



**Marine tethysuchian crocodyliform from the ?Aptian-Albian  
(Early Cretaceous) of the Isle of Wight, England**

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3 Marine tethysuchian crocodyliform from the ?Aptian-Albian (Early Cretaceous)  
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6 of the Isle of Wight, England  
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44 RUNNING HEAD: Cretaceous tethysuchian from England  
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3 ABSTRACT. A marine tethysuchian crocodyliform from the Isle of Wight, most likely from  
4 the Upper Greensand Formation (late Albian, Early Cretaceous), is described. However, we  
5 cannot preclude it being from the Ferruginous Sands Formation (late Aptian), or more  
6 remotely, the Sandrock Formation (late Aptian-early Albian). The specimen consists of the  
7 anterior region of the right dentary, from the tip of the dentary to the incomplete fourth  
8 alveolus. This specimen increases the known geological range of marine tethysuchians back  
9 into the late Early Cretaceous. While we refer it to *Tethysuchia incertae sedis*, there are seven  
10 anterior dentary characteristics which suggest a possible relationship with the Maastrichtian-  
11 Eocene clade Dyrosauridae. We also review 'middle' Cretaceous marine tethysuchians,  
12 including putative Cenomanian dyrosaurids. We conclude that there is insufficient evidence  
13 to be certain that any known Cenomanian specimen can be safely referred to Dyrosauridae, as  
14 there are some cranial similarities between basal dyrosaurids and Cenomanian-Turonian  
15 marine 'pholidosaurids'. Future study of middle Cretaceous tethysuchians could help unlock  
16 the origins of Dyrosauridae and improve our understanding of tethysuchian  
17 macroevolutionary trends.  
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**Key words:** Albian – Aptian – Cretaceous – England – Tethysuchia – Upper Greensand  
Formation.

## INTRODUCTION

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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 *et al.*, 2001; Jouve *et al.* 2005a, 2006a; Barbosa *et al.*, 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 Paleocene and Eocene (e.g. Buffetaut 1976, 1978, 1982; Jouve 2005, 2007; Jouve *et al.* 2005a, 2005b, 2006a, 2008; Barbosa *et al.*, 2008; Hill *et al.*, 2008; Hastings *et al.* 2010, 2011). However, the origins of this clade are poorly understood due to a paucity of fossils from the 'middle' Cretaceous.

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A phylogenetic definition of Tethysuchia was recently proposed by Andrade *et al.* (2011: S102) as: "the clade composed of *Pholidosaurus purbeckensis* (Mansell-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 *et al.* (2011: S259) as: "a stem-based group name including *Pholidosaurus schauburgensis* (Meyer, 1841) and all taxa closer to it than to *Dyrosaurus phosphaticus* (Thomas, 1893) or *Pelagosaurus typus* Bronn, 1841".  
  
  
explicit phylogenetic definition has been proposed for Dyrosauridae or Elosuchidae.

Phylogenetic analyses consistently finds Dyrosauridae to be holophyletic (e.g. Wu *et al.*, 2001; Jouve, 2005; Jouve *et al.* 2005a, 2006a, 2008; Barbosa *et al.*, 2008; Young &

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3 Andrade, 2009; Hastings *et al.* 2010, 2011; Andrade *et al.*, 2011; Fortier *et al.*, 2011). The  
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5 holophyly of Pholidosauridae however, is not always recovered. Pholidosauridae has either  
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7 been found to be a paraphyletic grade of taxa closely related to Dyrosauridae (Wu *et al.*,  
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9 2001; Jouve *et al.* 2005a, 2008; Barbosa *et al.*, 2008; Young & Andrade, 2009; Hastings *et al.*  
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11 2010, 2011; Andrade *et al.*, 2011), holophyletic (Fortier *et al.*, 2011), or holophyletic with   
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13 *Elosuchus* being outside the clade comprising Dyrosauridae and Pholidosauridae (Jouve *et*  
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15 *al.*, 2006a). Martin & Buffetaut (2012) and Martin *et al.* (in press) also found Pholidosauridae  
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17 to be holophyletic, but as no dyrosaurids were included in those analyses they never tested  
18  
19 whether pholidosaurids constitute a natural group. When Pholidosauridae is found to be  
20  
21 paraphyletic, the sister taxon of Dyrosauridae varies between *Terminonaris* (Wu *et al.*, 2001;  
22  
23 Jouve *et al.* 2005a, 2008; Barbosa *et al.*, 2008), *Oceanosuchus* (Young & Andrade, 2009) and  
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25 *Elosuchus* (Hastings *et al.* 2010, 2011); although *Oceanosuchus* was only included in the  
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27 analysis of Young & Andrade (2009). As such, the internal evolutionary relationships of  
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29 Tethysuchia are in flux. This has important implications for tethysuchian evolution, in  
30  
31 particular for our understanding of dyrosaurid origins, and whether dyrosaurids and the  
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33 marine 'pholidosaurids' *Terminonaris* and *Oceanosuchus* constitute a single marine radiation  
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35 or several independent ones.

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40 One of the major issues hampering resolution in these analyses is the paucity of  
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42 'middle' Cretaceous (Barremian-Turonian) marine tethysuchians, thus affecting our  
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44 understanding of character polarity. In those phylogenetic analyses where 'pholidosaurids' are  
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46 paraphyletic, all potential dyrosaurid sister taxa (*Elosuchus*, *Oceanosuchus* and  
47  
48 *Terminonaris*) are from this time span (see Mook 1933, 1934; de Lapparent de Broin, 2002;  
49  
50 Wu *et al.*, 2001; Hua *et al.*, 2007). Furthermore, the earliest potential dyrosaurids are  
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52 Cenomanian in age (Buffetaut & Lauerjat, 1978; Buffetaut *et al.*, 1990). Therefore,  
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3 investigating specimens from the Barremian-Turonian stages will be key to elucidating the  
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5 early evolution of Tethysuchia.  
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7           Here we describe a long known but previously unstudied tethysuchian crocodyliform.  
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9 This specimen, the anterior-most part of a right dentary (NHMUK PV OR36173), is most  
10  
11 likely from the Upper Greensand Formation of England (late Albian, Early Cretaceous).  
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13 Although this specimen was discovered over 150 years ago, it has only been briefly  
14  
15 mentioned once in the literature. Furthermore, it is of importance due to its unusual  
16  
17 morphology and geological age. The presence of a marine tethysuchian in the late Early  
18  
19 Cretaceous of England would indicate that tethysuchians moved into the marine realm earlier  
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21 than previously realised.  
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## 27           ABBREVIATIONS

### 28                   INSTITUTIONAL

29  
30 MIWG, the Museum of Isle of Wight Geology (now IWCMS- the Isle of Wight County  
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32 Museum Service, incorporating Dinosaur Isle museum and visitor attraction); NHMUK,  
33  
34 Natural History Museum, London, England, United Kingdom.  
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### 41                   ANATOMICAL

42  
43 D1, first dentary alveolus; D2, second dentary alveolus; D3, third dentary alveolus; D4,  
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45 fourth dentary alveolus; for, foramen; rug, rugose patch; sym, symphysis.  
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## 50           HISTORICAL INFORMATION

51  
52 The anterior right dentary (NHMUK PV OR36173) was purchased by the British Museum  
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54 (Natural History), in October 1861 from a Mr Simmons. In the NHMUK specimen register,  
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56 NHMUK PV OR36173 is listed as an ‘anterior portion of left upper jaw with four teeth  
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3 sockets, of a crocodylian reptile. Greensand ? Shanklin, I. of Wight'. The only mention of the  
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5 specimen we can find in the literature is by Lydekker (1889: 179), who identified NHMUK  
6  
7 PV OR36173 as *Polyptychodon interruptus*, and states that it is: "apparently the extremity of  
8  
9 the left premaxilla". Why he referred NHMUK PV OR36173 to Pliosauridae, and thought it  
10  
11 might be *Polyptychodon interruptus*, was not stated. Amongst the specimen labels is a note  
12  
13 left by Dr Leslie Noé, dated 23rd August 1999, in which he states: 'This jaw fragment is not  
14  
15 pliosaurian [? crocodylian]'. This taxonomic note is what brought NHMUK PV OR36173 to  
16  
17 our attention.  
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#### 20 21 22 23 GEOLOGICAL INFORMATION

