

The skull of the giant predatory pliosaur *Rhomaleosaurus cramptoni*: implications for plesiosaur phylogenetics

Adam S. Smith · Gareth J. Dyke

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Abstract The predatory pliosaurs were among the largest creatures ever to inhabit the oceans, some reaching gigantic proportions greater than 15 m in length. Fossils of this subclade of plesiosaurs are known from sediments all over the world, ranging in age from the Hettangian (approximately 198 Myr) to the Turonian (approximately 92 Myr). However, due to a lack of detailed studies and because only incomplete specimens are usually reported, pliosaur evolution remains poorly understood. In this paper, we describe the three dimensionally preserved skull of the giant Jurassic pliosaur *Rhomaleosaurus cramptoni*. The first phylogenetic analysis dedicated to in-group relationships of pliosaurs allows us to hypothesise a number of well-supported lineages that correlate with marine biogeography and the palaeoecology of these reptiles. Rhomaleosaurids comprised a short-lived and early diverging lineage within pliosaurs, whose open-water top-predator niche was filled by other pliosaur taxa by the mid-late Jurassic.

Keywords Reptiles · Plesiosaurs · Phylogenetics · Anatomy · Cladistics

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A. S. Smith · G. J. Dyke
School of Biology and Environmental Science,
University College Dublin,
Belfield,
Dublin 4, Republic of Ireland

Present address:

A. S. Smith (✉)
Department of Geology, Trinity College Dublin,
Dublin 2, Republic of Ireland
e-mail: assmith@tcd.ie

Introduction

Plesiosaurs are one of the most familiar groups of Mesozoic marine reptiles. Carnivorous, secondarily aquatic and predominantly marine, these animals ranged in length from less than 2 m up to more than 17 m (Tarlo 1959; Buchy et al. 2003; Noè et al. 2004). However, the evolutionary history and palaeobiology of plesiosaurs remains poorly understood: Recent phylogenetic analyses (O’Keefe 2001; Druckenmiller 2006) have revealed some consensus but debate remains, especially regarding relationships of one early diverging branch, pliosaurs.

Plesiosaurs have long been classified into groups of uncertain monophyly (e.g. Seeley 1892; Persson 1963; Brown 1981; O’Keefe 2001; Druckenmiller 2006). Traditional arrangements recognise two morphotypes—large-headed and short-necked ‘pliosauromorphs’ and small-headed and long-necked ‘plesiosauromorphs’—but encompass other forms that have defied robust phylogenetic placement (O’Keefe 2001). *Rhomaleosaurus* is a large plesiosaur that shares some characteristics with both ‘pliosauromorph’ and ‘plesiosauromorph’ lineages. Because *Rhomaleosaurus* had a long neck compared to other pliosaurs and a gigantic head (Figs. 1a,b and 2), resolving its position within plesiosaur phylogeny is important if we are to better understand and document the evolution of feeding and locomotor adaptations amongst these reptiles (O’Keefe 2002).

Here, we describe the three-dimensional skull of the holotype specimen of *Rhomaleosaurus cramptoni*, one of the largest and best preserved ‘pliosauromorph’ plesiosaurs known (Fig. 2). The original description of this taxon is short and outdated (Carte and Bailey 1863); re-description is warranted because this skull was prepared in 2006. We use newly revealed anatomical data to

