A revision of the deep-water teleosauroid crocodylomorph *Teleosaurus megarhinus* Hulke, 1871 from the Kimmeridge Clay Formation (Late Jurassic) of England, UK (#25493)

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A revision of the deep-water teleosauroid crocodylomorph *Teleosaurus megarhinus* Hulke, 1871 from the Kimmeridge Clay Formation (Late Jurassic) of England, UK

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Teleosauroids were a successful group of semi-aquatic crocodylomorphs that were an integral part of coastal marine/lagoonal faunas during the Jurassic. Their fossil record suggests that the group declined in diversity and abundance in deep water deposits during the Late Jurassic. One of the few known teleosauroid species from the deeper water horizons of the Kimmeridge Clay Formation is '*Teleosaurus*' *megarhinus* (Hulke, 1871), a poorly studied, gracile longirostrine form. The holotype is an incomplete snout from the *Aulacostephanus autissodorensis* Sub-Boreal ammonite Zone of Kimmeridge, England. The only other referred specimen is an almost complete skull from the slightly older *A. eudoxus* Sub-Boreal ammonite Zone of Quercy, France (unfortunately the whereabouts of this specimen is unknown). Recently, the validity of the species has been called into question. Here we describe an incomplete teleosauroid, DORCM G.05067i-v, (an anterior rostrum with three osteoderms and an isolated tooth crown) from the same horizon and locality as the holotype. We demonstrate that DORCM G.05067i-v is referable to '*Teleosaurus*' *megarhinus*, that the species is indeed a valid taxon, and establish a new monotypic genus, *Bathysuchus*. *Bathysuchus megarhinus* comb. nov. has a unique combination of characters: strongly ventrally deflected anterior margin of the premaxilla; five premaxillary alveoli, the posterior-most being considerably reduced in size; anterodorsally oriented external nares; conical teeth bearing carinae that are only visible on the apical third of the crown. In our novel phylogenetic analysis, *Bathysuchus megarhinus* is found to be in a subclade containing *Mycterosuchus nasutus* and *Teleosaurus cadomensis*. Based on the reduction in dermatocranial and osteoderm ornamentation we hypothesise that *B. megarhinus* was one of the few teleosauroids beginning to evolve a more pelagic lifestyle. The reduction in ornamentation is mirrored in *Aeolodon priscus*, a species with a well-preserved post-cranial skeleton and has a similar low level of ornamentation.

A REVISION OF THE DEEP-WATER TELEOSAUROID CROCODYLOMORPH *TELEOSAURUS MEGARHINUS* HULKE, 1871 FROM THE KIMMERIDGE CLAY FORMATION (LATE JURASSIC) OF ENGLAND, UK

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Key words: Crocodylomorpha, Kimmeridgian, Teleosauroidea, UK

ABSTRACT

Teleosauroids were a successful group of semi-aquatic crocodylomorphs that were an integral part of coastal marine/lagoonal faunas during the Jurassic. Their fossil record suggests that the group declined in diversity and abundance in deep water deposits during the Late Jurassic. One of the few known teleosauroid species from the deeper water horizons of the Kimmeridge Clay Formation is '*Teleosaurus*' *megarhinus* (Hulke, 1871), a poorly studied, gracile longirostrine form. The holotype is an incomplete snout from the *Aulacostephanus autissodorensis* Sub-Boreal ammonite Zone of Kimmeridge, England. The only other referred specimen is an almost complete skull from the slightly older *A. eudoxus* Sub-Boreal ammonite Zone of Quercy, France (unfortunately the whereabouts of this specimen is unknown). Recently, the validity of the species has been called into question. Here we describe an incomplete teleosauroid, DORCM G.05067i-v, (an anterior rostrum with three osteoderms and an isolated tooth crown) from the same horizon and locality as the holotype. We demonstrate that DORCM G.05067i-v is referable to '*Teleosaurus*' *megarhinus*, that the species is indeed a valid taxon, and establish a new monotypic genus, *Bathysuchus*. *Bathysuchus megarhinus* comb. nov. has a unique combination of characters: strongly ventrally deflected anterior margin of the premaxilla; five premaxillary alveoli, the posterior-most being considerably reduced in size; anterodorsally oriented external nares; conical teeth bearing carinae that are only visible on the apical third of the crown. In our novel phylogenetic analysis, *Bathysuchus megarhinus* is found to be in a subclade containing *Mycterosuchus nasutus* and *Teleosaurus cadomensis*. Based on the reduction in dermatocranial and osteoderm ornamentation we hypothesise that *B. megarhinus* was one of the few teleosauroids beginning to evolve a more pelagic lifestyle. The reduction in ornamentation is

mirrored in *Aeolodon priscus*, a species with a well-preserved post-cranial skeleton and has a similar low level of ornamentation.

INTRODUCTION

Teleosauroid thalattosuchians were a successful group of semi-aquatic Jurassic crocodylomorphs that were an abundant part of marine/lagoonal faunas for most of the Jurassic to the Early Cretaceous of Europe, Asia and Africa (Andrews 1909; Andrews 1913; Buffetaut et al. 1981; Lepage et al. 2008; Young et al. 2016; Fanti et al. 2016; Jouve et al. 2016; Johnson et al. 2018). Teleosauroids underwent a severe decline across the Middle-Late Jurassic boundary at Sub-Boreal and Boreal latitudes, but in remained numerically and taxonomically abundant in the Late Jurassic of the Tethys and continental Europe (Young et al. 2014a, 2014b; Foffa et al. 2015; Johnson et al. 2015; Johnson et al. 2017).

The teleosauroid fossil record is particularly scarce in the Late Jurassic Kimmeridge Clay Formation (KCF; Kimmeridgian-Tithonian, ~157-148 Ma) of the UK (Young and Steel 2014) where rare fossilised remains are almost exclusively limited to isolated tooth crowns (NHMUK PV R 1774) and osteoderms (MJML K2158 and BRSMG Ce9826; CAMSM J.29481; OUMNH J.77970-1) (Seeley 1869; Young and Steel, 2014; Foffa et al. *in press*). The only exceptions are the cranial remains of an enigmatic longirostrine teleosauroid, *'Teleosaurus' megarhinus* from the deep-water deposits of the Kimmeridgian of Dorset (Hulke 1871; Delair 1958; Vignaud et al. 1993). Thus, this species is vital to understand not only the systematics of Teleosauroidea, but also their palaebiogeography and ecology, in particular those teleosauroids that adapted to living in deep-water environments.

Herein we describe a new specimen of *'Teleosaurus' megarhinus* (DORCM G.05067i- v) that reveals new information on this enigmatic taxon. The revision of the new and already available material revealed a unique combination of characters that validates the species, and helps defines a new genus. With the aid of an updated and expanded teleosauroid phylogenetic dataset we are able to test the relationships of this new taxon within Teleosauroidea.

Historical background

The holotype of *Teleosaurus megarhinus* (NHMUK PV OR 43086) was discovered in the winter of 1870 in the Kimmeridge Clay Formation strata at Kimmeridge Bay (Dorset). J.C. Mansel sent the specimen to J.W. Hulke to be described (Hulke 1871; Delair 1958). After comparisons with other specimens, Hulke assigned the specimen to *Teleosaurus* (without supporting the decision) and proposed the specific designation *megarhinus* based on the 'dilation of the terminal nostril' that he remarked as 'greater than in any other *Teleosaurus* known to me' (sic Hulke, 1871, pp. 442). Lydekker (1888) later referred the species to the genus *Steneosaurus*.

A skull from near Quercy (France) was referred to '*Steneosaurus*' cf. *megarhinus* based on premaxillary and maxillary tooth count, and stratigraphic occurrence (Vignaud et al., 1993). Vignaud et al. (1993) also compared '*S.*' *megarhinus* with other longirostrine teleosauroids from the Late Jurassic of Europe (*Steneosaurus deslongchampsianus* and *Aeolodon priscus*), and considered '*S.*' *megarhinus* to be a valid taxon, but they could only find tooth counts as being able to differentiate the three species. Vignaud (1997) noticed differences in the dentition (tooth count and crown shape proportions) between *Steneosaurus leedsi* Andrews, 1909, and '*S.*' *megarhinus*.

Curiously, Pierce et al. (2009) hypothesised that '*Steneosaurus*' *megarhinus* was a synonym of *Steneosaurus leedsi*. Although, under the rules of the ICZN Code this would have resulted in '*S.*' *megarhinus* being the senior subjective synonym not *S. leedsi* (contra Pierce et al., 2009 that had *S. leedsi* as the senior synonym). It would also create a species that lasted for approximately 12 million years, and was morphologically distinct at both chronostratigraphic termini. However, the teleosauroid species diagnoses of Pierce et al. (2009) have been criticised as being diagnostic only to the generic level or use characters that describe all teleosauroids (Martin & Vincent 2013, p. 194). Contra Pierce et al. (2009, p. 1067), we cannot find any mention of Oxfordian specimens referred to '*S.*' *megarhinus*, by Vignaud (1995) or anyone else.

