EARTH AND ENVIRONMENTAL SCIENCE
TRANSACTIONS OF THE ROYAL SOCIETY
OF EDINBURGH

CAMBRIDGE
UNIVERSITY PRESS

An unusual small-bodied crocodyliform from the Middle Jurassic of Scotland, UK, and potential evidence for an early diversification of advanced neosuchians

Journal:	*Earth and Environmental Science Transactions of the Royal Society of Edinburgh*
Manuscript ID	Draft
Manuscript Type:	Spontaneous Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Yi, Hong-yu; Grant Institute, School of Geosciences; Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology Tennant, Jonathan; Imperial College London, Earth Science and Engineering Young, Mark; University of Edinburgh, School of GeoSciences Challands, Thomas; University of Edinburgh, School of GeoSciences Foffa, Davide; Grant Institute, School of Geosciences Hudson, John; University of Leicester, Department of Geology Ross, Dugald; Staffin Museum, Earth Sciences Brusatte, Stephen; Grant Institute, School of Geosciences; National Museums Scotland, Earth Sciences
Keywords:	Isle of Skye, Mesozoic, Duntulm Formation, Eusuchia origin

SCHOLARONE™
Manuscripts

An unusual small-bodied crocodyliform from the Middle Jurassic of Scotland, UK, and

potential evidence for an early diversification of advanced neosuchians

HONGYU YI[1, 2], JONATHAN P. TENNANT[3*], MARK T. YOUNG[1], THOMAS J.

CHALLANDS[1], DAVIDE FOFFA[1], JOHN D. HUDSON[4], DUGALD A. ROSS[5], *and*

STEPHEN L. BRUSATTE[1, 6]

[1] School of GeoSciences, Grant Institute, The King's Buildings, University of Edinburgh, James

Hutton Road, Edinburgh EH9 3FE, UK

[2] Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences,

Beijing, 100044, China

[3] Department of Earth Science and Engineering, Imperial College London, London, SW6 2AZ,

UK

[4] Department of Geology, University of Leicester, University Road, Leicester LEI 7RH

[5] Staffin Museum, 6 Ellishadder, Staffin, Isle of Skye IV51 9JE, UK

[6] National Museums Scotland, Chambers Street, Edinburgh EH1 1JF, UK

[#]These authors listed alphabetically

* Corresponding author: jon.tennant.2@gmail.com

RUNNING HEAD: Middle Jurassic crocodyliform from Scotland, UK

ABSTRACT

The Middle Jurassic is a poorly sampled time interval for non-marine neosuchian crocodyliforms, which obscures our understanding of the origin and early evolution of major clades. Here we report a lower jaw from the Middle Jurassic (Bathonian) Duntulm Formation of the Isle of Skye, Scotland, UK, which consists of an isolated and incomplete left dentary and part of the splenial. Morphologically, the Skye specimen closely resembles Cretaceous hylaeochampsids, including *Pachycheilosuchus* and *Pietraroiasuchus*, in having a proportionally short mandibular symphysis, shallow dentary alveoli, a strongly laterally compressed dentary, and inferred weakly heterodont dentition. It differs from other crocodyliforms in that the Meckelian canal is dorsoventrally expanded posterior to the mandibular symphysis and drastically constricted at the 6th alveolus. We tentatively refer the new specimen to cf. Hylaeochampsidae sp. which, together with the presence of *Theriosuchus* sp. from the Valtos Formation and indeterminate neosuchians from the Kilmaluag Formation, indicates the presence of a previously unrecognized highly diverse crocodyliform fauna in the Middle Jurassic of Skye, and Europe more generally. This new specimen indicates that small-bodied neosuchians were present, and ecologically and taxonomically diverse, in nearshore environments in the Middle Jurassic of the UK.

Key words: Isle of Skye, Mesozoic, Duntulm Formation, Eusuchia origin

Modern crocodiles and alligators are the only living members of Crocodyliforms, a group of archosaurs whose evolutionary history spans about 200 million years (Whetstone and Whybrow, 1983; Benton and Clark, 1988; Bronzati et al., 2015; Mannion et al., 2015). The Middle Jurassic was a key period in their evolution, with thalattosuchians rapidly diversifying in the marine realm (e.g., Gasparini and Chong, 1977; Young et al., 2010, 2011; Wilberg, 2015). Much less is known about the non-marine crocodyliforms from this time, however. Apparently terrestrial and freshwater species were stuck in a low point of their diversity, although this could be an artefact of the notoriously poor Middle Jurassic fossil record. Sparse sampling during this interval complicates our understanding of non-marine crocodyliform diversification patterns (Bronzati et al., 2015; Mannion et al., 2015; Tennant et al., 2016), meaning that new Middle Jurassic fossils are critical.

Indeed, non-marine crocodyliform faunas during the Middle Jurassic remain poorly understood compared with other geological intervals. During the Late Jurassic, most crocodyliforms in Europe were goniopholidids and atoposaurids (Andrade et al., 2011; Young et al., 2016; Tennant et al., in press), and at the same time small-bodied sphenosuchian and protosuchian-grade taxa were widely distributed in other parts of the world (Gao, 2001; Clark et al., 2004; Göhlich et al., 2005; Pol et al., 2013). By the Early Cretaceous, the European faunas comprised a more diverse assemblage of neosuchians, including goniopholidids, pholidosaurids, bernissartiids, putative atoposaurids, and hylaeochampsids (e.g., Salisbury and Naish, 2011; Sweetman et al., 2015). Depending on the systematic position of these Cretaceous neosuchian clades, ghost lineages imply that some of these major lineages may have gotten their start during the dark period of the

Middle Jurassic (e.g., Bernissartiidae, Hylaeochampsidae, Paralligatoridae, and Pholidosauridae: Bronzati et al., 2015; Turner, 2015; Tennant et al., 2016).

The problem, however, is that there are few places where Jurassic (and in particular Middle Jurassic) crocodyliforms can be found. Non-marine fossil-bearing beds of the Jurassic are sparsely distributed in China (Gao, 2001; Maisch et al., 2003; Fu et al., 2005), Kyrgyzstan (Averianov, 2000), parts of Europe (Evans and Milner, 1994; Kriwet et al., 1997; Knoll et al., 2013; Knoll and López-Antoñanzas, 2014; Young et al., 2016), and Russia (Kuzmin et al., 2013), and these have yielded some crocodyliform fossils. Furthermore, there are undescribed crocodyliform teeth of this age from Thailand (Tong et al., 2002) and possible remains from Madagascar (Dal Sasso and Pasini, 2003; Flynn et al., 2006), but these are fragmentary. The vast majority of Middle Jurassic crocodyliform fossils are isolated specimens from microvertebrate localities—limited evidence that makes it difficult to assign these fossils to higher-level clades, which in turn hinders our understanding of the origin and early evolution of these groups that would later go on to great diversity and success in the Cretaceous and beyond.

Here we report a new crocodyliform lower jaw from the Middle Jurassic of the Isle of Skye, Scotland, UK (Fig. 1). This study is part of an ongoing investigation of the world-class Middle Jurassic vertebrate fossil record of Skye, led by the PalAlba Group (Brusatte et al., 2015a, 2015b; Brusatte and Clark, 2015; Young et al., 2016). Previously identified crocodyliforms from Skye include indeterminate remains (Evans et al., 2006; Wills et al., 2014) and a partial skeleton (Evans and Waldman, 1996) from Cladach a'Ghlinne (Fig. 1B) and a partial lower jaw assigned to *Theriosuchus* sp. (Young et al., 2016) from Valtos (Fig. 1B). The new specimen represents a hitherto unknown small-

bodied taxon from the Middle Jurassic Skye tetrapod assemblage, and has implications for the diversity and ecology of non-marine crocodyliforms of the poorly-sampled Middle Jurassic.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA.

IPFUB, Institut für Paläontologie der Freie Universität Berlin, Berlin, Germany.

NHMUK, Natural History Museum, London, UK.

NMS, National Museums Scotland, Edinburgh, UK.

PC-1, provisional specimen number for *Pietraroiasuchus ormezzanoi* Buscalioni et al., 2011 at Museo Regionale di Scienze Naturali di Torino, Italy.

SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, USA.

1. Systematic Palaeontology

CROCODYLIFORMES BENTON & CLARK, 1988

MESOEUCROCODYLIA WHETSTONE & WHYBROW, 1983

NEOSUCHIA BENTON & CLARK, 1988

cf. Hylaeochampsidae sp.

Specimen

NMS G.2016.21.1: an isolated and incomplete, three-dimensionally preserved left lower jaw, including much of the dentary and part of the splenial. It is broken posterior to where the Meckelian canal enters the dentary.

6

Differential diagnosis

A small-bodied crocodyliform, differing from other members of the group in the following features: Meckelian canal dorsoventrally expanded posterior to the mandibular symphysis and constricted at the 6th alveolus; mandibular symphysis mediolaterally thin and dorsoventrally broad; nutrient foramina present medial to the tooth row, with a one-to-one association with the tooth sockets from teeth 4-8; lateral nutrient foramina evenly spaced, forming a row that curves dorsally at the 6th alveolus; the 5th dentary tooth socket smaller than the 4th and 6th and slightly raised from the tooth row.

Locality

The specimen was collected from bed 46 of the type section of the Duntulm Formation at the southern part of the exposures (NG407 734) at Cairidh Ghlumaig, Isle of Skye, Scotland, United Kingdom (Morton and Hudson, 1995:Figs. 35-36, Table 2) (Fig. 1C).

