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Macroevolutionary trends in the genus *Torvoneustes* (Crocodylomorpha: Metriorhynchidae) and discovery of a giant specimen from the Late Jurassic of Kimmeridge, UK

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The metriorhynchid crocodylomorph fauna of the Late Jurassic Kimmeridge Clay Formation (KCF) of the UK was highly diverse. One genus from this Formation, *Torvoneustes*, was unique in evolving dentition similar to known chelonivorous crocodylomorphs and enlarged attachment sites for the pterygoideus adductor musculature. Here we report the largest known *Torvoneustes* specimen, the occipital region of a large cranium that was discovered on the shore of Brandy Bay, Dorset, UK (KCF). We also report three tooth crowns discovered during the 19th century from Oxfordshire that can also be referred to *Torvoneustes*. The partial braincase is unique in having: verticalized basioccipital tuberosities that have thickened ventral margins, the notch between the basioccipital tuberosities is a narrow inverted 'U'-shape and a subrectangular-shaped carotid canal foramina. The presence of 'occipital fossae' (deep concavities with the hypoglossal foramina in their dorsomedial corners) and carotid foramina with raised rims relative to the basioccipital posterior surface, allow us to refer it to *Torvoneustes*. Although incomplete, the exceptional size of the specimen demonstrates that *Torvoneustes* attained larger body lengths than previously supposed (3.7–4.7 m). Comparing the dimensions of this specimen to other metriorhynchids suggests that at least some *Torvoneustes* specimens rivalled *Plesiosuchus manselii* in body length.

ADDITIONAL KEYWORDS: body-size – Geosaurinae – Kimmeridgian – macroevolution – Metriorhynchoidea – *Torvoneustes*.

INTRODUCTION

Metriorhynchids were a species-rich and successful group of marine crocodylomorphs that lived during the Mesozoic era. This clade adapted to a pelagic lifestyle by evolving a body-plan superficially reminiscent of ichthyosaurs and dolphins, including: hydrofoil-like forelimbs, a highly regionalized caudal vertebral column with a hypocercal tail, loss of osteoderms and enlarged salt glands (e.g. Fraas, 1902; Andrews, 1913; Fernández & Gasparini, 2000, 2008; Herrera *et al.*, 2013; Sachs *et al.*, 2019). During the Late Jurassic, metriorhynchids were especially diverse. This is best seen in the open-shelf Kimmeridge Clay Formation (Kimmeridgian–Tithonian) of the UK. Numerous macrophagous metriorhynchids of the subclade Geosaurini are found in this Formation, showing variation in: snout shape, tooth count, gape mechanics, occlusion mechanics, tooth crown and serration morphologies, and body-size (Andrade *et al.*, 2010; Young *et al.*, 2011, 2012a, b, 2013a, b; Foffa *et al.*, 2018a). Thus, these taxa may have evolved distinct morphofunctional complexes in order to limit interspecific competition by subdividing available niches [much like in extant ecosystems; see Young *et al.* (2011, 2012a and the references therein].

Here, we describe a three-dimensionally preserved occiput of a metriorhynchid from the lower Kimmeridgian Clay Formation (Upper Kimmeridgian) of Brandy Bay, Dorset, UK. This specimen can be

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*Corresponding author. E-mail: mark.young@ed.ac.uk referred to the genus *Torvoneustes*, based on three occipital characteristics. Its large size suggests that *Torvoneustes* could grow to larger body-sizes than previously supposed. Moreover, presence of the verticalized basioccipital tuberosities in this specimen provides more evidence that the genus *Torvoneustes* was undergoing rapid morphofunctional evolution during the Kimmeridgian. We also describe three tooth crowns from Shotover Hill, Oxfordshire, UK. Discovered during the 19th century, they are possibly the youngest known of *Torvoneustes* specimens.

ABBREVIATIONS

Institutional

BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; MANCH, Manchester Museum, Manchester, UK; MJML, Museum of Jurassic Marine Life, Kimmeridge, Dorset, UK; NHMUK PV, vertebrate palaeontology collection of the Natural History Museum, London, UK (OR, old register; R, reptiles); OUMNH, Oxford University Museum of Natural History, Oxford, UK; PETMG, Peterborough Museum & Art Gallery, Peterborough, UK.

Anatomical

XII, hypoglossal foramen (=cranial nerve XII); bo, basioccipital; eo, exoccipital–opisthotic complex; fm, foramen magnum; ic, foramen for the carotid artery and vein; oc, occipital condyle; of, occipital fossa; so, supraoccipital.

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA HAY, 1930 (*SENSU* NESBITT, 2011)

THALATTOSUCHIA FRAAS, 1901 (*SENSU* YOUNG & ANDRADE, 2009)

METRIORHYNCHIDAE FITZINGER, 1843 (*SENSU* YOUNG & ANDRADE, 2009)

GEOSAURINAE LYDEKKER, 1889 (*SENSU* YOUNG & ANDRADE, 2009)

GEOSAURINI LYDEKKER, 1889 (*SENSU* CAU & FANTI, 2011)

TORVONEUSTES ANDRADE *ET AL*., 2010

Type species

Dakosaurus carpenteri Wilkinson *et al.*, 2008 (following Recommendation 67B of the ICZN Code). Now referred to as *Torvoneustes carpenteri* (Wilkinson *et al.*, 2008) Andrade *et al.*, 2010.

TORVONEUSTES SP.

(FIGS 1, 2C, 3C)

Specimen

MJML K1707 – incomplete occipital region of the skull.

Locality

Brandy Bay, Dorset, England, UK.

