Filling the ‘Corallian Gap’: re-description of a metriorhynchid crocodylomorph from the Oxfordian (Late Jurassic) of Headington, England

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(Received 2 December 2012; final version received 17 December 2012; first published online 21 January 2013)

Re-description of a long-known, but little studied, metriorhynchid crocodylomorph from the Oxfordian of England begins to help fill the ‘Corallian Gap’. This ‘Gap’ represents a paucity of vertebrate remains from the Oxfordian of England. Filling the ‘Corallian Gap’ has important implications for our understanding of metriorhynchids from England, especially as there was a shift in this ecosystem from being metriorhynchine dominated in the older Oxford Clay Formation, to a geosaurine-dominated fauna in the younger Kimmeridge Clay Formation. The re-description of the specimen reveals that it is a member of the derived subclade Geosaurini, which most likely pertains to the genus *Torvoneustes*.

**Keywords:** Crocodylomorpha; Corallian Gap; Geosaurini; Metriorhynchidae; Oxfordian; *Torvoneustes*

1. Introduction

Metriorhynchids were a successful evolutionary radiation of marine crocodylomorphs that lived during the Middle Jurassic – Early Cretaceous. They evolved numerous adaptations to their pelagic lifestyle, including a hypocercal tail and loss of osteoderm cover (e.g. Fraas 1902; Andrews 1913; Young et al. 2010). Although metriorhynchids are well represented from the Oxford Clay Formation (OCF) (Callovian–lower Oxfordian, Middle Jurassic) and the Kimmeridge Clay Formation (Kimmeridgian-Tithonian, Late Jurassic) of England (Table 1), metriorhynchids are very poorly known from the intermediate formations (collectively referred to as the Corallian Group).

The Corallian Group is a series of formations that range from the lower Oxfordian to the uppermost Oxfordian (Cope 2006). It lies above the older OCF, and is overlain by the younger Kimmeridge Clay Formation. Although metriorhynchids are common in both of these formations (see Table 1; Andrews 1913; Young et al. 2012), they are very rare in the Corallian Group. This results in an approximate 6 million year gap in the English metriorhynchid fossil record (the ‘Corallian Gap’). This gap is significant as the metriorhynchid Sub-Boreal fauna shifts from being metriorhynchine dominated in the Callovian (species with elongate snouts and high tooth counts) to being geosaurine dominated in the Kimmeridgian (species with foreshortened/broadened snouts, low tooth counts and serrated dentition) (Andrews 1913; Young et al. 2012; Table 1).

The ‘Corallian Gap’ hampers our understanding of how, and when, the Sub-Boreal ecosystem shifted and the evolution of metriorhynchids in the Late Jurassic. Here I re-describe an incomplete, but three dimensionally preserved metriorhynchid skull from the Oxfordian of Headington, England. As this specimen is from the ‘Corallian Gap’, it will begin to help us understand this dramatic shift in metriorhynchid ecosystem occupation.

1.1 Institutional abbreviations

AMNH, American Museum of Natural History, New York City, NY, USA; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; CAMSM, Sedgwick Museum, Cambridge, UK; GLAHM, Hunterian Museum, Glasgow, UK; LIECT, New Walk Museum and Art Gallery, Leicester, UK; MGCL, Musée Géologique Cantonal, Lausanne, Switzerland; MJML, Museum of Jurassic Marine Life, Kimmeridge, Dorset, UK; MANCH, Manchester Museum, Manchester, UK; NHMUK, Natural History Museum, London, UK; NMING, National Museum of Ireland, Dublin, Ireland; NMW, National Museum of Wales (National Museum Cardiff, Amgueddfa Genedlaethol Caerdydd), Cardiff, UK; OU/MNH, Oxford University Museum of Natural History, Oxford, UK; PETMG, Peterborough Museum and Art Gallery, Peterborough, UK; RMS, Royal Museum of Scotland, Edinburgh, UK; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

2. Historical overview of MANCH L6459

The specimen (MANCH L6459) was acquired by MANCH from Mr P. Manning on 21 December 1904.
Table 1. List of metriorhynchid specimens from the Jurassic of England based on my personal observations.