The validity problem of '*S.*' *megarhinus* is due to the use of overall upper jaw tooth count as the sole means to differentiate the taxon from other teleosauroids (e.g. Vignaud et al. 1993; Pierce et al. 2009). The characteristic shape of the premaxilla, the extreme lateral expansion of the premaxilla, the arrangement of the premaxilla alveoli, and number of premaxillary alveoli are not mentioned. Thus, it is not surprising that the validity of the species has been questioned.

Few phylogenetic analyses have included '*S.*' *megarhinus*. The first to include the species recovered '*S.*' *megarhinus* as the sister taxon to *Teleosaurus cadomensis* Lamouroux, 1820, this was based on prefrontal characters (Mueller-Töwe 2006). The supertree analysis of Bronzati et al. (2012) considered *'S.' megarhinus* as valid, and found it sister taxon to *Teleosaurus cadomensis*. Subsequently, the validity and systematics of '*Teleosaurus*' *megarhinus* have not been investigated. Moreover, as this taxon has rarely been included in phylogenetic analyses, we do not know which radiation of teleosauroids migrated into deep water ecosystems in the Late Jurassic.

Institutional abbreviations— **BHN,** Musée-sur-Mer, Boulogne, France (closed over a decade ago); **BRSMG,** Bristol Museum and Art Gallery, Bristol, England, UK; **CAMSM,** Sedgwick Museum, Cambridge, England, UK; **DORCM**, Dorset County Museum, Dorchester, England, UK; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MJML**, Museum of Jurassic Marine Life – the Steve Etches Collection, Kimmeridge, England, UK; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **MNHNL**, Muséum national d'Histoire naturelle Luxembourg, Luxembourg City, Luxembourg; **NHMUK PV**, vertebrate palaeontology collection of the Natural History Museum, London, UK (OR, old register; R, reptiles); **NHMW**, Naturhistorisches Museum Wien, Vienna, Austria; **OUMNH**, Oxford University Museum of Natural History, Oxford, England, UK; **PN**, collection number for Palaeontological Research and Education Centre, Maha Sarakham University, Thailand; **PRC**, Palaeontological Research and Education Centre, Maha Sarakham University, Thailand; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Baden-Württemberg, Germany

GEOLOGICAL SETTING AND PALEOENVIRONMENT

Both NHMUK OR 43086 and DORCM G.05067i-v were found in same locality Kimmeridge Bay (Dorset, England UK) of the Kimmeridge Clay Formation (Fig. 1) (KCF; Kimmeridgian-Tithonian, ~157-148 Ma). In England the KCF continuously outcrops onshore from Dorset to Yorkshire, and continue offshore as one of the main source rock for the North Sea oil industry. Other important KCF localities in the UK are in Scotland on the west shores of the Isle of Skye (Inner Hebrides) and southern Sutherland. The KCF comprises a succession of silicoclastic marine deposits dominated by calcareous organic-rich mudstones, claystones, and siltsones, frequently intercalated with oil-rich shales, and concetional horizons (Cox and Gallois 1981; Gallois 2004). The KCF is traditionally subdivided into Lower KCF (*Pictonia baylei* to *Aulacostephanus autissodorensis* ammonite Zone – Kimmeridgian) and Upper KCF (*Pectinates elegans* to *Virgapavlovia fittoni* ammonite Zones – early Tithonian). The KCF is part of the Ancholme Group that spanning the Middle-Late Jurassic offers a continuous lithostratigraphic and fossil record of an epicontinental sea (Jurassic Sub-Boreal Seaway) that covered large part of the British Isles at that time. The KCF is part of a long term transgressive cycle that started in the middle Oxfordian following a regression phase in the Callovian-early Oxfordian (Coe 1992; Coe 1995; Cox 2001; Gallois 2004; Weedon et al 2004). The Kimmeridgian strata of the KCF record a deepening phase of the Jurassic Sub-Boreal Seaway, during a period of high global sea levels (Cox 2001). The KCF strata at Kimmeridge Bay spans the middle part of the Kimmeridgian stage (*Aulacostephanus eudoxus* to *Pectninatites wheatleyensis* ammonite Subzones). Thus, this section likely represents the deepest basin (outer-shelf environment, water depth of 150-200 m) (Gallois 2004) where teleosauroid fossils have been found (see Discussion).

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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)

BATHYSUCHUS, gen. nov. (Figs 2–4)

ZooBank Life Science Identifier (LSID) for genus: urn:lsid:zoobank.org:act: [To be added upon acceptance]

Type Species— *Bathysuchus megarhinus* gen. et comb. nov. (type by monotypy).

Etymology— Meaning deep water crocodile ‘βαθύς (*bathus*)’ is Ancient Greek for ‘deep’, and - ‘σοῦχος (*soûkhos*)’ is Ancient Greek for crocodile

Diagnosis— Same as for the only known species (type by monotypy).

BATHYSUCHUS MEGARHINUS, gen. et comb. nov.

v**1871* *Teleosaurus megarhinus* nov. sp.; Hulke, p. 442-443, pl. 18, fig.1-3

v *1872* *Steneosaurus morinicus* (sic) nov. sp.; Sauvage, p. 180

v *1874* *Steneosaurus morinicus* Sauvage; Sauvage, p. 38-40

v *1888* *Steneosaurus megarhinus* (Hulke, 1871) – Lydekker, p. 117

v *1936* *Steneosaurus megarhinus* (Hulke, 1871) – Kuhn, p. 39

v *1936* *Steneosaurus morinicus* Sauvage 1874 – Kuhn, p. 33

v *1958* *Teleosaurus megarhinus* Hulke, 1871 – Delair, p. 57

v *1973* *Steneosaurus megarhinus* (Hulke, 1871) – Steel, p. 33

v *1973* *Steneosaurus morinicus* Sauvage 1874 – Steel, p. 32

v *1986* *Steneosaurus morinicus* Sauvage 1874 – Buffetaut et al., p. 80-81

v 1993 *Steneosaurus* cf. *megarhinus* (Hulke, 1871) – Vignaud et al., p.1509-1514, fig.2

v *2006* *Steneosaurus megarhinus* (Hulke, 1871) – Mueller-Töwe

v *2009* *Steneosaurus leedsi* (Andrews, 1909) – Pierce et al.

v *2012* *Steneosaurus megarhinus* (Hulke, 1871) – Bronzati et al.

ZooBank Life Science Identifier (LSID) for species: urn:lsid:zoobank.org:act: [To be added upon acceptance]

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Holotype— The specimen NHMUK PV OR 43086 is an incomplete and severely diagenetically damaged and partially reconstructed snout (including fragments of maxilla, and premaxillae).

Referred specimens— DORCM G.05067i-v is an incomplete snout (i), including most of the premaxillae and limited portion of the anterior part of maxillae, that was found in the same locality and horizon of the type species. Three well preserved osteoderms (ii-iv) and a complete tooth (v) were also found associated.

Another specimen from Francoulès, Quercy area, France (*A. eudoxus* ammonite Zone) was referred to *'Steneosaurs'* cf. *megarhinus*. This specimen is a diagenetically damaged skull consisting of parts of the snout and post orbital region. Only the anterior part of the mandibular symphysis is preserved. This specimen is perhaps a juvenile (Vignaud et al. 1993). Unfortunately, this cannot be verified because the whereabouts of this specimen is currently unknown. BHN 2R 95, a mandibular symphysis (holotype of *Steneosaurus morinicus* in Sauvage, 1872) – according to Vignaud (1995) is the same taxon as Quercy specimen.

Type locality— Kimmeridge Bay, Dorset, England, United Kingdom.

Type horizon— *A. autissodorensis* ammonite Zone, Kimmeridge Clay Formation.

Diagnosis— Longirostine teleosauroid crocodylomorph with the following unique combination of characters (autapomorphic characters are indicated by an asterisk): the premaxillae have five alveoli (shared with *Platysuchus multiscrobiculatus* Berckhemer, 1929, *Teleosaurus cadomensis*); the P1 and P2 alveoli do not form a couplet, but are still oriented to the anterior margin of the premaxilla* (*Machimosaurus* has an analogous character, but caused by the reduction in premaxillary tooth count to three, in that genus the P2 and P3 alveoli are oriented to the lateral margin of the premaxilla); in dorsal view the external nares has an ‘8’ shaped external nares, created by the enlarged anterior and posterior processes of the premaxilla*; the external nares are anteriorly oriented (shared with *Steneosaurus brevior* Blake, 1876, *Mycterosuchus nasutus* Andrews, 1913, *Platysuchus multiscrobiculatus*, Chinese teleosauroid previously referred to as *Peipehsuchus* (see Li 1993) , Thai teleosauroids PN-16-20 and PRC 239); anterior-posteriorly reduced length of the external nares: more than 67% of the premaxillae total length is posterior to the external nares (shared with ‘*Steneosaurus’ gracilirostris*, Chinese teleosauroid, Thai teleosauroid PN-16-20); the lateral expansion of the premaxilla is very pronounced*; the premaxillae anterior and anterolateral margins are strongly anteroventrally deflected and extend ventrally (shared with *Steneosaurus brevior Mycterosuchus nasutus, Platysuchus multiscrobiculatus* Chinese teleosauroid, Thai teleosauroids PN-16-20 and PRC 239); inconspicuously ornamented maxilla dorsal surface (shared with Chinese teleosauroid, Thai teleosauroids PN-16-20 and PRC 239, *Aeolodon priscus* von Sömmerring, 1814); maxillary ornamentation consisting of a shallow irregular patterns of ridges and rugose anastomosing grooves*; maxilla interalveolar spacing is longer than adjacent alveoli; lack of apical tooth ornamentation*; the ornamental pits on the dorsal osteoderms are circular and regularly organised in alternate rows on the osteoderms (shared with *Aeolodon priscus*).