24  
25 The right partial dentary (NHMUK PV OR36173) was discovered at Shanklin, Isle of Wight,  
26  
27 England, United Kingdom. The exact formation that yielded it is, however, unclear. It was  
28  
29 referred to the Upper Greensand Formation by Lydekker (1889), but the NHMUK specimen  
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31 register refers to it as from: 'Greensand ?'. Therefore, verifying that it is actually from the  
32  
33 Upper Greensand Formation, and not from one of the Lower Greensand Group formations  
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35 exposed at Shanklin is important (see Fig. 1). In order to determine this, one of us (TP)  
36  
37 examined the fossils in the MIWG (IWCMS) and the rocks at Shanklin. Descriptions of the  
38  
39 deposits of the Lower Greensand and Selborne Groups on the Isle of Wight have been given  
40  
41 by White (1921), Wach & Ruffell (1991), Insole *et al.* (1998), and Hopson *et al.* (2008).  
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46 Numerous marine reptiles are known from the Ferruginous Sands Formation (Lower  
47  
48 Greensand Group) of the Isle of Wight. The members of the Ferruginous Sands Formation  
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50 exposed at the lower part of the cliffs at Shanklin (Knock Cliff to Hope Beach) are: the Old  
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52 Walpen Chine Member (XII), the New Walpen Chine Member (XIII) and Member XIV (un-  
53  
54 named). If the provenance of NHMUK PV OR36173 is one of these members, we would  
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56 expect it to be very dark brown or black in colour with a dark matrix (this being due to the  
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3 iron-rich nature of the sediment), as is the case in the exceptionally rare ornithopod bones and  
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5 a number of ichthyosaur vertebrae (e.g. MIWG.5376) from Member VI which are black-dark  
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7 brown. However, we cannot discount that NHMUK PV OR36173 may have come from an  
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9 isolated calcareous lens in one of these members. As such, the possibility of a Ferruginous  
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11 Sands Formation origin cannot currently be completely ruled out.  
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14 Overlying the Ferruginous Sands Formation at Shanklin is the Sandrock Formation  
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16 (Fig. 1). This formation is a mixture of blue silty clay and yellow sands, and is considered to  
17  
18 have been deposited during a time when cyclical sea-level changes preserved a number of  
19  
20 wide estuaries and near-shore mud-flats (see Wach & Ruffel, 1991). Fossil plants discovered  
21  
22 from this formation are typically pale (white), fragmentary and crumble easily. While we  
23  
24 think it is unlikely that the Sandrock Formation is the origin of NHMUK PV OR36173, the  
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26 lack of any suitable reptilian material for comparison means we cannot entirely discount the  
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28 possibility.  
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32 The final, and highest, formation from the Lower Greensand Group exposed is the  
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34 Monks Bay Sandstone Formation (formerly known as the Carstone Formation of the Isle of  
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36 Wight) (Fig. 1). This overlies the Sandrock Formation. It is very gritty, with large iron-rich  
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38 sandstone nodules and has a dark brown colouration. Vertebrate fossils are unreported in this  
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40 formation, and we exclude this as the possible origin of NHMUK PV OR36173.  
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43 The Lower Greensand Group is overlain by the Selborne Group, with two formations  
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45 exposed (Fig. 1): the Gault Formation (Albian) and the Upper Greensand Formation (Albian-  
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47 Cenomanian). The Selborne Group was deposited in a marine setting, with the Gault  
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49 Formation forming in a mid- or outer-shelf environment, while the Upper Greensand  
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51 Formation was formed in a shallow offshore shelf and in lower shoreface zones related to an  
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53 eastward-prograding shoreline (Hopson, 2011).  
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3 At Shanklin, the clays/mudstones of the Gault Formation are dark in colour which  
4 results in dark fossils. The general colouration and matrix of NHMUK PV OR36173 appears  
5 similar to the central part of the Upper Greensand Formation, the 'Malm Rock' or Freestone, a  
6 pale grey-green glauconitic sandstone/siltstone which have iron-rich sandy nodules within  
7 (division D of Jukes-Browne & Hill, 1900). This thick sequence lies above the basal 'Passage  
8 Beds' (division A of Jukes-Browne & Hill, 1900) and below the Chert Beds (division E of  
9 Jukes-Browne & Hill, 1900).  
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18 However, it must be appreciated that a considerable amount of time (over 150 years)  
19 has passed since NHMUK PV OR36173 was collected. Therefore, the external surface may  
20 have altered as it dried out and oxidised. Based on general specimen colouration and matrix,  
21 the Upper Greensand Formation seems like the most probable origin of NHMUK PV  
22 OR36173. As stated above, we cannot preclude the possibility that NHMUK PV OR36173  
23 originated from the Sandrock Formation or from an isolated calcareous lens in Member XII,  
24 Member XIII or Member XIV of the Ferruginous Sands Formation.  
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34 Is NHMUK PV OR36173 reworked from an earlier, Jurassic, horizon? Not only is the  
35 morphology of NHMUK PV OR36173 distinct from any known Jurassic taxon (see  
36 description below), but a drifted block of Jurassic material would needed to have travelled  
37 many kilometres from the nearest exposed Jurassic outcrop to have become entombed in the  
38 marine Greensands. We find this to be an unlikely scenario.  
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## 50 SYSTEMATIC PALAEOLOGY

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52 CROCODYLIFORMES BENTON & CLARK, 1988

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54 MESOEUCROCODYLIA WHETSTONE & WHYBROW, 1983

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56 NEOSUCHIA BENTON & CLARK, 1988  
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TETHYSUCHIA BUFFETAUT, 1982

TETHYSUCHIA *INCERTAE SEDIS*

*Specimen*

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

*Locality*

Shanklin, Isle of Wight, England, United Kingdom.

*Horizon and age*

Most likely from the 'Malm rock' or Freestone, Upper Greensand Formation, Selborne Group (late Albian, Early Cretaceous). However, it could be from an isolated calcareous lens from one of three members within the Ferruginous Sands Formation, Lower Greensand Group (late Aptian, Early 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 (late Aptian-early Albian, Early Cretaceous), as there are no known suitable fossils from this formation to compare it with.

## 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

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2  
3 external (= lateral and ventral) surfaces of the dentary are gently convex, with numerous  
4 large, sub-circular foramina that are mostly widely spaced (Figs. 2-3). The external surface  
5 ornamentation is composed of numerous, very small sub-circular pits. This ornamentation  
6 pattern remains constant along the element. The medial contractions between alveoli (and the  
7 raised alveolar rims, especially the D3 and D4) suggest that the premaxillary teeth would  
8 have occluded lateral to the interalveolar spaces on the dentary (i.e. in an overbite or  
9 interlocking manner) (Figs. 2, 4).

10  
11 On the dorsal surface of the dentary, the three anterior-most alveoli are completely  
12 preserved and the anterior section of the fourth (Fig. 4). All of the preserved alveoli are very  
13 large, but vary in size and shape. There is also variation in interalveolar spacing. The first  
14 dentary alveolus (D1) is orientated dorsally and slightly anteriorly (Figs. 2, 4-5). The D1  
15 alveolus is oval in shape, orientated along the anteroposterior axis of the dentary, with an  
16 anteroposterior length of 48 mm and a mediolateral width of approximately 38 mm. Between  
17 the D1 and D2 alveoli, there is a minimum interalveolar space of 17 mm. The D2 alveolus is  
18 notably smaller and also oval in shape, having an anteroposterior length of 25 mm. Between  
19 the D2 and D3 alveoli, there is a minimum interalveolar space of 14 mm. The D3 alveolus is  
20 smaller than the D2 alveolus and slightly more circular in shape, with an anteroposterior  
21 length of 21 mm. Between the D3 and D4 alveoli, there is a minimum interalveolar space of 9  
22 mm. The D4 alveolus is incomplete, but it would have been considerably larger than the D2  
23 and D3. The D4 alveolus has a transverse width of approximately 35 mm. Each alveolus has  
24 a slight, or noticeable, raised rim. In the D1 and D3 they are barely noticeable, in the D2 the  
25 rim is more strongly developed, while the D4 has a very large and well-developed rim.