| Formation         | Metriorhynchines | Geosaurines |
|-------------------|------------------|-------------|
| OCF               | AMNH FR 997; CAMSM J64297, J64398, J64900, J64918; GLAHM V942, V963, V964, V965, V971, V973, V974, V975, V982, V983, V984, V985, V987, V988, V989, V996, V1004, V1015, V1027, V1140, V1142, V1143; LEICT G118.1987 (provisional number), G1301.1899, G148.1956.25; MGCL 9959, 9960; NHMUK PV R1529, R1530, R1666, R2030, R2031, R2032, R2033, R2036, R2041, R2042, R2044, R2049, R2051, R2053, R2054, R2055, R2056, R2058, R2065, R2069, R3014, R3016, R3540, R3899, R3900, R3906, R4762, R5793, R6859, R6860; NMING F16892, F21731; NMW 19.96 G21; PETMG R8, R10, R20, R42, R24, R72, R180; RMS M150; SMNS 10115, 10116 | CAMSM J64267; GLAHM V972, V993, V995, V1145; LEICT G563.1901; NHMUK PV R486, R1994, R2039, R2618, R3321, R3541, R3699, R3700, R3804, R3939, R4763; PETMG R19, R176 |
| Corallian Group   |                  |             |
| Kimmeridge Clay   | CAMSM J29475; MJML K435; OUMNH J1439, J29823, J50426 | MANCH L6459 |

Notes: From the OCF, there are 74 definitive metriorhynchines (79.6%) and 19 geosaurines (20.4%). From the Kimmeridge Clay Formation, there are 5 definitive metriorhynchines (17.9%) and 23 geosaurines (82.1%). (1) From both formations there are still numerous specimens that are currently undiagnostic and (2) I have excluded diagnostic isolated teeth from the OCF in GLAHM, as I cannot be sure whether they were not once associated with more complete specimens. Subfamily diagnoses based on data in Young and Andrade (2009) and Young et al. (2010, 2012).
Unfortunately, there is no historical information associated with the specimen.

The specimen was originally described by Watson (1911), the only time this specimen has been mentioned in the literature. Watson (1911) referred the specimen to Metriorhynchus cf. hastifer, as he believed the specimen was a member of the genus Metriorhynchus. On the basis of the specimen’s robust nature and relatively broad snout, he considered only three described species to be comparable: Metriorhynchus hastifer, Metriorhynchus brachyrhynchus and Metriorhynchus palpebrosus. Watson (1911, p. 7) dismissed MANCH L6459 being a member of Metriorhynchus brachyrhynchus due to (1) its snout tapering more slowly, (2) not as great a disparity between the width of the nasals at the anterior region and the posterior region, (3) larger gap between the nasals and premaxillae (although the premaxillae are not preserved in MANCH L6459, the gap would have been far larger than in any Metriorhynchus brachyrhynchus specimen) and (4) the palate is more ‘profoundly channelled’. Although the palate is poorly preserved in MANCH L6459, the ‘channeling’ of the palate (concavity) is notable. Watson (1911, p. 7) dismissed MANCH L6459 being a member of Metriorhynchus palpebrosus due to (1) its lower maxillary tooth count, Metriorhynchus palpebrosus has 18 alveoli in the region of the skull that is preserved in MANCH L6459, which only has 10 in the same space and (2) MANCH L6459 has a more strongly ‘channelled’ palate.

Interestingly, Watson (1911, p. 8) showed that MANCH L6459 and Metriorhynchus hastifer differ in the following ways: (1) in Metriorhynchus hastifer the snout tapers more slowly than in MANCH L6459, (2) in Metriorhynchus hastifer the nasals are shorter and (3) in Metriorhynchus hastifer the widest part of the preorbital skull is formed by the nasals. Watson (1911) considered MANCH L6459 to be a well-marked variety of Metriorhynchus hastifer, but hesitated on naming it as the specimen is so poorly preserved.