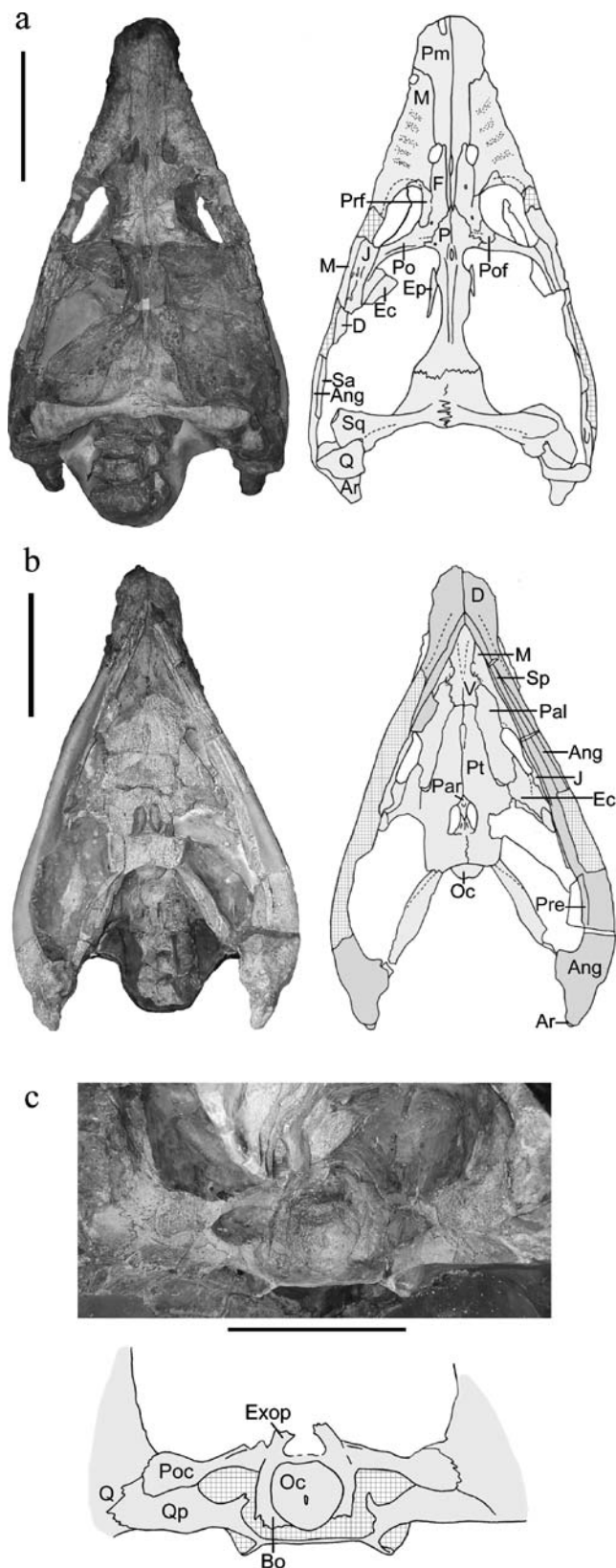


Fig. 1 Photos and drawings of the skull of NMING F8785, *R. cramptoni*: **a** dorsal view, **b** ventral (palatal) view, and **c** posterior view. Cross-hatching in **a** and **b** indicates restored areas, in **c** it represents matrix; dotted lines indicate ridges (scale bar is 30 cm)

present a novel phylogenetic hypothesis for pliosaur relationships.

Material and methods

NMING F8785 (National Museum of Ireland, Natural History), a complete articulated adult specimen (Fig. 2) including the skull (Fig. 1a,b), was unearthed in 1848 in an alum quarry at Kettleless, near Whitby, on the Yorkshire coast of the UK (late Upper Lias, Toarcian; approximately 178 Myr) and was displayed as a centrepiece at the 1853 meeting of the British Association in Dublin. Stored and encased in concrete in Dublin ever since, the specimen became the holotype of *R. cramptoni* (Carte and Bailey 1863). The total length of NMING F8785 was around 7 m (Fig. 2); skull length along the dorsal midline is 88 cm. A cladistic analysis was performed using PAUP (version 3.04; Swofford 2000; see S1 for characters and S2 for the data matrix) comprising 39 taxa, 93 characters and the sauropterygian *Cymatosaurus* (Rieppel 2000) as an out-group.

