Journal of Vertebrate Paleontology

ISSN: 0272-4634 (Print) 1937-2809 (Online) Journal homepage: www.tandfonline.com/journals/ujvp20

Re-evaluating body size in the Middle Jurassic pliosaur *Liopleurodon ferox* Sauvage, 1873

Edward O. Bartlett, David M. Martill & Roy E. Smith

To cite this article: Edward O. Bartlett, David M. Martill & Roy E. Smith (16 Jul 2026): Re-evaluating body size in the Middle Jurassic pliosaur *Liopleurodon ferox* Sauvage, 1873, Journal of Vertebrate Paleontology, DOI: 10.1080/02724634.2026.2691149

To link to this article: https://doi.org/10.1080/02724634.2026.2691149

Journal of Vertebrate Paleontology e2691149 (18 pages)
Published with license by the Society of Vertebrate Paleontology
DOI: 10.1080/02724634.2026.2691149

ARTICLE

RE-EVALUATING BODY SIZE IN THE MIDDLE JURASSIC PLIOSAUR *LIOPLEURODON FEROX* SAUVAGE, 1873

EDWARD O. BARTLETT, [1]* DAVID M. MARTILL, [1] and ROY E. SMITH [1]
[1]School of the Environment and Life Sciences, University of Portsmouth, Portsmouth PO1 3QL, U.K., eddie.bartlett@port.ac.uk, david.martill@port.ac.uk, roy.smith@port.ac.uk

ABSTRACT—*Liopleurodon ferox* is a macropredatory pliosaurid plesiosaur from the Callovian (Middle Jurassic) of Europe. Several near-complete skeletons are known from the Peterborough Member of the Oxford Clay Formation of eastern England and approximately equivalent strata in north France. Disparate total lengths between 5.7 and 25 m have been reported for *L. ferox*, influencing paleoecological interpretations and length estimates for large pliosaurs. An updated model of *Liopleurodon* proportions and measurements is presented here, reconstructed from a near-complete skull and two well-preserved specimens with extensive postcranial remains. The skull comprises a larger proportion of the total skeletal length (24%) than a previously reported skull:body ratio of 1:5, and greater than the skull:body ratio of sympatric pliosaurs, indicating an ability to capture relatively larger prey. Intervertebral spacing (set at 10% based on other well-preserved plesiosaurians) was included in the final length determinations. By isometrically scaling a dataset of 37 specimens attributed to *L. ferox*, a total length range of 2.46–8.09 m is calculated. *Liopleurodon* is the largest aquatic tetrapod and apex predator of the Oxford Clay Formation paleoecosystem. Applying the new model to a range of indeterminate Oxford Clay pliosaurids as well as some Late Jurassic taxa, pliosaurs are calculated to reach total lengths up to 12.2 m, evolving gigantism by the Middle Jurassic and maintaining their position as apex predators for ~80 my until they were superseded by mosasaurs in the late Turonian of the Upper Cretaceous.

SUPPLEMENTARY FILES—Supplementary files are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Bartlett, E. O., Martill, D. M., & Smith, R. E. (2026) Re-evaluating body size in the Middle Jurassic pliosaur *Liopleurodon ferox* Sauvage, 1873. *Journal of Vertebrate Paleontology*. https://doi.org/10.1080/02724634.2026.2691149

Submitted: July 13, 2025
Revisions received: May 14, 2026
Accepted: May 19, 2026

INTRODUCTION

Pliosauridae (Reptilia, Sauropterygia) are a family of Mesozoic marine reptiles; early members from the Lower Jurassic resemble plesiosauroids with small skulls and long necks (Benson & Druckenmiller, 2014; Benson et al., 2012). The derived pliosaurid clade, Thalassophonea, are characterized by large skulls, often with massive, deep-rooted caniniform teeth, proportionally short necks, four near equal-sized flippers, and often attaining large body lengths of over 10 m (Andrews, 1913; Benson et al., 2013; Noè & Gómez-Pérez, 2022; Noè et al., 2004). Most taxa likely were generalist carnivores, with some occupying the niche of apex predator (Benson & Druckenmiller, 2014; Fischer et al., 2022; McHenry, 2009), although some may have been specialist feeders on larger teuthoids and fish (Martill, 1992; Noè, 2001). Thalassophoneans first appeared in the Middle Jurassic (Bajocian) and persisted to the early Late Cretaceous (Turonian), existing for ~80 my (Angst & Bardet, 2016; Sachs et al., 2023; Sato et al., 2023). Despite a global distribution and some well-preserved, near complete specimens (Andrews, 1913; Fischer et al., 2017; Knutsen et al., 2012; Noè & Gómez-Pérez, 2022; Páramo-Fonseca et al., 2016, 2018), pliosaurs are often highly incomplete, making generic identification difficult, and thus accurately calculating body size for these animals has been difficult. Accurate determination of body size is reliant on well-preserved specimens for length estimates, but such specimens are extremely rare. Plesiosaurs have a unique bauplan of fusiform bodies, four well-developed hydrofoil flippers and a short, tapered tail, lacking modern analogues (Andrews, 1913; Cruickshank et al., 1996; Halstead, 1989; Noè et al., 2004; O'Keefe, 2002). Body size is an important factor influencing the prey range of a macro predator, so estimating total body length (TBL) is crucial for paleobiological and paleoecological reconstructions of pliosaurs and understanding how they regulated their ecosystems as top predators. In addition, knowledge of their size will contribute to our understanding of their coexistence with other secondarily aquatic reptiles, including other pliosaurids.

Liopleurodon ferox (Sauvage, 1873) is a well-known thalassophonean pliosaurid from the Middle Jurassic (Callovian) Oxford Clay Formation (OCF) of England (Andrews, 1913) and

*Corresponding author.

Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.

Published online 16 Jul 2026

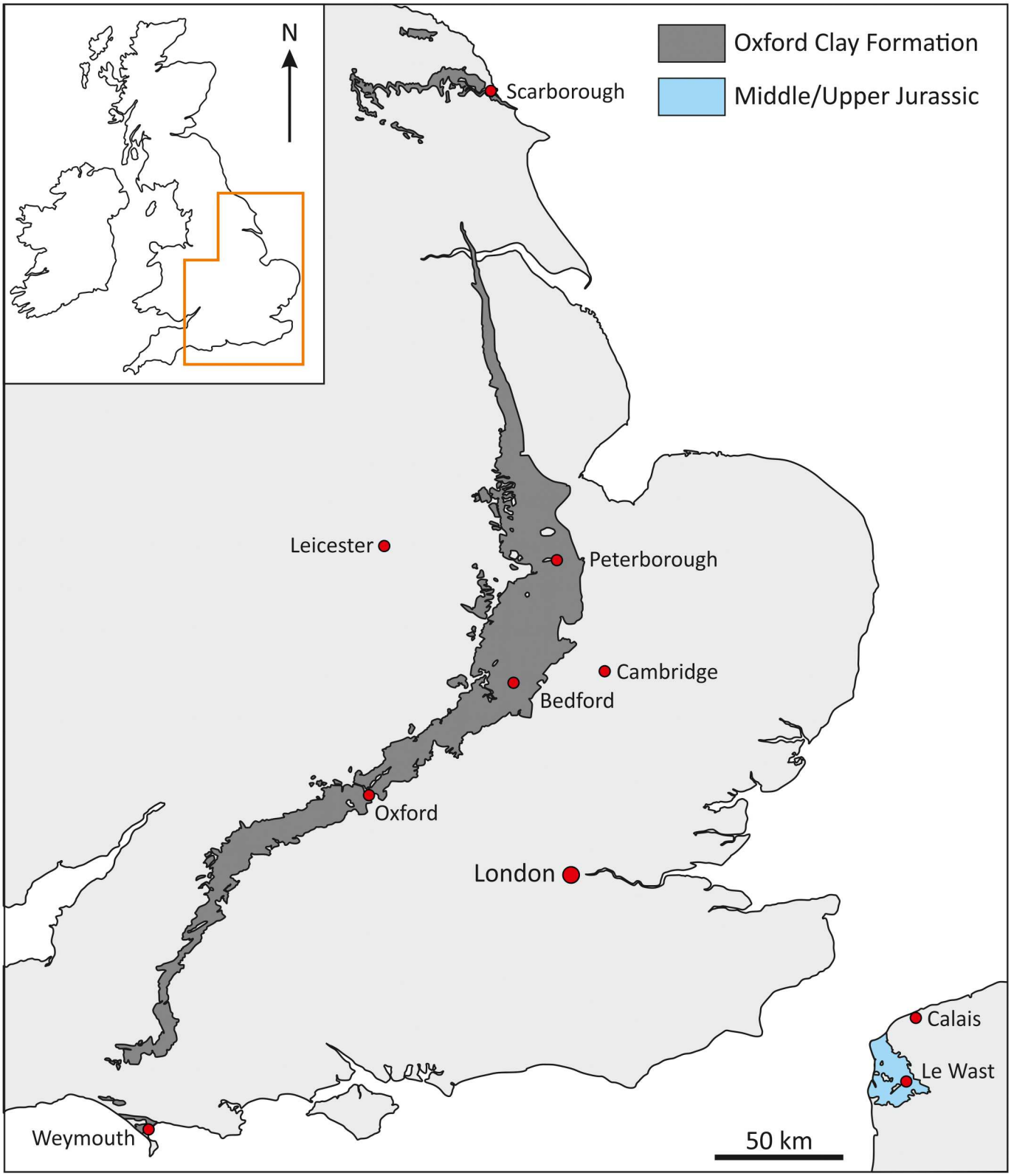

FIGURE 1. Map of the Oxford Clay Formation outcrop in eastern England and north-western France. The Paleontological Collection of the University of Tübingen, Germany was also visited. Adapted from Hudson and Martill (1994).

equivalent strata in northwest France (Sauvage, 1873; Vincent et al., 2024). It is among the earliest of thalassophoneans to be known from near-complete skeletons (Andrews, 1913). Consequently, *Liopleurodon* has become a benchmark for systematic studies and size comparisons of thalassophoneans (Ketchum & Benson, 2022; McHenry, 2009). However, a

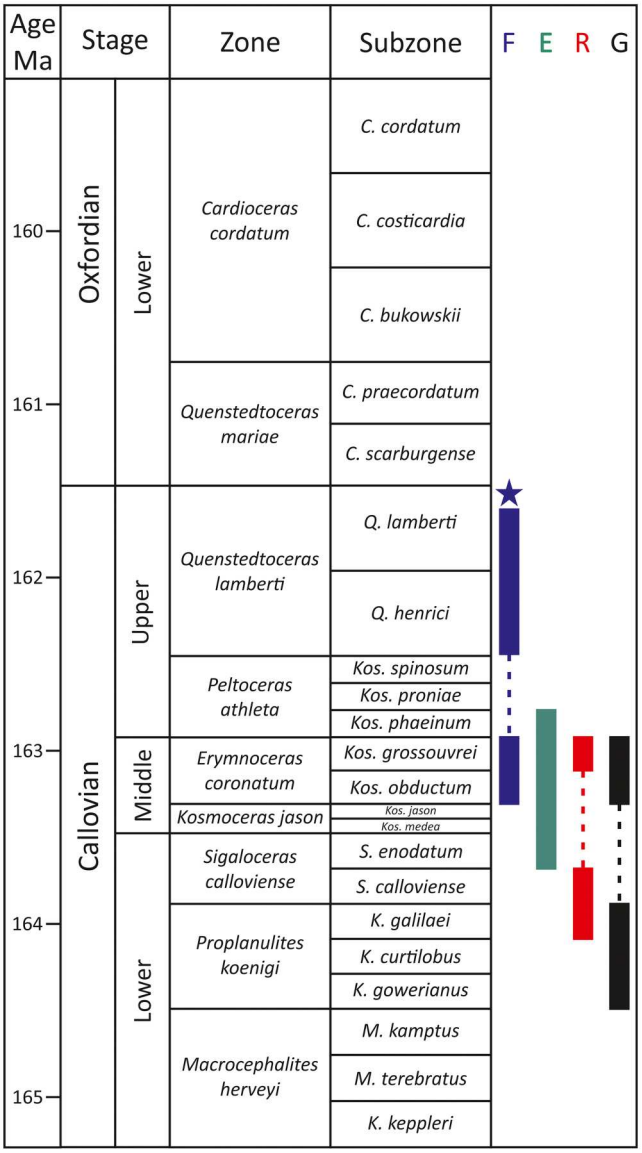

FIGURE 2. Stratigraphic and geographic distribution of *Liopleurodon ferox* in Europe. Callovian and lower Oxfordian ammonite biozonation of Western Europe adapted from Martill and Hudson (1991), correlated to the time scale of Gradstein et al. (2020). Occurrence data from Sauvage (1873), Andrews (1913), Rauhut et al. (2016), Sachs and Nyhuis (2018), and Zverkov et al. (2024). **Abbreviations**: **E**, England, **F**, France; **G**, Germany; **R**, Russia. Star represents the holotype.

complicated taxonomic history stemming from the diagnosis of the holotype, an isolated caniniform tooth (BHN 3R 197) originally described by Sauvage (1873), has led to the referral of many Callovian–Tithonian pliosaurid specimens to the genus (Halstead, 1971; Halstead, 1989; Martill & Hudson, 1991; Tarlo, 1960). This has resulted in a wide range of size estimates from 6.39 m to the astonishing 25 m presented in the 1999 BBC TV series *Walking with Dinosaurs* (Martill & Naish, 2000; Martill et al., 2023; Noè et al., 2003). A reconstruction of the skeleton of *Liopleurodon* by Newman and Tarlo (1967) has frequently been used to represent and estimate the length of other thalassophoneans (Martill et al., 2023; McHenry, 2009). While it was originally intended as a generalized pliosaur, the reconstruction was partly based upon NHMUK PV R 8322, a large, incomplete pliosaurid consisting of a mandibular symphysis and a partial postcranial skeleton from the Oxford Clay Formation, that was estimated at 10.97 m (Newman & Tarlo, 1967). The reconstruction was considered by McHenry (2009) to be supplemented by the postcrania of CAMSM J.35990, another large pliosaurid from the Kimmeridge Clay Formation, while the reconstruction's skull resembles GPIT-PV-30093, a pliosaur identified as *L. ferox* from the Oxford Clay Formation of England (Noè, 2001), therefore likely making their restoration a chimaera of three taxa. All three specimens have at one point been referred to *L. ferox*: NHMUK PV R 8322 was accessioned under *L. ferox*, CAMSM J.35990 was assigned to *Liopleurodon macromerus* (Halstead, 1989), and GPIT-PV-30093 has been identified as *L. ferox* or a synonym of the taxon since Linder's (1913) description. Thus, Newman and Tarlo's (1967) reconstruction has often been referred to as *Liopleurodon* and has been included in many size estimations (Knutsen et al., 2012; Martill & Hudson, 1991; Martill et al., 2023; McHenry, 2009; O'Keefe, 2002). However, both NHMUK PV R 8322 and CAMSM J.35990 have since been referred to Pliosauridae indet. and *Pliosaurus* cf. *kevani*, respectively, and consequently the reconstruction of Newman and Tarlo (1967) cannot be confidently used as a basis for the proportions and total length of *L. ferox* (Benson et al., 2013; McHenry, 2009; Noè, 2001; Smith, 2021). Here we present a new range of estimates for body size of *L. ferox*, based on the proportions of a well-preserved skull and two specimens preserving partial crania and postcranial material confidently referred to the taxon. The new model is also applied to a dataset of large, but fragmentary specimens from Middle Jurassic Oxford Clay Formation that might represent distinct taxa.

