



# A NEW GENUS OF PLIOSAUR (REPTILIA: SAUROPTERYGIA) FROM THE LOWER JURASSIC OF HOLZMADEN, GERMANY

by ADAM. S. SMITH\* and PEGGY VINCENT†

\*Natural History Division, National Museum of Ireland, Merrion Street, Dublin 2, Ireland; e-mail adsmith@museum.ie

†Muséum National d'Histoire Naturelle de Paris, Département Histoire de la Terre, CNRS UMR 7207, 57 rue Cuvier, CP 38, 75231 Paris Cedex 05, France; e-mail pvincent@mnhn.fr

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**Abstract:** The exquisitely preserved holotype of the pliosaur '*Rhomaleosaurus*' *victor* (SMNS 12478) is described from the Toarcian Posidonien-Schiefer (Upper Lias, Lower Jurassic) of Holzmaden (Baden-Württemberg), Germany. The specimen presents a novel combination of synapomorphies and unique morphometric proportions separating it from *Rhomaleosaurus sensu stricto* and warranting the erection of a new genus, *Meyerasaurus* gen. nov. Historically, the name '*Thaumatosaurus*' has been interchangeable with *Rhomaleosaurus* and is frequently associated with SMNS 12478 in the literature. However, this is an invalid taxon and cannot be reinstated. The anatomy of *Meyerasaurus victor* is compared in detail with other pliosaurs, and its taxonomic affinity is reviewed. *M. victor* belongs to the family Rhomaleosauridae and shares several anatomical characters with *Rhomaleosaurus*

including a short and robust premaxillary rostrum (length-to-width ratio *c.* 1.0), parallel premaxilla–maxilla sutures anterior to the nares, vomers contacting the maxillae posterior to the internal nares, and *c.* 28 cervical vertebrae minus the atlas–axis. The known geographical distribution of *Rhomaleosaurus*, which previously extended across the German and English palaeobiogeographical zones, is reduced to the English zone as a consequence of the referral of SMNS 12478 to a new genus. This is significant because it contributes to an ongoing trend of increasing generic separation between the German and English zones, while increasing the generic diversity within the German zone itself.

**Key words:** Plesiosauria, Pliosauroida, Posidonien-Schiefer, '*Thaumatosaurus*', *Rhomaleosaurus victor*, *Meyerasaurus*.

PLESIOSAURIANS are a group of predatory marine reptiles whose stratigraphical range extends from the uppermost Triassic (Rhaetian) to the uppermost Cretaceous (Maastrichtian) (Persson 1963; Storrs 1994). They form a significant component of the Lias (Early Jurassic) marine reptile fauna in Europe. In particular, the Posidonien-Schiefer (Toarcian) of Holzmaden, Baden-Württemberg in south-western Germany has yielded many excellently preserved specimens and received considerable research attention (Maisch and Rücklin 2000; O'Keefe 2004; Grossmann 2006, 2007). The plesiosaurs found within these deposits are always significantly outnumbered by ichthyosaurs (Hauff 1921, 1953; Hauff and Hauff 1981). The long-necked plesiosauroids *Hydrorion* (Grossmann, 2007), and *Seeleyosaurus* (White, 1940) (Grossmann 2006, 2007) are the most abundant taxa within the plesiosaur assemblage. Pliosauroids on the other hand are rare; only two species are currently known from the Posidonien-Schiefer. The pliosaurid *Hauffiosaurus zanoni* O'Keefe, 2001 is known from a single specimen (HAUFF 'Uncatalogued') described briefly by O'Keefe

(2001) and is currently under study by one of the authors (PV). The second pliosauroid taxon is the rhomaleosaurid *Rhomaleosaurus victor* (Fraas, 1910), which forms the topic of this paper. The family Rhomaleosauridae is not recognized by all workers and recent cladistic analyses of plesiosaurs conflict in this area, with O'Keefe (2001) and Smith and Dyke (2008) both recognizing a distinct rhomaleosaurid clade whereas Druckenmiller and Russell (2008) do not.

Seeley (1874) introduced *Rhomaleosaurus* as a new name for *Plesiosaurus cramptoni* based on a specimen (NMING F8785) that is the holotype for the genus and for the family Rhomaleosauridae (Smith and Dyke 2008). Numerous species have since been allocated to this genus, including SMNS 12478. Many of these specimens have been redescribed since; *Rhomaleosaurus zetlandicus* (Phillips, 1854) was described by Taylor (1992a, b); *Rhomaleosaurus megacephalus* (Stutchbury, 1846) by Cruickshank (1994); *Rhomaleosaurus thornstoni* (Andrews, 1922a) by Cruickshank (1996); *Rhomaleosaurus cramptoni* (Carte and Bailly, 1863) by Smith and Dyke (2008); and

*Rhomaleosaurus propinquus* (Tate and Blake 1876) by Vincent and Smith (2009). Smith and Dyke (2008) recognized that the genus *Rhomaleosaurus* is polyphyletic with respect to *Maresaurus*, *Sthenosaurus*, *Macroplata* and *Eurycleidus* and considered '*Rhomaleosaurus*' *megacephalus* and '*Rhomaleosaurus*' *victor* as generically separate from *Rhomaleosaurus sensu stricto*. Vincent and Smith (2009) recognized *R. propinquus* as a junior synonym of *R. zetlandicus*. Consequently, the number of species referred to *Rhomaleosaurus* has been reduced, and the systematic position of many taxa formerly referred to *Rhomaleosaurus* needs reassessment.

