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First and most northern occurrence of a thalattosuchian crocodylomorph from the Jurassic of the Isle of Skye, Scotland

Kim J. Kean[1]*, Davide Foffa[2], Michela M. Johnson, Mark T. Young[1], Gert Greitens, Stephen L. Brusatte[1]

[1]School of Geosciences, University of Edinburgh, Grant Institute, The King's Buildings, James Hutton Road, Edinburgh EH9 3FE, UK

[2] National Museums Scotland, Chambers St, Edinburgh EH1 1JF, UK

*Corresponding author (email:kean.kim.j@gmail.com)

Abstract:

The Jurassic was a key interval for the evolution of dinosaurs, crocodylomorphs, and many other vertebrate groups. In recent years, new vertebrate fossils have emerged from the Early-Middle Jurassic of the Isle of Skye, Scotland; however, much more is known about Skye's dinosaur fauna than its crocodylomorphs. Here we report new crocodylomorph material collected from Jurassic marine deposits at Prince Charlie's Cave on the north east coast of Skye. The specimen is a small cobble containing postcranial elements from an individual that is considerably larger in size than previous crocodylomorphs described from Skye. Based on features of the vertebrae and osteoderms, the specimen is assigned to Thalattosuchia, an extinct clade of semiaquatic/pelagic crocodylomorphs. Specifically, the sub-circular and bean-shaped pit ornamentation on the dorsal surface of the osteoderms in alternating rows suggest affinities with the semi-aquatic lineage Teleosauroidea. Although the ornamentation pattern on the osteoderms is most similar to *Macrospondylus* (*"Steneosaurus"*) *bollensis*, we conservatively assign the specimen to Teleosauroidea indeterminate. Regardless of its precise affinities and fragmentary nature, the specimen is the first thalattosuchian discovered in Scotland and is the most northerly reported Jurassic thalattosuchian globally, adding to our understanding of the palaeobiogeography and evolution of this group.

Introduction

Crocodylomorpha is a highly diverse clade of archosaurian reptiles with a long evolutionary history that spans over 200 million years from the Late Triassic to the present (Irmis et al., 2013). While modern crocodylomorph diversity is limited to semiaquatic ambush predators, extinct species experimented with an enormous variety of niches and modes of life ranging from small terrestrial cursorial insectivores and armoured herbivores (Crush, 1984; Buckley et al., 2000; O'Connor et al., 2010), to large terrestrial apex predators (Zanno et al., 2015; Godoy et al., 2014), and even some fully marine forms (Andrews, 1913; Young et al., 2010; Schwab et al., 2020).

Thalattosuchians were the only crocodylomorph clade, and the only archosaurs, that transitioned to a fully marine pelagic lifestyle. This transition occurred during the Jurassic, which therefore represents a key time in the evolutionary history of the group. Thalattosuchia is divided into two subgroups: Metriorhynchoidea, which includes the fully aquatic Metriorhynchidae (Young et al., 2010), and the primarily semi-aquatic Teleosauroidea (Johnson et al., 2015, 2017, 2018, 2020a,b,c; Foffa et al., 2019). The fossil record of Thalattosuchia spans from the Early Jurassic to the Early Cretaceous; however, it is patchy and strongly influenced by a few high-diversity European localities (Lagerstätten effect) in the Early, late-Middle, and Late Jurassic (Benson et al., 2010). Only a few million years after their initial appearance, both thalattosuchian lineages had achieved near-global distribution by the Middle Jurassic, with species known from Sub-Boreal, Continental and Tethyan Europe (e.g. Andrews, 1913; Cau and Fanti, 2011; Parrilla-Bel et al., 2013; Chiarenza et al., 2015), North America (Buffetaut, 1979; Wilberg, 2015), South America (Gasparini et al., 2000, 2005; Fernández and Gasparini, 2000; Fernández et al., 2011; Herrera et al., 2013a; Herrera, 2015), Siberia (Efimov, 1988), India (Phansalkar et al., 1994), and Africa (Fara et al., 2002; Haddoumi et al., 2016; Jouve et al., 2016; Dridi and Johnson, 2020). However, unlike other contemporaneous marine reptile groups, neither thalattosuchian lineage apparently inhabited high latitudes (Delsett et al., 2015; Zverkov et al., 2015a, b; Roberts et al., 2020), perhaps due to physiological constraints (Mannion et al. 2015; Séon et al., 2020). To date, teleosauroids and metriorhynchoids from the Middle-Late Jurassic of Yorkshire, England, represent the northern-most published occurrence of the clade (Benton and Taylor, 1984; Foffa et al., 2018a).

Here we report new crocodylomorph material (NMS G.2020.11.1) from the Jurassic of the Isle of Skye, Scotland. This new specimen is the sixth crocodylomorph taxon (Table 1) (Evans and Waldman, 1996; Wills et al., 2014; Young et al., 2016; Yi et al., 2017) from the increasingly diverse tetrapod assemblage of the Jurassic lagoonal/coastal deposits of Skye (Clark, 1993; Anquetin, 2010; Brusatte et al., 2015; Young et al., 2016; dePolo et al., 2018, 2020; Panciroli et al., 2017, 2018, 2019). Extensive comparisons with contemporaneous terrestrial and marine tetrapods demonstrate that this specimen shares affinities with thalattosuchian teleosauroids. Therefore, it represents the first known occurrence of thalattosuchian crocodylomorphs from the Isle of Skye (and Scotland), the most northern occurrence of the group globally, and provides new insights on the palaeogeography and early evolution of teleosauroids. Note that throughout the text, we refer to the recently published teleosauroid taxonomy provided by Johnson et al. (2020c), with species previously referred to as "*Steneosaurus*" originally indicated in brackets.

Institutional Abbreviations:

CAMSM – Sedgwick Museum of Earth Sciences, Cambridge, UK; IVPP – Institution of Palaeontology and Palaeoanthropology, Beijing, China; MNHN – Muséum National d'Histoire Naturelle, Paris, France; NHMUK – Natural History Museum, London, UK; NMS – National Museum of Scotland, Edinburgh, UK; PETMG – Peterborough Museum and Art Gallery, Peterborough, UK; SMNS – Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SNHM – Staatliches Naturhistorisches Museum Braunschweig, Braunschweig, Germany.

1.   Geological Background

The Inner Hebrides boasts one of the most complete fossiliferous Middle Jurassic sequences in the world, and the Isle of Skye, in particular, has become a globally important site for Jurassic research (Clark, 1993, 2001, 2018; Morton and Hudson, 1995; Anquetin, 2010; Wills et al., 2014; Brusatte et al., 2015; Young et al., 2016; Yi et al., 2017; dePolo et al., 2018, 2020; Panciroli et al., 2017, 2018, 2019). The specimen described here was found in 2018 by Gert Greitens as a loose cobble at Prince Charlie's Cave, north of Portree (Fig. 1). As the cobble was not found in situ, it is difficult to determine its exact age and stratigraphic origin. Nevertheless, we can derive some hints of its provenance by comparing the matrix surrounding the specimen with the lithology of the geological formations exposed in the area. Fortunately, the Jurassic succession of Prince Charlie's Cave is

90 one of the most complete of the Hebrides Basin, and spans from the uppermost Pliensbachian

91 (~190.8 – 182.7 Ma - Early Jurassic) to the Bajocian (~170.3 – 168.3 Ma - Middle Jurassic), as

92 described by Morton (2004). Here we summarise the main lithological features of each unit and

93 invite the reader to refer to Morton (2004) for a more detailed account.