Geological and Geographic Context

The holotype of *L. ferox* is a single tooth crown (BHN 3R 197) discovered near the village of Le Wast near Boulogne-sur-Mer, north-west France, in mudstones of the Lamberti ammonite biozone (upper Callovian; Figs. 1, 2; Sauvage, 1873). These strata are equivalent to the Stewartby Member of the English Oxford Clay Formation (Martill & Hudson, 1991). Thus the holotype specimen is likely to be approximately 1 my younger than specimens referred to *Liopleurodon* from the English Oxford Clay Formation that come from the Peterborough Member of the OCF.

The Oxford Clay Formation crops out across southern and eastern England, from Weymouth, Dorset to Scarborough, North Yorkshire (Fig. 1), where it is divided into three members, the lower Peterborough Member, dominated by bituminous clays and shales with numerous thin shell beds, and the Stewartby and Weymouth members, consisting of brownish-gray mudstones with intermittent calcareous shell beds (Cox & Sumbler, 2002; Martill & Hudson, 1991). This transitions into gray blocky mudstones in the upper two members with, in some places, the Lamberti limestone (upper Callovian) separating the upper Callovian Stewartby Member from the lower Oxfordian Weymouth Member marks the boundary between the Middle and Upper Jurassic. Vertebrate fossils are commonly found in Bed 10 of the Peterborough Member in the Jason ammonite biozone at Peterborough (Figs. 1, 2), within the Oxford Clay (Martill, 1985), as evidenced by the extensive Leeds collection of fossil reptiles (1867–1917; Andrews, 1910, 1913; Hudson & Martill, 1994; Leeds, 1956; Martill & Hudson, 1991; Noè, 2001).

Besides the holotype tooth crown, other material referred to *Liopleurodon* includes 20 specimens referred to *Liopleurodon* by Andrews (1913) and a recently described and well-preserved postcranial skeleton from Saint-Laon, Department de la Vienne in western France (specimen number ComCom Thouarsais_-Geol.0121). The specimen was found in the argillaceous limestones of Saint-Laon, known as "calcaires en platins" (Vincent

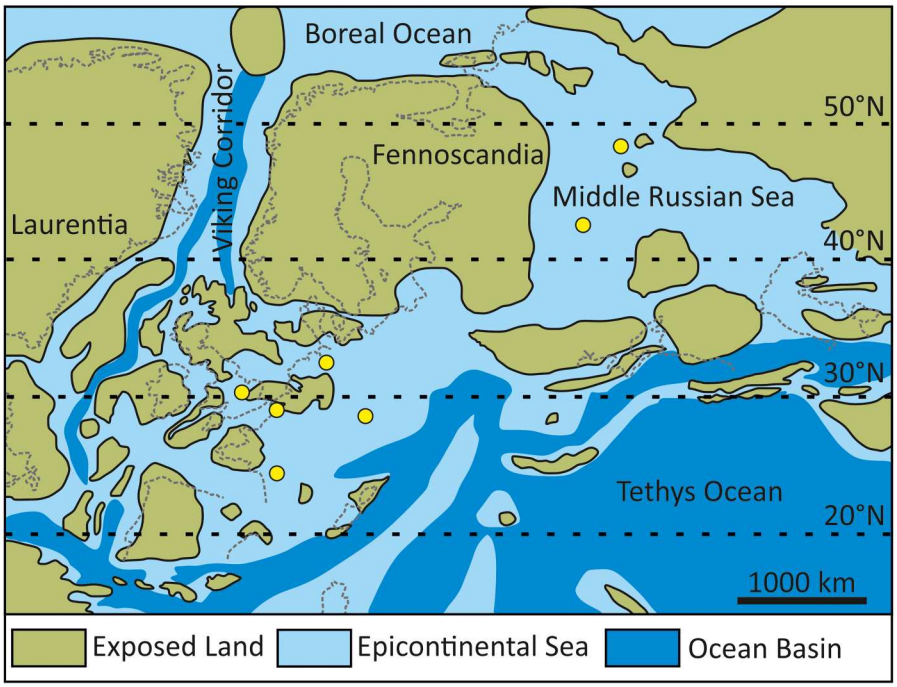

FIGURE 3. Paleogeographic map of Callovian Europe with circles marking localities where *Liopleurodon ferox* specimens have been discovered. Adapted from Vickers et al. (2021) and Zverkov et al. (2024). Occurrence data from Sauvage (1873), Andrews (1913), Rauhut et al. (2016), Zverkov et al. (2024), and Vincent et al. (2024).

et al., 2024:4). Lithological evidence, including ferruginous ooids present in the matrix indicate that the specimen comes from the Coronatum ammonite biozone and thus coeval with the upper part of the Peterborough Member of the Oxford Clay Formation of eastern England (Fig. 2; Vincent et al., 2024). Specimens of *L. ferox* have come from the lower–middle Callovian Ornatenton Formation in North Rhine-Westphalia (northwest Germany), Hildesheim (north-central Germany) and Lauffen (southwest Germany; Michelis et al., 1996; Noè, 2001; Rauhut et al., 2016; Sachs & Nyhuis, 2018). The majority of specimens were found in the Coronatum ammonite biozone (middle Callovian; Fig. 2; Michelis et al., 1996; Rauhut et al., 2016) excluding RPMH uncataloged, an isolated crown from Hildesheim from the lower Callovian Macrocephalites Clay of the Koenigi ammonite biozone (Fig. 2; Mönnig, 1995; Sachs & Nyhuis, 2018). Presently, this specimen represents the oldest occurrence of *L. ferox* in the lower Callovian. Material identified as *L. ferox* has also been documented from European Russia (Zverkov et al., 2024). These Russian specimens were discovered in the Unzha River Basin of Makariev district of the Kostroma Oblast and the Mikhalovcement quarry in the Mikhaylov district of Ryazan Oblast. The Russian specimens were found in the Koenigi, Calloviense, and Coronatum ammonite biozones (Fig. 2), corresponding to the same ammonite biozonation schemes used in Western Europe, and thus dating the Russian examples to the lower–middle Callovian (Zverkov et al., 2024). Thus, *Liopleurodon* would seem to have a stratigraphic range of lower Callovian to upper Callovian, equating to approximately 3.24 my (see Discussion; Fig. 2) and a geographic range that extends from eastern England to slightly east of Moscow.

The beginning of the Callovian was marked by a significant marine transgression (Haq, 2018), with a European low-lying archipelago largely inundated by a shallow (0–100 m) epicontinental sea and positioned ~20° further south than today (Fig. 3; Barron et al., 2012; Callomon, 2020; Martill & Hudson, 1991). The climate was warm and humid with mean surface water temperatures around 21°C based on aragonitic temperatures derived from the common ammonite *Kosmoceras* (Barron et al., 2012; Cox & Sumbler, 2002). The paleoenvironment of the Peterborough Member is well studied (Martill, 1985; Hudson & Martill, 1991, 1994); it represents a shallow epeiric sea (Fig. 3) with fluctuating benthic oxygen levels and at times a 'soupy' seafloor substrate. The water column was nutrient-rich and highly productive, with a high total organic carbon reaching 14% in bed 10 (Cox & Sumbler, 2002; Hudson & Martill, 1994). Episodes of high sedimentation would rapidly bury remains, accounting for the exceptional preservation and the quantity of vertebrate fossils recorded (Hudson & Martill, 1994; Martill & Hudson, 1991). A eustatic sea level rise connected the Boreal, Western European, Middle Russian seas and the Tethys Ocean via a system of straits (Fig. 3), surrounded by the European archipelago (Barron et al., 2012; Callomon, 2020; Zverkov et al., 2024). This connection is seen by the mixing of previously endemic ammonites such as the boreal Kosmoceratidae appearing in European strata in the early Callovian (Callomon, 2020).

MATERIALS AND METHODS

Data Collection

A data set of 20 specimens of *L. ferox* (Table S1, Supplementary File 1) was assembled through visits to the collections of BEDFM, CAMSM, GPIT, LEICT, NHMUK, OUMNH, and PETMG (Fig. 1). Photographs of specimens were taken using a Nikon D3100 and a Google Pixel 5, and manipulated in CorelDRAW X8 (Corel Corporation, 2016). Dimensions were measured using vernier digital calipers and a measuring tape for larger specimens. The data set is supplemented with a further 17 *L. ferox* specimens (Table S1, Supplementary File 1) reported in the literature (Andrews, 1913; Michelis et al., 1996; Noè, 2001; Noè et al., 2003; Sachs & Nyhuis, 2018; Tarlo, 1960; Vincent et al., 2024; Zverkov et al., 2024).

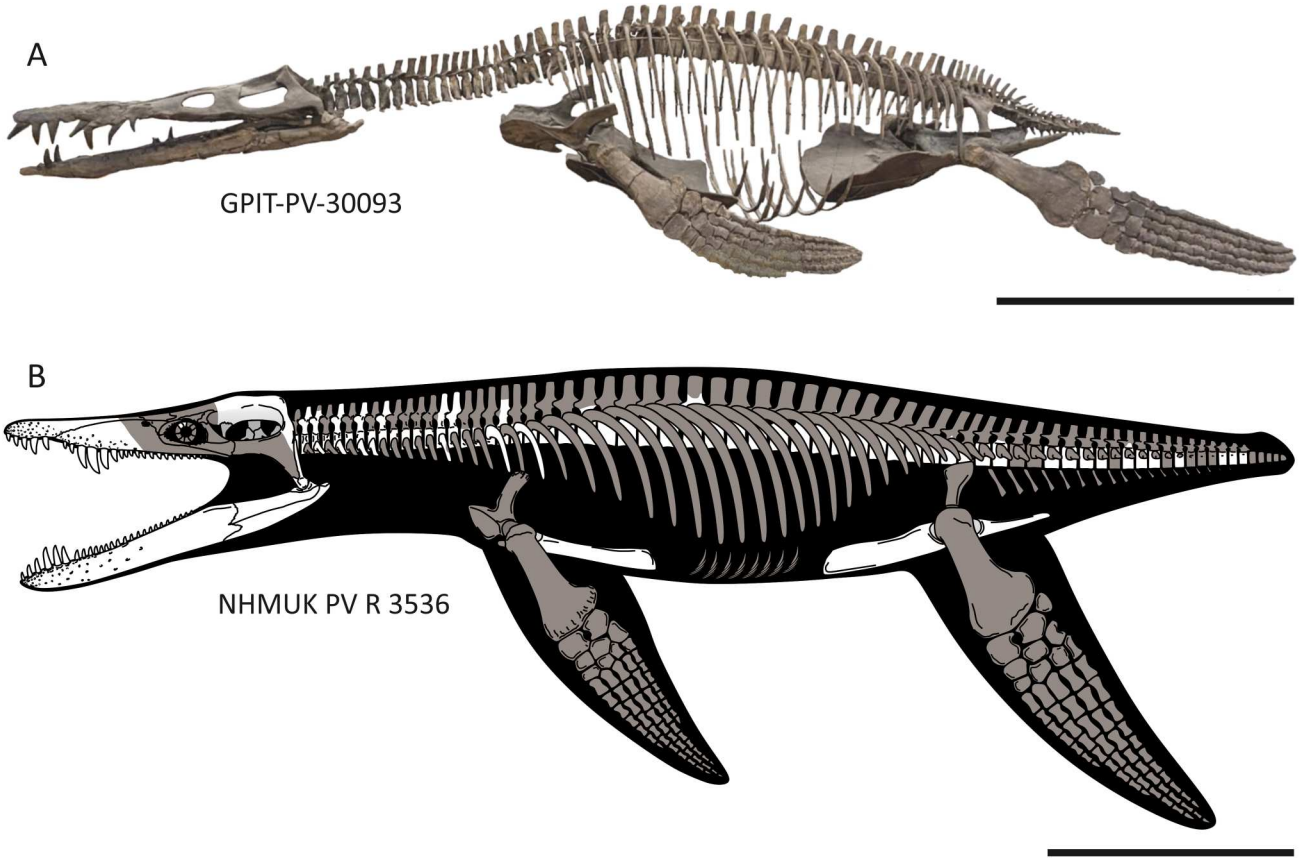

FIGURE 4. Well-preserved specimens of *Liopleurodon ferox* in left lateral view. **A**, GPIT-PV-30093; **B**, skeletal of NHMUK PV R 3536 representing all elements during data collection (right scapula, femur, and tibia are preserved). Scale bar equals 1 m.

