



Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola

A truly gigantic pliosaur (Reptilia, Sauropterygia) from the Kimmeridge Clay Formation (Upper Jurassic, Kimmeridgian) of England

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ARTICLE INFO

Article history:

Received 1 July 2022

Received in revised form 17 April 2023

Accepted 24 April 2023

Available online xxxx

Keywords:

Sauropterygia

Pliosauridae

Late Jurassic

Kimmeridgian

Giant-size

England

ABSTRACT

Four isolated cervical vertebrae from the Kimmeridge Clay Formation (Upper Jurassic, Kimmeridgian) of Abingdon, Oxfordshire, England are identified as from a pliosaurid plesiosaurian sauropterygian on account of their shortness relative to width and height, their near platycoelous nature and the location of tall rib facets on the centrum body. They are noteworthy for their size, with a maximum width of 269 mm, maximum height of 222 mm and maximum length of 103 mm. Simple scaling and comparisons with cervical vertebrae of Mid Jurassic pliosaurus *Peloneustes* and *Liopleurodon*, and the Early Cretaceous *Stenohynchosaurus* and *Sachiasaurus* suggest a total body length of between ~9.8 m and 14.4 m for the Abingdon Kimmeridge Clay pliosaur. Likely the true length was towards the higher end of this range.

A genus and species cannot be confidently determined on the basis of the described material, but they likely belong to *Pliosaurus* sp. or a similar animal, for which a precise neck length is not known. We estimate a neck length of 0.77 m for *Pliosaurus* ?*brachyspondylus* based on the average cervical lengths provided for specimen CAMSM J.35991.

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1. Introduction

Pliosauromorphs were generally large (> 4 m), obligate secondarily aquatic sauropterygian reptiles, characterised by a massive skull, a proportionally short neck, barrel-like body with four large wing-like flippers tapering to a blunt point, and a short, tapered tail (e.g., Andrews, 1913; Cruickshank et al., 1996; Taylor, 1992; Noè et al., 2004; Ketchum and Benson, 2011; Schumacher et al., 2013; Fischer et al., 2015). Some forms reached gigantic proportions and may have been among the largest Mesozoic marine predators (Phillips, 1871; Longman, 1924; Tarlo, 1959a, 1959b, 1960; Martill and Naish, 2000; Buchy et al., 2003; Hampe, 2005; Foffa et al., 2014; Zverkov and Pervushov, 2020; Noè and Gomez-Pérez, 2021). They were distributed world-wide and range from the Early Jurassic to the end of the Cretaceous (e.g., Hampe, 1992; Gasparini, 2009; Knutsen et al., 2012; Benson et al., 2013; Angst and Bardet, 2016; Bastiaans et al., 2021; Noè and Gomez-Pérez, 2021). Pliosaurus display several skeletal modifications that are noteworthy when compared with their close relatives, the Plesiosauroidea (long-necked plesiosaurs). Notably, they have elongated mandibular symphyses in which several teeth lie alongside each other in tooth pairs, and a

dentition that includes massive fang-like crowns with robust enamel ribbing, and strongly curved roots and crown (Sauvage, 1873; Leeds, 1956; Sassoon et al., 2015). In addition, their main propodials (humeri and femora) are remarkably similar and may be difficult to distinguish when found in isolation.

Despite their spectacular size, pliosaurids were relatively unknown in the public domain, until airing of the BBC TV animated documentary series *Walking with Dinosaurs* in 1999 when, in the episode, *Cruel Sea* a 'star' animal, the Middle Jurassic pliosaur *Liopleurodon* was controversially claimed to have been 25 m in length and to have weighed perhaps 150 tonnes (see Martill and Naish, 2000). There is no unambiguous fossil evidence for any of these claims, with near complete *Liopleurodon ferox* skeletons indicating a length closer to 6.4 m (Noè et al., 2003). There are, however, a number of isolated pliosaur bones from the Oxford Clay (Callovian to Oxfordian) and Kimmeridge Clay (Kimmeridgian to Tithonian) formations of southern and eastern England that are from considerably larger individuals, though their generic identity remains largely unknown, as do their total dimensions (Martill and Naish, 2000).

Large to gigantic pliosaurus are also reported from the marine Cretaceous (Kear, 2003; Noè and Gomez-Pérez, 2021). Of these, the genus *Kronosaurus* (Aptian–Albian) (note that this taxon is now restricted to the non-diagnostic holotype jaw fragment and is regarded as a nomen dubium (Noè and Gomez-Pérez, 2021)) perhaps reached a length in excess of 9 m (Kear, 2003). This taxon's validity is questioned by some authors and a replacement genus, *Monquirasaurus*, has been proposed for a South American specimen previously attributed to *Kronosaurus*

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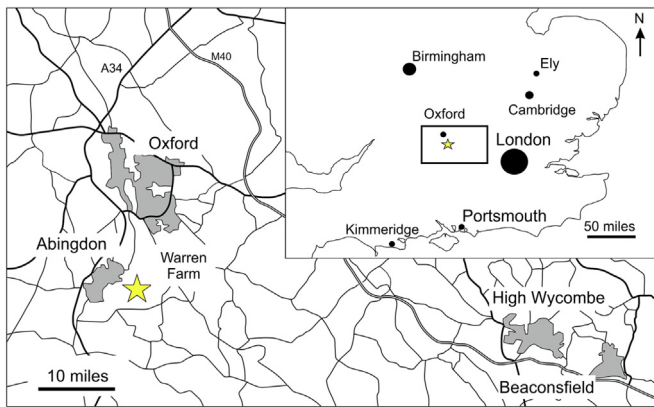


Fig. 1. Map of the region around Abingdon showing the location (starred) of the discovery site of the four pliosaur cervical vertebrae ABGCH 1980.191.1038–41. The location of two other important Late Jurassic pliosaur sites, Kimmeridge and Ely are also indicated.

(Noè and Gomez-Pérez, 2021). Note also that these authors have assigned some Australian examples of *Kronosaurus* to the new genus *Eiectus*.

Here we describe four associated pliosaur cervical vertebral centra from the Kimmeridge Clay Formation of south-central England (Fig. 1) and one from eastern England that are noteworthy for their extremely large size and provide some bearing as to the maximum size that some Late Jurassic pliosaurus may have achieved.

2. Materials and methods

Four cervical vertebral centra from the Abingdon Kimmeridge Clay Formation (ABGCH 1980.191.1038–1041), and a single anterior cervical vertebral centrum from the Kimmeridge Clay Formation of Ely, Cambs (YORYM: 2006.19) were used for this analysis (see Table 1).

The four Abingdon cervical centra were topographically scanned using an Einscan Pro+ scanner and 3D models processed using Geomagic design X. Images of the scans were captured in this software.

Specimens (Figs. 2–5) were measured using a calibrated ruler. Additional digital photographs were taken using a Nikon D3300 and are available in the SI. Images were processed using CorelDraw X8. Scaling was achieved by simple multiplication of length dimensions compared with those of related, but more complete pliosaur genera, including *Liopleurodon*, *Peloneustes*, *Sachisaurus* and *Stenorhynchosaurus* where cervical vertebra length could be determined as a proportion of the skeleton's total length.

2.1. Quantitative analysis

The quantitative analysis employed here was kept as simple as possible. We identified several complete skeletons across a range of pliosaurid taxa from the literature (see Tables 2, 3). The vertebral count for the Kimmeridgian/Tithonian *Pliosaurus* from the Late Jurassic remains unknown and is thus of limited value for this analysis.

The skeletons employed were divided into four discrete segments; skull, neck, trunk and tail (Fig. 7), and the percentage length of each segment was calculated (Table 2). The number of cervical vertebrae for each taxon's neck was derived from counts reported in the literature. To determine the original neck length of the Abingdon (and York) pliosaurus the average cervical length of the specimens described here was multiplied by the cervical count of the chosen comparative taxa. Once a neck length was determined, a total animal length was calculated using the segment proportions of the comparative taxa (see Table 2 and Fig. 7).

Institutional abbreviations. **ABGCH**, Abingdon County Hall Museum, Abingdon, UK; **CAMSM**, Sedgwick Museum of Earth Sciences, University of Cambridge, Downing St, Cambridge CB2 3EQ, UK; **DORCM**, Dorset County Museum, Dorchester, UK; **GPIT**, Geologisch-Palaäontologisches Institut Tübingen, Geschwister-Scholl-Platz, 72074 Tübingen, Germany; **MJML**, The Etches Collection, Kimmeridge, Wareham, Dorset, UK; **MP**, Universidad Nacional de Colombia, administrated by the Colombian geological survey (SGC: Servicio Geológico Colombiano); **MS-AS RK**, Institute of Zoology, Kazakhstan; **NHMUK** (formerly **BMNH**), Natural History Museum, London, UK; **NMINH**, National Museum of Ireland Natural History; **OUNMH** Oxford University Museum of Natural History, Oxford, United Kingdom; **PMO**, University of Oslo Natural History Museum, Norway; **YORYM** Yorkshire Museum, Museum Gardens, Museum Street, York, YO1 7FR, UK.

