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MORPHOLOGY OF THE CAUDAL VERTEBRAE IN *RHOMALEOSAURUS ZETLANDICUS* AND A REVIEW OF THE EVIDENCE FOR A TAIL FIN IN PLESIOSAURIA

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ABSTRACT

The holotype of the large plesiosaurian *Rhomaleosaurus zetlandicus* from the Toarcian (Lower Jurassic) of England comprises an almost complete skeleton, including the caudal vertebral series. The osteology of the tail is described and two morphological characteristics are interpreted as evidence for a caudal fin in *Rhomaleosaurus*: 1. A distinct node consisting of two relatively anteroposteriorly shortened vertebrae; and 2. Laterally compressed terminal caudal centra. This inference is based on osteological correlates derived from other marine reptile groups that possessed a vertically oriented bilobed dermal tail fin in life (ichthyosaurs, thalattosuchian crocodylomorphs, and mosasaurs). This corroborates evidence from other plesiosaurian taxa and suggests that a caudal fin may have been widespread among plesiosaurians, with implications for locomotion and behavior.

INTRODUCTION

Plesiosaurians are an iconic group of extinct marine reptiles with an extensive stratigraphic range spanning approximately 135 million years from the early Jurassic to the late Cretaceous (Ketchum and Benson, 2010). Plesiosaurians belong the diapsid group Sauropterygia, and were adapted for aquatic life, with a sturdy trunk region and four large wing-like limbs, used to propel themselves through water (Robinson, 1975). This paraxial or appendicular locomotory style represents an unusual deviation from the general convergent trend towards axial (oscillatory) locomotion in the majority of derived secondarily aquatic reptiles (Robinson, 1975; Massare, 1988; Storrs, 1993; Motani et al., 1996; Motani, 2005; Lindgren et al., 2010, 2013). Plesiosaurians were entirely carnivorous and comprised an important component of oceanic ecosystems during the Mesozoic Era (Massare, 1987). They exhibit a variety of body plans ranging between two extremes: short-necked large-headed 'pliosauromorphs' and long-necked small-headed 'plesiosauromorphs' (O'Keefe, 2002; O'Keefe and Carrano, 2005). Recent studies have demonstrated that plesiosaurian body proportions were evolutionarily plastic and that these two extreme morphotypes arose multiple times independently in several clades (Bakker, 1993; O'Keefe, 2002; O'Keefe and Carrano, 2005; Benson and Druckenmiller 2013; Benson et al., 2013).

Rhomaleosaurids are a clade of Early–Middle Jurassic plesiosaurians, morphologically intermediate between the plesiosauromorph and pliosauromorph extremes (Cruickshank 1994; Smith and Dyke, 2008). Although the cranial anatomy of rhomaleosaurids has received considerable research attention and is generally well understood (Cruickshank 1994, 1996; Gasparini, 1997; Sato and Wu, 2008; Smith and Dyke, 2008; Smith and Vincent 2010; Vincent and Benson, 2012), the postcranial anatomy of these plesiosaurians is more poorly known. This paper provides a description of the caudal vertebrae in the rhomaleosaurid *Rhomaleosaurus zetlandicus* (Phillips, in Anon, 1854) to improve knowledge of the caudal anatomy in this taxon, and plesiosaurians in general.

Institutional Abbreviations—NHMUK, The Natural History Museum, London, UK; NMING, National Museum of Ireland (Natural History Division), Dublin, Ireland; MB, Naturkundemuseum Berlin, Germany; USNM, Smithsonian Institution, Washington, D.C; WM, Whitby Museum, UK; YORYM, Yorkshire Museum, UK.

MATERIALS AND METHODS

The holotype of the large-headed plesiosaurian *Rhomaleosaurus zetlandicus* (YORYM G503) from the Lower Jurassic (Toarcian) of the Yorkshire Coast, UK, comprises an almost complete skeleton. The skull was described and figured by Taylor (1992a) and the postcranial skeleton was briefly described with an emphasis on its taphonomy and preservation (Taylor, 1992b). The caudal series is complete (with the possible exception of one or two terminal vertebrae) and forms the basis of the present study. The tail of a referred specimen of *Rhomaleosaurus zetlandicus* is incomplete (WM851.S, previously '*Rhomaleosaurus* *propinquus*') and is therefore unavailable for comparison (Vincent and Smith, 2009).

There is no major taphonomic distortion of any of the elements in YORYM G503 (Taylor, 1992b). They are preserved in three dimensions allowing accurate measurement of vertebral dimensions. The tail vertebrae were consecutively numbered from the first caudal vertebra (v1) to the terminal-most vertebra (a partial centrum, v32). Vertebra 3 (at the proximal base of the tail) is damaged, precluding accurate measurement. It therefore provides a natural break to the measured sequence, which extends from v4 (proximally) to v32 (distally). Measurements of the vertebrae were taken using callipers to the nearest tenth of a millimeter (Table 1). For consistency, anteroposterior vertebral length was measured along the median ventral surface of the centrum, and dorsoventral height and mediolateral width were taken from the anterior articular face of the centrum. The anterior face was selected to include the partially preserved distal-most vertebra (v32) in the results. To quantify variation in proportions along the caudal vertebral column, two indices were calculated. 1. Relative centrum length along the vertebral column was quantified using a vertebral length index (VLI) (Brown, 1981), where length is expressed as a percentage of the average centrum diameter (in this case, the average diameter calculated from height and width measurements from the anterior surface). 2. Relative width of the articular faces along the vertebral column was quantified as a simple index, where width is expressed as a percentage of vertebral height. The sequence of vertebrae in Figures 1–7 represent the sequence as mounted, however, vertebrae 6, 10, 13, and 14, are oriented back-to-front, so this was corrected for in the analysis (the measurements were taken from the anatomically anterior faces). Otherwise, there are no obviously misplaced or out of position centra in the sequence. Finally, to assess whether *Rhomaleosaurus* had a dermal tail fin or not, a suite of comparative osteological correlates was compiled based on other marine reptiles (Table 2).

ANATOMICAL DESCRIPTION

Taylor (1992b) identified at least 33 caudal vertebrae in *Rhomlaeosaurus zetlandicus* but only 32 were identified in the present study. It is difficult to confidently identify the transition from sacral to caudal vertebrae in the genus *Rhomaleosaurus* because the rib facets never return entirely to the centrum (Figure 3A, D, and see below), which may account the discrepancy in vertebral counts. At the distal-most end of the sequence the anterior part of v32 is preserved (Figures 1A, 7G, I–L) so only height and width measurements could be taken from this vertebra. There may be at least two terminal vertebrae missing according to Taylor (1992b). The relative proportions of the measured caudal vertebrae (v4–32) are presented in Table 1 and Figure 2. Few neural spines, ribs, or chevrons are preserved with the specimen, so the following description concentrates on the vertebral centra.

Most of the caudal centra (v1–24) have concave sub-hexagonal anterior and posterior faces (Figures 3E, H, K, 4B, D, 5B, E, H, K, 6E, F, 7B), anteroposteriorly concave lateral surfaces, and flat ventral surfaces. The facets for the caudal ribs are situated dorsally on the lateral surface of the centrum, have raised rims, and always retain a connection to the neural arch (Figure 1, 3A, D, G, J, 4A, C, 5A, D, G, J 6A-D). The rib facets decrease steadily in size posteriorly and are completely absent in the terminal vertebrae 22–32 (Figures 1A, B, 6A–D, 7A, D, G, J). In vertebra 21 the rib facets are asymmetrical in that the left facet is significantly smaller and less pronounced than the right (Figure 6A,B). Asymmetrical caudal vertebrae have been documented in other plesiosaurs (e.g. Wilhelm and O'Keefe, 2010), where they have been interpreted as pathological in origin. There is no supporting evidence for pathology in the tail of *Rhomaleosaurus zetlandicus* (YORYM G503), and so the asymmetry in v21 is considered non-pathological. The neural arch facets have diamond shaped outlines, and the base of the neural canal is constricted midlength and bears longitudinally oriented rugosities anteriorly (Figure 4E, 5C,I, 6C, 7C). All of the caudal centra bear anteroposteriorly oriented rugose ornamentation on their lateral and ventral surfaces. A pair of widely spaced nutritive foramina is situated on the ventral surface of the centrum in v1–20, located mid-centrum length and slightly medial to the chevron facets (Figures 1C, D, 3F, L, 4F, 5F, L, 6D). These ventral nutritive foramina are absent in distal vertebrae 21–32, but nutritive foramina are sometimes present on the lateral surfaces of the distal vertebrae, e.g. v27 (Figure 7A, D). The chevron facets in vertebrae 16–32 are relatively large and formed by the posteroventral and anteroventral surfaces of the centrum, whereas in v1–15 they are relatively small and formed by the posteroventral surfaces only (i.e. anterior chevron facets are completely absent or diminutive) (Figures 3F, L, 4F, 5F, L). Vertebrae 23 and 24 are notably shortened relative to the rest of the caudal sequence and form a distinct node (Figures 1, 2, 6A, B, G–J). These two conspicuous vertebrae participate equally towards a pair of relatively enlarged chevron facets (Figure 6J). The posteroventral margin of v23 is concave (Figure 6J), in contrast to the convex posteroventral margin present in every other caudal vertebra. There is no fusion, distortion or rugosity to suggest this node is a pathology, and it is therefore

TABLE 1. Measurement data and calculated ratios/indices for the caudal vertebrae in YORYM G503, the holotype of *Rhomaleosaurus zetlandicus*.