Specimen Referral to *Liopleurodon*

The majority of the specimens from collection visits had only been identified to the family Pliosauridae, or to "*Pliosaurus ferox*" and the nomen dubium "*Pliosaurus grandis*." This required the reidentification of material using a combination of sources for *L. ferox*: the holotype diagnosis (Sauvage, 1873) and the amended diagnoses and descriptions of more complete specimens (Andrews, 1913; Noè, 2001; Tarlo, 1960; Vincent et al., 2024). The dentitions of GPIT-PV-30093 (Fig. 4A) and NHMUK PV R 3536 (Fig. 4B) were compared to images of the holotype tooth crown BHN 3R 197 to independently assess their identification from previous studies (Andrews, 1913; Noè, 2001; Tarlo, 1960). A revised diagnosis of *L. ferox* and the validity of the holotype was not explored, as this requires further research. The diagnosis given below is an amended version from previous authors as used by Vincent et al. (2024). Specimens have been further divided into isolated material and more complete specimens represented by multiple elements or cranial material that are generally more confidently referrable to *Liopleurodon* (see Table S1, Supplementary File 1 for distinction). This is reflected in the ranges of TBLs presented in the results.

Morphometric Analysis

Two near-complete skeletons, GPIT-PV-30093 and NHMUK PV R 3536 (Fig. 4), were used to determine the body segment proportions of *L. ferox* and to determine how they differed from the composite reconstruction of Newman and Tarlo (1967). GPIT-PV-30093 and NHMUK PV R 3536 preserve incomplete crania. Accordingly, they were scaled against NHMUK PV R 2680 (Andrews, 1913; Noè, 2001), which preserves a complete cranium. The skull was measured along the dorsal midline from the anterior of the cranium to the basioccipital; the vertebral column was measured along the ventral midline of the centra (Table 1). The tails of both specimens are incomplete (Figs. 4, 5), which seems to be typical of even well-preserved pliosaurids (Andrews, 1913; McHenry, 2009; Páramo-Fonseca et al., 2016, 2018), with GPIT-PV-30093 preserving 11 caudal vertebrae (the mount has been extended with additional casts) and NHMUK PV R 3536 preserving 14 caudal vertebrae. *Peloneustes philarchus* from the Oxford Clay Formation preserves 28 caudal vertebrae and Andrews (1913) also states that *Pliosaurus* preserves 25–30. Accordingly, the tail of *L. ferox* is reconstructed here with a caudal vertebral count conservatively estimated at 25, using the average caudal length of the preserved vertebrae (Tables 1 and 2). The mounted skeleton (GPIT-PV-30093, Fig. 4A) has been considered to be a composite (Martill et al., 2023). It also contains several plaster replica vertebrae that may be artificially extending the length of the vertebral column. Based on personal observations by the lead author, the mounted skeleton is likely composed of one specimen, as noted by Noè (2001), except for the left ilium (Linder, 1913), therefore it is a sufficiently reliable specimen to use in combination with NHMUK PV R 3536 for morphometric assessment. The total skeletal length refers to the total length exclusive of intervertebral spacing, and is used to compare proportions. The two specimens were divided into discrete segments of skull, neck, torso (including sacral region), and tail as per Martill et al. (2023; see Table 1). The boundary between the neck-

TABLE 1. The preserved and estimated skeletal lengths of the two specimens preserving postcrania used to determine the proportions of *Liopleurodon ferox*. Skull length estimated scaling from NHMUK PV R 2680.

Specimen No.		Skull length (m)	Neck length (m)	Torso length (m)	Tail length (m)	Total skeletal length (m)
GPIT-PV-30093	Preserved	0.83	0.78	1.39	0.41	3.41
	Estimated	0.97	0.85	1.39	0.92	4.14
NHMUK PV R 3536	Preserved	0.78	1.03	1.81	0.72	4.82
	Estimated	1.27	1.03	1.81	1.29	5.39

torso and the torso-tail was taken at the glenoid and acetabulum of the pectoral and pelvic girdles respectively. Each segment was then converted into a percentage of the total skeletal length and rounded to the nearest whole number.

Scaling

To calculate the total body length estimates for fragmentary specimens, scaling was achieved by the simple multiplication and division of measured lengths of congruent elements in GPIT-PV-30093 and NHMUK PV R 3536 (Fig. 4). Among the most common elements were teeth (Table S1, Figs. S2, S3, Supplementary File 1). Pliosaur dentition can be highly anisodont, usually with massive teeth anteriorly becoming significantly smaller posteriorly. This is especially marked in *Liopleurodon* which possesses large caniniform teeth in the premaxilla and mandibular symphysis, but much smaller teeth posteriorly in the mandibular rami (Noè, 2001; Sassoon et al., 2015). To avoid overestimates, isolated crowns were assumed to be the largest in the tooth row (see Discussion). This value (crown height) was divided by the crown height of the largest crown associated with NHMUK PV R 3536 (Table 2). The scaling factor produced is multiplied by the total skeletal length of NHMUK PV R 3536. Another common skeletal element within many of the specimens represented by partial postcranial remains are vertebrae (Table S1, Supplementary File 1). These were scaled by multiplying the ventral length of the centra by the number of missing vertebrae (Table 2) to produce a total length for a specific segment, which was then input into the proportions of *L. ferox* to estimate total length. As previously mentioned, specimens have been separated into two categories based on the completeness of each specimen to determine how the results are affected by scaling from isolated material (Table S1, Supplementary File 1).

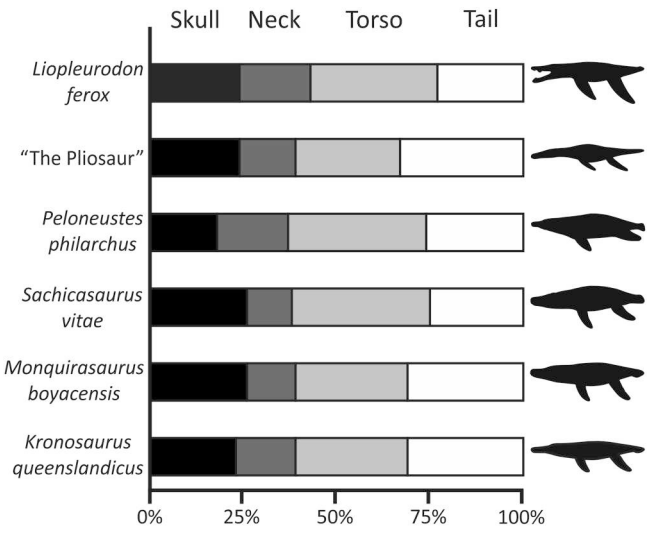

FIGURE 5. The segmented body proportions of pliosaur genera *Liopleurodon*, *Peloneustes*, *Sachicasaurus*, *Monquirasaurus*, *Kronosaurus*, and a composite reconstruction of *Liopleurodon* by Newman and Tarlo (1967). The tails of the Cretaceous pliosaurs *Sachicasaurus*, *Monquirasaurus*, and *Kronosaurus* were reconstructed to a vertebral count of 25 to be consistent with the reconstructed tail of *Liopleurodon*; this may represent an overestimate of the tail length.

Reconstructing Intervertebral Cartilage

Plesiosaurs have platycoelous vertebrae bearing a cartilaginous intervertebral disc (Wintrich et al., 2020). The intervertebral discs can comprise a significant portion of the total body length of the vertebral column, upwards of 20% (Evans, 1993; Troelsen, 2019). For this reason the intervertebral cartilage is incorporated into the total body length estimates, and thus the total body length/total length refers to the total skeletal length and intervertebral spacing combined. Well-preserved, articulated plesiosaur specimens can provide data on the original spacing of the vertebrae. Troelsen (2019) shows that the spacing length scales with centrum length in two specimens of *Thalassiodracon hawkinsii*. An analysis of 17 plesiosaur specimens that preserve the original spacing was performed from specimens figured in the literature, and the intervertebral spacing as a percentage of centrum length was recorded in Table S2, Supplementary File 1. This resulted in an average spacing length of 12% of centrum length; a conservative 10% was applied to the vertebral column of *L. ferox*. As the skull occupies a significant portion of the TBL (~25%) in pliosaurs, only the vertebral column was multiplied by 10%. Adding the skull length to this value resulted in an overall increase of 8% of the TBL, which was applied to the estimates derived from our scaling.

Institutional Abbreviations—**BEDFM**, The Higgins Art Gallery and Museum, Bedford, U.K. **BHN**, Musée d'Histoire Naturelle, Boulogne-sur-Mer, France; **CAMSM**, Sedgwick Museum of Earth Sciences, Cambridge, U.K.; **ComCom Thouarsais**, Community of Communes of Thouarsais, Thouars, France; **GPIT**, Paleontological Collection of the University of Tübingen, Tübingen, Germany; **LEICT**, Leicester Museum and Art Gallery, Leicester, U.K.; **NHMUK**, Natural History Museum, London, U.K.; **OUMNH**, Oxford University Museum of Natural History, Oxford, U.K.; **PETMG**, Peterborough Museum & Art Gallery, Peterborough, U.K.

Anatomical Abbreviations—**ap**, apex; **ar**, articular; **av**, alveolus; **aw**, apical wear; **c**, coronoid; **cr**, crown; **crj**, crown-root junction; **d**, dentary; **dac**, dentary alveolar channel; **er**, enamel ridge; **ms**, mandibular symphysis; **msa**, mandibular symphyseal angle; **na**, neural arch; **naf**, neural arch facet; **ncf**, neural canal floor; **np**, notochordal pit; **ns**, neural spine; **pmx**, premaxilla; **poz**, postzygapophysis; **prz**, prezygapophysis; **rap**, retroarticular process; **rf**, rib facet; **rl**, ridgelet; **ro**, root; **sa**, surangular; **scf**, subcentral foramen; **vs**, ventral sulcus.

SYSTEMATIC PALEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA De Blainville, 1835
Family PLIOSAURIDAE Seeley, 1874
Clade THALASSOPHONEA Benson and Druckenmiller, 2014

TABLE 2. *Liopleurodon* measurements based on reconstructed vertebral columns.

Specimen No.	Crown height (mm)	Average cervical vertebra length (mm)	Cervical vertebrae count	Average dorsal vertebra length (mm)	Dorsal vertebrae count	Average caudal vertebra length (mm)	Caudal vertebrae count
GPIT-PV-30093	73	37.4	22	60.4	23	36.8	25
NHMUK PV R 3536	88	46.6	22	78.5	23	51.6	25

Genus *LIOPLEURODON* Sauvage, 1873
LIOPLEURODON FEROX Sauvage, 1873

Below is a truncated synonymy list, highlighting the original description, changes in genus and/or specific designation, and major anatomical descriptions:

Liopleurodon ferox Sauvage, 1873:377, pl. VIII, fig. 1 (original description).

Polyptychodon ferox (Sauvage, 1873): Sauvage, 1880:544.

Pliosaurus ferox (Sauvage, 1873): Lydekker, 1888:353.

Liopleurodon ferox Sauvage, 1873: Blake, 1905:23, figs. 1–2.

Pliosaurus ferox (Sauvage, 1873): Sauvage, 1912:189.

Pliosaurus grandis (Sauvage, 1873): Linder, 1913:55, figs. 34–35, 38.

Pliosaurus ferox (Sauvage, 1873): Andrews, 1913:2, figs. 1–7, pls 1–2.

Pliosaurus ferox (Sauvage, 1873): von Huene, 1934:31, figs. 1–26.

Pliosaurus pachydeirus Seeley, 1869: Tarlo, 1959:440.

Pliosaurus ferox (Sauvage, 1873): Delair, 1959:72.

Liopleurodon ferox Sauvage, 1873: Tarlo, 1960:151, fig. 3e, pls. 24, 28, figs. 2–2b.

Liopleurodon pachydeirus (Seeley, 1869): Tarlo, 1960:151, fig. 3f, pls. 25, 28, figs. 1–1b.

Liopleurodon ferox Sauvage, 1873: Persson, 1963:25.

Liopleurodon ferox Sauvage, 1873: Noè, 2001:26, figs. 22–107.

Liopleurodon ferox Sauvage, 1873: Vincent et al., 2024:5, figs. 2–8.

Holotype—BHN 3R 197, a single tooth crown in the Musée d'Histoire naturelle de Lille, France.

Referred Specimens—See Table S1, Supplementary File 1.

Diagnosis—Modified from Vincent et al. (2024). Conical tooth crown with subcircular cross-section with coarse apicobasal ridges and less well-developed intercalated ridges; labial face smooth; crown-root base vermiculated by short reticulated ridgelets (Sauvage, 1873). Cervical vertebrae short (length half or less than height or width); double-headed anterior cervical rib articulations; ventral lip present on cervical centrum anteriorly but no ventral keel; long epipodials (Andrews, 1913; Tarlo, 1960). See Noè (2001) for cranial characters.

Locality, Horizon, and Age—The holotype tooth is from Le Wast near Boulogne-sur-Mer, northern France (Sauvage, 1873). Other material used to diagnose the taxon comes from the Jason to Coronatum zones of the Middle Jurassic (middle Callovian) Peterborough Member, Oxford Clay Formation (Andrews, 1913); Lamberti zone (upper Callovian) of the Stewartby Member, Oxford Clay Formation (Martill & Hudson, 1991).