3. Geographic and geological context

The vertebrae described here were discovered during temporary excavations at Warren Farm, in the River Thames Valley near Abingdon in Oxfordshire (51° 39' 46.0"N 01° 15' 01.9"W; Fig. 1), but presently there are no exposures at this locality. The Thames floodplain here is covered with Pleistocene and Holocene alluvial deposits that overlie the Kimmeridge Clay Formation and in some places Early Cretaceous strata. At this locality it is the Kimmeridge Clay Formation that underlies the alluvial gravel, and the vertebrae described here are, not unreasonably, assumed to come from this horizon.

4. Results

4.1. Systematic palaeontology

Sauropterygia Owen, 1860
 Plesiosauria de Blainville, 1835
 Pliosauroida Welles, 1943
 Pliosauridae Seeley, 1874
 Thalassophonea Benson and Druckenmiller, 2014
 Genus and species indet. ?*Pliosaurus* sp. Owen, 1841.

Material. Four isolated and partly worn cervical vertebrae from Abingdon. Accession numbers: ABGCH 1980.191.1038, 1039, 1040, 1041 (Figs. 2–6).

Curation information. The original label for this material states: 'Two slightly abraded enormous cervical centra. Found seven feet below the ground level, in Kimmeridge Clay. Field reservoir site adjacent to backwater

Table 1
 Dimensions of four cervical vertebral centra of a gigantic pliosaur from the Upper Jurassic Kimmeridge Clay Formation of Abingdon, Oxfordshire, and a single anterior cervical centrum from the same formation of ?Ely, Cambridgeshire.

Vertebra spec. no.	Max. width (mm)	Max. height (mm)	Max. length (mm)
ABGCH 1980.191.1041	217	191	95
ABGCH 1980.191.1040	252	218	103
ABGCH 1980.191.1039	234	207	79
ABGCH 1980.191.1038	269	222	95
YOYRM: 2006.19	202	167	86

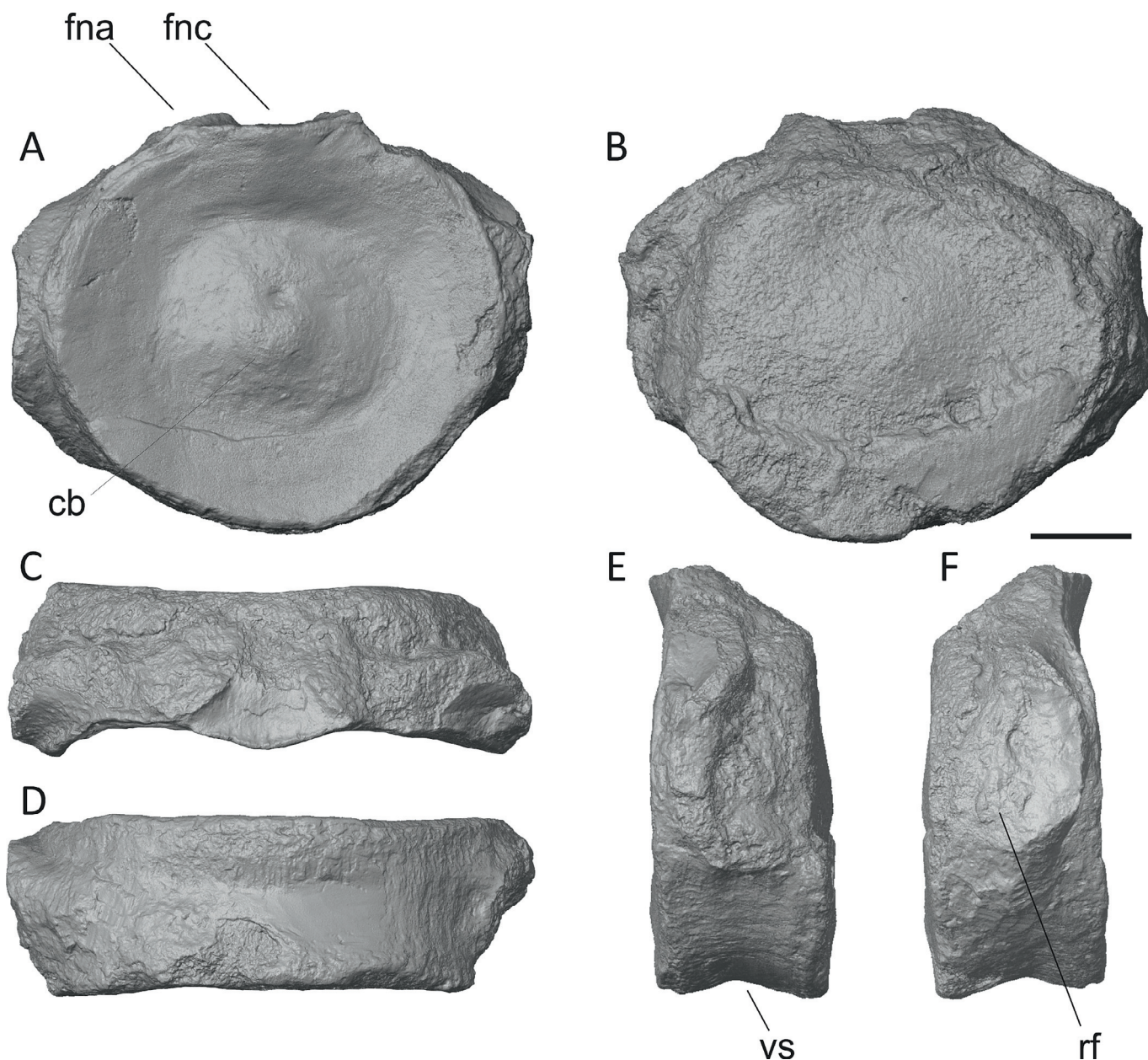


Fig. 2. Digital three-dimensional scan images of pliosaur cervical vertebral centrum ABGCH 1980.191.1038 from the Kimmeridge Clay Formation of Warren Farm, Abingdon. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, left lateral view; F, right lateral view. Scale bar = 50 mm. Abbreviations: cb, central boss; fna, facet for neural arch; fnc, floor of neural canal; rf, rib facet; vs, ventral sulcus.

of R. Thames, opposite Warren Farm, Cullham. Discovered in 1979 by "White Horse Contractors Limited" and presented on indefinite loan by Mr J. Koster in April, 1980'.

Locality. Warren Farm, Abingdon, Oxfordshire, National Grid reference SU 519 964. Lat/Long (deg.) 51° 39' 46.0"N 01° 15' 01.9"W.

Horizon. Reported as Kimmeridge Clay Formation. According to the British Geological Survey (BGS) (Digimap: digimap.edina.ac.uk), this locality lies on the mapped boundary of the undifferentiated Amphill Clay (Oxfordian) and Kimmeridge Clay (Kimmeridgian to lower Tithonian) formations and the Aptian Lower Greensand Group. Adherent mudstone matrix on the specimen shows the specimen to come from the former, and most likely the Kimmeridge Clay Formation due to its proximity to the upper boundary of the two undifferentiated formations. In addition, vertebrate remains are extremely rare in the

Amphill Clay Formation, but occur frequently in the Kimmeridge Clay Formation of Oxfordshire, Wiltshire and Dorset (Martill et al., 2020).

Description. The four vertebral centra are variously worn with some slight breakage in places. There is also some compaction damage, but the measurements taken are deemed reliable (Table 1). The vertebrae are identified as pliosauromorph partly on account of their occurrence in a marine mudrock well-known for pliosaur remains, and they differ markedly from those of other marine reptiles reported from the same strata (e.g., ichthyopterygians, thalattosuchians and chelonians). Anatomically, their platycoelous nature, approximately circular outline, aspect ratios and rib articulations with an approximately figure of eight outline (e.g., Fig. 2F) are features found in pliosaur cervicals. In addition, they are identified as pliosaurid on account of the shortness of the vertebral centra relative to their height and width (in Plesiosauroidea the