Vertebra Number	Length (Ventral)	Length (Dorsal)	Width (Anterior)	Height (Anterior)	VLI	Ratio Length: Width	Ratio Length: Height	(Width/ Height) *100
4	49.7	?	94.1	88	54.6	0.53	0.56	106.9
5	49.6	?	92.1	90.5	54.3	0.54	0.55	101.8
6	47.2	?	94.3	87.0	52.1	0.50	0.54	108.4
7	46.6	45.0	92.8	85.0	52.4	0.50	0.55	109.2
8	43	40.0	89.3	82.3	50.1	0.48	0.52	108.5
9	45.9	42.7	85.8	81.6	54.8	0.53	0.56	105.1
10	42.5	39.5	84.5	79.5	51.8	0.50	0.53	106.3
11	42.6	37.6	82.4	76.0	53.8	0.52	0.56	108.4
12	44.0	42.8	79.0	76.9	56.4	0.56	0.57	102.7
13	39.3	41.5	79.0	70.1	52.7	0.50	0.56	112.7
14	38.0	38.8	77.0	72.0	51.0	0.49	0.53	106.9
15	42.8	39.5	74.0	68.4	60.1	0.58	0.63	108.2
16	42.5	36.8	73.4	72.0	58.5	0.58	0.59	101.9
17	38.5	35.0	72.4	68.9	54.5	0.53	0.56	105.1
18	35.0	39.9	67.1	68.0	51.8	0.52	0.51	98.7
19	36.1	37.7	63.0	63.8	56.9	0.57	0.57	98.7
20	37.1	38.7	64.2	65.4	57.3	0.58	0.57	98.2
21	36.1	32.5	62.8	60.5	58.6	0.57	0.60	103.8
22	34.3	32.5	57.1	58.0	59.6	0.60	0.59	98.4
23	26.0	26.5	65.5	59.5	41.6	0.40	0.44	110.1
24	21.0	19.1	61.2	60.0	34.7	0.34	0.35	102.0
25	34.1	28.5	49.0	49.0	69.6	0.70	0.70	100.0
26	31.1	25.0	48.6	46.4	65.5	0.64	0.67	104.7
27	23.1	22.5	46.5	41.0	52.8	0.50	0.56	113.4
28	26.8	23.2	35.0	39.2	72.2	0.77	0.68	89.3
29	23.1	20.0	29.0	36.3	70.8	0.80	0.64	79.9
30	15.0	20.2	23.3	39.2	48.0	0.64	0.38	59.4
31	21.8	15.0	21.0	33.8	79.6	1.04	0.64	62.1
32	?	?	12.8	26.5	–	–	–	48.3

regarded as anatomically natural. The vertebral centra posterior to the node (vertebrae 25–32) become increasingly mediolaterally compressed (Figures 1, 2, 7), and their articular faces dorsoventrally oriented sub-rectangles (Figure 7B, E, H, K). Small cracks on the right ventrolateral surface of v31 and v32 (Figure 7G) indicate a minimal amount of postmortem compression, which accounts for some, but not all, of the mediolateral compression in these vertebrae. The sudden shift in vertebral morphology at the node coincides with a subtle ventral displacement of the vertebrae, or a kink in the tail (Figure 6A, B; Smith, 2007), but the preservation is too poor to positively identify this morphology.

ANALYSIS

Evidence for a Dermal Tail Fin in Mesozoic Marine Reptiles—Direct soft tissue evidence for a bilobed dermal tail fin in ichthyosaurs is provided by exceptionally preserved specimens from the Sulphur Mountain Formation (Lower–Middle Triassic) of British Columbia (Nicholls and Manabe, 1999; Motani, 2005) Lower Triassic deposits of China (Motani et al., 1996; but see Nicholls and Manabe, 1999; and Motani, 2005); Charmouth Mudstone Formation (Sinemurian) of England (Martill, 1995); Posidona Shale (Toarcian) of Germany (Wiman, 1920, 1946; McGowan, 1992; Lingham-Soliar, 2001; Motani, 2005) and Solnhofen Formation (Tithonian) of Germany (Bardet and Fernandez, 2000). A similarly well-preserved

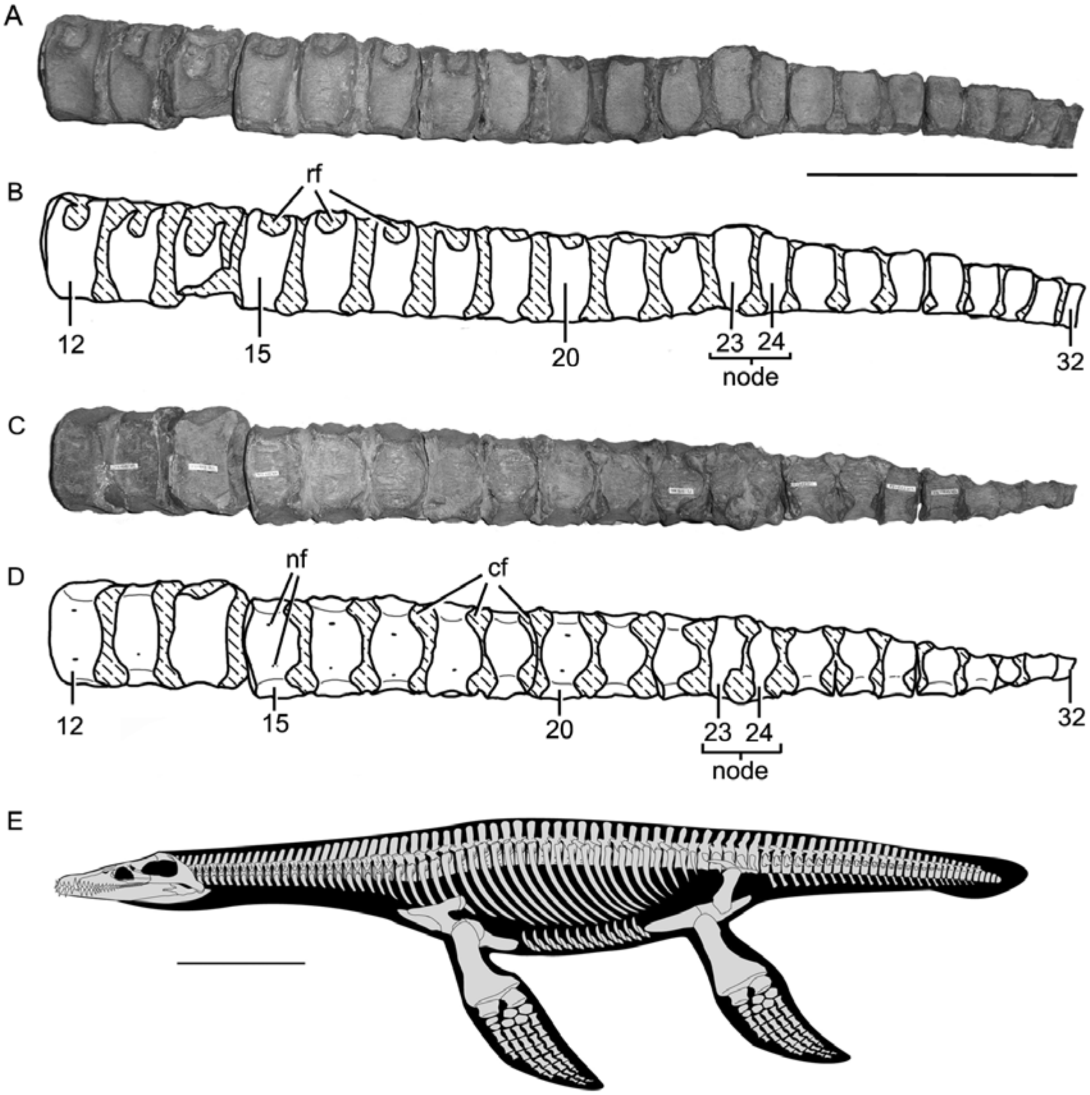

FIGURE 1. The posterior portion of the articulated series of caudal vertebrae (caudal vertebrae 12-32) in YORYM G503, the holotype of *Rhomaleosaurus zetlandicus*, A. photograph and B. interpretive illustration of the series in left lateral view, C. photograph and D. interpretive illustration of the series in ventral view. The region labelled “node” indicates the position of two foreshortened vertebrae. E. Reconstruction of the skeleton and outline of *Rhomaleosaurus* showing a vertically oriented dermal tail fin (from Smith and Dyke 2008). Abbreviations: cf, chevron facets; nf, nutritive foramina; rf, rib facets. Scale bar in A–D = 200 mm, scale bar in E = 1000 mm.