94

95 Surrounding the cave are almost continuous sea cliffs of the Scalpay Sandstone Formation

96 (Pliensbachian-Toarcian). Stratigraphically the Scalpay Sandstone Formation is overlain by the

97 Portree Shale Formation (Toarcian, ~182.7 – 174.1Ma), which is thicker and more complete at

98 Prince Charlie's Cave than elsewhere in the Hebrides Basin, and is itself overlain by the Raasay

99 Ironstone Formation (Toarcian) and Dun Caan Shale Member (Toarcian). The Scalpay Sandstone

100 Formation consists of a grey, fine-medium grained sandstone that has been extensively

101 bioturbated, and contains marine invertebrates such as crinoids, bivalves, brachiopods, and

102 ammonites. At its base, the Portree Shale Formation is a claystone which becomes silty and sandy,

103 and contains belemnites. Moving up the beds are light-dark grey claystones containing ammonites,

104 and the top of the succession is defined by scattered iron-ooliths and abundant belemnites. The

105 Raasay Ironstone Formation is divided into three parts; a basal section of crystalline calcareous

106 ironstones, or ferruginous limestones; a middle section of claystone with two bands of ironstone

107 nodules; and a top section consisting of a light-medium grey oolitic ironstone. Both ammonites

108 and belemnites are found throughout the Raasay Formation, with belemnites being particularly

109 abundant in the middle section. Overlaying the Raasasy Formation is the dark-grey micaceous

110 shale of the Dun Caan Shale Member which has no ammonites (Morton, 2004; Morton and

111 Hudson, 1995).

112

113 NMS G.2020.11.1 is a cobble of claystone with a fine-grained clay matrix that is well-cemented

114 and grey in colour. This may indicate that the cobble belongs to the Portree Shale Formation,

115 suggesting a lower Toarcian age (~182.7 Ma) for the specimen, which would place it in the Early

116 Jurassic. With that said, because the specimen was found loose and water worn, it has certainly

117 been reworked, and it therefore could have derived from nearly any Jurassic-aged unit along the

118 east coast of the Trotternish Peninsula of Skye, so we conservatively consider it Early to Middle

119 Jurassic in age here.

120

2.   Systematic Palaeontology

Specimen. *NMS G.2020.11.1*: a small cobble containing eight complete and partial osteoderms, three incomplete vertebrae, and additional rib fragments. The osteoderms are fragmented and due to the low contrast between matrix and bones in the μCT-scans, diagnostic features can only be observed clearly on two of the osteoderms. The vertebrae are also incomplete; the neural spine is present in only one of the vertebrae, which has a single complete transverse process. In the remaining vertebrae the neural spine is missing, and the transverse processes are either absent or incomplete. There are no chevrons or cervical ribs preserved.

Locality. Collected by G. G. at Prince Charlie's Cave, north of Portree (the cobble was not found in situ).

Preparation and Scanning. As the majority of the fossil material in NMS G.2020.11.1 is embedded in the matrix, the specimen was subjected to X-ray computed tomography (CT) scanning by Dr. Thomas Davies using a Nikon XT H 225 μCT scanner at the Palaeobiology Lab of the University of Bristol. Digital segmentation of the fossils from the matrix was conducted by Kim Kean at the University of Edinburgh, School of GeoSciences, using Materialise Mimics 20. 0.

3.   Description

NMS G.2020.11.1 is a 14 cm long, 8 cm wide, and 4 cm tall cobble (Fig. 2). It contains at least eighteen bones: three vertebrae, eight osteoderms, and seven ribs, plus other fragmentary unidentified elements, all associated in a fine grained, grey, well-cemented, clay matrix. The bones are well preserved but slightly damaged. The cobble has been rounded, likely by attrition and hydraulic action while it was in the North Atlantic Ocean. The bones that can be seen on the surface of the cobble have been damaged by these erosional processes, in particular the vertebrae, which are all incomplete as a result.

3.1 Vertebrae

Three incomplete vertebrae are preserved in NMS G.2020.11.1 (Fig. 3). They are all partially exposed on the surface of the cobble and weathered to varying degrees. The neural spine and a prezygapophysis are preserved on one of the three vertebrae (Fig. 3A). The postzygapophyses are missing in all vertebrae, and only two have preserved transverse processes. The transverse

processes (Fig. 3A and B) are long and wide, with rounded distal ends. They are broadened anteroposteriorly and show the diapophyseal and parapophyseal rib attachments . The neural spine is partially preserved and has been tilted approximately 35º laterally relative to the centrum; it is rectangular in lateral view, thin, and taller than the centrum at approximately 3.44 cm tall (Fig. 3A). The single preserved prezygapophysis is ellipsoidal in shape and extends slightly anterior to the articular surface of the centrum. The centra of all three vertebrae are spool-shaped, anteroposteriorly elongated, taller than wide, and amphicoelous. In ventral and lateral views, the centra show the typical hourglass figure of crocodylomorph vertebrae (Fig. 3) (Andrews, 1913; Young et al., 2013; Johnson et al., 2017). The exact position of the vertebrae along the spinal column is unclear, but the absence of rib attachment on the centra rules out a cervical position. Similarly, the absence of sacral ribs, or caudal chevrons/haemal arches indicate that these centra do not come from the sacral or caudal regions. Instead, the long, spool-shaped centra, and the elongated transverse processes with separated rib attachments, demonstrate that these are vertebrae from the middle-posterior dorsal section of the vertebral column (Andrews, 1913; Romer, 1956). As the neural arch is largely missing in the third preserved vertebra (Fig. 3C), it is possible that the neurocentral suture was open, which would indicate that this individual was not yet fully mature (Brochu, 1996; Herrera et al., 2013b), although its exact ontogenetic stage is unclear.

3.2 Osteoderms

As the bones in NMS G.2020.11.1 are disarticulated and have not maintained their in-vivo association, it is impossible to say with confidence if the osteoderms originated from the dorsal or ventral series. The osteoderms are rectangular- or triangular-shaped with a flat, pitted dorsal surface, and a slightly convex and smooth ventral surface. There are eight osteoderms in the block in total, five of which could be confidently segmented due to low contrast in the µCT data (Figs. 4, 5). The most complete osteoderms are shown in Fig. 4. The osteoderm in Fig. 4A is rectangular in shape; it is approximately 5 cm in length and 3 cm in width. It is ornamented with well separated bean-shaped, sub-circular, and sub-triangular pits that are arranged into alternate rows. The osteoderm shown in Fig. 4B is comparatively thin and irregular in shape. It is approximately 4 cm in length and ranges in width from 6 to 2 cm as it tapers to a point. The unfragmented edges of the osteoderm suggest that its irregular shape is not due to erosion or wear. The pits ornamenting the surface are circular and sub-triangular and decrease in size as they radiate out from the centre.

The osteoderms depicted in Fig. 5 are incomplete, and around 3 cm in width and 1.5-3 cm in length. The pits are bean-shaped and sub-circular, and arranged into alternating rows, similar to the pattern observed in Fig. 4A. The difference in shape and pit pattern of Fig. 4B could be reflective of the osteoderms belonging to different areas of the body (Vickaryous and Hall, 2008). A keel is absent on all the osteoderms observed, however, we do not consider this a reliable diagnostic character as ornamentation on the osteoderms of crocodylomorphs is formed by the resorption and redeposition of cortical bone. Therefore, pits and ridges are routinely altered, eroded, or filled during ontogeny (Clarac et al., 2015). In addition, the prominence of a keel can vary greatly within individuals of a single species. Given that a keel is absent in NMS G.2020.11.1, we have focused on comparisons between the pit ornamentation of sacral osteoderms amongst teleosauroids, which are generally diagnostic.

3.3 Other fragments

There are several ribs and unidentifiable bone fragments in NMS G.2020.11.1. In cross-section the ribs are semi-circular. The most complete fragment as shown in Fig. 5D is 16 cm long and approximately 1 cm in diameter in the rib body, and has a similar morphology to the thoracic ribs of the Middle Jurassic teleosauroid from Tunisia described by Dridi and Johnson (2020). The rib has a break towards the distal end of the rib body, but when complete it was likely uniformly curved distally. The proximal end of the rib is double headed with a tuberculum and capitulum. The capitulum would have been in contact with the parapophysis of the transverse process. It would appear that the tuberculum is rounded, however this, along with finer details of the rib's morphology, are difficult to discern due to the low contrast between it and the surrounding matrix in the μCT-scan.

4.   Crocodylomorph Affinity of NMS G.2020.11.1

The Inner Hebrides were home to diverse terrestrial and marine faunas during the Jurassic. Since the earliest discoveries by Hugh Miller (1858), an ever increasing variety of amphibians (Evans and Waldman, 1996), lepidosauromorphs (Waldman and Evans, 1994), turtles (Anquetin, 2010), dinosaurs (Clark, 2018; dePolo et al., 2018, 2020), ichthyosaurs (Brusatte et al., 2015), plesiosaurs (Clark, 1993), crocodylomorphs (Evans and Waldman, 1996; Wills et al., 2014; Young et al., 2016;

Yi et al., 2017), and mammaliamorphs (Waldman and Savage, 1972; Panciroli et al., 2017, 2018, 2019) have been reported, represented both by body and trace fossils.