Possible additional characters— As we cannot locate the Quercy specimen, we cannot double-check whether these additional characters are valid. However, if they are then the diagnosis can be expanded to include the following characters (autapomorphic characters are indicated by an asterisk): absence of frontal ornamentation*; in dorsal view, the rostrum narrows markedly immediately in front of the orbits (shared with *Teleosaurus cadomensis*, *Mycterosuchus nasutus* and the Thai teleosauroid PN-16-20); in dorsal view, the minimum interorbital width across the frontal is broader than the orbital width (shared with *Steneosaurus bollensis* Jäger, 1828, *Platysuchus multiscrobiculatus*, *Teleosaurus cadomensis*, *Steneosaurus brevior*, and *Steneosaurus gracilirostris* Westphal 1961); small and reduced occipital tuberosities.

Remarks. The Quercy specimen has a basicranial length of 78 cm, which using the body length questions of Young et al. (2016) yields a 4 m long size estimate. Based on the skull proportions of the most complete specimen (the Quercy specimen), the largest known *Bathysuchus megarhinus* individual (NHMUK OR 43086) would have had a basicranial length of approximately 85 cm, and using the body length questions of Young et al. (2016) gives an estimate of 435 cm.

Geographical and Stratigraphic Range. Kimmeridgian of England (*A.autissodorensis* ammonite Zone) and France (*A. eudoxus* ammonite Zone)

DESCRIPTION

Cranial elements

Premaxillae. The premaxillae of *Bathysuchus megarhinus* are ladle-shaped elements with a strongly convex dorsal side and strongly concave ventral surface (Figs. 2-3). The premaxillae of the holotype (NHMUK PV OR 43086) each bear five alveoli, of which the posterior one is strongly reduced and nearly posteriorly oriented (Fig. 2). The same feature has been reported by

Vignaud et al. (1993) for the Quercy specimen. Unfortunately, the P5 alveoli are difficult to see in DORCM G.05067i due to the poor preservation of the premaxilla posterior to the P4 alveoli and of the premaxilla-maxilla suture (Fig. 3). Such a high alveolar count is unusual amongst teleosauroids, being known only in *B*. *megarhinus*, *P*. *multiscrobiculatus* (MNHNL TU895, SMNS 9930) and *T*. *cadomensis* (MNHN.F AC 8746) (Lamouroux 1820; Westphal 1961, 1962; Johnson et al. 2018). The P1 and P2 alveoli are laterally aligned and do not form a couplet, (which differs in other teleosauroids such as *Lemmysuchus obtusidens*, where the P1 and P2 alveoli are only separated by a thin lamina; see Johnson et al. 2017). The lateral margin of the premaxillae are strongly laterally expanded, so that the P3-P4 alveoli are anteroposteriorly aligned on a more lateral plane than the external margin of the P2 alveoli. Posterior and lateral to the P2 alveoli there is a noticeable diastema between the P2 and P3 alveoli. The P3 and P4 alveoli are also well separated, and the P5 alveoli are oriented posteriorly.

The external nares are well preserved in both NHMUK OR 43086 and DORCM G.05067i, and are characteristically ‘8-shaped’ in dorsal and anterior views (Figs. 2E and 3A, E). Overall the external nares constitute a small length of the entire premaxillae that develop posteriorly for more than 67% of its entire length, considerably longer than in *A*. *priscus* (MNHN.F.CNJ 78), which is approximately 60-65%. The anterior and posterior medial margin of the external nares is made by two bulbous projections of the premaxillae in anterior and dorsal direction (Hulke 1871) (Figs. 2E and 3E). The anterior margin of the external nares of *B*. *megarhinus* (DORCM G.050671i) is weakly ornamented by fine ridges.

The premaxillae in both NHMUK PV OR 43086 and DORCM G.05067i are laterally expanded in line with the P3-P4 alveoli, and are strongly ventrally deflected (Figs. 2-3). A noticeable effect of the ventral deflection of the premaxillae is that the P1-P3 alveoli are on a ventral plane compared to the rest of the snout dentition, including the P4 alveoli, which is dorsal to them and slightly posteriorly oriented (Figs. 2B, D and 3B, D). As reported by Hulke (1871), the P4 alveoli are the largest alveoli in the premaxilla, and the P1 and P5 alveoli are the smallest. In dorsal view the premaxillae contact the maxillae with a 'V-shaped' suture that posteriorly reached to level to the M3 alveoli (or was slightly posterior the alveoli) (Figs. 2A and 3A). In ventral view, the same suture has a horizontal (square-shaped) profile with the most anterior side reaching in between the P3 and P4 alveoli (Figs. 2C and 3C). The ornamentation of the dorsal surface of the premaxillae is weak, as in *A. priscus* (MNHN.F.CNJ 78) and considerably less pronounced than in *M. nasutus* (NHMUK PV R 3577 and CAMSM J1420) (Figs. 2-3).

Maxillae. The maxillae are only partially preserved in NHMUK PV OR 43086 and DORCM G.05067i, and their suture(s) with posterior elements cannot be assessed in these specimens (Figs. 2-3); however, they are more completely preserved in the Quercy specimen (see Vignaud 1995). The maxillae form a substantial part of the rostrum, with sub-parallel lateral margins in dorsal view. The rostrum is dorsoventrally flattened (oval in cross section with a horizontal long axis) (Fig. 2F).

With reference to photographs and line drawings of the Quercy specimen (fig. 2 Vignaud et al. 1993; Plate 12, Vignaud 1995), the rostrum of *B. megarhinus* makes up approximately 71% when compared with ~73% in *M. nasutus* (NHMUK PV R 3577, CAMSM J1420) and *A. priscus* (MNHN.F.CNJ 78), as well as ~74% in *P. multiscrobiculatus* (SMNS 9930) (its closest relatives). The rostral length in teleosauroids ranges from ~55-75% (with *Machimosaurus mosae* Sauvage & Liénard, 1879, having the lowest snout/basicranial length ration in teleosaurids and *M. nasutus, 'Steneosaurus' deslongchampsianus* Lennier, 1887, and *A. priscus* the highest). This suggests that snout length is a plastic feature in teleosauroids, with different clade that independently diverged from the plesiomorphic longirostry towards extreme longirostrine or mesorostrine/brevirostrine morphologies (see Discussion). The dorsal and lateral surfaces of NHMUK PV OR 43086 and DORCM G.05067i are weakly ornamented with a shallow network of ridges, rugosities and anastomosing grooves (Figs. 2-3). The density and depth of the maxilla ornamentation varies in teleosauroids, and in semi-aquatic taxa the loss of dermatocranial and osteoderm ornamentation has been linked to a pelagic lifestyle (Young et al. 2013; Clarac et al. 2017) (see Discussion). This is similar to metriorhynchids, which plesiomorphically had well ornamented dermatocrania that independently became 'smoother' in numerous lineages through time (Young et al. 2013).

Given the incomplete preservation of all known specimens, it is impossible to provide a precise tooth count for *B. megarhinus*. The Quercy referred specimen (Vignaud et al. 1993; Vignaud 1995) has 28-30 preserved maxillary alveoli (~24 most anterior alveoli are preserved on each side of NHMUK PV OR 43086 and only the three anterior most the right maxillae of DORCM G.05067i). The maxilla interalveolar spacing is regular and as wide as adjacent alveolar length or more, this can be seen in all specimens (Figs. 2C-3C). The palatines are not visible in any of the English specimens, but Vignaud et al. (1993) reported for the French specimen that these bones occupy the entire width of the beginning of the snout, and the maxillae are reduced to thin lateral bands. It is not possible to accurately estimate the anterior extent of the palatine-maxillae suture in relation to the tooth count, but it certainly does not extend more than ~5 cm anterior to the beginning of the posterior end of the snout, roughly corresponding to the M27-M30 alveoli (see Vignaud et al. 1993).

Teeth. DORCM G.05067v is the only tooth that is well preserved enough to allow description (Fig. 4). The crown is small, only ~17 mm in apicobasal length, with a high crown base average diameter/ crown height ratio (~2.5). The crown is sub-circular, only slightly laterally compressed and weakly curved in medial direction. The enamel is finely ornamented by continuous parallel apicobasally aligned ridges that are densely packed and low-relief. The ridges do not reach the apex of the tooth, but stop two-thirds up the crowns in both the mature and unerupted teeth (left P4 and M2). DORCM G.05067v has one visible carina for each anterior and posterior margin. The carinae are easier to detect on the apical third of the crown, and they are smooth as no denticles can be observed (even using optical aids). Following the Massare (1987) functional classification of Mesozoic marine reptile teeth, *B. megarhinus* (DORCM G.050761v) falls in the 'Pierce' guilds, as well as the other longirostrine teleosauroids in the dataset.