specimen of the metriorhynchid thalattosuchian crocodylomorph *Racheosaurus* from the Mörnsheim Formation (Tithonian), Germany (Fraas, 1902; Young et al., 2010) provides soft-tissue evidence for a dorsoventrally expanded tail fin with a dorsal dermal lobe in derived crocodylomorphs. A large bilobed dermal tail fin has been inferred in the derived mosasaurs *Plotosaurus* and *Platecarpus* based on compelling osteological evidence (Lindgren et al., 2007, 2010), and there is direct soft tissue evidence for this in a specimen of the mosasaur *Prognathodon* from the Muwaqqar Chalk Marl Formation (Maastrichtian), Jordan (Lindgren et al., 2013). Since there is direct evidence for a dermal tail fin in these marine reptiles, osteological correlates can be established and used to infer a fin in other taxa. Table 2 summarizes the osteological correlates of a dermal caudal fin in these three major groups of Mesozoic marine reptiles, and also provides details of the distribution of these correlates among selected plesiosaurian genera. Four osteological correlates are identified: Mediolaterally compressed distal caudal vertebrae. Mediolaterally compressed distal caudal centra are present in derived ichthyosaurs (Andrews, 1910; Buchholtz, 2001),

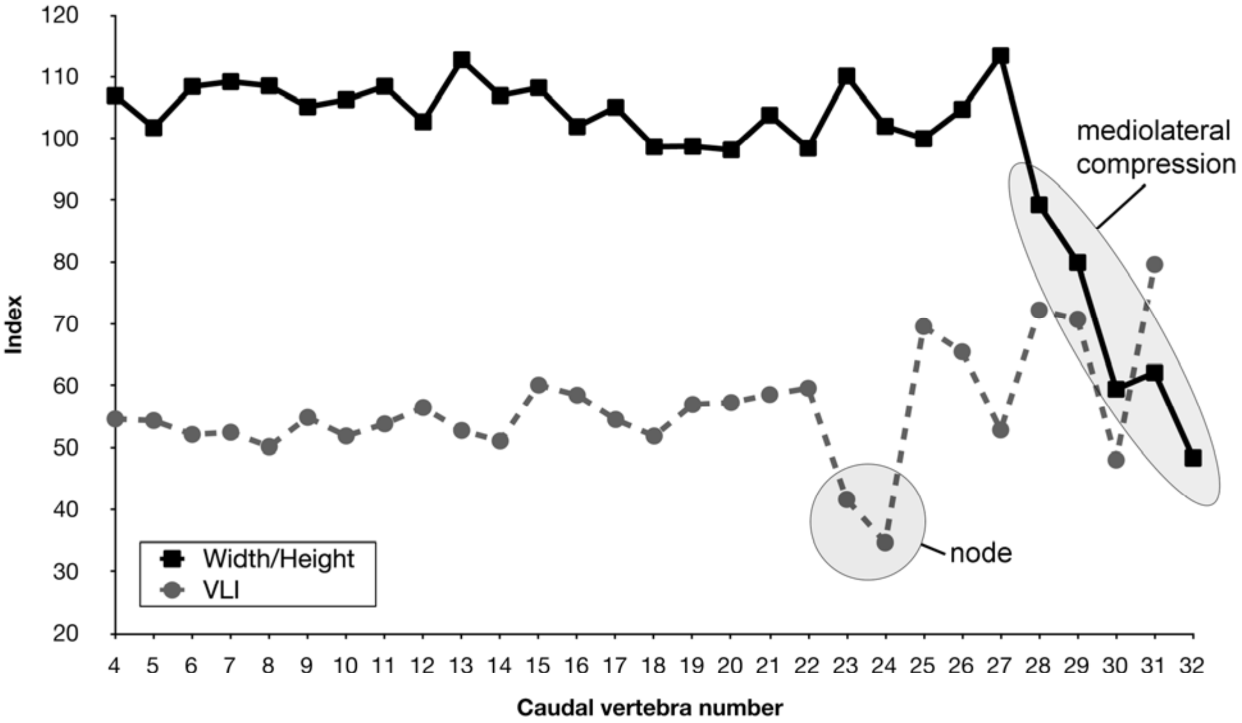

FIGURE 2. Graph showing the proportions of caudal vertebrae four to 32 in YORYM G503, the holotype of *Rhomaleosaurus zetlandicus*. See text for explanation of indices. Only the anterior face of vertebra 32 is preserved so there is no VLI measurement for this element. Note that vertebrae 23 and 24 are foreshortened and form a distinct node. Vertebra thirty is also notably foreshortened, and the last seven preserved vertebrae become increasingly compressed mediolaterally. The sequence of vertebrae represents the order as mounted, which appears to be correct.

thalattosuchian crocodylomorphs (Andrews 1913), and mosasaurs (Lindgren et al., 2008). Mediolateral compression of the vertebrae is associated with a mediolaterally compressed dermal tail fin.

A caudal node. A short sequence of conspicuous vertebrae, described here as a 'node', is present in ichthyosaurs (Merriam, 1908; Andrews, 1910; McGowan, 1989, 1992; Buchholtz, 2001) and thalattosuchian crocodylomorphs (*Metriorhynchus*, Andrews, 1913). In mosasaurs a similar node is formed by a short sequence of anteroposteriorly shortened intermediate vertebrae (Lindgren et al., 2007, 2008, 2010). This region is regarded as the point of origin for a dermal lobe in ichthyosaurs, thalattosuchians, and mosasaurs.

Ventral displacement of the vertebral column. Ventral displacement of the vertebral column results in a hypocercal fluke in ichthyosaurs (Merriam, 1908; Andrews, 1910; McGowan, 1989, 1992; Buchholtz, 2001), crocodylomorphs (Fraas, 1902; Young et al., 2010) and mosasaurs (Lindgren et al., 2007, 2010, 2013). This ventrally directed fluke supported the ventral lobe of a bilobed caudal fin in these taxa. The degree of ventral displacement is related to deflection caused by the caudal node, but can also be present along the length of the fluke itself due to wedge shaped vertebrae (Lindgren, 2007, 2013). High angle tail bends in ichthyosaurs supported high aspect ratio caudal fins (Bucholtz, 2001).

A region of reversed inclination of the neural spines. The angle of inclination of the neural spine changes along the vertebral column in ichthyosaurs (Buchholtz, 2001) and mosasaurs (Lindgren et al., 2007, 2008, 2013). This shift is correlated with a dorsal lobe of the tail fin.