SMNS 12478, the holotype of '*Rhomaleosaurus*' *victor*, was briefly re-examined by O'Keefe (2001), but it has not been properly described in the literature since the original description a century ago (Fraas 1910). Given this fact and the current state of flux within plesiosaur palaeontology in general, modern description and systematic review of SMNS 12478 is vital. The specimen was damaged during a bombing raid on the city of Stuttgart in 1944, but the fossil was rescued from the wreckage, and the missing and damaged parts were reconstructed based on the original description. Despite this incident, the fossil is still well preserved and complete and has been figured as an exemplar plesiosaur specimen by numerous authors over the last 120 years (e.g. Nicholson and Lydekker 1889; Williston 1914, 1925; Romer 1933, 1956; O'Riordan 1983; Hauff and Hauff 1981; Storrs 1993; Smith 2008a).

This paper provides a detailed re-examination of the skull and postcranium of SMNS 12478, the holotype of '*Rhomaleosaurus*' *victor*. Complete plesiosaurs preserving the skull and postcranium in association are extremely rare and thus highly important. Given the excellent state of completeness, together with its stratigraphical position early in the history of plesiosaurs, a thorough modern description of '*R. victor*' is vital for understanding the evolution and origins of plesiosaurs, and it will also form a sound basis for understanding the anatomy of other early plesiosaurs. A detailed comparison of SMNS 12478 with other taxa, especially those pertaining to *Rhomaleosaurus*, confirms that it represents a new genus. Finally, we assess the significance of our findings for the diversity and palaeobiogeographical distribution of Toarcian plesiosaurs.

*Institutional abbreviations.* HAUFF, Urwelt Museum Hauff, Holzmaden, Germany; LEICS, Leicestershire Museums, Arts and Records Services, Leicester, UK; BMNH, Natural History Museum, London, UK; NMING, National Museum of Ireland – Natural History, Dublin, Ireland; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; YORYM, Yorkshire Museum, York, UK.

*Anatomical abbreviations.* a, angular; aiv, anterior interpterygoid vacuity; ar, articular; at, atlas; bo, basioccipital; bop, basioccipital

basipterygoid process; d, dentary; ec, ectopterygoid; en, external naris; eo?, exoccipital opisthotic; gl, glenoid fossa; hy, hyoid element; imf, intermandibular foramen; in, internal nares; mx, maxilla; oc, occipital condyle; orb, orbit; pa, prearticular; pal, palatine; paf, palatal fenestra; piv, posterior interpterygoid vacuities; pmx, premaxilla; ps, parasphenoid; pt, pterygoid; ptfl, lateral flange of pterygoid; q, quadrate; sa, surangular; sq, squamosal; sp, splenial; v, vomer.

## RHOMALEOSAURUS OR 'THAUMATOSAURUS'?

SMNS 12478 was first described by Fraas (1910) under the name '*Thaumatosauros*' *victor*. Historically, the genus *Rhomaleosaurus* has been interchangeable with '*Thaumatosauros*'. The confusion between these two taxa arose from taxonomic inconsistency between Richard Lydekker and Harry G. Seeley, two prolific nineteenth-century palaeontologists who both 'refused steadfastly to recognize the generic and specific names proposed by one another' (Tarlo 1960, p. 148). Seeley named *Rhomaleosaurus* in 1874 based on a specimen already named *Plesiosaurus cramptoni* (Carte and Baily, 1863) (NMING F8785); however, Lydekker (1889a, b, 1891) regarded *Rhomaleosaurus* as a synonym of '*Thaumatosauros*', a genus named by von Meyer (1841) on the basis of fragmentary skull, vertebral and limb material from Württemberg, Germany ('*Thaumatosauros oolithicus*'). Meyer (1856) provided a full description and figured the holotype material of '*T. oolithicus*' in a later paper. The subsequent use of '*Thaumatosauros*' (over *Rhomaleosaurus*) was most noticeable and influential in Lydekker's catalogues of the fossil Reptilia and Amphibia produced for the British and Irish Natural History Museums (Lydekker 1889b, 1891). Fraas (1910) recognized both generic names in his original description of SMNS 12478 but followed Lydekker, referring SMNS 12478 to the new species '*Thaumatosauros*' *victor*. The name '*Thaumatosauros*' was adopted by many other researchers (e.g. Brandes 1914; von Huene 1921; Williston 1925; Storrs 1993) and used in many popular texts (e.g. Nicholson and Lydekker 1889; Williston 1914; Romer 1933, 1956; O'Riordan 1983; Hauff and Hauff 1981). This genus became popularized due to the exceptional preservation of SMNS 12478 (Tarlo 1960).