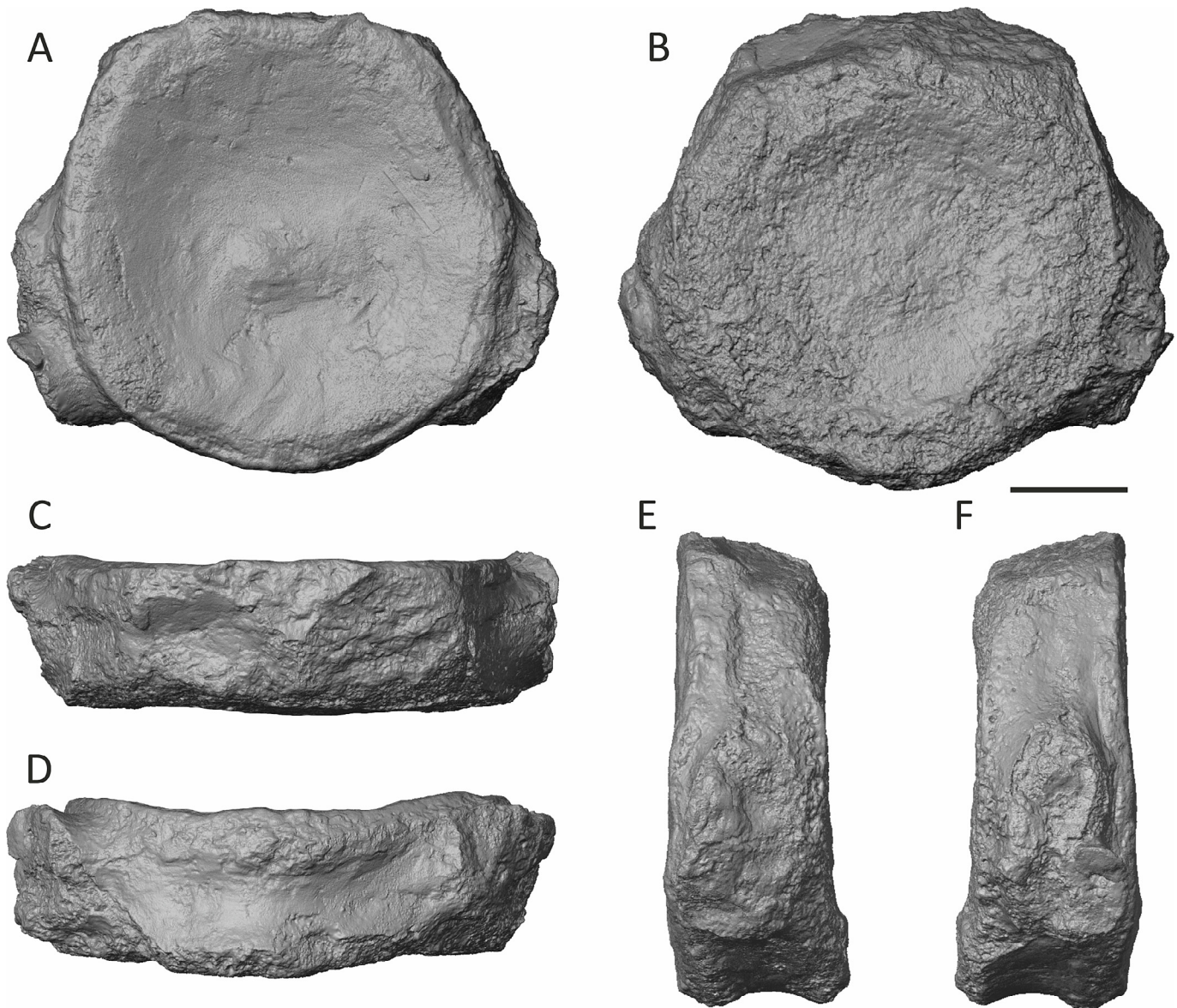


Fig. 3. Digital three-dimensional scan images of pliosaur cervical vertebral centrum ABGCH 1980.191.1039 from the Kimmeridge Clay Formation of Warren Farm, Abingdon. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, left lateral view; F, right lateral view. Scale bar = 50 mm.

cervical vertebrae are proportionally longer (Brown, 1981)). They are tentatively identified as *Thalassophonea* on account of size only. All *Thalassophonea* are large animals (Benson and Druckenmiller, 2014).

All four vertebrae are identified as cervicals on account of their aspect ratios, the presence of rib facets on the centrum sides, and their relative positions on the centrum body. The anterior and posterior ventral margins of the centrum are raised with respect to the surface of the centrum body, thus forming a sulcus that extends around the basal third of the centrum, dying out laterally on both sides. The posterior rim is deeper than the anterior rim when seen in lateral view (e.g., Fig. 5E, F). Facets for the neural arches are moderately dish-shaped, cover all the dorsal surface except for the central region where the neural canal was located, and descend slightly down the lateral margins of the centra (Fig. 4C). Facets for the cervical ribs are located high on the lateral margins of two centra, and they appear to merge with the base of the facet for the neural arch (Fig. 4F), suggesting that they are the most posterior cervical vertebrae likely from just anterior to the first pectoral vertebra.

Some slight damage obscures the detail, and it cannot be completely ruled out that the vertebra is a first pectoral. In centrum ABGCH 1980.191.1041 the rib facets are lower with the top margin of the facet at a point approximately half the height of the centrum, and its lower margin at a point approximately one quarter the height. The facets are clearly double-headed and located more anteriorly on the centrum sides (Figs. 4 F, 5F), suggesting they are from a more anterior position in the neck. A conspicuous mammillate boss in the middle of the centrum also suggests a posterior position in the neck (Tarlo, 1959a, 1959b).

Remarks. The Kimmeridge Clay Formation has yielded a high diversity of marine reptiles, including ichthyosaurs, crocodylians, and turtles (Martill et al., 2020), and a variety of sauropterygians (Ketchum and Benson, 2020). An ichthyosaurian identity for the new material is excluded on account of the lack of deeply dish-shaped anterior and posterior faces on the centra. In addition, in ichthyosaurs the double-headed rib facets are represented by two separate circular projections, contrasting

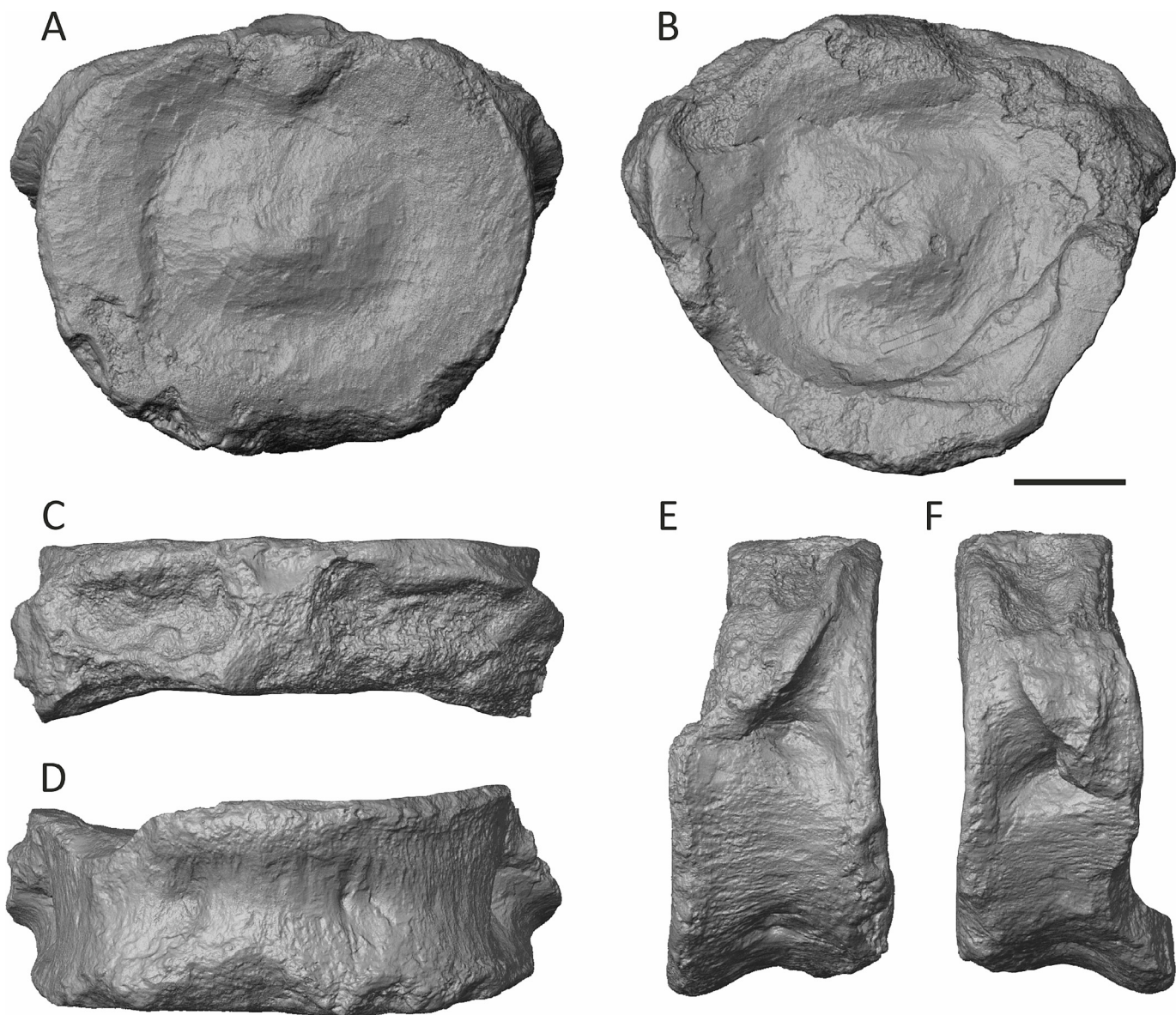


Fig. 4. Digital three-dimensional scan images of pliosaur cervical (or possibly first pectoral: see Sachs et al., 2013 for discussion) vertebral centrum ABGCH 1980.191.1040 from the Kimmeridge Clay Formation of Warren Farm, Abingdon. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, left lateral view; F, right lateral view. Scale bar = 50 mm. Note that the rib facets sit high on the centrum suggesting this is a more posterior cervical vertebra, and may even be the first pectoral.