The Case for a Tail Fin in *Rhomaleosaurus*— *Rhomaleosaurus zetlandicus* presents two osteological correlates for a vertically oriented dermal tail fin (Table 2): a distinct node, and mediolaterally compressed distal vertebral centra (Figures 1, 2, 6G–J, 7). A vertically oriented dermal tail fin can therefore be inferred for *Rhomaleosaurus* (Figure 1E). In addition, a subtle ventral displacement of the vertebrae at the node may be present (Figures 1A, B, 6A–B) but preservation is too poor to positively identify this morphology. The angle of the neural spines and the size and morphology of the chevrons is unknown in *Rhomaleosaurus*,

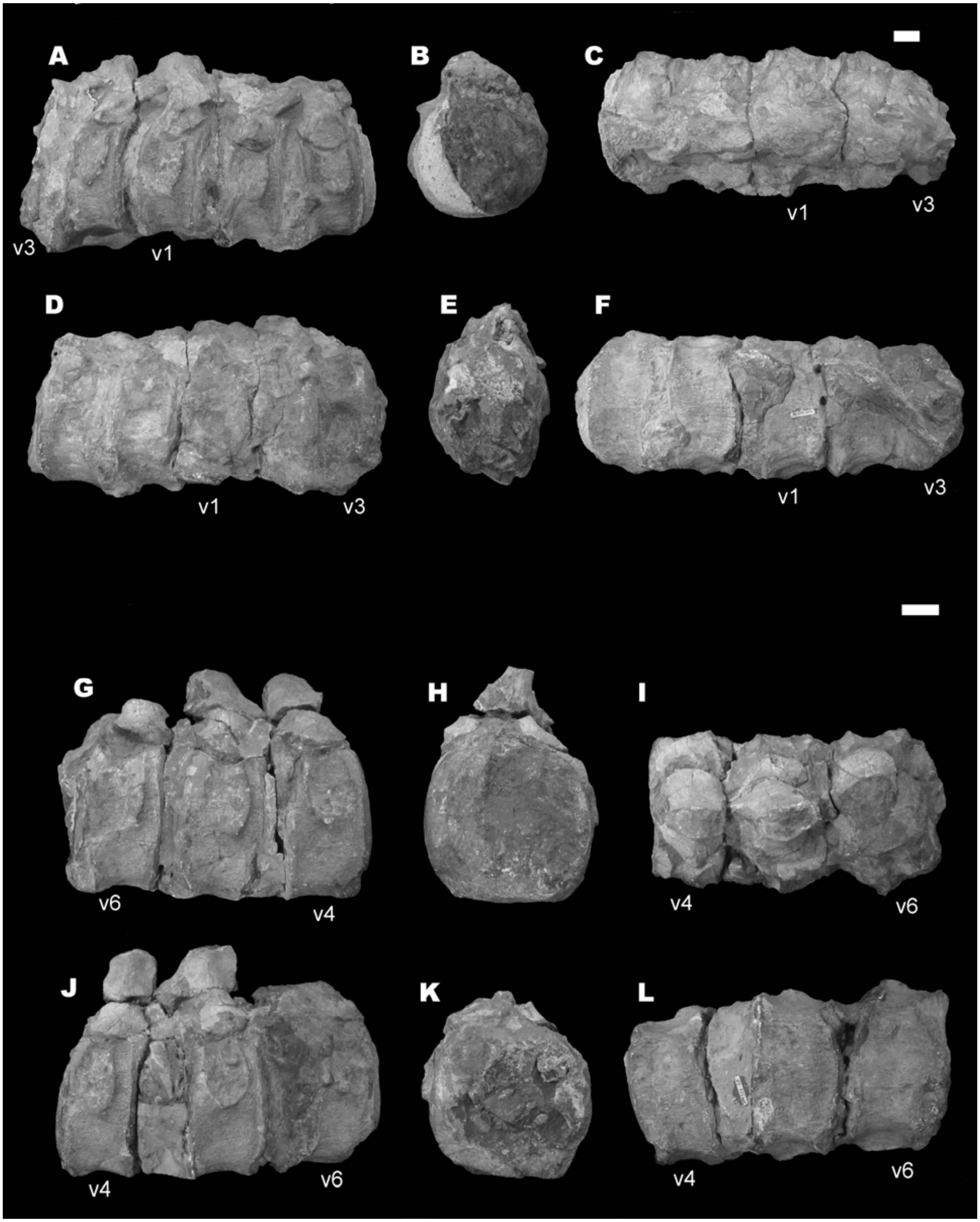

FIGURE 3. Posterior sacral vertebrae and caudal vertebrae one–six in *Rhomaleosaurus zetlandicus* (YORYM G503). A–F, posterior sacral vertebrae and caudal vertebrae one–three in A, right lateral, B, anterior, C, dorsal, D, left lateral, E, posterior, and F, ventral view. G–L, caudal vertebrae four–six in G, right lateral, H, anterior, I, dorsal, J, left lateral, K, posterior, and L, ventral view. Scale bar = 20 mm.

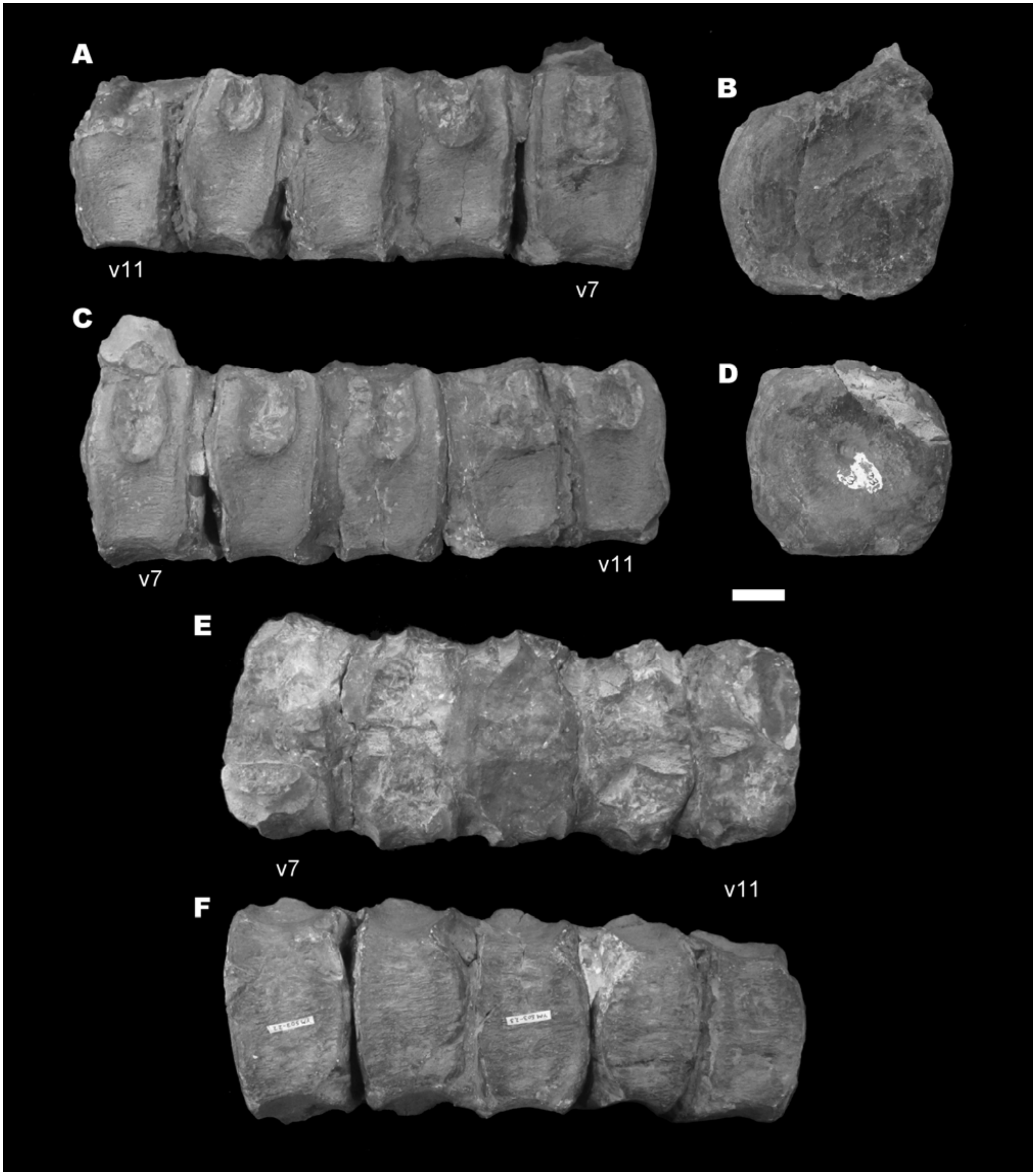

FIGURE 4. Caudal vertebrae seven–11 in *Rhomaleosaurus zetlandicus* (YORYM G503). A, right lateral, B, anterior, C, left lateral, D, posterior, E, dorsal, and F, ventral view. Scale bar = 20 mm.

however, the enlarged chevron facets situated on the ventral surface of the caudal node (Figures 1C, D, 6G–J) may indicate an increase in chevron size in this region. The caudal vertebral series is incomplete or obscured in other *Rhomaleosaurus* specimens. The caudal series is incomplete in *Rhomaleosaurus thorntoni* (NHMUK R4853; Andrews, 1922) and a referred specimen of *R. zetlandicus* (WM 851.S; Vincent and Smith, 2009). In *R. cramptoni* (NMING F8785) the tail appears to be complete (Smith, 2007), but it is obscured by paint and plaster. In the closely related *Meyerasaurus victor* (Fraas 1910) the tail is almost completely preserved but the associated chevrons obscure the centra (Smith and Vincent, 2010).