26  
27 The medial border of the D2 and D3 alveoli are either in the same sagittal plane ~~line~~  
28 as, or lateral to, the lateral border of the D1 alveolus (Fig. 4). Overall the dorsal surface of the  
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3 dentary is mainly flat, with numerous large foramina medial to the D2 and D3 alveoli. The  
4  
5 largest foramen is medial to the D3 alveolus.  
6

7 ~~When seen in~~ lateral view (Fig. 2), the dorsal margin of the dentary is concave  
8  
9 between the D1 and D4 alveoli. This results in the D2 and D3 alveoli being ventral in the  
10  
11 transverse plane to the D1 and D4 alveoli. Moreover, the D2 and D3 alveoli are orientated  
12  
13 slightly dorsolaterally. When seen in lateral view, the ventral margin is distinctly curved, and  
14  
15 is convex. It rises dorsally anteriorly, and is noticeable ventral to the first two dentary alveoli.  
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19 In medial view, the preservation is poor but the symphyseal suture is partially visible  
20  
21 (Fig. 6). However, the dentary appears to be 'hollow' posteroventral to the D3 and D4 alveoli.  
22  
23 Anteriorly, the dentary is a solid bone which would have created a firm **interdentary contact**.  
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25 Ventral to the D3 there is a concave surface that forms the boundary from the 'hollow' and  
26  
27 solid regions of the dentary. Posteriorly, bivalve encrustations and bivalve fossils are  
28  
29 preserved within this 'hollow' region.  
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33 We cannot determine how far much of the symphyseal surface is preserved, although  
34  
35 it is likely that it extended posterior to the fourth alveolus. Based on the preserved region, the  
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37 dentary appears to be from a mesorostrine or longirostrine taxon (based on the long, narrow  
38  
39 and dorsoventrally shallow dentary). It is similar to other tethysuchians like '*Elosuchus felixi*  
40  
41 (de Lapparent de Broin, 2002) and Dyrosauridae (e.g. Hill *et al.*, 2008; Hastings *et al.*, 2010).  
42  
43 There is no trace of the splenial, but we would not expect there to be since the splenial does  
44  
45 not reach as far anteriorly as the fourth alveolus in other tethysuchian taxa (e.g. de Lapparent  
46  
47 de Broin, 2002; Hill *et al.*, 2008; Hastings *et al.* 2010, 2011; Adams *et al.*, 2011).  
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49  
50 In posterior view, ~~we can see a cross section through the dentary~~ (Fig. 7). As noted by  
51  
52 Lydekker (1889: 179) there are large cancelli in the diploë. The dentary is highly cancellous,  
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54 with thicker cortical bone along the ventral and lateroventral margins of the bone; whereas  
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56 the dorsal and dorsolateral margins have very thin cortical bone. Adjacent to the cortical  
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3 bone, the cancelli immediately internal to the thickest cortical bone are larger than those  
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5 adjacent to thinner cortical bone.  
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## 8 9 10 DENTITION

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12 Only two, incomplete, *in situ* tooth crowns are preserved (Fig. 4). The *in situ* tooth crowns  
13  
14 are in the first and third alveoli. In the first alveolus there is an erupting replacement tooth  
15  
16 crown. The crown is only partially visible, with only the apical half of the lingual surface  
17  
18 exposed. In the third alveolus there is a cross-section through the base of a fully erupted tooth  
19  
20 crown. The crown has a diameter of 11-12 mm.  
21

22  
23 Based on the two *in situ* tooth crowns, the dentition would have been caniniform in  
24  
25 morphology, i.e. single cusped and labiolingually compressed. The basal section is oval in  
26  
27 cross-section, being wider mesiodistally than labiolingually. The incomplete preservation of  
28  
29 the crowns makes it impossible to make any further comments on the carinal or overall crown  
30  
31 morphologies.  
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## 34 35 36 37 38 DISCUSSION

### 39 40 EXCLUDING NHMUK PV OR36173 FROM PLESIOSAURIA

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42 We agree with Dr Leslie Noé that the referral of NHMUK PV OR36173 to Pliosauridae, and  
43  
44 *Polyptychodon interruptus*, is incorrect. There are a number of plesiosaurian characteristics  
45  
46 that are lacking in NHMUK PV OR36173, which allow us to confidently exclude NHMUK  
47  
48 PV OR36173 from Sauropterygia. These include:  
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52 1) The pattern of large-to-small teeth in NHMUK PV OR36173 is unknown in  
53  
54 Plesiosauria (first and fourth dentary alveoli being considerably larger than the second and  
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56 third alveoli; Fig. 4). To our knowledge there is no known plesiosaurian in which the first  
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3 dentary alveous (D1) is larger than the second and third alveoli. In fact in all plesiosaurian  
4 dentaries, the D1 is smaller (or at least subequal) than the immediately posterior alveoli. This  
5 is seen in Rhomaleosauridae (Smith, 2007), Pliosauridae (Andrews, 1913; Tarlo, 1960;  
6 Benson *et al.*, 2011; Ketchum & Benson, 2011; Sassoon *et al.*, 2012; Albright *et al.*, 2007a),  
7 Leptocleididae (Druckenmiller & Russell, 2008) and Polycotyliidae (Carpenter, 1996;  
8 Albright *et al.*, 2007b).

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16 2) Eosauropterygians have a distinctive tooth replacement pattern. Their replacement  
17 teeth originate in separate temporary alveoli, recognisable by aligned foramina on the dorsal  
18 surface of the dentaries. Developing teeth grow within these, until the temporary and  
19 functional alveoli fuse (Owen, 1840; von Huene, 1923; Rieppel, 2001; Shang, 2007). The  
20 erupting teeth grow in a shallow groove medial to each functional alveolus. The separation  
21 between primary and secondary alveoli can be short or large. However, tooth replacement in  
22 thecodont groups (including Crocodylomorpha) involves the replacement teeth developing in  
23 shallow pits in the lingual side of the functional alveolus, and then migrating into the primary  
24 tooth pulp cavity through resorption pits in the old base (Edmund 1960, 1969; Kieser *et al.*,  
25 1993). Consequently, and in contrast to eosauropterygians, the entire process remains hidden  
26 inside the dentigerous bone. An exception to this pattern is in polycotyliids, where the  
27 secondary alveoli are placed below the functional teeth and so are hidden within the bone  
28 (O'Gorman & Gasparini, 2013). NHMUK PV OR36173 is clearly thecodont, with a  
29 replacement tooth erupting within dentary alveolus one (Fig. 4).

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47 3) No plesiosaurians have a symphyseal region of the dentary that is as large and  
48 continuously flat as in NHMUK PV OR36173 (Fig. 4). In plesiosaurians the alveoli occupy  
49 the largest part of the dorsal surface. Medial to the alveoli, there is usually a groove, although  
50 sometimes the alveoli and groove are separated by paradental plates (e.g. Ketchum &  
51 Benson, 2011; Benson *et al.*, 2011). In Pliosauridae replacement alveoli develop within the  
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3 symphyseal groove. Only medial to the groove is there a flat dorsal surface. The lack of the  
4  
5 symphyseal dorsal groove in NHMUK PV OR36173, and its large flat dorsal surface does not  
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7 support referral to Pliosauridae.  
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#### 10 11 NHMUK PV OR36173 WITHIN CROCODYLOMORPHA 12 13