The Duntulm Formation (Bathonian, Middle Jurassic) is part of the Great Estuarine Group, (Anderson, 1948), which crops out in portions of the northwest Highlands of Scotland, including the Isles of Skye, Raasay, Eigg, and Muck (Harris and Hudson, 1980). It consists of sedimentary rocks of marginal marine and non-marine lagoonal and fluvial origin, deposited in the Hebrides Basin during the Bathonian of the Middle Jurassic (Harris and Hudson, 1980).

Seven formations belong to the Great Estuarine Group (Fig. 1A). The upper formations of the Group, following an initial transgression across the fluvial deltas of the

Valtos Formation, were deposited during a phase of marine regression (Andrews, 1985), which shows a transition from shelly limestone, shale, and mudstone in the Duntulm Formation (Andrews and Walton, 1990), to interbedded shale, fine grained limestone and dolomite (with desiccation cracks) and fine-grained sandstones in the freshwater lagoonal Kilmaluag Formation, and finally to silty clay, coarse sandstone, and intraformational conglomerates in the fluvial Skudiburgh Formation (Andrews, 1985).

The Duntulm Formation represents the nearest approach to marine conditions within the Great Estuarine Group, and the strata from which NMS G.2016.21.1 was collected have one of the most marine-dominated molluscan fauna within the Duntulm Formation as a whole. In these beds, the small oyster *Praeexogyra hebridica*, which forms nearly monotypic shell beds that dominate much of the formation, is joined by bivalve genera such as *Camptonectes*, *Placunopsis*, *Corbula*, and *Modiolus*, and by echinoid spines, all typical of contemporaneous shallow marine deposits in England. The trace fossil *Thalassinoides* indicates the presence of burrowing crustaceans.

With that said, the facies is not simple marine. Cyanobacterial ('algal') limestones interbedded with the oyster-bearing limestones show evidence of both subaerial exposure and freshwater flushing (Andrews, 1986). Carbon, oxygen, and strontium isotopic studies of the oysters show that the lagoons where they lived were at times isolated from the sea and suffered evaporation (Holmden and Hudson, 2003). An intercalation of strata bearing the bivalves *Unio* and *Neomiodon*, a few meters above where NMS G.2016.21.1 was discovered, emphasizes the potential for freshwater input, confirmed by the isotopic investigations. A scenario depicting the overall environment was presented by Hudson and Trewin (2003). Dinosaur fossils, most notably the trackways of large sauropods, are

now known from the lower part of the formation (Brusatte et al., 2015b), northeast of where NMS G.2016.21.1 was collected.

Bed 46, from which the crocodyliform specimen came, is more sandy than the surrounding beds. Unlike them, it yields the freshwater alga *Bothrococcus*, probably washed in along with the sand (Andrews and Walton, 1990). However, its dominant fauna is of marine-related genera.

In NMS G.2016.21.1, the matrix surrounding the bone is greenish grey sandstone that weathers to a buff-orange colour (Fig. 1D). Besides the crocodyliform jaw, the matrix preserves fish scales, fish teeth, and shells of the oyster *Praeexogyra hebridica*. The small oysters are preserved isolated and broken, confirming a high-energy near-shore environment. It may be that the crocodyliform was part of the marine fauna that invaded the oyster lagoons at times of maximum marine influence.

Preparation and scanning

Physical preparation exposed the medial surface of the jaw and most of the dorsal surface of the tooth row, whereas the lateral surface and the anterior tip of the dentary remain embedded within the matrix. We used high-resolution X-ray computed tomography (HRCT) to visualize the entire specimen, including the embedded portions (Fig. 2). We scanned the fossil in a custom-build machine (constructed and operated by Dr Ian Butler) at the School of GeoSciences, University of Edinburgh, using a 240 kv GE X-ray generator. The scan has a resolution of 44 μm, which was performed under 2.8 w power and with a 0.8 mm Aluminium filter.

2. Description

The lower jaw is preserved in three-dimensions, showing no obvious taphonomic distortion or post-mortem damage, aside from the break at the posterior end. The specimen is proportionally narrow, measuring 28 mm anteroposteriorly, 6 mm dorsoventrally at the deepest point, and less than 4 mm labiolingually (Fig. 2). The posterior margin terminates at the 13th dentary alveolus (D13); therefore, we cannot assess the total number of dental teeth (Fig. 2A-B). The irregular shape of this posterior margin suggests it represents a fracture rather than the anterior margin of the external mandibular fenestra. This means that the specimen preserves the anterior part of the left dentary and a small fragment of the splenial (Fig. 2E-H). The angular and surangular are not preserved, and we cannot distinguish whether a mandibular fenestra was present.

Dentary: In dorsal view, the dentary (and thus the tooth row) forms a sigmoidal arcade that is labially concave at the 5th alveolus (D5) (Fig. 2A–B). The dental arcade occupies almost the entire mediolateral width of the occlusal surface of the lower jaw, similar to *Pachycheilosuchus trinquei* Rogers, 2003 (SMU 75278: Rogers, 2003). The anterior tooth row is raised from an edge that extends medially between the 1st and 8th alveoli (D1–D8) and provides an elongate articulation surface with the splenial. Nutrient foramina are present medial to the tooth row. Anterior to the 4th alveolus (D4), the foramina are irregularly distributed on the articulation surface for the splenial. From the 4th alveolus to the 8th (D4–D8), one foramen is located posterior to each tooth socket in the raised tooth row (Fig. 2B).

In lateral view, the dentary has a straight dorsal margin and a concave ventral margin. It gradually tapers dorsoventrally towards the anterior tip and medially into the

symphysis (Fig. 2C–2D). A series of ten evenly-spaced nutrient foramina occupy the lateral external surface of the bone. These foramina are positioned ventrally, following the curvature of the ventral margin of the dentary.

Medially, an anteroposteriorly short mandibular symphysis fully occupies the anterior tip of the dentary. The symphysis extends posteriorly to the 3rd alveolus (D3) and terminates anteriorly as a rounded edge. The symphyseal surface bears longitudinal striations for articulation, distinct from the 'starburst' morphology of *Theriosuchus* (Young *et al*., 2016). The Meckelian canal opens directly posterior to the symphysis and continues along the entire length of the preserved dentary; it is marked by a distinct dorsoventral constriction at the 6th alveolus (D6), followed by a trumpet-shaped expansion that opens to the truncated posterior margin of the dentary. A large nutrient foramen is located in the Meckelian canal posterior to the constricted area and beneath the 10th alveolus (D10). A small fragment of splenial is preserved at the posteroventral margin of the dentary, and it does not appear to have contributed to the symphysis.

The ventral profile of the dentary is labiolingually narrow. The dentary curves towards the midline of the skull from the 5th alveolus (D5) to the anterior tip (Fig. 2A–2B, 2G–2H).

We digitally mirrored the specimen to reconstruct a composite full lower jaw for NMS G.2016.21.1. The reconstructed mandibles display a tapering tip at the symphysis (Fig. 3), compared with the more rounded or U-shape outline in most crocodyliforms.

Alveoli: The dentary preserves 13 tooth alveoli, each separated by an interalveolar septum. These septa vary in thickness, with those between D1–D3 being almost absent, those surrounding the D5 alveolus being marginally wider, and subsequent posterior

septa being approximately uniform in width. No teeth are preserved fully or partially *in situ*, nor are any associated teeth present within the surrounding matrix. The preserved tooth sockets are shallow, extending no deeper than the dorsal margin of the Meckelian canal. We infer mild heterodonty in the lower jaw dentition. The alveoli measure approximately 1.5 mm in diameter, except that the 1st and 5th sockets, which are about half the size of adjacent ones (Fig. 2A-B). Therefore, it is likely that NMS G.2016.21.1 had two tooth 'waves'. The first four alveoli (D1–D4) are longitudinally elongated and labiolingually compressed, whereas the posterior alveoli (D5–D13) are round in shape.

Developmental stage: The lack of dermal ornamentation and small size suggest that the specimen was not skeletally mature at the time of preservation. In extant crocodylians, dermal ornamentation is present but weak in young individuals and develops into prominent pits and rugosities in adults (Mook, 1921; Joffe, 1967). However, several fossil crocodyliforms represented by mature specimens have a smooth or weakly pitted external surface of the skull, including the atoposaurids *Alligatorellus* and *Alligatorium*, the protosuchian *Zosuchus davidsoni* Pol and Norell, 2004 and various metriorhynchid genera (e.g., Young et al., 2013; Tennant and Mannion, 2014).

The dentary of NMS G.2016.21.1 as preserved measures 28 mm, with 13 alveoli (D1–D13). A row of the same number of dentary alveoli measures 30 mm in *Theriosuchus guimarotae* Schwarz and Salisbury, 2005 (IPFUB Gui Croc 8109: Schwarz and Salisbury, 2005), 40–45 mm in *Pachycheilosuchus trinquei* (SMU 75278: Rogers, 2003; Fig. 5) and *Pietraroiasuchus ormezzanoi* Buscalioni et al., 2011 (PC-1: Buscalioni et al., 2011), and about 65 mm in *Goniopholis* (NHMUK PV OR 48300: Salisbury, 2002) , which all appear to be represented by anatomically mature specimens. NMS

G.2016.21.1 thus is smaller than an adult, and generally matches the size of a subadult, when compared with other small-bodied neosuchians.