Osteoderms. Three osteoderms, two dorsal and one ventral (DORCM G.05067i-iv) are preserved (Fig. 5). Based on their respective rectangular and sub-circular shape the dorsal osteoderms presumably come from one of the paramedian series of the dorsal series (DORCM G.05067ii) (Fig. 5A-B) and the anterior tail (DORCM G.05067iv) (Fig. 5C-D). All osteoderms are ornamented with small circular/sub-circular pits that are organised in alternate rows unlike in the usual 'starbust' patterns of tear-drop/irregular shaped pits as in most teleosauroids (e.g. machimosaurins; see Young et al (2014), Johnson et al (2017)). The regular shape and arrangement of these pits is similar to the one observed in *A. priscus* (MNHN.F.CNJ 78). The caudal osteoderm, DORCM G.05067iv, has a well-developed medial keel that is not present in the other two osteoderms (Fig. 5A, C). The third osteoderm, DORCM G.05067iii, somewhat differs from the others in the fact that the ornamental pits are more widely separated from one another and has a flat external surface (Fig. 5E-F).

Overall, the osteoderms of *B. megarhinus* are poorly ornamented compared to other teleosauroids (e.g. see Andrews 1913; Johnson et al. 2017), a character shared with *A. priscus* (MNHN.F.CNJ 78).

PHYLOGENETIC ANALYSIS

Methods

We conducted a phylogenetic analysis to test the evolutionary relationships of *Bathysuchus megarhinus* gen. nov. within Thalattosuchia using a modified version of the dataset provided by Ősi et al. (in review), which is continuously being updated, as it forms the foundation of the ongoing Crocodylomorph SuperMatrix Project. The dataset consists of a merged matrix combining the two datasets originally published by Young et al. (2016), following which both matrices were then revised and expanded; hereafter we refer to it as the Hastings + Young matrix (H+Y matrix). The dataset was first presented in Ristevski et al. (2018); however, it has been extensively updated subsequently (see Ősi et al. (in review) for full details). All data are summarised in Supplementary data files.

The current iteration of the H+Y dataset consists of 142 crocodylomorph OTUs (seventy-two of which represent thalattosuchians, including twenty teleosauroids, seven basal metriorhynchoids and forty-two metriorhynchids) scored for 454 characters. Of these 454 characters, 25 characters representing morphoclines were treated as ordered (7, 28, 36, 49, 57, 98, 164, 166, 174, 205, 225, 228, 234, 264, 274, 330, 357, 362, 372, 407, 410, 420, 421, 423, 435) and *Postosuchus kirkpatricki* Chatterjee, 1985 was used as the outgroup taxon. For the H+Y dataset the differences between our analyses and those presented by Ősi et al. (in review) are: (1) the addition of the two Thai teleosauroid OTUs; (2) the rescoring of *B. megarhinus*; (3) the rescoring of the Chinese teleosauroid OUT; and (4) a slight re-organisation of the character list, with two new anatomical sections (palaeoneuroanatomy and craniomandibular pneumaticity). The character scoring for *B. megarhinus* was based on first-hand examination of the holotype by DF, MMJ and MTY, as well as first-hand examination of the referred specimen *Bathysuchus* by DF. Due to the poor preservation and incompleteness of these specimens, *B. megarhinus* was scored for 60 out of 454 characters (13.2%).

The cladistic analysis of the dataset was conducted using TNT 1.5 Willi Hennig Society Edition (Goloboff et al. 2008; Goloboff and Catalano 2016), following the methodology used in Young et al. (2016). Memory settings were increased with General RAM set to 900 Mb and the maximum number of trees to be held set to 99,999. Cladogram space was searched by means of the 'New Technology search' option in TNT (Sectorial Search, Ratchet, Drift, and Tree fusing) with 1000 random-addition replicates (RAS). In addition, we increased the default setting for the iterations of each method (except for Tree fusing, which was kept at 3 rounds). In the Sectorial Search we ran 1000 Drift cycles (for selections of above 75) and 1000 starts and fuse trees 1000 times (for selections below 75), as well as 1000 rounds of Consensus Sectorial Searches (CSSs) and Exclusive Sectorial Searches (XSSs). For Ratchet, the program used 1000 ratchet iterations set to stop the perturbation when 1000 substitutions were made or 99% of the swapping was reached. Lastly, in Drift, the analysis included 1000 Drift cycles set to stop the perturbation when 1000 substitutions were made or 99% of the swapping was reached.

Furthermore, we ran an additional analysis in which the *B. megarhinus* OTU included character scores based on the Quercy specimen. For this analysis, we scored 98 out of 454 characters (21.5%) using the H+Y dataset and conducted the analysis in 'New Technology search' option in TNT (Sectorial Search, Ratchet, Drift, and Tree fusing) with 1000 random-addition replicates (RAS), as detailed above.

Results

The first H+Y phylogenetic analysis produced 102 most parsimonious cladograms (MPCs) with 1488 steps (ensemble consistency index (CI) = 0.412; ensemble retention index (RI) = 0.840; rescaled consistency index (RCI) = 0.346; ensemble homoplasy index (HI) = 0.588). The overall strict consensus topology recovered from this analysis produced few changes from that presented by Ristevski et al. (2018) and Ősi et al. (in review). *Bathysuchus megarhinus* was found to be in a stable position, forming a clade with the Thai specimen (PN-16-20) and the Chinese teleosauroid (IVPP V 10098) (Fig. 6A). This subclade is in a polytomy with *Platysuchus multiscrobiculatus*, *Steneosaurus brevior*, *Mycterosuchus nasutus*, *Teleosaurus cadomensis* and the Thai specimen (PRC-239) (Fig. 6B). *Steneosaurus gracilirostris* was recovered as the basal-most teleosauroid.

Our second analysis (which includes scores for the Quercy specimen in the *B. megarhinus* OTU) produced 75 MPCs with 1491 steps (CI = 0.411; RI = 0.840; RCI = 0.345; HI = 0.589). The strict consensus topology produced many changes from the first analysis. *Bathysuchus megarhinus* continued to be in a stable but has moved its position, and presented as most closely related to the clade containing *Mycterosuchus nasutus* and *Teleosaurus cadomensis*. The Thai specimen (PN-16-20) was found to be the sister taxon of the Chinese teleosauroid (IVPP V 10098); in turn, the subclade's sister taxon is the second Thai specimen (PRC-239). *Steneosaurus gracilirostris* was once again recovered as the basal-most teleosauroid.

In both analyses, the overall picture of crocodylomorph interrelationships found are similar to those found in previous iterations of this merged dataset (Ristevski et al., 2018; Smith et al., in review; et al., Ősi in review): the rauisuchian *Postosuchus kirkpatricki* lies outside the clade that unites all other taxa (i.e. Crocodylomorpha), with 'sphenosuchians' forming a grade of more derived taxa. Protosuchidae and *Fruitachampsa callisoni* Clark, 2011 are recovered as basal crocodyliforms. The remaining taxa comprise Mesoeucrocodylia, which includes a clade formed by *Eopneumatosuchus colberti* Crompton and Smith, 1980 + Thalattosuchia, and the other clade being Metasuchia. Metasuchia contains two sub-clades, Notosuchia and Neosuchia. Within Thalattosuchia, both Teleosauroidea and Metriorhynchoidea are both recovered as monophyletic. In Metriorhynchoidea, *Pelagosaurus typus* Bronn, 1841 is found to be a basal metriorhynchoid, and Metriorhynchidae, Metriorhynchinae, Rhacheosaurini, Geosaurinae and Geosaurini are all found to be monophyletic. Within Teleosauroidea, *Steneosaurus gracilirostris* is the basal-most species, with two large subclades recovered. These two large subclades include: (1) a group of very poorly known genera and species (e.g. *Teleosaurus*, *Platysuchus* and *Mycterosuchus*) that are predominately long-snouted, and (2) the typical '*Steneosaurus*' group along with the durophagous species. Within the second subclade, the tribe Machimosaurini is recovered (consisting of *Lemmysuchus* and *Machimosaurus*; see Young et al. (2014); Jouve et al. (2016); Young et al. (2016); Johnson et al. (2017); Ősi et al. (in review)).

