Marine tethysuchian crocodyliform from the ?Aptian-Albian (Lower Cretaceous) of the Isle of Wight, UK

MARK T. YOUNG1,2*, LORNA STEEL3, DAVIDE FOFFA4, TREVOR PRICE5, DARREN NAISH2 and JONATHAN P. TENNANT6

1Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, The King’s Buildings, Edinburgh EH9 3JW, UK
2School of Ocean and Earth Science, National Oceanography Centre, University of Southampton, Southampton SO14 3ZH, UK
3Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK
4School of Earth Sciences, University of Bristol, Wills Memorial Building, Bristol BS8 1RJ, UK
5Dinosaur Isle Museum, Sandown, Isle of Wight PO36 8QA, UK
6Department of Earth Science and Engineering, Imperial College London, London SW6 2AZ, UK

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A marine tethysuchian crocodyliform from the Isle of Wight, most likely from the Upper Greensand Formation (upper Albian, Lower Cretaceous), is described. However, we cannot preclude it being from the Ferruginous Sands Formation (upper Aptian), or more remotely, the Sandrock Formation (upper Aptian-upper Albian). The specimen consists of the anterior region of the right dentary, from the tip of the dentary to the incomplete fourth alveolus. This specimen increases the known geological range of marine tethysuchians back into the late Lower Cretaceous. Although we refer it to Tethysuchia incertae sedis, there are seven anterior dentary characteristics that suggest a possible relationship with the Maastrichtian-Eocene clade Dyrosauridae. We also review ‘middle’ Cretaceous marine tethysuchians, including putative Cenomanian dyrosaurids. We conclude that there is insufficient evidence to be certain that any known Cenomanian specimen can be safely referred to Dyrosauridae, as there are some cranial similarities between basal dyrosaurids and Cenomanian-Turonian marine ‘pholidosaurids’. Future study of middle Cretaceous tethysuchians could help unlock the origins of Dyrosauridae and improve our understanding of tethysuchian macroevolutionary trends. © 2014 The Linnean Society of London, Biological Journal of the Linnean Society, 2014, 113, 854–871.


INTRODUCTION

Tethysuchian crocodyliforms were a highly successful group, some of which returned to a marine lifestyle during the latter part of the Mesozoic and early Cenozoic. Many species superficially resembled extant gharials in having enlarged supratemporal fenestrae, an elongate, tubular snout, and a high tooth count (e.g. Koken, 1887; Mook, 1933, 1934; Wu, Russell & Cumbaa, 2001; Jouve et al., 2005a, 2006a; Barbosa, Kellner & Viana, 2008). Tethysuchia was one of several crocodyliform clades that survived the end-Cretaceous mass-extinction event, with the subclade Dyrosauridae continuing to radiate and diversify during the Palaeocene and Eocene (e.g. Buffetaut, 1976, 1978, 1982; Jouve, 2005, 2007; Jouve et al., 2005a, 2006a; Jouve, Bouya & Amaghzaz, 2005b, 2008; Barbosa et al., 2008; Hill et al., 2008; Hastings et al., 2010; Hastings, Bloch & Jaramillo, 2011, in press). However, the origins of this clade are...
poorly understood owing to a paucity of fossils from the ‘middle’ Cretaceous.

A phylogenetic definition of Tethysuchia was recently proposed by Andrade et al. (2011: S102) as: ‘the clade composed of *Pholidosaurus purbeckensis* (Mansel-Pleydell, 1888) and *Dyrosaurus phosphaticus* (Thomas, 1893), their common ancestor and all its descendants’. This definition encompasses Dyrosauridae and Pholidosauridae, and possibly Elosuchidae. Although curiously, this is not the case in the phylogenetic analysis of Andrade et al. (2011), as Elosuchidae was recovered outside the *Pholidosaurus + Dyrosaurus* clade. Moreover, Andrade et al. (2011) proposed that Elosuchidae be used for the clade consisting of *Elosuchus*, *Sarcosuchus*, and *Vectisuchus*. Also, a phylogenetic definition of Pholidosauridae was recently proposed by Fortier, Perea & Schultz (2011: S259) as: ‘a stem-based group name including *Pholidosaurus schaumburgensis* (Meyer, 1841) and all taxa closer to it than to *D. phosphaticus* (Thomas, 1893) or *Pelagosaurus typus* Bronn, 1841’. No explicit phylogenetic definition has been proposed for Dyrosauridae or Elosuchidae.

Phylogenetic analyses consistently find Dyrosauridae to be holophyletic (e.g. Wu et al., 2001; Jouve, 2005; Jouve et al., 2005a, 2006a, 2008; Barbosa et al., 2008; Young & Andrade, 2009; Hastings et al., 2010, 2011, in press; Andrade et al., 2011; Fortier et al., 2011). The holophyly of Pholidosauridae, however, is not always recovered. Pholidosauridae has either been found to be a paraphyletic grade of taxa closely related to Dyrosauridae (Wu et al., 2001; Jouve et al., 2005a, 2008; Barbosa et al., 2008; Young & Andrade, 2009; Hastings et al., 2010, 2011, in press; Andrade et al., 2011), holophyletic (Fortier et al., 2011; and in one of the analyses of the Jouve et al., 2006a data set in Hastings et al., in press), or holophyletic with *Elosuchus* being outside the clade comprising Dyrosauridae and Pholidosauridae (Jouve et al., 2006a; and in one of the analyses of the Jouve et al., 2006a data set in Hastings et al., in press). Martin & Buffetaut (2012) and Martin et al. (2014b) also found Pholidosauridae to be holophyletic, but as no dyrosaurids were included in those analyses they never tested whether pholidosaurids constitute a natural group. When Pholidosauridae is found to be paraphyletic, the sister taxon of Dyrosauridae varies between *Terminonaris* (Wu et al., 2001; Jouve et al., 2005a, 2008; Barbosa et al., 2008; Hastings et al., in press), *Oceanosuchus* (Young & Andrade, 2009), and *Elosuchus* (Hastings et al., 2010, 2011), although *Oceanosuchus* was only included in the analysis of Young & Andrade (2009). As such, the internal evolutionary relationships of Tethysuchia are in flux.