The mandibular symphysis of NMS G.2016.21.1 is distinctly expanded dorsoventrally and constricted mediolaterally, with low striations on the articulating surface. Absence of deep articulation rugosities may be indicative of a young individual, which is consistent with the smooth lateral surface of the dentary and small size of the specimen.

The shape of the mandibular symphysis, however, remains reasonably stable through ontogeny in extant crocodylians. We examined the lower jaw of *Alligator mississippiensis* Daudin, 1802 through ontogeny using skeletal specimens from the AMNH collection (Fig. 4). The mandibular symphysis retains its mediolateral expansion from hatchling-sized juveniles (AMNH R7129; Fig. 4A-B), to medium sized young individuals (AMNH R7140; Fig. C-D), and into skeletal maturity (AMNH R66645; Fig. 4E-F). If *Alligator* is a good model for the ontogeny of the taxon NMS G.2016.21.1 belongs to, this indicates that the mediolateral constriction of the mandibular symphysis observed in NMS G.2016.21.1 may not be an ephemeral juvenile feature, but also present in adult individuals, and therefore could be potentially diagnostic of a possible new taxon (although we do not name a new taxon here, given the incomplete nature of the specimen and its likely juvenile status).

3. Crocodyliform affinity of NMS G.2016.21.1

A diverse array of archosaurs, lepidosaurs, choristoderes, stem mammals, and marine reptiles are known from the Middle Jurassic of the Isle of Skye (e.g., Waldman

and Savage, 1972; Clark et al., 1995; Evans and Waldman, 1996; Evans et al., 2006; Wills et al., 2014; Brusatte and Clark, 2015; Brusatte et al., 2015a, 2015b; Close et al., 2016; Young et al., 2016).

NMS G.2016.21.1 differs from lepidosaurs and choristoderes in having thecodont dentition with rounded alveoli and a single row of nutrient foramina on the lateral surface (Romer, 1956; Gao and Fox, 1998). It also differs from thecodont ichthyosaurs in having shallow tooth sockets: some Triassic ichthyosaurian taxa have thecodont dentition, but their tooth roots attach deeply in the jaw bones (Motani, 1997). The lack of tooth replacement pits in the dentary contrasts with multiple rows of dentary teeth observed in eosauropterygians (Sassoon et al., 2015). Among archosaurs, NMS G.2016.21.1 differs from dinosaurs in the long Meckelian canal extending into the mandibular symphysis (Romer, 1956; Holliday and Nesbitt, 2013). A pterosaur affinity is unlikely, based upon the short mandibular symphysis and abundant lateral nutrient foramina of NMS G.2016.21.1.

Among pseudosuchian archosaurs, crocodyliforms and some derived 'sphenosuchians' (Nesbitt, 2011) have a Meckelian canal present through the dentary symphysis, which is not the case in NMS G.2016.21.1. Furthermore, 'sphenosuchians' have a proportionally longer mandibular symphysis than NMS G.2016.21.1 (Colbert and Mook, 1951; Clark and Sues, 2002; Clark et al., 2004; Pol et al., 2004), and therefore, we exclude NMS G.2016.21.1from these other groups, and refer it to a small-bodied, sub-adult crocodyliform.

4. Taxonomic Comparisons within Crocodyliformes

The preserved dentary measures 28 mm, which suggests that it belonged to a small individual with an estimated total skull length of less than 100 mm. Although the specimen may represent a juvenile, it contains distinctive features that are not known to be ontogenetic variants in other crocodyliforms.

The mandibular ramus is slender and labiolingually compressed, with a short symphysis. This excludes the specimen from large-bodied aquatic clades that evolved elongate symphyseal sutures and lower jaws, such as Thalattosuchia, which are the most commonly discovered and diverse Jurassic crocodyliforms (e.g., Andrews, 1913; Pierce and Benton, 2006; Young et al., 2010). Among taxa considered to be 'protosuchians', species with a similarly short mandibular symphysis differ from NMS G.2016.21.1 in having a fused symphyseal region. For example, *Zosuchus davidsoni* and *Gobiosuchus kielanae* Osmólska, 1972 both have labiolingually expanded anterior tips of the fused mandibles (Osmólska et al., 1997; Pol and Norell, 2004). Within Notosuchia, numerous genera have anteriorly tapering mandibles with short symphyses, including *Araripesuchus* (Pol and Apesteguía, 2005; Turner, 2006), *Notosuchus* (Fiorelli and Calvo, 2008), and *Malawisuchus* (Gomani, 1997). However, the shape of the dentary in notosuchians is much more sigmoid than in NMS G.2016.21.1, and no notosuchian remains have yet been found from the Jurassic. Therefore, we can exclude reference of NMS G.2016.21.1 to Notosuchia.

Among small-bodied neosuchians, NMS G.2016.21.1 differs from another crocodyliform known from Skye, *Theriosuchus* (Young et al., 2016; Tennant et al., in press), in the relative degree of heterodonty, the proportionally shorter symphysis, the mediolateral extension of the dentary arcade, and the degree of ornamentation on the

external dentary surface. In addition, while the dentary of atoposaurids is poorly known, NMS G.2016.21.1 can be excluded from *Alligatorium* by its straight dorsal margin and excluded from *Atoposaurus* and *Alligatorellus* due to the lack of a splenial contribution to the symphysis (Tennant and Mannion, 2014; Tennant et al., in press). NMS G.2016.21.1 is distinct from *Montsecosuchus*, a small-bodied neosuchian from the Early Cretaceous of Spain with an uncertain phylogenetic position (see Buscalioni and Sanz, 1990; Tennant et al., in press), due to the lack of dentary ornamentation and the relative curvature of the dentary in ventral view.

NMS G.2016.21.1 is similar, however, to some other small-bodied neosuchians. It shares several dentary characters with hylaeochampsids (sensu Turner, 2015), including the implied mild heterodont dentition, lack of a fully-developed caniniform tooth (implied by the absence of any greatly enlarged alveoli), and most dentary alveoli being similar in diameter. NMS G.2016.21.1 closely resembles the putative hylaeochampsids *Pachycheilosuchus trinquei* (Rogers, 2003) from the Early Cretaceous of Texas, USA and *Pietraroiasuchus ormezzanoi* (Buscalioni et al., 2011) from the Early Cretaceous of Italy (Fig. 5). Similar to *P. trinquei*, NMS G.2016.21.1 has a labiolingually compressed mandibular ramus, particularly at the symphyseal region (Fig. 5A-B). In comparison, most small-bodied neosuchians display varying degrees of labiolingual expansion at the anterior tip of the dentary (Fig. 5C, figure 3 of Young et al., 2016, and figure 8 of Young et al., 2014). Also shared with *P. trinquei* is a row of nutrient foramina on the lateral surface of the dentary, evenly spaced and ventrally positioned, which is a unique feature among neosuchians (Fig. 6A-B). In addition, NMS G.2016.21.1 and *P. trinquei* share a short mandibular symphysis that terminates posteriorly near the 3rd alveolus (Fig. 6C-D).

Although similar to some hylaeochampsids in many regards, NMS G.2016.21.1 also has some potentially distinctive characteristics, which could be diagnostic of a new species or the result of ontogenetic variation. For example, the morphology of the interalveolar septa might distinguish NMS G.2016.21.1 from other hylaeochampsids sensu Turner (2015). The dentary alveoli of NMS G.2016.21.1 have narrow interalveolar spaces, indicating tightly packed dentition. *Pachycheilosuchus trinquei* has tightly packed teeth, but their spacing is slightly wider anteriorly than in NMS G.2016.21.1. *Pietraroiasuchus ormezzanoi* has interalveolar spaces which are subequal to the diameter of the adjacent alveoli (Fig. 5C; Buscalioni et al., 2011), as well as an arcuate dental arcade that shifts from a lateral position anteriorly to a medial position posteriorly. In *Acynodon* the teeth are tightly packed in the upper jaw, and the lower jaw has similarly tightly packed teeth with no interalveolar septae anteriorly. A parallel row of medially positioned nutrient foramina is also present in the occlusal surface of the dentary based on *Acynodon iberoccitanus* (Martin, 2007; Delfino et al., 2008), yet the number and position of these foramina differ from NMS G.2016.21.1.

Dorsoventral expansion of the Meckelian canal is potentially diagnostic of NMS G.2016.21.1 (Fig. 6E), as it is absent in other neosuchians, such as *Pachycheilosuchus trinquei*, whose Meckelian canal forms a narrow groove at the anterior tip (Fig. 6F). Also potentially diagnostic are the faint longitudinal marks on the mandibular symphyseal surface of NMS G.2016.21.1 (Fig. 6E), whereas deep articulation ridges are present in other neosuchians (Young et al., 2016: Fig. 2D).

Based on the above comparisons, we tentatively associate NMS G.2016.21.1 with hylaeochampsids, pending further discovery of additional skull and postcranial material,

and additional systematic work on this group. Further understanding of ontogenetic changes in the lower jaw of crocodyliforms will help to assess the phylogenetic position of NMS G.2016.21.1.

5. Discussion

NMS G.2016.21.1 is the first known definitive crocodyliform from the Middle Jurassic Duntulm Formation, and it contributes a new member to the Mesozoic archosaur assemblage of the Isle of Skye (Clark et al., 1995; Evans and Waldman, 1996; Evans et al., 2006; Wills et al., 2014; Brusatte and Clark, 2015; Brusatte et al., 2015b; Young et al. 2016).