Systematic paleontology

- Plesiosauria de Blainville 1835
- Pliosauroida Seeley 1874
- Rhomaleosauridae (Nopsca 1928)
- *Rhomaleosaurus* Seeley 1874
- *R. cramptoni* (Carte and Bailey 1863)

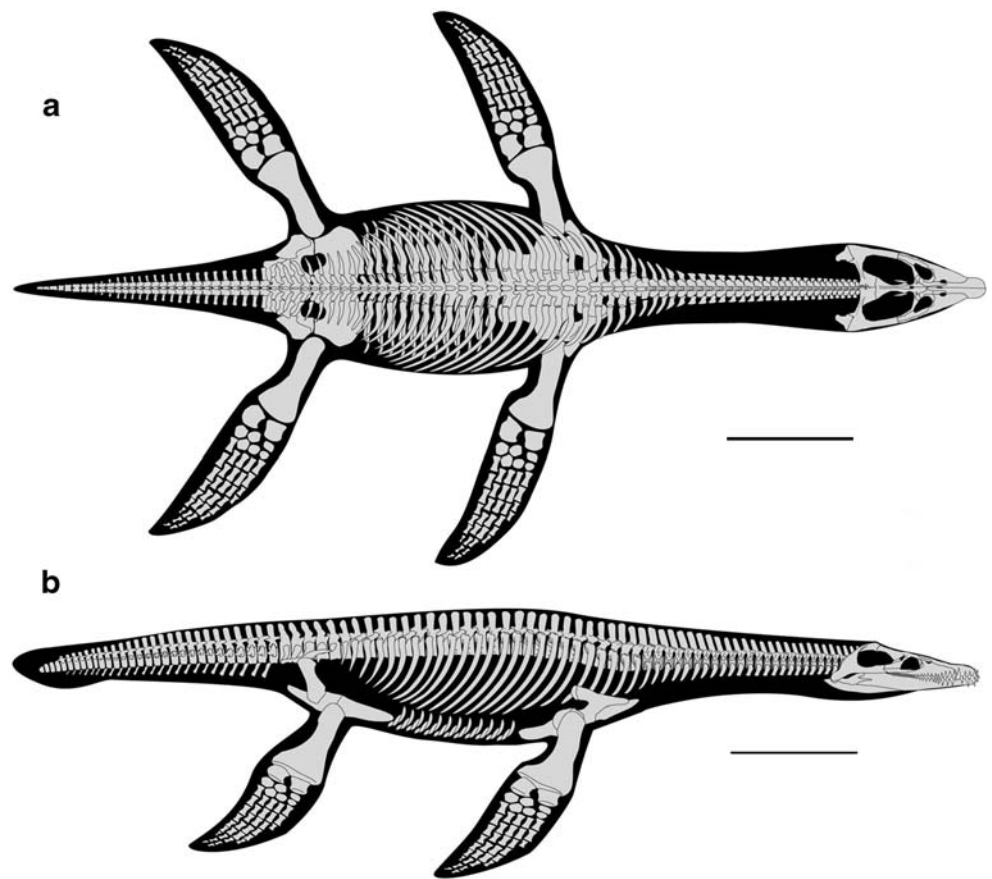
Revised diagnosis

Rhomaleosaurus is a large pliosaur characterised by the following apomorphic combination of skull characters, as identified by phylogenetic analysis: (1) rounded dorsomedian foramen situated between the nares, (2) foramina present on the frontals, (3) premaxilla–maxilla sutures run parallel to each other anterior to the nares, (4) palatine excluded from internal naris (choanae), (5) length and width of premaxillary rostrum subequal, (6) short mandibular symphysis (length/width=0.60–0.89), (7) rounded bulb/bump protruding from the medial margin of the retroarticular process and (8) presence of a quadrate foramen.

