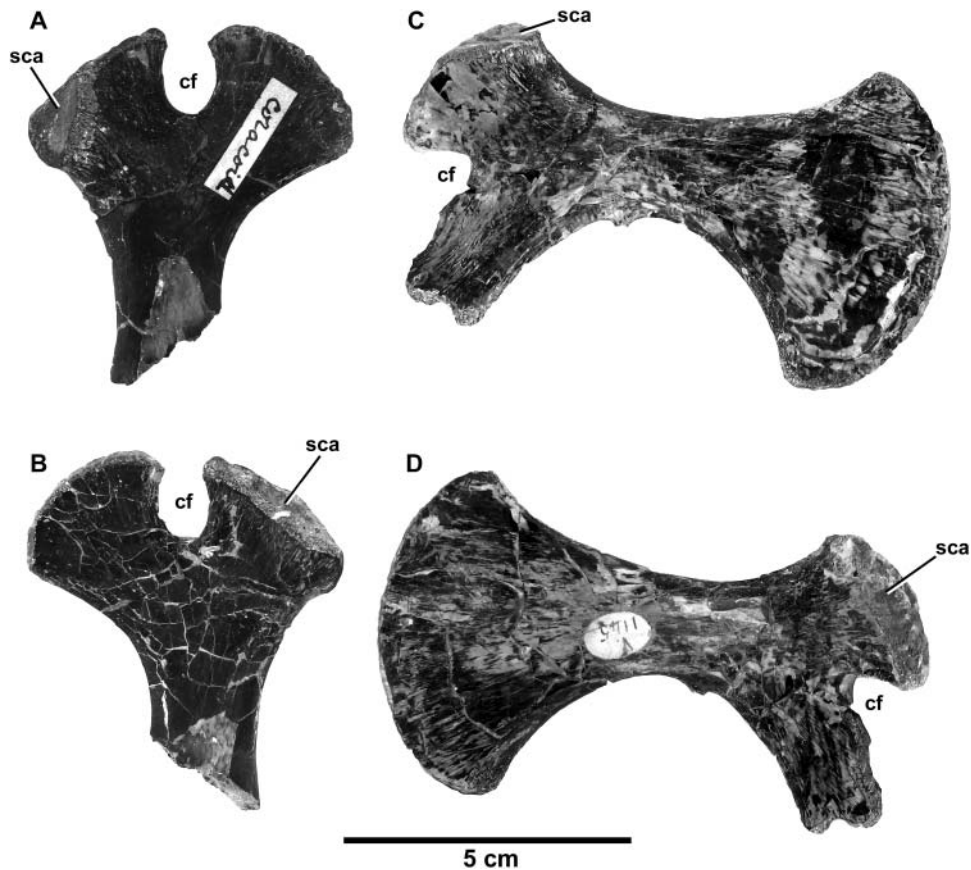
Figure 15. *Tyrannoneustes lythrodectikos* sp. nov., GLAHM V1145. Right coracoid in: **A**, lateral view; **B**, medial view. Left coracoid in: **C**, medial view; **D**, lateral view.

Figure 16. *Tyrannoneustes lythrodectikos* sp. nov. Ilium of GLAHM V972 in: **A**, lateral view; **B**, medial view. Ilium of GLAHM V1145 in: **C**, lateral view; **D**, medial view.

Figure 17. *Tyrannoneustes lythrodectikos* sp. nov., holotype, GLAHM V972. Ischium in: **A**, dorsal view; **B**, lateral view; C, medial view.

similar to that of other metriorhynchids (e.g. Fraas 1902; Andrews 1913). The ilium of GLAHM V972 measures 39 mm along the dorsal border, with a maximum anterioposterior length of 48.5 mm. The ilium of GLAHM V1145 measures 41 mm along the dorsal border, with a maximum dorsoventral length of 66 mm and a maximum anterioposterior length of 50 mm.

The ilium of this species differs from those of other Oxford Clay metriorhynchids in the following ways. First, in lateral view, the dorsal margin of the articulation facet that contributes to the acetabulum is horizontally oriented, rather than ventrally oriented as in *M. superciliosus* (GLAHM V995) and *S. brachyrhynchus* (GLAHM V1142). Second, the dorsal border of the ilium is short in *Tyrannoneustes*, as in medial view it terminates prior to the ilium contribution to the acetabulum, rather than terminating approximately level to the mid-point of the ilium acetabulum contribution in *M. superciliosus* (GLAHM V995) and *S. brachyrhynchus* (GLAHM V1142).

Ischium. The left ischium of GLAHM V972 is preserved, but only from the neck of the ischium to the proximal articulation facets (Fig. 17). The ischium blade is not preserved. The proximal end of the ischium is divided into two processes. However, unlike other metriorhynchids (e.g. Andrews 1913; Wilkinson *et al*. 2008), there is no deep notch separating them, but rather a medially directed convex ridge. This ridge forms a prominent curve along the medial margin.

The tip of the anterior process in GLAHM V972 differs from *M. superciliosus*, as the latter has a distinct and bulbous articulation surface for the pubis (NHMUK PV R2054, NHMUK PV R2775, NHMUK PV R6859). In geosaurines, however, there is no variation in cross-sectional width between the articulation surface and the rest of the anterior process, e.g. GLAHM V972, *S. brachyrhynchus* (GLAHM V995, NHMUK PV R3804), *Torvoneustes carpenteri* (BRSMG Cd7203) and *D. maximus* (Fraas 1902). As with *D. maximus* the articulation facet for the pubis in GLAHM V972 is a complex surface (hills and troughs) restricted to the anterior margin of the process. This is distinct from its contemporary metriorhynchids (*S. brachyrhynchus* and *M. superciliosus*) which both have a rounded and smooth articulation at the end of the anterior process; the lack of obvious articulation facets in those taxa is why Andrews (1913) believed there was cartilage in this area.

The dorsal articulation surface of the larger posterior process – which contributes to the acetabulum – in GLAHM V972 is also distinct from other Oxford Clay metriorhynchids. *Tyrannoneustes lythrodectikos* has a more complex (i.e. deeper troughs and hills) articulation facet for the ilium than seen in *M. superciliosus* (GLAHM V990), and the ischial contribution to the acetabulum is distinct. In *M. superciliosus* (GLAHM V990) and *S. brachyrhynchus*

(GLAHM V995) the ischial contribution to the acetabulum is a laterally directed, slightly concave semi-circular basin, whereas in GLAHM V972 it is a laterally directed, deeply concave basin and semi-ellipsoidal in shape.

Femur. The femur is a robust bone with the sigmoidal shape seen in all other metriorhynchids (Fig. 18). In comparison with *Gracilineustes leedsi* (NHMUK PV R3015), *Torvoneustes carpenteri* (BRSMG Cd7203) and *Dakosaurus maximus* (Fraas, 1902), the femur of *Tyrannoneustes lythrodectikos* is more sigmoidal. The fourth trochanter is absent, a character shared by all metriorhynchids (Andrews 1913). The femur is 258 mm in total proximal-distal length, with a proximal head width of 43 mm and a distal head width of 33 mm.

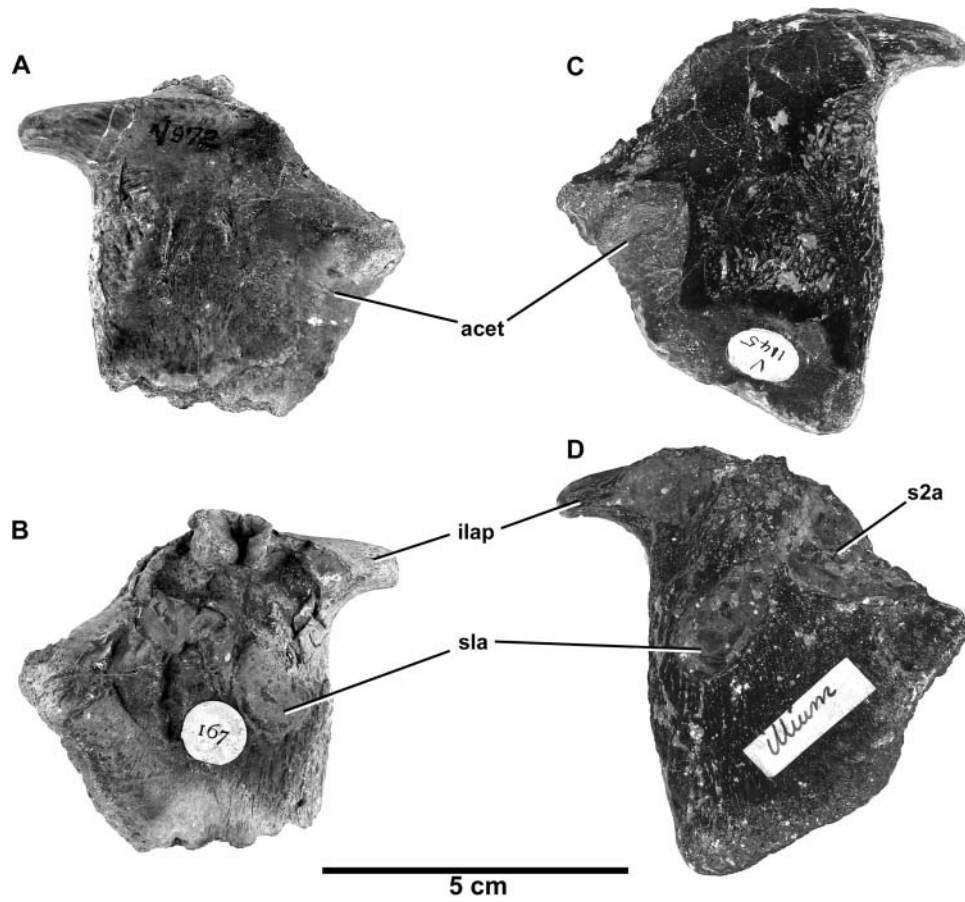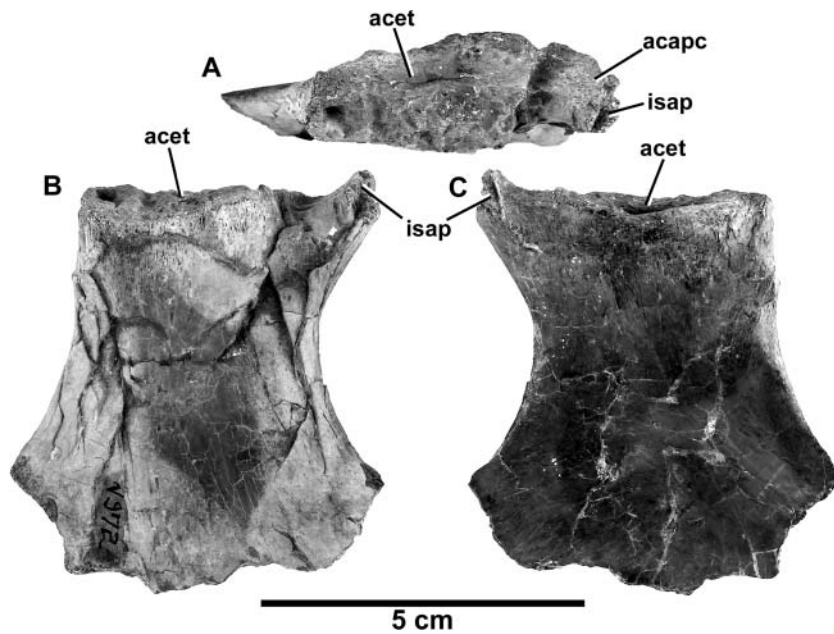**Figure 18.** *Tyrannoneustes lythrodectikos* sp. nov., GLAHM V1145. Femur in: **A**, lateral view; **B**, medial view.