NMS G.2016.21.1 differs from other crocodyliforms currently known from Skye. *Theriosuchus* sp. (Young et al., 2016) is represented by an incomplete lower jaw from the Valtos Formation (Fig. 1A). It has deep dentary ornamentation, strongly heterodont alveoli, and a unique 'starburst' morphology on the articular surface of the mandibular symphysis (NMS G. 2014.52.1: Young et al., 2016, Fig. 2D), none of which are present in NMS G.2016.21.1. Isolated neosuchian remains are also known from the Kilmaluag Formation, which is stratigraphically immediately above the Duntulm Formation (Evans and Waldman, 1996; Evans et al., 2006; Wills et al., 2014). The Kilmaluag material—comprising teeth, osteoderms, and incomplete postcranial skeletons—is not directly comparable with NMS G.2016.21.1 due to lack of overlapping skeletal elements. It is possible that these specimens belong to the same taxon as NMS G.2016.21.1, and if so one or more of them would make more suitable holotypes, which is one reason we do not name NMS G.2016.21.1 here. These Kilmaluag specimens are currently under study, so

their systematics and relationships with NMS G.2016.21.1 will become clearer in the future. What NMS G.2016.21.1 unequivocally tells us, however, is that there were various small-sized neosuchians in the near-shore ecosystems of the Isle of Skye during the Middle Jurassic.

The morphological resemblance of NMS G.2016.21.1 to advanced neosuchians, and in particular to hylaeochampsids, implies that Hylaeochampsidae might have originated much earlier in the Jurassic than previously recognized based on their purely Cretaceous fossil record (Norell and Clark, 1990; Pol et al., 2009; Turner, 2015). *Hylaeochampsa vectiana* Owen, 1874 is known from the Early Cretaceous of the Isle of Wight (southern coast of the United Kingdom). *Pachycheilosuchus trinquei* and *Pietraroiasuchus ormezzanoi* are from the Early Cretaceous (Rogers, 2003; Buscalioni et al., 2011), and they were distributed in the proto-Atlantic and Tethyan realms. The rest of the family is known from the Late Cretaceous of Europe (Clark and Norell, 1992; Martin, 2007; Delfino et al., 2008a, 2008b; Puértolas-Pascual et al., 2014). NMS G.2016.21.1, therefore, potentially extends the temporal range of hylaeochampsids into the Middle Jurassic, and geographically into the north of the United Kingdom, which would be the most palaeogeographically northern occurrence of this clade.

Pachycheilosuchus trinquei was originally described as a possible atoposaurid (Rogers, 2003), but Turner (2015) recovered it at the base of Eusuchia. Other studies have found *P. trinquei* either in a more basal position within Neosuchia, closer to the split with Tethysuchia (Adams, 2014), or as a derived neosuchian but not a eusuchian (Narváez et al., 2015). Recently, Tennant et al. (in press) found conflicting relationships for this taxon, including a possible derived non-eusuchian neosuchian position. The

phylogeny of Turner (2015) is consistent with Buscalioni et al. (2011) in the monophyly

of Hylaeochampsidae, despite that the latter study found *Pietraroiasuchus ormezzanoi* as

the sister group of *P. trinquei* (but did not sample *Acynodon*). The incompleteness of

NMS G.2016.21.1 hinders a rigorous phylogenetic analysis of hylaeochampsids, but new

dentary characters are observed in multiple members of the clade and will be important in

future systematic evaluations of neosuchians. The mandibular symphysis extends less

than 3 tooth positions in NMS G.2016.21.1, *P. trinquei* (Rogers, 2003), and *P.*

ormezzanoi (Buscalioni et al., 2011), and it is shorter than 5 tooth positions in *Acynodon*

iberoccitanus (Martin, 2007). In all these taxa, the dentary alveoli extend no deeper than

the dorsal margin of the Meckelian canal. This suggests that a short mandibular

symphysis and shallow dentary alveoli are potential synapomorphies of hylaeochampsids.

Several clades of small-to-medium-sized Mesozoic neosuchians have been

suggested to be closely positioned to the origin of Eusuchia, including

Hylaeochampsidae, Susisuchidae, Bernissartiidae, and Paralligatoridae, although the

taxonomic compositions of these clades vary among more recent crocodyliform

phylogenies (Turner and Sertich, 2010; Adams, 2014; Turner, 2015). There was an early

divergence in the Early Jurassic (Adams, 2014; Turner, 2015) between large-bodied and

primarily aquatic neosuchian clades (Pholidosauridae and Dyrosauridae) and the

relatively smaller-bodied, terrestrial or semi-aquatic clades. Yet little is known about

neosuchians before the Late Jurassic due to a patchy non-marine fossil record (Mannion

et al., 2015; Tennant *et al*., 2016). The earliest definitive record of pholidosaurid material

comes from the Late Jurassic of Uruguay and France (Fortier et al., 2011). The Bathonian

age for the putative pholidosaurid *Anglosuchus* was questioned by Watson (1911), and the specimens referred to this taxon cannot be located.

Discovery of a potential hylaeochampsid from the Middle Jurassic indicates that small body size, which is widespread among basal eusuchians, emerged early in Neosuchia. We remain cautious in this conclusion, however, because the incomplete nature and likely juvenile status of NMS G.2016.21.1 preclude an accurate estimate of adult body size. Further investigation is required to elucidate the distribution, mode, and magnitude of body size evolution among advanced neosuchians and basal eusuchians, and we suggest that the discovery of new Middle Jurassic fossils from places like the Isle of Skye may hold the key.

6. Conclusion

The new lower jaw from the Isle of Skye is an important fossil that helps shed light on the evolution of crocodyliforms during the mysterious Middle Jurassic interval. We tentatively refer the specimen to Hylaeochampsidae due to its similarity with *Pachycheilosuchus trinquei* and *Pietraroiasuchus ormezzanoi*. While it has several distinctive dentary characters, particularly in the Meckelian canal and mandibular symphysis, we do not refer it to a new taxon due to its incompleteness, but further discoveries may reveal that it does belong to a diagnostic new species. Along with other discoveries from Skye, this new specimen shows that early, small-bodied, non-marine neosuchians were diversifying in the Middle Jurassic, during a time when their fossil record is extremely poor.

7. Acknowledgements

8. References

Adams, T. L. 2014. Small crocodyliform from the Lower Cretaceous (Late Aptian) of central Texas and its systematic relationship to the evolution of Eusuchia. Journal of Paleontology 88:1031–1049.

Anderson, F. W. 1948. Algal beds in the Great Estuarine Series of Skye. Proceedings of the Royal Physical Society of Edinburgh 23:123–142.

Andrade, M. B., R. Edmonds, M. J. Benton, and R. Schouten. 2011. A new Berriasian species of *Goniopholis* (Mesoeucrocodylia, Neosuchia) from England, and a review of the genus. Zoological Journal of the Linnean Society 163:S66–S108.

Andrews, C. W. 1913. A descriptive catalogue of the marine reptiles of the Oxford clay,

part two. London: British Museum (Natural History), 285pp pp.

Andrews, J. E. 1985. The sedimentary facies of a late Bathonian regressive episode: the Kilmaluag and Skudiburgh Formations of the Great Estuarine Group, Inner Hebrides, Scotland. Journal of the Geological Society 142:1119–1137.

Andrews, J. E. 1986. Microfacies and geochemistry of algal limestones from the Middle Jurassic of Scotland. Sedimentology 33:499-520

Andrews, J. E., and W. Walton. 1990. Depositional environments within Middle Jurassic oyster-dominated lagoons: an integrated litho-, bio- and palynofacies study of the Duntulm Formation (Great Estuarine Group, Inner Hebrides). Transactions of the Royal Society of Edinburgh: Earth Sciences 81:1–22.

Averianov, A. O. 2000. *Sunosuchus* sp. (Crocodylomorpha, Goniopholididae) from the Middle Jurassic of Kirghisia. Journal of Vertebrate Paleontology 20:776–779.

Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodyli a; pp. 295–338 in M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods. vol. 1: Amphibi. Clarendon Press, Oxford.

Brinkmann, W. 1992. Die Krokodilier-Fauna aus der Unter-Kreide (Ober Barremium) von Uña (Provinz Cuenca, Spanien). Berliner Geowissenschaftliche Abhandlungen (E) 5:1–143.

Bronzati, M., F. C. Montefeltro, and M. C. Langer. 2015. Diversification events and the effects of mass extinctions on Crocodyliformes evolutionary history. Royal Society Open Science 2:140385.

Brusatte, S. L., M. T. Young, T. J. Challands, N. D. L. Clark, V. Fischer, N. C. Fraser, J. J. Liston, C. C. J. Macfadyen, D. A. Ross, S. Walsh, and M. Wilkinson. 2015a.

Ichthyosaurs from the Jurassic of Skye, Scotland. Scottish Journal of Geology 51:43–55.

Brusatte, S. L., and N. D. L. Clark. 2015. Theropod dinosaurs from the Middle Jurassic (Bajocian – Bathonian) of Skye, Scotland. Scottish Journal of Geology 51: 157-164.

Brusatte, S. L., T. J. Challands, D. A. Ross, and M. Wilkinson. 2015b. Sauropod dinosaur trackways in a Middle Jurassic lagoon on the Isle of Skye , Scotland. doi:10.1144/sjg2015-005.

Buscalioni, A. D., and J. L. Sanz. 1990. *Montsecosuchus depereti* (Crocodylomorpha, Atoposauridae), new denomination for *Alligatorium depereti* Vidal, 1915 (Early Cretaceous, Spain): redescription and phylogenetic relationships. Journal of Vertebrate Paleontology 10:244–254.