14 The most commonly discovered marine crocodylomorph clade from the Mesozoic is  
15  
16 Thalattosuchia. However, the Aptian-Albian age of NHMUK PV OR36173 makes a  
17  
18 thalattosuchian identification unlikely. Teleosaurids are currently only known from the  
19  
20 Jurassic, as the only definitive Early Cretaceous specimen (from the Valanginian of France)  
21  
22 was recently re-described and re-identified as a metriorhynchid (Young *et al.*, in press).  
23  
24 Moreover, the anterior dentary morphologies of teleosaurids do not match NHMUK PV  
25  
26 OR36173 (Fig. 8). In teleosaurids the anterior region is: spatulate, with the maximal width  
27  
28 being present at the level of the D3 alveolus; the D3 and D4 alveoli are closely set; there are  
29  
30 no enlarged foramina medial to the alveoli; and the alveolar margin is convex at the D3-D4  
31  
32 region, resulting in those alveoli being positioned dorsal to the D1 and D2 alveoli (e.g. Fig.  
33  
34 10C; Andrews, 1913; Hua, 1999; Lepage *et al.*, 2008; Martin & Vincent, 2013). Accordingly,  
35  
36 we can safely disregard a teleosaurid origin for this specimen.  
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41 However at least four lineages of the other thalattosuchian clade, Metriorhynchidae,  
42  
43 survived into the Early Cretaceous (Young *et al.*, in press), and there is an indeterminate  
44  
45 specimen from the Barremian of Spain (Parrilla-Bel *et al.*, 2012). We can exclude NHMUK  
46  
47 PV OR36173 from pertaining to any of these lineages (*Cricosaurus*, *Dakosaurus*, *Geosaurus*  
48  
49 and *Plesiosuchina*) as they all have the following dentary characteristics: the D1 and D4  
50  
51 alveoli are not enlarged relative to the other anterior alveoli, festooning along the alveolar  
52  
53 margin is either absent or only subtle, no enlarged foramina are present medial to the alveoli,  
54  
55 and the dentary alveoli lack raised rims (e.g. Fig. 8B; Fraas, 1902; Gasparini & Dellapé,  
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3 1976; Pol & Gasparini, 2009; Young & Andrade, 2009; Young *et al.*, 2012; Herrera *et al.*,  
4  
5 2013). Therefore, there is no reason to assume a thalattosuchian origin for NHMUK PV  
6  
7 OR36173.  
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10 From non-marine Barremian-Aptian deposits of the Isle of Wight, numerous  
11 crocodylomorph clades are known. There is a new bernissartiid (genus and species currently  
12 in press), the atoposaurid *Theriosuchus* sp., the goniopholidid *Anteophthalmosuchus hooleyi*,  
13  
14 the ?goniopholidid/elosuchid/pholidosaurid *Vectisuchus leptognathus*, the enigmatic  
15  
16 neosuchian *Leiokarinosuchus brookensis* and the basal eusuchian *Hylaeochampsia vectiana*  
17  
18 (see Salisbury & Naish, 2011; Sweetman *et al.*, in press). *Vectisuchus*, *Leiokarinosuchus* and  
19  
20 *Hylaeochampsia* lack the anterior dentary, and are thus not comparable to NHMUK PV  
21  
22 OR36173.  
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27 While no dentaries are known for *Hylaeochampsia vectiana*, the anterior dentary is  
28 known for two Albian hylaeochampsid species: *Pachycheilosuchus trinquei* from Texas,  
29  
30 USA and *Pietraroiiasuchus ormezzano* from the southern Apennines, Italy. Both species are  
31  
32 interpreted as living in shallow, near-shore, brackish environments (Rogers, 2003; Buscalioni  
33  
34 *et al.*, 2011). However, their dentaries do not resemble the Shanklin specimen (NHMUK PV  
35  
36 OR36173). In hylaeochampsids, the anterior tip of the dentary is laterally convex in dorsal  
37  
38 view, resulting in a broad anterior dentary (D1-D6 region) with each successive alveolus  
39  
40 being lateral to the preceding one (Fig. 80). Also, their symphyses are short (terminating  
41  
42 level to the fourth or sixth dentary alveolus) and the dentaries lack concavities (i.e.  
43  
44 festooning) along the alveolar margins. Furthermore, the D1 and D4 alveoli are not larger  
45  
46 than the D2 or D3 alveoli. Rogers (2003: 132) described *Pachycheilosuchus trinquei* as  
47  
48 having: "Rough pitting and grooves sculpture the ventral surface and a row of nutrient  
49  
50 foramina parallels the labial margin", this differs from the low-relief ornamentation pattern  
51  
52 and the large foramina that are arranged across the dentaries lateral and ventral surfaces in  
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3 NHMUK PV OR36173. As such, we can confidently exclude NHMUK PV OR36173 from  
4  
5 Hylaeochampsidae.  
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8 The only longirostrine clade of eusuchians known from the Cretaceous are  
9  
10 Gavialoidea. Gavialoids are known from the Maastrichtian (Late Cretaceous) to the present  
11  
12 day, with numerous 'thoracosaurine' species known from Maastrichtian-Paleocene marine  
13  
14 deposits (e.g. Brochu 2004, 2006; Hua & Jouve, 2004; Delfino *et al.*, 2005; Jouve *et al.*,  
15  
16 2006b). The Shanklin specimen however, does not resemble basal gavialoids. The anterior  
17  
18 region of the dentary of the Maastrichtian species *Eothoracosaurus mississippiensis* has  
19  
20 circular D1 alveoli; the D2 alveoli are larger than the D1, D3 and D4 alveoli; a diastema is  
21  
22 present between the D2 and D3 alveoli; the D3 and D4 alveoli are closely set, although they  
23  
24 do not form a 'couplet'; and large foramina on the dorsal surface of the dentary adjacent to the  
25  
26 alveoli are absent (Fig. 8P; Brochu, 2004). The anterior region of the dentary of the  
27  
28 Paleocene species *Eosuchus lerichi* has: circular D1 alveoli; the D1-D4 alveoli are similar in  
29  
30 diameter, with the D3 alveoli being slightly smaller; a diastema is present between the D2  
31  
32 and D3 alveoli; and large, widely separated foramina are present on the dorsal surface of the  
33  
34 dentary immediately medial to the alveoli (Delfino *et al.*, 2005). The anterior region of the  
35  
36 dentary of the Paleocene species *Argochampsia krebsi* is poorly preserved. However, the  
37  
38 alveolar diameters are similar with the D2 alveoli being slightly smaller than the D1, D3 and  
39  
40 D4 alveoli (Jouve *et al.*, 2006b). As the anterior dentary morphologies seen in basal  
41  
42 gavialoids differ from NHMUK PV OR36173, combined with the long inferred ghost range,  
43  
44 we cannot refer the specimen to that clade.  
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50 The Shanklin specimen (NHMUK PV OR36173) does not resemble any  
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52 goniopholidid. In goniopholidids, the anterior tip of the dentary is laterally convex in dorsal  
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54 view, resulting in it being wider than the region posterior to the D4 alveolus (Fig. 8M-N;  
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56 Salisbury *et al.*, 1999; Salisbury, 2002; Schwarz, 2002). The D1 alveolus is mediolaterally  
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3 wider than it is anteroposteriorly long; the D3 and D4 alveoli are both larger than the D1 and  
4 D2 alveoli; and the ventral and lateral surfaces of the anterior part of the dentary are covered  
5 with small, closely spaced pits (Salisbury *et al.*, 1999; Salisbury, 2002; Schwarz, 2002).  
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9 Additionally, the anteriormost part of the dentary is often out-turned in goniopholidids (e.g.  
10 *Goniopholis crassidens* (Fig. 9) and *G. tenuidens*; Owen, 1879, Pl. 1, Fig. 1; Salisbury 2002  
11 as cf. *Goniopholis* sp.). In view of these marked differences, there is no reason to regard  
12 NHMUK PV OR36173 as a member of Goniopholididae.  
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18 The Shanklin specimen can additionally be excluded from the semi-aquatic basal  
19 neosuchian group Atoposauridae (Gervais, 1871), which persisted from the Middle Jurassic  
20 to the latest Cretaceous (Evans & Milner, 1994; Martin *et al.*, 2010). Multiple individuals of  
21 *Theriosuchus pusillus* (Owen, 1879) are known from the Early Cretaceous of the UK. The  
22 mandibular symphysis of one well preserved specimen (NHMUK PV OR48262) is 10 mm  
23 long, and has seven alveoli adjacent (Fig. 10). *Theriosuchus* has a heterodont dentition, and  
24 the first seven teeth are all of the pseudocaniniform morphotype similar to NHMUK PV  
25 OR36173. The D1 alveoli border the symphysis at its most anterior point, the gap between  
26 the D1 and D2 alveoli is approximately equal to that between the D2 and D3 alveoli; while  
27 the D3 to D7 alveoli are conjoined. The lateral margin of the anterior snout is heavily  
28 ornamented, and has numerous heterogeneously spaced foramina, all approximately 0.5-1mm  
29 in diameter, as is also the case in the other western European species *T. guimarotae* (Schwarz  
30 & Salisbury, 2005) and *T. ibericus* (Brinkmann, 1992). *Theriosuchus* differs from NHMUK  
31 PV OR36173 in the relative sizes of the first four alveoli, with the D1-3 alveoli all being  
32 equal and smaller than the D4 alveoli, and the aforementioned heterogeneous spacing.  
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3 differences, we can exclude NHMUK PV OR36173 from being regarded as a large marine  
4  
5 atoposaurid.  
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7 The anterior end of the dentary is well preserved in several taxa conventionally or  
8  
9 putatively considered members of Pholidosauridae. In *Pholidosaurus schauburgensis* from  
10  
11 the Berriasian of Germany, the anterior region is spatulate and widest at the level of the D2  
12  
13 alveoli (Koken 1887). There is a sizeable gap between the D1 and D2 alveoli and the D2 and  
14  
15 D3 alveoli, while the D3 and D4 alveoli are closely set (Koken, 1887). 

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18 In the large-bodied 'pholidosaurids' *Sarcosuchus hartti*, *S. imperator* and '*Sunosuchus*'  
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20 *thailandicus* the anterior dentaries are spatulate with the maximal width at the level of the D4  
21  
22 alveoli (Fig. 8D; Buffetaut & Taquet, 1977; Buffetaut & Ingavat, 1984; Martin *et al.*, in  
23  
24 press). In these taxa, the D1 and D2 alveoli are small, and substantially smaller than D3  
25  
26 alveoli. In '*Sunosuchus*' *thailandicus* the D4 alveoli are greatly enlarged relative to the D1-D3  
27  
28 alveoli. In '*Sunosuchus*' *thailandicus* the D4 alveoli are greatly enlarged relative to the D1-D3  
29  
30 alveoli (Buffetaut & Taquet, 1977; Martin *et al.*, in press), while in *Sarcosuchus hartti* and *S.*  
31  
32 *imperator* the D3 and D4 alveoli are both enlarged (Buffetaut & Taquet, 1977).  
33