This has important implications for tethysuchian evolution, in particular for our understanding of dyrosaurid origins, and whether dyrosaurids and the marine ‘pholidosaurids’ *Terminonaris* and *Oceanosuchus* constitute a single marine radiation or several independent ones.

One of the major issues hampering resolution in these analyses is the paucity of ‘middle’ Cretaceous (Barremian–Turonian) marine tethysuchians, thus affecting our understanding of character polarity. In those phylogenetic analyses in which ‘pholidosaurids’ are paraphyletic, all potential dyrosaurid sister taxa (*Elosuchus*, *Oceanosuchus*, and *Terminonaris*) are from this time span (see Mook, 1933, 1934; Wu et al., 2001; de Lapparent de Brion, 2002; Hua et al., 2007). Furthermore, the earliest potential dyrosaurids are Cenomanian in age (Buffetaut & Lauverjat, 1978; Buffetaut, Bussert & Brinkmann, 1990). Therefore, investigating specimens from the Barremian–Turonian stages will be key to elucidating the early evolution of Tethysuchia.

Here we describe a long-known, but previously unstudied, tethysuchian crocodyliform. This specimen, the anterior-most part of a right dentary (NHMUK PV OR36173), is most probably from the Upper Greensand Formation of England (upper Albian, Lower Cretaceous). Although this specimen was discovered over 150 years ago, it has only been briefly mentioned once in the literature. Furthermore, it is of importance as a result of its unusual morphology and geological age. The presence of a marine tethysuchian in the late Lower Cretaceous of the UK would indicate that tethysuchians moved into the marine realm earlier than previously realized.

**ABBREVIATIONS**

**INSTITUTIONAL**

MIWG, the Museum of Isle of Wight Geology (now IWCMS – the Isle of Wight County Museum Service, incorporating Dinosaur Isle museum and visitor attraction); MNHN, Muséum national d’histoire naturelle, Paris, France; NHMUK, Natural History Museum, London, UK.

**ANATOMICAL**

D1, first dentary alveolus; D2, second dentary alveolus; D3, third dentary alveolus; D4, fourth dentary alveolus; for, foramen; rug, rugose patch; sym, symphysis.

**HISTORICAL INFORMATION**

The anterior right dentary (NHMUK PV OR36173) was purchased by the British Museum (Natural
History) in October 1861 from a Mr Simmons. In the NHMUK specimen register, NHMUK PV OR36173 is listed as an ‘anterior portion of left upper jaw with four teeth sockets, of a crocodilian reptile. Greensand? Shanklin, I. of Wight’. The only mention of the specimen we can find in the literature is by Lydekker (1889: 179), who identified NHMUK PV OR36173 as the pliosaurid, *Polyptychodon interruptus*, and states that it is: ‘apparently the extremity of the left premaxilla’. Why he referred NHMUK PV OR36173 to Pliosauridae, and thought it might be *P. interruptus*, was not stated. Amongst the specimen labels is a note left by Dr Leslie Noé, dated 23 August 1999, in which he states: ‘This jaw fragment is not pliosaurian [? crocodilian]’. This taxonomic note is what brought NHMUK PV OR36173 to our attention.

GEOLoGICAL INFORMATION

The right partial dentary (NHMUK PV OR36173) was discovered at Shanklin, Isle of Wight, UK. The exact formation that yielded it is, however, unclear. It was referred to the Upper Greensand Formation by Lydekker (1889), but the NHMUK specimen register refers to it as from: ‘Greensand?’. Therefore, verifying that it is actually from the Upper Greensand Formation, and not from one of the Lower Greensand Group formations exposed at Shanklin, is important (see Fig. 1). In order to determine this, one of the authors (T.P.) examined the fossils in the MIWG (IWCMS) and the rocks at Shanklin. Descriptions of the deposits of the Lower Greensand and Selborne Groups on the Isle of Wight have been given by White (1921), Wach & Ruffell (1991), Insole, Daley & Gale (1998), and Hopson, Wilkinson & Woods (2008).

Numerous marine reptiles are known from the Ferruginous Sands Formation (Lower Greensand Group) of the Isle of Wight. The members of the Ferruginous Sands Formation exposed at the lower part of the cliffs at Shanklin (Knock Cliff to Hope Beach) are: the Old Walpen Chine Member (XII), the New Walpen Chine Member (XIII), and Member XIV (un-named). If the provenance of NHMUK PV OR36173 is one of these members, we would expect it to be very dark brown or black in colour with a dark matrix (this being caused by the iron-rich nature of the sediment), as is the case in the exceptionally rare ornithopod bones and a number of ichthyosaur vertebrae (e.g. MIWG.5376) from Member VI, which are dark brown/black. However, we cannot discount that NHMUK PV OR36173 may have come from an isolated calcareous lens in one of these members. As

Figure 1. Map of the Isle of Wight showing Shanklin (A), with the geological column of formations exposed there (B). [A and B are modified from Hopson (2011).] Photographs of the formations exposed near Shanklin, at Luccombe Chine (C), and Knock cliff (D).

such, the possibility of a Ferruginous Sands Formation origin cannot currently be completely ruled out.

Overlying the Ferruginous Sands Formation at Shanklin is the Sandrock Formation (Fig. 1). This formation is a mixture of blue silty clay and yellow sands, and is considered to have been deposited during a time when cyclical sea-level changes preserved a number of wide estuaries and near-shore mud flats (see Wach & Ruffel, 1991). Fossil plants discovered from this formation are typically pale (white), fragmentary, and crumble easily. Although we think it unlikely that the Sandrock Formation is the origin of NHMUK PV OR36173, the lack of any suitable reptilian material for comparison means that we cannot entirely discount the possibility.

The final, and highest, formation from the Lower Greensand Group exposed is the Monks Bay Sandstone Formation (formerly known as the Carstone Formation of the Isle of Wight) (Fig. 1). This overlies the Sandrock Formation. It is very gritty, with large iron-rich sandstone nodules and has a dark-brown coloration. Vertebrate fossils are unreported in this formation, and along with the iron-rich deposits (which would make fossils darker in colour), we exclude this as the possible origin of NHMUK PV OR36173.