Description and comparison

The skull of NMING F8785 is preserved three dimensionally (Fig. 1a–c). The premaxillae form a short rounded spatulate rostrum with a total of five tooth positions each. The occiput is deep and the jaws as preserved are fully

Fig. 2 Full body reconstruction of *Rhomaleosaurus* in **a** dorsal and **b** lateral view (scale bar is 1 m)



occluded. Large oval nares are positioned close to (53 mm away from) the orbits as in all plesiosaurs and there is a lozenge-shaped dorsomedian foramen bordered by a raised margin on the midline between the external nares (Fig. 1a); this character is also seen in *R. zetlandicus* and *R. propinquus*. Taylor (1992) noted the presence of this feature in *R. victor* and a cleft was also figured for this taxon by Fraas (1910; Taf. X).

Anterior to the external nares is a sharp median ridge; this feature is also developed in all species of *Rhomaleosaurus* and forms a crest in *Umoonasaurus* (Kear et al. 2006). Unlike most plesiosaurs, the premaxillae do not diverge immediately anterior to the nares and the premaxilla–maxilla sutures run parallel, as is also the case in *R. zetlandicus*, *R. propinquus*, *R. thorntoni* and *Maresaurus* (Smith 2007). Each maxilla produces a triangular flange that protrudes dorsally between the frontal and the prefrontal. The frontals are elongate bones separated medially by a long posterior premaxillary process; each sends a broad anterior process to the external naris margin and almost excludes the premaxilla from the margin of the external naris (Fig. 1a). The frontals are also separated in all other Toarcian plesiosaurs, whereas they contact in the older *R. megacephalus* (Cruickshank 1994).

The anteromedial border of the orbit is formed by the prefrontal. There is a distinct postorbital ridge and the parietal bears a square lateral process. A lozenge-shaped pineal foramen is situated on the midline between the fused parietals (Fig. 1a). The postfrontals are small triangular elements that contribute to the posteromedial margins of the orbit. Each postorbital ridge forms the majority of the postorbital bar while the jugal is elongate and forms the posterolateral margin of each orbit. The squamosals are large tri-radiate elements forming the entire posterior margins of the supratemporal fenestrae and expand into a squamosal–parietal plate as described for *R. zetlandicus* (Taylor 1992) and also present in *R. propinquus* and *R. megacephalus* (Smith 2007).

A convex posterior bulb is formed where the squamosals meet on the midline; anteriorly, they contact the parietal along a transverse inter-digitating suture forming an expanded plate (Fig. 1a). There is a quadrate foramen between the squamosal and quadrate at the dorsal tip of the quadrate; this foramen is also present in *R. zetlandicus* (Taylor 1992).

The palate of NMING F8785 is complete (Fig. 1b). The fused vomers extend posteriorly between the choanae and expand laterally to wrap around the posterior margin of

each to contact the maxilla. This is also the case in *R. zetlandicus*, *R. thornstoni* and *R. victor*, whereas in *R. megacephalus*, the palatines in these specimens do contact the internal naris. A raised bump is formed at the anterior part of the vomer–palatine suture (Fig. 1b), also present in *R. zetlandicus* (Smith 2007). Posteriorly, the vomers contact the pterygoids on the midline along a straight, transversely orientated suture and the maxilla forms the lateral margin of each internal naris. The pterygoids are large plate-like elements; there is no open anterior interpterygoid vacuity, although the pterygoids are separated on the midline and filled by bone (parasphenoid?). This contrasts with the narrow open anterior interpterygoid vacuities in *R. megacephalus* (Cruickshank 1994), as well as the broad anterior interpterygoid vacuity in *R. victor* (Fraas 1910). The pterygoids form a square plate caudal to the posterior interpterygoid vacuities and meet medially (Fig. 1b). The cultriform process is exposed on the palate; it is short with a ventrally facing concave surface. The cultriform process is short as in all other species of *Rhomaleosaurus*, but it is completely absent in *R. victor*. There are small (20 mm long) but distinct lateral palatal vacuities between the palatines and pterygoids, and the suborbital fenestrae are large and elongate, widest anteriorly, slightly pinched towards the posterior and expanded again slightly at the posterior border (Fig. 1b). The flat face of the prominent ectopterygoid boss is directed ventrolaterally and the surface is distinctly ornamented with pits (as in crocodylians) indicating the presence of a plate of cartilage.