As with all other metriorhynchids (Fraas 1902; Andrews 1913; Wilkinson *et al*. 2008), the proximal head extends medially into the acetabulum. The articular surface of the proximal head is noticeably triangular in dorsal aspect (due to the enlargement of the posteromedial tuber), and is directed medially. Moreover, the articular surface of the proximal head is restricted to the dorsal and medial surfaces; there is no contribution from the lateral surface. The enlargement of the posteromedial tuber is more pronounced in GLAHM V972 than in *M. superciliosus* (GLAHM V990), *G. leedsi* (NHMUK PV R3015) and *S. brachyrhynchus* (GLAHM V995). The enlargement of the posteromedial tuber gave a greater medial deflection of the femoral head in GLAHM V972, resulting in a more adducted femur from the pelvis than in other contemporaneous Oxford Clay metriorhynchids; this would have enabled a greater arc of adduction.

Because the medially deflected proximal head would have rested on the ischial contribution of the acetabulum (i.e. the concave basin), and because the proximal head of the femur is triangular and does not have an articular surface extanding onto its lateral surface, the range of possible hind limb motion would have been restricted to dorsoventral and anteroposterior movement.

Remarks. The Late Oxfordian '*Dakosaurus*' teeth from the Wapienno quarry of Poland (Jentzsch 1884; Gallinek 1895, 1896; Radwańska & Radwańska 2003) are very similar in form to those herein referred to *Tyrannoneustes* (Zatoń 2007, 2010 pers. comm.). However, until they are described their exact taxonomic affinity remains uncertain.

Evolutionary relationships of *Tyrannoneustes lythrodectikos*

Methods

We undertook a series of phylogenetic analyses to assess the evolutionary relationships of *Tyrannoneustes lythrodectikos* within Metriorhynchidae. These analyses are based on a revised version of the taxon and character dataset of Young *et al*. (2011a). The character scores for *Suchodus brachyrhynchus* and *Suchodus durobrivensis* were combined due to the subjective synonymy of these species (see appendix of Young *et al*. 2011a). This caused character state conflicts for characters 112 and 134. Therefore, these characters were coded as polymorphic: (0,1) and (1,2), respectively. Twelve new characters were added, and all characters were re-examined (leading many to be rephrased/reworded to reduce ambiguity). Furthermore, the character list was reorganised into progressive anatomical order: cranium, mandible, dentition, appendicular skeleton, axial skeleton, and then osteoderms. These revisions were based on examinations of GLAHM and NHMUK material,

photographs of specimens from other institutions, and the relevant literature. The only new taxon added to the analysis was *Tyrannoneustes lythrodectikos*. See Online Supplementary Material for the revised character list and scores.

The phylogenetic analysis was carried out with TNT v1.1 (Willi Hennig Society Edition) (Goloboff *et al*. 2008). Treespace was searched using a heuristic search algorithm with tree-bisection-reconnection (TBR) branch swapping and 1000 random addition replicates. The analysis was then subjected to the advanced search methods in TNT, namely: sectorial searched, tree fusion, ratchet and drift; again for 1000 random addition replicates. The default settings for the advanced search methods were changed to increase the iterations of each method per replicate: now 100 sectorial search drifting cycles, 100 ratchet iterations, 100 drift cycles and 100 rounds of tree fusion per replicate. This tree-space search procedure was repeated for five different random start seeds.

Two further phylogenetic analyses were run, using only a pruned selection of metriorhynchoid taxa, to elucidate geosaurine evolutionary relationships. *Teleidosaurus calvadosii* was used as the outgroup taxon (as previous studies have found it to be the basal-most metriorhynchoid; Wilkinson *et al*. 2008, Young & Andrade 2009; Young *et al*. 2011a), and the ingroup consisted of all well-preserved geosaurines (i.e. the Argentine Geosaurinae indeterminate and the Mexican *Dakosaurus* sp. were removed) and the four most complete metriorhynchine species (*M. superciliosus*, *G. leedsi*, *R. gracilis* and *C. suevicus*). What differs between the two additional analyses is the inclusion of NHMUK PV R486, an isolated tooth herein referred to as Geosaurinae indeterminate. The first of the pruned phylogenetic analyses did not include this specimen, whilst the second pruned analysis did. As these analyses have only 18 and 19 taxa respectively, an implicit enumeration search was run using TNT v1.1 (Willi Hennig Society Edition). Nodal support was evaluated using non-parametric bootstrapping (Felsenstein 1985) with 1000 replicates, using implicit enumeration searching, and Bremer support values.

Results

From the first phylogenetic analysis, three most parsimonious cladograms were recovered (length = 410; CI = 0.646; RI = 0.871; RC = 0.563). The topology of the strict consensus of these cladograms is identical to that reported by Young *et al*. (2011a) with the following exceptions: (1) *Pelagosaurus typus* was found to be the basal-most metriorhynchoid (however, we must stress that only one teleosaurid was included in the present analysis), and (2) *Tyrannoneustes lythrodectikos*, which is first included in the present analysis, was found to be the sister taxon of the clade Geosaurini (Fig. 19).

The second phylogenetic analysis returned one most parsimonious cladogram (length = 140; CI = 0.864; RI = 0.855; RC = 0.739) (Fig. 20). The strict consensus
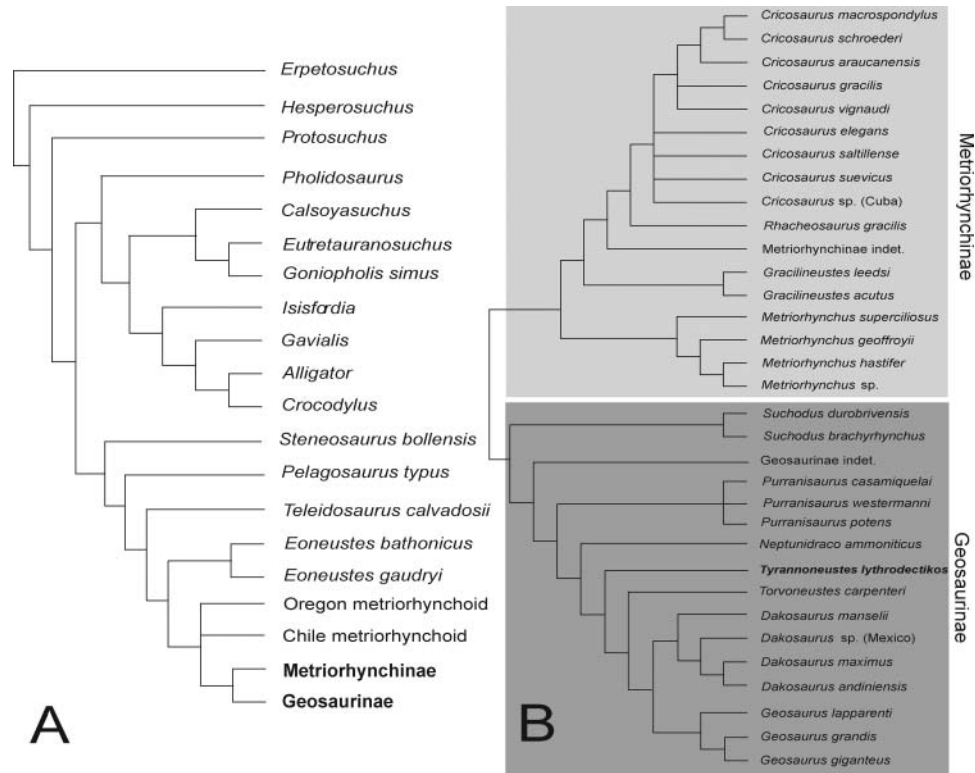
Figure 19. Strict consensus topology of the first phylogenetic analysis. This analysis investigated the phylogenetic relationships of *Tyrannoneustes lythrodectikos* sp. nov. within Crocodylomorpha. Note the sister-group evolutionary relationship between *T. lythrodectikos* and Geosaurini. Three most parsimonious cladograms: length = 414; ensemble consistency index (CI) = 0.635; ensemble retention index (RI) = 0.863; rescaled consistency index (RC) = 0.548. The evolutionary relationships of non-metriorhynchid crocodylomorphs (**A**) and metriorhynchids (**B**) are separated for ease of visualisation.

recovered the same relationships within Geosaurinae as the strict consensus of the first analysis. Very strong support was found for the clades: *Rhacheosaurus + Cricosaurus* (bootstrap = 97%; Bremer Support = 3), and *Dakosaurus maximus + D. andiniensis* (bootstrap = 92%; Bremer Support = 3). Strong support was found for: *Geosaurus* (bootstrap = 77%; Bremer Support = 2) and Geosaurinae (bootstrap = 80%; Bremer Support = 2). Moderate support was found for: *Geosaurus giganteus + G. grandis* (bootstrap = 56%) and Geosaurini (bootstrap = 55%).

The third phylogenetic analysis returned five most parsimonious cladograms (length = 141; CI = 0.858; RI = 0.850; RC = 0.729) (Fig. 21). The clade Geosaurini is no longer recovered as NHMUK PV R486 forms a large polytomy with *Tyrannoneustes*, *Torvoneustes*, the clade of *Geosaurus* species and the clade of *Dakosaurus* species. Clearly, the inclusion of NHMUK PV R486 disrupts the resolution of geosaurine interrelationships (i.e. it acts as a wildcard taxon due to its large amount of missing data and conflicting character scores). It is evident, therefore, that the referral of NHMUK PV R486 to *Dakosaurus* by Andrade *et al*. (2010) was premature, and we consider this tooth as Geosaurinae indet. here. Very strong support was

found for the clade *Rhacheosaurus + Cricosaurus* (bootstrap = 96%; Bremer Support = 3). Strong support was found for the clade: *Dakosaurus maximus + D. andiniensis* (bootstrap = 71%), *Geosaurus* (bootstrap = 79%; Bremer Support = 2) and Geosaurinae (bootstrap = 75%; Bremer Support = 2). Moderate support was found for: *Geosaurus giganteus + G. grandis* (bootstrap = 57%) and *Dakosaurus* (bootstrap = 51%).