Both phylogenetic analyses agree upon numerous aspects:

1. The positioning and monophyly of Thalattosuchia
2. The separation of Thalattosuchia into two clades: Teleosauroidea and Metriorhynchoidea
3. That *Pelagosaurus typus* is a basal metriorhynchoid, and *Steneosaurus gracilirostris* is the basal-most known teleosauroid
5. The monophyly of Teleosauroidea
6. Two large sub-clades within Teleosauroidea
7. The monophyly of Machimosaurini

What these two analyses do not agree upon is the position of *Bathysuchus megarhinus*. It is, however, consistently found to be a member of a large unnamed sub-clade consisting of *Steneosaurus brevior*, *Platysuchus multiscrobiculatus*, *Teleosaurus cadomensis*, *Mycterosuchus nasutus*, and the East Asian teleosauroids. Without the character scores for the Quercy specimen, *B. megarhinus* is only known from two partial rostra, one complete tooth crown and three osteoderms. Thus, it is unsurprising that in disrupts the internal relationships of this sub-clade of poorly-studied teleosauroids. Including the Quercy scores greatly improves the stability of this sub-clade, and moves *B. megarhinus* away from the East Asian teleosauroids and into a clade with *Teleosaurus*, *Mycterosuchus* and *Platysuchus*.

DISCUSSION

French *Bathysuchus megarhinus* specimens

As mentioned above, Vignaud et al. (1993) referred a partial skull to *'Steneosaurus'* cf. *megarhinus* from Quercy in France. Unfortunately, we have been unable to location the specimen. The skull is slender and gracile, with an extremely anteroposterior elongated rostrum (Vignaud 1995). The premaxilla has all the characteristic features of NHMUK PV OR 43086 and DORCM G.05067i as described above. The nasals are triangular is shape as in other thalattosuchians and do not contact the premaxilla (e.g. Andrews, 1913). In dorsal view, the rostrum narrows markedly immediately anterior to the orbits, which is shared with Thai teleosauroid (PN-16-20), *Teleosaurus cadomensis* (MNHN.F AC 8746), *Aeolodon priscus* (MNHN.F.CNJ 78) and *Mycterosuchus nasutus* (NHMUK PV R 3677). The minimum interorbital width across the frontal is broader than the orbital width, shared with *Steneosaurus* *bollensis* (SMNS 51753), *Platysuchus multiscrobiculatus* (SMNS 9930), *Teleosaurus cadomensis* (MNHN.F AC 8746), *Steneosaurus brevior* (NHMUK PV OR 14781), *Steneosaurus gracilirostris* (NHMUK PV OR 14792). The maxillae are anteroposteriorly elongated with sub-parallel lateral margins as in other teleosauroids (e.g. *Lemmysuchus obtusidens* NHMUK PV R 3168). Once peculiar feature is the reported lack of ornamentation on the frontal (note that Vignaud et al. (1993) suggested that this feature may be representative of a juvenile). The supratemporal fenestrae are large and anteroposteriorly elongated (sub-rectangular in shape) and the occipital tuberosities are small and reduced as in other teleosauroids such as *S. leedsi* (NHMUK PV R 3806) (excluding *Steneosaurus heberti* Morel de Glasville, 1876 (MNHN.F 1890-13), in which they are large and bulbous). The teeth are slender and apicobasally elongated, with pointed apices. Vignaud (1995) also referred an anterior fragment of the mandible (BHN 2R 25; the holotype of *Steneosaurus morinicus* Sauvage, 1872) as *'T'. megarhinus.*

Comparisons with other teleosauroids

Bathysuchus megarhinus shares a number of characters with other teleosauroids, most notably with some long-snouted taxa (e.g. *Mycterosuchus nasutus* NHMUK PV R 3577). As mentioned in the description, the high premaxillary alveolar count (five) is unusual, and is only seen in *B. megarhinus* (NHMUK PV OR 43086, DORCM G.05067i, Quercy specimen), *P. multiscrobiculatus* (MNHNL TU895, SMNS 9930) and *T. cadomensis* (Lamouroux 1820; Westphal 1961, 1962). The peculiar premaxillary alveolar distribution of the P1-P2 and the P3-P4 alveoli are characteristic of both *B. megarhinus* (NHMUK PV OR 43086, DORCM G.050671i) and *M. nasutus* (NHMUK PV R 3577), and it is one of a number of features that are unique to these two taxa. The anterior bulbous projections of the premaxillae processes seen in *B. megarhinus* (DORCM G.050671i) are also present in *M. nasutus* (CAMSM J .1420), but are absent in other teleosauroids such as *S. leedsi* (NHMUK PV R 3806), the Chinese teleosauroid (IVPP V 10098) and *A. priscus* (MNHN.F CNJ 78). *Bathysuchus megarhinus* shares three premaxilla features in common with *P. multiscrobiculatus* (SMNS 9930, MNHNL TU895), *S. brevior* (NHMUK PV OR 14781), *M. nasutus* (NHMUK PV R 3577), the Chinese teleosauroid (IVPP V 10098) and both Thai teleosauroids (PN-16-20, PRC-239):

(1) the premaxillae anterior and anterolateral margins are strongly anteroventrally deflected and extend ventrally. In other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806) the anterior and anterolateral premaxillary margins are not anteroventrally deflected and do not extend ventrally;

(2) the anterior nares face anteriorly. In other teleosauroids (e.g. *S. leedsi* NHMUK PV R 3806; *A. priscus* MNHN.F CNJ 78) the anterior nares face mainly dorsally; and

(3) the premaxilla is laterally expanded, in line with the P3-P4 alveoli and strongly ventrally deflected. In other teleosauroids (e.g. *A. priscus* MNHN.F CNJ 78) the premaxilla is not laterally expanded and in line with the P3-P4 alveoli.

The teeth of *B. megarhinus* are highly unusual, as the enamel ridges do not continue into the apical region (Fig. 4). This feature has not observed in any other described teleosauroid (e.g. *M. nasutus* NHMUK PV R 3677; *A. priscus* MNHN.F CNJ 78; *S. bollensis* MNHNL TU799), in which the enamel ridges are more densely packed and reach the apex. However, it is worth noting that it has been observed in an undescribed MNHN teleosauroid (one tooth in association with a partial skull) and NHMW 1884 (from the 'Lias' of Germany), which is labelled as

'Teleosaurus' (however, this tooth is laterally compressed, with discontinuous prominent ridges, more so than *Bathysuchus*).

Reduced ornamentation and possible pelagic adaptations in Teleosauroidea

The ornamentation of the maxillary dorsal and lateral surfaces of *B. megarhinus* (NHMUK PV OR 43086, DORCM G.05067i) is similar to the Chinese teleosauroid (IVPP V 10098), one Thai teleosauroid (PN-16-20) and *A. priscus* (MNHN.F CNJ 78) in that they are weakly ornamented with a shallow network of ridges, rugosities and anastomosing grooves. This differs from other taxa (e.g. *M. nasutus* NHMUK PV R 3577; *S. brevior* NHMUK PV OR 14781) that have a strongly ornamented rostrum.

The shape and arrangement of *B. megarhinus* (DORCM G.050671i) osteoderm pits is also similar to those observed in *A. priscus* (MNHN.F.CNJ 78). These pits are fairly large, but overall few in number and they are well separated from one another. However, there is a notable difference in that the thoracic osteoderms of *B. megarhinus* are not keeled, whereas longitudinal keels are present on all osteoderm in *A. priscus* (MNHN.F.CNJ 78), even the cervical ones. The ornamentation of the dorsal-sacral osteoderms of *B. megarhinus* (DORCM G.05067i) also radically differs from the irregular, reticular pattern seen in *M. nasutus* (NHMUK PV R 3577, CAMSM J.1420).

The pronounced reduction in dermatocranial and osteoderm ornamentation is shared between *B. megarhinus* and *A. priscus*, and is unique to these two species within Teleosauroidea. The shift from highly ornamented dermal bone/ossifications to low levels of ornamentation (or no ornamentation) is characteristic of the shift from amphibious to pelagic forms (Clarac et al.

2017). Clarac et al. (2017) outlined a possible mechanism for the increase in bone ornamentation in amphibious pseudosuchians, as a way to increase their basking efficiency. As dermatocranial and osteoderm ornamentation is highly vascularised, the overlying soft tissue can drive heat radiation to the bones. As such, it is curious that both *B. megarhinus* and *A. priscus* independently begin to reduce the size and thickness of their osteoderms, as well as lose, or heavily reduce their ornamentation. While the post-cranium of *B. megarhinus* is largely unknown, the skeleton of *A. priscus* is not. The *A. priscus* specimen MNHN.F.CNJ 78 has proportionally very small dorsal osteoderms, a proportional shortening of the tibiae, and the reduction of the forelimb with it becoming more flipper-like. Thus by the Late Jurassic at least one longirostrine teleosauroid (*A. priscus*) was beginning to evolve a more pelagic lifestyle. Without more of the post-cranium we cannot be certain as to whether the same was true for *B. megarhinus*, however it would explain the presence of a teleosauroid in a deep-water ecosystem. It would also show that two different teleosauroid sub-clades were evolving into pelagic forms by the end of the Jurassic.