3. Ambiguity over the locality and horizon of MANCH L6459

When Watson (1911) originally described MANCH L6459, he stated that the specimen came from Quarry Field, Headington, and that it was from the Lower Calcareous Grit. Unfortunately, this is the most detailed locality and horizon information recorded, as no further information is associated with the specimen.

Headington Quarry is the name of a village, east of Oxford and Old Headington, which was established around the ‘Headington stone’ quarry pits during the seventeenth century (although there had been a hamlet at this site for quarry workers for over a 100 years previously; Anonymous 2010). These quarries produced ‘Headington stone’, which was used in the construction of many of the buildings in Oxford. Today, the villages of ‘Old’ Headington, New Headington and Headington Quarry are in the eastern suburbs of Oxford.

The Headington Enclosure Award of 1804 resulted in the Headington area being enclosed in four large fields, which were subdivided into public and private ‘carriage ways and driftways’, bridle roads, foot paths, plots of common land, plots awarded to individuals, etc. The four large fields were North Field, South Field, Pound Field and Quarry Field. The ‘Headington stone’ quarries (some shown in Figure 1) were within Quarry Field. Although there had been numerous quarry pits in this area, by the time the 1881 British Ordnance Survey Map was made, only three were still in use (Anonymous 2010).

The Workhouse, or Corporation, Pit (renamed the Magdalen Pit once it was taken over by Magdalen College, Oxford; more recently it was renamed the ‘Headington Quarry’ by Oxford City Council) was the last of the ‘Headington stone’ quarries to close during the twentieth century. This quarry, along with the Crossroads Pit (or Rock Edge quarry as Oxford City Council renamed it), exposes the Wheatley Limestone Member of the Stanford Formation, which overlies the Beckley Sand Member of the Kingston Formation (Figures 1, 2; Wright 2001a, 2001b). During the twentieth century, the Beckley Sand Member of the Kingston Formation was only exposed early in the century at the Crossroads Pit, whereas the basal unit of the Beckley Sand Member at the Magdalen Pit was mostly covered by quarries for ‘Headington stone’.

Figure 1. Map of the Corallian Limestone outcrop in the Headington area. Showing the positions of the Magdalen Quarry Pit, Crossroads Quarry Pit and Windmill Quarry Pit. Modified from Wright (2001a, 2001b).
Pit was only exposed early in the century as well (see Wright 2001a, 2001b and references therein).

Watson (1911) originally stated that MANCH L6459 came from the Lower Calcareous Grit. The classical division of the Corallian Group was into the Lower Calcareous Grit, the Coral Rag and the Upper Calcareous Grit (proceeding from the geologically oldest to youngest). The Coral Rag of Oxfordshire is currently referred to as the Wheatley Limestone Member of the Stanford Formation (see Cobbing et al. 2004; Cope 2006; although see Wright 2001b for a discussion on reef facies at Quarry Field). As such, the specimen must have come from an older unit (if Watson 1911 was correct). Based on the geological columns for two of the Quarry Field pits (Magdalen Pit and Crossroads Pit; see Figure 2), that unit would have been the Beckley Sands Member of the Kingston Formation. No older unit has been reported for these sites (see Wright 2001a, 2001b and references therein). As this member was only broadly exposed very early in the twentieth century (its exposure in the nineteenth century is unknown), this fits with the specimen being acquired by MANCH in 1904 (i.e. had the specimen been discovered in the 1920s when the exposure of the Beckley Sand Member was limited, or if exposed at all, then the specimen would have been less likely to have originated in this Member).

In summary, the exact quarry pit MANCH L6459 was discovered in is unknown, as is the bed the specimen was found from. However, it was most likely from one of the three surviving post-1881 pits. Finally, as the specimen was historically considered to have been from the Lower Calcareous Grit (Watson 1911), this suggests that it was from what today is considered the Beckley Sands Member of the Kingston Formation. If the Lower Calcareous Grit determination proves to be wrong, then the only unit the specimen could pertain to is the Wheatley Limestone Member of the Stanford Formation (Figure 2). This would still put the specimen in the ‘Corallian Gap’, which means that the specimen is still from the middle Oxfordian (Cope 2006).