In all three phylogenetic analyses, a clade of metriorhynchid super-predators was recovered: Geosaurini + *Tyrannoneustes*. This clade is supported by the following characters: enlargement of the dentition (character 134) and the coronoid process ventral to both the retroarticular process and glenoid fossa (i.e. ventral deflection of the coronoid process relative to the raised jaw joint) (character 111). The poor support for the clade Geosaurini + *Tyrannoneustes* is largely a result of the incomplete preservation of *Tyrannoneustes lythrodectikos* and its immediate sister taxon, *Neptunidraco ammoniticus*. *Tyrannoneustes lythrodectikos* lacks the skull, while *N. ammoniticus* is known from a skull, mandible and anterior cervical vertebrae preserved in cross section in limestone. The state of preservation of *N. ammoniticus* precludes understanding of
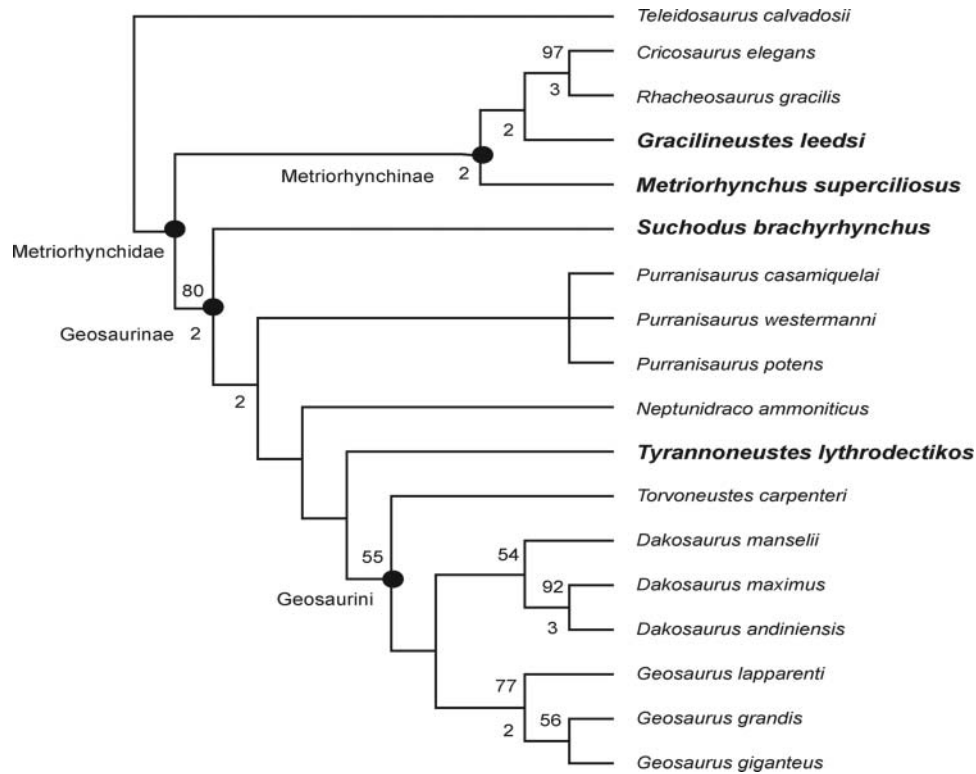
Figure 20. Strict consensus topology of the second phylogenetic analysis. This analysis was a pruned version of the first analysis (Fig. 19), to investigate the phylogenetic relationships of *Tyrannoneustes lythrodectikos* sp. nov. within Geosaurinae. Three most parsimonious cladograms: length = 143; CI = 0.881; RI = 0.835; RC = 0.764. Bootstrap values of 50% or more are reported above nodes, while Bremer Support values of greater than one are reported below nodes. Taxa from the Oxford Clay Formation are in bold.

its mandibular morphology in relation to gape. As such, we cannot discount that *N. ammoniticus* also exhibited the increased gape present in Geosaurini + *Tyrannoneustes*.

All species within the clade Geosaurini have dentition with a contiguous serrated edge on both the mesial and distal margins. Within Geosaurini, *Torvoneustes* has incipient microscopic true denticles combined with false-ziphodont serrations (see below), while *Geosaurus* and *Dakosaurus* both had true ziphodont serrations but lack conspicuous enamel ornamentation. Therefore, one monophyletic clade of ziphodonts was recovered. This suggests that ziphodonty evolved once among metriorhynchids, in the common ancestor of *Torvoneustes*, *Geosaurus* and *Dakosaurus*.

Revised dental descriptions for other metriorhynchids from the Oxford Clay Formation

In order to understand better the unusual dental morphology of *Tyrannoneustes* and explore the acquisition and evolu-

tion of dental characters (some of which surely have functional implications) in metriorhynchids, we studied the carinal morphology of contemporaneous metriorhynchids from the Oxford Clay Formation (*Metriorhynchus superciliosus*, *Gracilineustes leedsi* and *Suchodus brachyrhynchus*; Figs 22–25) and the basal-most member of Geosaurini (*Torvoneustes carpenteri*; Fig. 26) using scanning electron microscopy. This allows us to present a revised dental description for all metriorhynchids from the remarkable, niche-partitioned marine crocodylomorph fauna of the Oxford Clay Sea. Furthermore, we present revised and emended diagnoses of the various Oxford Clay Formation species, which helps to clarify and differentiate the many marine crocodylomorphs from this classic fauna (many of which are often found represented by fragmentary specimens that can easily be confused with each other). In order to facilitate taxon differentiation we have provided a table (Table 1) contrasting defining characteristics.

Metriorhynchus superciliosus (Blainville, 1853)
(Figs 22A–C, 23)

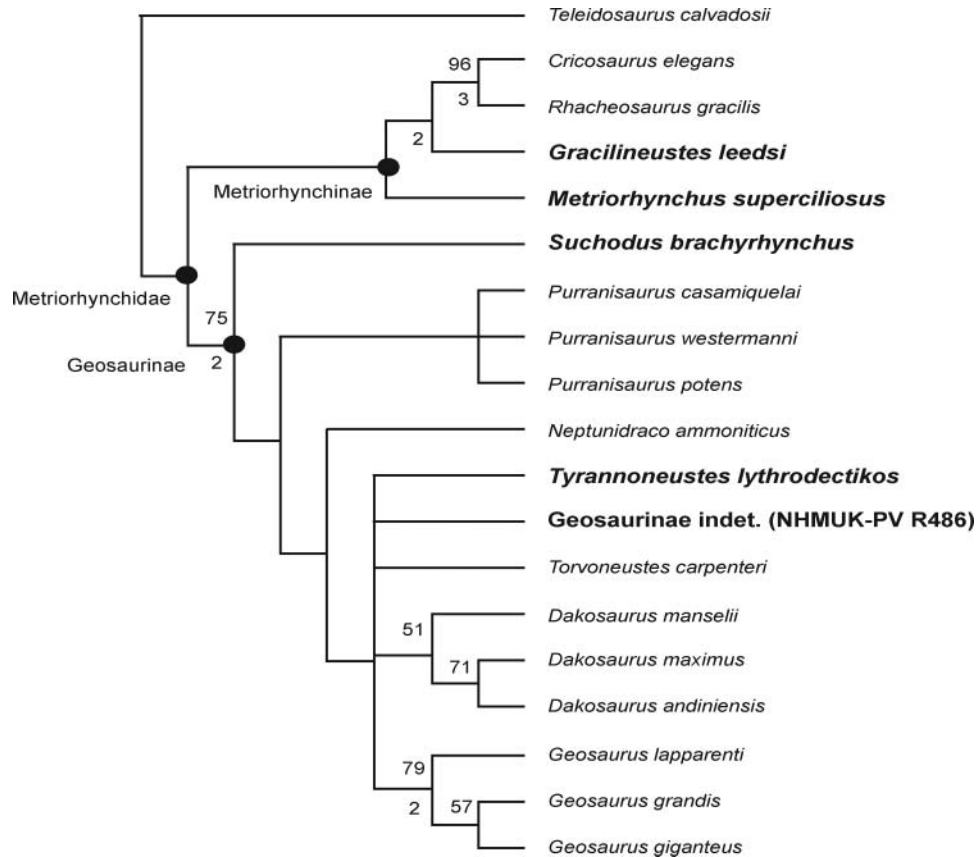**Neotype.** MNHN 8903, incomplete skull.

Figure 21. Strict consensus topology of the third phylogenetic analysis. This analysis is a pruned version of the first analysis (Fig. 19), to investigate what effect the inclusion of Geosaurinae indeterminate (NHMUK PV R486) had on the inter-relationships of Geosaurinae. Five most parsimonious cladograms: length = 144; CI = 0.875; RI = 0.827; RC = 0.754. Bootstrap values of 50% or more are reported above nodes, while Bremer Support values of greater than one are reported below the nodes. Taxa from the Oxford Clay Formation are in bold.

Type locality. Calvados, France. Marnes de Dives Formation, Late Callovian, Middle Jurassic.

Emended diagnosis. Metriorhynchid thalattosuchian with conical teeth with little mediolateral compression; crowns have a continuous smooth keel at mesial and distal edges; enamel on labial and lingual surfaces have conspicuous ornamentation composed of accessory ridges orientated to the apicobasal axis of the crown. Enamel ornamentation is stronger on the lingual face than on the labial face. Maxillae hold between 20 and 26 teeth; dentaries hold between 18 and 25 teeth, with 13 to 16 of those adjacent to the mandibular symphysis. The skull is narrow with a mesorostrine snout (*sensu* Young *et al*. 2010), with a maximum known basicranial length of 830 mm. Nasals and premaxillae always separated, ranging from 50–132 mm. Both the frontal and prefrontal bones have conspicuous ornamentation, although the frontal ornamentation is highly variable. Approximately 90° angle formed by the lateral and medial processes of the frontal, with the rostromedial border of the supratemporal

fossa (intratemporal flange) being either rounded or forming a right angle. A thin sclerotic ring composed of seven ossicles, which does not encompass the entire orbit. The deltopectoral crest is moderately developed, with the width of the humerus distal articular head being greater than the width of the deltopectoral crest projecting out from the humerus shaft.

Updated dental description. The teeth of *Metriorhynchus superciliosus* are single cusped and conical; they are slightly mediolaterally compressed (although newly erupted crowns can be strongly mediolaterally compressed, e.g. NHMUK PV R3016, see Fig. 22B, C) and curve lingually (Figs 22, 23). No constriction is present at the crown/root junctions, but the boundary is evident due to colour and texture. No facets are evident on either the labial or lingual faces (see Young & Andrade 2009; Andrade *et al*. 2010). Crowns are strongly ornamented, with ornamentation formed by apicobasally aligned ridges. These short to moderate length ridges are discontinuous,
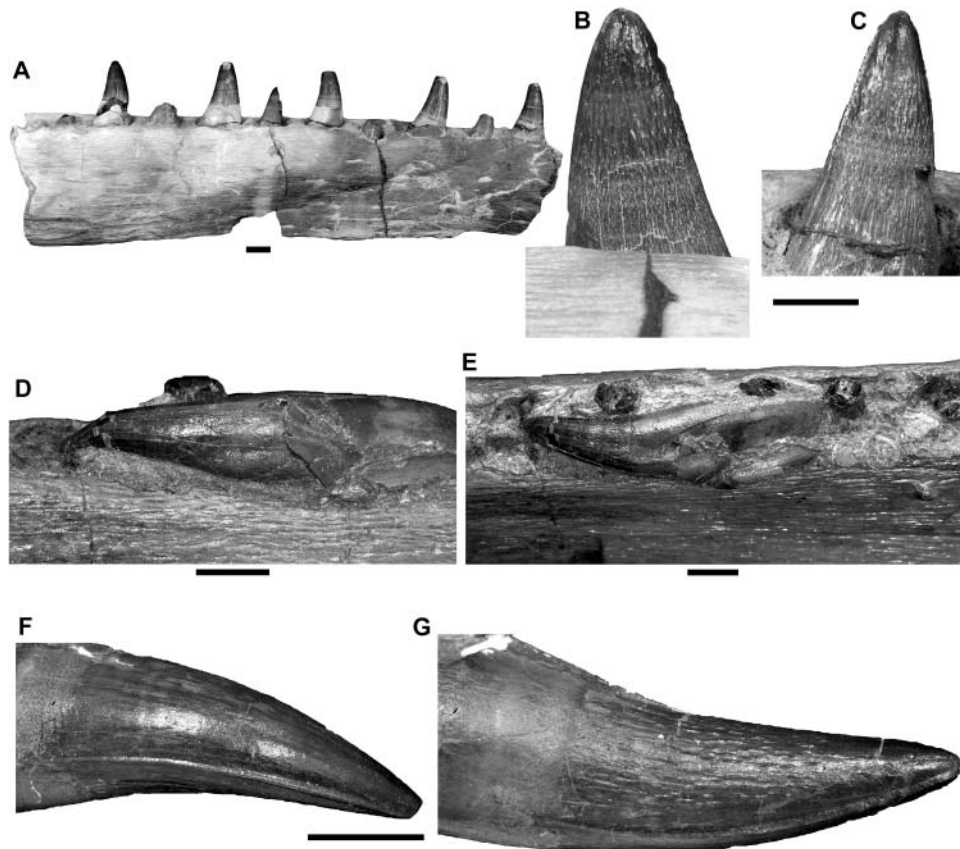
Figure 22. Comparative Oxford Clay Formation metriorhynchid dental morphology. **A-C**, *Metriorhynchus superciliosus* (Blainville), NHMUK PV R3016: **A**, mandibular fragment in lateral view; **B**, replacement tooth in labial view; **C**, replacement tooth in lingual view. **D**, **E**, *Gracilineustes leedsi* (Andrews), NHMUK PV R2042: **D**, tooth in carinal view; **E**, tooth in labial view. **F**, **G**, *Suchodus brachyrhynchus* (Eudes-Deslongchamps), NHMUK PV R3804: **F**, tooth in oblique carinal-labial view; **G**, tooth in lingual view. All scale bars = 5 mm.

and are well developed on the lingual face but more poorly developed on the labial face (although replacement teeth are strongly ornamented on both surfaces, see Fig. 22B, C). Using light microscopy the ridges can be easily distinguished from one another. Unlike the carinae, these ridges have no contribution from the underlying dentine (see Schmidt 1948). The ridges have been suggested to be a way of mechanically strengthening the teeth against transverse breakage (Schmidt 1948). In newly erupted teeth the ornamentation is intense, with the ridges more closely packed and becoming coarser away from the smooth apex. No serrations are present on the carinae of *M. superciliosus*; neither true denticles nor false-serrations created the conspicuous superficial ornamentation of enamel (false-ziphodonty). Split or supernumerary carinae were not found on any tooth (*sensu* Beatty & Heckert 2009).