The Lower Greensand Group is overlain by the Selborne Group, with two formations exposed (Fig. 1): the Gault Formation (Albian) and the Upper Greensand Formation (Albian–Cenomanian). The Selborne Group was deposited in a marine setting, with the Gault Formation forming in a mid- or outer-shelf environment, whilst the Upper Greensand Formation was formed in a shallow offshore shelf and in lower shoreface zones related to an eastward-prograding shoreline (Hopson, 2011).

At Shanklin, the clays/mudstones of the Gault Formation are dark in colour, which results in dark fossils. The general coloration and matrix of NHMUK PV OR36173 appears similar to the central part of the Upper Greensand Formation, the ‘Malm Rock’ or Freestone, a pale grey/green glauconitic sandstone/siltstone that contains iron-rich sandy nodules (division D of Jukes-Browne & Hill, 1900). This thick sequence lies above the basal ‘Passage Beds’ (division A of Jukes-Browne & Hill, 1900) and below the Chert Beds (division E of Jukes-Browne & Hill, 1900).

However, it must be appreciated that a considerable amount of time (over 150 years) has passed since NHMUK PV OR36173 was collected. Therefore, the external surface may have altered as it dried out and oxidized. Based on general specimen coloration and matrix, the Upper Greensand Formation seems like the most probable origin of NHMUK PV OR36173. As stated above, we cannot preclude the possibility that NHMUK PV OR36173 originated from the Sandrock Formation or from an isolated calcareous lens in Member XII, Member XIII, or Member XIV of the Ferruginous Sands Formation.

Is NHMUK PV OR36173 reworked from an earlier, Jurassic, horizon? Not only is the morphology of NHMUK PV OR36173 distinct from any known Jurassic taxon (see the description below), but a drifted block of Jurassic material would needed to have travelled many kilometres from the nearest exposed Jurassic outcrop to have become entombed in the marine Greensands. We find this to be an unlikely scenario.

SYSTEMATIC PALAEONTOLOGY
CROCODYLIFORMES BENTON & CLARK, 1988
MESOEUCROCODYLIA WHETSTONE & WHYBROW, 1983
NEOSUCHIA BENTON & CLARK, 1988
TETHYSUCHIA BUFFETAUT, 1982
TETHYSUCHIA INCERTAE SEDIS

Specimen
NHMUK PV OR36173, the anterior region of the right dentary.

Locality
Shanklin, Isle of Wight, UK.

Horizon and age
Most likely from the ‘Malm rock’ or Freestone, Upper Greensand Formation, Selborne Group (upper Albian, Lower Cretaceous). However, it could be from an isolated calcareous lens from one of three members within the Ferruginous Sands Formation, Lower Greensand Group (upper Aptian, Lower Cretaceous): the Old Walpen Chine Member (XII), the New Walpen Chine Member (XIII), or Member XIV (un-named). Moreover, we cannot entirely discount the Sandrock Formation, Lower Greensand Group (upper Aptian–lower Albian, Lower Cretaceous), as there are no known suitable fossils from this formation for comparison.

DESCRIPTION
DENTARY

Only the anterior region of the right dentary is preserved. It is approximately 130 mm in anteroposterior length. Overall, the preservation is good, other than it being broken posteriorly. There is no evidence of post-mortem mediolateral compression or shearing. The external (= lateral and ventral) surfaces of the dentary are gently convex, with numerous large, subcircular foramina that are mostly widely spaced...
The external surface ornamentation comprises numerous, very small, subcircular pits. This ornamentation pattern remains constant along the element. The medial contractions between alveoli (and the raised alveolar rims, especially the D3 and D4) suggest that the premaxillary teeth would have occluded lateral to the interalveolar spaces on the dentary (i.e. in an overbite or interlocking manner) (Figs 2–4).

On the dorsal surface of the dentary, the three anterior-most alveoli are completely preserved, along with the anterior section of the fourth (Fig. 4). All of the preserved alveoli are very large in proportion to the overall size of the bone, but vary in size and shape. There is also variation in interalveolar spacing. The first dentary alveolus (D1) is orientated dorsally and slightly anteriorly (Figs 2, 4–5). The D1 alveolus is oval in shape, orientated along the anteroposterior axis of the dentary, and has an anteroposterior length of 48 mm and a mediolateral width of approximately 38 mm. Between the D1 and D2 alveoli, there is a minimum interalveolar space of 17 mm. The D2 alveolus is notably smaller and also oval in shape, having an anteroposterior length of 25 mm. Between the D2 and D3 alveoli there is a minimum interalveolar space of 14 mm. The D3 alveolus is smaller than the D2 alveolus and is slightly more circular in shape, with an anteroposterior length of 21 mm. Between the D3 and D4 alveoli there is a minimum interalveolar space of 9 mm. The D4 alveolus is incomplete, but it would have been considerably larger than the D2 and D3 alveoli. The D4 alveolus has a transverse width of approximately 35 mm. Each alveolus has a slight, or noticeable, raised rim. In the D1 and D3 alveoli they are barely noticeable, in the D2 alveolus the rim is more strongly developed, whilst the D4 alveolus has a very large and well-developed rim.
The medial border of the D2 and D3 alveoli are either in the same sagittal plane, or lateral to, the lateral border of the D1 alveolus (Fig. 4). Overall, the dorsal surface of the dentary is mainly flat, with numerous large foramina medial to the D2 and D3 alveoli. The largest foramen is medial to the D3 alveolus.

In lateral view (Fig. 2), the dorsal margin of the dentary is concave between the D1 and D4 alveoli. This results in the D2 and D3 alveoli being ventral in the transverse plane to the D1 and D4 alveoli. Moreover, the D2 and D3 alveoli are orientated slightly dorsolaterally. When seen in lateral view, the ventral margin is distinctly curved, and is convex. It rises dorsally anteriorly, and is noticeable ventral to the first two dentary alveoli.