Horizon and age

Aulacostephanus autissiodorensis Sub-Boreal ammonite Zone, lower Kimmeridge Clay Formation. Upper Kimmeridgian, Upper Jurassic.

Description

The specimen (MJML K1707) was collected on 3 December 2005 by Mr Steve Etches, on the shore of the eastern corner of Brandy Bay, Dorset, UK. The specimen only preserves the occipital region of the cranium. It has a maximum dorsoventral height of 175 mm, a maximal width of 160 mm and an anteroposterior depth of 150 mm.

Supraoccipital: The supraoccipital forms the dorsomedial part of the occipital region of the skull (Fig. 1). When seen in occipital view, the supraoccipital is trapezoid-shaped, being broader dorsally than ventrally. However, it is poorly preserved, in particular the left-side where the specimen is both broken and has undergone deformation. We cannot determine whether the concave external surface is solely due to deformation or if the supraoccipital would have been slightly concave *in vivo*. The lateral contact with the exoccipital–opisthotic cannot be determined on the left-side of the supraoccipital, but is visible on the right. This suture is oriented dorsolaterally, but neither termini of this suture can be discerned. Dorsally, the skull is badly damaged and worn, and towards the foramen magnum it is hard to see where the suture naturally ended. Thus, we cannot determine with certainty if the supraoccipital contributed to the dorsal margin of the foramen magnum. The contact with the parietal is also not preserved as the dorsal surface of the supraoccipital is damaged and worn.

Exoccipital–opisthotic: The exoccipital–opisthotic forms the medial and lateral parts of the preserved occipital surface (Fig. 1). It is not possible to discern whether the exoccipital and the opisthotic have fused to form an otoccipital, due to damage and preservation. A possible suture between the exoccipital and opisthotic was noted for the holotype of *Torvoneustes*

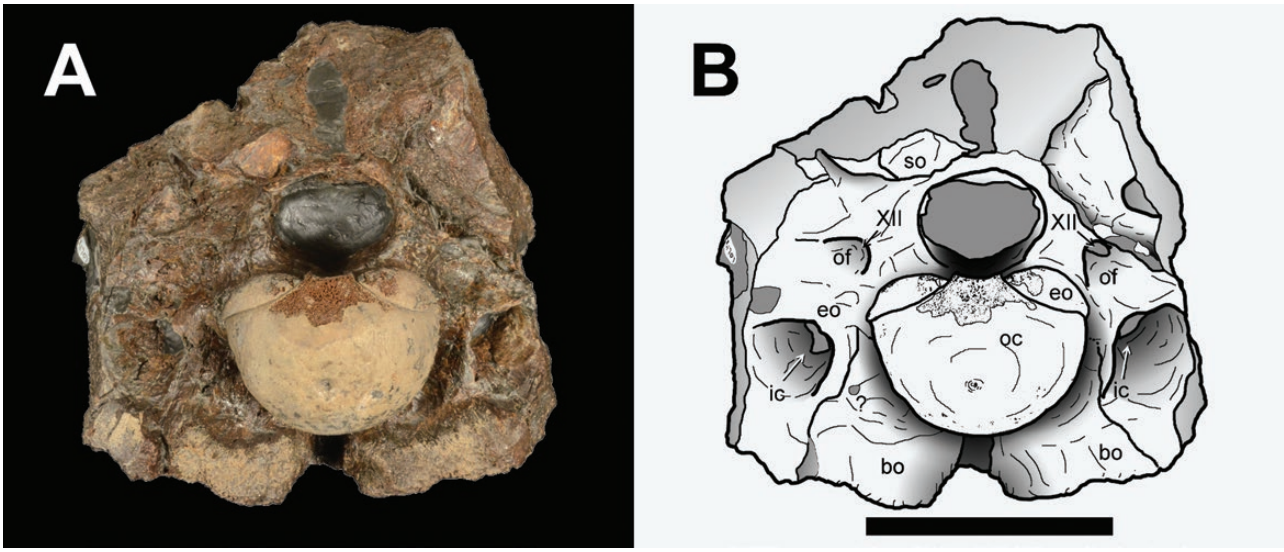

Figure 1. *Torvoneustes* sp. MJML K1707. A, photograph. B, interpretative drawing. See text for anatomical abbreviations. Scale bar = 10 cm.

coryphaeus by Young *et al.* (2013a), although it remains unclear whether there was delayed ossification in the thalattosuchian cranium. The only preserved sutures are with the supraoccipital and the basioccipital. Sutural contacts with the quadrates, parietal and squamosals are either not preserved or the relevant regions of the specimen are too badly damaged. The exoccipital–opisthotic contacts the supraoccipital along its medial margin dorsally. Ventral to its contact with the supraoccipital, the exoccipital–opisthotic forms most of the foramen magnum, including the lateral walls (but we cannot determine whether it also forms the dorsal wall; see 'Supraoccipital' above), and the ventrolateral corners. These paired ventrolateral projections form part of the occipital condyle, contacting the basioccipital. The suture between the exoccipital–opisthotic and the basioccipital continues ventrolaterally until it reaches the ventral margin of the skull. Neither paroccipital processes are preserved.