Gracilineustes leedsi (Andrews, 1913)
(Figs 22D, E, 24)

Holotype. NHMUK PV R3540, dorsoventrally crushed skull, premaxillae not preserved.

Type locality. Near Peterborough, Cambridgeshire, England. Peterborough Member, Oxford Clay Formation, Middle Callovian, Middle Jurassic.

Emended diagnosis. Metriorhynchid thalattosuchian with conical teeth with moderate to strong mediolateral compression; crowns have a continuous smooth keel at mesial and distal edges; enamel on labial and lingual surfaces has ornamentation composed of accessory ridges orientated to the apicobasal axis of the crown, the ridges are low and become rarer near the apex. Maxillae hold between 33 and 38 teeth; dentaries hold between 30 and 37 teeth, while 18 to 20 of those are adjacent to the mandibular symphysis. The skull is narrow with a meso-to-longirostrine snout (*sensu* Young *et al*. 2010), with a maximum known basicranial length of 580 mm. Nasals and premaxillae always separated, ranging from 50–100 mm. Both the frontal and prefrontal bones are smooth, lacking conspicuous ornamentation. Approximately 90 degree angle formed by the lateral and medial processes of the frontal, with the rostromedial border of the supratemporal fossa (intratemporal flange) being either rounded or forming a right angle. The deltopectoral crest
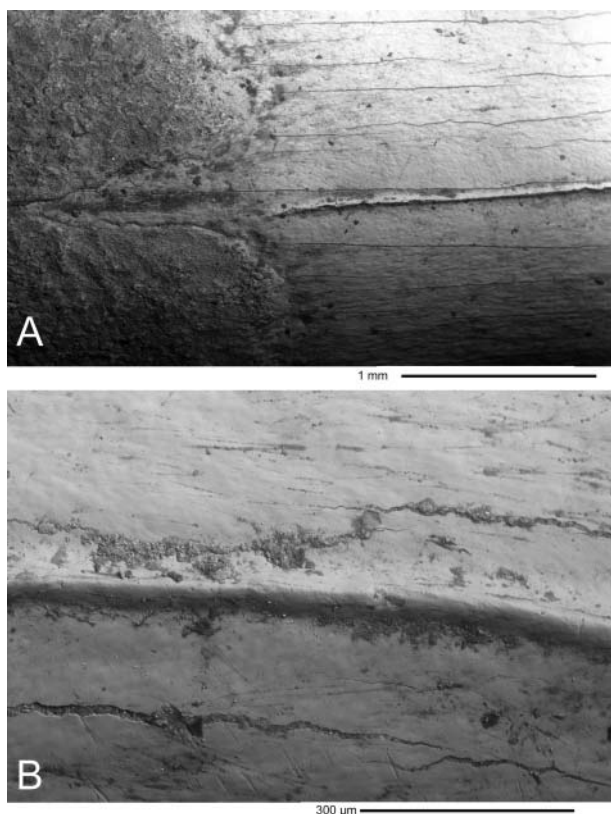
Figure 23. *Metriorhynchus superciliosus* (Blainville), GLAHM V1002, tooth. Backscattered SEM micrographs. **A**, carina near the crown base; **B**, close-up of carina.

is poorly developed, with the width of the humerus distal articular head being greater than the width of the deltopectoral crest projecting out from the humerus shaft, and in lateral view the crest is a gentle convex curve rather than a distinct triangular shape.

Updated dental description. The teeth of *Gracilineustes leedsi* are single cusped and conical; they are moderately to strongly mediolaterally compressed and curve lingually. No constriction is present at the crown/root junctions, but the boundary is evident due to colour and texture. No facets are evident on either the labial or lingual faces (see Young & Andrade 2009; Andrade *et al*. 2010). Crowns are strongly ornamented, which is formed by apicobasally aligned ridges, as with *M. superciliosus* these ridges are better developed on the lingual face than on the labial face. The labial surface has pronounced enamel ridges that are few in number and proceed along most of the crown (Fig. 22D, E). No true denticles are present on the carinae of *G. leedsi*, and split or supernumerary carinae were not found on any tooth (Fig. 24). The teeth of *G. leedsi* do not bear false serrations (false-ziphodont carinae).

Suchodus brachyrhynchus
(Eudes-Deslongchamps, 1868a)
(Figs 22F, G, 25)

Neotype. NHMUK PV R3700, skull lacking the tip of the premaxilla.

Type locality. Near Peterborough, Cambridgeshire, England. Peterborough Member, Oxford Clay Formation, Middle Callovian, Middle Jurassic.

Emended diagnosis. Metriorhynchid thalattosuchian with laminar teeth with moderate to strong mediolateral compression; crowns have a continuous keel at mesial and distal edges; enamel on labial surface lacks conspicuous ornamentation, while the lingual surface possesses poorly developed apicobasally aligned accessory ridges. Poorly defined microscopic true denticles present on both keels; denticles do not procede along the entire carina; in labial or lingual view the height of the denticles weakly influence the height of the keel (i.e. poorly serrated edge). Maxillae hold between 12 and 18 teeth; dentaries hold between 12 and 17 teeth, while seven or eight of those are adjacent to the mandibular symphysis. The skull is broad with a mesorostrine snout (*sensu* Young *et al*. 2010), with a maximum known basicranial length of 853 mm. Nasals and premaxillae either contact or separated by up to 38 mm. Both the frontal and prefrontal bones have conspicuous ornamentation. Approximately 90° angle formed by the lateral and medial processes of the frontal; the rostromedial border of the supratemporal fossa (intratemporal flange) is acutely angled. The deltopectoral crest is well developed, with: the width of the humerus distal articular head is subequal to the width that the deltopectoral crest projects out from the humerus shaft.

Updated dental description. The teeth of *Suchodus brachyrhynchus* are single cusped and laminar, with moderate to strong mediolateral compression and curve lingually (Fig. 22F, G). No constriction is present at the crown/root junctions, but the boundary is evident due to colour and texture. No facets are evident on either the labial or lingual faces (see Young & Andrade 2009; Andrade *et al*. 2010). Crowns lack conspicuous ornamentation on the labial surface, but have moderate ornamentation on the lingual face, formed by apicobasally aligned ridges. As with *Tyrannoneustes*, poorly defined microscopic true denticles are present on both mesial and distal keels (Fig. 25). They do not proceed along the entire carina (heterogeneous), and appear in small groups (2–10). In labial or lingual views the height of the denticles either does not or very slightly influences the height of the keel (i.e. little or no serrated edge). However, the denticles are better developed than observed in *Tyrannoneustes*. Split or supernumerary carinae were not found on any tooth.
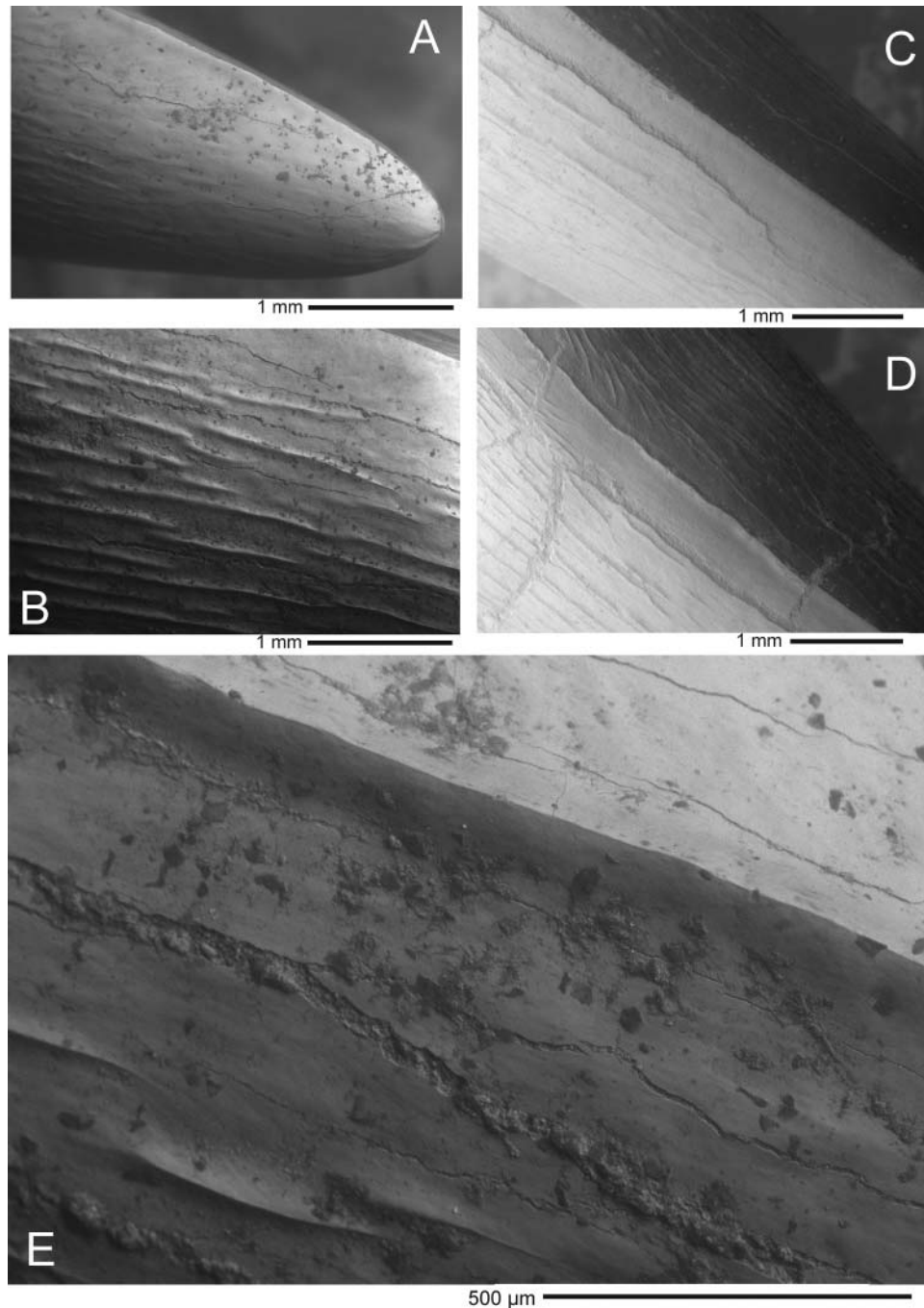
Figure 24. *Gracilineustes leedsi* (Andrews), GLAHM V1009, tooth. Backscattered SEM micrographs. **A**, **B**, crown apex and enamel ornamentation; **C**, **D**, enamel ornamentation on either side of a carina; **E**, close-up of carina.