CONCLUSIONS

Here, we describe a new specimen of '*T*'. *megarhinus* (DORCM G.05067i-v) as well as figure and describe the holotype (NHMUK PV OR 43806), demonstrate that it is indeed a valid species and establish a new monotypic genus, *Bathysuchus*, for the taxon. It has five autapomorphies and shares six characters with a large unnamed sub-clade of teleosauroids (*Steneosaurus brevior, Teleosaurus cadomensis, Platysuchus multiscrobiculatus, Mycterosuchus nasutus* and unnamed taxa from Eastern Asia). This suite of characteristics falsifies the hypothesis that *B. megarhinus* is a subjective synonym of *S. leedsi* (which lacks all of these characters). Unfortunately, we were unable to find the French skull referred to *B. megarhinus*. Based on the pronounced reduction in dermatocranial and osteoderm ornamentation, we hypothesise that *B. megarhinus* had evolved a pelagic lifestyle. This helps to explain its paradoxical discovery in the deep-water Dorset succession of the Kimmeridge Clay Formation. This ornamentation reduction is also seen in *Aeolodon priscus*, a species with a known post-cranium and shows skeletal evidence for this shift. If correct, then by the end of the Jurassic two lineages of teleosauroids were evolving a pelagic lifestyle.

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REFERENCES

Andrews CW. 1909. XXXVIII. – On some new steneosaurs from the Oxford Clay of Peterborough. *Annals and Magazine of Natural History* 3: 299–308. DOI:10.1080/00222930908692579.

Andrews, C.W. 1913. A descriptive catalogue of the marine reptiles of the Oxford Clay, Part Two. London: British Museum (Natural History).

Bronzati, M., Montefeltro, F. C., Langer, M. C. 2012. A species-level supertree of Crocodyliformes. *Historical Biology* 24: 598–606.

Buffetaut, E., Termier, G., Termier, H. 1981. A teleosaurid (Crocodylia, Mesosuchia) from the Toarcian of Madagascar and its palaeobiological significance. *Paläontologische Zeitschrift* 55: 313–319.

Chatterjee, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Paleontology* 21(part1): 83–127.

Clarac, F., Buffrénil, V. de, Brochu, C., Cubo, J. 2017. The evolution of bone ornamentation in Pseudosuchia: morphological constraints versus ecological adaptations. *Biological Journal of the Linnean Society* 121: 395–408.

Coe, A.L. 1992. The Oxfordian and Portlandian. In Coe, A.L., Hesselbo, S.P., Parkinsson, D.N., and Jenkyins, H.C. (Ed.) Sequence Stratigraphy of the Dorset Jurassic, a field guide. Sequence Stratigraphy of European Basins, CNRS-IFP, Dijon, France 37–81.

Coe, A.L. 1995. A comparison of the Oxfordian successions of Dorset, Oxfordshire and Yorkshire. In Taylor, P.D. (Ed.) Field Geology of the British Jurassic 151–172.

Cox, B.M. 2001. In Wright, J.K., and Cox, B.M. British Upper Jurassic Stratigraphy, Geological Conservation Review Series, No. 21, Joint Nature Conservation Committee, Peterborough, 266pp.

Delair, J.B. 1958. The mesozoic reptiles of Dorset. *Proceedings of the Dorset Natural History and Archaeological Society* 79: 47–72.

Hulke, J.W. 1871. Note on a Fragment of a Teleosaurian snout from Kimmeridige Bay, Dorset. *Quarterly Journal of the Geological Society of London* 17: 442–443.

Eudes-Deslongchamps, E. 1867–1869. Notes Paléontologiques. Caen and Paris, France, 320–392 pp.

Fanti, F. Miyashita, T., Cantelli, L., Mnasri, F., Dridi, J., Contessi, M., and Cau, A. 2016. The largest thalattosuchian (Crocodylomorpha) supports teleosaurid survival across the Jurassic-Cretaceous boundary. *Cretaceous Research* 61: 263–274.

Foffa, D., Young, M.T., and Brusatte, S.L. 2015. Evidence of macrophagous teleosaurid crocodylomorphs in the Corallian Group (Oxfordian, Late Jurassic) of the UK. *PeerJ* 3:e1497.

Foffa, D., Young, M.T., and Brusatte, S.L. *in press.* Filling the Corallian gap: new information on Late Jurassic marine reptile faunas from England. *Acta Palaeontologica Polonica* DOI [unavailable yet]

Fraas, E. 1901. Die Meerkrokodile (Thalattosuchia n. g.) eine neue Sauriergruppe der Juraformation. *Jahreshefte des Vereins für vaterländische Naturkunde inWürttemberg* 57:409–418.

Fitzinger, L. J. F. J. 1843. Systema Reptilium. Vindobonae: Braumüller et Seidel Press, Wien, Austria. ? pp.

Gallois, R.W. 2004. The Kimmeridge Clay: the most intensively studied formation in Britain. *Open University Geological Journal* 25: 33–38.

Geoffroy Saint-Hilaire, E. 1831. Recherches sur de grands sauriens trouvés à l'état fossile aux confins maritimes de la Basse-Normandie, attribués d'abord au crocodile, puis déterminés sous les noms de *Teleosaurus* et *Steneosaurus*. *Mémoires de l'Académie des Sciences* 12: 1–138.

Goloboff, P. A., Farris, J. S., Nixon, K. C. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.

Goloboff, P. A., Catalano, S. A. 2016. TNT version 1.5, including a full implementation of phylogeneticmorphomet rics. Cladistics 32: 221–238.

Hay, O. P. 1930. Second bibliography and catalogue of the fossil vertebrata of North America 2. Carnegie Institute Washington Press, Washington, DC. Jäeger CF. 1828. Über die fossile Reptilien, welche in Württemberg aufgefunden worden sind. Stuttgart: J. B. Metzler.

Johnson, M.M., Young, M.T., Steel, L., and Lepage, Y. 2015. *Steneosaurus edwardsi* (Thalattosuchia, Teleosauridae), the largest known crocodylomorph of the Middle Jurassic. *Biological Journal of the Linnean Society* 115: 911–918.

Johnson, M.M., Young, M.T., Steel, L., Foffa, D., Smith, A.S., Hua, S., Havlik, P., Howlett, E.A., and Dyke, G. 2017. Re-description of '*Steneosaurus' obtusidens* Andrews, 1909, an unusual macrophagous teleosaurid crocodylomorph from the Middle Jurassic of

England. *Zoological Journal of the Linnean Society* zlx035, https://doi.org/10.1093/zoolinnean/zlx035

Johnson, M.M. Young, M.T., Brusatte, S.L., Thuy, B., and Weis, R. 2018. A catalogue of teleosauroids (Crocodylomorpha: Thalattosuchia) from the Toarcian and Bajocian (Jurassic) of southern Luxembourg. *Historical Biology* DOI: 10.1080/08912963.2018.1427090

Jouve, S., Mennecart, B., Douteau, J, Jalil, N.-E. 2016. The oldest durophagous teleosaurid (Crocodylomorpha, Thalattosuchia) from the Lower Bathonian of Central High Atlas, Morocco. *Palaeontology* 59: 863–876.

Kuhn, O. 1936. Crocodilia. In: Fossilium Catalogus, Animalia. W. Quenstedt Ed, Berlin, 1, 75: 1-144.

Lamouroux, M. 1820. Sur le crocodile fossile trouve´ dans les carrie`res du bourg d'Allemagne, a` un quart de lieue de Cean. *Annales Générales des Sciences Physiques* 3:160–164.

Lennier, G. 1887. Description des fossiles du Cap de la Hève. *Bulletin de la Société Géologique de Normandie. Le Havre* 12: 17–98.

Lepage, Y., Buffetaut, E., Hua, S., Martin, J.E., and Tabouelle, J. 2008. Catalogue descriptif, anatomique, géologique et historique des fossiles présentés à l'exposition Les Crocodiliens fossiles de Normandie. *Bulletin de la Société Géologique de Normandie et des Amis du Muséum du Havre* 95: 5–152.

Li, J. 1993. A new specimen of *Peipehsuchus teleorhinus* from Ziliujing Formation of Daxion, Sichuan. *Vertebrata PalAsiatica* 31: 85-94.

Martin, J.E., Vincent, P. 2013. New remains of *Machimosaurus hugii* von Meyer, 1837 (Crocodylia, Thalattosuchia) from the Kimmeridgian of Germany. *Fossil Record* 16: 179–196.

Massare, J.A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology* 7: 121–137.

Mueller-Töwe, I.J. 2006. Anatomy, phylogeny, and palaeoecology of the basal thalattosuchians (Mesoeucrocodylia) from the Liassic of Central Europe. Unpublished PhD thesis, Universität Mainz, Germany.

Nesbitt, N. J. 2011. The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* 352:1–292.

Ősi, A., Young, MT., Galácz, A., Rabi, M. In review. A new large-bodied thalattosuchian crocodyliform from the lower Jurassic (Toarcian) of Hungary, with further evidence of the mosaic acquisition of marine adaptations in Metriorhynchoidea. *PeerJ*.

Pierce, S. E., Angielczyk, K. D., Rayfield, E. J. 2009. Morphospace occupation in thalattosuchian crocodylomorphs: skull shape variation, species delineation and temporal patterns. *Palaeontology* 52: 1057–1097.