There are several foramina for nerves and blood vessels on the posterior surface of the exoccipital–opisthotic. The foramen magnum is the largest opening on the occipital surface, situated at the skull midline between the supraoccipital, the exoccipital–opisthotic and the basioccipital. It is suboval-shaped, being wider mediolaterally than tall dorsoventrally. Dorsolateral to the occipital condyle on both sides of the skull midline are large fossae (Figs 1, 2). These 'occipital fossae' are deep depressions that, based on current knowledge, are only found in *Torvoneustes* among thalattosuchians. These structures were first, and until now only, observed on the holotype of *T. coryphaeus* Young *et al.*, 2013a. We cannot assess whether this feature is diagnostic of *Torvoneustes* at the generic level, because the holotype of *T. carpenteri* does not preserve the area (Wilkinson *et al.*, 2008). In the dorsomedial corner of each 'occipital fossa' is the foramen for the hypoglossal nerve (=cranial nerve XII), just as in *T. coryphaeus* (Figs 1, 2). The region surrounding the hypoglossal foramina is variable in Metriorhynchidae, with some species having no evidence of occipital fossae ['*Metriorhynchus*' cf. *durobrivensis* (Wenz, 1968; Lepage *et al.*, 2008); although this specimen is slightly worn]. Other taxa have a slight concavity in this region [*Plesiosuchus manselii* (Hulke, 1870), Young *et al.*, 2012a; *Dakosaurus andiniensis* Vignaud & Gasparini, 1996, Pol & Gasparini, 2009], whereas in '*Metriorhynchus*' cf. *westermanni* Gasparini, 1980 (Fernández *et al.*, 2011: fig. 1c) and *Tyrannoneustes lythrodectikos* Young *et al.*, 2013 (Foffa & Young, 2014: fig. 11a) there is a shallow concavity that has a distinct dorsal/dorsomedial border, but no lateral or ventral borders (i.e. the depressions are 'open' laterally and ventrally; Fig. 1). However, in MJML K1707 and *T. coryphaeus* (Young *et al.*, 2013a), the 'occipital fossae' are enclosed laterally by the exoccipital–opisthotic, and ventrally by a thin lamina of bone that also forms the dorsal margin of the carotid artery foramen. In those taxa with a shallow concave depression in this region, the depression and the carotid foramen are noticeably separated (e.g. *Plesiosuchus manselii*, *Tyrannoneustes lythrodectikos* and '*Metriorhynchus*' cf. *westermanni*; Fernández *et al.*, 2011; Young *et al.*, 2012a; Foffa & Young, 2014).

The foramina for the cerebral carotid canals (=foramen caroticum posterius) are the second-largest openings on the occipital surface (Figs 1, 2). These foramina form funnel-like structures that open posteroventrally.

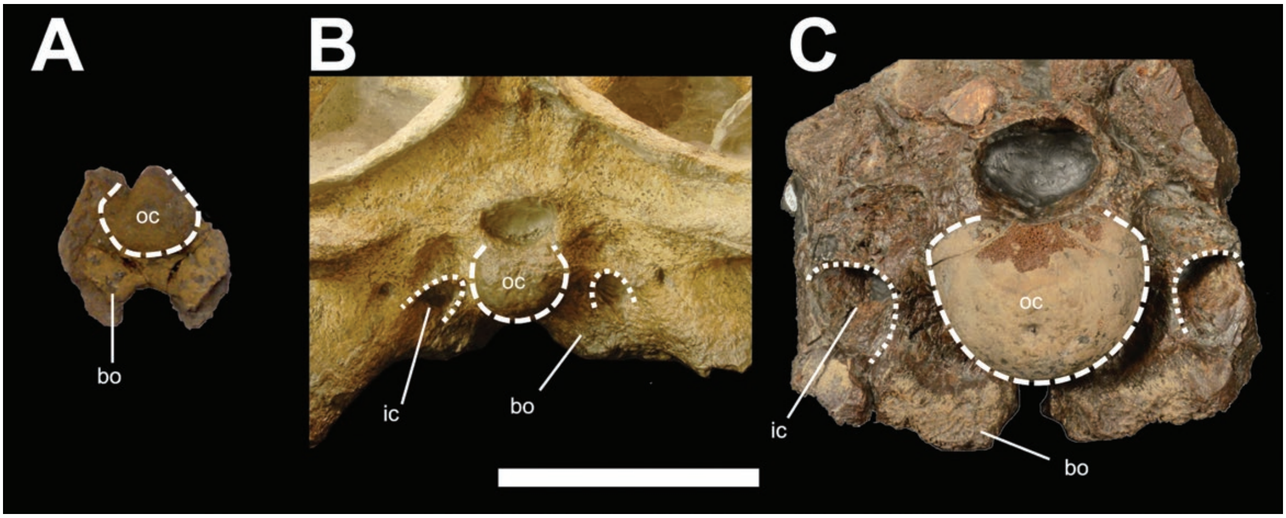

Figure 2. Comparative plate of occipital condyle–basioccipital complex of *Torvoneustes* species. A, *Torvoneustes carpenteri*, holotype BRSMG Ce17365. B, *Torvoneustes coryphaeus*, holotype MJML K1863. C, *Torvoneustes* sp., MJML K1707. Scale bar = 10 cm.

In most other thalattosuchians these foramina are largely flush with the occipital surface (Wenz, 1968; Lepage *et al.*, 2008; Jouve, 2009; Pol & Gasparini, 2009; Fernández *et al.*, 2011; Young *et al.*, 2012a; Foffa & Young, 2014; Herrera *et al.*, 2015), but here they are raised relative to the basioccipital surface immediately medial to them. This morphology is also present in the holotype of *T. coryphaeus* (Young *et al.*, 2013a: fig. 8).