Torvoneustes carpenteri
(Wilkinson, Young & Benton, 2008)
(Fig. 26)

Holotype. BRSMG Cel7365, incomplete skull.

Type locality. Westbury, Wiltshire, England. Lower Kimmeridge Clay Formation, Upper Kimmeridgian, Upper Jurassic.

Emended 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*
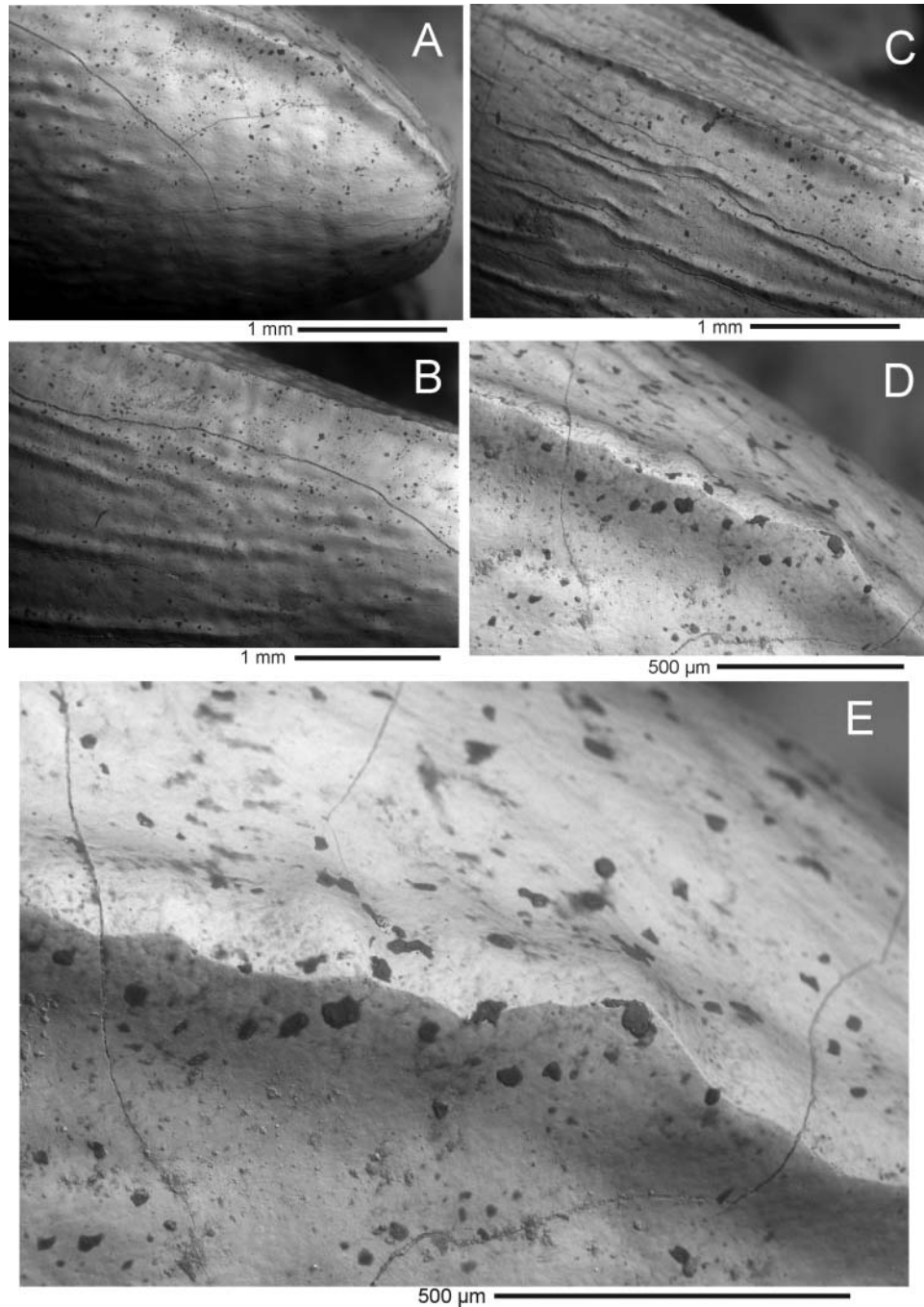
Figure 25. *Suchodus brachyrhynchus* (Eudes-Deslongchamps), GLAHM V1439, tooth. Backscattered SEM micrographs. **A**, crown apex; **B**, **C**, enamel ornamentation; **D**, **E**, close-up of carina.

(50°), but less than in species of *Metriorhynchus* (60–70°); number of teeth in each jaw ramus estimated at 14, similar to *D. maximus* and *D. andiniensis* (12–16), and far fewer than in any species of *Metriorhynchus* (typically 22–29) (modified from Wilkinson *et al*. 2008); acute angle formed by the lateral and medial processes of the frontal; small preorbital fenestra present (not homologous to the archosaurian antorbital fenestrae, see Fernández & Herrera 2009), enclosed within an oblique preorbital fossa; lacrimal-prefrontal fossa present (modified from Young & 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) and true denticles; 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,
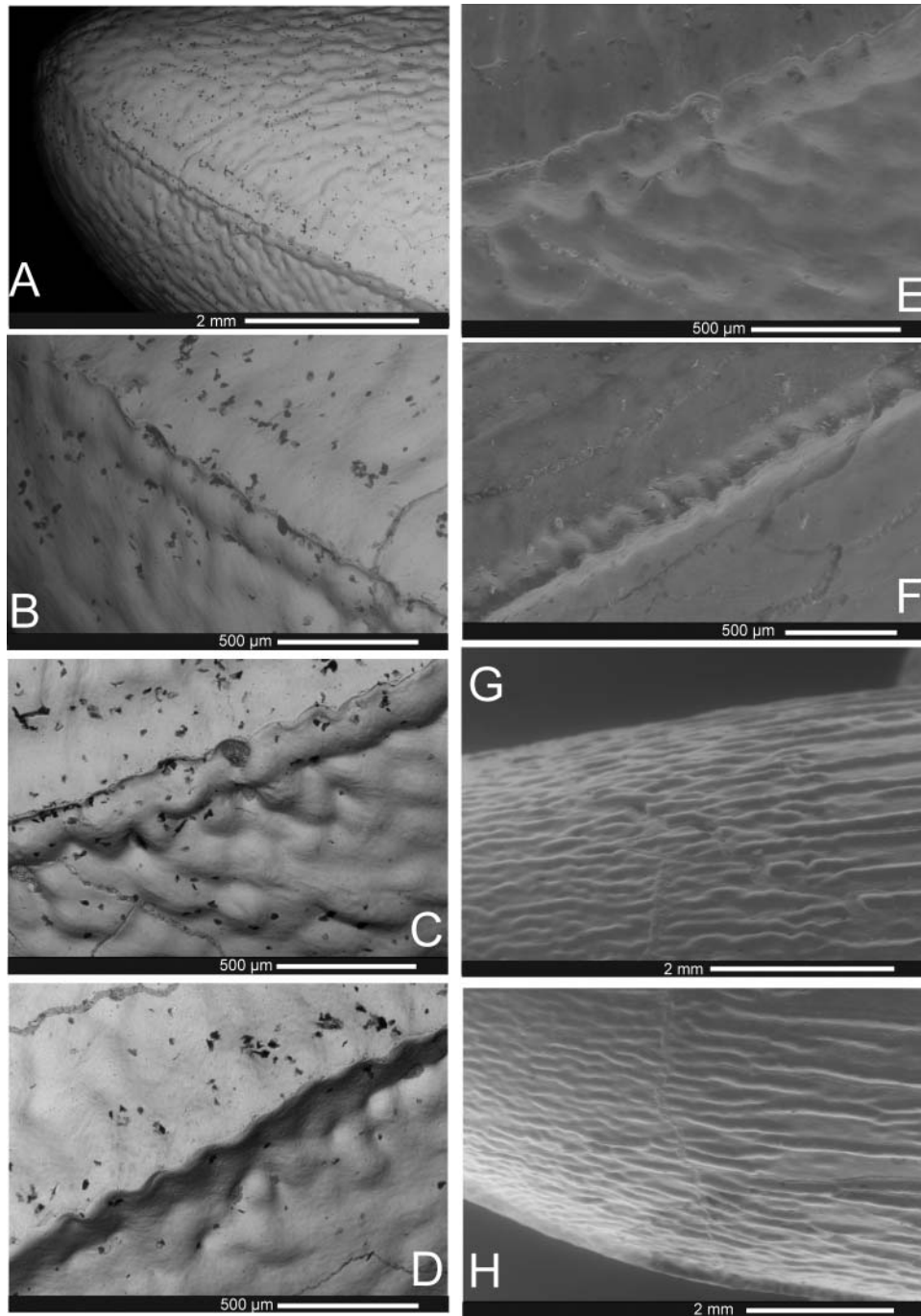
Figure 26. *Torvoneustes carpenteri* (Wilkinson, Young & Benton), BRSMG Cd7203, tooth. **A–D**, secondary electron SEM micrographs of the carina and apex; **E**, **F**, backscattered SEM micrographs of the carina; **G**, **H**, backscattered micrographs of the enamel ornamentation.

terminating prior to the preorbital fossa (modified from Andrade *et al*. 2010).

Updated dental description. Dental characters of *Torvoneustes carpenteri* have been described previously by Grange & Benton (1996), Wilkinson *et al*. (2008) and Andrade *et al*. (2010). The only update we make herein regards serration morphology (Fig. 26). Neither Grange & Benton (1996) nor Wilkinson *et al*. (2008) mentioned serrations. Andrade *et al*. (2010), however, used SEM to report that the dentition was false-ziphodont (i.e. the 'serrations' are created on the surface of the carinal keel by the conspicuous superficial ornamentation of enamel). Recent re-examination of SEM data of *T. carpenteri* teeth suggests the serration morphology may be more complex than previously supposed.

Table 1. List of characters to differentiate between the various metriorhynchid species found in the Peterborough Member of the Oxford Clay Formation.

Characters		*Metriorhynchus superciliosus*	*Gracilineustes leedsi*	*Suchodus brachyrhynchus*	*Tyrannoneustes lythrodectikos*
Dentition	Premaxillary alveoli count	3	3	3	?
	Maxillary alveoli count	20–26	33–38	12–18	?
	Dentary alveoli count	18–25	30–37	12–17	12
	Dentary alveoli adjacent to symphysis	13–16	18–20	7–8	10
	Enamel ornamentation	Conspicuous ornamentation on both surfaces composed of accessory ridges orientated to the apicobasal axis of the crown	Ornamentation largely inconspicuous to the naked eye. Composed of apicobasal ridges that are low and become rarer near the apex	Labial surface lacks conspicuous ornamentation, the lingual surface has possesses short but high apicobasal ridges	Ornamentation inconspicuous, apicobasal ridges on both surfaces are restricted to the base of the crown, and are low, well-spaced and very short
Cranium	Microscopic denticles	No	No	Yes	Yes
	Frontal surface texture	Ornamented	Smooth	Ornamented	?
	Squamosal overlap of the paraoccipital process (in dorsal aspect)	Small, the paraoccipital process projects further posteriorly than the squamosal	Small, the paraoccipital process projects further posteriorly than the squamosal	Extensive, projecting further posteriorly than the paraoccipital process itself	?
	Shape of the prefrontal expansion over the orbits (in dorsal aspect)	Lateral margin forms a convex curve	Lateral margin forms a convex curve	Lateral margin forms a 90 degree angle giving it a distinct triangular shape	?
	Palatine rostral development along the midline	Adjacent to 18th maxillary alveoli	Adjacent to 19th maxillary alveoli	Adjacent to 10th maxillary alveoli	?
	Palatine with two non-midline anterior processes (one on either side of the mid-line)	Yes, both separate from the mid-line and the maxilla alveolar border. Terminate adjacent to the 15th maxillary alveoli	Yes, both separate from the mid-line but lateral margin sutures with the maxilla alveolar border. Terminate adjacent to the 8th maxillary alveoli	No	?