with the merged double facets of pliosaurid cervical centra (e.g., Andrews, 1913). A crocodylomorph origin is similarly discounted on account of the overall shortness of the centra, as in all marine Mesozoic crocodylomorphs the centra are longer than wider or high. Despite its fully marine depositional setting the Kimmeridge Clay Formation has yielded a number of non-avian dinosaurs, including remains of sauropods (e.g., *Duriatitan humericristatus* (Barrett, 2020)). Once again, it is possible to exclude a sauropod origin for the four new centra. In sauropods, cervical centra are elongate and usually opisthocoelous and have multiple laminae. Sauropod dorsal vertebrae may have centra similar to those of pliosaurids, but those of sauropods lack rib facets on the lateral margins of the centrum. The anterior caudal vertebrae of some sauropods may have similarities with pliosaur cervical vertebrae in that they sometimes display reduced length to width/height aspect ratios (Wedel and Taylor, 2013; see also Holwerda et al., 2019). Caudal vertebrae one and two in sauropods may possess a rib facet on the centrum sides, but these facets are generally absent from caudals three

posteriorly (see, for example, *Tambatitanis Saegusa and Ikeda, 2014; Giraffatitan Wedel and Taylor, 2013*). Two of the new vertebrae (1980.191.1038 and 1980.191.1039) clearly possess double-headed rib facets, whereas the condition is a little less clear in the other two. In addition, sauropod caudal vertebrae possess two pairs of facets ventrally for the articulation of the chevrons: no such facets occur on the vertebrae described here. The cervical vertebrae of pliosaurids are distinguished from those of other plesiosaurians on being short relative to their height. Those of long-necked plesiosaurs from the Kimmeridge Clay Formation, such as *Colymbosaurus* and *Kimmerosaurus* are almost equidimensional in height, length and width (Ketchum and Benson, 2020).

Additional material. One cervical vertebra from Ely, Cambs, accession number YORYM: 2006.19. Precise locality and horizon information is not available for this accession.

Although a new label on this specimen lists the locality as Dorset, an older label glued to the specimen states the locality as Ely,

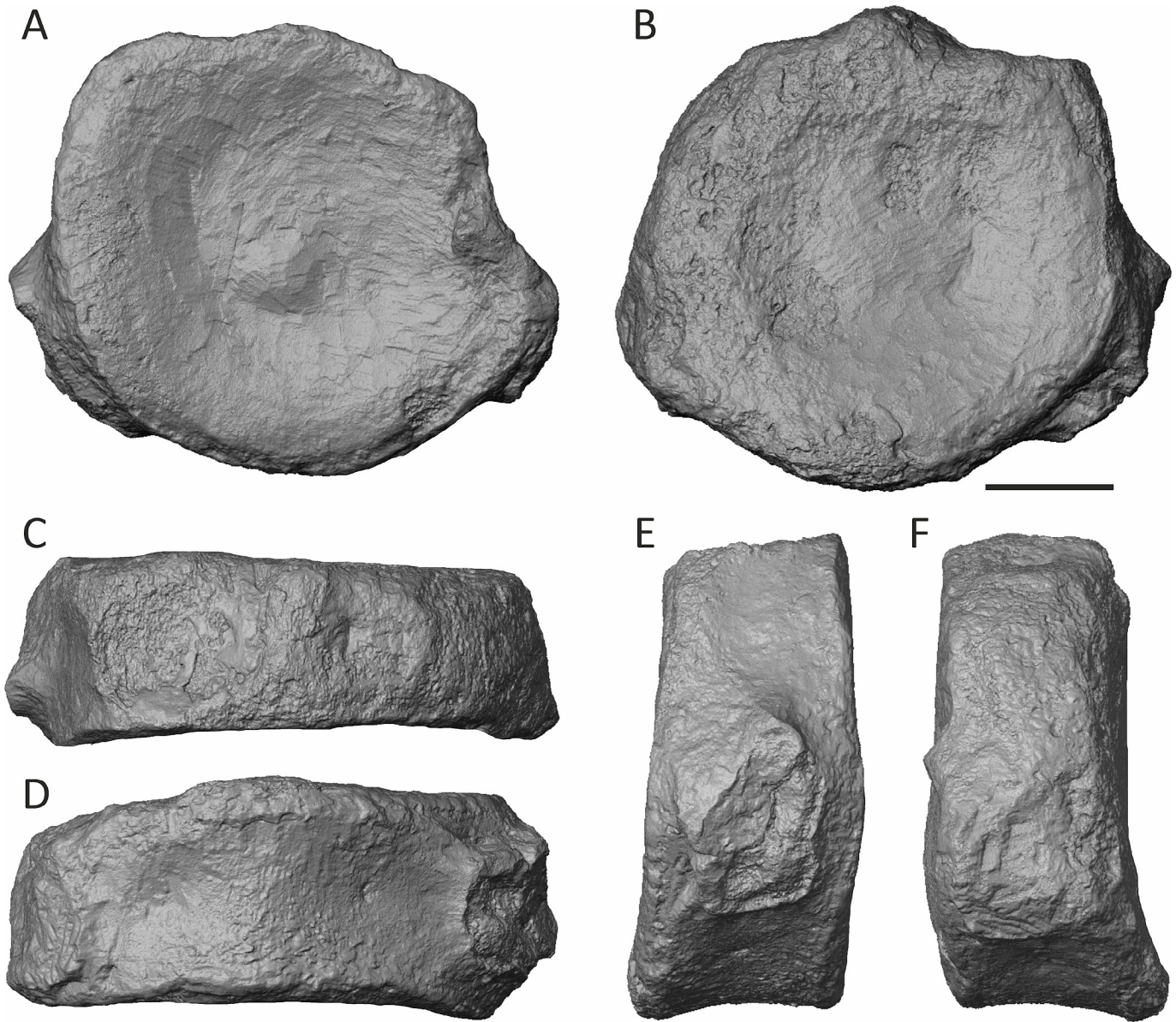


Fig. 5. Digital three-dimensional scan images of pliosaur cervical vertebral centrum ABGCH 1980.191.1041 from the Kimmeridge Clay Formation of Warren Farm, Abingdon. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, left lateral view; F, right lateral view. Scale bar = 50 mm.

Cambridgeshire, which is here considered more likely. The horizon is highly likely the Kimmeridge Clay as pits at Ely excavate this formation whilst the coast at Kimmeridge exposes only the Kimmeridge Clay Formation.

4.2. Quantitative analysis

The overall largest of the four centra, ABGCH 1980.191.1038, has a maximum width of 269 mm, a height of 222 mm, and a length of 95

Table 2
Body segments of selected pliosaur genera as percentages of total length. Fractions of 1% have been rounded up or down.

Taxon	Skull	Neck	Torso	Tail	Reference
<i>Peloneustes philarchus</i> NHMUK R. 3318 GPIT-PV-30091	18	19	37	27	Andrews, 1913
<i>Liopleurodon ferox</i> NHMUK R. 3536	24	15	28	34	Andrews, 1913
<i>Sachicasaurus vitae</i> MP111209-1	25	11	46	18	Páramo-Fonseca et al., 2018
<i>Stenorhynchosaurus munozi</i> SGC VL17052004-1	21	17	49	13 (est.)	Páramo-Fonseca et al., 2016

Table 3
Pliosaur cervical vertebral counts. Only species of genera mentioned in the text are included.