Occipital condyle: The occipital condyle is subcircular in posterior view, slightly mediolaterally wider at its dorsal margin than ventrally. There is a small depression at the centre of the posterior surface. The condyle is mostly formed by the basioccipital, with the exoccipital–opisthotics contributing only to the dorsolateral corners. The gap between the corners, filled by the basioccipital, comprises most of the dorsal margin of the condyle and the ventral margin of the foramen magnum (Fig. 1). This is the normal condition within Thalattosuchia, and is seen in other teleosaurids, basal metriorhynchoids, metriorhynchine metriorhynchids and basal geosaurine metriorhynchids (Andrews, 1913; Pierce & Benton, 2006; Lepage *et al.*, 2008; Jouve, 2009; Foffa & Young, 2014). However, in some derived geosaurine metriorhynchids, the exoccipital–opisthotic forms the entire dorsal margin of the occipital condyle when these two processes fuse together (*Plesiosuchus manselii* Young *et al.*, 2012a; *Torvoneustes coryphaeus* Young *et al.*, 2013a). The holotype of *T. carpenteri*, preserves most of the basioccipital portion of the occipital condyle (Wilkinson *et al.*, 2008). Unfortunately, the dorsal margin of the occipital condyle is broken and worn.

Basioccipital: In addition to constituting the majority of the occipital condyle, the basioccipital forms the ventromedial part of the occipital region of the cranium (Figs 1, 2). The suture between the exoccipital–opisthotic and the basioccipital is clearly seen on the occipital condyle, and is also visible laterally and ventrally to the condyle. Here, the lateral contact between the exoccipital–opisthotic and basioccipital is a subtle suture that projects ventrolaterally from the occipital condyle to the lateral margin of the basioccipital tuberosity (=basal tuber), and is medial to the enlarged carotid foramen. The left and right tuberosity extend ventrally from the ventral edge of the braincase in occipital view. They have a distinctive subrectangular shape, with a notably thickened distal region. This morphology is distinctly different from most other geosaurine metriorhynchids, where they tend to be rounded and project ventrolaterally such as in *Dakosaurus andiniensis* (Pol & Gasparini, 2009), '*Metriorhynchus*' *brachyrhynchus* (Andrews, 1913; NHMUK PV R 3699, NHMUK PV R 3700, NHMUK PV R 3804; Fig. 3a), *Plesiosuchus manselii* (Young *et al.*, 2012a; NHMUK PV R 1089, NHMUK PV OR 40103; Fig. 3d, e), *Purranisaurus potens* (Herrera *et al.*, 2015) and *Tyrannoneustes lythrodectikos* (Foffa & Young, 2014; PETMG R176; Fig 3b). The braincase of '*Metriorhynchus*' cf. *westermanni* has prominent tuberosities that are ventrolaterally orientated, but have a blunter ventral margin (Fernández *et al.*, 2011). The occiput of MJML K1707 also differs from these taxa in having the tuberosities that are medially close to one another, resulting in the intertuberosity notch being very small (Fig. 3c). Unfortunately, in the holotype of *Torvoneustes carpenteri* these tuberosities

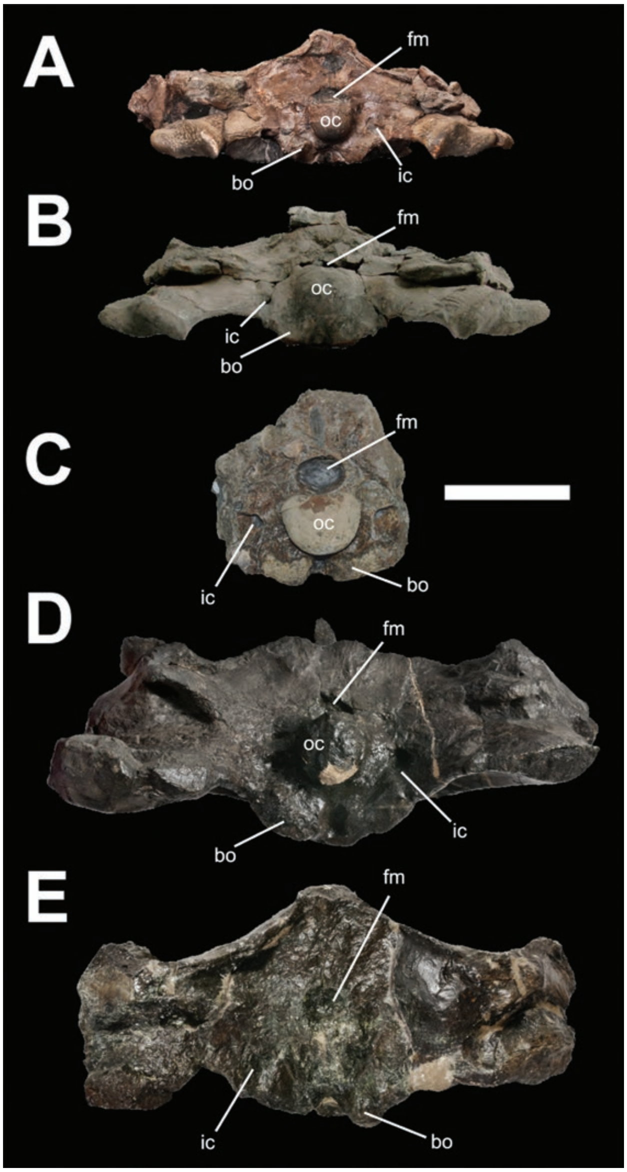

Figure 3. Comparative plate of occipital condyle–basioccipital complex of geosaurines. A, '*Metriorhynchus*' *brachyrhynchus*, referred specimen NHMUK PV R 3804. B, *Tyrannoneustes lythrodectikos,* referred specimen PETMG R176. C, *Torvoneustes* sp., MJML K1707. D, *Plesiosuchus manselii*, referred specimen NHMUK PV R 1089. E, *Plesiosuchus manselii*, holotype NHMUK PV OR 40103. Scale bar = 10 cm.

are poorly preserved (Wilkinson *et al.*, 2008), and the holotype of *T. coryphaeus* is damaged in this region (Young *et al.*, 2013a). Between the tuberosities is a deep fossa, within which is the foramen for the medial pharyngeal tube that forms part of the median pharyngeal sinus system.