In medial view, the preservation is poor but the symphyseal suture is partially visible (Fig. 6). However, the dentary appears to be ‘hollow’ posteroverentral to the D3 and D4 alveoli. Anteriorly, the dentary is a solid bone, which would have created a firm mandibular symphysis. Ventral to the D3 there is a concave surface that forms the boundary from the ‘hollow’ and solid regions of the dentary. Posteriorly, bivalve encrustations and bivalve fossils are preserved within this ‘hollow’ region.

We cannot determine how much of the symphyseal surface is preserved, although it is likely that it extended posterior to the fourth alveolus. Based on the preserved region, the dentary appears to be from a mesorostrine or longirostrine taxon (based on the long, narrow and dorsoventrally shallow dentary). It is similar to other tethysuchians such as ‘Elosuchus’ felixi (de Lapparent de Broin, 2002) and Dyrosauridae (e.g. Hill et al., 2008; Hastings et al., 2010). There is no trace of the splenial, but we would not expect there to be because the splenial does not reach as far anteriorly as the fourth alveolus in other tethysuchian taxa (e.g. de Lapparent de Broin, 2002; Hill et al., 2008; Hastings et al., 2010, 2011; Adams et al., 2011).

In posterior view, the bone is exposed in cross section (Fig. 7). As noted by Lydekker (1889: 179) there are large cancelli in the diploë. The dentary is highly cancellous, with thicker cortical bone along the ventral and lateroventral margins of the bone, whereas the dorsal and dorsolateral margins have very thin cortical bone. Adjacent to the cortical bone, the cancelli immediately internal to the thickest cortical bone are larger than those adjacent to thinner cortical bone.

**Dentition**

Only two, incomplete, in-situ tooth crowns are preserved (Fig. 4). The in-situ tooth crowns are in the first and third alveoli. In the first alveolus there is an
erupting replacement tooth crown. The crown is only partially visible, with only the apical half of the lingual surface exposed. In the third alveolus there is a cross section through the base of a fully erupted tooth crown. The crown has a diameter of 11–12 mm.

Based on the two in-situ tooth crowns, the dentition would have been caniniform in morphology (i.e. single cusped and labiolingually compressed). The basal section is oval in cross section, being wider mesiodistally than labiolingually. The incomplete preservation of the crowns makes it impossible to make any further comments on the carinal or overall crown morphologies.

DISCUSSION
EXCLUDING NHMUK PV OR36173 FROM PLESIOSAURIA
We agree with Dr Leslie Noé that the referral of NHMUK PV OR36173 to Pliosauridae and P. interruptus is incorrect. There are a number of plesiosaurian characteristics that are lacking in NHMUK PV OR36173, allowing us to exclude, with confidence, NHMUK PV OR36173 from Sauropterygia. These include the following.

1. The pattern of large-to-small teeth in NHMUK PV OR36173 (in which the first and fourth dentary alveoli are considerably larger than the second and third alveoli; Fig. 4) is unknown in Plesiosauria. To our knowledge there is no known plesiosaurian in which the first dentary alveous (D1) is larger than the second and third alveoli. In all plesiosaurian dentaries, the D1 is smaller (or at least subequal) than the immediately posterior alveoli. This is seen in Rhomaleosauridae (Smith, 2007), Pliosauridae (Andrews, 1913; Tarlo, 1960; Albright, Gillette & Titus, 2007a; Benson et al., 2011; Ketchum & Benson, 2011; Sassoon, Noé & Benton, 2012), Leptocephalidae (Druckenmiller & Russell, 2008), and Polycotylidae (Carpenter, 1996; Albright, Gillette & Titus, 2007b).

2. Eosauropterygians have a distinctive tooth-replacement pattern. Their replacement teeth originate in separate temporary alveoli, recognizable by aligned foramina on the dorsal surface of the dentaries. Developing teeth grow within these, until the temporary and functional alveoli fuse (Owen, 1840; von Huene, 1923; Rieppel, 2001; Shang, 2007). The erupting teeth grow in a shallow groove medial to each functional alveolus. The separation between primary and secondary alveoli can be short or large. However, tooth replacement in thecodont groups (including Crocodylomorpha) involves development of the replacement teeth in shallow pits in the lingual side of the functional alveolus, and then migration into the primary tooth pulp cavity through resorption pits in the old base (Edmund, 1960, 1969; Kieser et al., 1993). Consequently, and in contrast to eosauropterygians, the entire process remains hidden inside the dentigerous bone. An exception to this pattern is in polycoptylids, in which the secondary alveoli are placed below the functional teeth and so are hidden within the bone (O’Gorman & Gasparini, 2013). NHMUK PV OR36173 is clearly thecodont, with a replacement tooth erupting within the first dentary alveolus (Fig. 4).

3. No plesiosaursians have a symphyseal region of the dentary that is as large and continuously flat as in NHMUK PV OR36173 (Fig. 4). In plesiosaursians, the alveoli occupy the largest part of the dorsal surface. There is usually a groove medial to the alveoli, although sometimes the alveoli and groove are separated by paradental plates (e.g. Benson et al., 2011; Ketchum & Benson, 2011). In Pliosauridae, replacement alveoli develop within the symphyseal groove. Only medial to the groove is there a flat dorsal surface. The lack of a
symphyseal dorsal groove in NHMUK PV OR36173, and its large flat dorsal surface, does not support referral to Pliosauridae.

NHMUK PV OR36173 WITHIN CROCODYLOMORPHA

The most commonly discovered marine crocodylomorph clade from the Mesozoic is Thalattosuchia. However, the Aptian-Albian age of NHMUK PV OR36173 makes a thalattosuchian identification unlikely. Teleosaurids are currently only known from the Jurassic, as the only definitive Lower Cretaceous specimen (from the Valanginian of France) was recently redescribed and reidentified as a metriorhynchid (Young et al., 2014). Moreover, the anterior dentary morphologies of teleosaurids do not match NHMUK PV OR36173 (Fig. 8). In teleosaurids the anterior region is as follows: spatulate, with the maximal width being present at the level of the D3 alveolus; the D3 and D4 alveoli are closely set; there are no enlarged foramina medial to the alveoli; and the alveolar margin is convex at the D3–D4 region, resulting in those alveoli being positioned dorsal to the D1 and D2 alveoli (e.g. Fig. 10C; Andrews, 1913; Hua, 1999; Lepage et al., 2008; Martin & Vincent, 2013). Accordingly, we can safely disregard a teleosaurid origin for this specimen.