Taxon	Spec. no.	No. CV	Av. length (cm)	Est. neck length (cm)	Horizon	Reference
<i>Peloneustes philarchus</i>	NHMUK PV R 3318	21/22	2.63	57.86	Oxford Clay Fm.	Andrews, 1913
<i>P. philarchus</i>	NHMUK PV R 2679	2 + 12	Unknown	Unknown	Oxford Clay Fm.	Andrews, 1913
<i>P. philarchus</i>	NHMUK PV R 2440	1 + 19	Mid C = 3.3	> 66.00	Oxford Clay Fm.	Andrews, 1913
<i>P. philarchus</i>	NHMUK PV R 2439	2 + 18	Mid C = 3.4	68.00	Oxford Clay Fm.	Andrews, 1913
<i>P. philarchus</i>	NHMUK R 2438	2 + 19	Mid C = 3.7 Av. = 2.98	63.62	Oxford Clay Fm.	Andrews, 1913
<i>P. philarchus</i>	NHMUK R 2441	1 + 19	Unknown	Unknown	Oxford Clay Fm.	Andrews, 1913
<i>Peloneustes evansi</i>	CAMSM J46909	2 + 19	Unknown	Unknown	Oxford Clay Fm.	Seeley, 1877; Andrews, 1913
	NHMUK PV 47837, PV R 1713, PV R 1713a					
<i>P. evansi</i>	NHMUK PV R 3891	2 + 16	Av. = 4.3	> 78.30	Oxford Clay Fm.	Andrews, 1913
<i>P. evansi</i>	NHMUK PV R 2445	2 + 13	Av. = 3.55	> 53.35	Oxford Clay Fm.	Andrews, 1913
<i>P. evansi</i>	NHMUK PV R. 2437	2 + 17	Av. 3.9	> 66.30	Oxford Clay Fm.	Andrews, 1913
<i>Simolestes vorax</i>	NHMUK PV R 3319	2 + ~18	3.2	~64.00	Oxford Clay Fm.	Andrews, 1913
<i>Liopleurodon ferox</i>	NHMUK PV R 3536	2 + 20	Av. 5.07	107.00	Oxford Clay Fm.	Andrews, 1913
<i>L. ferox</i>	NHMUK PV R 2446	10	Av. 4.4	> 40.40	Oxford Clay Fm.	Andrews, 1913
<i>Liopleurodon cf. rossicus</i>	MS-AS RK 7/13–1958		4.9	Neck length est. for 20 CVs = 98.00	Upper Jurassic, Tithonian	Malakhov, 1999
<i>Pliosaurus funkei</i>	PMO 214.135 Holotype	Only 3 preserved	6.82	Neck length est. for 20 CVs = 136	Agardhfjellet Fm. Upper Jurassic, Volgian	Knutsen et al., 2012
<i>Sachiasaurus vitae</i>	MP111209–1	2 + 12	9.88	137		Páramo-Fonseca et al., 2018

mm (Table 1). The longest of the four centra is ABGCH 1980.191.1040, with a length of 103 mm (Fig. 4). The average length of all four centra is 93 mm, however, the length of ABGCH 1980.191.1039 is excluded from the analysis due to heavy damage to its posterior surface, and as such its true length cannot be determined. Consequently, we use the average length of the three complete centra of ~98 mm. We compare the Abingdon pliosaur neck with the Jurassic genera *Liopleurodon* and *Peloneustes*, and the Early Cretaceous genera *Sachiasaurus* and *Stenorhynchosaurus*. A neck length can be calculated for the Abingdon pliosaur using *Pliosaurus* (maximum cervical count 19: Tarlo, 1959a) and *Simolestes* (cervical count 22: Andrews, 1913), but note that in both *Pliosaurus* and *Simolestes*, there is no complete skeleton known, such that the proportion of the total skeleton length occupied by the neck cannot be determined. Furthermore, for *Pliosaurus* Tarlo (1959a) provided centrum lengths of only five vertebrae of the cervical series. Using the average length of 40.7 mm (see Tarlo, 1959a, table on p. 287 for cervical lengths), we estimate the length of the neck of *Pliosaurus* sp. specimen CAMSM J 35991 at 0.77 m. In *Liopleurodon* the maximum cervical vertebral count is 22, in *Peloneustes* it is 21 for *P. evansi* and 22 for *P. philarchus* (Andrews, 1913), for *Sachiasaurus* the cervical count is 14 (Páramo-Fonseca et al., 2018) and in *Stenorhynchosaurus* the count is 17 (Páramo-Fonseca et al., 2016). Thus, if the four vertebrae described here derive from one of these or a closely related taxon, then its neck length can be calculated using the average length of the cervical centrum (= 98 mm) multiplied by the cervical count. This provides a minimum neck length based on the low cervical count of *Sachiasaurus* ($n = 14$) of 1.37 m to a maximum based on *Peloneustes*, *Liopleurodon* and *Simolestes* all with a cervical count of 22 of 2.16 m. Note that excluding vertebra 1980.191.1040 which may be a first pectoral (see description above) from the analysis, these values are 1.33 m and 2.09 m respectively, thus the ambiguity in the identification of this vertebra has only a minor effect on the result.

In the Mid Jurassic pliosaur *Peloneustes* the complete neck is ~19% of the total skeleton length whereas it is only ~15% in *Liopleurodon*. Thus, a total body length of between 10.8 m and 11.4 m is calculated for the Abingdon pliosaur based on the two species of *Peloneustes*, whilst a total skeletal length of 14.4 m is obtained using the proportions of *Liopleurodon*.

Comparison with the Early Cretaceous pliosaur *Stenorhynchosaurus*, which had at least 17 cervical vertebrae, including the atlas and axis

(Páramo-Fonseca et al., 2016), and a neck to skeletal total length of 17% gives a total body length for the Abingdon pliosaur of 9.8 m. Similarly, a comparison with *Sachiasaurus* gives a body length of 12.5 m. Therefore, the total skeletal length estimates for the Abingdon pliosaur based on those taxa with complete or near complete skeletons give a range of 9.8 m to 14.4 m (Table 4).

5. Discussion

The large size of the four Abingdon cervical centra begs the question as to how large the original animal was. Secondarily aquatic tetrapods are well known for achieving large, and even immense sizes across a wide variety of mammalian and reptilian clades (Nicholls and Manabe, 2004; Lomax et al., 2018). The largest extant aquatic mammals, the baleen whales such as the blue whale *Balaenoptera musculus*, achieve lengths of up to 30 m (Mizroch et al., 1984), and weights of 130 tonnes (190 tonnes has been reported) (Lockyer, 1976) but the lengths and masses of the largest marine reptiles remain somewhat contentious. Such is the nature of the fossil record that complete skeletons of *Pliosaurus* are exceedingly rare. Claims for seemingly incredible sizes of pliosaurs were made (*Mea culpa* DMM) in the well-known TV animated documentary series 'Walking with Dinosaurs' and have been critiqued in detail in the well-respected science blog 'The Plesiosaur Directory' by Smith (see link in references). Claims for lengths of up to 25 m for pliosauromorphs have generally been dismissed, whilst claims of 18 to 20 m have been considered reasonable by some authors (Martill and Naish, 2000; McHenry, 2009), but have been rejected by others (Noë et al., 2004). Complete skeletons capable of supplying accurate length data are rare occurrences within Pliosauroida. The longest complete articulated pliosauromorph skeleton from the Early Jurassic is that of *Rhomaleosaurus cramptoni* at 7 m total length (Smith and Dyke, 2008). The type specimen of *Rhomaleosaurus cramptoni*, from the Toarcian Alum Shales of Kettlewell, North Yorkshire is now stored in Dublin (spec. no. NMINH F8785) (Smith, n.d. web site). In the Middle Jurassic (Callovian) the pliosaur *Liopleurodon* from the Peterborough Member of the Oxford Clay Formation is credited with a length of around 9.1 m (McHenry, 2009), but the 'complete' skeletons of the taxon held in several museums (Tübingen, NHMUK, Paris) are likely