Ristevski, J., M. T. Young, M. B. Andrade, and A. K. Hastings. 2018. A new species of *Anteophthalmosuchus* (Crocodylomorpha, Goniopholididae) from the Lower Cretaceous of the Isle of Wight, United Kingdom, and a review of the genus. *Cretaceous Research* 84: 340–383.

Sauvage, M. H. E. 1872. Note sur les reptiles fossiles: *Bulletin de la Société géologique de France,* 3rd series, n. 1, p. 365-386.

Sauvage, M. H. E. 1874. Mémoires sur les Dinosauriens et les Crocodiliens des terrains jurassiques de Boulogne-sur-Mer. *Mémoires de la Société Géologique de France*, Paris 10: 1-58.Sauvage, H.-E., Liénard, F. 1879. Memoire sur le genre *Machimosaurus*. *Mémoires de la Société Géologique de France*, 3ème série 4: 1–31.

Steel, R. 1973. Crocodylia. In: Encyclopedia of Palaeoherpetology (edit. Kuhn, O.). Gustav Fischer, Stuttgart, Part 16: 1-16.

Vignaud, P., Lange-Badre, B., Hantzpergue, P., Dutrieux, M., Maury G. 1993. Découverte d'un crâne de Teleosauridae dans la Zone à *Eudoxus* du Kimméridgien supérieur quercynois (France). *Comptes rendus de l'Académie des Sciences*, Paris 2: 1509-1514.

Vignaud, P. 1995. Les Thalattosuchia, crocodiles marins du Mésozoique: Systématique phylogénétique, paléoécologie, biochronologie et implications paléogéographiques. Unpublished PhD thesis, Université de Poitiers, 410 pp.

~~Vignaud, P., Lange‐Badre, B., Hantzpergue, P., Dutrieux, M., and Maury, G. 1993. Découverte d'un crane de Teleosauridae dans la Zone à Eudoxus du Kimméridgien supérieur quercynois (France).~~ ~~*Académie des sciences (France). Comptes rendus de l'Académie des sciences. Série 2, Mécanique, physique, chimie, sciences de l'univers, sciences de la terre*~~ ~~317: 1509–1514.~~

Weedon, G.P., Coe, A.L., and Gallois, W. Cyclostratigraphy, orbital tuning and inferred productivity for the type Kimmeridge Clay (Late Jurassic), Southern England. Journal of the Geological Society 161: 655-666, https://doi.org/10.1144/0016-764903-073

Westphal, F. 1961. Zur Systematik der deutschen und englischen Lias-Krokodilier. *Neues Jahrbuch für Geologie und Paläontologie* 113:207–218.

Westphal, F. 1962. Die krokodilier des Deutschen und Englischen oberen Lias. *Palaeontographica, Abteilung A* 116: 23–118.

Young, M. T., and M. B. Andrade. 2009. What is *Geosaurus*? Redescription of *Geosaurus giganteus* (Thalattosuchia: Metriorhynchidae) from the Upper Jurassic of Bayern, Germany. Zoological Journal of the Linnean Society 157(3):551–585. Doi: 10.1111/j.1096-3642.2009.00536.x

Young, M.T., Andrade, M.B., Etches, S., and Beatty B.L. 2013. A new metriorhynchid crocodylomorph from the Lower Kimmeridge Clay Formation (Late Jurassic) of England, with implications for the evolution of dermatocranium ornamentation in Geosaurini. *Zoological Journal of the Linnean Society* 169(4):820–848.

Young, M.T., and Steel, L. 2014. Evidence for the teleosaurid crocodylomorph genus Machimosaurus in the Kimmeridge Clay Formation (Late Jurassic) of England, *Historical Biology: An International Journal of Paleobiology* 26(4): 472–479.

Young, M.T., Hua, S., Steel, L., Foffa, D., Brusatte, S.L., Thüring, S., Mateus, O., Ruiz-Omeñaca, J.I., Havlik, P., Lepage, Y., and Andrade, M.B. 2014a. Revision of the Late Jurassic teleosaurid genus *Machimosaurus* (Crocodylomorpha, Thalattosuchia). *Royal Society Open Science*, 1, 140222.

Young, M.T., Steel, L., Brusatte, S.L., Foffa, D., and Lepage, Y. 2014b. Tooth serration morphologies in the genus *Machimosaurus* (Crocodylomorpha, Thalattosuchia) from the Late Jurassic of Europe. *Royal Society Open Science* 1, 140269.

Young, M.T., Márton, R., Bell, M.A., Foffa, D., Steel, L., Sachs, S., and Peyer. K. 2016. Big-headed marine crocodyliforms and why we must be cautious when using extant species as body length proxies for long-extinct relatives. *Palaeontologia Electronica* 19(3): 1–14.

Figure Captions

Figure 1. *Bathysuchus megarhinus* stratigraphic and palaeogeographic distribution in the Kimmeridgian – early Tithonian of Europe. Map modified from Ron Blakey © (http://cpgeosystems.com/).

Figure 2. NHMUK PV OR 43086, holotype of *Bathysuchus megarhinus* gen. et. sp. nov. from the Kimmeridgian of Kimmeridge Bay, Dorset, England, UK. A, middle and anterior rostrum in dorsal view. B, rostrum in right lateral view. C, rostrum in ventral view. D, rostrum in left lateral view. E, premaxilla in anterior view. F, maxillae in posterior view. Scale bar equals 10 cm.

Figure 3. DORCM G.05067i, anterior rostrum of referred specimen of *Bathysuchus megarhinus* gen. et. sp. nov. from the Kimmeridgian of Kimmeridge Bay, Dorset, England, UK. A, anterior maxillae and premaxillae in dorsal view. B anterior maxillae and premaxillae in right lateral view. C, anterior maxillae and premaxillae in ventral view. D, anterior maxillae and premaxillae in in left lateral view. E, premaxilla in anterior view. Scale bar equals 10 cm.

Figure 4. DORCM G.05067iv tooth of *Bathysuchus megarhinus* gen. et. sp. nov. A, tooth in labial view. B, tooth medial-mesial view. C, tooth in lingual view. D, tooth in mesial-medial view. Scale bar equals 3 cm.

Figure 5. DORCM G.05067ii-iv osteoderms of *Bathysuchus megarhinus* gen. et. sp. nov. A. Dorsal-sacral osteoderm DORCM G.05067ii in dorsal view. B. Dorsal-sacral osteoderm

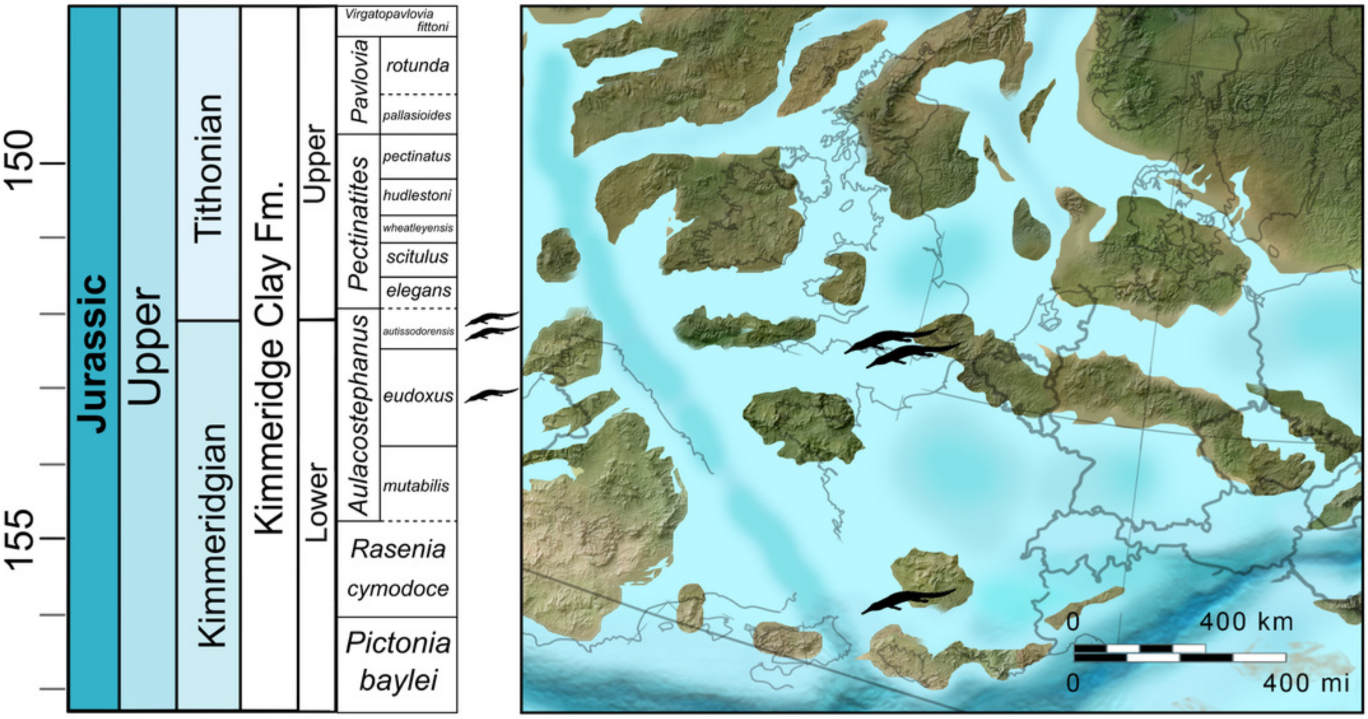
DORCM G.05067ii in ventral view. C. Caudal osteoderm DORCM G.05067iv in dorsal view. D, Caudal osteoderm DORCM G.05067iv in ventral view. E, ?ventral osteoderm DORCM G.05067iii in view. F, ?ventral osteoderm DORCM G.05067iv in dorsal view. Scale bar equals 3 cm.