RESULTS

Proportions of *Liopleurodon ferox*

The various proportions of the skeletons of GPIT-PV-30093 and NHMUK PV R 3536 (Fig. 4) do not differ significantly, with just 1% difference between body segments, despite over a meter difference in total body length (Table 1). This suggests a near isometric growth for *Liopleurodon* and that the new model for determining total length can be reliably applied for determining the overall size of individuals known only from fragmentary material. Skeletal length proportions were used for comparisons to eliminate uncertainty from reconstructing intervertebral spacing. The new model of *L. ferox* comprised of three specimens possesses the same skull-to-total length ratio of 1:4 as the composite reconstruction by Newman and Tarlo (1967). However, the new model presented here differs in that the postcranial skeleton has a proportionally longer neck and torso, and a shorter tail (Fig. 5). The postcranial proportions resemble those of the contemporaneous pliosaur *Peloneustes* (see Fig. 5), although the skull occupies a smaller proportion (18%) of the total length. Skull-to-total length ratios appear to be relatively conservative across the larger macropredatory pliosaur genera as the skull percentage in Cretaceous pliosaurs (*Sachicasaurus*, *Monquirasaurus*, and *Kronosaurus*) varies by only ~3% from that of *Liopleurodon* and is consistently around 1:4 (Fig. 5). Whether this is true for all macrophagous pliosaurs remains to be determined. *Liopleurodon* has a proportionally longer neck than the Cretaceous pliosaurs *Sachicasaurus vitae* and *Monquirasaurus boyacensis* (McHenry, 2009; Páramo-Fonseca et al., 2018), both having the shortest neck proportionally at 13% of the total body length.

Total Body Length Estimates

Representative specimens of *L. ferox* GPIT-PV-30093, NHMUK PV R 2680, and NHMUK PV R 3536 are estimated at 4.47 m, 5.04 m, and 5.82 m TBL, respectively, including a factor for intervertebral spacing. The total dataset of 37 *L. ferox* specimens documents a wide range of TBLs (Table S1, Supplementary File 1; Fig. 6), with the smallest estimated at

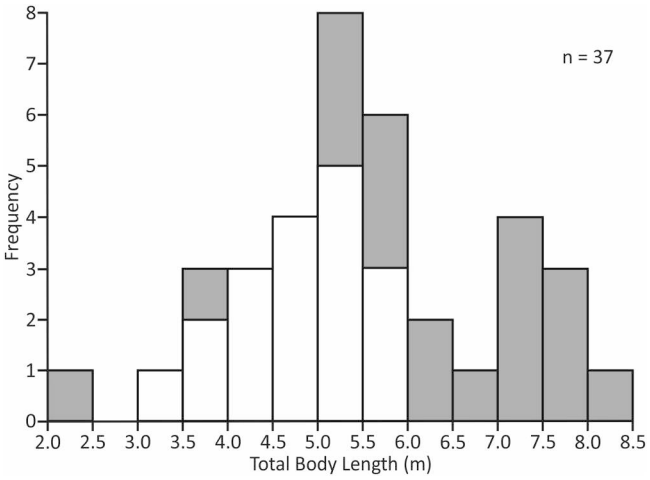

FIGURE 6. Histogram of total body length in *Liopleurodon ferox*. White bars represent the more complete sample, and gray bars represent isolated specimens.

FIGURE 7. Smallest and largest estimated *Liopleurodon ferox* tooth specimens. **A**, labial view of the largest estimated specimen (NHMUK PV R 4747); **B**, lingual view; **C**, labial view of the smallest estimated specimen (OUMNH J.3871); **D**, lingual view. Scale bar equals 50 mm.

2.46 m based on a crown height of 38 mm (Fig. 7A, B), while the largest is a 425 mm tooth, the crown height measures 125 mm and an estimated TBL of ~8.09 m (Fig. 7C, D). The average TBL of *L. ferox* is 5.6 m, where Fig. 7 shows the most frequent TBL was between 5.0–6.0 m across 14 specimens. Separating out the TBLs of the isolated elements from more complete specimens shows that the extremes of the estimates stem from the isolated specimens, while more complete material show a more constrained range of 3.2–5.96 m (Fig. 6). The average TBL of the more complete specimens is 4.8 m with the most frequent TBL between 5.0–5.5 m with five specimens, contrasting with the greater average TBL of 6.29 m for isolated elements and the most frequent TBLs between 5.5–6.0 m and 7.0–7.5 m. An unequal variances t-test indicates that there is a statistically

FIGURE 8. Indeterminate pliosaur dorsal vertebral centrum (GPIT-PV-42022) from the Peterborough Member (middle Callovian) of the Oxford Clay Formation of Peterborough. **A**, anterior view; **B**, posterior view; **C**, dorsal view; **D**, lateral view; **E**, ventral view. Scale bar equals 50 mm.

significant difference between the samples (t: 3.93, $p < 0.001$), demonstrating that the larger body size estimates within the total dataset are disproportionately represented by isolated elements. Therefore, the broader size distribution observed in the total dataset likely reflects increased uncertainty and potential over- and underestimation associated with scaling from isolated material. The total dataset supports the presence of large individuals of *Liopleurodon*, but more complete specimens indicate that TBLs exceeding 6 m may be less common than the total dataset suggests, where 22% of the sample is

TABLE 3. Indeterminate Oxford Clay Formation pliosaurid specimens and total body length estimates scaled up based on the proportions of *Liopleurodon*. Lower and upper limit size ranges are provided for specimens that could not be reliably calculated.

Specimen No.	Material	Total body length (m)
GPIT-PV-42022	Dorsal vertebra	8.91
PETMG:R274	3 pectoral vertebrae	7.02–12.01
NHMUK PV R 8322	Partial skeleton	7.52–12.20

estimated to be ≥ 7 m TBL (see Supplementary File 1). Higher TBLs may therefore represent rare instances of *Liopleurodon*, or a preservational bias against large individuals. The average TBL of *Liopleurodon* was likely ~5 m as seen in the more complete sample and the total dataset (Fig. 6). Compared to previously estimated TBLs, the average length found here is in the range of 5.7 m and 6.39 m, as reported by McHenry (2009) and Noè et al. (2003), but the larger dataset increases the potential upper size range of *L. ferox* by almost 2 m. However, our total dataset does not include any examples approaching the size estimated for *Liopleurodon* of 10.97 m by Newman and Tarlo (1967), based on indeterminate pliosaurid specimens NHMUK PV R 8322 and CAMSM J.35990. The 25 m provided in Walking with Dinosaurs (Martill & Naish, 2000) far exceeds the average and maximum TBL estimates in this dataset (see Martill et al., 2023).

Large Pliosaurids in the Oxford Clay Formation

The results clearly show that *L. ferox* was a large pliosaur, possibly reaching lengths of up to 8.09 m, and considerably greater than coeval taxa such as *Eardasaurus* and *Peloneustes* (Andrews, 1913; Ketchum & Benson, 2022) and comparable to other large pliosaurs (Benson et al., 2013; Knutsen et al., 2012; McHenry, 2009; Noè & Gómez-Pérez, 2022; Páramo-Fonseca et al., 2018). However, three specimens (GPIT-PV-42022, PETMG:R274, and NHMUK PV R 8322) from the Oxford Clay Formation were identified as belonging to much larger pliosaur individuals than those in the dataset but could not be identified beyond indeterminate Pliosauridae.

GPIT-PV-42022—Specimen consists of an isolated dorsal vertebral centrum and partial neural arch with a height of 168.11 mm, width of 169.3 mm, and length of 122.03 mm. The specimen museum label records it was discovered in Peterborough and is of Callovian age, which strongly indicates the Oxford Clay Formation as its source. The vertebra was identified as a pliosaurid dorsal centrum due to its platycoelous articular surfaces with near circular outline, presence of a notochordal pit, concave lateral surfaces, lack of rib facets on the centrum margins, neural arch facets and neural arch occupying almost the entirety of dorsal surface, neural canal narrow, and large nutritive foramina present ventrally (as seen in Fig. 8; Andrews, 1913; Tarlo, 1960). The size of the vertebra also suggests it belongs to Pliosauridae rather than Plesiosauroidea, but there are no diagnostic characters that permit a genus-level identification (Tarlo, 1959). The ventral length of the vertebra is 122.03 mm, ~2 times larger than the average dorsal length in Table 2, resulting in a TBL of 8.91 m (Table 3). This far exceeds the upper limit of *L. ferox* and suggests that larger pliosaurs existed during the Callovian.

PETMG:R274—Three large vertebrae were found in association in Beeby's pit, Yaxley in Cambridgeshire. The strata formerly exposed at Beeby's pit are the Kellaways Sand Formation and the overlying Peterborough Member of the Oxford Clay Formation (Hudson & Martill, 1994). The centra are heavily damaged from pyrite decay (Fig. 9), although the label attached states that efforts to consolidate and conserve the vertebrae have been attempted. The vertebrae (Fig. 9) can be identified as pliosaurian on account of their centra being platycoelous with circular articular surfaces, a subcentral ventral foramina and distinctive aspect ratios (height/width > length; Brown, 1981). The vertebrae are likely pectorals as the single-headed rib facets are situated high on the lateral margins of the centrum (Fig. 9), merging with the neural arch facets (Tarlo, 1959). To estimate the TBL of PETMG:R274, a range of 7.02–12.01 m (Table 3) was calculated based on scaling the average length of the vertebrae (96 mm) as either part of the neck or the body. The lower estimate is within the upper range of *Liopleurodon* (based on the total dataset) while the upper estimate indicates a pliosaur approaching the maximum TBL of the clade (14.4 m; Martill et al., 2023). Realistically, the TBL of PETMG:R274 likely lies between the two estimates and, despite its precise value, the specimen shows further evidence of gigantic pliosaurs in Callovian seas.

NHMUK PV R 8322—This specimen is a pliosaurid mandibular symphysis (Fig. 10), with partial vertebral column, ribs, pelvic girdle, and hind limb from the Coronatum ammonite biozone of the Peterborough Member, Oxford Clay Formation at Coronation pit, Stewartby, Bedfordshire, U.K. With no dentition preserved and only 5 alveolar pairs in the symphysis (Fig. 10) compared to the 6.5 alveolar pairs in *L. ferox* (Fig. 4B), the Stewartby pliosaur cannot be confidently assigned to *Liopleurodon*. The sympatric pliosaur *Simolestes vorax* has a symphysis with 5 alveolar pairs, however, the symphysis of NHMUK PV R 8322 has an oval outline (Fig. 10), as in *Liopleurodon* and unlike the diamond shape seen in *Simolestes*. Furthermore, the width: length ratio of the symphysis of 0.83 is significantly different from both *L. ferox* and *S. vorax* at 0.5–0.6 and 1.02 respectively, while the symphyseal angle in lateral view is 138° compared to 145–155° in *Simolestes* and the gently curved ventral surface in *Liopleurodon* (McHenry, 2009; Noè, 2001). The dorsal surface is obscured by a medial fragment of the premaxilla preserved dorsally; the alveolar septa are partially preserved, based on this we cautiously estimate a premaxillary tooth count of 5, as seen in both *L. ferox* and *S. vorax*. Damage on the ventral surface makes it difficult to determine the presence of a ventral keel and the extent of the dentary-splenial contact. NHMUK PV R 8322 was likely assigned to *L. ferox* as Tarlo's (1960) diagnosis of the genus includes a range of 5–7 symphyseal alveolar pairs. As stated above, *L. ferox* possesses 6.5 alveolar pairs and based on the description here, the Stewartby pliosaur cannot be confidently assigned to either *Simolestes* or *Liopleurodon* and it is currently regarded as Pliosauridae indet. This result further weakens the use of Newman and Tarlo's (1967) reconstruction as *Liopleurodon* and highlights the need for an updated skeletal model for *Liopleurodon*. Due to a difference in symphyseal length:width ratio to *Liopleurodon*, a range of TBLs was calculated based on scaling the symphysis using a length of 400 mm or width of 330 mm compared to *L. ferox*, resulting in a wide TBL range of 7.52–12.2 m (Table 3). Newman and Tarlo (1967) reconstructed the Stewartby pliosaur at 10.97 m, while McHenry (2009) provided a range of 9.1–15.12 m based on similar methodology. Both previous estimates for NHMUK PV R 8322 are within the range presented here, and the median is similar to the lower estimate of McHenry (2009). The estimate calculated here (7.52 m) based on symphyseal length indicates a sizeable pliosaur rivaling the largest specimens of *Liopleurodon* (Fig. 7C, D; Table S1, Supplementary File 1). Similarly, the length (12.2 m) determined from symphyseal width represents another extremely gigantic Callovian pliosaur, whose true length was likely somewhere within the range 7.5–12.2 m.