4. **Systematic paleontology**

Crocodylomorpha Hay, 1930 (sensu Walker, 1970)  
Thalattosuchia Fraas, 1901 (sensu Young and Andrade, 2009)  
Metriorhynchidae Fitzinger, 1843 (sensu Young and Andrade, 2009)  
Geosaurinae Lydekker, 1889 (sensu Young and Andrade, 2009)  
Geosaurini Lydekker, 1889 (sensu Cau and Fanti, 2011)  
*cf. Torvoneustes* (Figures 3–5)

4.1 **Specimen**

MANCH L6459, incomplete, but three-dimensionally preserved skull.

4.2 **Locality**

Headington, Oxfordshire, England, UK. Note that Headington is sometimes spelt as ‘Heddington’, especially in the nineteenth century literature. This is not to be confused with Heddington in Wiltshire, England. During the seventeenth century, two manor houses were built in the Headington area; the largest was the Manor of Headington, whereas the smaller house was the Manor of Heddington. This appears to be the source of confusion.

4.3 **Horizon and age**

As noted above, the specimen is most likely from the Beckley Sand Member of the Kingston Formation (middle Oxfordian in age).
5. Description

5.1 General comments on the cranium

Only some cranial bones are preserved, but they are undistorted (MANCH J6459; Figures 3–5). However, many bones are not preserved and are thus unknown in cf. Torvoneustes; these include the premaxillae, lacrimalis, jugals, palatines, pterygoids, ectopterygoids, parietal, postorbitals, squamosals, quadratojugalts, quadrates, supraoccipital, exoccipital, basioccipital, basisphenoid, laterosphenoids and proötics. No teeth are preserved, nor are any mandibular or post-cranial elements.

5.2 Maxilla

The maxillae are incompletely preserved, and nothing can be noted about their anterior margins (Figure 3). The external surfaces of the maxillae are slightly convex and have moderate to strong anteroposteriorly aligned grooves and raised ridges (Figures 3, 4). MANCH J6459 lacks the aligned set of large neurovascular foramina that extend posteroventrally from the preorbital fossa in Dakosaurus andiniensis and Dakosaurus maximus (Pol and Gasparini 2009; Young et al. 2012).

In dorsal view, the maxillae contact the anterior processes of the nasals along their medial margins (Figure 3). Anterior to the nasals, the left and right maxillae suture along their medial margins. Although the premaxillae are absent and the premaxilla–maxilla suture cannot be determined, based on other metriorhynchids the maxillae would have contacted the premaxillae anteriorly, and the midline maxillary contact would have separated the premaxillae from the nasals (Fraas 1902; Andrews 1913; Pol and Gasparini 2009; Young et al. 2012).

In palatal view (Figure 5), the left maxilla has nine preserved complete alveoli, whereas the right maxilla has seven complete alveoli, the distal remains of a more mesial alveolus, and two eroded distal alveoli. As such, 10 alveoli can be discerned on the right maxilla. These are arranged so that left and right correspond in size and shape and mesiodistal position. This indicates that the maxillary tooth count was at least 10, although it was clearly greater because the anterior region, and the posterior-most region, of the maxillae is missing. Based on how much of the skull is preserved, it is unlikely that any more than four or five maxillary alveoli are missing.

