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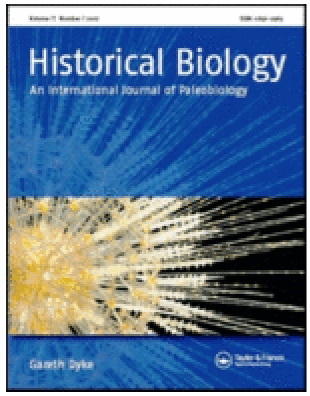

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Evidence of thalattosuchian crocodylomorphs in the Portland Stone Formation (Late Jurassic) of England, and a discussion on Cretaceous teleosauroids

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We report the first definite specimen of a thalattosuchian crocodylomorph from the Portland Stone Formation of England. This specimen (an isolated tooth crown) can be referred to the teleosauroid genus *Machimosaurus* based on its conical shape, distinctive enamel ornamentation and lack of carinae. Understanding the faunal composition of the Portland Stone Formation is key to elucidating the distinct shift in crocodylomorph taxa that occurred during the Tithonian-to-Berriasian in Europe. One of the most striking aspects of this faunal shift is the hypothesised extinction of Teleosauroidea in Europe. The presence of *Machimosaurus* in the Portland Stone Formation supports the hypothesis that the localised marine regression in Europe at the Jurassic–Cretaceous boundary, and the resultant habitat loss, contributed to the absence of teleosauroids in Europe during the Berriasian. However, the fossil record of thalattosuchians during the Cretaceous is notorious scarce. We review the purported Cretaceous record of teleosauroids, and agree that closer to the equator this clade survived for at least 20 million years after the Jurassic–Cretaceous boundary.

Keywords: Crocodylomorpha; England; Portland Stone Formation; Tithonian; Teleosauroidea

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1. Introduction

In southern England there is a distinct faunal shift in crocodylomorph taxa from the Tithonian-to-Berriasian (i.e. crossing the Jurassic–Cretaceous boundary). During the Tithonian, pelagic metriorhynchid thalattosuchians are overwhelmingly the most abundant component of the crocodylomorph fauna, with teleosauroid thalattosuchians being a rare component (see Young and Steel in press for a recent overview). By the Berriasian, the crocodylomorph fauna of southern England is significantly different, being composed of the neosuchian genera *Theriosuchus*, *Goniopholis* and *Pholidosaurus* (e.g. Benton and Spencer 1995; Salisbury 2002; Andrade et al. 2011; Tennant et al. 2016). However, the falling sea levels in Europe across the Tithonian-Berriasian (Hallam, 1988, 2001) is most likely the cause of this shift, especially as *Theriosuchus* and *Goniopholis* are known from freshwater Jurassic strata in Europe (e.g. Schwarz 2002; Young et al. 2016), with pholidosaurids also known from the Jurassic (Fortier et al. 2011). Moreover, metriorhynchid biodiversity peaks coincide with high sea levels and the greater number of shallow marine formations, and biodiversity troughs coincide with low sea levels and lower numbers of shallow marine formations (Young, 2009; Young et al. 2010).

However, when this regionalised shift occurred is still not understood. This is because the late Tithonian thalattosuchian fossil record is exceptionally poor, restricted to the exceptional fossils from Argentina (e.g. Gasparini et al. 2006; Fernández et al. 2019). In England, thalattosuchian fossils from the Tithonian are exclusively ~~come~~ known from the

Kimmeridge Clay Formation (e.g. Benton and Spencer 1995; Young and Steel in press). The crocodylomorph fauna from geological younger strata, such as the Portland Stone Formation, are unknown. Here we begin to rectify this issue by describing an incomplete tooth crown from the Portland Stone Formation of the Isle of Portland, which we assign to the teleosauroid genus *Machimosaurus*.

1.1 Institutional Abbreviation

MB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany;. **MNHN,** Muséum national d'Histoire naturelle, Paris, France.

2. Systematic Palaeontology

Crocodylomorpha Hay, 1930 (*sensu* Nesbitt, 2011)

Thalattosuchia Fraas, 1901 (*sensu* Young and Andrade, 2009)

Teleosauroidea Geoffroy Saint-Hilaire, 1831 (*sensu* Young and Andrade, 2009)

Machimosaurus von Meyer, 1837 (emendation von Meyer, 1838)

Type species

Machimosaurus hugii von Meyer, 1837

Machimosaurus sp.