However, at least four lineages of the other thalattosuchian clade, Metriorhynchidae, survived into the Early Cretaceous (Young et al., 2014), and there is an indeterminate specimen from the Barremian of Spain (Parrilla-Bel et al., 2012). We can exclude NHMUK PV OR36173 from pertaining to any of these lineages (Cricosaurus, Dakosaurus, Geosaurus, and Plesiosuchina) as they all have the following dentary characteristics: the D1 and D4 alveoli are not enlarged relative to the other anterior alveoli; festooning along the alveolar margin is either absent or only subtle; no enlarged foramina are present medial to the alveoli; and the dentary alveoli lack raised rims (e.g. Fig. 8B; Fraas, 1902; Gasparini & DellaPé, 1976; Pol & Gasparini, 2009; Young & Andrade, 2009; Young et al., 2012; Herrera, Gasparini & Fernández, 2013). Therefore, there is no reason to assume a thalattosuchian origin for NHMUK PV OR36173.

From non-marine Barremian–Aptian deposits of the Isle of Wight, numerous crocodylomorph clades are known. There is a new bernissartiid (genus and species currently in press), the atoposaurid Theriosuchus sp., the goniopholid Anteopthalamosuchus hooleyli, the ?goniopholid/elasuchid/pholidosaurid Vectisuchus leptognathus, the enigmatic neosuchian Leiokarinosuchus brookensis, and the basal eusuchian Hylaeochampsia vectiana (see Salisbury & Naish, 2011; Sweetman et al., in press). Vectisuchus, Leiokarinosuchus, and Hylaeochampsia lack the anterior dentary, and are thus not comparable with NHMUK PV OR36173. Based on the size and shape of the supratemporal fenestrae of L. brookensis, it was likely to have been a longirostrine form (Salisbury & Naish, 2011).

Although no dentaries are known for H. vectiana, the anterior dentary is known for two Albian hylaeochampsid species: Pachycheilosuchus trinquei from Texas, USA, and Pietraroiasuchus ormezzanoi from the southern Apennines, Italy. Both species are interpreted as living in shallow, near-shore, brackish environments (Rogers, 2003; Buscalioni et al., 2011). However, their dentaries do not resemble the Shanklin specimen (NHMUK PV OR36173). In hylaeochampsids, the anterior tip of the dentary is laterally convex in dorsal view, resulting in a broad anterior dentary (D1–D6 region), with each successive alveolus being lateral to the preceding one (Fig. 8O). Also, their symphyses are short (terminating level to the fourth or sixth dentary alveolus) and the dentaries lack concavities (i.e. festooning) along the alveolar margins. Furthermore, the D1 and D4 alveoli are not larger than the D2 or D3 alveoli. Rogers (2003: 132) described P. trinquei as having: ‘Rough pitting and grooves sculpture the ventral surface and a row of nutrient foramina parallels the labial margin’; this differs from the low-relief ornamentation pattern and the large foramina that are arranged across the lateral and ventral surfaces of the dentaries in NHMUK PV OR36173. As such, we can confidently exclude NHMUK PV OR36173 from Hylaeochampsidae.

The only longirostrine clade of eusuchians known from the Cretaceous are Gavialoidea. Gavialoids are known from the Maastrichtian (Late Cretaceous) to the present day, with numerous ‘thoracosaurine’ species known from Maastrichtian–Paleocene marine deposits (e.g. Brochu, 2004, 2006; Hua & Jouve, 2004; Delfino, Piras & Smith, 2005; Jouve et al., 2006b). The Shanklin specimen, however, does not resemble basal gavialoids. The anterior region of the dentary of the Maastrichtian species Eotherosaurus mississipiensis has circular D1 alveoli; the D2 alveoli are larger than the D1, D3, and D4 alveoli; a diastema is present between the D2 and D3 alveoli; the D3 and D4 alveoli are closely set, although they do not form a ‘couplet’; and large foramina on the dorsal surface of the dentary adjacent to the alveoli are absent (Fig. 8P; Brochu, 2004). The anterior region of the dentary of the Palaeocene species, Eosuchus lerichi, has: circular D1 alveoli; D1–D4 alveoli of similar diameters, with the D3 alveoli being slightly smaller; a diastema between the D2 and D3 alveoli; and large, widely separated foramina on the dorsal surface of the dentary, immediately medial to
the alveoli (Delfino et al., 2005). The anterior region of the dentary of the Paleocene species, *Argochampsa krebzi*, is poorly preserved. However, the alveolar diameters are similar, with the D2 alveoli being slightly smaller than the D1, D3, and D4 alveoli (Jouve et al., 2006b). As the anterior dentary morphologies seen in basal gavialoids differ from NHMUK PV OR36173, combined with the long inferred ghost range, we cannot refer the specimen to that clade.

The Shanklin specimen (NHMUK PV OR36173) does not resemble any goniopholidid. In
goniopholidids, the anterior tip of the dentary is laterally convex in dorsal view, resulting in it being wider than the region posterior to the D4 alveolus (Fig. 8M, N; Salisbury et al., 1999; Salisbury, 2002; Schwarz, 2002). The D1 alveolus is mediolaterally wider than it is anteroposteriorly long; the D3 and D4 alveoli are both larger than the D1 and D2 alveoli; and the ventral and lateral surfaces of the anterior part of the dentary are covered with small, closely spaced pits (Salisbury et al., 1999; Salisbury, 2002; Schwarz, 2002). Additionally, the anterior-most part of the dentary is often out-turned in goniopholidids (e.g. Goniopholis sp. (Fig. 9) and Goniopholis tenuidens; Owen, 1879, Pl. 1, fig. 1; Salisbury 2002 as cf. Goniopholis sp.). In view of these marked differences, there is no reason to regard NHMUK PV OR36173 as a member of the Goniopholididae.