34 In the marine 'pholidosaurids' *Terminonaris browni* and *T. robusta*, the anterior region  
35  
36 of the dentary is slightly spatulate shape, its maximal width being at the level of the D3  
37  
38 alveoli (Fig. 8I; Mook 1933, 1934). The D1 and D2 alveoli are notably smaller than the D3   
39  
40 and D4 alveoli, and the rest of the alveoli adjacent to the symphysis. The anterior region  of  
41  
42 the dentary is unknown in the 'pholidosaurids' *Oceanosuchus boecensis* (Hua *et al.*, 2007;  
43  
44 Lepage *et al.*, 2008) and *Vectisuchus leptognathus* (Buffetaut & Hutt, 1980; Salisbury &  
45  
46 Naish, 2011).  
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49 The elosuchid/'pholidosaurid' *Elosuchus cherifiensis* also has a spatulate anterior  
50  
51 dentary region, the maximal width being at the level of the D2 and D3 alveoli (Fig. 8J-K; de  
52  
53 Lapparent de Broin, 2002). The D1 alveoli are enlarged compared to the D2-D4 alveoli, with  
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55 the D3 alveoli being smallest of the anterior alveoli (de Lapparent de Broin, 2002). The line  
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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 sub-circular to sub-oval in shape. The holotype of '*Elosuchus felixi*', however, closely resembles NHMUK PV OR36173 in having: 1) a D1 alveolus where the anteroposterior axis is greater than the mediolateral axis, 2) the D1 alveolus is much larger than the D2 and D3 alveoli, and 3) the anterior dentary is not spatulate (de Lapparent de Broin, 2002). These similarities are also present in dyrosaurids (Fig. 8E-H; Hill *et al.*, 2008; Hastings *et al.* 2010, 2011). There is one noticeable difference between '*E. felixi*' and NHMUK PV OR36173: in '*E. felixi*' the D4 alveolus is not dorsal to the D2-D3 alveoli, it is however, ventral to them and orientated somewhat posteriorly (when seen in lateral view). This is caused by a second strong concavity along the dorsal margin of the dentary in this taxon (see de Lapparent de Broin, 2002: Figure 2N).

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-D3 alveoli (Fig. 8). 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 a slightly/moderate anterior orientation as well. Also seen in: *Cerrejonisuchus improcerus* (Hastings *et al.*, 2010), *Dyrosaurus 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 *Argochampsa krebsi* (Jouve *et al.*, 2006b) and *Eothoracosaurus mississippiensis* (Brochu, 2004).

3. The numerous, large foramina on the lateral and ventral surfaces of the dentary that are widely spaced. Also seen in: *Arambourgisuchus khouribgaensis* (Jouve *et al.*, 2005a) and *Dyrosaurus phosphaticus* (Jouve, 2005).
4. Concave dorsal margin of the dentary between the D1 and D4, resulting in the D2 and D3 alveoli being slightly dorsolaterally orientate (e.g. a festooned anterior dentary). Also seen in: *Dyrosaurus 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. Also seen in: *Phosphatosaurus gavialoides* (Hill *et al.*, 2008).
6. The external ornamentation on the dentary is of low relief and not conspicuous. Also seen in: *Arambourgisuchus 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), neither is the dentary 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).


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).

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3 Furthermore, NHMUK PV OR36173 also lacks the mediolaterally expanded anterior dentary  
4 seen in 'pholidosaurids' and teleosaurids, and also differs in alveolar configuration (Fig. 8).  
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6 Moreover, the alveolar configuration and dentary shape of NHMUK PV OR36173 are similar  
7  
8 to those of both dyrosaurids and '*Elosuchus felixi*' (Fig. 8). Although, the prominent  
9  
10 concavities present along the dentary alveolar margin in '*E. felixi*' are noticeably different  
11  
12 from NHMUK PV OR36173 and result in '*E. felixi*' specimens having a very different  
13  
14 orientation of the D4 alveoli when seen in lateral view. Numerous other characteristics (listed  
15  
16 above) suggest a close relationship between NHMUK PV OR36173 and Dyrosauridae. There  
17  
18 is one anterior dentary characteristic that dyrosaurids share that NHMUK PV OR36173 lacks:  
19  
20 a diastema/gap between the D2 and D3 alveoli. In view of this combination of dentary  
21  
22 characters, we conservatively identify NHMUK PV OR36173 as *Tethysuchia incertae sedis*.  
23  
24 More complete material and inclusion within a comprehensive phylogenetic analysis would  
25  
26 enable testing of whether or not NHMUK PV OR36173 is the sister taxon to Dyrosauridae, or  
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28 if it is a 'pholidosaurid'-grade marine taxon.  
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### 36 'MIDDLE' CRETACEOUS MARINE TETHYSUCHIANS

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38 The best known 'middle' Cretaceous marine tethysuchians are *Terminonaris browni* and *T.*  
39  
40 *robusta* from North America (middle Cenomanian-middle Turonian) and *Oceanosuchus*  
41  
42 *boecensis* (early Cenomanian) from France (Mook 1933, 1934; Wu *et al.*, 2001; Hua *et al.*,  
43  
44 2007; Lepage *et al.*, 2008; Adams *et al.*, 2011). From the late Cenomanian of Bavaria,  
45  
46 Germany a large, incomplete upper jaw from a longirostrine taxon has been referred to  
47  
48 *Terminonaris cf. browni* (Buffetaut & Wellnhofer, 1980). *Terminonaris* and *Oceanosuchus*  
49  
50 differ from dyrosaurids in having: 1) more strongly ornamented skull and lower jaw bones, 2)  
51  
52 a premaxilla without an anterodorsally projecting process anterior to the external nares, 3) a  
53  
54 dorsally orientated external nares, 4) five premaxillary alveoli instead of four, 5) the anterior  
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3 margin of the premaxilla is sub-vertical and extends ventrally relative to the rest of the  
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5 element (i.e. the 'pholidosaurid beak'), 6) they lack the D2-D3 diastema/gap seen in  
6  
7 dyrosaurids, and 7) they also lack the small D7 alveoli seen in dyrosaurids. The anterior  
8  
9 region of the dentary is not preserved in *Oceanosuchus*, but the anterior region of the dentary  
10  
11 of *Terminonaris* is slightly spatulate (Mook 1933, 1934; Wu *et al.*, 2001; Adams *et al.*,  
12  
13 2011). As such, these taxa still had classic 'pholidosaurid' characteristics (Hua *et al.*, 2007;  
14  
15 Fortier *et al.*, 2011).

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17  
18 It should be noted that some putative pholidosaurid (*sensu* Fortier *et al.*, 2011) and  
19  
20 elosuchid (*sensu* Andrade *et al.*, 2011) apomorphies are also found in the basal-most known  
21  
22 dyrosaurid *Chenanisuchus lateroculi* (Jouve *et al.*, 2005b). Fortier *et al.* (2011) stated that the  
23  
24 medial margin of the orbit (in dorsal view) is mostly formed by the prefrontal, with the  
25  
26 frontal only slightly participating in the medial margin, is a pholidosaurid apomorphy.  
27  
28 However, this also occurs in *Chenanisuchus lateroculi* (Jouve *et al.*, 2005b), and  
29  
30 goniopholidids (see the figures in Andrade & Hornung, 2011). Andrade *et al.* (2011) stated  
31  
32 that the frontal being concave with the medial borders of the orbit being upturned is an  
33  
34 elosuchid apomorphy. However, this also occurs in the pholidosaurids *Pholidosaurus*  
35  
36 *purbeckensis* (Salisbury, 2002), *P. schauburgensis* (Koken, 1887), *Oceanosuchus boecensis*  
37  
38 (Hua *et al.*, 2007; Lepage *et al.*, 2008), *Terminonaris robusta* (Mook, 1934) and the  
39  
40 dyrosaurid *Chenanisuchus lateroculi* (Jouve *et al.*, 2005b; Hill *et al.*, 2008). Therefore, in  
41  
42 some aspects, cranial variation between 'pholidosaurids' and basal dyrosaurids is less marked  
43  
44 than originally thought. 