Although NMS G.2020.11.1 is largely incomplete and poorly preserved, it still yields a suite of vertebral and osteodermal characters that distinguishes it from contemporaneous taxa previously reported on the Isle of Skye. The following vertebral and osteodermal characters suggest a crocodylomorph affinity for NMS G.2020.11.1:

i) Long hourglass-shape and amphicoelous vertebral centra (Fig. 3) (Andrews, 1913; Young et al., 2013; Johnson et al., 2017). Turtles also have vertebrae with an hourglass centrum (Joyce et al., 2009; Pérez-García, 2012). However, as in *Eileanchelys waldmani* from Skye, the vertebrae of turtles differ from those of crocodylomorphs and NMS G.2020.11.1 in being platycoelous (Joyce et al., 2009; Anquetin, 2010; Pérez-García, 2012). An affinity with dinosaurs can also be ruled out based on the morphology of the vertebrae in NMS G.2020.11.1. Although the dorsal vertebrae of ornithischians are typically longer than they are tall as is the case with NMS G.2020.11.1, they do not have a ventral surface as strongly concave as those in crocodylomorphs and NMS G.2020.11.1 (Galton, 1985). The vertebrae of saurischians are similarly distinct; the dorsals of sauropods, for example, are typically opisthocoelous and ornamented by deep pleurocoelous fossae (Romer, 1956; Wilson et al., 2011; Wilson, 2012). Pleurocoels (pneumatic fossae and foramina) are also seen in the dorsals of theropods, whose centra tend to be platycoelous (Romer, 1956; Rauhut, 2005). Furthermore, saurischians typically have a series of thin laminae on their dorsal vertebrae, but these are absent in NMS G.2020.11.1 (Wilson et al., 2011; Wilson, 2012). Amongst marine reptiles, the vertebrae of ichthyosaurs are amphicoelous, but are very short and their centra are not hourglass-shaped (McGowan and Motani, 2003). The vertebrae of plesiosaurs do not possess an "hourglass" profile, and the transverse processes of their dorsal vertebrae are rod-like, not plate-like as in crocodylomorphs and NMS G.2020.11.1. The transverse processes also diverge from the centra at an angle from the sagittal plane in plesiosaurs, whereas they are perpendicular to the centra in crocodylomorphs and NMS G.2020.11.1 (Andrews, 1910, 1913).

ii) Double rib attachment (diapophyses and parapophyses) on the transverse process (Fig. 3). Double-headed ribs are not exclusive to crocodylomorphs, and are also seen in ichthyosaurs and dinosaurs, whilst marine reptiles such as plesiosaurs and turtles have single-headed ribs (McGowan and Motani, 2003; Huh et al., 2011; Kim et al., 2011). However, the morphology of the rib attachments differs among these groups. In ichthyosaurs the diapophyses and parapophyses are located on the lateral surfaces of the centra of the dorsal vertebrae (McGowan and Motani, 2003). In the anterior dorsals of saurischian dinosaurs the parapophysis lies on the centrum and migrates to the neural arch in the middle and posterior dorsal vertebrae (Wilson et al., 2011). In the dorsal vertebrae of crocodylomorphs the parapophyses and diapophyses are located on the transverse process (Andrews, 1913), as is the case in NMS G.2020.11.1.

iii) Presence and shape of osteoderms (Figs. 4, 5). Amongst species in the Jurassic terrestrial and marine faunas of Skye, an integumentary skeleton of dermal bone is present in turtles, lepidosauromorphs, and archosaurs (Waldman and Evans, 1994; Vickaryous and Sire, 2009; Anquetin, 2010; Wills et al., 2014). However, the carapace of turtles and lepidosaurian scales differ substantially from the thick, disc-shaped osteoderms of archosaurs (Vickaryous and Sire, 2009). Amongst Early-Middle Jurassic archosaurs, osteoderms can be found in the vast majority of pseudosuchians (the larger group of crocodylomorphs and close relatives) and some ornithischian dinosaurs (e.g. stegosaurs and ankylosaurs). Osteoderms are also present in non-archosaurian archosauriformes such as the Triassic Proterochampsia and Doswelliidae (Cerda et al., 2015; Ezcurra 2016). Some of these groups can be readily excluded as potential identities for NMS G.2020.11.1. Non-crocodylomorph pseudosuchians and non-archosaurian archosauromorphs did not survive into the Jurassic. The osteoderms of stegosaurs take the form of unornamented and enlarged dermal plates that are organised in rows along the dorsolateral body surface (de Buffrenil et al., 1986; Main et al., 2005; Maidment et al., 2015). Ankylosaur osteoderms are often characterised by a keel and a dendritic pattern of vascularised furrows that radiate away from the keel and randomly organised pits on the dorsal surface (Burns, 2008). By contrast the pitted osteoderms present in NMS G.2020.11.1 resembles those of crocodylomorphs in shape, ornamentation, size, and association with the vertebral column (Burns et al., 2013; Schwarz et al., 2017).

275 Overall, the size and combination of vertebral and osteodermal characters demonstrates that NMS
276 G.2020.11.1 can be referred to a relatively large-bodied crocodylomorph. As several
277 crocodylomorph taxa have been reported from the Jurassic of Skye (Table 1) over the last two
278 decades (Evans and Waldman, 1996; Wills et al., 2014; Young et al., 2016; Yi et al., 2017), the
279 next section aims to clarify whether NMS G.2020.11.1 belongs to any of these taxa. Note that all
280 previous Skye crocodylomorphs come from Middle Jurassic rocks, whereas the provenance of
281 NMS G.2020.11.1 cannot be substantiated beyond the Jurassic generally (as discussed above).

282

4.1 Taxonomic comparisons with other Early and Middle Jurassic crocodylomorphs

284 Here we compare NMS G.2020.11.1 to Early and Middle Jurassic crocodylomorph clades found
285 on Skye, as well as worldwide. We have divided them into non-thalattosuchian crocodylomorphs,
286 namely Goniopholididae, Atoposauridae and Pholidasauridae, and thalattosuchian
287 crocodylomorphs.

288

4.1.1 Non-thalattosuchian crocodylomorphs

290 The crocodylomorph material known from Skye (Table 1) includes an incomplete dentary of a
291 hylaeochampsid-like taxon (Yi et al., 2017), a partial lower jaw from the atoposaurid *Theriosuchus*
292 (Young et al., 2016), a disarticulated incomplete postcranial skeleton from a goniopholidid (Evans
293 and Waldman, 1996), a left pubis from an indeterminate mesoeucrocodylian (Wills et al., 2014),
294 and a tooth and disarticulated osteoderms from an indeterminate neosuchian (Wills et al., 2014).
295 These specimens demonstrate that Skye hosted a variety of small-sized neosuchians in nearshore
296 environments during the Middle Jurassic. However, none of these groups share the same vertebral
297 and osteodermal characteristics as NMS G.2020.11.1, and were significantly smaller in body size
298 than NMS G.2020.11.1.

299

300 **Indeterminate neosuchian (Wills et al., 2014) -** Two previous crocodylomorph specimens
301 containing osteoderms have been reported from the Jurassic of Skye: NHMUK PV R 36713
302 (assigned by Wills et al. (2014) to Neousuchia indet.) and G.1992.47.6 (assigned to
303 Goniopholididae, discussed below). NHMUK PV R 36713 was found in the Kilmaluag Formation
304 on the southwest Elgol Peninsula of Skye and contains thirteen partial osteoderms. Some of the
305 more complete osteoderms show an overall quadrilateral structure ornamented by a straight

longitudinal keel and circular to oval pits (Fig. 6A) (Wills et al., 2014). The largest of the osteoderms is approximately 20 mm wide (Wills et al., 2014), which is significantly smaller than the osteoderms of NMS G.2020.11.1, which are up to 50 mm in width. Most pits ornamenting the osteoderms in NHMUK PV R 36713 are circular, with a few that are oval in shape (Fig. 6A) (Wills et al., 2014). The pits on NMS G.2020.11.1 are more varied in shape, with some that are circular, oval, and bean-shaped (Figs. 4, 5).