The basicranium of NMING F8785 is exposed in ventral and posterior view (Fig. 1c). The parasphenoid forms a sharp ventral keel and merges into the basi-sphenoid posteriorly, while the occipital condyle of the basioccipital extends beyond the posterior margin of the pterygoid plates (Fig. 1c). There is no evidence for the exposure of the basioccipital on the posterior-most ventral surface of the palate between the pterygoids in *R. cramptoni*, as inferred for *R. zetlandicus* (Taylor 1992). A dorsoventrally orientated oval pit is present on the posterior of the occipital condyle. The occipital condyle is situated dorsal to the level of the pterygoid plates of the quadrate–pterygoid flange. The posterior margin of the foramen magnum slopes posteriorly so that the dorsal parts of each exoccipital–opisthotic and all of the supraoccipital are obscured by matrix. The paroccipital process is a splint of bone angled posteriorly and slightly ventrally. Distally, this process forms a spatula, which contacts the quadrate–pterygoid flange. Proximally, the paroccipital process and quadrate–pterygoid flange are separated but, distally, they unite for half of their length before broadly contacting the medial wall of the squamosal and quadrate flange (Fig. 1c).

Fig. 3 Strict consensus tree for pliosaurs (a) and close up of the Rhomaleosauridae (50% majority-rule consensus) (b) with skull cartoons. This clade is supported by the following apomorphies: diminutive contact of premaxilla with external naris (except *Archaeonectrus*; confidence interval (CI)=0.667), accessory grooves on the palatal surface (CI=1.0); bowed mandible (except *Archaeonectrus*, shared with *Plesiosaurus*, *Simolestes*; CI=0.5); between 27 and 29 cervical vertebrae (except *Macroplata*; CI=0.571); nutritive foramina on cervical vertebrae sunk in deep depressions (shared with *L. clemati*, *Dolychorhynchops*; CI=0.5); large nutritive foramina on cervical vertebrae (except *Macroplata*, shared with *Dolychorhynchops*, *L. clemati*; CI=0.286)