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47 While dyrosaurids are well known from the Maastrichtian onwards, their pre-  
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49 Maastrichtian fossil record is relatively poor. Two maxillary fragments from the Campanian  
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51 of Egypt pertain to a longirostrine crocodyliform tentatively referred to *Dyrosaurus*  
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53 (Churcher & Russell, 1992; Churcher, 1995). The earliest potential dyrosaurids are  
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3 Cenomanian in age. A partial dentary (mid-symphyseal region) from the middle Cenomanian  
4 marine deposits of Portugal was noted to be reminiscent of dyrosaurids (Buffetaut &  
5 Lauerjat, 1978). However, its incomplete nature means that no firm conclusions can be  
6  
7 drawn as to its affinities. Skull fragments (frontal, parietal and left postorbital) and  
8  
9 incomplete vertebrae from Cenomanian lacustrine deposits of Sudan were referred to  
10  
11 Dyrosauridae indet. by Buffetaut *et al.* (1990). The dorsal vertebrae have very large  
12  
13 hypapophyses as is the case in dyrosaurids (i.e. blade-like, flattened laterally, rounded  
14  
15 ventrally and anteroposteriorly long) (e.g. see the figures in Storrs, 1986; Jouve & Schwarz,  
16  
17 2004; Jouve *et al.*, 2005a; Schwarz *et al.*, 2006). *Terminonaris robusta* also has noticeable  
18  
19 hypapophyses on some vertebrae, but they are much lower and are a different shape (see Fig.  
20  
21 4 in Wu *et al.*, 2001). The skull fragments were considered to be from a primitive dyrosaurid  
22  
23 by Buffetaut *et al.* (1990), as they have: 1) more strongly ornamented cranial bones, 2) a  
24  
25 smaller anterolateral process on the left postorbital than that of other dyrosaurids, 3) a  
26  
27 broader intertemporal bar than dyrosaurids (i.e. between the supratemporal fenestrae), and 4)  
28  
29 a dorsal region of the postorbital pillar that is only slightly medially inclined. Unfortunately,  
30  
31 the anterolateral process of the left postorbital is broken, so its size cannot be properly  
32  
33 judged. However, large anterolateral processes of the postorbitals are also seen in  
34  
35 *Terminonaris browni* (Mook, 1933), *T. robusta* (Wu *et al.*, 2001) and *Oceanosuchus*  
36  
37 *boecensis* (Hua *et al.*, 2007; Lepage *et al.*, 2008). These examples further highlight how  
38  
39 certain marine 'pholidosaurid' and dyrosaurid cranial morphologies overlap and appear to be  
40  
41 homologous. As such, only the vertebrae (which Buffetaut *et al.*, 1990 could not be certain  
42  
43 were associated with the skull fragments), reliably suggest a dyrosaurid, not indeterminate  
44  
45 tethysuchian, origin for this material. Note that the presence of the Sudanese material in non-  
46  
47 marine deposits does not imply that during the Cenomanian some putative dyrosaurids were  
48  
49 restricted to freshwater environments, as there is growing evidence that dyrosaurids  
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3 successfully exploited both freshwater and saltwater environments (see Khosla *et al.*, 2009  
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5 and the references therein).  
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## 10 11 CONCLUSIONS 12

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14 Herein we describe a tethysuchian crocodyliform from the Aptian-Albian (most likely the late  
15 Albian) of England from at Shanklin on the Isle of Wight. The single known specimen is the  
16 anterior region of a right dentary, and it increases the known geological range of marine  
17 tethysuchians back into the late Early Cretaceous. Within Tethysuchia this mandibular  
18 fragment has certain characteristics which suggest a possible relationship with Dyrosauridae:  
19 (1) enlarged dentary alveolus one relative to the second and third alveoli; (2) dentary alveolus  
20 one is mainly dorsally orientated but is slightly anteriorly orientated; (3) numerous large  
21 foramina on the lateral and ventral surfaces of the dentary that are widely spaced; (4) concave  
22 dorsal margin of the dentary between the first and fourth dentary alveoli which results in the  
23 second and third dentary alveoli being slightly dorsolaterally orientated; (5) large foramina on  
24 the dorsal surface of the dentary medial to the second and third alveoli; (6) external  
25 ornamentation on the dentary is of low relief; and (7) anterior dentary is not laterally  
26 expanded forming a 'spatulate' morphology. However, establishing a new taxon for this  
27 specimen must await the discovery of more complete remains.  
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45 We consider there to be no firm evidence that any known 'middle' Cretaceous  
46 tethysuchian is either a dyrosaurid or an especially close relative of that clade, especially as  
47 some putative apomorphies for 'Pholidosauridae'/Elosuchidae are also found in the basal-  
48 most known dyrosaurids. Only future studies of new discoveries, and/or unrecognised  
49 museum specimens from this key time span, will elucidate the tethysuchian radiation into the  
50 marine realm and the origin of Dyrosauridae.  
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## FIGURE CAPTIONS

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

Figure 2. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in lateral view, (A) photograph, (B) line drawing.

Figure 3. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in ventral view, (B) photograph, (C) line drawing.

Figure 4. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in dorsal view, (A) photograph, (B) line drawing.

Figure 5. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in anterior view, (A) photograph, and (B) line drawing.

Figure 6. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in medial view, (A) photograph, (B) line drawing.

Figure 7. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in posterior view, (A) photograph, and (B) line drawing.

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3 Figure 8. The anterior ends of right dentaries of select crocodylomorphs compared to  
4 NHMUK PV OR36173 (some are mirrored relative to the original figures); all are shown in  
5 isolation from the left dentary. (A) NHMUK PV OR36173, (B) metriorhynchid *Plesiosuchus*  
6 *manselii* (after Young *et al.*, 2012), (C) teleosaurid *Machimosaurus hugii* (after Martin &  
7 Vincent, 2013), (D) ‘pholidosaurid’ *Sarcosuchus imperator* (after Buffetaut & Taquet 1977),  
8 (E) dyrosaurid *Phosphatosaurus gavialoides* (after Hill *et al.*, 2008), (F) dyrosaurid  
9 *Hyposaurus* ‘morphotype 1’ (after Jouve, 2007), (G) dyrosaurid *Hyposaurus* ‘morphotype 2’  
10 (after Jouve, 2007), (H), dyrosaurid *Rhabdognathus* sp. (after Jouve, 2007), (I)  
11 ‘pholidosaurid’ *Terminonaris robusta* (after Mook, 1934), (J–K) elosuchid *Elosuchus*  
12 *cherifiensis* (after de Lapparent de Broin, 2002), (L) ‘pholidosaurid’ ‘*Sunosuchus*’  
13 *thailandicus* (after Buffetaut & Ingavat, 1984), (M) ‘*Goniopholis*’ *phuwiangensis* (after  
14 Buffetaut & Ingavat, 1983), (N) goniopholidid *Goniopholis baryglyphaeus* (after Schwarz,  
15 2002), (O) hylaeochampsid *Pietraroiasuchus ormezzanoi* (after Buscalioni *et al.*, 2011), (P)  
16 gavialoid *Eothoracosaurus mississippiensis* (after Brochu, 2004). The reconstructions are not  
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38 Figure 9. *Goniopholis crassidens*, NHMUK PV R1807, referred specimen. Anterior region of  
39 the dentary in dorsal view, (A) photograph, (B) line drawing.  
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45 Figure 10. *Theriosuchus pusillus*, NHMUK PV OR48262, referred specimen. Anterior region  
46 of the left dentary in dorsal view, (A) photograph, (B) line drawing.  
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51 Figure 11. Stratigraphic ranges of relevant Early Cretaceous crocodylomorph lineages,  
52 plotted against time and compared with the possible age range of the Shanklin specimen  
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(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.

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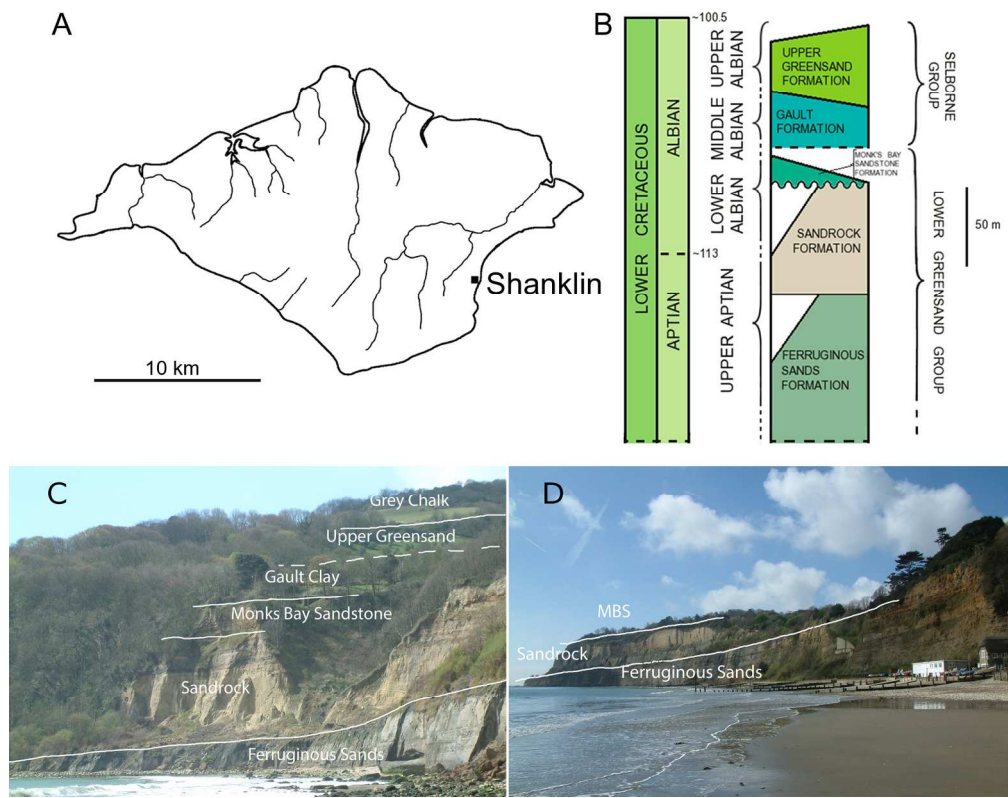