Buscalioni, A. D., P. Piras, R. Vullo, M. Signore, and C. Barbera. 2011. Early eusuchia crocodylomorpha from the vertebrate-rich Plattenkalk of Pietraroia (Lower Albian , southern Apennines, Italy). Zoological Journal of the Linnean Society 163:S199–S227.

Clark, J. M., and M. A. Norell. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. American Museum Novitates 1–19.

Clark, J. M., and H. Sues. 2002. Two new basal crocodylomorph archosaurs from the Lower Jurassic and the monophyly of the Sphenosuchia. Zoological Journal of the Linnean Society 136:77–95.

Clark, J. M., X. Xu, C. A. Forster, and Y. Wang. 2004. A Middle Jurassic "sphenosuchian" from China and the origin of the crocodylian skull. Nature

430:1021–1024.

Clark, N. D. L., Boyd, J. D., Dixon, R. J., and Ross, D. A. 1995. The first Middle Jurassic dinosaur from Scotland: a cetiosaurid? (Sauropoda) from the Bathonian of the Isle of Skye. Scottish Journal of Geology 31:171-176.

Close, R. A., Davis, B. M., Walsh, S., Wolniewicz, A. S., Friedman, M., and Benson, R. B. J. 2015. A lower jaw of *Palaeoxonodon* from the Middle Jurassic of the Isle of Skye, Scotland, sheds new light on the diversity of British stem therians. Palaeontology 59:155-169.

Colbert, E. H., and C. C. Mook. 1951. The Ancestral Crocodilian *Protosuchus*. Bulletin of the American Museum of Natural History 97:143–182.

Dal Sasso, C., and G. Pasini. 2003. First record of pterosaurs (Diapsida, Archosauromorpha, Pterosauria) in the Middle Jurassic of Madagascar. Atti Della Societa Italiana Di Scienze Naturali E Del Museo Civico Di Storia Naturale in Milano 144:281–296.

Daudin, F. M. 1802. Le crocodile du Mississipi, p. 412–416. In Histoire Naturelle, Générale et Particulière des Reptiles; ouvrage faisant suit à l'Histoire Naturelle générale et particulière, composée par Leclerc de Buffon; et rédigée par C. S. Sonnini, membre de plusieurs Sociétés savantes. Tome Second. F. Dufart, Paris.

Delfino, M., J. E. Martin, and E. Buffetaut. 2008a. A new species of *Acynodon* (Crocodylia) from the Upper Cretaceous (Santonian – Campanian) of Villaggio del Pescatore, Italy. Palaeontology 51:1091–1106.

Delfino, M., V. Codrea, A. Folie, P. Dica, P. Godefroit, and T. Smith. 2008b. A complete skull of *Allodaposuchus precedens* Nopcsa, 1928 (Eusuchia) and a reassessment of

the morphology of the taon based on the Romanian remains. Journal of Vertebrate Paleontology 28:111–122.

Evans, S. E., P. M. Barrett, J. Hilton, R. J. Butler, M. E. H. Jones, M.-M. Liang, J. C. Parish, E. J. Rayfield, D. Sigogneau-Russell, and C. J. Underwood. 2006. The Middle Jurassic vertebrate assemblage of Skye, Scotland. Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota, Abstracts and Proceedings: 36–39.

Evans, S. E., and A. R. Milner. 1994. Middle Jurassic microvertebrate assemblages from the British Isles; pp. 303–321 in N. C. Fraser and H. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press.

Evans, S. E., and M. Waldman. 1996. Small reptiles and amphibians from the Middle Jurassic of Skye, Scotland. Museum of Northern Arizona Bulletin 60:219–226.

Fiorelli, L., and J. O. Calvo. 2008. New remains of *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes : Mesoeucrocodylia) from Late Cretaceous of Neuquén, Patagonia, Argentina. Arquivos Do Museu Nacional, Rio de Janeiro 66:83–124.

Flynn, J. J., S. R. Fox, M. Parrish, L. Ranivoharimanana, and A. R. Wyss. 2006. Assessing diversity and palaeoecology of a Middle Jurassic microvertebrate assemblage from Madagascar; pp. 476–489 in J. D. Harris, S. G. Lucas, J. A. Spielmann, M. G. Lockley, A. R. C. Milner, and J. I. Kirkland (eds.), The Triassic–Jurassic terrestrial transition. New Mexico Museum of Natural History and Science Bulletin 37. Authority of the State of New Mexico, Albuquerque.

Gao, K., and R. C. Fox. 1998. New choristoderes (Reptilia: Diapsida) from the Upper Cretaceous and Palaeocene, Alberta and Saskatchewan, Canada, and phylogenetic

relationships of Choristodera. Zoological Journal of the Linnean Society 124:303–
353.

Gao, Y. 2001. A new species of *Hsisosuchus* (Mesoeucrocodylia) from Dashanpu,
Zigong Municipality, Sichuan Province. Vertebrata PalAsiatica 39:177–184.

Gasparini, Z. B., and G. Chong. 1977. *Metriorhynchus casamiquelai* n. sp. (Crocodilia,
Thalattosuchia), a marine crocodile from the Jurassic (Callovian) of Chile, South
America. Neues Jahrbuch Für Geologie Und Paläontologie, Abhandlungen 153:341–
360.

Göhlich, U. B., L. M. Chiappe, J. M. Clark, and H.-D. Sues. 2005. The systematic
position of the Late Jurassic alleged dinosaur *Macelognathus* (Crocodylomorpha:
Sphenosuchia). Canadian Journal of Earth Sciences 42:307–321.

Gomani, E. M. 1997. A crocodyliform from the Early Cretaceous Dinosaur Beds,
northern Malawi. Journal of Vertebrate Paleontology 17:280–294.

Harris, J. P., and J. D. Hudson. 1980. Lithostratigraphy of the Great Estuarine Group
(Middle Jurassic), Inner Hebrides. Scotish Journal of Geology 16:231–250.

Holliday, C. M., and S. J. Nesbitt. 2013. Morphology and diversity of the mandibular
symphysis of archosauriforms. Geological Society, London, Special Publications
379:555–571.

Holmden, C., and J. D. Hudson. 2003. 87/86Sr and Sr/Ca investigation of Jurassic
mollusks from Scotland: implications for paleosalinities and the Sr/Ca ratio of
seawater. Geological Society of America, Bulletin 115:1249 - 1264.

Hudson, J. D., and N.H. Trewin. 2003 Chapter 11, Jurassic in Trewin, N. editor, *The
Geology of Scotland* (4th edition). The Geological Society, London.

Joffe, J. 1967. The "dwarf" crocodiles of the Purbeck Formation, Dorset: a reappraisal. Palaeontology 10:629–639.

Knoll, F., and R. López-Antoñanzas. 2014. The vertebrate fauna from the "stipite" layers of the Grands Causses (Middle Jurassic, France). Frontiers in Ecology and Evolution 2:48:doi: 10.3389/fevo.2014.0048.

Knoll, F., G. Cuny, P.-O. Mojon, R. López-Antoñanzas, and D. Huguet. 2013. A new vertebrate-, ostracod-, and charophyte-bearing locality in the Middle Jurassic of the Grands Causses (southern France). Proceedings of the Geologists' Association 124:525–529.

Kriwet, J., O. W. M. Rauhut, and U. Gloy. 1997. Microvertebrate remains (Pisces, Archosauria) from the Middle Jurassic (Bathonian) of southern France. Neues Jahrbuch Für Geologie Und Paläontologie Abhandlungen 206:1–28.

Kuzmin, I. T., P. P. Skutschas, O. I. Grigorieva, and S. A. Krasnolutskii. 2013. Goniopholid Crocodylomorph from the Middle Jurassic Berezovsk Quarry locality (Western Siberia, Russia). Proceedings of the Zoological Institute RAS 317:452–458.

Mannion, P. D., R. B. J. Benson, M. T. Carrano, J. P. Tennant, J. Judd, and R. J. Butler. 2015. Climate constrains the evolutionary history and biodiversity of crocodylians. Nat Commun 6:8438.

Martin, J. E. 2007. New material of the Late Cretaceous globidontan *Acynodon iberoccitanus* (Crocodylia) from southern France. Journal of Vertebrate Paleontology 27:362–372.

Mook, C. C. 1921. Individual and age variations in the skulls of recent Crocodilia.

Bulletin of the American Museum of Natural History 44:51–66.

Morton, N., and J. D. Hudson. 1995. Field guide to the Jurassic of the isles of Raasay and Skye, Inner Hebrides, NW Scotland. pp 209 -280 in Taylor, P. D. (editor)*, Field Geology of the British Jurassic.* Geological Society, London.

Motani, R. 1997. Temporal and spatial distribution of tooth implantations in ichthyosaurs; pp. 81–103 in J. M. Callaway and E. L. Nicholls (eds.), Ancient Marine Reptiles. Academic Press, San Diego, USA.

Nesbitt, S. J. 2011. The Early evolution of Archosaurs: relationships and the origin of major clades. Bulletin of the American Museum of Natural History 1–292.

Norell, M. A., and J. M. Clark. 1990. A reanalysis of *Bernissartia fagesii*, with comments on its phylogenetic position and its bearing on the origin and diagnosis of the Eusuchia. Bulletin - Institut Royal Des Sciences Naturelles de Belgique. Sciences de La Terre 60:115–128.