DISCUSSION

Plesiosaurians are sometimes portrayed with a vertically oriented caudal fin on the end of the tail (e.g. Dames, 1895; Woodward, 1896; Zarnik, 1925; Newman and Tarlo, 1967). This trend may have been initiated when Richard Owen noted the terminal caudal vertebrae in a Lower Jurassic plesiosaurian (*Archaeonectrus rostratus*) were compressed and “probably supported some development of the terminal dermal expanse” (Owen, 1865, p. 26). The only known soft-tissue evidence for a caudal fin in a plesiosaur was described in the holotype of *Seeleyosaurus guilelmiimperatoris* (MB R.1992; Dames, 1895), for which a black carbonaceous silhouette was identified at the tip of the tail. This taxon was subsequently restored with a large diamond-shaped caudal fin at the tip of the tail (Dames, 1895; Zarnik, 1925). This specimen has since been covered with paint, obscuring any preserved soft tissue, so this evidence cannot currently be verified. Later depictions of plesiosaurians with a caudal fin have been based on this single piece of soft-tissue evidence. For example, ‘*Plesiosaurus*’ *macrocephalus* has been portrayed with a diamond-shaped dermal tail fin (Woodward, 1896), and Tarlo (1957) speculated on the presence of a tail fin in pliosaurs, including a triangular fin in a reconstruction of the pliosaurid *Liopleurodon* (Newman and Tarlo, 1967).

Other authors have considered the osteology of plesiosaurian tails and how it might relate to the soft tissue anatomy. The tails of some plesiosaurians have been observed to “turn up slightly near the extremity, as though for the support of a small terminal fin” (Williston, 1914, p. 80; without further details). Wilhelm (2010) described the tail of the cryptoclidids *Cryptoclidus* and *Muraenosaurus* and interpreted lateral compression of the caudal vertebrae, changes in caudal rib and neural spine morphology, and a fused pygostyle-like structure, as evidence for a tail fin. In particular, the distal-most neural spines become inclined anteriorly, and the 17th caudal neural arch is relatively larger and more anteroposteriorly expanded than those preceding it. Wilhelm (2010, p. 48 fig. 3.6) therefore reconstructed the tail of *Cryptoclidus* with a dorsal dermal lobe. Similarly, O’Keefe et al. (2011) reconstructed the closely related cryptoclidid *Tatenectes* with a dermal tail fin. A node of the kind described in *Rhomaleosaurus zetlandicus* has not been observed in any other plesiosaur taxa, even specimens with complete tails, suggesting it may be an autapomorphy of this taxon. However, fused caudal vertebrae, and pygostyle-like structures, have been described in several other plesiosaurians belonging to a variety of clades (Dames, 1895; Wegner, 1914; Welles, 1943; Kear et al., 2006; Kear, 2006; Wilhelm, 2010; Kubo et al., 2012). In *Seeleyosaurus* (Dames, 1895) the neural arches of the four terminal vertebrae are fused to each other, in *Brancasaurus* (Wegner, 1914) the neural arches of the seven terminal vertebrae are fused, and in *Archaeonectrus* an uncertain number of terminal vertebrae are fused (Wegner, 1914). In *Cryptoclidus* five to six terminal caudal vertebrae are fused into a pygostyle-like structure (Wegner, 1914; Wilhelm, 2010), in *Morenosaurus* the terminal five vertebrae are “fused into a pointed mass” (Welles, 1943 p.166), in *Umoonasaurus* at least five terminal vertebrae are fused (Kear et al., 2006; Kear, 2006), and in *Albertonectes* seven terminal vertebrae are heavily fused into a “dorsoventrally flattened structure” (Kubo et al., 2012, p. 562), although the dorsoventral flattening is possibly a taphonomic artefact (Kubo et al., 2012). The presence of such a pygostyle in adults might be a synapomorphy of Cryptoclidia (Benson and Druckenmiller 2013, char 195). The widespread presence of partial or complete fusion of the terminal caudal vertebrae in multiple different plesiosaurs, shows that it is not of pathological origin. The significance of the pygostyle-like structures is unclear, but it may be related to a dermal tail fin. Fraas (1910) and Wegner (1914) even proposed a mediolaterally expanded tail, or horizontal tail fin, in plesiosaurians, on the basis of the pygostyle-like structure (and well-developed lateral processes [caudal ribs]). Ketchum and Smith (2010) described wedge shaped caudal vertebrae (caudal vertebrae 17 and 18) midway along the tail in *Macroplata*, resulting in a ventral deflection of the distal portion of the tail. In conjunction with the evidence presented here for *Rhomaleosaurus*, there is therefore a growing body of osteological evidence suggesting a dermal tail fin was present in a variety of plesiosaurian taxa (including rhomaleosaurids, cryptoclidids, leptoclidids, and basal plesiosauroids).

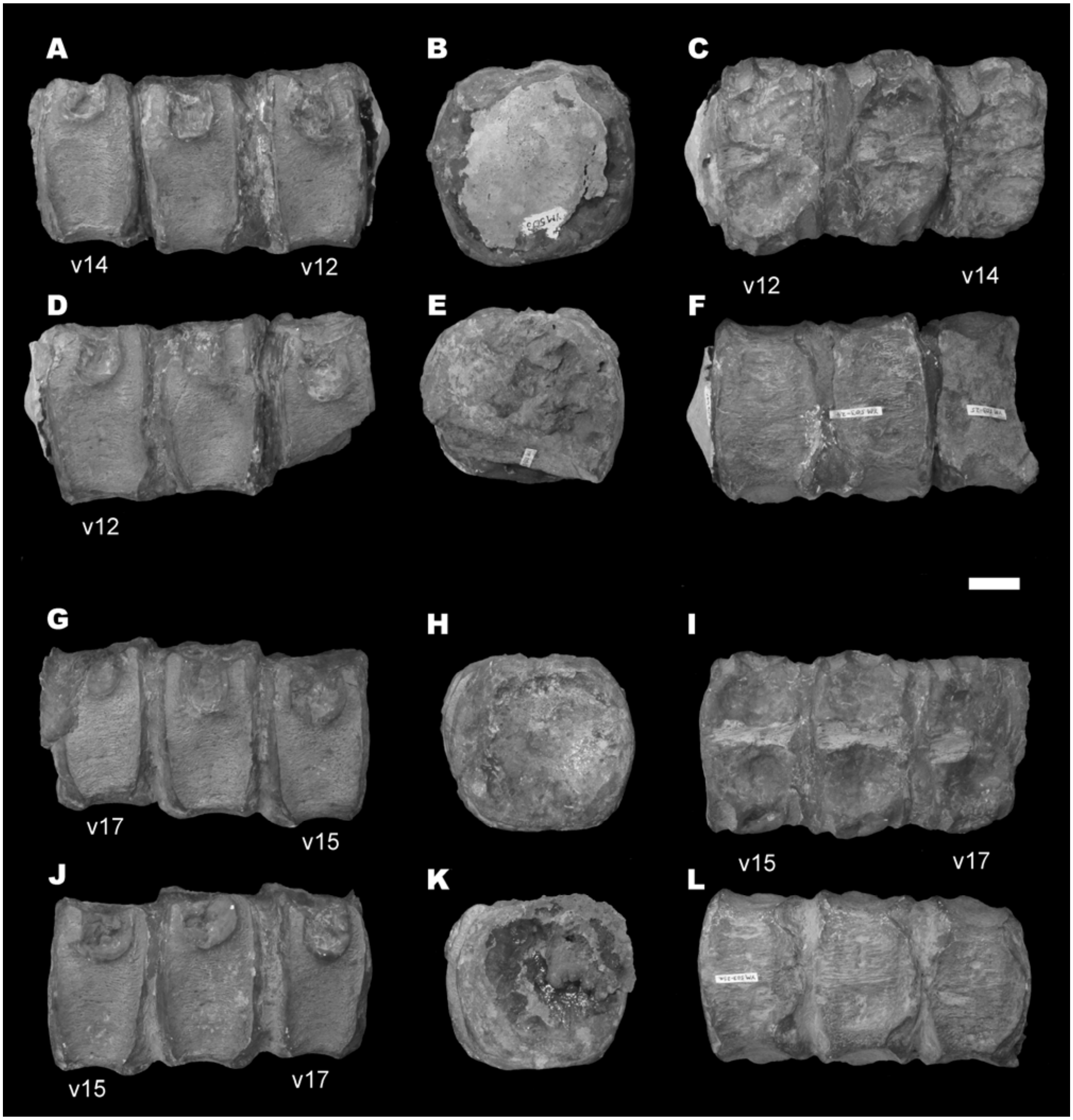

FIGURE 5. Caudal vertebrae 12–17 in *Rhomaleosaurus zetlandicus* (YORYM G503). A–F, caudal vertebrae 12–14 in A, right lateral, B, anterior, C, dorsal, D, left lateral, E, posterior, and F, ventral view. G–L, caudal vertebrae 15–17 in G, right lateral, H, anterior, I, dorsal, J, left lateral, K, posterior, and L, ventral view. Scale bar = 20 mm.