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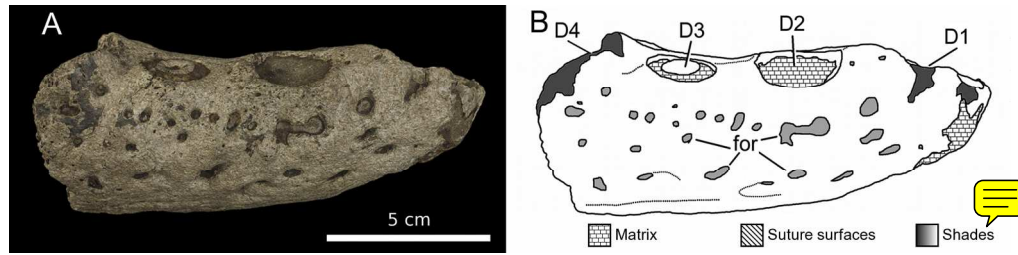


Figure 2. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in lateral view, (A) photograph, (B) line drawing.  
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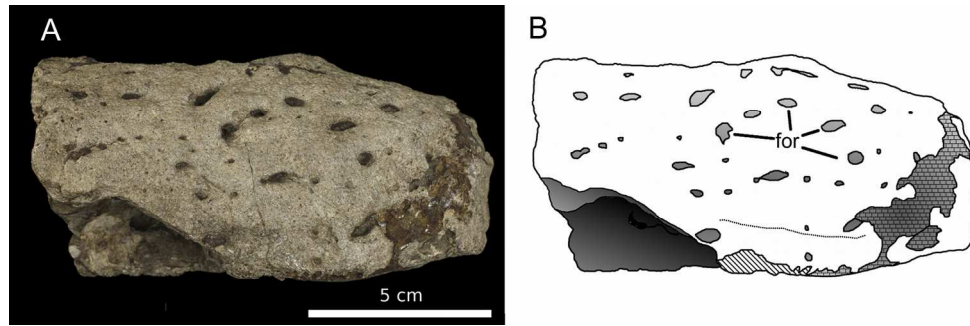


Figure 3. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in ventral view, (B) photograph, (C) line drawing.  
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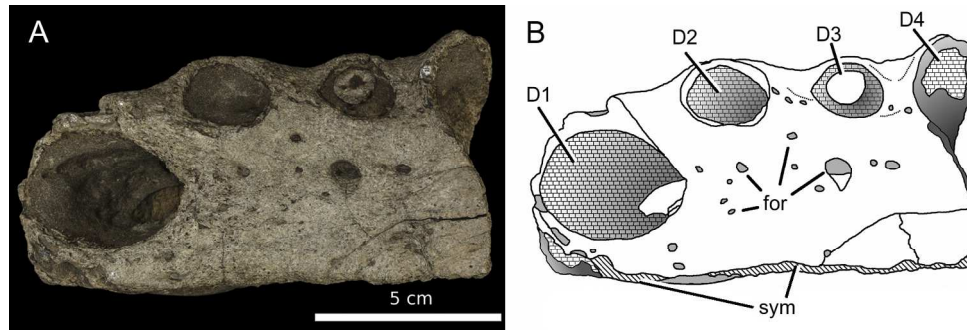


Figure 4. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in dorsal view, (A) photograph, (B) line drawing.  
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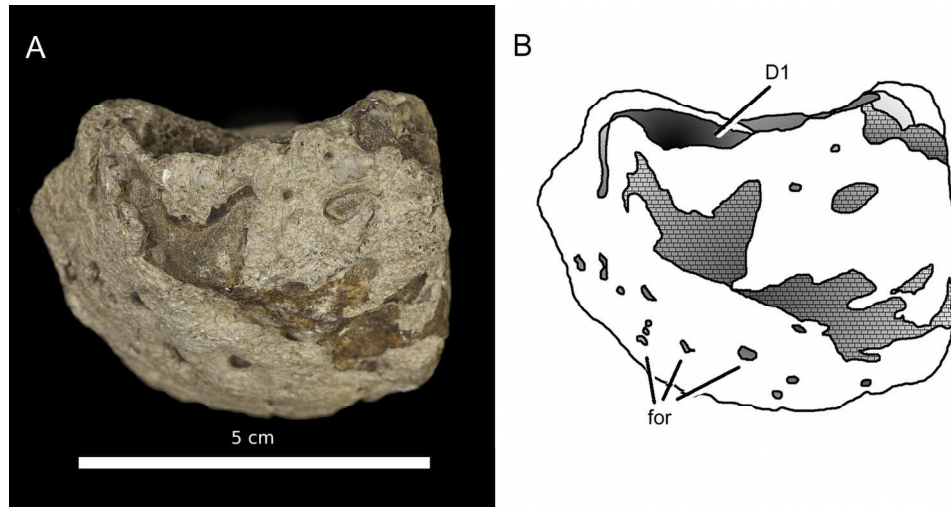


Figure 5. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in anterior view, (A) photograph, and (B) line drawing.  
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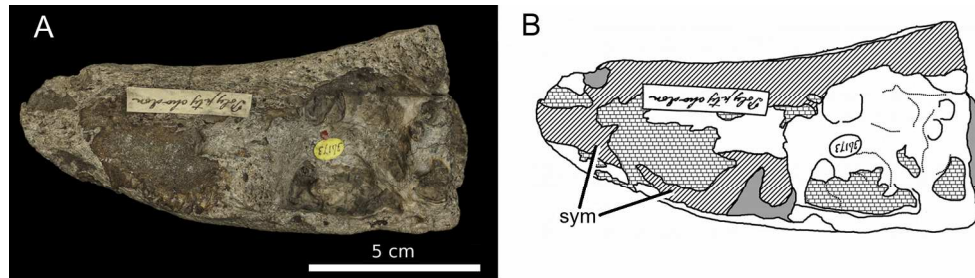


Figure 6. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in medial view, (A) photograph, (B) line drawing.  
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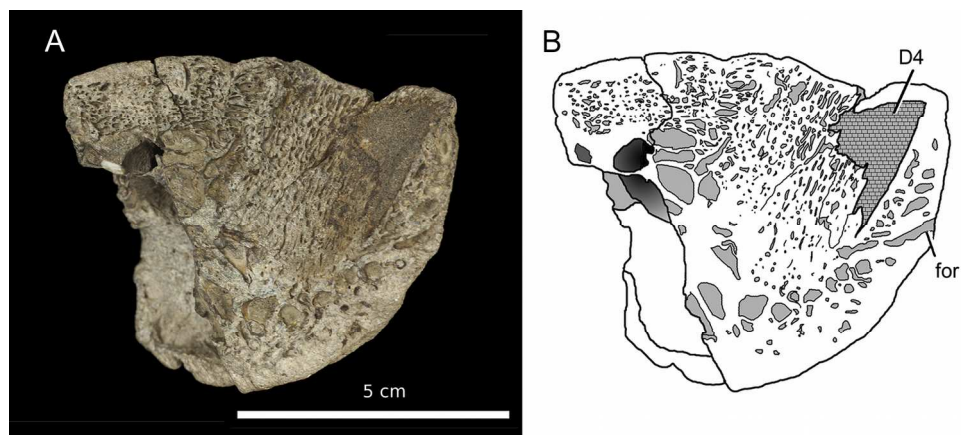