TORVONEUSTES SP.

(FIG. 4)

Specimens

OUMNH J.50061, OUMNH J.50079–J.50085: incomplete isolated tooth crowns and roots.

Locality

Shotover Hill, Oxfordshire, England, UK.

Horizon and age

Unknown horizon from the Kimmeridge Clay Formation. The deposits from this locality are almost entirely Early Tithonian in age, with the only Kimmeridgian horizon being the *Pictonia baylei* Sub-Boreal ammonite Zone (earliest Kimmeridgian) (Cox, 2001: fig. 2.52). Most likely Lower Tithonian, Upper Jurassic.

Description

Overall, these tooth crowns (Fig. 4) are exceptions, similar to those of *Torvoneustes carpenteri* (see: Andrade *et al.*, 2010; Young *et al.*, 2013b), such that if they originated from the type locality, they would be assigned to *T. carpenteri*. The tooth crowns have a caniniform morphology and are single-cusped, conical with little labiolingual compression and are poorly curved lingually (Fig. 4). However, looking at the crown and root, there is a noticeable lingual curvature (e.g. Fig. 4F). The apices of the teeth are broken and/or rounded, with no evidence of the natural apex preserved. Overall, the teeth retain their labiolingual width along most of their apicobasal length.

All the tooth crowns lack a constriction at the crown–root junction, although the boundary is evident due to the change in colour and texture. They also lack cingula (a ridge at the base of the crown) and accessory cusps/denticles. The are no apicobasal troughs or flutings (see: Foffa *et al.*, 2017, 2018). Moreover, the teeth lack the apicobasal facets on the labial surfaces, and the 'laminar' crown cross-sections seen in *Geosaurus* and *Ieldraan* (e.g. Young & Andrade, 2009; Andrade *et al.*, 2010; Foffa *et al.*, 2017, 2018). The teeth also lack the 'carinal flanges' and carinal (mesiodistal) macrowear seen in *Dakosaurus* (Young *et al.*, 2012a, b, 2015). The weak 'carinal flanges', which are preeminent at the mid-crown, and strong distal curvature of the mesial margin, which are diagnostic for Plesiosuchina, are also not present (see: Young *et al.*, 2012a; Chiarenza *et al.*, 2015).

All tooth crowns preserve mesial and distal carinae, but there are no split or supernumerary ones. In the apical region, the superficial enamel ornamentation

Figure 4. *Torvoneustes* sp. teeth, OUMNH J.50085 (A, D, G), J.50082 (B, E, H), J.50083 (C, F, I). Scale bar = 5 cm.

contacts the carinal keel (=false serrations). These could only be properly observed with the use of optical aids. The labial and lingual surfaces are heavily ornamented, with the same characteristic enamel ornamentation pattern seen in other *Torvoneustes* species (Andrade *et al.*, 2010; Young *et al.*, 2013b; Barrientos-Lara *et al.*, 2016). In the basal-to-mid crown regions, the enamel ornamentation is composed of numerous elongate apicobasal ridges, while in the apical region, the ornamentation shifts to being composed of shorter ridges that form an anastomosed pattern.

DISCUSSION

Referral of MJML K1707 to *Torvoneustes*

The occiput (MJML K1707) described herein can be referred to *Torvoneustes* based on comparison with the holotype of *T. coryphaeus* (Fig. 2). This referral is supported by three characteristics not seen in any other thalattosuchian. Due to the incomplete preservation of *T. carpenteri* specimens, we cannot determine their nature in the type species.

1. The presence of well-defined 'occipital fossae' that have the hypoglossal foramen in their dorsomedial corner (Fig. 2). As discussed above, other geosaurines have a shallow concavity in this region, but other than *T. coryphaeus* and MJML K1707, no known specimen has both deeply concave fossae and fossae with well-defined limits (i.e. distinct lateral and ventral margins).
2. The carotid canal foramina margins are raised relative to the external surface of the basioccipital (Fig. 2). As mentioned above, in other thalattosuchians these foramina are largely flush with the occipital surface. However, in *T. coryphaeus* and MJML K1707, the external margins of the carotid foramina are raised, which results in them 'projecting' further posteriorly than the basioccipital posterior surface.
3. The ventral margin of the 'occipital fossae' and the dorsal margin of the carotid foramina are the same thin lamina of bone (Fig. 2). In taxa with a shallow concavity, the depressions are situated more dorsally than the carotid foramina, such that there is a 'flat' region of the exoccipital–opisthotic between them (Pol & Gasparini, 2009; Fernández *et al.*, 2011; Young *et al.*, 2012a; Foffa & Young, 2014; Herrera *et al.*, 2015). In *T. coryphaeus* and MJML K1707, both the 'occipital fossae' and the carotid foramina look to be proportionally larger than in other geosaurines. The carotid foramina, in particular, are very large in MJML K1707.

While MJML K1707 cannot be compared with the type species *T. carpenteri* for the fossae and carotid characteristics, we can compare the orientation of the basioccipital tuberosities and the posterior surface of the basioccipital ventral to the occipital condyle (Fig. 2):

1. In the *T. carpenteri* holotype, the basioccipital tuberosities are incompletely preserved. However, from what is preserved, they would have been orientated ventrolaterally, rather than ventrally as in MJML K1707.
2. The difference in basioccipital tuberosity orientated yields a different shape of intertuberosity notch. The *T. carpenteri* holotype has a broad, inverted

'U'-shape, whereas MJML K1707 has a much narrower inverted 'U'-shaped notch.