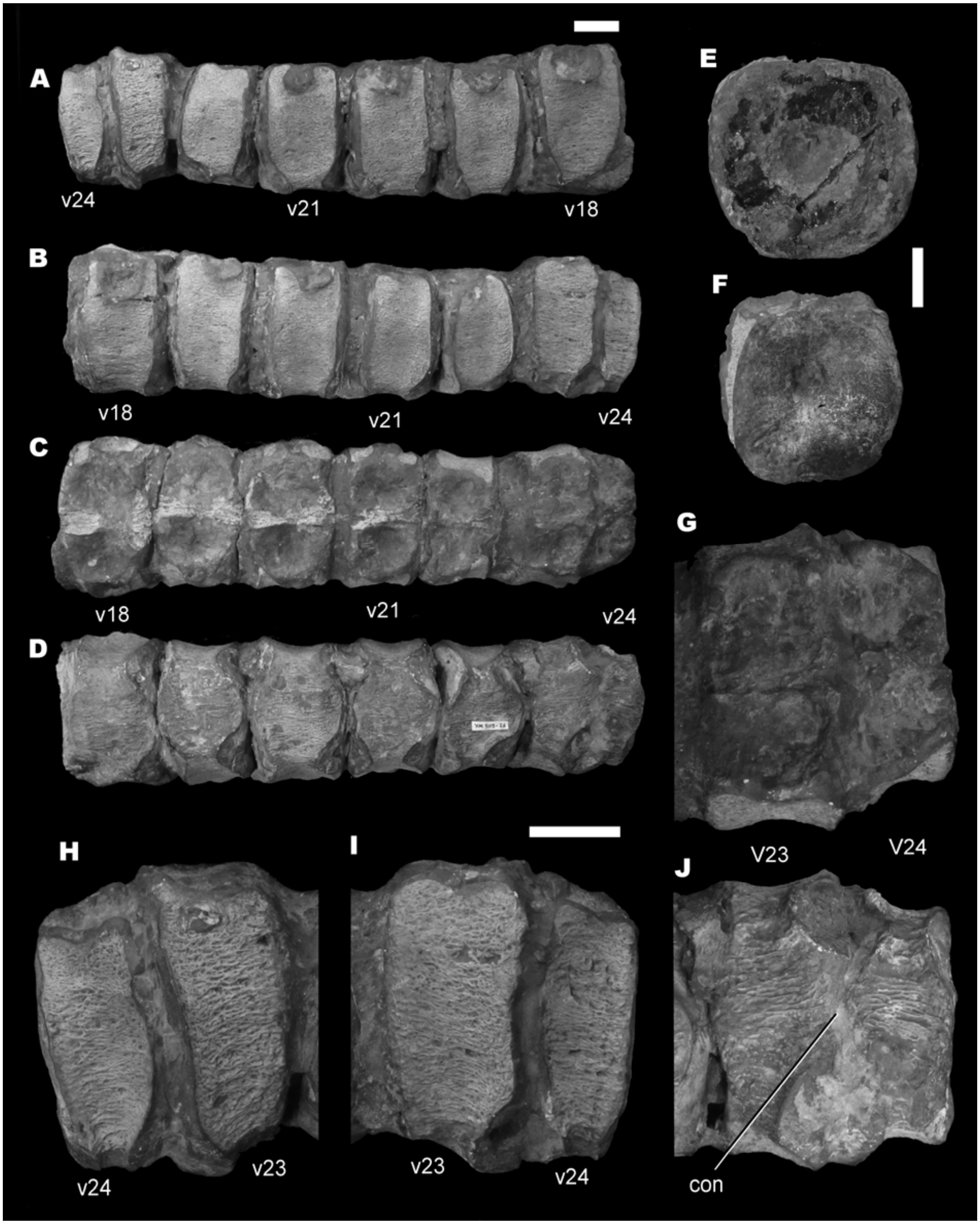

FIGURE 6. Caudal vertebrae 18–24 in *Rhomaleosaurus zetlandicus* (YORYM G503). A–F, caudal vertebrae 18–24 in A, right lateral, B, left lateral, C, dorsal, D, ventral, E, anterior, and F, posterior view. G–J, close up of caudal vertebrae 23–34, the node, in G, dorsal, H, right lateral, I, left lateral, J, ventral view. Note the asymmetry in v21. Abbreviations: con, concave posteroventral margin of v23. Scale bars = 20 mm.

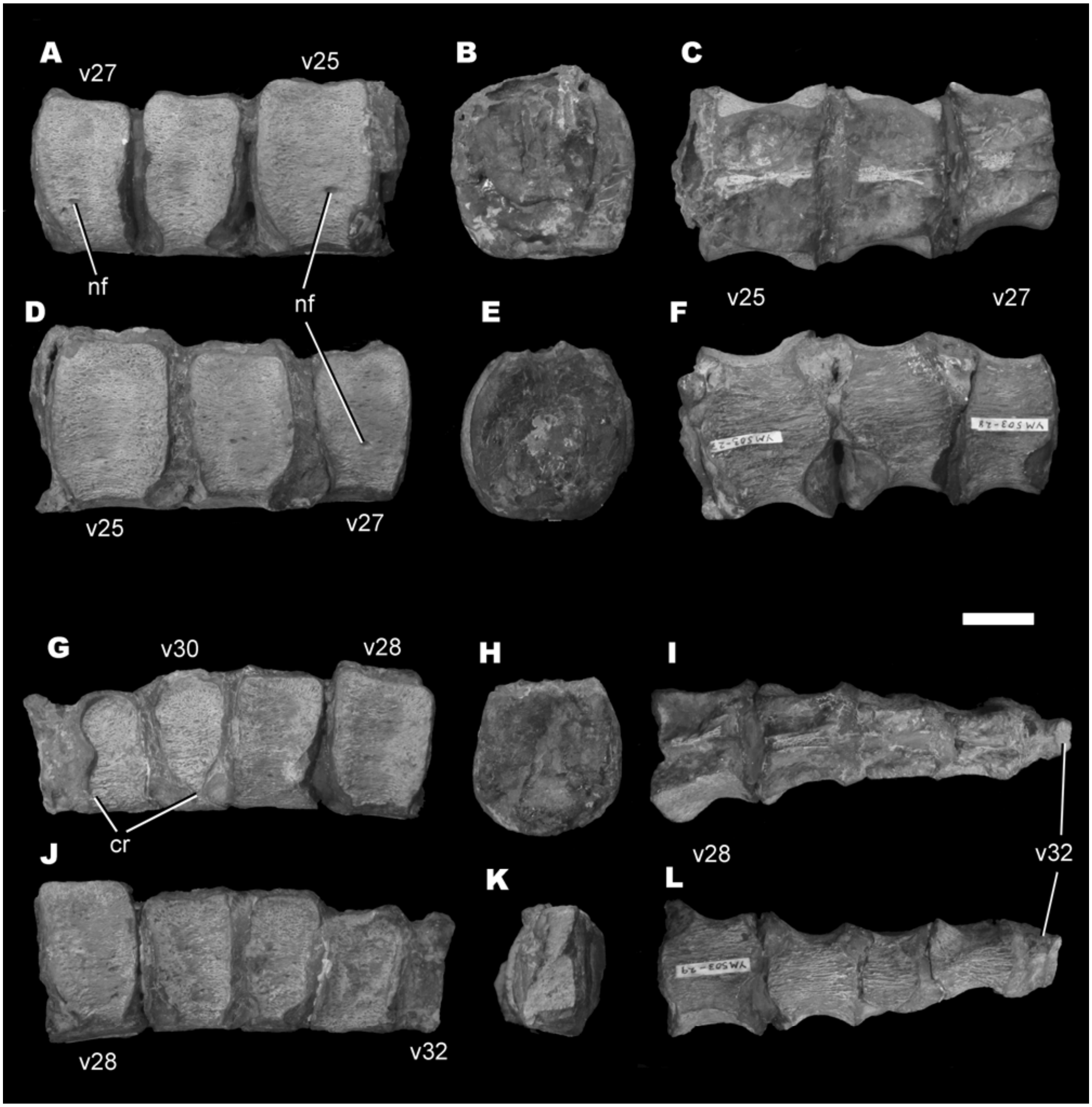

FIGURE 7. Caudal vertebrae 25–32 in *Rhomaleosaurus zetlandicus* (YORYM G503). A–F, caudal vertebrae 25–27 in A, right lateral, B, anterior, C, dorsal, D, left lateral, E, posterior, and F, ventral view. G–L, caudal vertebrae 28–32 in G, right lateral, H, anterior, I, dorsal, J, left lateral, K, posterior, and L, ventral view. Abbreviations: cr, cracks, nf, nutritive foramina. Scale bar = 20 mm.