The maxillary interalveolar spaces are all very small, being less than a quarter of the length of the immediate alveoli and typically far shorter (Figure 5). In other genera within Geosaurini, this pattern of extreme reduction in interalveolar spaces is also present (Plesiosuchus manselii and D. maximus Young et al. 2012; Torvoneustes carpenteri Grange and Benton, 1996). This pattern is
also observed in the Middle Jurassic geosaurine Metriorhynchus cf. durobrivensis (Wenz 1970). However, in teleosaurids (Andrews 1913), metriorhynchine metriorhynchids (such as Metriorhynchus superciliusus, NHMUK PV R6860) and basal geosaurine metriorhynchids (‘Metriorhynchus’ brachyrhynchus, NHMUK PV R3700; Andrews 1913), the maxillary interalveolar spaces are variable in size, ranging from being larger than the proceeding and preceding alveolus, to being half the size. Also in palatal view, the maxillae suture along the midline forming part of the secondary palate. The maxillary–palatine contact cannot be determined due to the poor preservation of the posterior region of the palate (Figure 5).
5.3 Nasals
The nasals are large, paired, unfused elements. In dorsal view, they are subtriangular in shape and broad (Figure 3). Along the midline, the dorsal surface of the nasals has a steep longitudinal depression (‘trenched morphology’), a metriorhynchoid apomorphy (a characteristic present in *Pelagosaurus*, *Teleidosaurus*, *Eoneustes* and *Metriorhynchidae*; Young et al. 2012). The anterior-most part of the nasals (= anterior process) contacts the maxillae along their anterolateral margins (Figures 3, 4). The anterior processes are particularly well ornamented, with a grooved-ridged pattern that is orientated to the long axis of the nasals. On the rest of the dorsal and lateral surfaces of the nasals, the ornamentation pattern is largely composed of sub-circular/elliptical pits, whereas the dorsal surface also has faint anteroposteriorly aligned grooves.

Along the posterior margin, the nasals contact the frontal and prefrontals (Figure 3). The right nasal is the best preserved in this region. It has the dorsoposterior process, and a small portion of the lateroposterior process. The dorsoposterior process contacts the frontal medially and the prefrontal laterally. Between the dorsoposterior process and the lateroposterior process, the right nasal contacts what is preserved of the right prefrontal (Figures 3, 4). Although most of the right lateroposterior process is missing, from what is preserved it would have formed part of the dorsal margin to the preorbital fossa (Figure 4).

5.4 Frontal
Only the anteromedial process of the frontal is preserved (Figures 3, 4). This process is wedge shaped and would have contacted the dorsoposterior processes of the nasal laterally. From what is preserved, it appears to be a single element lacking any evidence of an interfrontal suture on the external surface. The external surface is ornamented by grooves and ridges aligned anteroposteriorly.

5.5 Prefrontals
Only the anterior region of the right prefrontal is preserved (Figures 3, 4). The dorsal surface of the prefrontal is enlarged and expanded, and although it is incomplete it would have overhung the anterior third of the orbit as with other metriorhynchids (Fraas 1902; Andrews 1913). The external surface is slightly convex and is covered in large pits of irregular shape. Some of these pits merge and form short irregularly shaped grooves.
6. Phylogenetic analyses

6.1 Methods

I undertook two phylogenetic analyses to assess the evolutionary relationships of MANCH J6459 within Thalattosuchia. The analysis presented here is a revised version of the published taxon and character data-set of Young et al. (2012). The analysis presented here differs from that of Young et al. (2012) in that:

1. MANCH J6459 was added into the analysis.
2. The ‘Ricla crocodile’ was added into the analysis. This is a new genus and species, the name of which is currently in press (Parrilla-Bel et al. in press).
3. The ‘Mr Etches’ specimen was added into the analysis. This is a new taxon (Manuscript, in preparation) that helps to polarise characters in Geosaurini.
4. Cricosaurus saltillensis is re-coded following the description of a new specimen of this species by Buchy et al. (in press). Note that they also amended the specific epithet.
5. ‘Cricosaurus’ gracilis was removed from the current analysis as I am currently re-describing the specimen. This re-description will result in a more confident set of character scores for this taxon.
6. Eleven new characters were added to the character data-set.
7. The characters relating to dermatocranium ornamentation patterns have been restructured and recoded based on recent visits to NHMUK and OUMNH.
8. ‘Metriorhynchus’ brachyrhynchus has been partially recoded based on a recent visit to NHMUK. As noted by Young et al. (2012), the taxonomic status of Suchodus davorivensis is currently unknown and requires a re-description. As such it is not included in this analysis.