3. In the *T. carpenteri* holotype, the posterior surface of the basioccipital is broadly exposed ventral to the occipital condyle. However, in MJML K1707, this surface is only visible lateral to the occipital condyle, and then is reduced due to the thickened ventral margin of the basioccipital tuberosities. This is perhaps due to the ventrolateral orientation of the tuberosities in *T. carpenteri*, resulting in this surface being proportionally larger. Alternatively, the occipital condyle of MJML K1707 could also be proportionally larger, but because so little of the occipital surface of the *T. carpenteri* holotype is preserved, we cannot evaluate that possibility.

These differences mean we cannot refer MJML K1707 to *T. carpenteri*. We can also exclude MJML K1707 from *T. coryphaeus* due to:

1. The lack of fusion of the exoccipital–opisthotic processes on the dorsal margin of the occipital condyle. In *T. coryphaeus*, the resulting fusion of these two processes mean that the basioccipital is excluded from the dorsal margin of the occipital condyle (Young *et al.*, 2013a: fig. 8). In MJML K1707, these processes do not fuse, such that the basioccipital is exposed medially on the occipital condyle dorsal margin.
2. The distinctive subrectangular shape of the carotid foramina in MJML K1707. These foramina are subcircular in *T. coryphaeus* (Young *et al.*, 2013a: fig. 9).
3. The ventral orientation of the basioccipital tuberosities in MJML K1707. While incompletely preserved in *T. coryphaeus*, this species shares the same broad inverted 'U'-shaped inter-tuberosity notch as *T. carpenteri*, created by the ventrolateral orientation of the basioccipital tuberosities (see Young *et al.*, 2013a: fig. 8).

REFERRAL OF THE OUMNH TEETH TO *TORVONEUSTES*

The incomplete tooth crowns and roots (OUMNH J.50061, OUMNH J.50079–J.50085 described herein can be referred to *Torvoneustes*, as they have the following characters: (1) heavy enamel ornamentation composed of numerous discontinuous, apicobasally aligned ridges of high relief and density, (2) basal-to-mid crown has superficial enamel ornamentation composed of numerous apicobasal ridges, (3) apical region enamel ornamentation is composed of shorter ridges that form an anastomosed pattern and (4) in the apical region, the apicobasal ridges curve towards, and contact, the carinae (false serrations). This suite of characters is seen in *T. carpenteri* and *T. mexicanus* (Wieland, 1910) (Andrade *et al.*, 2010; Young *et al.*, 2013b; Barrientos-Lara *et al.*, 2016). Note that *T. coryphaeus* lacks false serrations (Young *et al.*, 2013a).

The contemporaneous thalattosuchian genera *Machimosaurus* and *Torvoneustes* had similar dentition, sharing an anastomosed enamel ornamentation pattern apically, basal-and-mid crown regions with apicobasally aligned ridges, false serrations in the apical region, poor lingual curvature and a blunt apex. However, *Machimosaurus hugii* von Meyer, 1837 has 'pseudodenticles' occurring along the superficial enamel ridges, and *Machimosaurus* spp. tooth crowns either lack carinae or have low carinae (Young *et al.*, 2014a, b). The OUMNH crowns lack 'pseudodenticles' and the carinae are prominent with the keel itself being well-developed (best seen in Fig. 4F). The latter is a characteristic that sets *Torvoneustes* apart even among other macrophagous metriorhynchids (Young *et al.*, 2013b).

OVERVIEW OF THE GENUS *TORVONEUSTES*

The oldest specimen potentially referable to the genus *Torvoneustes* is the incomplete skull MANCH L6459 from the Middle Oxfordian of Headington, Oxfordshire, UK. Young (2014) tentatively concluded it to be cf. *Torvoneustes*. This was due to the specimen lacking apomorphies of *Plesiosuchus*, *Dakosaurus* and *Geosaurus*, and that it shared the same external ornamentation morphology on the maxillae as *Torvoneustes coryphaeus*. The phylogenetic analysis of Young (2014) supported the weak referral to cf. *Torvoneustes*.

The oldest definitive *Torvoneustes* specimen is *T. coryphaeus*, known from a single incomplete skull (the holotype MJML K1863). The holotype was discovered in an exposure of the lower Kimmeridge Clay Formation in 2006 at the Studley Grange landfill site in the village of Lydiard Tregoze, west of Swindon, Wiltshire, UK. Based on the presence of a *Pictonia* ammonite in the carbonate concretion that yielded the holotype, *T. coryphaeus* comes from the *P. baylei* Sub-Boreal ammonite Zone (Young *et al.*, 2013a). This means *T. coryphaeus* is known from the base of the Early Kimmeridgian. Following Young *et al.* (2013a), *T. coryphaeus* can be distinguished from the other species and specimens in the genus *Torvoneustes* by: the posterior margin of the prefrontals having irregular 'notches', frontal anteromedial process reaches the same relative position as the anterior margin of the prefrontals, strong ornamentation of the external surface of the nasals and the frontal, the supraorbital notch forms an acute angle (less than 45 degrees), prefrontal posterolateral margin in dorsal view forms an acute angle, the maxillae continue posteriorly under the orbits, the maxillary tooth row terminates under the anterior half of the orbit, the maxillae have an estimated 17–19 teeth each and the superficial enamel ridges on the tooth crowns do not contact the carinae.