The Shanklin specimen can additionally be excluded from the semi-aquatic basal neosuchian group, Atoposauridae (Gervais, 1871), which persisted from the Middle Jurassic to the latest Cretaceous (Evans & Milner, 1994; Martin, Rabi & Csiki, 2010; Martin et al., 2014b). Multiple individuals of Theriosuchus pusillus (Owen, 1879) are known from the Lower Cretaceous of the UK. The mandibular rostrum of one well-preserved specimen (NHMUK PV OR48262) is 10 mm long and has seven alveoli (Fig. 10). Theriosuchus has a heterodont dentition, which is visible even without preserved or erupted tooth crowns, owing to the characteristic shift in alveolar shape/morphology (Brinkmann, 1992; Schwarz & Salisbury, 2005; NHMUK PV OR48262). NHMUK OV OR36173 lacks this shift in alveolar shape from subcircular (pseudocaniniform morphotype) to oval (labiolingually compressed teeth) alveoli. The D1 alveoli border the symphysis at its most anterior point; the gap between the D1 and D2 alveoli is approximately equal to that between the D2 and D3 alveoli; and the D3 to D7 alveoli are confluent. The lateral margin of the anterior snout is heavily ornamented, and has numerous heterogeneous spaced foramina, all approximately 0.5–1 mm in diameter, as is also the case in the other western European species Theriosuchus guimarotae (Schwarz & Salisbury, 2005) and Theriosuchus ibericus (Brinkmann, 1992). Theriosuchus differs from NHMUK PV OR36173 in the relative sizes of the first four alveoli, with the D1–3 alveoli all being equal in size and smaller than the D4 alveoli, and the aforementioned heterogeneous spacing. Additionally, the symphyseal surface has a slight dorsal curvature anteriorly, unlike the linear surface of NHMUK PV OR36173. Based on these marked differences and the overall size differences, we can exclude NHMUK PV OR36173 from being regarded as a large marine atoposaurid.

The anterior end of the dentary is well preserved in several taxa conventionally or putatively considered as members of the Pholidosauridae. In P.
schaumburgensis from the Berriasian of Germany, the anterior region is spatulate and widest at the level of the D2 alveoli (Koken, 1887). There is a sizeable gap between the D1 and D2 alveoli and the D2 and D3 alveoli, whereas the D3 and D4 alveoli are closely set (Koken, 1887). Moreover, the D3 and D4 alveoli are only slightly larger than the other dentary alveoli, all of which are similar in size (Koken, 1887).

In the large-bodied ‘pholidosaurids’, Sarcosuchus hartii, Sarcosuchus imperator, and ‘Sunosuchus’ thailandicus, the anterior dentaries are spatulate with the maximal width at the level of the D4 alveoli (Fig. 8D; Buffetaut & Taquet, 1977; Buffetaut & Ingavat, 1984; Martin et al., 2014a). In these taxa, the D1 and D2 alveoli are small, and substantially smaller than the D3 alveoli. In ‘S.’ thailandicus the D4 alveoli are greatly enlarged relative to the D1–D3 alveoli (Buffetaut & Taquet, 1977; Martin et al., 2014a), whereas in S. hartii and S. imperator the D3 and D4 alveoli are both enlarged (Buffetaut & Taquet, 1977).

In the marine ‘pholidosaurids’ Terminonaris browni and Terminonaris robusta, the anterior region of the dentary is slightly spatulate in shape, its maximal width being at the level of the D3 alveoli (Fig. 8I; Mook, 1933, 1934). The D1 and D2 alveoli are notably smaller than the D3 and D4 alveoli and the rest of the alveoli adjacent to the symphysis. The anterior region of the dentary is unknown in the ‘pholidosaurids’ Oceanosuchus boeensis (Hua et al., 2007; Lepage et al., 2008) and V. leptognathus (Buffetaut & Hutt, 1980; Salisbury & Naish, 2011). However, the spatulate premaxilla of O. boeensis suggests that the anterior region of the dentary was also spatulate, being similar to Terminonaris and other ‘pholidosaurids’.

The elosuchid/pholidosaurid Elosuchus cherifiensis also has a spatulate anterior dentary region, the maximal width being at the level of the D2 and D3 alveoli (Fig. 8J, K; de Lapparent de Broin, 2002). The D1 alveoli are enlarged compared with the D2–D4 alveoli, with the D3 alveoli being the smallest of the anterior alveoli (de Lapparent de Broin, 2002). The line drawings of de Lapparent de Broin (2002) make the shape of the D1 alveoli between the different E. cherifiensis specimens somewhat hard to judge, but they appear to be subcircular to suboval in shape.

The holotype of ‘E.’ felixi and the two lower jaws referred to this species, share some similarities with NHMUK PV OR36173. The ‘E.’ felixi specimens and NHMUK PV OR36173 share: (1) a D1 alveolus that is larger than the D2 and D3 alveoli; and (2) noticeably enlarged D4 alveoli relative to the other alveoli (de Lapparent de Broin, 2002; MNHN.F INA 21, MNHN.F INA 22, MNHN.F INA 25). Another shared characteristic is the position of the D4 alveoli in lateral view, which in both ‘E.’ felixi and NHMUK PV OR36173 is dorsal to the D2 and D3 alveoli. Note that de Lapparent de Broin (2002: fig. 2N) incorrectly showed in a figure the D4 alveolus as being ventral to the D2 and D3 alveoli, and orientated somewhat posteriorly. This is probably a result of the post-mortem deformation of the holotype (MNHN.F INA 25); however, the two other lower jaws are from much larger individuals (MNHN.F INA 21 and MNHN.F INA 22) and they share the same D4 position as NHMUK PV OR36173. There are, however, some noticeable differences between ‘E.’ felixi and NHMUK PV OR36173: (1) ‘E.’ felixi lacks the elongate anteroposterior axis of the D1 alveolus that is found in NHMUK PV OR36173; (2) the anterior dentary is gladius-shaped in ‘E.’ felixi – the anterior dentary of the holotype has a slight concavity along the lateral margin in dorsal/ventral views, but in the larger specimen, MNHN.F INA 21, this concavity is much more pronounced, and in both specimens the anterior dentary is widest at the level of the D4 alveoli; and (3) the gladius-shaped anterior dentary results in the bone tapering anterior to the D4 alveoli, whereas in NHMUK PV OR36173 the D2–D3 region is almost straight and is only slightly lateral to the D1.