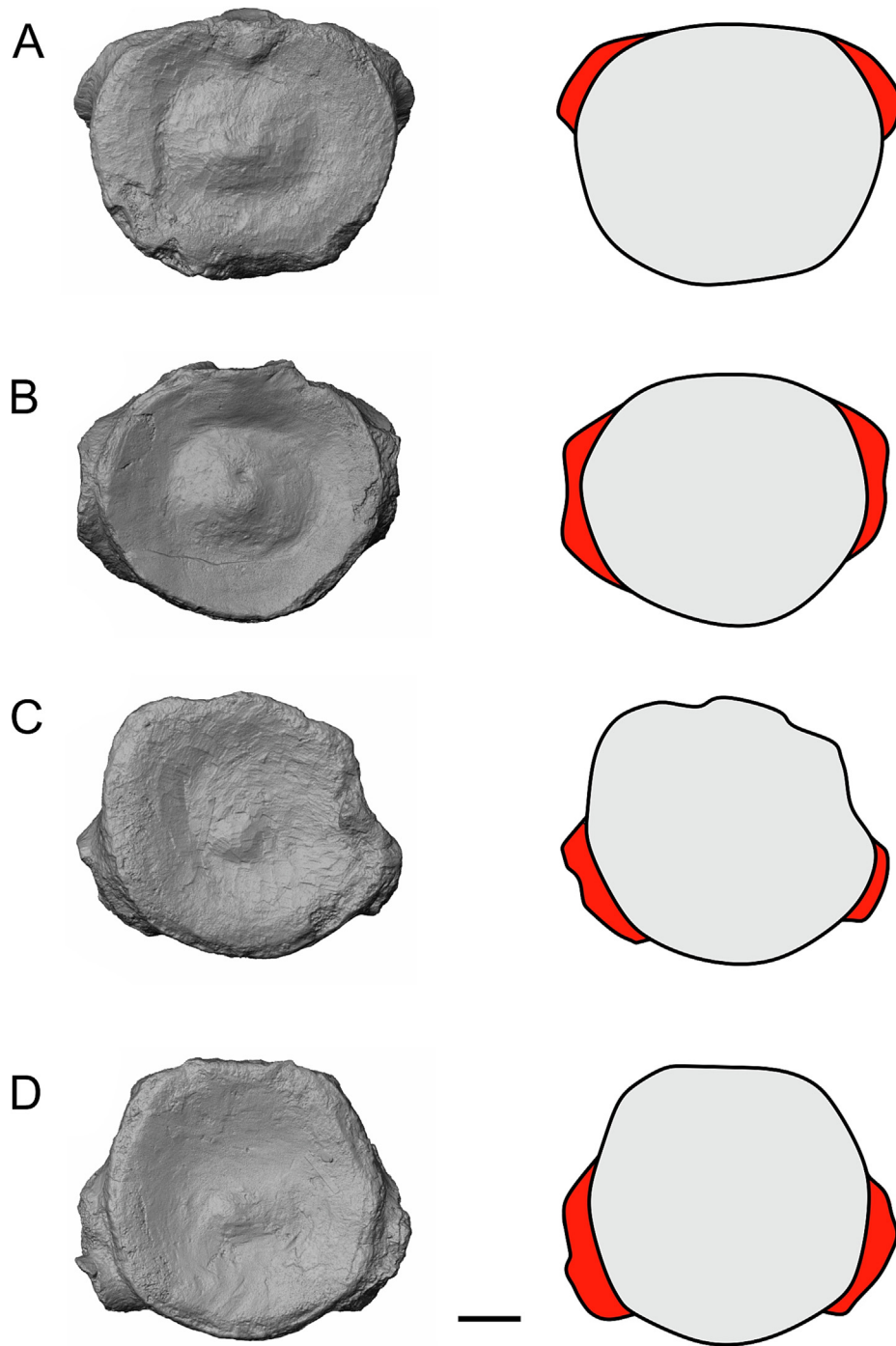


Fig. 6. Photographs and interpretive line drawings in either posterior or anterior views showing the position of the rib facets in red on the centrum arranged according to height. A, 1980.191.1040; B, 1980.191.1038; C, 1980.191.1041; D, 1980.191.1039.

composites. Nonetheless, there have been some very large fragments of Middle Jurassic pliosaurs from the Callovian part of the Oxford Clay Formation of Bedfordshire and Cambridgeshire in Eastern England (McHenry et al., 1996). In the Cretaceous, the genus *Kronosaurus* is often credited with a total length of 10.5 m (McHenry, 2009), and even larger at 12.8 m, a length thought to be highly exaggerated by McHenry (2009) (see above for taxonomic discussion and status of this genus).

The four Abingdon cervical vertebrae recorded here are confidently identified as those of a pliosauroid and are notable for their extreme

size. Indeed, the widths of the four Abingdon centra and the single York specimen are comparable with the largest reported by Zverkov and Pervushov (2020) for *Monquirasaurus boyacensis* (= *Kronosaurus boyacensis*) from the Aptian of Colombia. Despite being considerably damaged, sufficient features are present to identify them as cervical vertebrae, but it is not possible to be certain as to their exact position within the cervical series. The four vertebrae do not appear to comprise a series but some seem to represent mid cervical centra whilst others appear to be from a more posterior position in the neck based on the size and location of the cervical rib articulatory facets (Fig. 6).

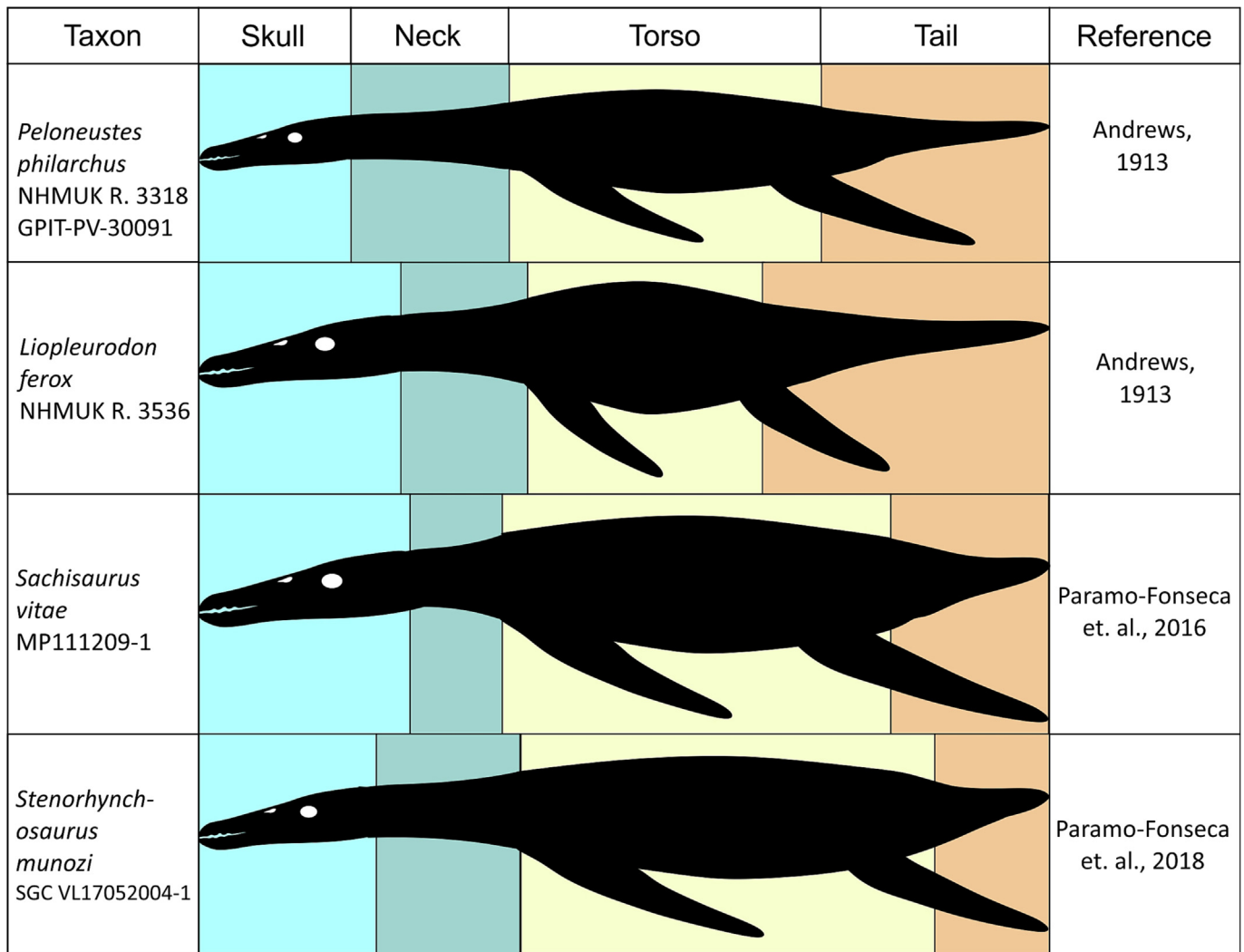


Fig. 7. Body segment proportions for the two Mid-Jurassic pliosauers *Peloneustes* and *Liopleurodon*, and two Early Cretaceous pliosauers *Sachiasaurus* and *Stenorhynchosaurus*. Percentage values for each segment are given in Table 2. The flippers on all silhouettes are schematic.

5.1. Other giant pliosauers from the Kimmeridge Clay

There have been a number of reports of giant pliosauromorphs from the Kimmeridge Clay Formation, and the earliest of which from the Kimmeridge Clay Formation of Market Rasen, Lincolnshire is detailed by Conybeare (1824), Owen (1842) and Phillips (1871). From this locality, a very large mandible, partial cranium, and

associated postcranial remains are the type of *Pliosaurus brachydeirus* Owen, 1841. Its mandible measures approximately 1.085 m in length (see Noè et al., 2004 for discussion). Similar sized pliosaur mandibles have also been reported from Cambridgeshire where *Pliosaurus brachyspondylus* (Owen, 1840) has a mandibular length of approximately 1.19 m (Seeley, 1869, Noè et al., 2004) and ‘*Pliosaurus grandis*’ (Owen, 1840) has a mandible of 1.7 m length. An

Table 4

Cervical counts and neck proportions for several Jurassic and Cretaceous pliosaur genera used to determine neck length and total skeletal length for the Abingdon and York pliosaur specimens. Percentage neck of skeletal length based on data from Table 2. Cervical count based on data in Table 3. Abingdon pliosaur neck length and total skeletal length calculated using average cervical length of 98 mm (see Table 1).