Goniopholididae - The dorsal osteoderms of Goniopholididae are plate-like, quadrilateral structures which are wider than long. The paramedial osteoderms of *Goniopholis*, for example, have a heavily ornamented dorsal surface, lack a keel, and are sub-rectangular and wider than long (Andrade et al., 2012; Wills et al., 2014). In contrast, cervical dorsolateral osteoderms from *Sunosuchus* described by Averianov (2000) are longer than wide and have a high longitudinal keel with oval-shaped pits arranged in alternating rows ornamenting the dorsal surface. Typically, the pits ornamenting the dorsal surface of Goniopholididae osteoderms are oval to circular in shape, while the anterior margin of the dorsal surface tends to be smooth (Fig. 6B) (Averianov, 2000; Kuzmin et al., 2013; Puértolas-Pascual et al., 2015; Puértolas-Pascual and Mateus, 2020). A partial postcranial skeleton with osteoderms discovered in the Kilmaluag Formation of Skye was assigned to Goniopholididae by Evans and Waldman (1996). This specimen (G.1992.47.6) is currently being held in the NMS collections and has significantly smaller osteoderms than NMS G.2020.11.1. The osteoderms in NMS G.2020.11.1 are also not as densely pitted as that of Goniopholididae indet. shown in Fig. 6B, nor are the pits as large. Whilst the pits are arranged in regular rows in both *Sunosuchus* and NMS G.2020.11.1, the pits in NMS G.2020.11.1 vary more in morphology than those in *Sunosuchus*.

***Theriosuchus* and Atoposauridae -** The *Theriosuchus* material previously described from Skye by Young et al. (2016) does not include osteoderms. Therefore, we will be making direct comparisons between NMS G.2020.11.1 and taxa closely related to *Theriosuchus*. In addition to *Theriosuchus* sp., atoposaurid taxa from the Jurassic include *Alligatorellus* sp., *Alligatorium* sp., *Atoposaurus* sp., and *Knoetschkesuchus langenbergensis* (Schwarz-Wings et al., 2011; Tennant and Mannion, 2014; Schwarz et al., 2017). The ventral osteoderms of these Late Jurassic atoposaurids tend to be quadrilateral in shape and ornamented with a shallow keel and circular pits

337 (Schwarz-Wings et al., 2011; Tennant and Mannion, 2014; Schwarz et al., 2017). NMS
338 G.2020.11.1 can be excluded from Atoposauridae in part because of its larger size. Atoposaurids
339 were characteristically very small in size, rarely reaching more than 1 m in overall body length
340 (Schwarz and Salisbury, 2005; Schwarz et al., 2017). Given that NMS G.2020.11.1 shows single
341 vertebrae 3-4 cm in length, the animal would have been significantly larger. In addition, the
342 osteoderms of NMS G.2020.11.1 do not show the same circular pitting as observed in atoposaurid
343 taxa.

344

345 **Pholidosauridae -** Pholidosaurids were common in freshwater and marginal marine environments
346 during the Late Jurassic and Early Cretaceous (Martin and Buffetaut, 2012). Their dorsal
347 osteoderms are typically rectangular in shape and are densely ornamented by small, deep, circular
348 and subcircular pits (Jouve and Jalil, 2020). With the thoracic osteoderms being highly elongated
349 mediolaterally (see Jouve and Jalil, 2020). This does not match the shape or ornamentation
350 observed in NMS G.2020.11.1.

351

352 **4.1.2   NMS G.2020.11.1 within Thalattosuchia**
353 Despite the diversity of crocodylomorphs on Skye, no evidence of thalattosuchians has previously
354 been recovered from the island, even though they are one of the most diverse crocodylomorph
355 clades of the Mesozoic (Pierce and Benton, 2006; Young et al., 2010, 2014; Young and Steel,
356 2014; Johnson et al., 2017; Foffa et al., 2019; Johnson et al., 2020c). This is puzzling for two
357 reasons: firstly, there are abundant marine deposits on Skye, and secondly, thalattosuchians were
358 relatively diverse in the Early and Middle Jurassic with multiple taxa found in the lagerstätten of
359 England (Andrews, 1910, 1913; Pierce and Benton, 2006; Brusatte et al., 2016; Foffa et al.,
360 2018a,b). Specifically, three teleosauroid taxa (*Plagiophthalmosuchus* [*"Steneosaurus"*]
361 *gracilirostris*, *Macrospondylus* [*"Steneosaurus"*] *bollensis*, and *Mystriosaurus*) (Westphal, 1961;
362 Walkden et al., 1987; Sachs et al., 2019), and one basal metriorhynchoid (*Pelagosaurus typus*)
363 (Pierce and Benton, 2006) are known from the Lower Jurassic of Southern England and Yorkshire;
364 and at least four teleosauroids (*Neosteneosaurus* [*"Steneosaurus"*] *edwardsi, Charitomenosuchus*
365 [*"Steneosaurus"*] *leedsi, Mycterosuchus nasutus, Lemmysuchus obtusidens*) (Andrews 1913;
366 Johnson et al., 2015, 2017; Foffa et al., 2018a,b), and seven metriorhynchids (*Ieldraan*
367 *melkshamensis, Suchodus durobrivensis, "Metriorhynchus" brachyrhynchus, Tyrannoneustes*

368 *lythrodectikos, Dakosaurus*–like specimens, *Metriorhynchus superciliosus, Gracilineustes leedsi*)

369 (Andrews, 1913; Young and Andrade, 2009; Young et al., 2012; Foffa and Young, 2014; Foffa et

370 al., 2017, 2018a,b, 2019), are known from the late Middle Jurassic of the Oxford Clay Formation.

371 The following paragraphs will be used to compare NMS G.2020.11.1 to worldwide Early and

372 Middle Jurassic teleosauroids and basal metriorhynchoids, with emphasis on taxa from England.

373 Due to the limited variation of vertebrae in teleosauroids we largely focus on differences in

374 osteoderm shape, thickness, and ornamentation. NMS G.2020.11.1 will not be compared with

375 metriorhynchids as they do not possess osteoderms (Young et al., 2013).

376

377 **Basal Metriorhynchoids -** Early Jurassic metriorhynchoids such as *Pelagosaurus typus* (Fig. 6C)

378 and *Magyarosuchus fitosi* (Fig. 6D) had osteoderms, unlike derived metriorhynchoids of the

379 family Metriorhynchidae. However, the osteoderms of all known basal metriorhynchoids differ

380 from those in NMS G.2020.11.1; for instance, the paramedial dorsal osteoderms of *Pelagosaurus*

381 *typus*, which are also sub-rectangular, have a very low keel, and a honey-comb pattern of pits

382 (Pierce and Benton, 2006), and are more densely ornamented (e.g. more numerous pits) than NMS

383 G.2020.11.1 (Fig. 6C). The dorsal osteoderms of *Magyarosuchus fitosi*, on the other hand, are

384 large, rectangular to slightly rounded in shape, and are ornamented with an anteroposterior dorsal

385 keel and irregularly shaped pits (Fig. 6D) (Ősi et al., 2018). The pits range from circular, ellipsoid,

386 bean-shaped, triangular to quadrangular morphologies, and show variations in size from small to

387 very large on the dorsal surface (Ősi et al., 2018). Whilst the pits ornamenting *M. fitosi* are

388 predominantly triangular in shape, NMS G.2020.11.1 is largely adorned by sub-circular and bean-

389 shaped pits. In addition, the disparity in size of pits is not as large in NMS G.2020.11.1 as it is in

390 *M. fitosi.*

391

392 **Early Jurassic Teleosauroids -** Specific teleosauroids that are known from the Early Jurassic

393 include *Pl. gracilirostris* (NHMUK PV OR 14792) (Fig. 7A), *Mystriosaurus laurillardi* (Fig. 7B),

394 *Platysuchus multiscrobiculatus* (SMNS 9930) (Fig. 7C), and *Ma. bollensis* (SMNS 51563) (Fig.