Osmólska, H. 1972. Preliminary note on a crocodilian from the Upper Cretaceous of Mongolia. Palaeontologia Polonica 27:43–47.

Osmólska, H., S. Hua, and E. Buffetaut. 1997. *Gobiosuchus kielanae* (Protosuchia) from the Late Cretaceous of Mongolia: anatomy and relationships. Acta Palaeontologica Polonica 42:257–289.

Owen, R. 1874. Supplement to the fossil Reptilia of the Wealden (*Hylaeochampsa*), Number 6. Monograph of the Palaeontographical Society London 27 (issue 125):1–7.

Pierce, S. E., and M. J. Benton. 2006. *Pelagosaurus typus* Bronn, 1841 (Mesoeucrocodylia: Thalattosuchia) from the Upper Lias (Toarcian, Lower Jurassic)

of Somerset, England. Journal of Vertebrate Paleontology 26:621–635.

Pol, D., and M. A. Norell. 2004. A new Crocodyliform from Zos Canyon, Mongolia.

American Museum Novitates 3445:1–36.

Pol, D., and S. Apesteguía. 2005. New *Araripesuchus* remains from the early Late

Cretaceous (Cenomanian – Turonian) of Patagonia. American Museum Novitates

3490:1–38.

Pol, D., A. H. Turner, and M. A. Norell. 2009. Morphology of the Late Cretaceous

Crocodylomorph *Shamosuchus djadochtaensis* and a discussion of neosuchian

phylogeny as related to the origin of eusuchia. Bulletin of the American Museum of

Natural History 324:1–103.

Pol, D., S. Ji, J. M. Clark, and L. M. Chiappe. 2004. Basal crocodyliforms from the

Lower Cretaceous Tugulu Group (Xinjiang , China), and the phylogenetic position

of *Edentosuchus*. 25:603–622.

Pol, D., O. W. M. Rauhut, A. Lecuona, J. M. Leardi, X. Xu, and J. M. Clark. 2013. A

new fossil from the Jurassic of Patagonia reveals the early basicranial evolution and

the origins of Crocodyliformes. Biological Reviews 88:862–872.

Puértolas-Pascual, E., J. I. Canudo, and M. Moreno-Azanza. 2014. The eusuchian

crocodylomorph *Allodaposuchus subjuniperus* sp. nov., a new species from the

latest Cretaceous (Upper Maastrichtian) of Spain. Historical Biology 26:91–109.

Rogers, J. V. 2003. *Pachycheilosuchus trinquei*, a new procoelous crocodyliform from

the Lower Cretaceous (Albian) Glen Rose Formation of Texas. Journal of Vertebrate

Paleontology 23:128–145.

Romer, A. S. 1956. Osteology of the reptiles; pp. 772 in Chicago: University of Chicago

Press.

Salisbury, S. W. 2002. Crocodilians from the Lower Cretaceous (Berriasian) Purbeck Limestone Group of Dorset, Southern England. Special Papers in Palaeontology 68:121–144.

Salisbury, S. W., and D. Naish. 2011. Crocodilians; pp. 305–369 in D. J. Batten (ed.), English Wealden Fossils. The Palaeontological Association (London).

Sassoon, J., D. Foffa, and R. Marek. 2015. Dental ontogeny and replacement in Pliosauridae. Royal Society Open Science 2.

Schwarz, D., and S. W. Salisbury. 2005. A new species of *Theriosuchus* (Atoposauridae, Crocodylomorpha) from the Late Jurassic (Kimmeridgian) of Guimarota, Portugal Une nouvelle espèce de Theriosuchus (Atoposauridae, Crocodylomorpha) du Jurassique supérieur (Kimméridgien) de Guimarota. 38:779–802.

Sweetman, S. C., U. Pedreira-segade, and S. U. Vidovic. 2015. A new bernissartiid crocodyliform from the Lower Cretaceous Wessex Formation (Wealden Group, Barremian) of the Isle of Wight, southern England. Acta Palaeontologica Polonica 60:257–268.

Tennant, J. P., and P. D. Mannion. 2014. Revision of the Late Jurassic crocodyliform *Alligatorellus*, and evidence for allopatric speciation driving high diversity in western European atoposaurids. PeerJ 2:e599:1–37.

Tennant, J. P., P. D. Mannion, and P. Upchurch. 2016. Environmental drivers of crocodyliform extinction across the Jurassic/Cretaceous transition. Proceedings of the Royal Society B: Biological Sciences 283:20152840.

Tennant, J. P., P. D. Mannion, and P. Upchurch. In Press. Evolutionary relationships and

systematics of Atoposauridae (Crocodylomorpha: Neosuchia): implications for the rise of Eusuchia. Zoological Journal of the Linnean Society.

Tong, H., E. Buffetaut, and V. Suteethorn. 2002. Middle Jurassic turtles from southern Thailand. Geological Magazine 139:687–697.

Turner, A. H. 2006. Osteology and phylogeny of a new species of *Araripesuchus* (Crocodyliformes : Mesoeucrocodylia) from the Late Cretaceous of Madagascar. 18:255–369.

Turner, A. H. 2015. A Review of *Shamosuchus* and *Paralligator* (Crocodyliformes, Neosuchia) from the Cretaceous of Asia. Plos One 10:e0118116.

Turner, A. H., and J. J. W. Sertich. 2010. Phylogenetic history of Simosuchus clarki (Crocodyliformes : Notosuchia) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology Meomoir 10 30:177–236.

Waldman, M., and Savage, R. J. G. 1972. The first Jurassic mammal from Scotland. Journal fo the Geological Society of London 128:119-125.

Watson, D. 1911. Notes on some British Mesozoic crocodiles. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 55:1–13.

Whetstone, K. N., and P. J. Whybrow. 1983. A "cursorial" crocodilian from the Triassic of Lesotho (Basutoland), southern Africa. Occasional Papers of the University of Kansas Museum of Natural History 106:1–37.

Wilberg, E. E. W. 2015. A new metriorhynchoid (Crocodylomorpha, Thalattosuchia) from the Middle Jurassic of Oregon and the evolutionary timing of marine adaptations in thalattosuchian crocodylomorph. Journal of Vertebrate Paleontology 35:e902846.

Wills, S., P. M. Barrett, and A. Walker. 2014. New dinosaur and crocodylomorph
material from the Middle Jurassic (Bathonian) Kilmaluag Formation, Skye,
Scotland. Scottish Journal of Geology 50:183–190.

Young, M. T., M. B. Andrade, S. Etches, and B. L. Beatty. 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 169:820–848.

Young, M. T., S. L. Brusatte, M. Ruta, and M. B. Andrade. 2010. The evolution of
Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): An integrated approach
using geometric morphometrics, analysis of disparity, and biomechanics. Zoological
Journal of the Linnean Society 158:801–859.

Young, M. T., M. A. Bell, M. B. Andrade, and S. L. Brusatte. 2011. Body size estimation
and evolution in metriorhynchid crocodylomorphs: implications for species
diversification and niche partitioning. Zoological Journal of the Linnean Society
163:1199–1216.

Young, M. T., S. L. Brusatte, B. L. Beatty, M. B.Andrade, and J. B. Desojo. 2012. Tooth-
On-Tooth Interlocking Occlusion Suggests Macrophagy in the Mesozoic Marine
Crocodylomorph *Dakosaurus*. 1158:1147–1158.

Young, M. T., L. Steel, D. Foffa, T. Price, D. Naish, and J. P. Tennant. 2014. Marine
tethysuchian crocodyliform from the ?Aptian-Albian (Lower Cretaceous) of the Isle
of Wight, UK. Biological Journal of the Linnean Society 113:854–871.

Young, M. T., J. P. Tennant, S. L. Brusatte, T. J. Challands, N. C. Fraser, N. D. L. Clark,
and D. A. Ross. 2016. The first definitive Middle Jurassic atoposaurid

(Crocodylomorpha, Neosuchia), and a discussion on the genus *Theriosuchus*.

Zoological Journal of the Linnean Society 176:443–462.

34

FIGURE CAPTIONS

Figure 1. Locality and geological context of NMS G.2016.21.1. (A) Stratigraphic occurrences of fossil crocodyliforms discovered from the Great Estuarine Group. (B) Map of the Isle of Skye, and fossil crocodyliforms are known from three localities: Duntulm (a), Valtos (b), and Cladach a'Ghlinne (c). (C) Geological context at the Duntulm locality (a). (D) The new specimen NMS G.2016.21.1. Scale bar = 10 mm.

Figure 2. CT models of NMS G.2016.21.1 and line drawings. (A-B), the specimen in dorsal view. (C-D), lateral view. (E-F), medial view. (G-H), ventral view. Anatomical abbreviations: d1, the 1st dentary tooth; d5, the 5th dentary tooth; d.sp, dentary articulation surface for the splenial; mg, Meckelian groove; n. fr, nutrient foramina; sp, splenial; sym, mandibular symphysis; v.sp, ventral articulation surface for the splenial. Scale bar = 10 mm.

Figure 3. Reconstructed CT models of the anterior mandibles of NMS G.2016.21.1. (A) Dorsal view. (B) Ventral view. Scale bar = 10 mm.

Figure 4. The mandibular symphysis of *Alligator mississippiensis* through ontogeny. Depicted are the left mandibular rami of a hatchling (AMNH R7129) in medial (A) and dorsal (B) view, a medium-sized individual (AMNH R7140) in medial (C) and dorsal (D) view, and an adult (AMNH R66645) in medial (E) and dorsal view (F). Scale bar = 10 mm.