(Figure 1)

Specimen

MB.R.4059, an incomplete isolated tooth crown.

Locality

Isle of Portland, Dorset, England, United Kingdom.

Horizon

Portland Stone Formation, Portland Group. Tithonian, Upper Jurassic.

3. Description

The tooth appears to have been broken in three places, first near the root-crown junction, second along its apicobasal axis, and finally in the apical region. Thus, the tooth does not preserve the root, at least one third of the crown in the basal-and-mid regions, and the entire apical region (Fig. 1). From what is preserved, the tooth crown would have had a conical shape, with slight mediolateral compression. The preserved external surface shows a slight curvature towards the apex. In *Machimosaurus* teeth this slight curvature occurs on the labial surface (Krebs 1967; Hua 1999; Lepage et al. 2008; Young et al. 2014a, 2014b). As such, the lingual surface is largely missing. Unfortunately, we cannot orientate the tooth mesially and distally.

Mesial and distal carinae are absent in MB.R.4059. Although the tooth crown is incomplete (Fig. 1), the carinae should still be visible as most of the crown is preserved. The presence, and morphology, of carinae is variable in *Machimosaurus*, ranging from being readily identifiable, being hard to distinguish from the superficial enamel ornamentation, to being completely absent (see Krebs 1967; Young et al. 2014b).

The preserved external surfaces of the enamel are covered by superficial ornamentation. It is composed of numerous, tightly packed apicobasally aligned ridges that are (sub)-parallel to one another. Most are continuous from the basal region to the preserved apical-most region, although shorter ridges are also present. As the apex is missing, the anticipated shift in enamel ornamentation to an anastomosed pattern cannot be seen.

4. Discussion

4.1 Referral of MB.R.4059 to Machimosaurus

The isolated tooth crown described herein has a suite of morphological characteristics that are only known in two genera of thalattosuchians, the teleosauroid *Machimosaurus* and the metriorhynchid *Torvoneustes* (von Meyer 1837; Krebs 1967; Hua 1999; Lepage et al. 2008; Andrade et al. 2010; Barrientos-Lara et al. 2016; Young et al. 2013, 2014a, 2014b):

1. Tooth crowns that are largely conical (poor mediolateral compression) - although this is variable between species in these genera, and across the tooth-row (for *Torvoneustes* see Barrientos-Lara et al. 2016).
2. Basal third to four-fifths of the tooth crown have numerous and tightly-packed apicobasally aligned enamel ridges that are (sub)parallel to one another, with most being continuous from the base to the apical region.

Based on this character suite we can safely refer MB.R.4059 to either *Machimosaurus* or *Torvoneustes*. We can exclude this tooth from *Torvoneustes* due to the lack of carinae. The dentition of *Torvoneustes* have strongly developed mesiodistal carinae (Andrade et al. 2010; Young et al. 2013; Barrientos-Lara et al. 2016), whereas in *Machimosaurus* the presence of carinae is variable across the tooth-row, including tooth crowns lacking carinae (Young et al. 2014a, 2014b).

These morphological features are characteristic of the 'crunch guild' of Massare (1987). As shown by Foffa et al. (2018), other Late Jurassic marine reptile groups from the Sub-Boreal seaway did not convergently evolve this character suite. Morphologically, the closest to these 'crunch guild' teeth, are those of the 'smash guild', occupied by ichthyosaurs. However, plicidentine enamel is considered an apomorphy of Ichthyosauria (Maxwell et al., 2011), a unique enamel ornamentation arrangement composed of apicobasal ridges interspaced with furrows.

4.2 Cretaceous teleosauroids

The thalattosuchian fossil record in the Cretaceous is notoriously poor, especially for teleosauroids. Young et al. (2014a) revised the genus *Machimosaurus* and found there to be no conclusive evidence of *Machimosaurus*, and thus teleosauroids, to be present in the Cretaceous. Fanti et al. (2016) described a new species from Tunisia, *Machimosaurus rex* Fanti et al. 2016, which they considered to be from the Early Cretaceous. While Fanti et al. (2016) considered *M. rex* to be from the Hauterivian, the age of *M. rex* is far from certain (see Martin et al. 2018; Cortes et al. in press). The possibility that the *M. rex* holotype is Tithonian in age cannot be discounted (M. Johnson pers. comm. 2019). Thus, *M. rex* cannot be taken as definitive evidence for the survival of teleosauroids into the Cretaceous.