The presence of a tail fin has potential implications for plesiosaurian behaviour in terms of swimming speed, manuverability and stability in the water column. Plesiosaurians propelled themselves through the water using four large wing-like flippers (Robinson, 1975; Frey and Riess, 1982; Godfrey, 1984; Riess and Frey, 1991; Lingham-Soliar, 2000; Carpenter et al., 2010). The evolutionary history of most other marine reptiles (and fully aquatic vertebrates in general) is dominated by a convergent trend towards axial locomotion, culminating in the tail-based propulsive system in ichthyosaurs, mosasaurs and thalattosuchian crocodylomorphs. A distinct lunate caudal fin evolved independently in each of these

TABLE 2. Summary of osteological correlates for a vertical dermal caudal fin and their distribution among marine reptile clades and individual plesiosaurian taxa. Symbols: ✓, present; X, absent; ?, uncertain

Taxonomic group		**Osteological correlate of tail fin**				**Soft tissue evidence**	**Tail fin present?**
		Mediolateral compression of distal vertebrae	**Ventral displacement along vertebral column**	**Distinct node: wedge-shape/ foreshortened vertebra(e)**	**Shift in angle of neural spines**		
Ichthyosauria		✓	✓	✓	?	✓	Yes (McGowan, 1992)
Thalattosuchia		✓	✓	✓	✓	✓	Yes (Fraas, 1902; Young et al. 2010)
Mosasauroidea		✓	✓	✓	✓	✓	Yes (Lindgren et al. 2007, 2008, 2010, 2013)
Plesiosauria	*Rhomaleosaurus* (present study)	✓	? (possible subtle ventral displacement)	✓	?	X	Inferred (present study)
	Cryptoclidus	✓	X	X	✓	X	Inferred (see Wilhelm, 2010)
	Muraenosaurus	✓	X	X	✓	X	Inferred (see Wilhelm, 2010)
	Seeleyosaurus	?	?	?	?	✓ (But unverified)	Inferred (Dames, 1895)
	Archaeonectrus	✓	?	?	?	X	Inferred (Owen, 1865)
	Macroplata	X	✓	✓	?	X	Inferred (Ketchum and Smith, 2010)

groups (Lindgren et al., 2010). Turtles adopted a paraxial locomotory repertoire, however, they are constrained by their carapace and plastron, and a requirement for the females to move on land to lay eggs, whereas plesiosaurs and their ancestors gave birth to live young in the water and were fully aquatic (Cheng et al., 2004; O'Keefe and Chiappe, 2011). The evolution of paraxial locomotion in plesiosaurs may be the direct result of evolutionary constraints developed in the ancestors of plesiosaurs (Storrs, 1993), but may also represent a solution to the problem of Carrier's Contraint (Cowen, 1996). However, the primitive diapsid ancestors of sauropterygians and the most basal members of the clade (pachypleurosaurs) swam using lateral undulations of the body and tail (Storrs, 1993), so there was a considerable behavioural shift from an axial to paraxial locomotory repertoire between basal sauropterygians and derived plesiosaurs. The paraxial condition in plesiosaurians is therefore unique among diapsid marine reptiles (Massare, 1988) and represents a deviation from the typical convergent trend towards tail-propelled (oscillatory) swimming seen in the majority of fully-aquatic vertebrates. Furthermore, the presence of two pairs of limbs for use in propulsive locomotion (but see Lingham-Soliar, 2000) is another unique adaptation among aquatic vertebrates. Given these adaptations for paraxial propulsion it is unlikely that the caudal fin, where present, was used as a propulsive organ. Instead, it may have been used to increase efficiency of the tail as rudder (Buckland, 1837), providing additional manuverability and stability during locomotion (Robinson, 1975). Wilhelm and O'Keefe (2010) suggested that rounded edges on the articular centrum facets in the proximal caudal vertebrae of a possible *Pantosaurus* skeleton (USNM 536965) may have increased lateral flexibility of the proximal tail and allowed it to play a role in locomotion. Experimental analysis will be required to determine the true function of the plesiosaur tail, and the exact outline of the dermal tail fin in different plesiosaurian clades remains speculative pending the discovery of specimens with preserved soft tissues.

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REFERENCES

Andrews, C. W. 1910. A descriptive catalogue of the marine reptiles of the Oxford Clay. Part I. British Museum (Natural History), London, 205 pp.

Andrews, C. W. 1913. A descriptive catalogue of the marine reptiles of the Oxford Clay. Part II. British Museum (Natural History), London, 202 pp.

Andrews, C. W. 1922. Note on the skeleton of a large plesiosaur *(Rhomaleosaurus thorntoni* sp. n.) from the Upper Lias of Northamptonshire. Annals and Magazine of Natural History 10:407–415.

Anon. 1854. Report of the Council of the Yorkshire Philosophical Society. Annual Report of the Yorkshire Philosophical Society for 1853:7–8.

Bakker, R. T. 1993. Plesiosaur extinction cycles — events that mark the beginning, middle and end of the Cretaceous. Special Papers of the Geological Association of Canada 39:641–664.

Bardet, N. and M. Fernandez. 2000. A new ichthyosaur from the Upper Jurassic Lithographic Limestones of Bavaria. Journal of Paleontology 74:503–511.

Benson, R. B. J. and P. S. Druckenmiller. 2013. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. Biological Reviews. 10.1111/brv.12038.

Benson, R. B. J., H. F. Ketchum, D. Naish, and L. E. Turner. 2013. A new leptocleidid (Sauropterygia, Plesiosauria) from the Vectis Formation (early Barremian – early Aptian; Early Cretaceous) of the Isle of Wight and the evolution of Leptocleididae, a controversial clade. Journal of Systematic Palaeontology 11:233–250.

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 (Natural History), Geology 35:253–347.

Buchholtz, E. A. 2001. Swimming styles in Jurassic ichthyosaurs. Journal of Vertebrate Paleontology 21:61–73

Buckland, W. 1837. The Bridgewater Treatises on the Power, Wisdom and Goodness of God as Manifested in the Creation: Treatise 6. Geology and Mineralogy Considered with Reference to Natural Theology. Pickering.

Carpenter, K., F. Sanders, B. Reed, J. Reed, and P. Larson. 2010. Plesiosaur swimming as interpreted from skeletal analysis and experimental results. Transactions of the Kansas Academy of Science 113:1–34.

Cheng, Y-N., X-C. Wu, and Q. Ji. 2004. Triassic marine reptiles gave birth to live young. Nature 432:383–386.

Cowen, R. 1996. Locomotion and respiration in aquatic air-breathing vertebrates. Pp. 337–352 in D. Jablonski, D. H. Erwin, and J. H. Lipps (eds.), Evolutionary Biology. University of Chicago Press.

Cruickshank, A. R. I. 1994. Cranial anatomy of the Lower Jurassic pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia: Plesiosauria). Philosophical Transactions of the Royal Society of London, Series B 343:247–260.

Cruickshank, A. R. I. 1996. The cranial anatomy of *Rhomaleosaurus thorntoni* Andrews (Reptilia, Plesiosauria). Bulletin of the Natural History Museum, London 52:109–114.

Dames, W. 1895. Die plesiosaurier der Süddeutschen Liasformation. Abhandlungen der Königlich Preussischen Akademie der Wissenschaften zu Berlin 1895:1–81.

Fraas, E. 1902. Die meer-krocodilier (Thalattosuchia) des oberen Jura unter specieller berücksichtigung von *Dacosaurus* und *Geosaurus*. Paleontographica 49:1–72.

Fraas, E. 1910. Plesiosaurier aus dem oberen Lias von Holzmaden. Palaeontographica, 57:105–140.

Frey, E. and J. Riess. 1982. Considerations concerning plesiosaur locomotion. Neues Jarbuch für Geologie und Paläontologie Abhandlungen 167:193–194.

Gasparini, Z. 1997. A new pliosaur from the Bajocian of the Neuquen Basin, Argentina. Palaeontology 40:135–147.

