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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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Manuscripts

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3 **Evidence of thalattosuchian crocodylomorphs in the Portland Stone Formation (Late**
4 **Jurassic) of England, and a discussion on Cretaceous teleosauroids**
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10 MARK T. YOUNG^{1*}, ~~and SVEN SACHS², and PASCAL ABEL³~~
11
12
13

14 ¹ School of GeoSciences, Grant Institute, The King's Buildings, University of Edinburgh, James
15 Hutton Road, Edinburgh, EH9 3FE, United Kingdom
16
17

18 ² Naturkunde-Museum Bielefeld, Abteilung Geowissenschaften, Adenauerplatz 2, 33602 Bielefeld,
19 Germany
20
21

22 ³ ~~Senckenberg Centre for Human Evolution and Palaeoenvironment, Eberhard-Karls-University~~
23 ~~Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany~~
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30 We report the first definite specimen of a thalattosuchian crocodylomorph from the Portland
31 Stone Formation of England. This specimen (an isolated tooth crown) can be referred to the
32 teleosauroid genus *Machimosaurus* based on its conical shape, distinctive enamel
33 ornamentation and lack of carinae. Understanding the faunal composition of the Portland
34 Stone Formation is key to elucidating the distinct shift in crocodylomorph taxa that occurred
35 during the Tithonian-to-Berriasian in Europe. One of the most striking aspects of this faunal
36 shift is the hypothesised extinction of Teleosauroidea in Europe. The presence of
37 *Machimosaurus* in the Portland Stone Formation supports the hypothesis that the localised
38 marine regression in Europe at the Jurassic–Cretaceous boundary, and the resultant habitat
39 loss, contributed to the absence of teleosauroids in Europe during the Berriasian. However,
40 the fossil record of thalattosuchians during the Cretaceous is notorious scarce. We review the
41 purported Cretaceous record of teleosauroids, and agree that closer to the equator this clade
42 survived for at least 20 million years after the Jurassic–Cretaceous boundary.
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3 **Keywords:** Crocodylomorpha; England; Portland Stone Formation; Tithonian;
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5 Teleosauroidea
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10 * **Corresponding author.** Email: marktyoung1984@gmail.com
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14 **1. Introduction**

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16 In southern England there is a distinct faunal shift in crocodylomorph taxa from the
17 Tithonian-to-Berriasian (i.e. crossing the Jurassic–Cretaceous boundary). During the
18 Tithonian, pelagic metriorhynchid thalattosuchians are overwhelmingly the most abundant
19 component of the crocodylomorph fauna, with teleosauroid thalattosuchians being a rare
20 component (see Young and Steel in press for a recent overview). By the Berriasian, the
21 crocodylomorph fauna of southern England is significantly different, being composed of the
22 neosuchian genera *Theriosuchus*, *Goniopholis* and *Pholidosaurus* (e.g. Benton and Spencer
23 1995; Salisbury 2002; Andrade et al. 2011; Tennant et al. 2016). However, the falling sea
24 levels in Europe across the Tithonian-Berriasian (Hallam, 1988, 2001) is most likely the
25 cause of this shift, especially as *Theriosuchus* and *Goniopholis* are known from freshwater
26 Jurassic strata in Europe (e.g. Schwarz 2002; Young et al. 2016), with pholidosaurids also
27 known from the Jurassic (Fortier et al. 2011). Moreover, metriorhynchid biodiversity peaks
28 coincide with high sea levels and the greater number of shallow marine formations, and
29 biodiversity troughs coincide with low sea levels and lower numbers of shallow marine
30 formations (Young, 2009; Young et al. 2010).
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51 However, when this regionalised shift occurred is still not understood. This is because
52 the late Tithonian thalattosuchian fossil record is exceptionally poor, restricted to the
53 exceptional fossils from Argentina (e.g. Gasparini et al. 2006; [Fernández et al. 2019](#)). In
54 England, thalattosuchian fossils from the Tithonian are exclusively come-known from the
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3 Kimmeridge Clay Formation (e.g. Benton and Spencer 1995; Young and Steel in press). The
4 crocodylomorph fauna from geological younger strata, such as the Portland Stone Formation,
5
6 are unknown. Here we begin to rectify this issue by describing an incomplete tooth crown
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8 from the Portland Stone Formation of the Isle of Portland, which we assign to the
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10 teleosauroid genus *Machimosaurus*.
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17 **1.1 Institutional Abbreviation**