395 7D). The Chinese teleosauroid (IVPP RV 10098), which was previously referred to as

396 *Peipehsuchus teleorhinus* (Li, 1993), may also be from the Early Jurassic. However, the

397 provenance of IVPP RV 10098 and the holotype (IVPP RV 48001) is somewhat uncertain, and so

398 the Chinese teleosauroid is considered to be Early-Middle Jurassic in age (Martin et al., 2018).

399 Osteoderms are known from all but *Mystriosaurus laurillardi* and the Chinese teleosauroid.
400 However, one particular specimen located at the Staatliches Naturhistorisches Museum (SNHM)
401 in Braunschweig, Germany (SNHM-IG-008-R), which was assigned to *"Steneosaurus"* af.
402 *bollensis* by Wincierz (1967) contains partial osteoderms, and is currently thought to belong to
403 *Mystriosaurus* sp. Comparisons will therefore be made between SNHM-IG-008-R and NMS
404 G.2020.11.1. It is important to note that a formal description is currently in preparation by MMJ
405 and colleagues, and is beyond the scope of this paper.
406
407 The osteoderms of *Pl. gracilirostris* are unfortunately poorly preserved, making direct
408 comparisons difficult. The osteoderms appear to have small, moderately spaced pits, and is
409 ornamented by a very weak keel (Fig. 7A). In contrast, the osteoderms of *Ma. bollensis* are
410 ornamented by numerous, relatively close pits which are semi-ellipsoidal in shape (Fig. 7D).
411 However, there is great variety in keel size within *Ma. bollensis*, whilst some have prominent
412 keels, other individuals of comparable size can have weak keels. *Platysuchus multiscrobiculatus*
413 has a weak keel on the osteoderms, with small, circular, numerous pits that are densely packed
414 together (Fig. 7C). The pits on the dorsal osteoderms of *Mystriosaurus* sp. are closely packed
415 together, ellipsoidal in shape, and are arranged in a subtle 'starburst' pattern (Fig. 7B).
416
417 The shape of the pits in NMS G.2020.11.1 are not dissimilar to those of *Ma. bollensis*, however
418 unlike the osteoderms of *Ma. bollensis*, *P. multiscrobiculatus*, and *Mystriosaurus* sp., those of
419 NMS G.2020.11.1 do not have densely packed pits or a keel. The pits on NMS G.2020.11.1 are
420 not arranged in any kind of 'starburst' pattern either, as is the case in *Mystriosaurus* sp.
421
422 **Middle Jurassic Teleosauroids -** Teleosauroid taxa from the Bathonian include *Teleosaurus*
423 *cadomensis* (Fig. 7E), *Yvridiosuchus boutilieri*, *Deslongchampsina larteti*, *Seldsienean*
424 (*"Steneosaurus"*) *megistorhynchus*, *Clovesuurdameredeor* (*"Steneosaurus"*) *stephani*, and
425 *Andrianavoay* (*"Steneosaurus"*) *baroni* (Fig. 7F); however, osteoderms are currently only known
426 from *T. cadomensis* (NMHUK PV R 119a) and *A. baroni* (NHMUK PV R 1999). The dorsal
427 osteoderms of *T. cadomensis* are similar to those of *Platysuchus*, in which they are ornamented by
428 a weak keel and numerous, small, circular, densely packed pits (Fig. 7E) (Johnson et al., 2020a).
429 Only a small fragment of dorsal osteoderm is preserved for *A. baroni* (Fig. 7F). It shows well

430 separated, moderately sized, and subcircular pits which resembles the pit ornamentation of NMS
431 G.2020.11.1. However, it is currently unclear where this osteoderm may have been along the body;
432 it is also important to note that *A. baroni* (NHMUK PV R 1999) is currently only known from
433 Madagascar (Newton, 1893).

435 More well-known, Callovian teleosauroids include *C. leedsi* (NHMUK PV R 3806) (Fig. 7G), *N.*
436 *edwardsi* (PETMG R178) (Fig. 7H), *Lemmysuchus obtusidens* (NHMUK PV R 3168) (Fig. 7I),
437 and *Mycterosuchus nasutus* (NHMUK PV R 2617) (Fig. 7J), all of which have well preserved,
438 multiple dorsal osteoderms. Those of *C. leedsi* are ornamented by a shallow keel and small-to-
439 large sub-circular and elliptical pits, arranged in a semi-circular pattern (Fig. 7G). In *N. edwardsi*
440 (Fig. 7H), the pits are few, subcircular and exceptionally large (especially in the middle of the
441 osteoderm). In *L. obtusidens* (Fig. 7I), the osteoderms display distinctive elongated pits that merge
442 together (notably along the lateral margin) as well as irregularly shaped, relatively close pits that
443 are arranged in a 'starburst' pattern. The pits on the osteoderms of *My. nasutus* are well separated
444 and are largely irregular in shape, some of which are bean-shaped. The osteoderms in this taxon
445 possess a relatively well developed keel (Fig. 7J). This pit pattern is not dissimilar to that of NMS
446 G.2020.11.1, which also has sub-circular and some bean-shaped pits arranged into alternate rows,
447 with the smallest pits on the edges of the osteoderm. However, among Teleosauroidea, the dorsal
448 osteoderms of *My. nasutus* are unusually large and thick (DF. pers. obs. on NHMUK PV R 2617
449 and CAMSM J. 1420), which are features not seen in NMS G.2020.11.1.

451 In summary, NMS G.2020.11.1 was recovered from marine beds, and is significantly larger than
452 any crocodylomorph material previously discovered on Skye. Its vertebral morphology and
453 osteoderm ornamentation exclude an affinity between NMS G.2020.11.1 and any other
454 crocodylomorph clade previously described from the Isle of Skye. Instead, the osteoderms of NMS
455 G.2020.11.1 most closely resemble those of the Early Jurassic thalattosuchian teleosauroid *Ma.*
456 *bollensis*, indicating that it is most likely a teleosauroid, which is concordant with its large body
457 size, Jurassic age, and aquatic provenance. However, we acknowledge that NMS G.2020.11.1 is
458 composed of fragmentary material which are of limited diagnostic utility. Therefore, we do not
459 attempt to assign NMS G.2020.11.1 to a specific taxon and instead conservatively consider it
460 Teleosauroidea indeterminate.

5.   Discussion

Research over the last two decades has shown that Skye was home to a diverse crocodylomorph fauna of small-bodied, non-pelagic, neosuchians such as goniopholidids, atoposaurids and a hylaeochampsid-like taxon in the Jurassic (Evans and Waldman, 1996; Young et al., 2016; Yi et al., 2017). Not only is NMS G.2020.11.1 the first evidence of larger semi-aquatic crocodylomorphs on Skye during the Jurassic, it is also the most northerly thalattosuchian discovered to date. Previously the most northern thalattosuchians were recovered from the Blue Lias of Yorkshire on the east coast of England (Benton and Taylor, 1984; Foffa et al., 2018a).

The distribution of thalattosuchians appears to be more restricted than that of other marine reptiles. Marine pseudosuchians, including thalattosuchians, inhabited waters between palaeolatitudes of ~44°N and ~38°S (Mannion et al., 2015). With a palaeolatitude of ~40°N, Scotland was within the upper limits of this hypothesised habitable range for thalattosuchians (Nunn et al., 2009). Other marine tetrapods (e.g. ichthyosaurs and plesiosaurs) had a wider latitudinal range between ~69°N and 42°S (Mannion et al., 2015); and unlike thalattosuchians, pelagic sauropterygians and ichthyosaurs have been discovered much further north of Scotland, in Svalbard and Siberia (Delsett et al., 2015; Rogov et al., 2018; Zverkov et al., 2015a,b, 2018, 2019a,b). One possible explanation for this discrepancy is that plesiosaurs and ichthyosaurs were fully homeothermic endotherms, possibly being able to maintain their core temperatures between 32–40ºC (Bernard et al., 2010; Motani, 2010; Séon et al., 2020).