Figure 5. Lower jaw comparisons between NMS G.2016.21.1 and Early Cretaceous hylaeochampsids. (A) The Duntulm specimen (NMS G.2016.21.1). (B) *Pachycheilosuchus trinquei* (SMU75279). Photograph by D. Winkler. (C) *Pietraroiasuchus ormezzanoi* (PC-1, modified from Buscalioni et al., 2011).

Figure 6. Morphological comparisons between NMS G.2016.21.1 (A, C, E) and *Pachycheilosuchus trinquei* (SMU75279: B, D, F). (A–B) Dentary in lateral view, and a row of nutrient foramina evenly distributes along the lateroventral margin in both taxa. Arrows point to nutrient foramina in *P. trinquei*. (C–D) Dentary in dorsal view, showing a short mandibular symphysis in both taxa denoted by arrows. (E–F) The Meckelian canal expands dorsoventrally in the new specimen but constricts anteriorly in *P. trinquei*. Not to scale.
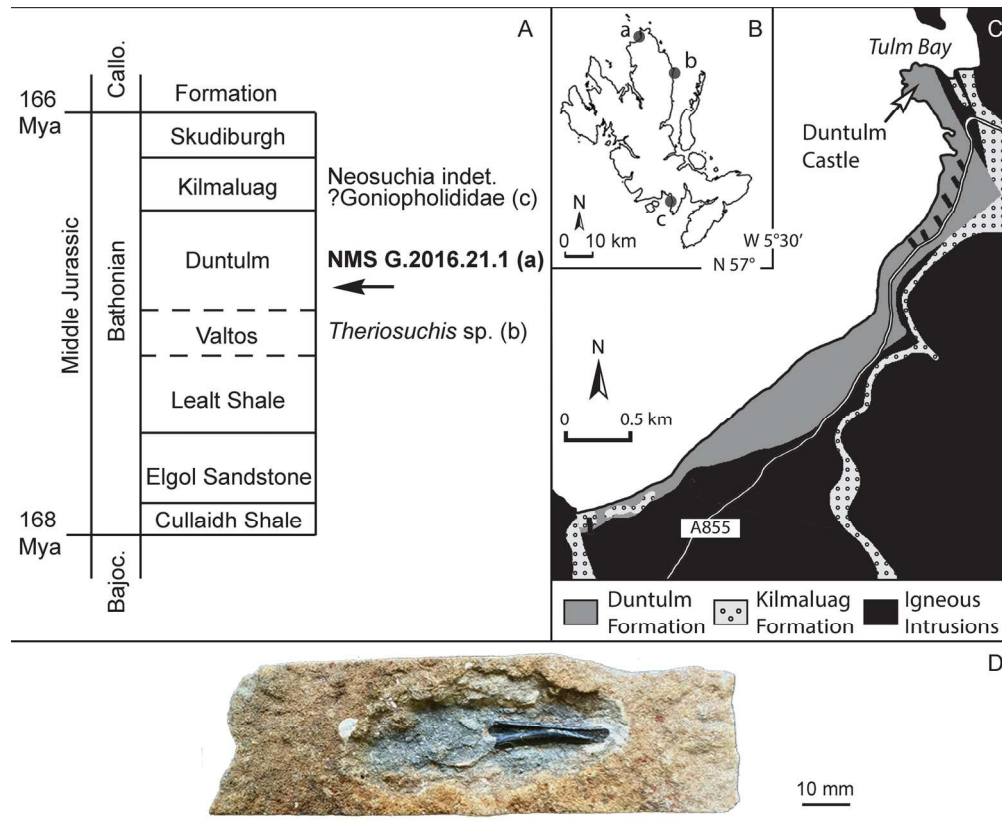
Figure 1. Locality and geological context of NMS G.2016.21.1. (A) Stratigraphic occurrences of fossil crocodyliforms discovered from the Great Estuarine Group. (B) Map of the Isle of Skye, and fossil crocodyliforms are known from three localities: Duntulm (a), Valtos (b), and Cladach a'Ghlinne (c). (C) Geological context at the Duntulm locality (a). (D) The new specimen NMS G.2016.21.1. Scale bar = 10 mm.
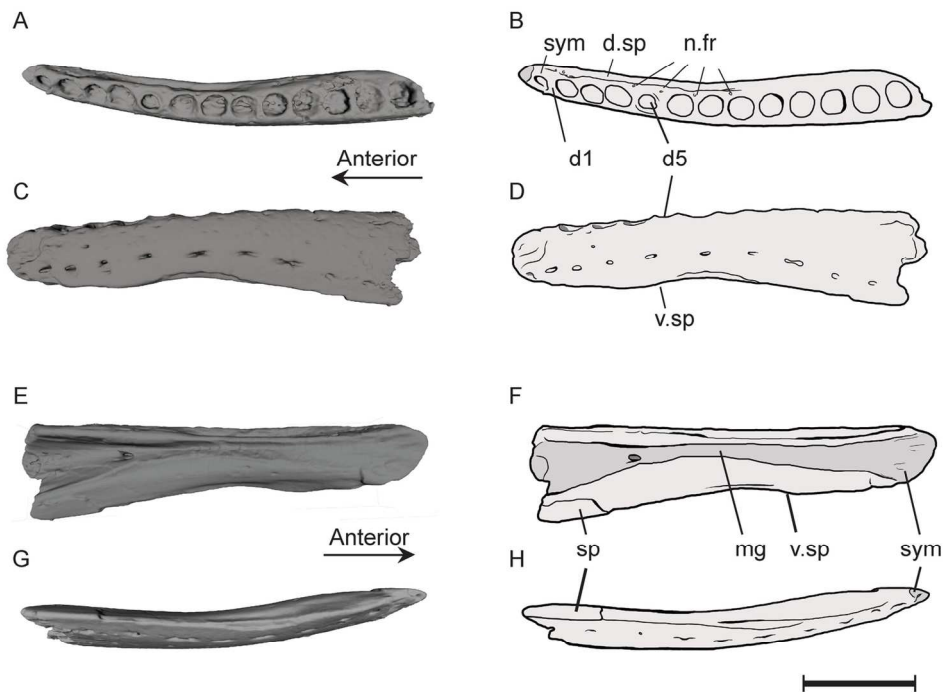152x125mm (300 x 300 DPI)

Figure 2. CT models of NMS G.2016.21.1 and line drawings. (A-B), the specimen in dorsal view. (C-D), lateral view. (E-F), medial view. (G-H), ventral view. Anatomical abbreviations: d1, the 1st dentary tooth; d5, the 5th dentary tooth; d.sp, dentary articulation surface for the splenial; mg, Meckelian groove; n. fr, nutrient foramina; sp, splenial; sym, mandibular symphysis; v.sp, ventral articulation surface for the splenial. Scale bar = 10 mm.
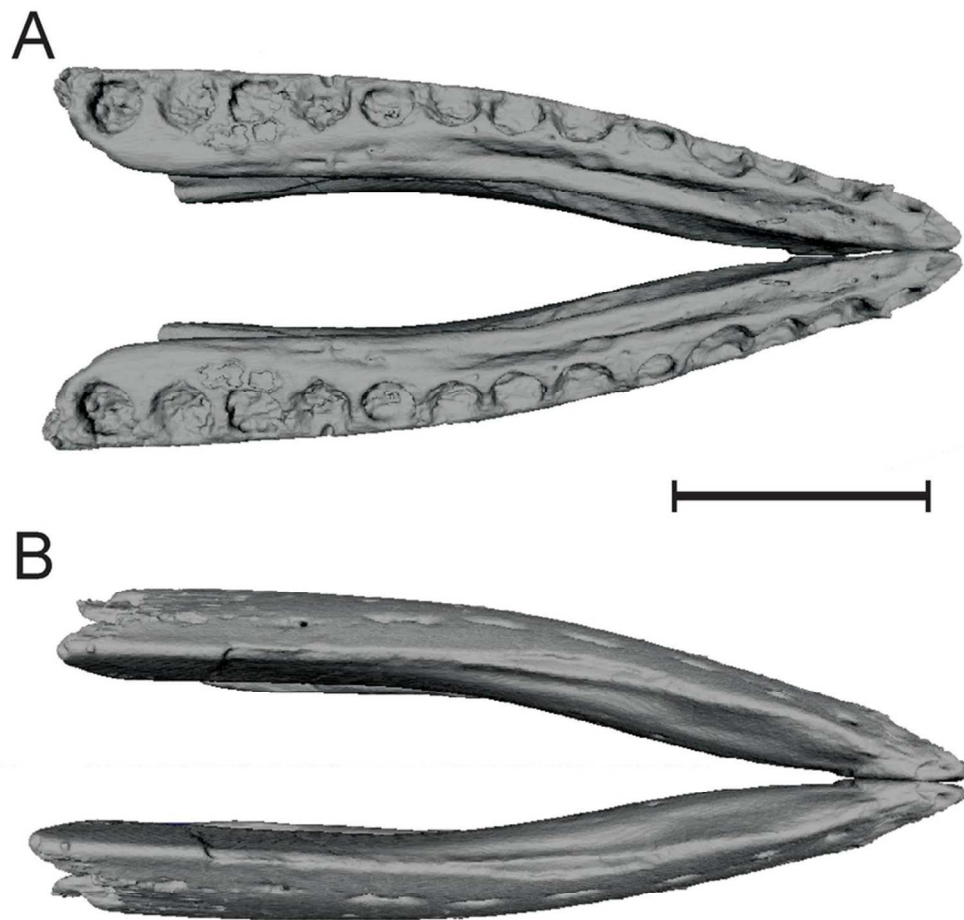142x108mm (300 x 300 DPI)