This results in a data-set of 251 characters and 75 taxa (see Supplementary Material for the Nexus file and the list of characters and coding sources). The two phylogenetic analyses were carried out using Tree analysis using New Technology (TNT) v1.1 (Willi Hennig Society Edition; Goloboff et al. 2008). They differed in that (1) the first analysis had all characters treated as unordered, whereas (2) in the second analysis 43 multi-state characters were treated as ordered (transformational sequences). The following characters were ordered in the second analysis: 1, 7, 8, 11, 15, 27, 40, 41, 44, 45, 49, 52, 58, 60, 71, 88, 89, 93, 99, 127, 130, 136, 137, 155, 156, 158, 162, 164, 174, 187, 189, 190, 191, 192, 207, 211, 223, 229, 236, 239, 241, 242, 248. Other than the ordering of those 43 characters, the analyses were identical.

Tree-space was searched using the advanced search methods in TNT, namely sectorial search, tree fusion, ratchet and drift, 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. All characters were treated with equal weight. Character polarity was determined with reference to a pre-defined non-crocodylomorph outgroup taxon (Postosuchus kirkpatricki). Nodal support was evaluated using non-parametric bootstrapping with 1000 replicates, using tree bisection and reconnection searching.

6.2 Results

From the first (unordered) phylogenetic analysis (Figure 6), 20 most parsimonious cladograms were recovered (cladogram length = 679 steps, CI = 0.490, RI = 0.851, RC = 0.417). The topology of the strict consensus of these cladograms differs from that reported by Young et al. (2012) in the following ways:

1. The addition of MANCH J6459, which is found to be in an unresolved clade with Torvoneustes carteri and the newly added ‘Mr Etches’ specimen.’
2. The addition of the ‘Ricla crocodile’ and the recoding of Cricosaurus saltillensis make the interrelationships within the subclade Rhachiosaurini less unresolved.
3. The recoded phylogenetic scores for ‘Metriorhynchus’ brachyrhynchus give it a more derived position within Geosaurinae. Previously, it was the basal-most taxon, now it is in an unresolved position with Neptunidraco ammonitics. The South American ‘Metriorhynchus’ taxa are now the basal-most members of Geosaurinae.

Very strong support was found for the clades: Thalattosuchia (bootstrap = 97%), Machimosaurus including ‘Steneosaurus’ obtusidens (bootstrap = 94%), Notosuchidae (bootstrap = 92%), metriorhynchoids more derived than Teleidosaurus calvoaeus (bootstrap = 92%), metriorhynchoids more derived than Pelagosaurus typus (bootstrap = 90%), Dukosaurus (bootstrap = 88%), Eusuchia (bootstrap = 88%), Crocodylus (bootstrap = 87%), crown-group Crocodylia (bootstrap = 86%) and Atoposauridae (bootstrap = 81%).

There is strong-to-moderate support for the clades: Machimosaurus hugii + Machimosaurus mosai (bootstrap = 74%), Notosuchia (bootstrap = 72%), Crocodyliformes (bootstrap = 71%), Geosaurini (bootstrap = 66%), Mesoeucrocodylia (bootstrap = 64%).
Figure 6. Strict consensus of 20 most parsimonious cladograms, showing the phylogenetic relationships of MANCH J6459 within Metriorhynchoidea when all characters are unordered. Note that MANCH J6459 forms an unresolved clade with Torvoneustes carpenteri and ‘Mr Etches’ specimen’. Cladogram length = 679 steps; ensemble consistency index, CI = 0.490; ensemble retention index, RI = 0.851; rescaled consistency index, RC = 0.417. Bootstrap values are given above or below the relevant node.

Geosaurus (bootstrap = 69%), Metriorhynchus hastifer + Metriorhynchus sp. (bootstrap = 66%) and Teleosaurus + Platypterygius (bootstrap = 65%).

The second (ordered) phylogenetic analysis (Figure 7) returned 181 most parsimonious cladograms (Cladogram length = 716 steps, CI = 0.469, RI = 0.857, RC = 0.402).