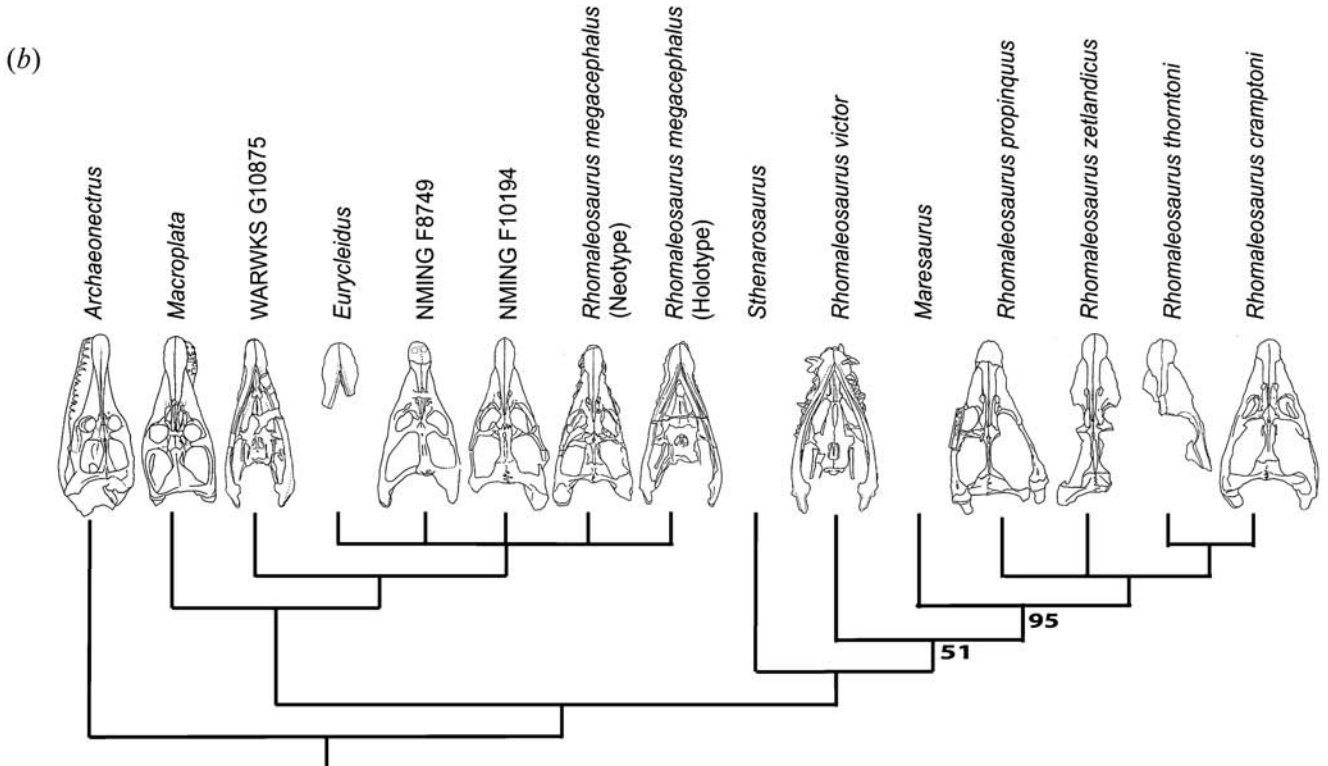
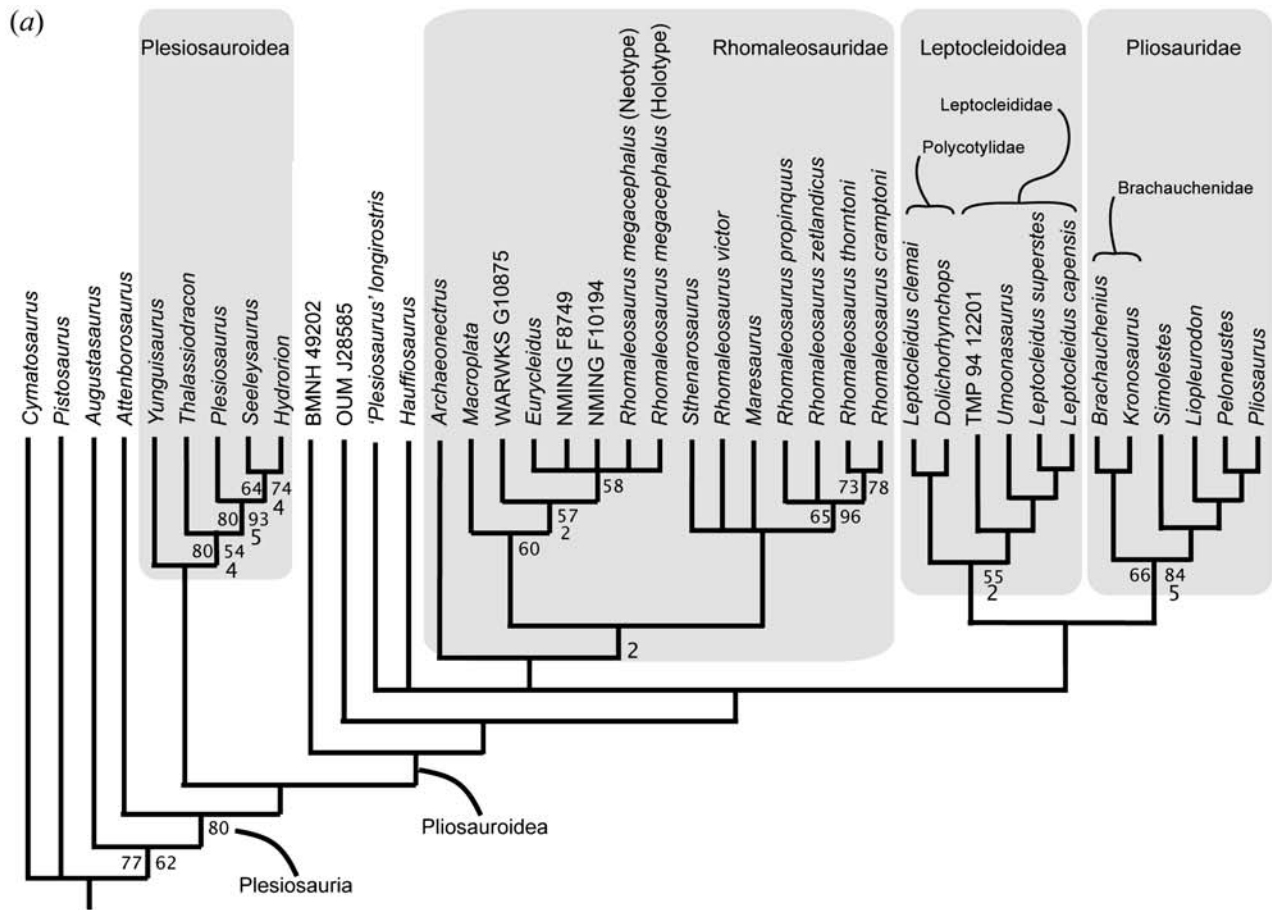
Discussion