While Jurassic thalattosuchians do not show evidence for homeothermic endothermy, with large-bodied teleosauroids potentially being 'gigantothermic' (like modern saltwater crocodiles), metriorhynchids may have been endothermic but poorly homeothermic (see Séon et al., 2020). Young et al. (2010) hypothesized that the closure of the external mandibular fenestrae in metriorhynchids was due to them no longer requiring mouth-gape basking to thermoregulate, a behaviour which teleosauroids likely utilized to raise their body temperatures, similar to extant crocodylians (Séon et al., 2020). This may have restricted teleosauroids to warmer, more hospitable climates and rendered more pole-ward habitats unfeasible. However, among extant crocodylians the American and Chinese alligators (*Alligator mississippiensis* and *Alligator*

492   *sinensis*) are able to inhabit temperate climates, and have the greatest tolerance to cold
493   environments of living crocodylomorphs, surviving by brumating in the winter, either underwater
494   or in burrows (e.g. Lang, 1987).

495

496   There is growing evidence that symplesiomorphically, crocodylomorphs had some form of
497   homeothermic and/or endothermic thermophysiology (Seymour et al., 2004; Summers, 2005; de
498   Ricqlès et al., 2008; Farmer and Sanders, 2010; Legendre et al., 2016). It has been hypothesised
499   that thalattosuchians reverted to poikilothermic ectothermy when they became aquatic ambush
500   predators during the Early Jurassic (Seymour et al., 2004; Mannion et al., 2015). Séon et al. (2020)
501   suggested that endothermy may have been 'reactivated' as metriorhynchids became better adapted
502   to an active pelagic lifestyle. Because of this difference in thermoregulatory strategy,
503   metriorhynchoids were likely less restricted by palaeolatitude than teleosauroids (Séon et al.,
504   2020). In recent years, several major disparities in the ecological niches and modes of life between
505   metriorhynchoids and teleosauroids have been uncovered using skeletal, neuroanatomical, and
506   geochemical data (e.g. Foffa et al., 2018b; Schwab et al., 2020; Séon et al., 2020).

507

508   **6.   Conclusion**

509   Here we report the discovery of new crocodylomorph material recovered from Jurassic marine
510   deposits on the Isle of Skye. NMS G.2020.11.1 is a small cobble containing partial vertebrae,
511   osteoderms, and ribs, from an animal larger than previous Jurassic crocodylomorphs described
512   from Skye. We establish that the material can be assigned to an indeterminate teleosauroid
513   thalattosuchian crocodylomorph based on vertebral and osteodermal characters. The pattern of the
514   pitting ornamenting the dorsal surface of the osteoderms, for instance, most closely resembles that
515   of the teleosauroid *Macrospondylus bollensis*. NMS G.2020.11.1 is consequently the first reported
516   thalattosuchian from Scotland, and the most northerly thalattosuchian material recovered to date
517   worldwide. NMS G.2020.11.1 is therefore an important specimen despite its fragmentary nature,
518   as it reveals further information on the palaeobiogeography of thalattosuchians during a poorly
519   sampled period of time. It suggests that other thalattosuchians may be found in Scotland in the
520   future, including other teleosauroids, and metriorhynchoids which were probably better adapted
521   for more northerly waters in the Jurassic.

522

7.   Acknowledgments

8.   References

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TABLES
Table 1: Summary of crocodylomorph specimens from the Middle Jurassic of Skye reported in the literature

FIGURE CAPTIONS

Figure 1: Map of Skye, Scotland, showing the geographical and geological context for the crocodylomorph specimen described here. Cross indicating location of Prince Charlie's Cave. Maps adapted from Brusatte et al. (2015) and Morton (2004).

Figure 2: (a) 3D model and (b) photograph of a cobble containing vertebrae, osteoderms, and ribs of a Teleosauroidea indet. from the Jurassic of Skye, Scotland. Scale bar 5cm.

Figure 3: Teleosauroidea indet. Vertebrae from the Jurassic of Skye, Scotland. A1–C6 series of three unassociated dorsal vertebrae from the Jurassic (NMS G.2020.11.1) in anterior, left lateral, posterior, right lateral, ventral, and dorsal views. Scale bar = 2cm
cent. = centrum; nc. = neural canal; ns. = neural spine; prz.= prezygapophyses; tp. = transverse process

Figure 4: Isolated Teleosauroidea indet. osteoderms from the Jurassic of Skye, Scotland (NMS G.2020.11.1) in dorsal, ventral, left lateral, right lateral, anterior, posterior views. Scale bar = 2cm.

Figure 5: Isolated Teleosauroidea indet. osteoderm fragments and rib from the Jurassic of Skye, Scotland (NMS G.2020.11.1). A–C osteoderms in dorsal and ventral views. D – rib in dorsal, ventral, left and right lateral views. Scale bar = 2cm.

Figure 6: Comparative plate of non-teleosauroid Jurassic crocodylomorph dorsal osteoderms. A – Neosuchia indet. (Wills et al., 2014) scale bar = 2cm; B – Goniopholididae indet. (Kuzmin et al., 2013) scale bar = 2cm; C – *Pelagosaurus typus* (MNHN.F RJN 463) scale bar = 2cm; D - *Magyarosuchus fitosi* (Ősi et al., 2018) scale bar = 5cm.