There are several anterior dentary characteristics which suggest a close relationship between NHMUK PV OR36173 and Dyrosauridae:

1. The D1 alveolus is enlarged relative to the D2 and D3 alveoli (Fig. 8). This is also seen in: Arambourgisuchus khouribgaensis (Jouve et al., 2005a), Dyrosaurus maghribensis (Jouve et al., 2006a), Hyposaurus ‘morphotypes 1 and 2’ and Rhabdognathus sp. (Jouve, 2007), and Phosphatosaurus gavialoides (Hill et al., 2008).

2. The D1 alveolus is mainly dorsally orientated, but there is also a slightly/moderate anterior orientation. This is also seen in: Cerrejonisuchus improcerus (Hastings et al., 2010), D. maghribensis (Jouve et al., 2006a), D. phosphaticus (Jouve, 2005), Hyposaurus ‘morphotypes 1 and 2’, and Rhabdognathus sp. (Jouve, 2007). This morphology is also seen in basal gavialoids such as A. krebsi (Jouve et al., 2006b) and E. mississippiensis (Brochu, 2004).

3. Numerous, large foramina on the lateral and ventral surfaces of the dentary that are widely spaced. This is also seen in: A. khouribgaensis (Jouve et al., 2005a) and D. phosphaticus (Jouve, 2005).

4. A concave dorsal margin of the dentary between the D1 and D4 alveoli, resulting in the D2 and D3 alveoli being slightly dorsolaterally orientated (i.e. a festooned anterior dentary). This is also seen in: D. phosphaticus (Jouve, 2005), Hyposaurus
'morphotypes 1 and 2', and *Rhabdognathus* sp. (Jouve, 2007).

5. Large foramina on the dorsal surface of the dentary, medial to the D2 and D3 alveoli. This is also seen in: *P. gavialoides* (Hill *et al*., 2008).

6. The external ornamentation on the dentary is of low relief and not conspicuous. This is also seen in: *A. khouribgaensis* (Jouve *et al*., 2005a), *Hyposaurus* 'morphotypes 1 and 2', and *Rhabdognathus* sp. (Jouve, 2007).

7. The anterior end of the dentary is not spatulate (as it is in the 'pholidosaurids' and teleosaurids discussed above) or gladius-shaped (as in 'E.' *felixi*), and the dentary is not laterally convex in dorsal view (which results in a distinctly wide anterior region, such as in goniopholidids and hylaeochampsids, discussed above). NHMUK PV OR36173 has a narrow anterior dentary, like that of longirostrine dyrosaurids (e.g. Jouve, 2007; Hill *et al*., 2008) and basal 'thoracosaurine' gavialoids (e.g. Brochu, 2004; Delfino *et al*., 2005; Jouve *et al*., 2006b) (see Fig. 8).

Note that characteristics 1–5 are also seen in *Crocodylus* spp. (NHMUK Earth Sciences comparative collection of extant reptiles), and are possibly related to an interlocking dentition and vertically festooned tooth row at the anterior-most region of the rostrum.

In summation, there were numerous clades of crocodylomorphs living during the 'middle' Cretaceous (Fig. 11). However, NHMUK PV OR36173 differs considerably from the basal eusuchian clade Hylaeochampsidae and the neosuchian clades Goniopholididae and Atoposauridae in alveolar configuration and dentary shape, and thus cannot be considered a member of these clades (Figs 8–10). Additionally, the anterior dentary morphology of basal gavialoids and metriorhynchid thalattosuchians differs from NHMUK PV OR36173 (Fig. 8). Furthermore, NHMUK PV OR36173 also lacks the mediolaterally expanded anterior dentary seen in 'pholidosaurids' and teleosaurids, and also differs in alveolar configuration (Fig. 8). The alveolar configuration and dentary shape of NHMUK PV OR36173 are similar to those of Dyrosauridae (Fig. 8), and numerous other characteristics (listed above) suggest a close relationship. There is one anterior dentary characteristic shared by dyrosaurids that NHMUK PV OR36173 lacks: a diastema/gap between the D2

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**Figure 11.** Stratigraphic ranges of relevant Lower Cretaceous crocodylomorph lineages, plotted against time and compared with the possible age range of the Shanklin specimen (NHMUK PV OR36173). Dotted lines represent parts of lineages for which fossils are unreported; arrows show that lineage persisted beyond the end of the Turonian.
and D3 alveoli. In view of this combination of dentary characters, we conservatively identify NHMUK PV OR36173 as Tethysuchia incertae sedis. More complete material and inclusion within a comprehensive phylogenetic analysis would enable testing of whether or not NHMUK PV OR36173 is the sister taxon to Dyrosauridae, or if it is a ‘pholidosaurid’-grade marine taxon.

**‘Middle’ Cretaceous marine tethysuchians**

The best known ‘middle’ Cretaceous marine tethysuchians are *T. brownii* and *T. robusta* from North America (middle Cenomanian–middle Turonian) and *O. boecensis* (lower Cenomanian) from France (Mook, 1933, 1934; Wu et al., 2001; Hua et al., 2007; Lepage et al., 2008; Adams et al., 2011). From the upper Cenomanian of Bavaria, Germany, a large, incomplete upper jaw from a longirostrine taxon has been referred to *Terminonaris cf. browni* (Buffetaut & Wellnhofer, 1980). *Terminonaris* and *Oceanosuchus* differ from dyrosaurids in having: (1) more strongly ornamented skull and lower jaw bones; (2) a premaxilla without an anterodorsally projecting process anterior to the external nares; (3) a dorsally orientated external nares; (4) five premaxillary alveoli instead of four; (5) a subvertical anterior margin of the premaxilla that extends ventrally relative to the rest of the element (i.e. the ‘pholidosaurid beak’); (6) absence of the D2–D3 diastema/gap seen in dyrosaurids; and (7) absence also of the small D7 alveoli seen in dyrosaurids. The anterior region of the dentary is not preserved in *Oceanosuchus*, but the anterior region of the dentary of *Terminonaris* is slightly spatulate (Mook, 1933, 1934; Wu et al., 2001; Adams et al., 2011). As such, these taxa still had classic ‘pholidosaurid’ characteristics (Hua et al., 2007; Fortier et al., 2011).