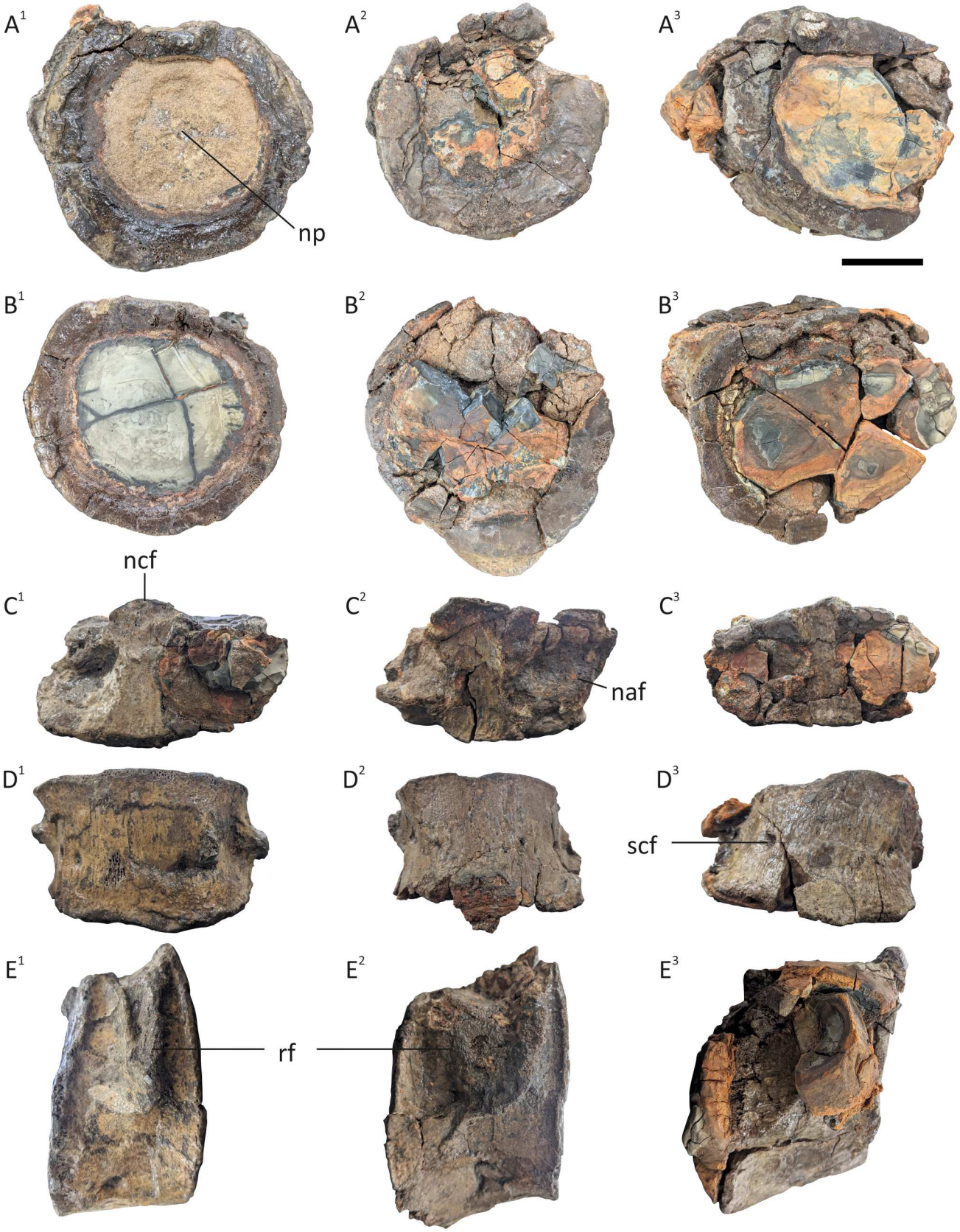

FIGURE 9. Three associated indeterminate pliosaur pectoral vertebral centra (PETMG:R274) from the Oxford Clay Formation of Peterborough, U.K. **A**, anterior view; **B**, posterior view; **C**, dorsal view; **D**, ventral view; **E**, lateral view. Scale bar equals 50 mm.

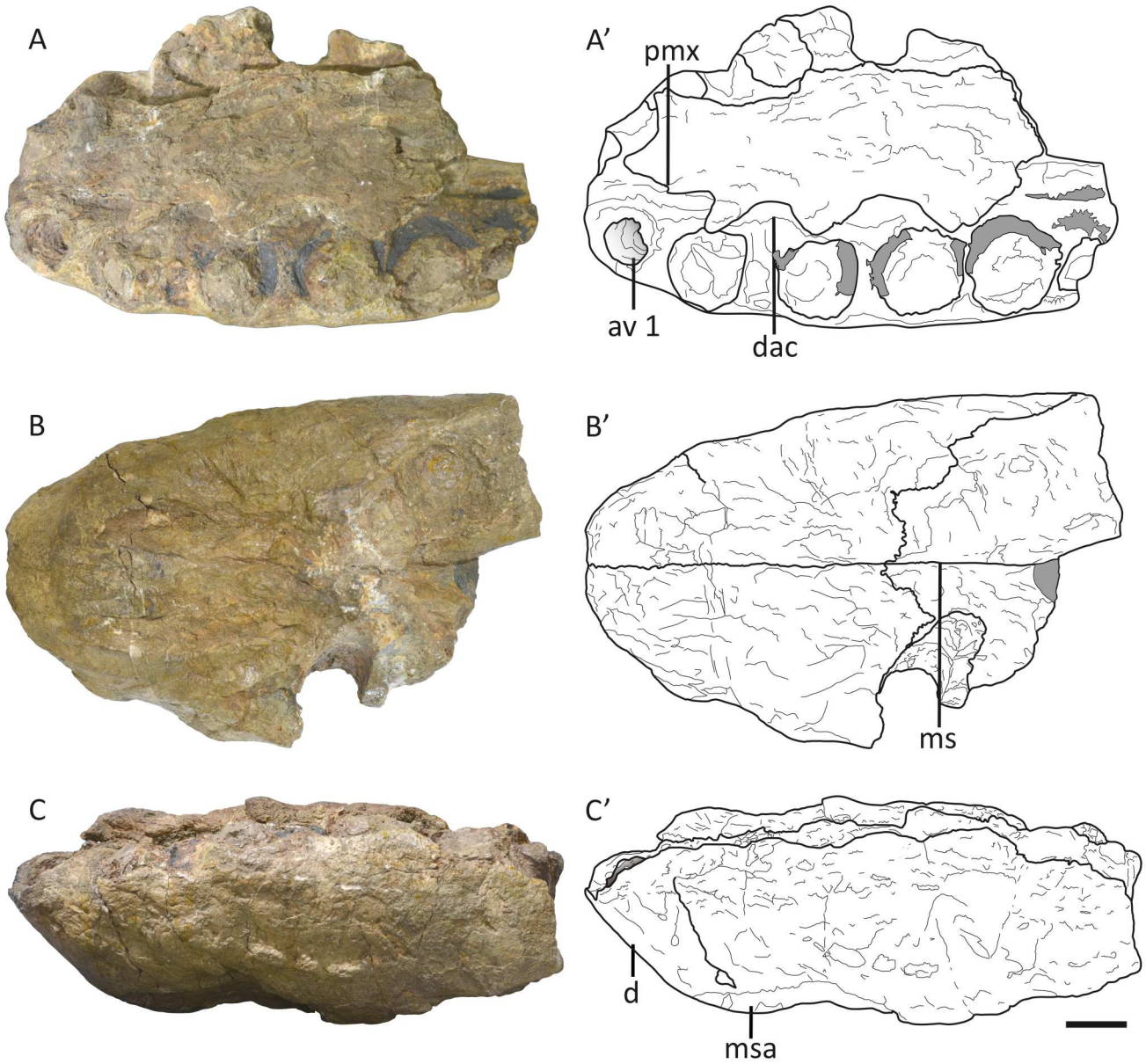

FIGURE 10. Anterior mandible fragment from an indeterminate pliosaur (NHMUK PV R 8322) from the Oxford Clay Formation of Stewartby, Bedfordshire, UK. **A**, dorsal view; **B**, ventral view; **C**, lateral view. Scale bar equals 50 mm.

DISCUSSION

Paleoecology of Gigantic Pliosaurs of the Oxford Clay Formation

The oldest record of *L. ferox* originates from the Koenigi ammonite biozone (lower Callovian) while the youngest *L. ferox* specimen is from the Lamberti zone, upper Callovian (Fig. 2). The Callovian spans 3.76 my (165.29–161.53 Ma; Gradstein et al., 2020) over seven ammonite biozones (Page, 1989; Fig. 2). Specimens attributed to *Liopleurodon* extend over six of these zones, therefore *Liopleurodon* is estimated to have existed for 3.24 my based on an average ammnonite zone duration of 0.54 my. *Liopleurodon* shared the Callovian seas throughout its 3.24 my existence with a diverse assemblage in the Oxford Clay Sea (Martill & Hudson, 1991), that included at least an additional five pliosaur genera, as well as the ichthyosaur *Ophthalmosaurus*, several long-necked plesiosaurs and at least two genera of marine Thalattosuchians (*Metriorhynchus*, *Neosteneosaurus*; Andrews, 1913; Brown, 1981; Cruickshank et al., 1996; Johnson et al., 2020; Ketchum & Benson, 2011, 2022; Martill & Hudson, 1991). The mean TBL of 4.8 m for more complete *L. ferox* specimens is comparable to maximum TBL estimates calculated for *Peloneustes*, *Eardasaurus*, *Simolestes*, and *Pachycostasaurus* (Table 4), while a maximum TBL of 5.96 m for *Liopleurodon* exceeds the total body length of its coeval pliosaurs by more than 1 m (Table 4). Based on the total dataset, the average *Liopleurodon* was almost 1 m longer than other Oxford Clay pliosaur taxa and could possibly attain even greater lengths of up to 8.09 m (Table 4), scaled from NHMUK PV R 4747 (Fig. 7C, D). Using interquadrate/glenoid distance as a proxy for gullet diameter (Fischer et al., 2022; Foffa et al., 2024) and scaling the Oxford Clay pliosaurs to an equivalent TBL (4 m), *L. ferox* has the second largest gullet (240 mm) after *S. vorax* (340 mm). Both taxa have significantly larger gullets than the more longirostrine pliosaurs *Eardasaurus* (151 mm), *Peloneustes* (181 mm), and *Marmornectes* (140 mm),

TABLE 4. Estimated maximum total lengths of some of the marine paleofauna of the Oxford Clay Formation.

Taxon	Total body length (m)	Reference
Leedsichthys problematicus	16.5	Liston et al. (2013)
'Stewartby pliosaur'	7.52–12.2	This study
Liopleurodon ferox (isolated)	8.09	This study
Neosteneosaurus edwardsi	6.6	Young et al. (2016)
Liopleurodon ferox (more complete)	5.96	This study
Muraenosaurus leedsi	5.2	Brown (1981)
Eardasaurus powelli	4.77	Ketchum and Benson (2022)
Ophthalmosaurus icenicus	4.5	Motani et al. (1999)
Marmornectes candrewi	4.27	This study
Peloneustes philarchus	4.21	This study
Cryptoclidus eurymerus	4	Brown (1981)
Simolestes vorax	3–4	Noè (2001)
Pachycostasaurus dawni	3.1	Cruickshank et al. (1996)

suggesting that *L. ferox* and *S. vorax* could capture and ingest relatively larger prey items than other sympatric pliosaurs. It is estimated that an 8.09 m *Liopleurodon* would have a gullet diameter of 487 mm, giving it an extremely broad prey range. This suggests a degree of niche partitioning between pliosaur taxa based on skull dimensions and absolute TBL. This corresponds with previous interpretations on the ecology of *L. ferox* and *S. vorax* as macrophagous generalists, while the longirostrine pliosaurs (*Peloneustes*, *Marmornectes*, and *Eardasaurus*) likely fed on small, agile prey (Fischer et al., 2022; Foffa et al., 2024; Martill, 1992; Massare, 1987; Noè, 2001). The skull of *Pachycostasaurus* is too poorly preserved to make any paleoecological inferences; however, the pachyostotic postcrania clearly indicates a unique paleoecology compared with the other Oxford Clay pliosaurs (Cruickshank et al., 1996; Noè, 2001). The upper size range of more complete *Liopleurodon* specimens is larger than most other marine reptiles from the Oxford Clay Formation (Table 4), such as *Cryptoclidus* and *Ophthalmosaurus*, estimated at 4 m and 4.5 m, respectively (Brown, 1981; Motani et al., 1999). *Neosteneosaurus*, a machimosaurid thalattosuchian, is estimated at 6.6 m TBL (Young et al., 2016), exceeding the largest *Liopleurodon* from the more complete sample (Fig. 6; Table 4). The dentition of *Neosteneosaurus* has been interpreted as placing within the pierce 1 guild, while the mandible is morphologically similar to durophagous machimosaurins (Foffa et al., 2024). *Neosteneosaurus* likely occupied a different ecological niche than *Liopleurodon*, which has been interpreted as a macrophagous generalist, despite attaining similar body sizes (Fischer et al., 2022; Foffa et al., 2024).

Due to its large body size, and robustness and gigantic size of its dentition, *Liopleurodon* was most likely the apex predator of the Oxford Clay Sea, a high trophic-level generalist carnivore preying on some of the above-mentioned taxa, in agreement with previous interpretations of *L. ferox* (Massare, 1987; Martill & Hudson, 1991; Martill et al., 1994; McHenry, 2009; Noè, 2001). Even the largest vertebrate of the Oxford Clay Formation, the 16.5 m planktivorous *Leedsichthys* (Liston et al., 2013), cannot be excluded as a potential prey source of an 8 m *Liopleurodon* (Table 4), with evidence of active predation by a crocodyliform on the frontal bone of the gigantic fish (Martill, 1986). While *Liopleurodon* was certainly a large macrophagous predator, the results presented here show that gigantic (up to 12.2 m), but indeterminate pliosaurids were also present in the Oxford Clay Formation (Tables 3 and 4). The lower size estimates for the indeterminate specimens rival the largest examples of *L. ferox* while the upper size limit exceeds that of *L. ferox* (Fig. 6). Precisely how these giant pliosaurs fit into the Oxford Clay paleoecosystem is currently unknown, especially as no dentition was preserved with the indeterminate specimens that may aid in inferring their diet.

Gigantism in Pliosaurs

Reevaluating the proportions and TBLs of *Liopleurodon* has ramifications for body size interpretations for all derived pliosaurs as *L. ferox* has frequently been used for scaling in other pliosaur genera (e.g., Buchy et al., 2003; Martill et al., 2023; Massare et al., 2014; McHenry, 2009). We consider the new *Liopleurodon* model more appropriate than previous methods of estimating TBL of Late Jurassic pliosaurs (Knutsen et al., 2012; Martill et al., 2023; McHenry, 2009), which are derivative of Newman and Tarlo's (1967) reconstruction, in lieu of specimens preserving most of the elements from all body segments. Our model is comprised of specimens currently referred to *L. ferox*, unlike Newman and Tarlo's (1967) reconstruction (see Introduction and description of NHMUK PV R 8322), and the updated proportions reflect this in their differences (Fig. 5). As demonstrated in the results, there is a level of conservatism between the skull-to-total length ratio of pliosaurs (Fig. 5) with a similarly proposed ecology (Fischer et al., 2022; Massare, 1987). Additionally, the postcranial proportions of non-brachaucheniine thalassophonean pliosaurids *Liopleurodon* and *Peloneustes* are remarkably

TABLE 5. Estimated total body lengths (TBL) of Late Jurassic pliosaurs scaled from *Liopleurodon ferox*.