Figure 7: Comparative plate of Jurassic thalattosuchians dorsal osteoderms. A – *Plagiophthalmosuchus gracilirostris* (NHMUK PV OR 14792) scale bar = 2cm; B – *Mystriosaurus* sp. (SNHM-IG-008-R) scale bar = 2cm; C – *Platysuchus multiscrobiculatus* (SMNS 9930) scale bar = 5cm; D – *Macrospondylus bollensis* (SMNS 51984) scale bar = 2cm; E – *Teleosaurus* sp. (NHMUK PV R 119a) scale bar = 2cm; F – *Andrianavoay baroni* (NHMUK PV R 1999) scale bar = 2cm; G – *Charitomenosuchus leedsi* (NHMUK PV R 3806) scale bar = 2cm; H – *Neosteneosaurus edwardsi* (PETMG R178) scale bar = 5cm; I – *Lemmysuchus obtusidens* (NHMUK PV R 3168) scale bar = 2cm; J – *Mycterosuchus nasutus* (NHMUK PV R 2617) scale bar = 5cm (A-D = Early Jurassic; E-J = Middle Jurassic (E-F = Bathonian; G-J = Callovian)). Note that the positioning of (F) is unknown.
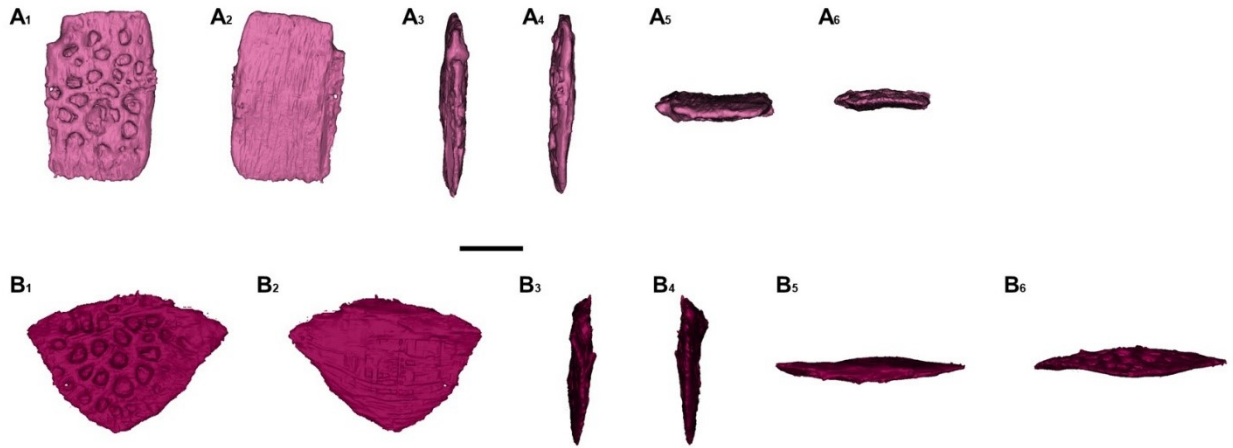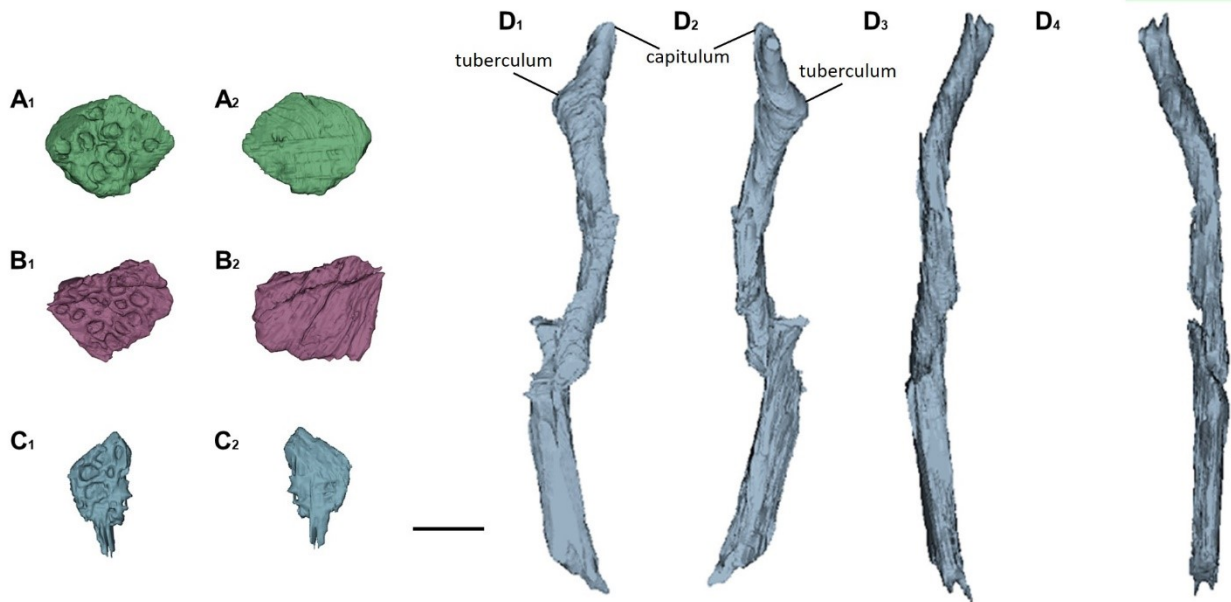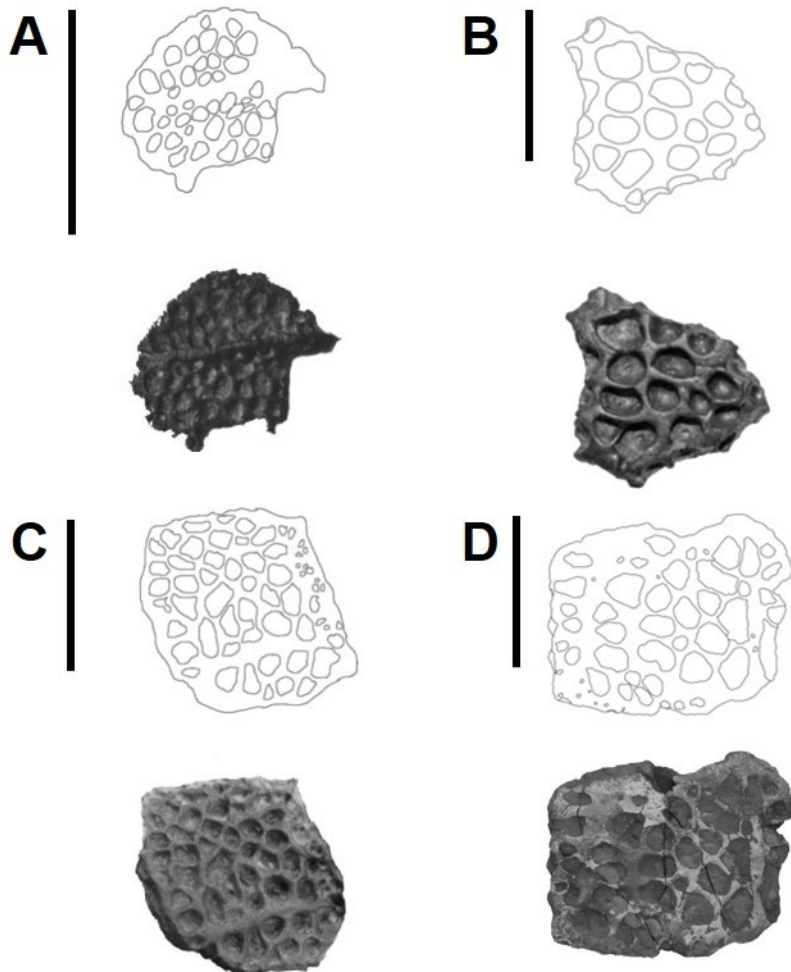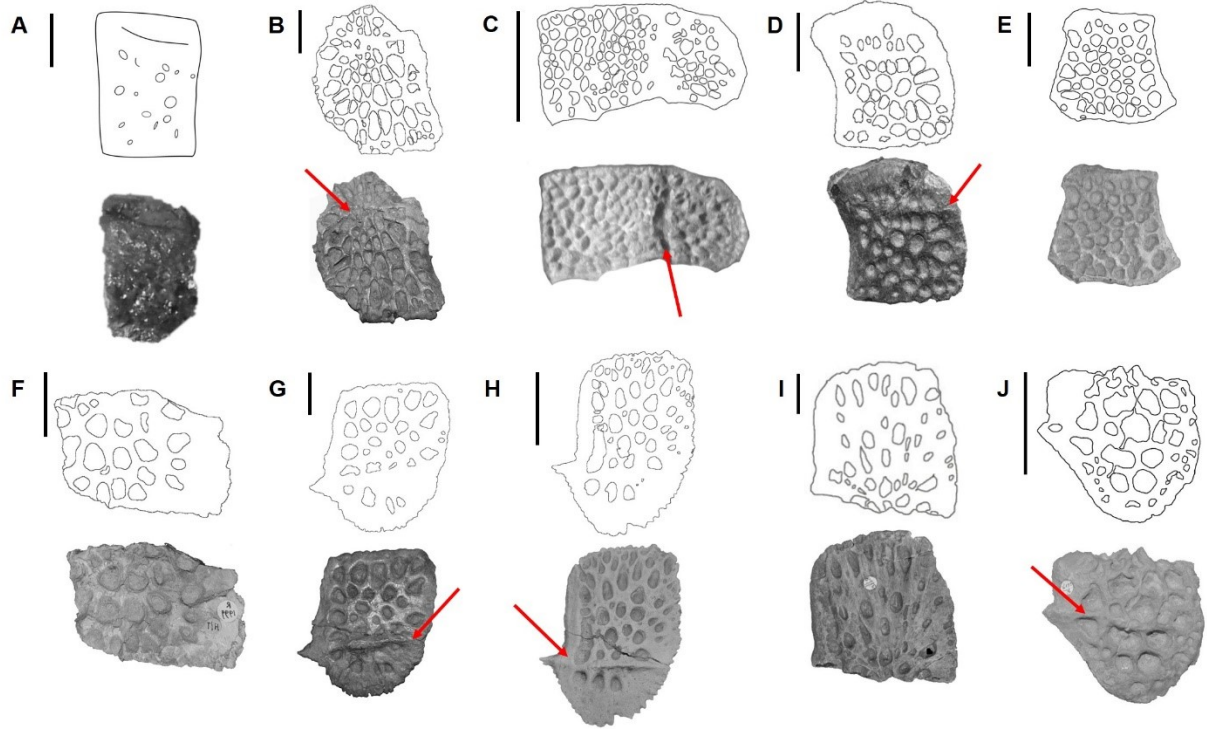