Figure 6. Results of the phylogenetic analyses, Simplified strict consensus trees of the 102 most parsimonious cladograms of Teleosauroidea within Crocodylomorpha. A. Strict consensus tree including the Quercy specimen of *Bathysuchus* cf. *megarhinus*. B. Strict consensus tree only including the Kimmeridge Bay specimens of *Bathysuchus megarhinus* (NHMUK PV OR 43086 and DORCM G.05067i-v).

Figure 1

Bathysuchus megarhinus stratigraphic and palaeogeographic distribution in the Late Jurassic (Kimmeridgian – early Tithonian).

Map modified from Ron Blakey © (http://cpgeosystems.com/).



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Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.

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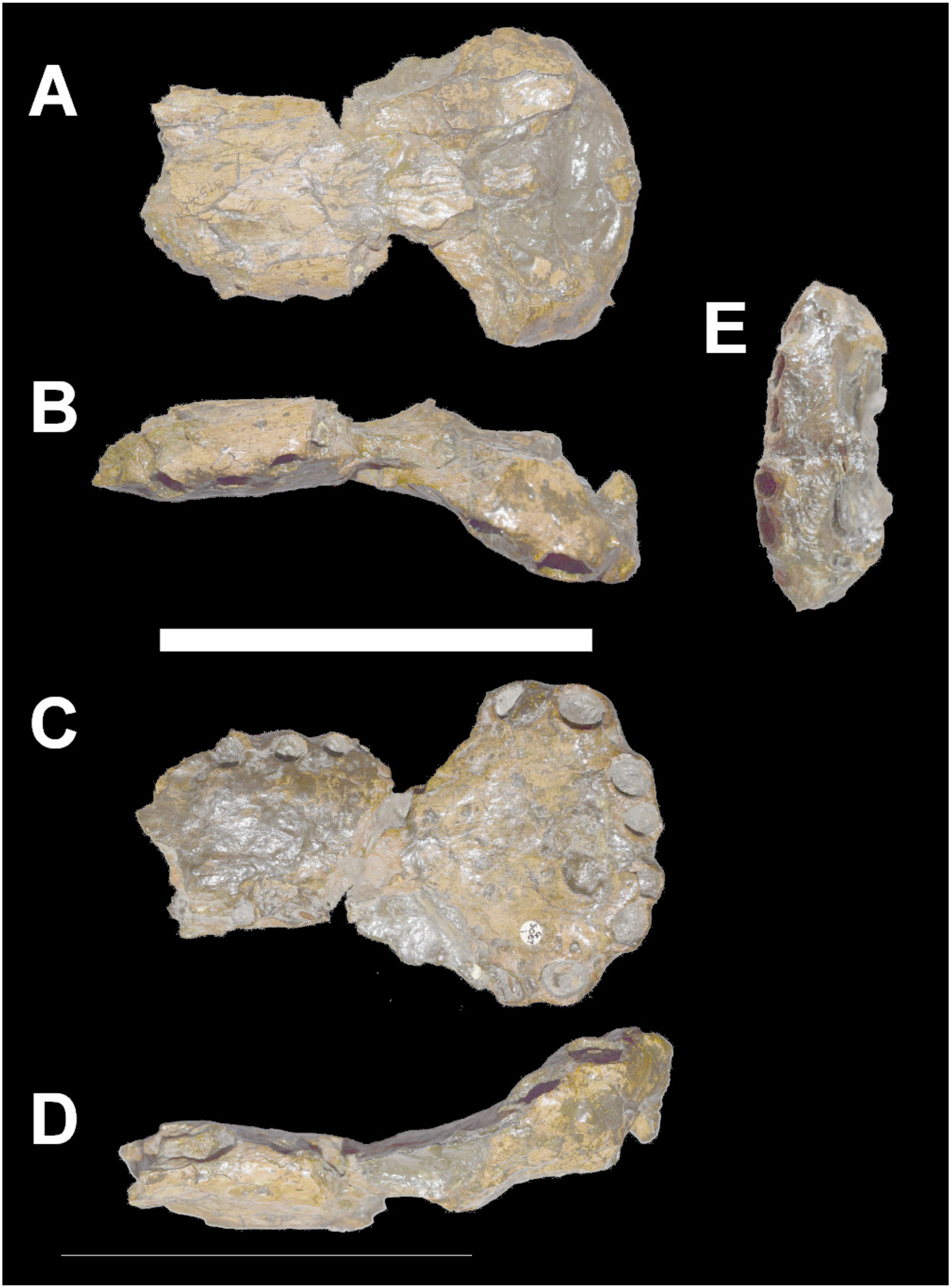
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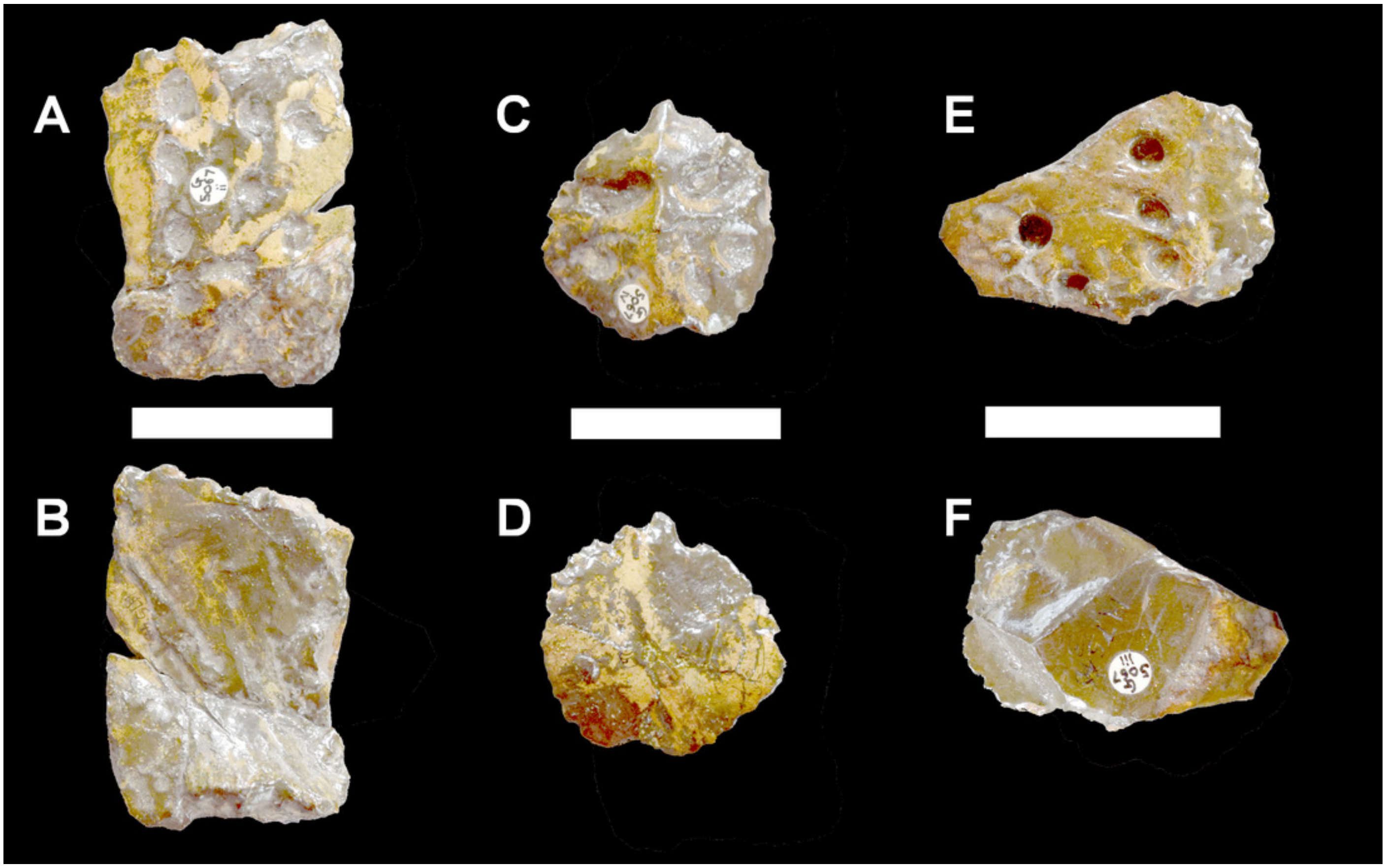

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