It should be noted that some putative pholidosaurid (*sensu* Fortier et al., 2011) and elosuchid (*sensu* Andrade et al., 2011) apomorphies are also found in the basal-most known dyrosaurids *Chenanisuchus lateroculi* (Jouve et al., 2005b) and a new genus and species (Hastings et al., in press). Fortier et al. (2011) stated that the medial margin of the orbit (in dorsal view) is mostly formed by the prefrontal, with the frontal participating only slightly in the medial margin, and is a pholidosaurid apomorphy. However, this also occurs in *C. lateroculi* (Jouve et al., 2005b), gen. et sp. nov. (Hastings et al., in press), and goniopholidids (see the figures in Andrade & Hornung, 2011). Andrade et al. (2011) stated that the frontal being concave, with the medial borders of the orbit being upturned, is an elosuchid apomorphy. However, this also occurs in the pholidosaurids *P. purbeckensis* (Salisbury, 2002), *P. schaumburgensis* (Koken, 1887), *O. boecensis* (Hua et al., 2007; Lepage et al., 2008), and *T. robusta* (Mook, 1934), and the dyrosaurid *C. lateroculi* (Jouve et al., 2005b; Hill et al., 2008). Therefore, in some aspects, cranial variation between ‘pholidosaurids’ and basal dyrosaurids is less marked than originally thought.

However, one region of the skeleton is profoundly different between the marine ‘pholidosaurids’ and dyrosaurids: the dorsal osteoderm. Like *S. hartii*, the marine taxa *T. robusta* and *O. boecensis*: (1) have subrectangular paravertebral dorsal osteoderms that are wider than they are anteroposteriorly long; (2) retain the stylofoveal joint (has a anterolateral process); (3) have a longitudinal keel; and (4) do not have accessory osteoderms (i.e. a biserial series, e.g. Buffetaut & Taquet, 1977; Wu et al., 2001; Hua et al., 2007). Dyrosaurids, however, lack the stylofoveal joint and longitudinal keels, they have accessory osteoderms lateral to the paravertebral series, and have a lateral process which creates a joint between the paravertebral osteoderm and the accessory osteoderm (see Schwarz, Frey & Martin, 2006). As such, while cranial variation between ‘pholidosaurids’ and basal dyrosaurids is less marked than is initially presumed, their difference in dorsal osteoderm morphologies are significant. These differences have the potential to be very useful in identifying dyrosaurids solely, or primarily, based on osteoderms.

Although dyrosaurids are well known from the Maastrichtian onwards, their pre-Maastrichtian fossil record is relatively poor. Two maxillary fragments from the Campanian of Egypt pertain to a longirostrine crocodyliform tentatively referred to *Dyrosaurus* (Churcher & Russell, 1992; Churcher, 1995). The earliest potential dyrosaurids are Cenomanian in age. A partial dentary (mid-symphysal region) from the middle Cenomanian marine deposits of Portugal was noted to be reminiscent of dyrosaurids (Buffetaut & Lauverjat, 1978). However, its incomplete nature means that no firm conclusions can be drawn as to its affinities. Skull fragments (frontal, parietal, and left postorbital) and incomplete vertebrae from Cenomanian lacustrine deposits of Sudan were referred to *Dyrosauridae indet.* by Buffetaut et al. (1990). The dorsal vertebrae have very large hypapophyses, as is the case in dyrosaurids (i.e. blade-like, flattened laterally, rounded ventrally, and anteroposteriorly long) (e.g. see the figures in Storrs, 1986; Jouve & Schwarz, 2004; Jouve et al., 2005a; Schwarz et al., 2006). *Terminonaris robusta* also has noticeable hypapophyses on some vertebrae, but they are much lower and are a different shape (see fig. 4 in Wu et al., 2001). The skull fragments were considered to be from a primitive dyrosaurid by Buffetaut et al. (1990), as they have: (1) more strongly ornamented cranial
CONCLUSIONS

Herein we describe a tethysuchian crocodyliform from the Aptian–Albian (most likely the upper Albian) of the UK from Shanklin on the Isle of Wight. The single known specimen is the anterior region of a right dentary, and it increases the known geological range of marine tethysuchians back into the late Lower Cretaceous. Within Tethysuchia this mandibular fragment has certain characteristics that suggest a possible relationship with Dyrosauridae: (1) an enlarged first dentary alveolus, relative to the second and third alveoli; (2) the first dentary alveolus is mainly dorsally orientated but is slightly anteriorly orientated; (3) numerous large foramina on the lateral and ventral surfaces of the dentary that are widely spaced; (4) a concave dorsal margin of the dentary between the first and fourth dentary alveoli, which results in the second and third dentary alveoli being slightly dorsolaterally orientated; (5) large foramina on the dorsal surface of the dentary medial to the second and third alveoli; (6) external ornamentation on the dentary is of low relief; and (7) anterior dentary is not laterally expanded forming a 'spatulate' morphology. However, establishing a new taxon for this specimen must await the discovery of more complete remains.

We consider there to be no firm evidence that any known ‘middle’ Cretaceous tethysuchian is either a dyrosaurid or an especially close relative of that clade, especially as some putative apomorphies for ‘Pholidosauridae’/Elosuchidae are also found in the basal-most known dyrosaurids. Only future studies of new discoveries, and/or unrecognized museum specimens from this key time span, will elucidate the tethysuchian radiation into the marine realm and the origin of Dyrosauridae.

REFERENCES