Taxon	Specimen No.	Age	Element	Previous TBL (m)	Revised TBL (m)	Source
Megalneusaurus rex	UW 4602	Oxfordian	Femur	9.2	8.25	Massare et al. (2014); Knight (1898)
Pliosaurus kevani	DORCM g.13,675	Kimmeridgian	Skull	10	9.17	Benson et al. (2013)
Pliosaurus brachydeirus	OUMNH J.9245	Kimmeridgian	Partial skeleton	-	4.88	Benson et al. (2013); Tarlo (1960)
Pliosaurus westburyensis	BRSMG Cc332	Kimmeridgian	Partial skeleton	-	5.92	Benson et al. (2013)
Pliosaurus carpenteri	BRSMG Cd6172	Kimmeridgian	Partial skeleton	8	8.27	Benson et al. (2013)
Abingdon pliosaur	ABBCH 1980.191.1038–1041	Kimmeridgian	4 cervical vertebrae	14.4	11.71	Martill et al. (2023)
Pliosaurus ?rossicus	OUMNH J.10454	Kimmeridgian	Mandible	11.74	9.01	Martill et al. (2023)
Monster of Aramberri	UANL-FCT-R2	Kimmeridgian	Vertebral column	11	7.6	Buchy et al. (2003)
Pliosaurus rossicus	PIN 2440/1	Tithonian	Anterior of rostrum, hind limb	10	9.59	Halstead (1971)
Pliosaurus funkei	PMO 214. 136	Tithonian	Partial skeleton	10	8.73	Knutsen et al. (2012)

similar, which is not shared with Newman and Tarlo's (1967) reconstruction (Fig. 5). Therefore, the new model is applied here to a range of Late Jurassic non-brachaucheniine thalassophonean pliosaurids, predominantly those from the Kimmeridge Clay Formation, U.K. (Table 5).

Late Jurassic pliosaurs were frequently calculated to measure 10 m TBL, reaching a maximum of 14.4 m (Table 5; Martill et al., 2023). This is substantially larger than previous *L. ferox* TBL estimates at 5.7 and 6.39 m (McHenry, 2009; Noè et al., 2003). Table 5 shows that Late Jurassic pliosaurs scaled using *L. ferox* frequently obtained total body lengths greater than the maximum TBL of *Liopleurodon* and other Oxford Clay pliosaurid taxa (Table 4). The upper range seen in Table 5 is similar to that of the indeterminate Oxford Clay pliosaurids described above (Table 3). *Megalneusaurus* is a large Oxfordian pliosaurid estimated at 8.25 m (Table 5), comparable in size to some of the largest *Pliosaurus* species. However, it must be cautioned that the taxon, represented primarily by appendicular remains from the Sundance Formation, U.S.A., is not the most reliable for TBL calculations (Knight, 1898; Knutsen et al., 2012; Massare et al., 2014; McHenry, 2009). The largest pliosaur specimen described appears to be an indeterminate Kimmeridgian pliosaur, represented by several vertebrae (ABBCH 1980.191.1038–1041) from Abingdon, Oxfordshire, U.K. (Martill et al., 2023). The estimated size of this animal is 11.71 m, reducing the previous estimate of 14.4 m (Martill et al., 2023). Despite this down-sizing, this specimen still indicates that pliosaurs attained massive body sizes in excess of 11.5 m. At the other end of the scale, the smallest species of *Pliosaurus*, *Pliosaurus brachydeirus* (OUMNH J.9245) is closer in TBL to the lower estimates of *L. ferox* and other Oxford Clay pliosaurs at 4.88 m (Fig. 6). The dramatic size difference between *P. brachydeirus* and other *Pliosaurus* species is possibly due to OUMNH J.9245 representing a juvenile (Benson et al., 2013; Knutsen, 2012; Tarlo, 1960). The Cumnor, Oxfordshire mandible (OUMNH J.10454) from the Kimmeridge Clay Formation is a gigantic specimen that measures 2.88 m along the mandible (Noè et al., 2004). A considerable portion of the length has been elongated using plaster; the TBL estimate provided here (9.01 m TBL) is calculated using symphyseal length, pending a full assessment of the preserved material (Bartlett et al., in prep). The TBL estimates presented here (Table 5) reinforce interpretations of pliosaurs as macrophagous apex predators, attaining gigantic TBLs of up to 11.71 m. These Late Jurassic forms were considerably larger than most Middle Jurassic pliosaurs, indicating an upwards trend of body size across the clade, in agreement with Benson et al. (2013). However, the potential upper TBL range of *Liopleurodon* and some indeterminate Oxford Clay Formation pliosaurids reduce the body size disparity between the Middle Jurassic and Late Jurassic pliosaurs (Fig. 6; Table 3). This suggests large body size in pliosaurs first appeared during the Middle Jurassic, with the advent of thalassophoneans beginning to occupy the macropredator niche (Sachs et al., 2023).

A sharp decrease in the maximum body length of pliosaur taxa during the earliest stages of the Cretaceous is observed, the Hauterivian pliosaurs *Makhaira* and *Luskhan* are 5–6.5 m TBL (Fischer et al., 2015; Fischer et al., 2017; Zverkov et al., 2018). This is attributed to a lack of diagnostic material as isolated elements from the Early Cretaceous of Russia and Germany indicate a higher diversity of pliosaurids than previously assumed, including the possible persistence of *Pliosaurus* into the Cretaceous (Sachs et al., 2018; Zverkov, 2015; Zverkov et al., 2018). Isolated crowns described by Zverkov et al. (2018) from the Berriasian and Valanginian are comparable in size to large crowns of *Liopleurodon* (Supplementary File 2). Therefore, it is likely gigantic TBLs persisted past the J-K boundary as later Early Cretaceous pliosaurs *Sachicasaurus*, *Monquirasaurus*, and *Kronosaurus* all have estimated TBLs of ~10 m (McHenry, 2009; Noè & Gómez-Pérez, 2022; Páramo-Fonseca et al., 2018), rivaling that of the largest Jurassic pliosaurs (Table 5). A large cervical centrum from the Cenomanian of Russia may represent a pliosaur with a 10 m TBL (Zverkov & Pervushov, 2020), suggesting the presence of gigantic pliosaurs in Early Cretaceous ecosystems right up until Oceanic Anoxic Event 2 (OAE2) at the Cenomanian–Turonian boundary. Subsequent to OAE2, one of the last representatives of Pliosauridae is the early Late Cretaceous pliosaur *Megacephalosaurus* (Schumacher et al., 2013). Estimated to have a TBL of 7.86 m, it is close in length to the potential upper size range of *L. ferox* (McHenry, 2009; Schumacher et al., 2013). Despite a smaller TBL than some of the Early Cretaceous pliosaurs, *M. eulerti* was still a large marine apex predator and dwarfed sympatric mosasaurs from the Western Interior Seaway (Schumacher, 2011). The results presented here (combined with Tables 4 and 5) show large-bodied pliosaurs (≥ 7 m) dominated Mesozoic marine ecosystems for ~80 my, in agreement with Sachs et al. (2023) and Sato et al. (2023). The extinction of gigantic pliosaurs is likely due to environmental shifts following Oceanic Anoxic Event 2 at the Cenomanian–Turonian boundary; it is unclear whether competition from polycotylids and large mosasauroids may have played a role in their extinction (Madzia & Cau, 2020; Schumacher, 2011; Takashima et al., 2024).

Comparison with other Gigantic Mesozoic Marine Reptiles

Pliosaurs were the largest sauropterygians, the potential upper size range of *L. ferox* (Fig. 6) surpassing the late Early Jurassic *Rhomaleosaurus*, estimated at 7 m TBL (Smith, 2007). The elasmosaurid plesiosaur *Albertonectes* from Alberta, Canada, was estimated to reach a remarkable 11.6 m TBL (Kubo et al., 2012), almost as long as the largest pliosaurs *Megalneusaurus* and the Abingdon cervical vertebrae (ABGCH 1980.191.1038–1041) at 11.64 and 11.71 m respectively (Table 5). It is postulated that similar gigantic lengths were obtained independently by Elasmosauridae and Pliosauridae as a method of reducing drag and increasing swimming efficiency (Gutarra et al., 2022). Ichthyosaurs and mosasaurs achieved total body lengths ≥ 10 m relatively early into their evolutionary history, less than 20 my after their first appearance (Lindgren et al., 2010; Polcyn et al., 2014; Sander et al., 2024). Both clades include taxa that exceed the maximum length of pliosaurs (Everhart, 2017; Lomax et al., 2024). The difference in maximum TBL may be related to the increased drag costs of up to 30% in appendicular locomotors such as plesiosaurs compared to axial locomotion; ichthyosaurs and mosasaurs could achieve the same swimming efficiency at larger body sizes due to their elongate shape (Gutarra et al., 2022). The axial locomotion of ichthyosaurs is highly advantageous for large TBLs as this style is beneficial for low-energy cruising, benefitting large animals with a wide foraging range (Gutarra & Rahman, 2021). A longer tail (hence a longer TBL) increases thrust generation (Gutarra & Rahman, 2021; Lindgren et al., 2010), suggesting that pliosaurs were mechanically limited to smaller TBLs than ichthyosaurs and mosasaurs due to higher drag and therefore energy costs involved with appendicular locomotion (Gutarra et al., 2022). The extent to which this limited maximum TBL in Mesozoic marine reptiles compared to environmental factors such as primary productivity, sea surface temperature, and sea level changes remains to be explored.

Limitations of the New *Liopleurodon ferox* Scaling Model

We consider the updated proportions and methods presented here improve upon previous methods of estimating total body length in *Liopleurodon* (McHenry, 2009; Newman & Tarlo,

1967; Noè et al., 2003), however, we recognize there are limitations with the model. *Liopleurodon*, as is the case for most pliosaur genera, suffers from a lack of sufficient material to fully determine the proportions of the animal. Near isometric growth is observed between GPIT-PV-30093 and NHMUK PV R 3536 (Fig. 4) but without well-preserved juvenile specimens, the growth allometry through ontogeny cannot be realistically determined in *Liopleurodon*, as can be seen in the skulls of *Stenorhynchosaurus* (Páramo-Fonseca et al., 2019). The specimens that formed the basis of the calculations to determine the proportions of *Liopleurodon* are nearly complete, although the length of the skulls of GPIT-PV-30093 and NHMUK PV R 3536 needed to be calculated using a third specimen, NHMUK PV R 2680, introducing another level of uncertainty. Some elements have been slightly deformed by taphonomic compaction, possibly altering the measurements and skewing the results very slightly. The composite status of GPIT-PV-30093 (Fig. 4A) is still under review and while this study considers the mounted skeleton to be a reliable source of *Liopleurodon* proportions based on personal observations, further research may dispute this. The complete caudal vertebral count and tail length are unknown in *Liopleurodon*. These had to be estimated from the number of caudal vertebrae in *Peloneustes* and Rhomaleosaurus, possessing 28 and 30 vertebrae each respectively (Andrews, 1913; Smith, 2007). A major issue with scaling dentition (which comprises the majority of the dataset) is that it is highly anisodont in *Liopleurodon* (Noè, 2001). The size and shape of the crowns are variable along the tooth row in both sets of jaws (Noè, 2001; Sassoon et al., 2015), with no method at present enabling the identification of the exact position of an isolated tooth within the jaw. A considerable margin of error is inevitable when isolated teeth are assumed to be the largest in the tooth row. Currently, a *L. ferox* specimen preserving a full dentition *in situ* is unknown, but further studies on the dental variability within and between specimens (e.g., Madzia et al., 2022) could elucidate the identity of crowns included in this dataset and enable refinement of the TBLs presented here. Isolated vertebrae also present a problem for TBL determination as this method employs the average centra length for each section and assumes isolated centra represents the average length of that section, leading to margins of error as seen in PETMG:R274 (Table 3). The TBL estimates provided here include a factor of 10% intervertebral spacing (8% overall when taking the skull into account) calculated from Table S2, Supplementary File 1. This factor is also subject to change based on the specimens included in the dataset and the discovery of well-preserved *Liopleurodon* specimens with the original intervertebral spacing. The new model can be used to estimate the TBL of different pliosaur genera as the proportions of *L. ferox* have been employed previously (Buchy et al., 2003; Martill et al., 2023; Massare et al., 2014; McHenry, 2009), although it should be noted that not all pliosaurs possess the same body proportions (Fig. 5), and scaling appendicular elements (Fig. S1, Supplementary File 1) is not necessarily reliable across separate species (Knutsen et al., 2012; McHenry, 2009). Despite all these factors, the new method employed here builds upon and refines previous efforts (Martill et al., 2023; McHenry, 2009; Noè et al., 2003), resulting in (hopefully) more reliable TBL estimates of *Liopleurodon* based on multiple well-preserved, near-complete skeletons and a large dataset.