Godfrey, S. J. 1984. Plesiosaur subaqueous locomotion: a reappraisal. Neues Jahrbuch für Geologie und Paläontologie 42:661–672.

Kear, B. J. 2006. Marine reptiles from the Lower Cretaceous of South Australia: elements of a high-latitude cold-water assemblage. Palaeontology 49:837–856.

Kear, B. J., N. I. Schroeder, and M. S. Y. Lee. 2006. An archaic crested plesiosaur in opal from the Lower Cretaceous high-latitude deposits of Australia. Biology Letters 2:615–619.

Ketchum, H. F. and R. B. J. Benson. 2010. Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon-sampling in determining the outcome of phylogenetic analyses. Biological Reviews 85:361–392

Ketchum, H. F., and A. S. Smith. 2010. The anatomy and taxonomy of *Macroplata tenuiceps* (Sauropterygia, Plesiosauria) from the Hettangian (Lower Jurassic) of Warwickshire, United Kingdom. Journal of Vertebrate Paleontology 30:1069–1081

Kubo, T., M. T. Mitchell, and D. M. Henderson. 2012. *Albertonectes vanderveldiei*, A new elasmosaur (Reptilia, Sauropterygia) from the Upper Cretaceous of Alberta. Journal of Vertebrate Palaeontology 32:557–572.

Lindgren, J., M. W. Caldwell, and J. W. M. Jagt. 2008. New data on the Postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp, 1942) (Upper Cretaceous: Maastrichtian), and the Taxonomic Status of P. tuckeri (Camp, 1942). Journal of Vertebrate Paleontology 28:1043–1054.

Lindgren, J., M. W. Caldwell, T. Konishi, and L. M. Chiappe. 2010. Convergent evolution in aquatic tetrapods: insights from an exceptional fossil mosasaur. PLoS ONE 5: e11998. doi:10.1371/journal.pone.0011998

Lindgren, J., J. W. M. Jagt, and M. W. Caldwell. 2007. A fishy mosasaur: the axial skeleton of *Plotosaurus* (Reptilia, Squamata) reassessed. Lethaia 40:153–160.

Lindgren, J., H. F. Kaddumi, and M. J. Polcyn. 2013. Soft tissue preservation in a fossil marine lizard with a bilobed tail fin. Nature Communications 4:2423.

Lingham-Soliar, T. 2000. Plesiosaur locomotion: is the four-wing problem real or merely an atheoretical exercise? Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 217:45–87.

Lingham-Soliar, T. 2001. The ichthyosaur integument: skin fibers, a means for a strong, flexible and smooth skin. Lethaia 34:287–302.

Martill, D. M. 1995. An ichthyosaur with preserved soft tissue from the Sinemurian of southern England. Palaeontology 38:897–903.

Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. Journal of Vertebrate Paleontology 7:121–137.

Massare, J. A. 1988. Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. Paleobiology 14:187–205

McGowan, C. 1989. The ichthyosaurian tailbend: a verification problem facilitated by computed tomography. Paleobiology 15:492–436.

McGowan, C. 1992. The ichthyosaurian tail: sharks do not provide an appropriate analogue. Palaeontology 35, 555–570.

Merriam, J. C. 1908. Triassic Ichthyosauria with special reference to the American forms. Memoirs of the University of California 1:1–196.

Motani, R. 2005. Evolution of fish-shaped reptiles (Reptilia: Ichthyopterygia) in their physical environments and constraints. Annual Review of Earth and Planetary Sciences 33:395–420.

Motani, R., H. You, and C. McGowan. 1996. Eel-like swimming in the earliest ichthyosaurs. Nature 382:347–48.

Newman, B. and B. Tarlo. 1967. A giant marine reptile from Bedfordshire. Animals 10:61–63.

Nicholls, E. L. and M. Manabe. 1999. The dorsal caudal fin of an Early Triassic ichthyosaur—the tale of the tail. Paludicola 2:182–89

O'Keefe, F. R. 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). Paleobiology 28:101–112.

O'Keefe, F. R., and M. T. Carrano. 2005. Correlated trends in the evolution of the plesiosaur locomotor system. Paleobiology 31:656–675.

O'Keefe, F. R. and L. M. Chiappe. 2011. Viviparity and K-selected life history in a Mesozoic marine plesiosaur (Reptilia, Sauropterygia). Science 333:870–873.

O'Keefe, F. R., H. P. Street, B. C. Wilhelm, C. D. Richards, and H. Zhu. 2011. A new skeleton of the cryptoclidid plesiosaur *Tatenectes laramiensis* reveals a novel body shape among plesiosaurs. Journal of Vertebrate Palaeontology 31:330–339.

Owen, R. 1865. A monograph on the fossil Reptilia of the Liassic Formations. Part 3. Sauropterygia. Monograph of the Palaeontographical Society 17: 1–40, pl. 1–16.

Riess, J. and E. Frey 1991.The evolution of underwater flight and the locomotion of plesiosaurs. Pp. 131–144 in J. M. V. Raynor and E. J. Wootton (eds.), Biomechanics in Evolution. Cambridge University Press.

Robinson, J. A. 1975. The locomotion of plesiosaurs. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 149:286–332.

Sato, T. and X.-C. Wu. 2008. A new Jurassic pliosaur from Melville Island, Canadian Arctic Archipelago. Canadian Journal of Earth Sciences 45:303–329.

Smith, A. S. 2007. Anatomy and systematics of the Rhomaleosauridae (Sauropterygia: Plesiosauria). Unpublished PhD thesis, School of Biology and Environmental Science, National University of

Ireland, University College Dublin.

Smith, A. S. and G. J. Dyke. 2008. The skull of the giant predatory pliosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics. Naturwissenschaften 95:975–980.

Smith, A. S. and P. Vincent. 2010. A new genus of pliosaur (Reptilia: Sauropterygia) from the Lower Jurassic of Holzmaden, Germany. Palaeontology 53:1049–1063.

Storrs, G. W. 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. American Journal of Science 293-A:63–90.

Tarlo, L. B. 1957. The scapula of *Pliosaurus macromerus* Phillips. Palaeontology 1:193–199.

Taylor, M. A. 1992a. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. Philosophical Transactions of the Royal Society of London, Series B 335:247–280.

Taylor, M. A. 1992b. Taxonomy and taphonomy of *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of the Yorkshire coast. Proceedings of the Yorkshire Geological Society 49:49–55.

Vincent, P. and R. B. J. Benson. 2012. *Anningasaura*, a basal plesiosaurian (Reptilia, Plesiosauria) from the Lower Jurassic of Lyme Regis, United Kingdom. Journal of Vertebrate Paleontology 32:1049–1063.

Vincent, P. and A. S. Smith. 2009: A redescription of *Plesiosaurus propinquus* Tate and Blake, 1876 (Reptilia, Plesiosauria), from the Lower Jurassic (Toarcian) of Yorkshire, England. Proceedings of the Yorkshire Geological Society 57:133–142.

Wegner, T. 1914. *Brancasaurus brancai* n. g. n. sp., ein Elasmosauridae aus dem Wealden Westfalens. Pp. 235-305 in F. Schoendorf (ed.), Branca-Festschrift. Gebrüda Bornträga, Berlin.

Welles, S. P. 1943. Elasmosaurid plesiosaurs with description of new material from California and Colorado. Memoirs of the University of California 13:125–254

Wilhelm, B. C. 2010. Novel anatomy of cryptoclidid plesiosaurs with comments on axial locomotion. M.S. thesis, Marshall University, Huntington, West Virginia, 76 pp.

Wilhelm, B. C. and F. R. O'Keefe. 2010. A new partial skeleton of a cryptoclidid plesiosaur from the Upper Jurassic Sundance Formation of Wyoming. Journal of Vertebrate Paleontology 30:1736–1742.

Williston, S. W. 1914. Water reptiles of the past and present. University of Chicago Press, Chicago, Illinois., 251 pp.

Wiman, C. J. 1920. Some reptiles from the Niobrara group in Kansas. Bulletin of the Geological Institute of Uppsala 18:9–18.

Wiman, C. J. 1946. Über ichthyosaurier und Wale. Senckenbergiana 27:1-11

Woodward, H. 1896. A guide to the fossil reptiles and fishes in the Department of Geology and Palaeontology. British Museum (Natural History). Dept. of Geology. 129 pp.

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

Zarnik, B. 1925. On the ethology of plesiosaurs, with contributions to the mechanism of the cervical vertebrae of recent sauropsids. Royal Morphological-Biological Institute, Zagreb, 1–26.