Taxon	Cervical count	% neck of skeletal length	Neck length of Abingdon pliosaur	Total skeletal length of Abingdon pliosaur	Neck length of YOYRM pliosaur	Total skeletal length of YOYRM pliosaur
<i>Liopleurodon</i>	22	15	2.16 m	14.4 m	1.89 m	12.6 m
<i>Peloneustes</i>	21/22	19	2.06/2.16 m	10.8/11.4 m	1.81/1.89 m	9.5/10.0 m
<i>Pliosaurus</i>	19	?	1.86 m	?	1.63 m	?
<i>Simolestes</i>	22	?	2.16 m	?	1.89 m	?
<i>Sachiasaurus</i>	14	11	1.37 m	12.5 m	1.20 m	11.0 m
<i>Stenorhynchosaurus</i>	17	17	1.67 m	9.8 m	1.46 m	8.6 m

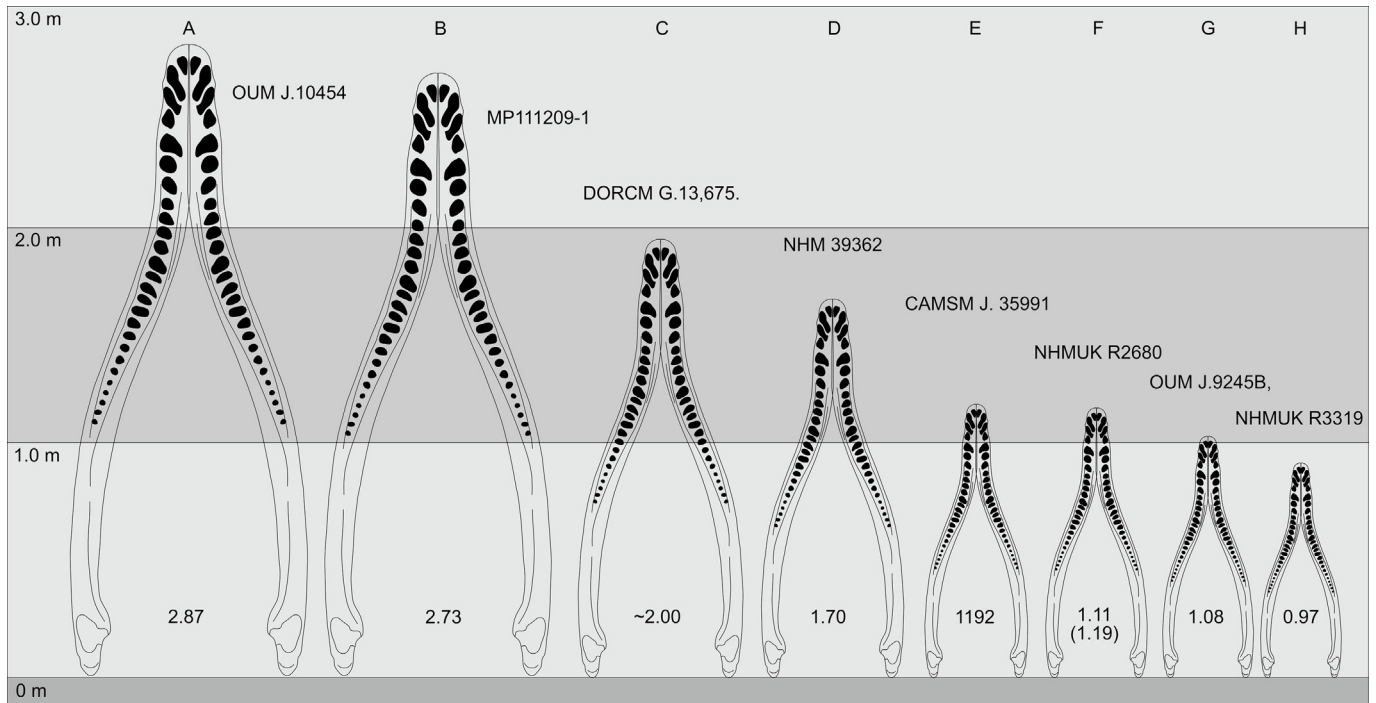


Fig. 8. A comparison of selected late Middle Jurassic and mid Late Jurassic pliosaur mandibles from the United Kingdom's Oxford and Kimmeridge Clay formations and a South American Cretaceous form. A, Oxford giant mandible, *Pliosaurus* sp. OUMNH J.10454; B, *Stenorhynchosaurus munozi* Páramo-Fonseca et al., 2016, SGC VL17052004-1; C, *Pliosaurus kevani* Benson et al., 2013, DORCM G.13.675; D, '*Pliosaurus grandis*' NHMUK 39362; E, *Pliosaurus brachyspondylus* (Owen, 1840) CAMSM J.35991; F, *Liopleurodon ferox* (Sauvage, 1873), NHMUK R2680, measurement from Andrews (1913). Proxy for mandibular length measured from premaxilla tip to posterior margin of articular along median line; G, *Pliosaurus brachydeirus* Owen, 1841, OUMNH J.9245; H, *Simolestes vorax* Andrews, 1909, NHMUK R3319. For ease of size comparison, the mandible outlines are stylised based on the left mandible of '*Pliosaurus grandis*' (Owen, 1840) as republished by Noè et al. (2004, fig. 3b) with the right side mirrored from the left. The value between the mandibular rami is the length of the mandible from the dentary tip to the post-articular processes measured along the median line.

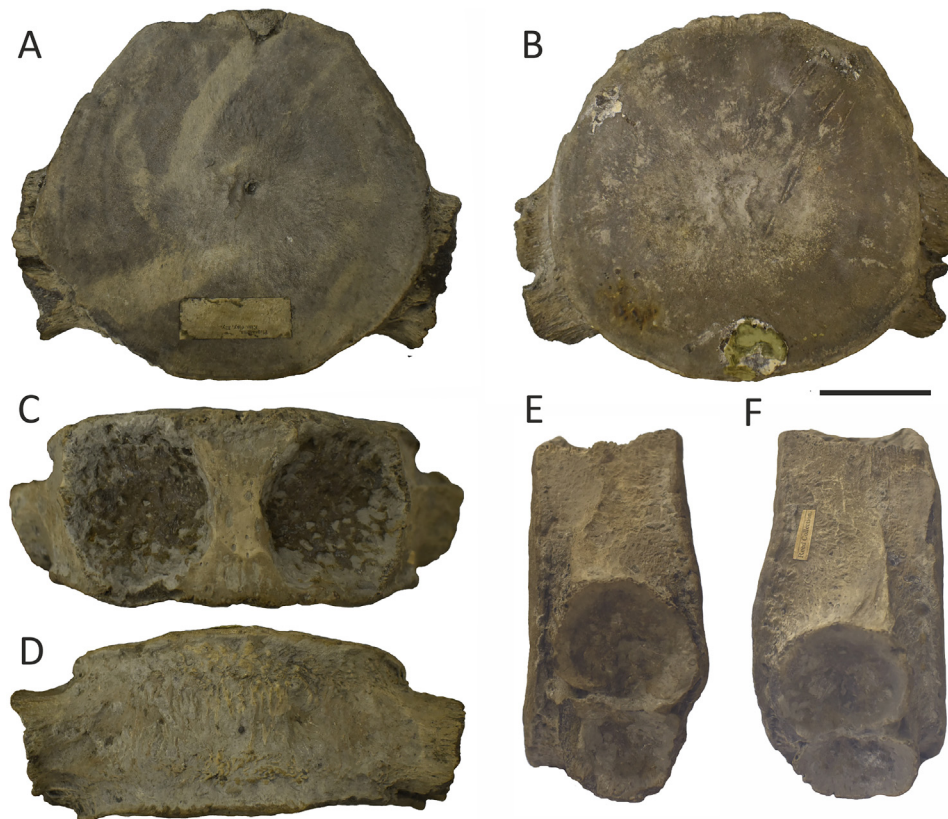


Fig. 9. Pliosaur cervical vertebral centrum YORYM: 2006.19 from the Kimmeridge Clay Formation of ?Ely, Cambridgeshire. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, left lateral view; F, right lateral view. Scale bar = 50 mm.

even larger giant pliosaur skull was more recently reported from the Kimmeridge Clay Formation of Dorset by Benson et al. (2013) in which the skull has a length of approximately 2 m. This specimen, assigned to a new species, *Pliosaurus kevani* (DORCM G.13,675), unfortunately lacks any associated postcranial remains. These skull specimens however pale into insignificance when compared to a gigantic mandible at Oxford Museum (OUMNH) from the Kimmeridge Clay Formation of Cumnor, Oxfordshire which is 2.88 m long (Noè et al., 2004) (Fig. 8A). The giant Oxford mandible was regarded as an example of *Stretosaurus macromerus* by Tarlo (1959a) although it is perhaps better regarded as *Pliosaurus* sp. (the generic name *Stretosaurus* is no longer valid: see Noè et al., 2004 and Hoare, 2015 for a taxonomic discussion on this subject: Benson et al., 2013 referred it to *P. rossicus*). Scaling the Oxford mandible to *Liopleurodon*, with a mandible length of 1.19 m, indicates, an animal with a total length of 11.74 m. Scaling the giant mandible with *Peloneustes philarchus* of the Oxford Clay Formation (using the complete skeleton held in Tübingen University Museum, specimen number GPIT-PV-30091) indicates a total body length of 13.98 m, a figure comparable with the dimensions derived from the four Abingdon vertebrae described above. However, it must be stated that some workers consider that the original preparators may have exaggerated the length of this giant mandible for greater visual effect. The amount of such exaggeration remains to be determined.