An incomplete fossil from late Barremian strata of Colombia was recently referred to Teleosauroidea (Cortes et al. in press). Unfortunately, no apomorphic characters were used to make this determination, with mesoeucrocodylian symplesiomorphies being used to justify the identification (e.g. hourglass-shaped amphiplatyan dorsal vertebral centra and osteoderms that are noticeably rectangular in shape). This is understandable, given that the specimen consists of dorsal vertebrae and ribs, dorsal and ventral trunk osteoderms, and epipodial elements preserved in matrix. Alas, the possibility of a pholidosaurid identification was not discussed. This is unfortunate as the large-bodied pholidosaurid *Sarcosuchus hartti* (Marsh, 1869) is known from the late Hauterivian-early Barremian of Brazil (Souza et al. 2019). Moreover, Cortes et al. (in press) estimated the body length of the Colombian specimen to be

9.6m (with 95% confidence internal of 7.6m – 13.4m), this size is more consistent with *Sarcosuchus* Broin & Taquet 1966 (O'Brien et al. 2019) than a teleosauroid (Young et al. 2016). However, the measurements of the dorsal osteoderms and their dorsal ornamentation are more consistent with a teleosauroid than a pholidosaurid. The shape of the dorsal vertebrae are also more reminiscent of a teleosauroid than *Sarcosuchus* (examining the *Sarcosuchus imperator* Broin & Taquet 1966 display skeleton in the MNHN), given their proportionally long centra.

Despite the short comings of the description and comparisons in Cortes *et al*. (in press), the taxonomic identification does appear to be correct. It yields an approximate 20 million-year gap between the Colombian indeterminate specimen and the late Tithonian *Machimosaurus* tooth described herein (MB.R.4059). Prior to the description of the MB.R.4059, the youngest definitive teleosauroids were from the early Tithonian of Europe, including *Aeolodon priscus* (von Sömmerring, 1814) and *Machimosaurus hugii* von Meyer (1837) (see Young et al. 2014a; Foffa et al. 2019; Young & Steel in press).

More diagnostic remains, and remains that have better age constraint, are needed before any definitive statements can be made regarding Cretaceous teleosauroids. However, closer to the equator it does appear that teleosauroids survived far longer than previously supposed, and grew to lengths rivalling even the largest Cretaceous neosuchians.

4.~~2~~3 Late Tithonian thalattosuchians in Europe

With the description of MB.R.4059, we have the first late Tithonian thalattosuchian known from Europe. Given the incredible diversity of European thalattosuchians in the early Tithonian (in particular metriorhynchids), it is highly likely that other fossils attributable to Thalattosuchia are currently in museum collections waiting to be described. We hope this paper will spur further investigation into these collections, as until more fossils are discovered and described, we cannot elucidate the dramatic shift in the crocodylomorph biota across the Jurassic-Cretaceous boundary.

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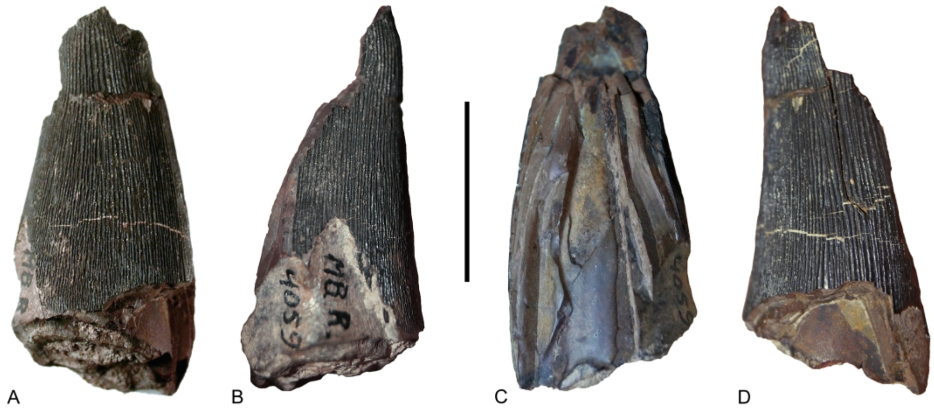
FIGURE CAPTION

Figure 1. *Machimosaurus* sp. MB.R.4059. Isolated tooth crown. A, lingual view, B, lingual view rotated towards basal cracked region, C, preserved labial view, and D, lingual view rotated away from basal cracked region. Scale bar is two centimetres.



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