The type species, *Torvoneustes carpenteri*, is known from an incomplete skull (the holotype BRSMG Ce17365), mandibular fragments, numerous vertebrae and ribs, humerus, left ischium, both femora and possible propodial elements (BRSMG Cd7203) and a partial mandible with an isolated tooth crown (MJML K225). The holotype and referred specimens were discovered in the quarries at the Lafarge cement works (formerly Blue Circle Industries) near Westbury, Wiltshire, UK. The specimens are from the lower Kimmeridge Clay Formation, *Aulacostephanus eudoxus* Sub-Boreal ammonite Zone (Wilkinson *et al.*, 2008). As such, all definitive *T. carpenteri* specimens are known from the same locality and are Late Kimmeridgian in age. Following Young *et al.* (2013a), *T. carpenteri* can be distinguished from the other species and specimens in the genus *Torvoneustes* by: four large 'finger-like' projections along the posterior margin of the prefrontals, frontal anteromedial process not reaching as far anteriorly as the same relative position as the anterior margin of the prefrontals, the lack of ornamentation of the external surface of the nasals and the frontal, the supraorbital notch is an open continuous curve forming an angle close to 90 degrees, prefrontal posterolateral margin in dorsal view is round forming an angle close to 90 degrees, the maxillae terminate anterior to the orbits, the maxillary tooth row terminates immediately posterior to the preorbital fossae, the maxillae have an estimated 14 teeth each and the tooth crowns have superficial enamel ridges that contact the carinae (false serrations).

From the Late Jurassic (presumed to be Kimmeridgian) of Mexico, *T. mexicanus* (Wieland, 1910) is known. Originally described as a plesiosaur, the holotype of *T. mexicanus* was reviewed and demonstrated to pertain to *Torvoneustes* (Barrientos-Lara *et al.*, 2016). As the specimen is a partial rostrum in an occlusal position, it cannot be compared with MJML K1707. Like *T. carpenteri*, *T. mexicanus* has false serrations, but the dentition of *T. mexicanus* is distinct from both European species in being more strongly compressed and having sharp apices (see: Barrientos-Lara *et al.*, 2016: fig. 3).

The isolated *Torvoneustes* tooth crowns (OUMNH J.50061, OUMNH J.50079–J.50085) from Shotover Hill, Oxfordshire (Fig. 4) can be excluded from *T. coryphaeus* due to the presence of the enamel ridges contacting the carinae (a morphology only seen in *T. carpenteri* and *T. mexicanus*). Unfortunately, like many historical specimens discovered in the 19th century from Shotover Hill, they lack precise geological data [see: Young *et al.* (2015) for the *Dakosaurus* tooth crowns also discovered during the 19th century at Shotover Hill]. However, they are most likely Early Tithonian in age, given the age of the rocks that crop out there (Cox, 2001) and how similar the tooth crowns are to those of *T. carpenteri*.

The differences between *Torvoneustes coryphaeus* and *T. carpenteri* are interesting. The geologically older species (*T. coryphaeus*) had longer maxillae, a greater maxillary tooth count, anteroposteriorly shorter suborbital fenestrae, more strongly ornamented dermatocranial bones and less heavily ornamented teeth than *T. carpenteri*. Therefore, there were several macroevolutionary trends in the genus *Torvoneustes*: (1) reduction in maxillary tooth count, (2) proportionally longer suborbital fenestrae and, presumably, enlarged *pterygoideus* musculature, (3) decreasing dermatocranium external ornamentation and (4) an increase in enamel surface ornamentation and the evolution of false serrations (enamel ridges contacting the carinae). This is supported by the Oxfordian cf. *Torvoneustes* skull, as it too has an ornamented dermatocranium and, from what is preserved, it had a relatively high tooth count. The dentition of the Mexican species *T. mexicanus* has sharper apices than the blunt teeth seen in *T. carpenteri* and *T. coryphaeus*, and, like *T. coryphaeus*, the tooth crowns of *T. mexicanus* show noticeable lingual curvature. Curiously, *T. mexicanus* has false serrations, but the overall level of enamel ornamentation is closer to *T. coryphaeus* than *T. carpenteri*. This suggests that the dentition of these three species shift from lingually curved tooth crowns with sharp apices (but still having the characteristic '*Torvoneustes*' enamel ornamentation pattern) to poorly curved tooth crowns that are subconical with blunt apices, false serrations apically and the entire tooth crown is more heavily ornamented.

With the addition of MJML K1707, we can add two additional morphological shifts in *Torvoneustes*: the ventralization of the basioccipital tuberosities and increasing body size. Whether the thickening of their ventral margin is apomorphic for MJML K1707 is currently unknown due to these tuberosities being incomplete in the *T. carpenteri* and *T. coryphaeus* holotypes. As this region is the insertion point for the head ventroflexion musculature in extant crocodylians (e.g. Snively & Russell, 2007; and the references therein), it suggests that in MJML K1707 there was a shift in head flexion or, perhaps, head stabilization during prey capture. Interestingly, thickened and verticalized basioccipital tuberosities are also present in the chelonivorous teleosauroid *Machimosaurus*, particularly in *M. hugii* (see: Young *et al.*, 2014: fig. 8). Given the similarity in tooth crowns between *Machimosaurus* and *Torvoneustes*, the shared morphology of the basioccipital tuberosities may be further evidence for durophagy in *Torvoneustes*. Alas, as no *Torvoneustes* cranium preserves the entirety of the occiput, we cannot elucidate what is happening.