A single, large cervical vertebra of a pliosaurid is registered in the collection of the Yorkshire Museum as specimen number YOYRM: 2006.19 (Fig. 9). Although a new label lists the locality as Dorset, an old label glued to the specimen states the locality as Ely, Cambridgeshire. The width and height of the specimen are slightly smaller than those measurements in the Abingdon specimens, and the length at 86 mm is close to the smallest length (88 mm) of the Abingdon specimens (average of 98 mm for the three well preserved Abingdon specimens). The smaller size of the height and width of the YOYRM specimen is likely due to its more anterior position in the neck as suggested by the very low position of the double headed rib facets (Fig. 9E, F). The size calculated for the YOYRM specimen using *Stenorhynchosaurus*, *Peloneustes*, *Sachiasaurus* and *Liopleurodon* as models (using the methodology outlined above) gives lengths of 8.6 m, 9.5 m, 11.0 m and 12.6 m respectively (see Table 4). As such, the YOYRM cervical vertebra, despite being of smaller height and width, may be from an animal of comparable size to the Abingdon example.

Finally, some large, but isolated pliosaur bones from the Kimmeridge Clay Formation are held in the Etches Collection including an extremely large mandible MJML K1, a femur and pair of pubes. They were collected from the Dorset coast of southern England (Etches and Clarke, 2010; Ketchum and Benson, 2020), and likely represent individuals of a comparable size to the Abingdon animal, but these remain to be studied in detail.

6. Conclusions

The four vertebral centra described here are clearly identifiable as those of a pliosaurid cervical series and, in coming from the Kimmeridge Clay Formation, are perhaps allied with *Pliosaurus*, or a closely related, but as yet undescribed taxon. Their immense size indicates an individual that, when alive, would have had a length of between 9.8 m and 14.4 m. The new material, although fragmentary, is clear evidence for a truly gigantic pliosaur species in the Late Jurassic, although not yet on a par with the fanciful claims made for *Liopleurodon* in the iconic BBC TV series *Walking With Dinosaurs*. Nevertheless, pliosaurs were extremely large predatory marine reptiles, and comparable in size with many of today's larger aquatic predators (Fig. 10). Compared with other aquatic vertebrates from the Kimmeridge Clay Formation, they were the true giants of the Jurassic seas (Fig. 11).

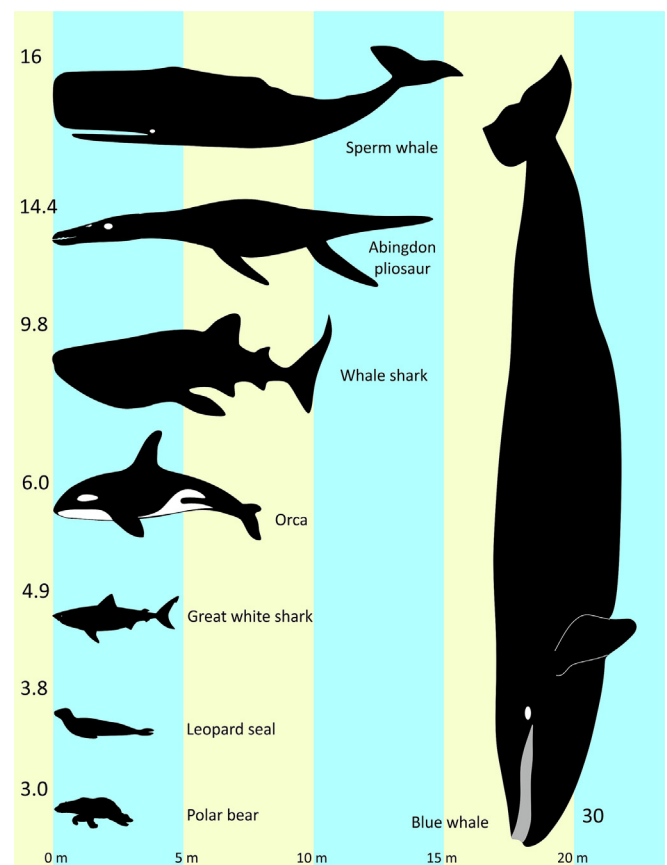


Fig. 10. Diagram placing the Abingdon pliosaur in a 'beauty contest' with a range of recent aquatic and semi-aquatic vertebrates to show the overall body sizes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are especially grateful to the staff and volunteers of Abingdon Museum, and give special mention to Dan Sancisi, Elin Bornemann and Jeff Wallis for their hospitality and assistance. We thank Sarah King of Yorkshire Museum for access to specimens in her care. Thanks to Nikolay Zherkov for valuable discussions and to Ingmar Werneburg for information on *Peloneustes* at Tübingen. Thanks to Steve Etches, Kimmeridge, for access to his amazing collection. DMM thanks Darren Naish (TetZoo) and Tim Haines (producer BBC *Walking with Dinosaurs*) for conversations (many years ago now) on the size of pliosaurs. We are grateful to our anonymous referees, who provided many thoughtful comments and greatly improved the manuscript. We are also delighted to thank Caroline Buttler for her editorial support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pgeola.2023.04.005>.

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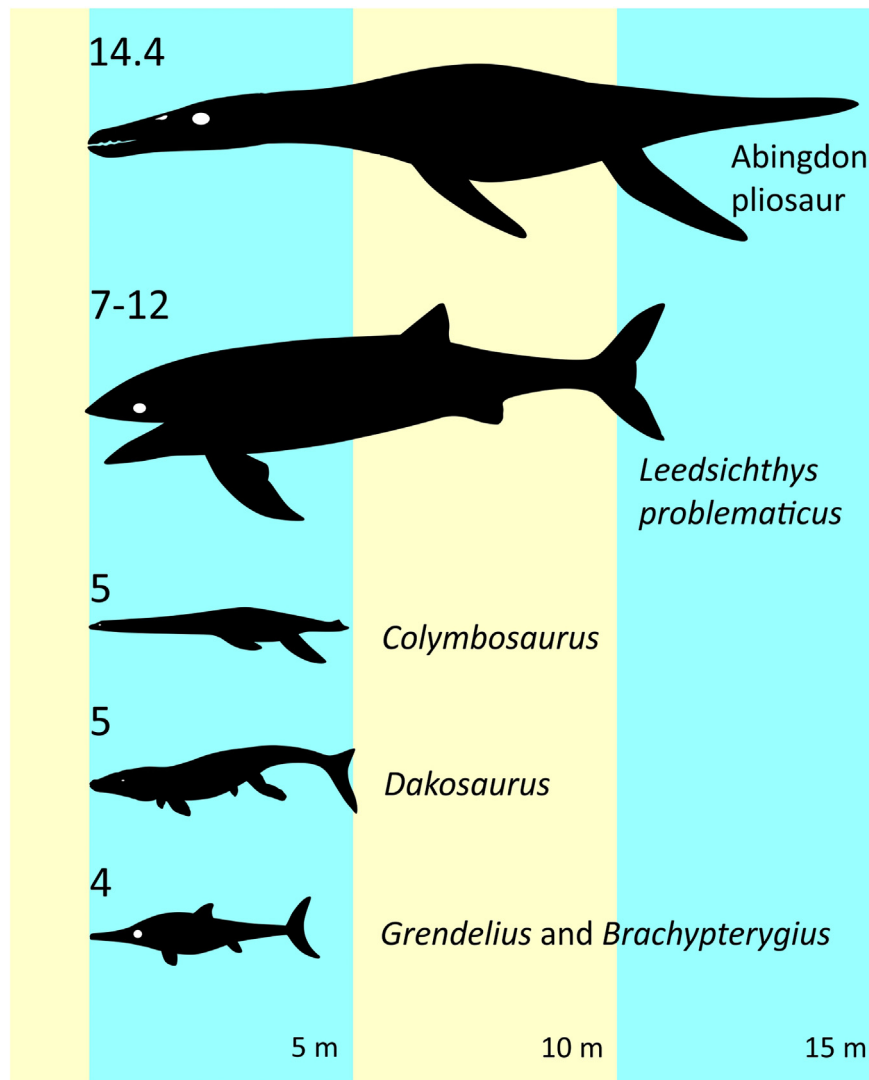


Fig. 11. The Abingdon pliosaur compared with other aquatic tetrapods and larger fish reported from the Kimmeridge Clay Formation of England and France. Note that there is not such a size difference between the larger estimates (~12 m) of the giant planktivorous pachycormid fish *Leedsichthys* and the Abingdon pliosaur.

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