Table 1. List of characters to differentiate between the various metriorhynchid species found in the Peterborough Member of the Oxford Clay Formation. *(Continued)*

Characters		*Metriorhynchus superciliosus*	*Gracilineustes leedsi*	*Suchodus brachyrhynchus*	*Tyrannoneustes lythrodectikos*
Mandible	Mandibular symphysis depth relative to mandible length	~4.5–6%	~4%	~7–8%	~5%
	Dentary tooth row ventrally displaced relative to jaw joint	No	No	No	Yes
	Coronoid process ventrally displaced relative to jaw joint	No	No	No	Yes
	Reception pits caused by the upper jaw tooth row	No	No	Yes, on the lateral margin of the dentary	Yes, sagittal plane between the dentary alveoli (D7-D12)
Vertebrae	Atlas hypocentrum length	Hypocentrum length subequal to odontoid process length	Hypocentrum length subequal to odontoid process length	Hypocentrum length greater than odontoid process length	?
	Cervical centra dimensions	Centrum length shorter than their height	Centrum length shorter than their height	Centrum length greater than their height	Centrum length and height subequal
Pectoral girdle	Deltopectoral crest shape	Distinctly triangular	Gentle convex curve	Distinctly triangular	Distinctly triangular
	Relative size of humerus and scapula	Scapula shorter than humerus	Humerus shorter than scapula	Scapula shorter than humerus	?
	Dorsal border of ilium acetabulum contribution	Orientated ventrally	?	Orientated ventrally	Orientated horizontal
Pelvic girdle	Ilium dorsal border relative to ilium acetabulum contribution	Terminates approximately level to mid-point of acetabulum	?	Terminates approximately level to mid-point of acetabulum	Terminates prior to acetabulum
	Ischium acetabulum contribution	Laterally-directed, slightly concave semi-circle	?	Laterally-directed, slightly concave semi-circle	Laterally-directed, deeply concave semi-ellipsoid
	Ischium acetabulum contribution and anterior process for the pubis	Clearly separated	?	Clearly separated	Connected by a medially-directed convex ridge
	Ischium process for the pubis	Articulation facet is rounded and smooth	?	Articulation facet is rounded and smooth	Articulation facet is complex (hills and troughs)

The carinae are homogenous, with a long, contiguous series of repetitive, isolated and isomorphic incipient true denticles that are microscopic (Fig. 26). Their dimensions typically do not exceed 300 μm (microziphodont). Identification of the denticles becomes progressively more subtle towards the apex. This is due to the heavy enamel ornamentation making differentiating denticles from ornamentation difficult (the denticles are the 'inflated base' observable in Andrade *et al*. 2010, fig. 6c), eventually impossible in many sections. This is coupled with the pronounced keel, which is considerably taller than the keels observed in *Geosaurus* and *Dakosaurus* (Pol & Gasparini 2009; Andrade *et al*. 2010). We now interpret *Torvoneustes carpenteri* as exhibiting both true-ziphodonty and an extensive ornamentation that contributes to the keel (which, in the absence of true-denticles, determines the false-ziphodont condition).

Super-predatory character evolution in metriorhynchids

Denticle evolution

Scanning electron microscopy reveals that the dentition of basal metriorhynchines (*Metriorhynchus* and *Gracilineustes*; Figs 22–24) lacks any form of serrations (either true- or false-ziphodonty). However, basal geosaurine genera (e.g. *Suchodus* and *Tyrannoneustes*; Figs 9, 10, 22 and 25) did possess true denticles. In these genera, very poorly defined microscopic true denticles are present on both keels. These denticles do not proceed contiguously along the entire carina (heterogeneous), but rather form short rows of up to 10 denticles. In both labial and lingual views the height of the denticles rarely influences the height of the keel (i.e. little to no serrated edge), in contrast to the typical ziphodont carinal morphology. These teeth are morphologically ziphodont (as they bear true denticles; Prasad & Broin 2002), but they are not functionally equivalent to the morphology that is generally considered ziphodont. This is due to the heterogenic nature of the denticles and the fact they probably did not create a functional saw. This morphology is herein referred to as incipient-microziphodonty (see Tables 2, 3).

Considering the subtle nature of the denticles (which require SEM to identify, and can be masked by enamel ornamentation) and their low density, it is easy to understand how this morphology was overlooked for so long. As such, there could be many reptilian taxa considered to be non-ziphodont which display this form of ziphodonty. Furthermore, this incipient-microziphodont morphology may provide insights into how ziphodonty arose in other predacious clades. As this morphology is present in two basal members of Geosaurinae, a clade whose more derived members possess true or false ziphodonty, it is probable that it is not only homologous to true/false ziphodonty to some degree, but also is an evolutionary precursor.

The genera of the super-predatory clade Geosaurini all possess serrated dentition (Fig. 27). The dentition of the genus *Torvoneustes* was described in Andrade *et al*. (2010) as false-ziphodont. Although it is true that superficial

Table 2. General categories for describing serrations and related structures along the carinae in Crocodylomorpha. False-ziphodonty (*sensu stricto*) and ziphomorphy are currently unknown in Metriorhynchidae. Taxa in bold are not metriorhynchids. Data for referring various metriorhynchid species comes from the current paper, Pol & Gasparini (2009) or Andrade *et al*. (2010), unless otherwise stated.

Morphology	Definition	Examples
Non-ziphodont	Carinae either absent, or present and composed of a smooth keel. No serrations present.	*Metriorhynchus superciliosus* *Gracilineustes leedsi*
Microziphodonty	Carinae heterogeneous/homogenous, with a series of repetitive isolated and isomorphic true denticles that are microscopic; whose dimensions typically do not exceed 300 μm. (Modified from Andrade *et al*. 2010).	*Geosaurus giganteus* *Geosaurus grandis* Geosaurinae indet. (NHMUK PV R486) *Dakosaurus* sp. (Ruiz-Omeñaca *et al*. 2010) *Suchodus brachyrhynchus* *Tyrannoneustes lythrodectikos* *Torvoneustes carpenteri*
Macroziphodonty	Carinae homogenous, with a long, contiguous series of repetitive isolated and isomorphic true denticles that are visible macroscopically. Dimensions typically exceed 300 μm. (Modified from Andrade 2010).	*Dakosaurus andiniensis* *Dakosaurus maximus* **Baurusuchidae** (Andrade 2010) **Peirosauridae** (Andrade 2010)
Ziphomorphy	Carinae heterogeneous, with anisomorphic, tuberous and well-spaced true denticles. No enamel ornamentation extending onto the carina (Andrade & Bertini 2008).	**Mariliasuchus** (Andrade 2010) **Sphagesaurus** (Andrade & Bertini 2008)
False-ziphodonty	Carinae homogenous, with 'serrations' created on the surface of the carinal keel by the conspicuous superficial ornamentation of enamel (Prasad & Broin 2002).	**Machimosaurus** (Prasad & Broin 2002) **Goniopholis** (Andrade *et al*. 2011)

Table 3. List of characters accompanied by a description, to elucidate the various serration morphologies in Metriorhynchidae. Data for referring various metriorhynchid species comes from the current paper, Pol & Gasparini (2009) or Andrade *et al*. (2010), unless otherwise stated.

Denticle size	Denticles contiguous	Incipient denticles?	Description	Examples
Macroziphodont	Yes	No, well developed	Carinae homogenous, with a long, contiguous series of repetitive isolated and isomorphic true denticles that are visible macroscopically. Dimensions typically exceed 300 μm.	*Dakosaurus andiniensis* *Dakosaurus maximus*
	Yes	No, well developed	Carinae homogenous, with a long, contiguous series of repetitive isolated and isomorphic true denticles that are microscopic; whose dimensions typically do not exceed 300 μm.	*Geosaurus giganteus* *Geosaurus grandis* Geosaurinae indet. (NHMUK PV R486) *Dakosaurus* sp. (Ruiz-Omeñaca *et al*. 2010)
	Yes	Yes, poorly developed	Carinae homogenous, with a long, contiguous series of repetitive isolated and isomorphic true denticles that are microscopic; whose dimensions typically do not exceed 300 μm. The denticles themselves are poorly defined and difficult to distinguish even under SEM.	*Torvoneustes carpenteri*
Microziphodont	No	Yes, poorly developed	Carinae heterogeneous, with a series of non-contiguous repetitive isolated and isomorphic true denticles that are microscopic. Series can be short (2) or moderate (~10), but are widely separate from one another, i.e. no contiguous series along the carina. Dimensions (length, width, height) typically do not exceed 300 μm. In labial or lingual view, the height of the denticles rarely influences the height of the keel (i.e. little or no serrated edge). The denticles themselves are poorly defined and difficult to distinguish even under SEM. No enamel ornamentation extending onto the carina.	*Tyrannoneustes lythrodectikos* *Suchodus brachyrhynchus*

enamel ornamentation contacts the carinae, there is also an 'inflated base' (see Andrade *et al*. 2010, fig. 6c). At the time we were unsure whether this 'base' was a row of denticles or part of the false-serrations. However, with the discovery of poorly defined ('incipient') denticles in Geosaurinae, we now interpret this 'base' as a row of microscopic denticles (Fig. 26; Table 3). Therefore we now characterize the carinal morphology as: poorly defined (incipient) microscopic true denticles present on both keels, the denticles proceed contiguously along the entire carina (homogenous), conspicuous superficial ornamentation of the enamel makes denticle identification difficult, especially towards the apex. As such, we now interpret *Torvoneustes* as exhibiting true-ziphodonty. This taxon highlights the difficulty that can arise when differentiating between true- and false-ziphodonty.

The dentition of the genus *Geosaurus* was characterized by Andrade *et al*. (2010) as microziphodont with well-defined microscopic true denticles present on both keels, which proceed contiguously along the entire carina (homogenous), and in both labial and lingual views the height of the denticles alters the height of the keel creating a serrated edge.

The dentition of the genus *Dakosaurus* was characterized in Andrade *et al*. (2010) as (micro- and macro)ziphodont, with: well-defined micro- or macroscopic true denticles present on both keels, the denticles proceed contiguously along the entire carina (homogenous), and in both labial and lingual views the height of the denticles alters the height of the keel creating a serrated edge. *Dakosaurus* is the only genus of metriorhynchid with denticles that are readily identifiable without the aid of SEM. Within *Dakosaurus* there is a trend towards decreased denticle density, and increasing denticle transverse width and apicobasal length in more derived species (Pol & Gasparini 2009; Andrade *et al*. 2010).