Figure 3. Reconstructed CT models of the anterior mandibles of NMS G.2016.21.1. (A) Dorsal view. (B) Ventral view. Scale bar = 10 mm.
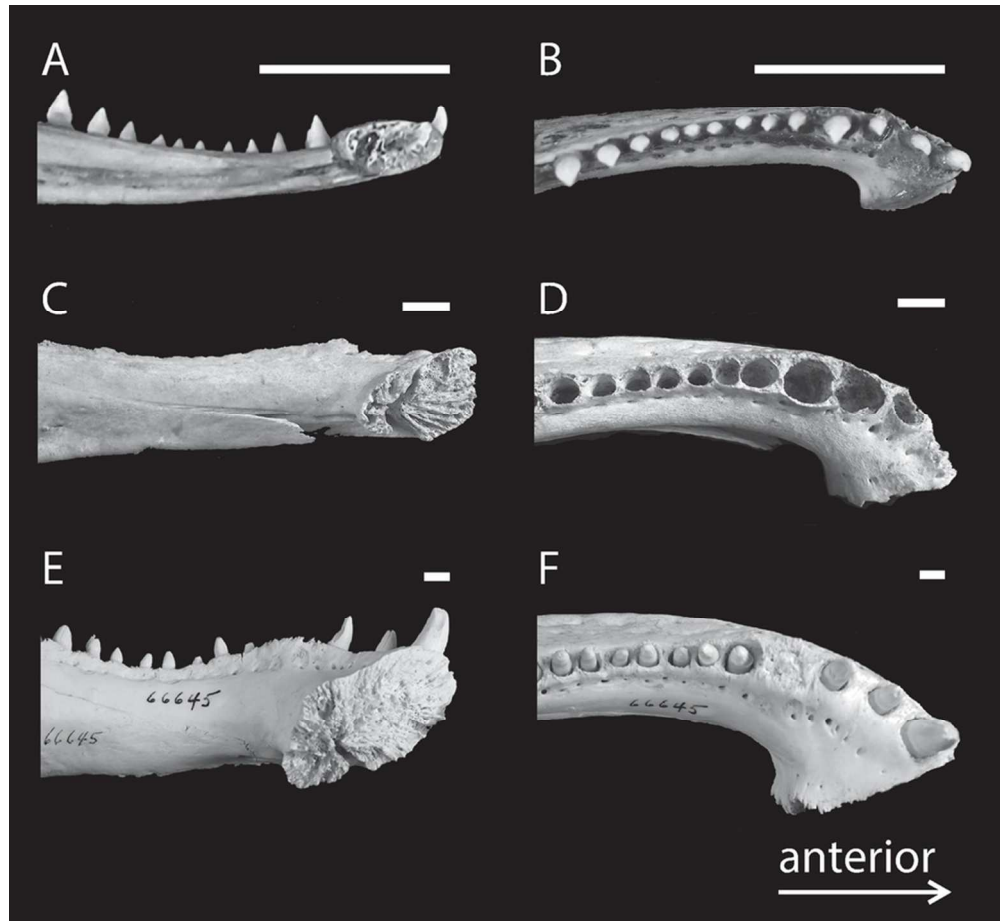76x76mm (300 x 300 DPI)

Figure 4. The mandibular symphysis of Alligator mississippiensis through ontogeny. Depicted are the left mandibular rami of a hatchling (AMNH R7129) in medial (A) and dorsal (B) view, a medium-sized individual (AMNH R7140) in medial (C) and dorsal (D) view, and an adult (AMNH R66645) in medial (E) and dorsal view (F). Scale bar = 10 mm.
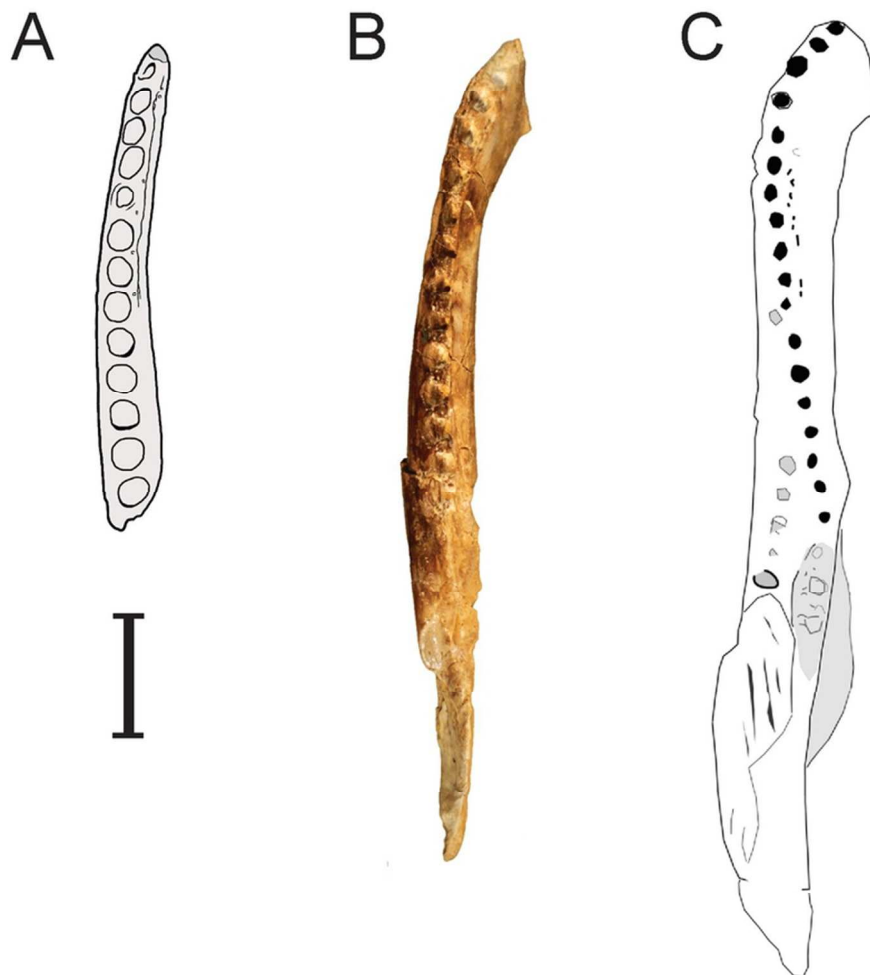81x74mm (300 x 300 DPI)

Figure 5. Lower jaw comparisons between NMS G.2016.21.1 and Early Cretaceous hylaeochampsids. (A) The Duntulm specimen (NMS G.2016.21.1). (B) Pachycheilosuchus trinquei (SMU75279). Photograph by D. Winkler. (C) Pietraroiasuchus ormezzanoi (PC-1, modified from Buscalioni et al., 2011). 76x76mm (300 x 300 DPI)
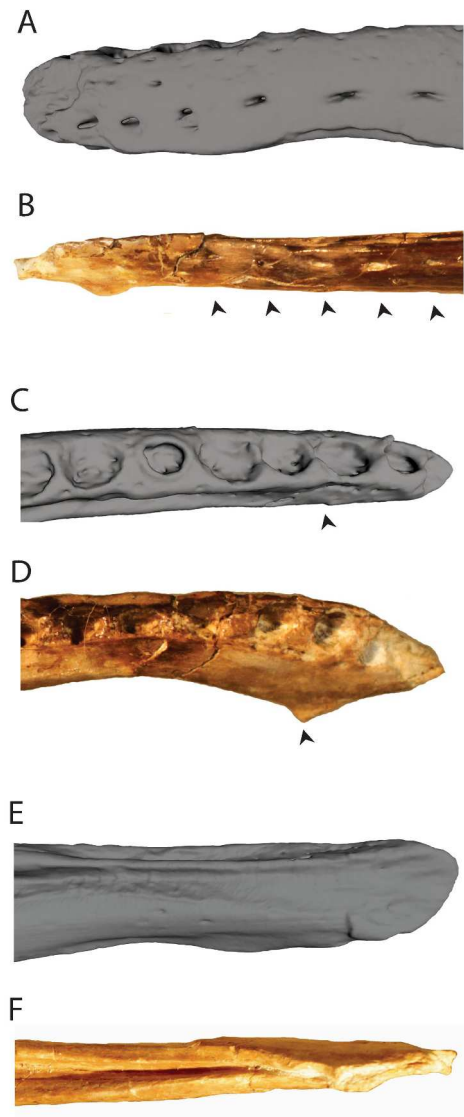
Figure 6. Morphological comparisons between NMS G.2016.21.1 (A, C, E) and Pachycheilosuchus trinquei (SMU75279: B, D, F). (A–B) Dentary in lateral view, and a row of nutrient foramina evenly distributes along the lateroventral margin in both taxa. Arrows point to nutrient foramina in P. trinquei. (C–D) Dentary in dorsal view, showing a short mandibular symphysis in both taxa denoted by arrows. (E–F) The Meckelian canal expands dorsoventrally in the new specimen but constricts anteriorly in P. trinquei. Not to scale. 177x414mm (300 x 300 DPI)