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19 **MB**, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; [MNHN](#),
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21 [Muséum national d'Histoire naturelle, Paris, France](#).
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26 **2. Systematic Palaeontology**

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

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

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

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

38 39 40 41 42 **Type species**

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44 *Machimosaurus hugii* von Meyer, 1837

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49 *Machimosaurus* sp.

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51 (Figure 1)

52 53 54 55 56 **Specimen**

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

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3 apical-most region, although shorter ridges are also present. As the apex is missing, the
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5 anticipated shift in enamel ornamentation to an anastomosed pattern cannot be seen.
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10 **4. Discussion**

11 **4.1 Referral of MB.R.4059 to *Machimosaurus***

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13 The isolated tooth crown described herein has a suite of morphological characteristics that are
14
15 only known in two genera of thalattosuchians, the teleosauroid *Machimosaurus* and the
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17 metriorhynchid *Torvoneustes* (von Meyer 1837; Krebs 1967; Hua 1999; Lepage et al. 2008;
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19 Andrade et al. 2010; Barrientos-Lara et al. 2016; Young et al. 2013, 2014a, 2014b):
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- 23
24 1. Tooth crowns that are largely conical (poor mediolateral compression) - although this
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26 is variable between species in these genera, and across the tooth-row (for
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28 *Torvoneustes* see Barrientos-Lara et al. 2016).
- 29
30 2. Basal third to four-fifths of the tooth crown have numerous and tightly-packed
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32 apicobasally aligned enamel ridges that are (sub)parallel to one another, with most
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34 being continuous from the base to the apical region.
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41 Based on this character suite we can safely refer MB.R.4059 to either *Machimosaurus*
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43 or *Torvoneustes*. We can exclude this tooth from *Torvoneustes* due to the lack of carinae. The
44
45 dentition of *Torvoneustes* have strongly developed mesiodistal carinae (Andrade et al. 2010;
46
47 Young et al. 2013; Barrientos-Lara et al. 2016), whereas in *Machimosaurus* the presence of
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49 carinae is variable across the tooth-row, including tooth crowns lacking carinae (Young et al.
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51 2014a, 2014b).
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54 These morphological features are characteristic of the ‘crunch guild’ of Massare
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56 (1987). As shown by Foffa et al. (2018), other Late Jurassic marine reptile groups from the
57
58 Sub-Boreal seaway did not convergently evolve this character suite. Morphologically, the
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3 closest to these ‘crunch guild’ teeth, are those of the ‘smash guild’, occupied by ichthyosaurs.
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5 However, plicidentine enamel is considered an apomorphy of Ichthyosauria (Maxwell et al.,
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7 2011), a unique enamel ornamentation arrangement composed of apicobasal ridges
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9 interspaced with furrows.
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12 13 14 15 **4.2 Cretaceous teleosauroids**