Results of the cladistic analysis are presented in Fig. 3a. A heuristic search strategy implemented in PAUP led to the generation of 2,114 equally most parsimonious trees (MPTs), each of 364 steps in length when a standard character ordering sequence is used (re-running the matrix by use of unordered characters results in no changes to major clade topologies).

Our hypothesis suggests the presence of three clades of pliosaurs—Pliosauridae, Rhomaleosauridae and Leptocleidoidea—in broad agreement with earlier studies (O’Keefe 2001; Druckenmiller 2006). The rhomaleosaurid lineage is proposed to be the sister taxon of the Pliosauridae and Leptocleidoidea, which comprise the traditionally defined ‘pliosauro-morph’ plesiosaurs (O’Keefe 2002; Fig. 3).

The strict consensus of the MPTs is shown in Fig. 3a—*R. cramptoni* is nested within a monophyletic Rhomaleosauridae, with the other named species in this genus and alongside the taxa *Archaeonectrus*, *Macroplata*, *Euycleidus*, *Sthenarosaurus* and *Maresaurus* (Fig. 3b). The genus *Rhomaleosaurus* is, however, not monophyletic and should therefore be restricted to encompass just *R. cramptoni* and its Toarcian relatives (i.e. *R. zetlandicus*, *R. thornstoni* and *R. propinquus*). *R. megacephalus* and *R. victor* do not belong to this genus; both taxa are currently under revision (Smith 2007). Although recovered in all MPTs, Rhomaleosauridae is supported by just one unambiguous synapomorphy, the presence of accessory grooves on the palatal surface (character 34; S1 characters). Additional characters that also support this lineage in the cladistic analysis are given in the caption to Fig. 3.

On the basis of our phylogenetic hypothesis (Fig. 3a), Rhomaleosauridae is restricted in age to the Lower Jurassic and early Middle Jurassic and comprises a short-lived early radiation of pliosaurs. *Maresaurus* is the youngest known member of this clade. Subsequent to their extinction, the open-water top-predator niche occupied by these marine reptiles was filled in the mid-late Jurassic by the shorter-necked pliosaurids; as suggested by O’Keefe (2002), these



marine reptiles diversified rapidly as marine predators, experimenting with a range of morphologies.

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