Although all three Geosaurini genera evolved very distinct serration morphologies, we can hypothesize about their ancestral morphology. Based on the optimisation of phylogenetic characters, we reconstruct the common ancestor of Geosaurini as having true microscopic denticles present on both keels that proceed contiguously along the
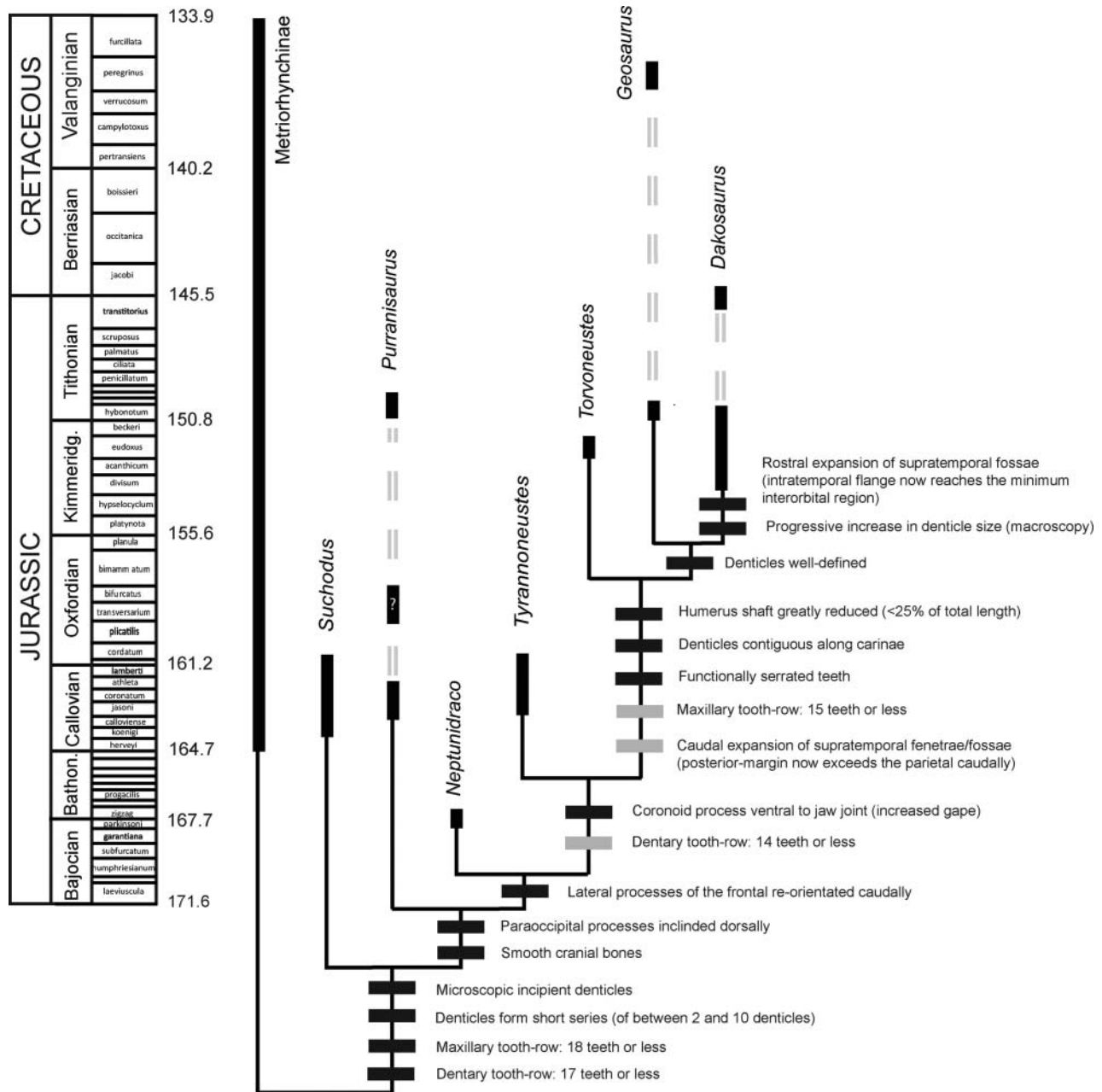
Figure 27. Calibrated cladogram of Geosaurinae highlighting the major marine and super-predatory adaptations of the clade. Black bars represent unambiguous synapomorphies, while grey bars represent ambiguous synapomorphies. Note that metriorhynchine symplesiomorphies are: (1) dentary and maxillary tooth rows with 20 or more alveoli and (2) teeth carinae with keels but lacking any serration morphologies.

entire carina (homogenous). Presently, the only taxa in which denticles are known to noticeably alter the height of the carinal keel (creating a notable serrated edge) are NHMUK PV R486, *Geosaurus giganteus*, *G. grandis*, the Spanish *Dakosaurus* tooth, *Dakosaurus maximus* and *D. andiniensis* (see Pol & Gasparini 2009; Andrade *et al.* 2010; Ruiz-Omeñaca *et al.* 2010). In *Torvoneustes carpenteri* we have two competing hypotheses as to why the denticles fail to noticeably alter the height of the keel: (1) this taxon

is the basal-most member of Geosaurini and has poorly defined ('incipient') denticles, as such a notable serrated edge is present only in more derived species; or (2) the interaction between superficial enamel ornamentation and the denticles with the pronounced keel (Fig. 26D, H) are derived characteristics for *Torvoneustes* that obliterate the conventional serrated edge. Although re-examination of the *Torvoneustes* holotype and referred specimens will be necessary, discovery of more geosaurines particularly from

the early Kimmeridgian and Oxfordian will be essential to help optimise these characteristics.

Denticle macroscopy. We posit that within Metriorhynchidae macroscopic denticles, the most common form of ziphodonty in terrestrial crocodylomorph clades evolved solely in the *Dakosaurus* lineage (Fig. 27). Currently, evidence from isolated teeth suggests this occurred during the Kimmeridgian. *Dakosaurus* crown morphology can be characterized as poorly compressed mediolaterally, very robust, lacking conspicuous enamel ornamentation and with well-defined macroscopic true denticles proceeding contiguously along the entire carinae. However, does any *Dakosaurus* specimen exhibit denticle microscopy? The Callovian-Oxfordian isolated tooth NHMUK PV R486 was previously considered the oldest confirmed *Dakosaurus* tooth. However, we do not consider it such because of its specific carinal morphology and enamel ornamentation, but rather conservatively consider it as Geosaurinae indeterminate (see above).

Interestingly, an isolated tooth referred to *Dakosaurus* from the Tereñes Formation (Late Kimmeridgian; see Schudack & Schudack 2002) of northern Spain exhibits microziphodonty (Ruiz-Omeñaca *et al*. 2010). Under light microscopy Ruiz-Omeñaca *et al*. (2010) found apicobasal aligned ridges, which coupled with the strong asymmetry of denticle densities along the mesial and distal carinae, suggest that this tooth may not belong to *Dakosaurus*. We provisionally retain the tooth in the genus *Dakosaurus* as the taxonomic affinity of *Dakosaurus manselii* is still in question. The holotype of *D. manselii* (NHMUK PV OR40103) lacks the large conspicuous denticles of *D. maximus* and *D. andiniensis*, and also has apicobasally aligned ridges (MTY pers. obs.). In addition, an ordered version of the Young *et al*. (2011a) phylogenetic analysis (see online supplementary material of Young *et al*. 2011a) found *D. manselii* to be the sister taxon of the clade *Geosaurus* + *Dakosaurus*. The removal of *manselii* from *Dakosaurus* was solely based on dental characters. Until *Dakosaurus manselii* is re-described (currently underway by the lead author) our understanding of the diversity of Kimmeridgian geosaurines will remain incomplete.

Currently, macroziphodonty in *Dakosaurus* is restricted to the final two Sub-Boreal ammonite zones of the Late Kimmeridgian and deposits younger in age. Two described species are macroziphodont: *D. maximus* (Andrade *et al*. 2010) and *D. andiniensis* (Pol & Gasparini 2009); while isolated teeth from the type localities of the Late Kimmeridgian 'species' *D. lissocephalus* and *D. primaevus* are also macroziphodont (both putative species are most probably junior synonyms of *D. maximus*; NHMUK PV OR20283, NHMUK PV OR32414). Unfortunately, the denticle morphology of *D. nicaeensis* (see Buffetaut 1982) and the un-named *Dakosaurus* species from the Kimmerid-

gian of Mexico (Buchy *et al*. 2007; Buchy 2008) cannot be observed due to poor preservation.

Stratigraphical range of metriorhynchid ziphodonty. As reported by Andrade *et al*. (2010) the stratigraphical range of microziphodonty is far longer than that of macroziphodonty in Metriorhynchidae. At first glance this appears to be in direct contrast with all other archosaurian groups, but without extensive investigation of carinal morphologies across all/most metriorhynchids using SEM there is no way to know the true prevalence of microziphodonty. As the denticle morphology in *Suchodus* and *Tyrannoneustes* can be referred to as microziphodonty (see Tables 2, 3), the known stratigraphical range of metriorhynchid microziphodonty extends from the middle Callovian to the upper Valanginian, a duration of approximately 25 million years. However, from the known stratigraphy of geosaurines (see Fig. 1) it is likely that denticles will be found in pre-Callovian specimens. Using a more restrictive definition of microziphodonty that excludes *Suchodus* and *Tyrannoneustes* (where the denticles are readily identifiable, i.e. not incipient, and they form a contiguous row; see Table 3), the known range of metriorhynchid microziphodonty extends from the upper Callovian/lower Oxfordian to the upper Valanginian, a duration of approximately 23 million years.

The stratigraphical range of macroziphodonty, which was at times contemporaneous with microziphodonty, is far more restricted. The oldest known macroziphodont *Dakosaurus* tooth is NHMUK PV OR20283 from the Sub-Boreal *Eudoxus* ammonite zone of the lower Kimmeridgian Clay Formation (upper Kimmeridgian), while the youngest known macroziphodont *Dakosaurus* specimen is from the lower-most Berriasian (*D. andiniensis*; Gasparini *et al*. 2006). This gives macroziphodonty a currently known stratigraphical duration of approximately 7 million years.

Although these stratigraphical ranges are the same as those reported by Andrade *et al*. (2010), the knowledge that incipient denticles are present in Callovian taxa extends the range of metriorhynchid ziphodonty back into the Middle Jurassic. The incipient-ziphodont morphology has thus far not been reported in other clades, but as with both microziphodonty and microziphodonty combined with false-serrations, the use of SEM is required for proper identification. It is likely that ziphodonty itself, as well as individual forms of it, was more temporally widespread and evolved earlier in metriorhynchids than currently thought, but testing this hypothesis awaits future discoveries.

Mandible shape. As outlined above, all metriorhynchids from the Oxford Clay Formation exhibit some ventral displacement of the dentary tooth row relative to the jaw joint (Fig. 6). In basal metriorhynchids (e.g. *Metriorhynchus superciliosus*: GLAHM V1141; *Gracilineustes leedsi*: NHMUK PV R3014, NHMUK PV R3015;

Suchodus brachyrhynchus: GLAHM V995, NHMUK PV R3804) the tooth row is located below the plane of the coronoid process, while the coronoid process is on the same plane as both the retroarticular process and the glenoid fossa (Fig. 6). Basal metriorhynchoids such as *Pelagosaurus typus* (Pierce & Benton 2006) and *Teleidosaurus calvadosii* (NHMUK PV R2681; Young *et al*. 2010, fig. 6) lack a distinct coronoid process, and the tooth row is only slightly below the retroarticular process and the glenoid fossa.

However, compared to other Oxford Clay metriorhynchids, the morphology in *Tyrannoneustes lythrodectikos* is extreme. In this taxon, the dorsally expanded and curved posterior region of the mandible effectively elevates the position of the quadrate articular condyle relative to the coronoid process and the dentary tooth row (therefore the dentary tooth row is further ventrally displaced) (Fig. 6). A similar morphology can be observed in *Dakosaurus andiniensis* (Gasparini *et al*. 2006; Pol & Gasparini 2009), *D. maximus* (SMNS 82043), *D. manselii* (NHMUK PV OR40103) and *Geosaurus giganteus* (NHMUK PV OR37020), in all cases associated with enlarged maxillary and dentary teeth. The discussion hereafter will refer to this extreme ventral displacement of the dentary (i.e. only that observed in *T. lythrodectikos* + Geosaurini). In these Geosaurini taxa, we hypothesize that the ventrally displaced dentary facilitated the enlargement of teeth. Large teeth, in turn, are beneficial for super-predatory behaviour as they have longer blade edges that are more efficient at slicing meat than smaller teeth. Although this mandibular morphology co-occurs with tooth-crowns that have an elongated apicobasal length, *T. lythrodectikos* has significantly smaller teeth than those observed in Geosaurini taxa. While this is true, tooth crown size in *T. lythrodectikos* is greater than its contemporaries (*Metriorhynchus superciliosus*: GLAHM V1141; *Gracilineustes leedsi*: NHMUK PV R3014, NHMUK PV R3015; *Suchodus brachyrhynchus*: GLAHM V995, NHMUK PV R3804), none of which exceed 2 cm in apicobasal length. Interestingly, by the Late Oxfordian (approximately 8 million years later) apicobasal length of metriorhynchid tooth-crowns dramatically increased to a maximum of 12 cm in *Dakosaurus nicaeensis* (Buffetaut 1982).