Figure 7. Strict consensus of 181 most parsimonious cladograms, showing the phylogenetic relationships of MANCH J6459 within Metriorhynchoidea when 43 multi-state characters are ordered. Note that MANCH J6459 forms an unresolved clade with Torvoneustes carpenteri and ‘Mr Etches’ specimen’. Cladogram length = 717 steps; ensemble consistency index, CI = 0.469; ensemble retention index, RI = 0.857; rescaled consistency index, RC = 0.402. Bootstrap values are given above or below the relevant node.

The topology of the strict consensus of these cladograms also finds MANCH J6459 to be in an unresolved clade with Torvoneustes carpenteri and ‘Mr Etches’ specimen’. This supports the referral of this specimen to cf. Torvoneustes. The topology of the strict consensus of these cladograms is highly unresolved (Figure 6). Young
et al. (2012) also found that the ordered analysis resulted in a loss of resolution in Neosuchia and Teleosauridae. However, here the loss of resolution is not as profound, with Neosuchia still recovered and teleosaurid interrelationships are unaffected. The primary differences between the first and second phylogenetic analyses are (1) the relationships between non-thalattosuchian species become less resolved and (2) the relationships within the subclade Rhachoeosaurini are better resolved.

Very strong support was found for the clades: Thalattosuchia (bootstrap = 96%), metriorhynchoids more derived than *Teleidosaurus* (bootstrap = 94%), *Crocodylus* (bootstrap = 89%), *Dakosaurus* (bootstrap = 88%), Notosuchidae (bootstrap = 87%), Eusuchia (bootstrap = 83%) and metriorhynchoids more derived than *Pelagosaurus* (bootstrap = 81%).

There is strong-to-moderate support for the clades: Metriorhynchidae + the two indeterminate metriorhynchoid specimens (bootstrap = 79%), Atoposauridae (bootstrap = 79%), *Machimosaurus* including *Steneosaurus* *obtusidens* (bootstrap = 76%), *Geosaurus* (bootstrap = 71%), *Metriorhynchus hastifer* + *Metriorhynchus* sp. (bootstrap = 71%), crown-group Crocodylia (bootstrap = 71%), *Teleosaurus* + *Platysuchus* (bootstrap = 69%), Crocodyliformes (bootstrap = 68%), *Machimosaurus hugii* + *Machimosaurus mosae* (bootstrap = 67%), *Eoneutes* (bootstrap = 65%), *Adamantinasuchus* + *Mariliasuchus* + *Sphagosaurs* (bootstrap = 65%), Metriorhynchidae (bootstrap = 64%), *Geosaurus* (bootstrap = 62%), *Cricosaurus* (excluding the putative Cuban species, bootstrap = 60%), Notosuchia (bootstrap = 60%)

These results show that the internal relationships within Geosaurini are currently poorly understood (Figures 6, 7). However, MANCH J6459 consistently forms a clade with the ‘Mr Etches’ specimen and *Tortoneustes carpenteri*.

7. Discussion
7.1 MANCH J6459 and Geosaurini
The specimen MANCH L6459 has the following apomorphies of the metriorhynchid subclade Geosaurini: (1) the reduction in maxillary tooth count (15 or fewer maxillary and dentary alveoli) and (2) the enlargement of the alveoli and their tight packing, such that the interalveolar spaces are all uniformly narrow (Young et al. 2012).

The specimen can be excluded from the Geosaurini genus *Dakosaurus* as: (1) it lacks the aligned set of maxillary neurovascular foramina ventral to the preorbital fenestrae and (2) the dorsal margin of the skull in concave. *Dakosaurus* has this set of maxillary foramina, and the dorsal margin of the skull is convex (Pol and Gasparini 2009; Young et al. 2012). As at least seven pairs of maxillary alveoli would have been anterior to the palatines (see Figure 5), MANCH J6459 is unlikely to pertain to the genus *Plesiosuchus* (in *Plesiosuchus manselli*), the anterior midline process of the palatines extends anteriorly level to the fourth maxillary alveoli; see Young et al. 2010). Furthermore, MANCH J6459 is unlike to be a member of *Geosaurus*, as there is no evidence of a maxillary overbite (reception pits on the palatal surface of the maxillae, medial to the maxillary tooth row, created by the dentary tooth crowns). In *Geosaurus giganteus* there is a maxillary overbite along the tooth row that creates a ‘scissor-like’ occlusion mechanism (Young and Andrade 2009). In the *Geosaurus giganteus* holotype and referred skull, the overbite creates large reception pits on the lateral surface of the dentaries (created by the maxillary tooth crowns; Young and Andrade 2009; Andrade et al. 2010).