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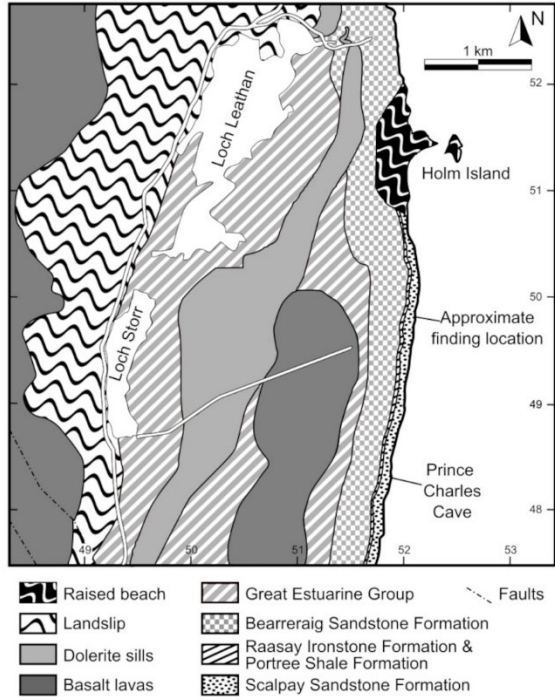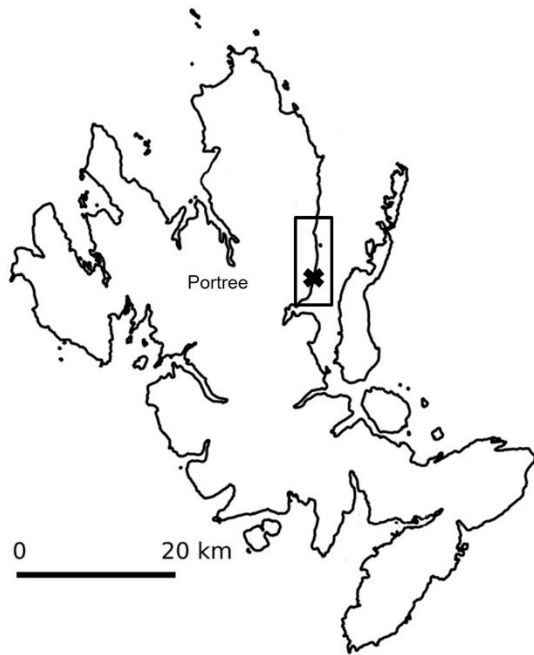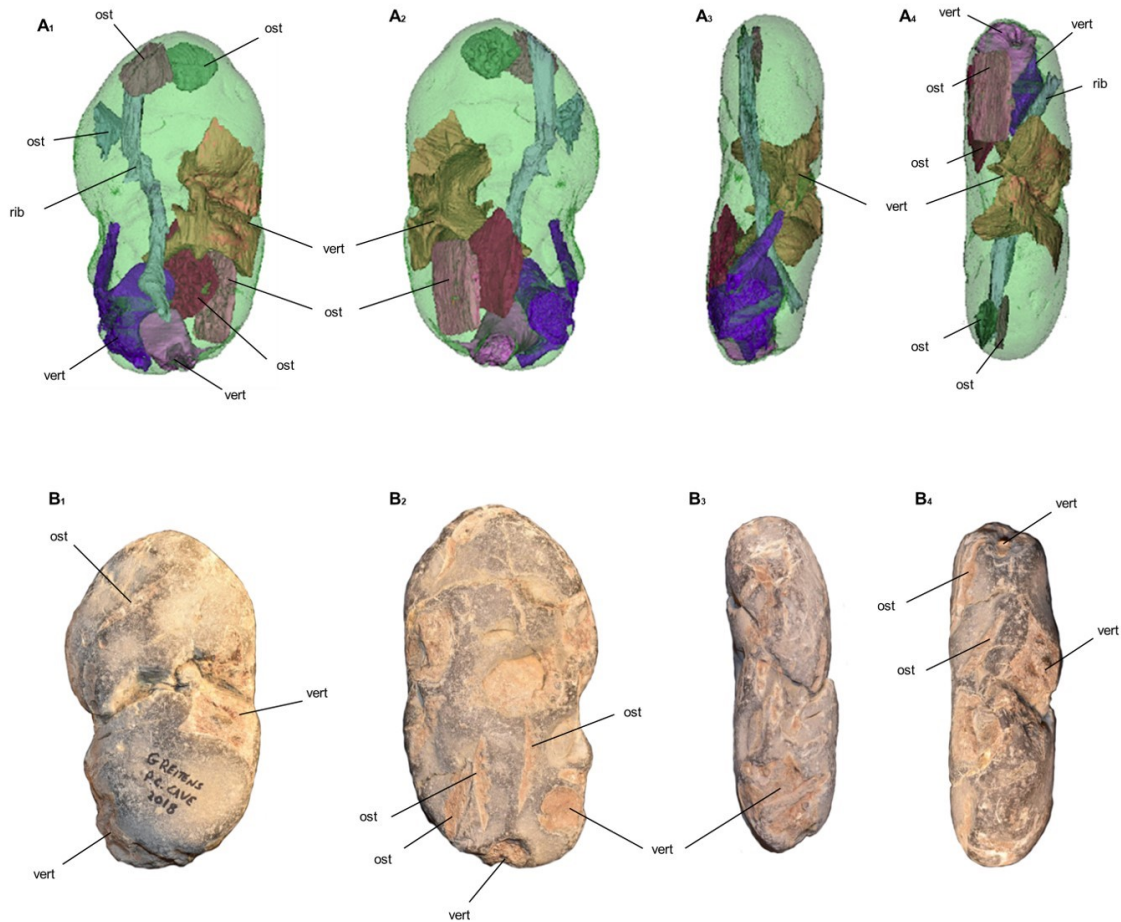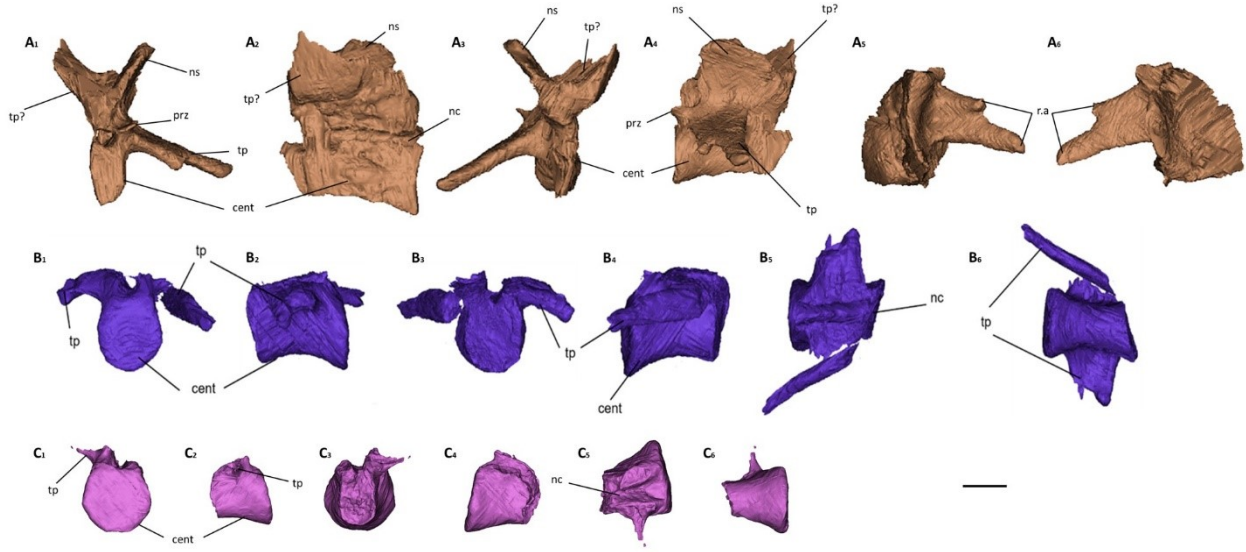
Age	Geology	Collection	Material	Reference	Taxon
Bathonian	Kilmaluag Formation	NMS G. 1992.47.6	Disarticulated partial postcranial skeleton	Evans and Waldman (1996)	Goniopholididae
Bathonian	Duntulum Formation	NMS G.2016.21.1	Incomplete left dentary and incomplete splenial	Yi et al. (2017)	Neosuchia cf. Hylaeochampsidae
Late Bajocian-Bathonian	Valtos Sandstone Formation	NMS G.2014.52	Anterior dentary	Young et al. (2016)	Theriosuchus
Bathonian	Kilmaluag Formation	NMS G.1992.47.51	Left pubis	Wills et al. (2014)	Indeteminate mesoeucrocodylian
Bathonian	Kilmaluag Formation	NHMUK R36713	Disarticulated osteoderms and single tooth	Wills et al (2014)	Neosuchia indet.

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