While increasing apicobasal length of the tooth-crowns would have been beneficial for feeding on large prey, there is a phylogenetic and temporal delay in observing a significant increase in tooth size after the acquisition of a ventral displacement of the dentary tooth row. Therefore the ventral displacement most probably arose as an adaptation for another function. A possible adaptation was for biting more efficiently into larger prey. Of course, it is theoretically possible for any metriorhynchid to bite into large prey as long as they have the necessary gape. However, in taxa with a relatively straight mandible and tooth row closer to being in-line with the jaw joint, such as *Metriorhynchus superciliosus*, the number of teeth that come into contact with
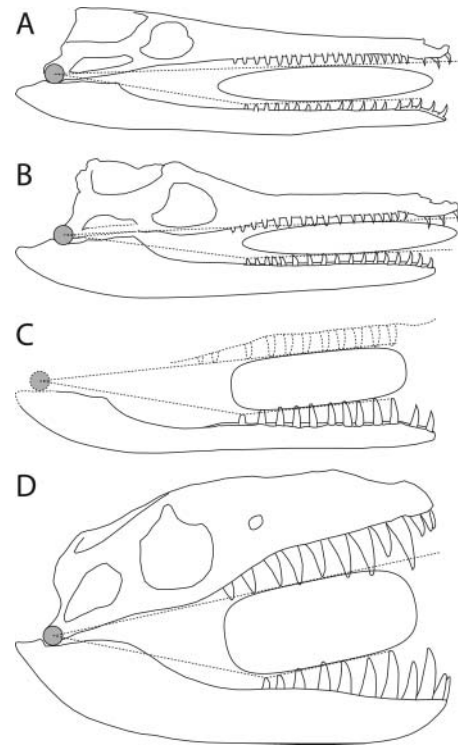

Figure 28. Optimum gape and prey size in *Tyrannoneustes* as compared to selected metriorhynchid taxa. **A**, *Metriorhynchus superciliosus* (Blainville); **B**, *Suchodus brachyrhynchus* (Eudes-Deslongchamps); **C**, *Tyrannoneustes lythrodectikos* sp. nov.; **D**, *Dakosaurus andiniensis* Pol & Gasparini. Optimum gape was determined by first drawing a line across the tips of the dentary tooth, then drawing a parallel line through the jaw joint, and finally, by taking the gape angle between that line and the tip of the posterior-most tooth. Optimum prey size would then be determined as the distance between the two parallel lines. *M. superciliosus* skull modified from Andrews (1913) and mandible of GLAHM V1141; *S. brachyrhynchus* is an original skull reconstruction of NHMUK PV R3804 and mandible reconstruction of NHMUK PV R3804 by Andrews (1913); *T. lythrodectikos*, GLAHM V972; *D. andiniensis*, redrawn from Gasparini *et al*. (2006).

prey tends to be low at wide gapes (Fig. 28). Combined with their small teeth, a low number of bite points does not allow for a firm grip. A bite is more efficient (regardless of gape) if multiple teeth can come into contact with prey simultaneously. This allows for a firm grip on prey. Thus the gape at which multiple teeth come into contact with prey would be the functionally optimal gape, herein coined 'optimum gape', and serves as a potential proxy for biomechanically optimal prey depth, or optimum prey size. We note, however, that optimum prey size does not necessarily reflect maximum prey size, since many predators are known to consume prey larger than their maximum gape (e.g. barracudas, see Grubich *et al.* 2008), but is a biomechanically predicted optimum prey size given the tooth row and mandibular morphology.

Optimum gape angle can be determined by: (1) drawing a straight line across the tips of the mandibular teeth; (2) drawing a second line through the jaw joint that is parallel to the first line; and (3) measuring the angle between the second line and the tip of the posterior most mandibular tooth (Fig. 28). In the metriorhynchine *M. superciliosus*, multiple teeth come into contact with prey at a gape angle of approximately 11° (Fig. 28). Optimum prey size is one that has a depth of around 8% of the mandibular length. The basal geosaurine *S. brachyrhynchus* has an optimum gape angle of approximately 10° with an optimum prey depth of 7% mandibular length. On the other hand, in the highly derived geosaurine, *D. andiniensis*, the optimum gape angle is approximately 23°, and optimum prey depth is about 19% of the mandibular length. *Tyrannoneustes lythrodectikos* is roughly intermediate in optimum gape angle (15°) and optimum prey size (13% of mandibular length). This fits well with its intermediate phylogenetic position between the basal *S. brachyrhynchus* and derived clade Geosaurini.

While it is well known that biting performances are reduced at wider gapes (a negative relationship exists between biting performance and gape, see Herring & Herring 1974; Dumont & Herrel 2003; Bourke *et al.* 2008), predatory taxa (such as mammalian carnivores) tend to exhibit adaptations for higher biting performances at wider gapes (Herring & Herring 1974). Our comparisons of optimum gape also reveal that derived geosaurines and *T. lythrodectikos* are better suited for biting into larger prey than the basal metriorhynchids *Metriorhynchus* and *Suchodus* (Fig. 28). Furthermore, *Tyrannoneustes*, *Torvoneustes*, *Geosaurus* and *Dakosaurus* exhibit adaptations that would be beneficial for wide gape biting. Firstly, since transmission of muscle force to bite force (i.e. mechanical advantage; Westneat 1994) is relatively lower at wide gapes than at narrow gapes (Dumont & Herrel 2003), a high overall mechanical advantage would compensate for such a loss. A reduction of the out-lever – foreshortening of the rostrum and the brevirostrine condition – is observed in Geosaurini (*Dakosaurus andiniensis* Pol & Gasparini 2009; *Geosaurus giganteus* Young & Andrade 2009; *Torvoneustes carpenteri* Wilkinson *et al.* 2008), an obvious adaptation for increasing mechanical advantage. Secondly, an increase in muscle force magnitude by enlargement of muscle cross-sectional areas is another way to compensate for low bite force at wide gape (Bourke *et al.* 2008). Geosaurin taxa display an increase in supratemporal fenestra diameter, (e.g. see character 35; compare *Dakosaurus andiniensis* (Pol & Gasparini 2009), *Geosaurus grandis* (Young & Andrade 2009) and *Torvoneustes carpenteri* (Wilkinson *et al.* 2008) to *Metriorhynchus superciliosus*, *Gracilineustes leedsi* and *Suchodus brachyrhynchus* in Andrews 1913), thus allowing for an increase in the area/volume available to house jaw adductor muscles, allowing for higher muscle force. Thirdly, geosaurines have sophisticated occlusal patterns:

Tyrannoneustes with in-line locking (see Fig. 7 and description above); *Dakosaurus* with tooth-tooth contact along the carinae (e.g. SMNS 81684, Young *et al.* 2012); and *Geosaurus* with maxillary overbite and dentition that would have created a scissor-like double-bladed occlusion (Young & Andrade 2009; Andrade *et al.* 2010). Unfortunately, the occlusal mechanism of *Torvoneustes carpenteri* is currently unknown. These sophisticated occlusal patterns combined with high crowns would have increased shearing surfaces.

An interesting point of observation is that while *D. andiniensis* accomplishes a higher optimum gape mostly through an anteriorly increasing crown height, *T. lythrodectikos* accomplishes this relying more on its strong ventral displacement of the dentary tooth row relative to the jaw joint (Fig. 28). *Dakosaurus andiniensis* also exhibits this unique mandibular morphology, but its functional importance regarding optimum gape is dwarfed in comparison to its unique crown height configuration. Meanwhile, *T. lythrodectikos* has comparatively smaller teeth, which are presumed to be more consistent in crown height along the dentary, so mandibular morphology plays a larger role in larger optimum prey size. Thus it could be argued that active predation and consumption of large prey evolved at the base of Geosaurini prior to the acquisition of both enlarged teeth and contiguously serrated teeth through ventral displacement of the dentary tooth row.

Although the concept of an optimum gape has been discussed previously from a biomechanical perspective (Bourke *et al.* 2008), its ecological implications remain unclear. Unlike gape-restricted predators, such as pike (Magnhagen & Heibo 2001), many predators (indeed most large terrestrial carnivores) are known to consume prey larger than their maximum gape, obviously accomplished by processing their food. Thus maximum gape may not equate to any ecological factor. Similarly, optimum gape suffers from this limitation, but unlike maximum gape, optimum gape is based on functional or biomechanical observations. Biomechanical analyses of biting performance at various gapes may reveal further insights into such adaptations in derived geosaurines.

Discussion

New discoveries, most notably the Late Aalenian 'Oregon crocodile' (Wilberg 2009) and the Late Bajocian-Early Bathonian *Neptunidraco ammoniticus* ('Portomaggiore crocodile': Cau & Fanti 2011), have led to a great increase in the total duration of ghost lineages within Metriorhynchidae, and especially Geosaurinae (see Figure 1). However, the description here of the new genus *Tyrannoneustes* from the Middle Jurassic helps to fill some of these gaps. Moreover, the discovery of *Tyrannoneustes lythrodectikos* represents a significant advance in our understanding

of the evolutionary history of super-predatory metriorhynchids. Not only has investigation of *Tyrannoneustes* revealed a hitherto unknown denticle morphology among metriorhynchids, it also reveals that this taxon shares a peculiar mandibular morphology with the super-predatory Geosaurini. Therefore *Tyrannoneustes* is currently the oldest known example of a super predator—a species well suited for feeding on prey as large or larger than itself—in the metriorhynchid fossil record.

Re-examination of long-known but understudied specimens from the Callovian of England show that the taxonomic, morphological and functional diversity of Middle Jurassic metriorhynchids is greater than previously understood. The phylogenetic analysis presented here clearly shows that the new species we describe pertains to a lineage of highly predacious meso-brevirostrine geosaurines (Figs 19–21).

Tyrannoneustes lythrodectikos sp. nov. represents a morphological and functional intermediate between basal geosaurines and the super-predatory Geosaurini, possessing a mosaic of plesiomorphic and derived characteristics. It shares with *Suchodus* a unique denticle morphology: a carinae composed of a series of non-contiguous repetitive isolated and isomorphic true denticles that are microscopic; which seemingly do not influence the height of the keel (i.e. little or no serrated edge). This morphology, which has never been recognised before, requires use of SEM, and could be prevalent in clades that evolve ziphodont dentition (especially, perhaps, during the early history of such clades). *Tyrannoneustes* shares with Geosaurini a mandibular morphology that facilitated enlargement of the teeth and increased optimum gape. Coupled with the increase in size, *Tyrannoneustes lythrodectikos* would have been a large-bodied marine predator that was well suited for feeding on larger prey items than other contemporaneous metriorhynchids.

The realisation that an isolated tooth, mandible and humerus (not from the same locality) cannot be referred to any known species of Oxford Clay metriorhynchid is intriguing. The tooth (NHMUK PV R486) and mandible (Lepage *et al*. 2008) are clearly from another large super-predatory species, while the humerus (GLAHM V1146) is from a species that is most probably better adapted to pelagic life. Nevertheless, it is premature to refer these three specimens to the same species, however tempting. It does suggest, however, that there is yet more to be discovered from the Oxford Clay Formation and that material in museum collections needs to be re-appraised with a more critical eye.

Acknowledgements

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