This leaves the genus *Tortoneustes*. The maxillary ornamentation pattern of MANCH J6459 matches *Tortoneustes carpenteri* and ‘Mr Etches’ specimen’: a pattern of grooves and ridges that are orientated anteroposteriorly. In *Geosaurus* the maxillae are ornamented with elliptical pits (Young and Andrade 2009), whereas in *Dakosaurus* the maxillae are ornamented with deep grooves and ridges along with numerous large elliptical pits (Young et al. 2012). Only *Plesiosuchus* shares the grooved-ridged maxillary ornamentation pattern (Young et al. 2012). However, as stated above, MANCH J6459 is unlikely to pertain to *Plesiosuchus* as it does not have the elongated palatines that are characteristic of this genus (Young et al. 2012). As the referral to *Tortoneustes* is weak, I refer to the specimen as cf. *Tortoneustes*.

7.2 The ‘Corallian Gap’
The presence of cf. *Tortoneustes* (MANCH L6459) shows that the subclade Geosaurini had already evolved by the middle Oxfordian. Members of this subclade had numerous craniodental adaptations for macrophagy (feeding on larger prey than their phylogenetic sister taxon). Unfortunately, MANCH L6459 is the only metriorhynchid skull known from the ‘Corallian Gap’. As such, when geosaurines began to dominate the Sub-Boreal marine ecosystems of Europe is unknown. However, it does show that macrophagous metriorhynchos were present by the middle Oxfordian.

Other than MANCH L6459, the only metriorhynchid specimens known from the ‘Corallian Gap’ are isolated teeth. These specimens include NHMUK PV OR36336-NHMUK PV OR36339 (from Malton in Yorkshire) and NHMUK PV OR47044 (two tooth crowns still embedded in matrix from). Lydekker (1888, p. 99) states that NHMUK PV OR47044 is from the ‘Calcareae Grit of Hedington, Oxfordshire’. As such, they were probably from the Quarry pits of Headington. There is, however,
confusion around the specimen number OR47044, as there is also a pliosaurid tooth from the Coral Rag Formation (also within the ‘Corallian Gap’) of Heddington registered under that number (L. Steel, pers. comm., 2012). Until this issue is resolved, I will forego describing these teeth.

Only by re-describing poorly preserved and little studied specimens from the ‘Corallian Gap’ of England, can we begin to understand the dramatic shift in metriorhynchid ecosystem composition in the Sub-Boreal seaways of Europe during the Jurassic. Furthermore, this will elucidate the evolution of the subclade Geosaurini and show when metriorhynchids began to occupy higher trophic levels in Jurassic marine ecosystems.

Acknowledgements

I would like to thank of David Gelthorpe of MANCH for permission to use the photographs of the specimen; and I would also like to thank Lorna Steel and Jonathan Jackson of the Natural History Museum London for preparing the photographs. I would like to thank Lorna Steel (NHMUK), Eliza Howlett (OUMNH), Steve Etches (MJML), Jeff Liston (GLAHM), Matt Lowe and Matt Riley (CAMS), Mark Evans (LEEP), Carl Mehlings (AMNH), Mike Taylor (RMS), Roger Clark (BRSMG), Glenys Wass (PETMG), Rainer Schoch (SMNS) and Manuel Riond (MGCL) for collections access and/or specimen photographs/information. Finally, I also thank Stephen Brusatte and an anonymous reviewer whose comments improved the quality of this paper.

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