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17 The thalattosuchian fossil record in the Cretaceous is notoriously poor, especially for
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19 teleosauroids. Young et al. (2014a) revised the genus *Machimosaurus* and found there to be
20
21 no conclusive evidence of *Machimosaurus*, and thus teleosauroids, to be present in the
22
23 Cretaceous. Fanti et al. (2016) described a new species from Tunisia, *Machimosaurus rex*
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25 Fanti et al. 2016, which they considered to be from the Early Cretaceous. While Fanti et al.
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27 (2016) considered *M. rex* to be from the Hauterivian, the age of *M. rex* is far from certain (see
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29 Martin et al. 2018; Cortes et al. in press). The possibility that the *M. rex* holotype is Tithonian
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31 in age cannot be discounted (M. Johnson pers. comm. 2019). Thus, *M. rex* cannot be taken as
32
33 definitive evidence for the survival of teleosauroids into the Cretaceous.
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37 _____ An incomplete fossil from late Barremian strata of Colombia was recently referred to
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39 Teleosauroidea (Cortes et al. in press). Unfortunately, no apomorphic characters were used to
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41 make this determination, with mesoeucrocodylian symplesiomorphies being used to justify
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43 the identification (e.g. hourglass-shaped amphiplatyan dorsal vertebral centra and osteoderms
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45 that are noticeably rectangular in shape). This is understandable, given that the specimen
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47 consists of dorsal vertebrae and ribs, dorsal and ventral trunk osteoderms, and epipodial
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49 elements preserved in matrix. Alas, the possibility of a pholidosaurid identification was not
50
51 discussed. This is unfortunate as the large-bodied pholidosaurid *Sarcosuchus hartti* (Marsh,
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53 1869) is known from the late Hauterivian-early Barremian of Brazil (Souza et al. 2019).
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55 Moreover, Cortes et al. (in press) estimated the body length of the Colombian specimen to be
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3 9.6m (with 95% confidence interval of 7.6m – 13.4m), this size is more consistent with
4 *Sarcosuchus* Broin & Taquet 1966 (O'Brien et al. 2019) than a teleosauroid (Young et al.
5 2016). However, the measurements of the dorsal osteoderms and their dorsal ornamentation
6 are more consistent with a teleosauroid than a pholidosaurid. The shape of the dorsal
7 vertebrae are also more reminiscent of a teleosauroid than *Sarcosuchus* (examining the
8 *Sarcosuchus imperator* Broin & Taquet 1966 display skeleton in the MNHN), given their
9 proportionally long centra.

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19 Despite the shortcomings of the description and comparisons in Cortes *et al.* (in
20 press), the taxonomic identification does appear to be correct. It yields an approximate 20
21 million-year gap between the Colombian indeterminate specimen and the late Tithonian
22 *Machimosaurus* tooth described herein (MB.R.4059). Prior to the description of the
23 MB.R.4059, the youngest definitive teleosauroids were from the early Tithonian of Europe,
24 including *Aeolodon priscus* (von Sömmerring, 1814) and *Machimosaurus hugii* von Meyer
25 (1837) (see Young et al. 2014a; Foffa et al. 2019; Young & Steel in press).

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

4.23 *Late Tithonian thalattosuchians in Europe*

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49 With the description of MB.R.4059, we have the first late Tithonian thalattosuchian known
50 from Europe. Given the incredible diversity of European thalattosuchians in the early
51 Tithonian (in particular metriorhynchids), it is highly likely that other fossils attributable to
52 Thalattosuchia are currently in museum collections waiting to be described. We hope this
53 paper will spur further investigation into these collections, as until more fossils are
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3 discovered and described, we cannot elucidate the dramatic shift in the crocodylomorph biota
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5 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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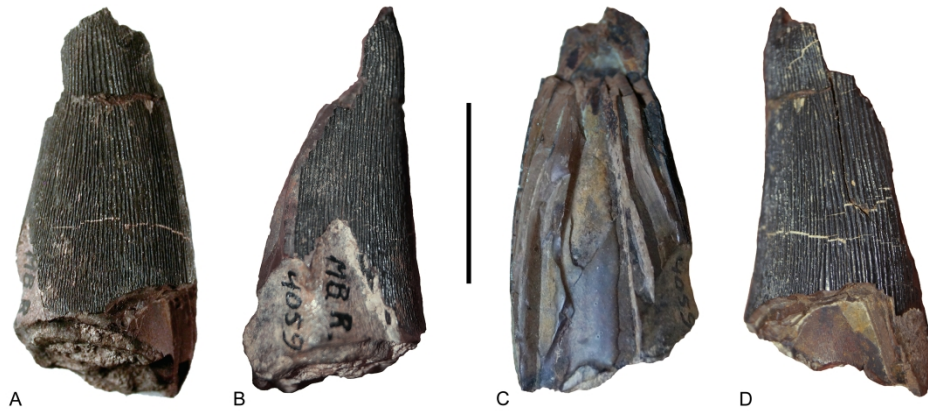


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184x79mm (600 x 600 DPI)