CONCLUSION

Based on two well-preserved specimens and a complete skull (Fig. 4), an updated model of *Liopleurodon* proportions is presented (Fig. 5). Scaling a dataset of 37 specimens (Table S1, Supplementary File 1), a range of 2.46–8.09 m TBL is calculated (Fig. 7). *Liopleurodon ferox* was the largest described pliosaur from the Oxford Clay Formation, and likely occupied the apex predator niche in the Callovian marine paleoecosystems for ~3.24 my. Indeterminate Oxford Clay Formation pliosaurid specimens estimated at 7.02–12.2 m TBL (Table 3) demonstrates that gigantism in pliosaurs (≥ 10 m) evolved during the late Middle Jurassic. When *Liopleurodon* proportions are applied to Late Jurassic specimens, pliosaurs of the Kimmeridgian and Tithonian attained lengths up to 11.71 m, and represent the largest sauropterygian clade to have existed. Despite not reaching the maximum reported lengths of some other Mesozoic marine reptiles (Triassic to Early Jurassic ichythosaurs and Late Cretaceous mosasaurs), gigantic pliosaurs dominated marine paleoecosystems from *L. ferox* in the Middle Jurassic (Callovian) until their extinction by the late Turonian, in the Late Cretaceous.

ACKNOWLEDGMENTS

We thank all the museum curators responsible for the numerous collections visited by EB during this study for their help locating and lifting difficult specimens. We thank I. Werneburg of GPIT, H. Southorn of LEICT, G. Wass of PETMG, L. Saul of BEDFM, M. Jones and M. Day of NHMUK, E. Nicholls of OUMNH, and M. Riley of CAMSM. We also thank D. Madzia for his advice, comments, and cooperation during this project. Thanks to H. Imran for producing an updated reconstruction of *L. ferox* used in this project. We thank reviewer V. Fischer and an anonymous referee, and editor E. Maxwell for their comments that improved the manuscript.

AUTHOR CONTRIBUTIONS

EOB: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing; DMM: Conceptualization, Methodology, Supervision, Writing – original draft, Writing – review & editing; RES: Investigation, Methodology, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing.

DATA AVAILABILITY STATEMENT

All data required to reproduce the results of this study are included in the main text or within the supplementary files.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

ORCID

Edward O. Bartlett http://orcid.org/0009-0009-9721-506X
David M. Martill http://orcid.org/0000-0002-3208-5702
Roy E. Smith http://orcid.org/0000-0001-9119-8865

SUPPLEMENTARY FILES

Supplementary File 1.docx: additional figures and tables of *Liopleurodon ferox* specimens and data of intervertebral spacing.

Supplementary File 2.xlsx: data set of raw measurements.

LITERATURE CITED

Andrews, C. W. (1910). IV.—Note on a mounted skeleton of a small pliosaur, *Peloneustes philarchus*, Seeley, sp. *Geological Magazine*, *7*(3), 110–112. https://doi.org/10.1017/s0016756800132960

Andrews, C. W. (1913). *A descriptive catalogue of the marine reptiles of the Oxford Clay: Based on the Leeds collection in the British Museum (Natural History), London (Part 2)*. British Museum.

Angst, D., & Bardet, N. (2016). A new record of the pliosaur *Brachauchenius lucasi* Williston, 1903 (Reptilia: Sauropterygia) of Turonian (Late Cretaceous) age, Morocco. *Geological Magazine*, *153*(3), 449–459. https://doi.org/10.1017/s0016756815000321

Barron, A. J. M., Lott, G. K., & Riding, J. B. (2012). *Stratigraphical framework for the Middle Jurassic strata of Great Britain and the adjoining Continental Shelf (Research report No. RR/11/06, v-156)*. British Geological Survey.

Benson, R. B. J., & Druckenmiller, P. S. (2014). Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. *Biological Reviews*, *89*(1), 1–23. https://doi.org/10.1111/brv.12038

Benson, R. B. J., Evans, M., & Druckenmiller, P. S. (2012). High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic Boundary. *PLoS ONE*, *7*(3), e31838. https://doi.org/10.1371/journal.pone.0031838

Benson, R. B. J., Evans, M., Smith, A. S., Sassoon, J., Moore-Faye, S., Ketchum, H. F., & Forrest, R. (2013). A giant pliosaurid skull from the Late Jurassic of England. *PLoS ONE*, *8*(5), e65989. https://doi.org/10.1371/journal.pone.0065989

Blainville de, H. D. (1835). Description de quelques espèces de reptiles de la Californie : précédée de l'analyse d'un système général d'erpétologie et d'amphibiologie. *Nouvelles Annales du Muséum (National) d'Histoire Naturelle, Paris*, *3*(4), 233–296.

Blake, J. F. (1905). A Monograph of the Fauna of the Cornbrash. Part I. Pages 1–100; Plates I–IX. *Monographs of the Palaeontographical Society*, *59*(282), 1–100. https://doi.org/10.1080/02693445.1905.12035520

Brown, D. S. (1981). The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the. Plesiosauria *Bulletin of the British Museum of Natural History*, *35*(4), 253–347.

Buchy, M., Frey, E., Stinnesbeck, W., & López-Oliva, J. G. (2003). First occurrence of a gigantic pliosaurid plesiosaur in the Late Jurassic (Kimmeridgian) of Mexico. *Bulletin de la Société Géologique de France*, *174*(3), 271–278. https://doi.org/10.2113/174.3.271

Callomon, J. H. (2020). The Middle Jurassic of western and northern Europe: its subdivisions, geochronology and correlations. *Geological Survey of Denmark and Greenland Bulletin*, *1*, 61–73. https://doi.org/10.34194/geusb.v1.4648

Corel Corporation. (2016). CorelDRAW (X8) [Computer Software].

Cox, B. M., & Sumbler, M. G. (2002). *Geological conservation review series: Ser. 26. British Middle Jurassic stratigraphy* (1st ed.). Joint Nature Conservation Committee.

Cruickshank, A. R. I., Martill, D. M., & Noè, L. F. (1996). A pliosaur (Reptilia, Sauropterygia) exhibiting pachyostosis from the Middle Jurassic of England. *Journal of the Geological Society*, *153*(6), 873–879. doi:10.1144/gsjgs.153.6.0873

Delair, J. B. (1959). The Mesozoic reptiles of Dorset: Part 2. *Proceedings of the Dorset Natural History and Archaeological Society*, *80*, 52–90.

Evans, M. (1993). *An investigation into the neck flexibility of two plesiosauroid plesiosaurs:* Cryptoclidus eurymerus *and* Muraenosaurus leedsii [Unpublished master's thesis]. University College London.

Everhart, M. J. (2017). *Oceans of Kansas: A Natural History of the Western Interior Sea (2nd ed.)*. Indiana University Press.

Fischer, V., Arkhangelsky, M. S., Stenshin, I. M., Uspensky, G. N., Zverkov, N. G., & Benson, R. B. J. (2015). Peculiar macrophagous adaptations in a new Cretaceous pliosaurid. *Royal Society Open Science*, *2*(12), 150552. doi:10.1098/rsos.150552

Fischer, V., Bennion, R. F., Foffa, D., MacLaren, J. A., McCurry, M. R., Melstrom, K. M., & Bardet, N. (2022). Ecological signal in the size and shape of marine amniote teeth. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1982), 1–9. https://doi.org/10.1098/rspb.2022.1214

Fischer, V., Benson, R. B. J., Zverkov, N. G., Soul, L. C., Arkhangelsky, M. S., Lambert, O., Stenshin, I. M., Uspensky, G. N., & Druckenmiller, P. S. (2017). Plasticity and convergence in the evolution of short-necked plesiosaurs. *Current Biology*, *27*(11), 1667–1676.e3. https://doi.org/10.1016/j.cub.2017.04.052

Foffa, D., Young, M. T., & Brusatte, S. L. (2024). Comparative functional morphology indicates niche partitioning among sympatric marine reptiles. *Royal Society Open Science*, *11*(5), 231951. doi:10.1098/rsos.231951

Gradstein, F. M., Ogg, J. G., Schmitz, M. D., & Ogg, G. (2020). *Geologic time scale 2020 (1st ed.)*. Elsevier.

Gutarra, S., & Rahman, I. A. (2021). The locomotion of extinct secondarily aquatic tetrapods. *Palaeontology*, *97*(1), 67–98.

Gutarra, S., Stubbs, T. L., Moon, B. C., Palmer, C., & Benton, M. J. (2022). Large size in aquatic tetrapods compensates for high drag caused by extreme body proportions. *Communications Biology*, *5*(1), 1–10. https://doi.org/10.1038/s42003-022-03322-y

Halstead, L. B. (1971). *Liopleurodon rossicus* (Novozhilov): A pliosaur from the lower Volgian of the Moscow Basin. *Palaeontology*, *14*, 566–570. https://www.biodiversitylibrary.org/part/173123

Halstead, L. B. (1989). Plesiosaur locomotion. *Journal of the Geological Society*, *146*(1), 37–40. doi:10.1144/gsjgs.146.1.0037

Haq, B. U. (2018). Triassic Eustatic Variations Reexamined. *GSA Today*, *28*(12), 4–9. doi:10.1130/GSATG381A.1

Hudson, J. D., & Martill, D. M. (1991). The Lower Oxford Clay: production and preservation of organic matter in the Callovian (Jurassic) of Central England. *Geological Society, London, Special Publications*, *58*(1), 363–379. doi:10.1144/GSL.SP.1991.058.01.23

Hudson, J. D., & Martill, D. M. (1994). The Peterborough Member (Callovian, Middle Jurassic) of the Oxford Clay Formation at Peterborough, UK. *Journal of the Geological Society*, *151*(1), 113–124. https://doi.org/10.1144/gsjgs.151.1.0113

Johnson, M. M., Young, M. T., & Brusatte, S. L. (2020). The phylogenetics of Teleosauroidea (Crocodylomorpha, Thalattosuchia) and implications for their ecology and evolution. *PeerJ*, *8*, e9808. https://doi.org/10.7717/peerj.9808

Ketchum, H. F., & Benson, R. B. J. (2011). A new pliosaurid (Sauropterygia, Plesiosauria) from the Oxford Clay Formation (Middle Jurassic, Callovian) of England: evidence for a gracile, longirostrine grade of Early–Middle Jurassic pliosaurids. *Palaeontology*, *86*, 109–129.

Ketchum, H. F., & Benson, R. B. J. (2022). A new pliosaurid from the Oxford Clay Formation of Oxfordshire, UK. *Acta Palaeontologica Polonica*, *67*(2), 297–315. https://doi.org/10.4202/app.00887.2021

Knight, W. C. (1898). Some new Jurassic vertebrates from Wyoming. *American Journal of Science*, *s4-5*(27), 186. https://doi.org/10.2475/ajs.s4-5.27.186

Knutsen, E. M. (2012). A taxonomic revision of the genus *Pliosaurus* (Owen, 1841a) Owen, 1841b. *Norwegian Journal of Geology*, *92*(2, 3), 259–276.

Knutsen, E. M., Druckenmiller, P. S., & Hurum, J. H. (2012). A new species of *Pliosaurus* (Sauropterygia: Plesiosauria) from the middle Volgian of central Spitsbergen, Norway. *Norwegian Journal of Geology*, *92*(2, 3), 235–258.

Kubo, T., Mitchell, M. T., & Henderson, D. M. (2012). *Albertonectes vanderveldei*, a new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. *Journal of Vertebrate Paleontology*, *32*(3), 557–572. https://doi.org/10.1080/02724634.2012.658124

Leeds, E. T. (1956). *The Leeds collection of fossil reptiles from the Oxford Clay of Peterborough*. Printed for the trustees and sold by B.H. Blackwell.

Linder, H. (1913). Beitrage zur Kenntnis der Plesiosaurier-Gattungen *Peloneustes* und *Pliosaurus*. In E. Koken (Ed.), *Geologische und palaeontologishe Abhandlungen* (pp. 339–406). Jena G. Fischer.

Lindgren, J., Caldwell, M. W., Konishi, T., & Chiappe, L. M. (2010). Convergent evolution in aquatic tetrapods: Insights from an exceptional fossil mosasaur. *PLoS ONE*, *5*(8), e11998. https://doi.org/10.1371/journal.pone.0011998

Liston, J., Newbrey, M. G., Challands, T. J., & Adams, C. E. (2013). Growth, age and size of the Jurassic pachycormid *Leedsichthys problematicus* (Osteichthyes: Actinopterygii). In G. Arratia, H. Schultze, & M. Wilson (Eds.), *Mesozoic fishes 5: Global diversity and evolution* (pp. 145–175). Verlag Dr. Friedrich Pfeil.