Additionally, if we take a literal reading of the fossil record, then during the Kimmeridgian there was a rapid increase in body size within *Torvoneustes*. The size of the occipital condyle shows that, MJML K1707 is the largest *Torvoneustes* specimen currently known (Figs 2, 5). Based on what is preserved, it is not possible to give a precise assessment of the size of MJML K1707. However, the occipital condyle width, and width across the basioccipital tuberosities are greater than those of currently largest known metriorhynchid, *Plesiosuchus manselii* NHMUK PV R 1089 (Fig. 5). Young *et al*. (2012a) estimated that NHMUK PV R 1089 had a basicranial length of 125.5 cm and a body length of 6.83 m (the total mandibular length of the specimen is 132.2 cm). Unfortunately, the scaling ratios of the occiput against the skull and body is unknown for metriorhynchids. Nevertheless, the braincases of MJML K1707 and NHMUK PV R 1089 are at least comparable in size, suggesting that MJML K1707 might have reached a body size rivalling the largest known metriorhynchid. This is marked larger than the 3.7 m body length estimate for Early Kimmeridgian species *T. coryphaeus*, and the 4.0–4.7 m length estimates for specimens of the Late Kimmeridgian species *T. carpenteri*. As the sample size of *Torvoneustes* specimens is unfortunately small, we cannot be certain whether this dramatic increase in body size is real or artefactual.

CONCLUSIONS

Herein we describe the occipital area of a large metriorhynchid crocodylomorph from the Kimmeridge Clay Formation of Dorset, UK. This specimen (MJML K1707) can be referred to the Late Jurassic genus *Torvoneustes* based on the presence of: 'occipital fossae', the raised rims of the carotid canal foramina, and that the 'occipital fossae' and carotid foramina share a common border that is reduced to a thin lamina. However, the specimen is unique in having: verticalized basioccipital tuberosities that have thickened ventral margins, a narrow inverted 'U'-shaped, inter-basioccipital tuberosity notch and subrectangular-shaped carotid artery foramina. Unfortunately, no *Torvoneustes* specimen preserves a complete occiput, thus we cannot confidently establish a new taxon and so we refer MJML K1707 to *Torvoneustes* sp. We also describe isolated tooth crowns referable to *Torvoneustes* that were discovered during the 19th century at Shotover Hill, Oxfordshire. These tooth crowns are, perhaps, the youngest known *Torvoneustes* specimens, and probably the first known from the Tithonian.

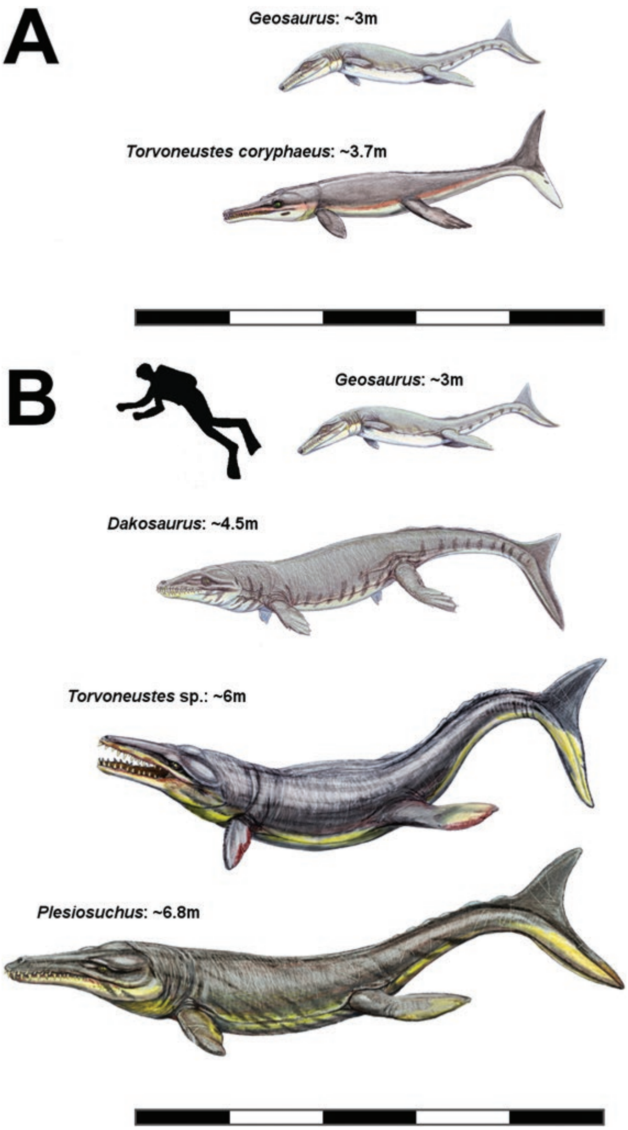

Figure 5. Life reconstructions showing the maximum known body lengths for geosaurine metriorhynchids present in the Kimmeridge Clay Formation. A, species known from the Lower Kimmeridgian. B, species known from the Upper Kimmeridgian–Lower Tithonian. The human diver is 1.8 m in height. All metriorhynchid life reconstructions are by Dmitry Bogdanov. Scale bar = 1 m.

The large size of MJML K1707 and the peculiar basioccipital tuberosity morphologies provides further evidence that during the Kimmeridgian, the genus *Torvoneustes* was undergoing rapid morphofunctional evolutionary changes. There is evidence for numerous macroevolutionary trends over this time-span: reduction of dermatocranium ornamentation, reduction in tooth count, increasing enamel ornamentation and the development of false serrations, blunter crown apices, tooth crowns losing their lingual curvature with crown cross-sections becoming more subconical, increasing suborbital fenestrae anteroposterior length, verticalization of the basioccipital tuberosities and, possibly, also increasing body size. These morphological shifts suggest that *Torvoneustes* was subject to strong selection pressures, possibly related to feeding on large-bodied prey.

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