Figure 7. *Tethysuchia incertae sedis*, NHMUK PV OR36173. Anterior region of the right dentary in posterior view, (A) photograph, and (B) line drawing.  
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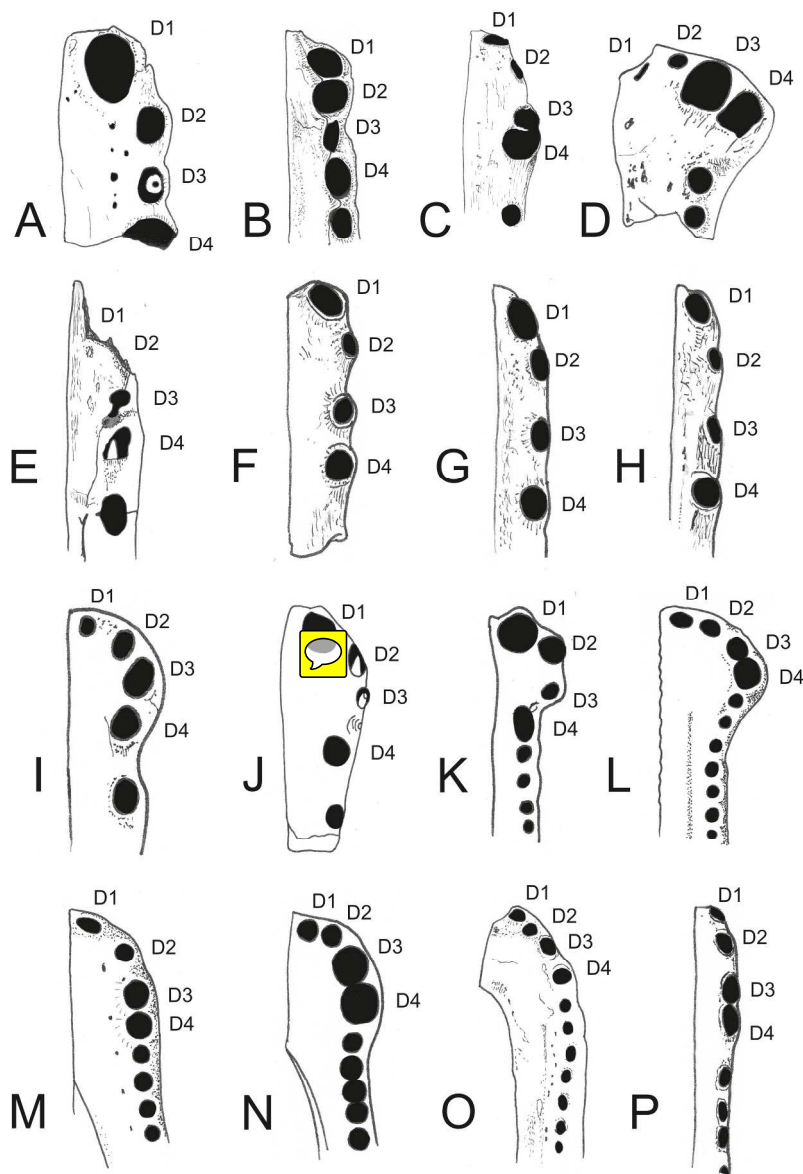


Figure 8. The anterior ends of right dentaries of select crocodylomorphs compared to NHMUK PV OR36173 (some are mirrored relative to the original figures); all are shown in isolation from the left dentary. (A) NHMUK PV OR36173, (B) metriorhynchid *Plesiosuchus manselii* (after Young et al., 2012), (C) teleosaurid *Machimosaurus hugii* (after Martin & Vincent, 2013), (D) 'pholidosaurid' *Sarcosuchus imperator* (after Buffetaut & Taquet 1977), (E) dyrosaurid *Phosphatosaurus gavialoides* (after Hill et al., 2008), (F) dyrosaurid *Hyposaurus* 'morphotype 1' (after Jouve, 2007), (G) dyrosaurid *Hyposaurus* 'morphotype 2' (after Jouve, 2007), (H), dyrosaurid *Rhabdognathus* sp. (after Jouve, 2007), (I) 'pholidosaurid' *Terminonaris robusta* (after Mook, 1934), (J–K) elosuchid *Elosuchus cherifiensis* (after de Lapparent de Broin, 2002), (L) 'pholidosaurid' '*Sunosuchus*' *thailandicus* (after Buffetaut & Ingavat, 1984), (M) 'Goniopholis' *phuwiangensis* (after Buffetaut & Ingavat, 1983), (N) goniopholidid *Goniopholis baryglyphaeus* (after Schwarz, 2002), (O) hylaeochampsid *Pietraroiiasuchus ormezzanoi* (after Buscalioni et al., 2011), (P) gavialoid *Eothoracosaurus mississippiensis* (after Brochu, 2004). The reconstructions are not to scale.

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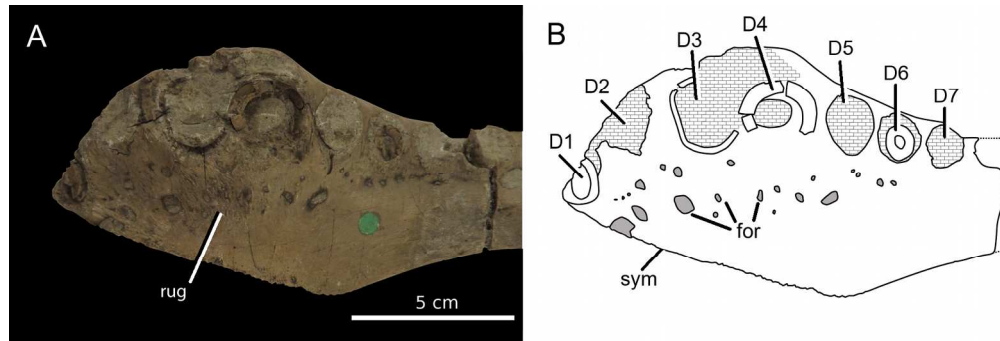


Figure 9. *Goniopholis crassidens*, NHMUK PV R1807, referred specimen. Anterior region of the dentary in dorsal view, (A) photograph, (B) line drawing.  
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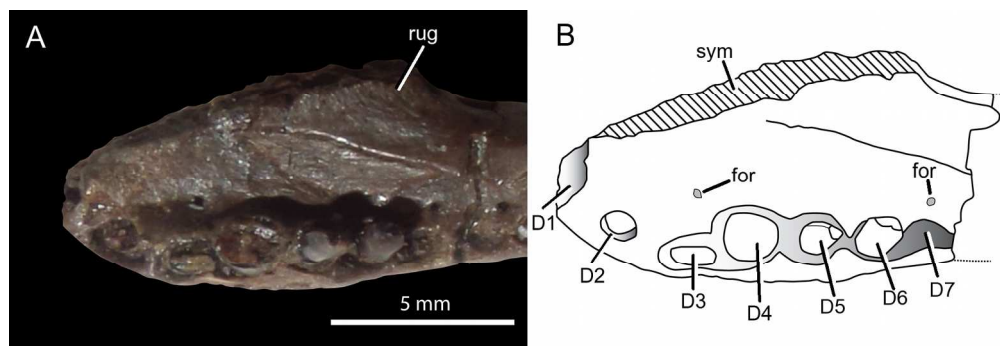


Figure 10. *Theriosuchus pusillus*, NHMUK PV OR48262, referred specimen. Anterior region of the left dentary in dorsal view, (A) photograph, (B) line drawing.  
167x56mm (300 x 300 DPI)

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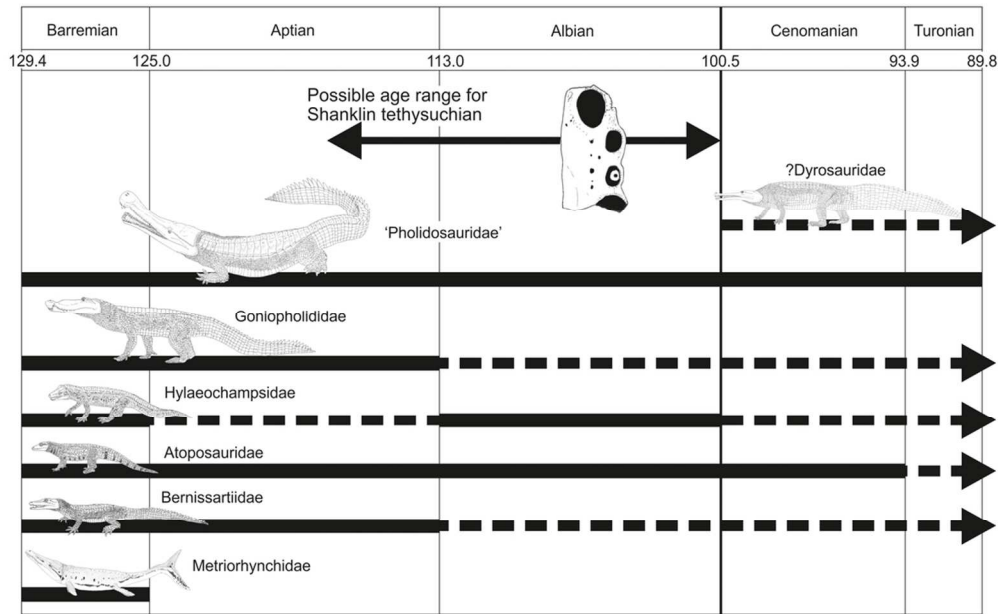


Figure 11. Stratigraphic ranges of relevant Early Cretaceous crocodylomorph lineages, plotted against time and compared with the possible age range of the Shanklin specimen (NHMUK PV OR36173). Dotted lines represent parts of lineages for which fossils are unreported; arrows show that lineage persisted beyond the end of the Turonian.

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Review