Lomax, D. R., De La Salle, P., Perillo, M., Reynolds, J., Reynolds, R., & Waldron, J. F. (2024). The last giants: new evidence for giant Late Triassic (Rhaetian) ichthyosaurs from the UK. *PLoS ONE*, *19*(4), e0300289. https://doi.org/10.1371/journal.pone.0300289

Lydekker, R. (1888). IV.—Notes on the Sauropterygia of the Oxford and Kimeridge Clays, mainly based on the Collection of Mr. Leeds at Eyebury. *Geological Magazine*, *5*(8), 350–356. doi:10.1017/S0016756800182160

Madzia, D., & Cau, A. (2020). Estimating the evolutionary rates in mosasauroids and plesiosaurs: Discussion of niche occupation in Late Cretaceous seas. *PeerJ*, *8*, e8941. doi:10.7717/peerj.8941

Madzia, D., Sachs, S., & Klug, C. (2022). Historical significance and taxonomic status of *Ischyrodon meriani* (Pliosauridae) from the Middle

Jurassic of Switzerland. *PeerJ*, *10*, e13244. https://doi.org/10.7717/peerj.13244
Martill, D. M. (1985). The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *311*(1148), 155–165. doi:10.1098/rstb.1985.0147
Martill, D. M. (1986). The stratigraphic distribution of fossil vertebrates in the Oxford Clay of England. *Mercian Geologist*, *10*(3), 161–186.
Martill, D. M. (1992). Pliosaur stomach contents from the Oxford Clay. *Mercian Geologist*, *13*(1), 37–42.
Martill, D. M., & Hudson, J. D. (1991). *Fossils of the Oxford Clay*. Palaeontological Association.
Martill, D. M., Jacobs, M. L., & Smith, R. E. (2023). A truly gigantic pliosaur (Reptilia, Sauropterygia) from the Kimmeridge Clay Formation (Upper Jurassic, Kimmeridgian) of England. *Proceedings of the Geologists' Association*, *134*(3), 361–373. https://doi.org/10.1016/j.pgeola.2023.04.005
Martill, D. M., & Naish, D. (2000). *Walking with Dinosaurs: The evidence*. BBC, London, UK.
Martill, D. M., Taylor, M. A., Duff, K. L., Riding, J., & Bown, P. R. (1994). The trophic structure of the biota of the Peterborough Member, Oxford Clay Formation (Jurassic), UK. *Journal of the Geological Society*, *151*(1), 173–194. https://doi.org/10.1144/gsjgs.151.1.0173
Massare, J. A. (1987). Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal of Vertebrate Paleontology*, *7*(2), 121–137. https://doi.org/10.1080/02724634.1987.10011647
Massare, J. A., Wahl, W. R., Ross, M., & Connely, M. V. (2014). Palaeoecology of the marine reptiles of the Redwater Shale Member of the Sundance Formation (Jurassic) of central Wyoming, USA. *Geological Magazine*, *151*(1), 167–182. https://doi.org/10.1017/s0016756813000472
McHenry, C.R. (2009). '*Devourer of gods': The palaeoecology of the Cretaceous pliosaur* Kronosaurus queenslandicus [Doctoral dissertation, University of Newcastle]. The University of Newcastle NOVA open access repository. https://hdl.handle.net/1959.13/935911
Michelis, I., Sander, P. M., Metzdorf, R., & Breitkreutz, H. (1996). Die Vertebratenfauna des Calloviums (Mittlerer Jura) aus dem Steinbruch Störmer (Wallücke, Wiehengebirge). *Geologie und Paläontologie in Westfalen*, *44*, 1–66.
Mönnig, E. (1995). Der Macrocephalen Oolith von Hildesheim. *Mitteilungen aus dem Roemer Museum*, *5*, 1–77.
Motani, R., Rothschild, B. M., & Wahl, W. (1999). Large eyeballs in diving ichthyosaurs. *Nature*, *402*(6763), 747. https://doi.org/10.1038/45435
Newman, B., & Tarlo, L. B. (1967). A giant marine reptile from Bedfordshire. *Animals*, *10*(2), 61–63.
Noè, L.F. (2001). *A taxonomic and functional study of the Callovian (Middle Jurassic) Pliosauroidea (Reptilia, Sauropterygia)* [Doctoral dissertation, University of Derby]. The University of Derby Repository. https://repository.derby.ac.uk/
Noè, L. F., & Gómez-Pérez, M. (2022). Giant pliosaurids (Sauropterygia; Plesiosauria) from the Lower Cretaceous peri-Gondwanan seas of Colombia and Australia. *Cretaceous Research*, *132*, 105122–27. https://doi.org/10.1016/j.cretres.2021.105122
Noè, L. F., Liston, J., & Evans, M. (2003). The first relatively complete exoccipital-opisthotic from the braincase of the Callovian pliosaur, *Liopleurodon*. *Geological Magazine*, *140*(4), 479–486. https://doi.org/10.1017/s0016756803007829
Noè, L. F., Smith, D. T. J., & Walton, D. I. (2004). A new species of Kimmeridgian pliosaur (Reptilia; Sauropterygia) and its bearing on the nomenclature of *Liopleurodon macromerus*. *Proceedings of the Geologists' Association*, *115*(1), 13–24. https://doi.org/10.1016/s0016-7878(04)80031-2
Owen, R. (1860). On the orders of fossil and recent Reptilia and their distribution in time. *Report of the British Association for the Advancement of Science*, *1859*, 153–166.
O'Keefe, F. R. (2002). The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). *Paleobiology*, *28*(1), 101–112. doi:10.1666/0094-8373(2002)028<0101:TEOPAP>2.0.CO;2
Page, K. (1989). A stratigraphical revision for the English lower Callovian. *Proceedings of the Geologists' Association*, *100*(3), 363–82. doi:10.1016/S0016-7878(89)80055-0
Páramo-Fonseca, M. E., Benavides-Cabra, C. D., & Gutiérrez, I. E. (2018). A new large pliosaurid from the Barremian (Lower Cretaceous) of Sáchica, Boyacá, Colombia. *Earth Sciences Research Journal*, *22*(4), 223–238. https://doi.org/10.15446/esrj.v22n4.69916
Páramo-Fonseca, M. E., Benavides-Cabra, C. D., & Gutiérrez, I. E. (2019). A new specimen of *Stenorhynchosaurus munozi* Páramo-Fonseca et al., 2016 (Plesiosauria, Pliosauridae), from the Barremian of Colombia: new morphological features and ontogenetic implications. *Journal of Vertebrate Paleontology*, *39*(4), e1663426. https://doi.org/10.1080/02724634.2019.1663426
Páramo-Fonseca, M. E., Gómez-Pérez, M., Noé, L. F., & Etayo-Serna, F. (2016). *Stenorhynchosaurus munozi*, gen. et sp. nov. a new pliosaurid from the upper Barremian (Lower Cretaceous) of Villa de Leiva, Colombia, South America. *Revista de La Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, *40*(154), 84–103. https://doi.org/10.18257/raccefyn.239
Persson, P. O. (1963). A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. *Lunds Universitets Årsskrift, N.F. Avdelningen*, *59*, 1–60.
Polcyn, M. J., Jacobs, L. L., Araújo, R., Schulp, A. S., & Mateus, O. (2014). Physical drivers of mosasaur evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *400*, 17–27. https://doi.org/10.1016/j.palaeo.2013.05.018
Rauhut, O. W. M., Hübner, T., & Lanser, K. (2016). A new megalosaurid theropod dinosaur from the late Middle Jurassic (Callovian) of north-western Germany: Implications for theropod evolution and faunal turnover in the Jurassic. *Palaeontologia Electronica*, *19.2.29A*, 1–48. https://doi.org/10.26879/654
Sachs, S., Hornung, J. H., Lallensack, J. N., & Kear, B. P. (2018). First evidence of a large predatory plesiosaurian from the Lower Cretaceous non-marine 'Wealden facies' deposits of northwestern Germany. *Alcheringa: An Australasian Journal of Palaeontology*, *42*(4), 501–508. doi:10.1080/03115518.2017.1373150
Sachs, S., Madzia, D., Thuy, B., & Kear, B. P. (2023). The rise of macropredatory pliosaurids near the Early–Middle Jurassic transition. *Scientific Reports*, *13*(1), https://doi.org/10.1038/s41598-023-43015-y
Sachs, S., & Nyhuis, C. (2018). Plesiosaurier-Funde aus dem Mittleren Jura von Hildesheim. *Naturhistorica*, *160*, 115–128.
Sander, P. M., Dederichs, R., Schaaf, T., & Griebeler, E. M. (2024). *Cymbospondylus* (Ichthyopterygia) from the Early Triassic of Svalbard and the early evolution of large body size in ichthyosaurs. *PalZ*, *98*(2), 275–290. https://doi.org/10.1007/s12542-023-00677-3
Sassoon, J., Foffa, D., & Marek, R. (2015). Dental ontogeny and replacement in Pliosauridae. *Royal Society Open Science*, *2*(11), 150384. https://doi.org/10.1098/rsos.150384
Sato, T., Nagai, K., Echizenya, H., Shinmura, T., Hikida, Y., & Soeda, Y. (2023). Pliosaurid (Reptilia: Sauropterygia) remains from the Upper Cretaceous of Japan, and their biostratigraphic and paleogeographic significance. *Cretaceous Research*, *150*, 105593. https://doi.org/10.1016/j.cretres.2023.105593
Sauvage, M. H. E. (1873). Notes sur les reptiles fossiles. *Bulletin de la Société Géologique de France (Paris)*, *3*(1), 365–380.
Sauvage, M. H. E. (1880). Synopsis des poissons et des reptiles des terrains Jurassiques de Boulogne-sur-Mer. *Bulletin de la Société Géologique de France (Paris)*, *3*(8), 524–547.
Sauvage, M. H. E. (1912). Les Plesiosaurides du terrain Jurassique du Boulonnais. *Bulletin de la Société Académique de l'Arrondissement de Boulogne-sur-Mer*, *9*, 186–215.
Schumacher, B. A. (2011). A '*Woollgari*-Zone Mosasaur' (Squamata; Mosasauridae) from the Carlile Shale (Lower Middle Turonian) of central Kansas and the stratigraphic overlap of early mosasaurs and pliosaurid plesiosaurs. *Transactions of the Kansas Academy of Science*, *114*(1 & 2), 1–14. https://doi.org/10.1660/062.114.0101
Schumacher, B. A., Carpenter, K., & Everhart, M. J. (2013). A new Cretaceous pliosaurid (Reptilia, Plesiosauria) from the Carlile Shale (middle Turonian) of Russell County, Kansas. *Journal of Vertebrate Paleontology*, *33*(3), 613–628. doi:10.1080/02724634.2013.722576
Seeley, H. G. (1869). *Index to the fossil remains of Ornithosauria, Aves, and Reptilia from the secondary strata, arranged in the Woodwardian Museum, Cambridge*. Cambridge University Press.

Seeley, H. G. (1874). Note on some of the generic modifications of the plesiosaurian pectoral arch. *Quarterly Journal of the Geological Society of London*, *30*(1-4), 436–449. https://doi.org/10.1144/gsl.jgs.1874.030.01-04.48

Smith, A. S. (2007). *Anatomy and systematics of the Rhomaleosauridae (Sauropterygia: Plesiosauria)* [Unpublished doctoral dissertation]. University College Dublin.

Smith, A. S. (2021, September 3). The Stewartby pliosaur and the 1967 *Liopleurodon* reconstruction. *Plesiosaur Directory*. https://plesiosauria.com/the-stewartby-pliosaur-and-the-1967-liopleurodon-reconstruction/

Takashima, R., Selby, D., Yamanaka, T., Kuwahara, Y., Nakamura, H., Sawada, K., Ikeda, M. A., Ando, T., Hayashi, K., Nishida, M., Usami, T., Kameyama, D., Nishi, H., Kuroyanagi, A., & Gyawali, B. R. (2024). Large igneous province activity drives oceanic anoxic event 2 environmental change across eastern Asia. *Communications Earth & Environment*, *5*(1), 1–7. https://doi.org/10.1038/s43247-024-01214-z

Tarlo, L. B. (1959). *Stretosaurus* gen. nov., a giant pliosaur from the Kimmeridge Clay. *Palaeontology*, *2*, 39–55.

Tarlo, L. B. (1960). A review of Upper Jurassic pliosaurs. *Bulletin of the British Museum of Natural History*, *4*(5), 147–189.

Troelsen, P. V. (2019). *Mobility and hydrodynamic implications of the long neck in plesiosaurs* [Doctoral dissertation, Liverpool John Moores University]. LJMU Research Online. https://doi.org/10.24377/ljmu.t.00010611

Vickers, M. L., Bernasconi, S. M., Ullmann, C. V., Lode, S., Looser, N., Morales, L. G., Price, G. D., Wilby, P. R., Hougård, I. W., Hesselbo, S. P., & Korte, C. (2021). Marine temperatures underestimated for past greenhouse climate. *Scientific Reports*, *11*(1), 1–7. https://doi.org/10.1038/s41598-021-98528-1

Vincent, P., Poncet, D., Rard, A., Robin, J., & Allemand, R. (2024). New remains of *Liopleurodon* (Reptilia, Plesiosauria) from the Middle Jurassic of western France and paedomorphosis within pliosaurids. *Palaeontologia Electronica*, *27*(2), 1–22. https://doi.org/10.26879/1280

von Huene, F. (1934). Ein grosser *Pliosaurus* aus dem schwabischen Ornatenton. *Jahresheften des Vereins für Vaterländische Naturkunde in Württemberg*, *90*, 31–46.

Wintrich, T., Scaal, M., Böhmer, C., Schellhorn, R., Kogan, I., Van Der Reest, A., & Sander, P. M. (2020). Palaeontological evidence reveals convergent evolution of intervertebral joint types in amniotes. *Scientific Reports*, *10*(1), 14106. https://doi.org/10.1038/s41598-020-70751-2

Young, M., Rabi, M., Bell, M., Foffa, D., Steel, L., Sachs, S., & Peyer, K. (2016). Big-headed marine crocodyliforms and why we must be cautious when using extant species as body length proxies for long-extinct relatives. *Palaeontologia Electronica*, *3*(30A), 1–14. https://doi.org/10.26879/648

Zverkov, N. G. (2015). On a typically Late Jurassic pliosaur from the Lower Cretaceous of Crimea. In E. Y. Baraboshkin, & D. E. Bykov (Eds.), *The International Scientific Conference on the Jurassic/Cretaceous boundary (September 7–13, Samara, Russia)—Proceedings volume* (pp. 86–94). Kassandra.

Zverkov, N., Arkhangelsky, M., Gulyaev, D., Ippolitov, A., & Shmakov, A. (2024). Callovian marine reptiles of European Russia. *Diversity*, *16*(5), 290. https://doi.org/10.3390/d16050290

Zverkov, N. G., Fischer, V., Madzia, D., & Benson, R. B. (2018). Increased pliosaurid dental disparity across the Jurassic–Cretaceous transition. *Palaeontology*, *61*(6), 825–846. https://doi.org/10.1111/pala.12367

Zverkov, N. G., & Pervushov, E. M. (2020). A gigantic pliosaurid from the Cenomanian (Upper Cretaceous) of the Volga Region, Russia. *Cretaceous Research*, *110*, 104419. doi:10.1016/j.cretres.2020.104419

Handling Editor: Erin Maxwell.