As early as 1922, Andrews (1922b) pointed out the insufficiency of the holotype of '*Thaumatosauros*' and created a new genus name (*Eurycleidus*) for Hettangian plesiosaurs formerly attributed to '*Thaumatosauros*'. However, Andrews (1922b) did not officially reject the name '*Thaumatosauros*', nor did he mention the Toarcian genus *Rhomaleosaurus*. Zittel (1932) also accepted the indeterminate nature of the type material of '*Thaumatosauros*'.

*saurus*' but did not formally reject it. Introducing more confusion, some authors have recognized *Rhomaleosaurus* and '*Thaumatosauros*' as distinct taxa (e.g. White 1940). Tarlo (1960) finally resolved the issue and formally rejected the genus '*Thaumatosauros*' due to its inadequate type material. Tarlo (1960) consequently referred SMNS 12478 to *Rhomaleosaurus*. Based on the descriptions and figures provided by Meyer (1841, 1856), the holotype material of '*Thaumatosauros oolithicus*' possesses no autapomorphies or character combinations upon which it can be considered valid. We therefore regard this taxon as a *nomen dubium*. The highest taxonomic level the specimen can be referred to is Pliosauroida *indet* based on the relatively short proportions of the cervical centra (their height exceeds length) (Brown 1981). Moreover, as shown below, '*Rhomaleosaurus victor*' is not referable to *Rhomaleosaurus*, and erection of a new genus for the reception of this material is therefore necessary.

## SYSTEMATIC PALAEOLOGY

Class REPTILIA Linnaeus, 1758

Superorder SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLIOSAUROIDEA (Seeley, 1874) Welles, 1943

Family RHOMALEOSAURIDAE (Nopcsa, 1928) Kuhn, 1961

Genus MEYERASAURUS gen. nov.

*Derivation of name.* The genus name *Meyerasaurus* honours the German palaeontologist Hermann von Meyer who proposed the now defunct generic name '*Thaumatosauros*' ('wonder reptile') once popularly applied to specimen SMNS 12478.

*Type species.* *Meyerasaurus victor* (Fraas, 1910). This genus is currently monospecific.

*Diagnosis.* As for the type and only species, *Meyerasaurus victor*.

*Meyerasaurus victor* (Fraas, 1910)

Text-figures 1–4

1910 *Plesiosaurus victor* Fraas, p. 114.

1910 *Thaumatosauros victor* Fraas, pp. 123–140, pls 8–10.

1932 *Eurycleidus victor* Zittel, p. 292.

1960 *Rhomaleosaurus victor* Tarlo, p. 178.

*Holotype.* SMNS 12478 (Text-figs 1–4), complete specimen exposed in ventral view.

*Range and distribution.* Holzmaden, Baden-Württemberg, Germany. Posidonien-Schiefer, Lias epsilon II, 3 (Unterer Schiefer),

*falciferum* ammonite Zone, *elegantulum-falciferum* Subzones, Lower Toarcian, Lower Jurassic (Röhl *et al.* 2001).

*Diagnosis.* Moderately sized pliosauroid with the following unique combination of characters: constricted rostrum; large broad anterior interpterygoid vacuity; lateral palatine vacuities between the palatines and pterygoids; absence of a cultriform process; pterygoids meet behind the posterior interpterygoid vacuities; basioccipital tubers visible and projecting beyond the posterior margin of the pterygoid plate; bowed mandible; reinforced and keeled spatulate symphysis; posteriorly inclined dorsal surface of retroarticular process; large teeth with lingual striations; interclavicle–clavicle complex with deep mesial notch and triangular lateral wings; scapulae separated on the midline; coracoids in contact along their entire length; humerus recurved and longer than femur; epipodials longer than wide; ten rows of gastralia. No autapomorphic characters were identified.

*Remarks.* *Meyerasaurus* differs from *Rhomaleosaurus* in its smaller overall size, presence of a broad open anterior interpterygoid vacuity, absence of a cultriform process, basioccipital tubers visible and projecting beyond the posterior margin of the pterygoid plate, posteriorly inclined dorsal surface of retroarticular process, coracoids in contact along their entire length and the possession of recurved humeri. *Meyerasaurus* also shows considerable proportional differences from *Rhomaleosaurus*: in relative terms, its skull is much smaller, the rostrum is shorter and wider, and the humeri are much larger than in *Rhomaleosaurus*.

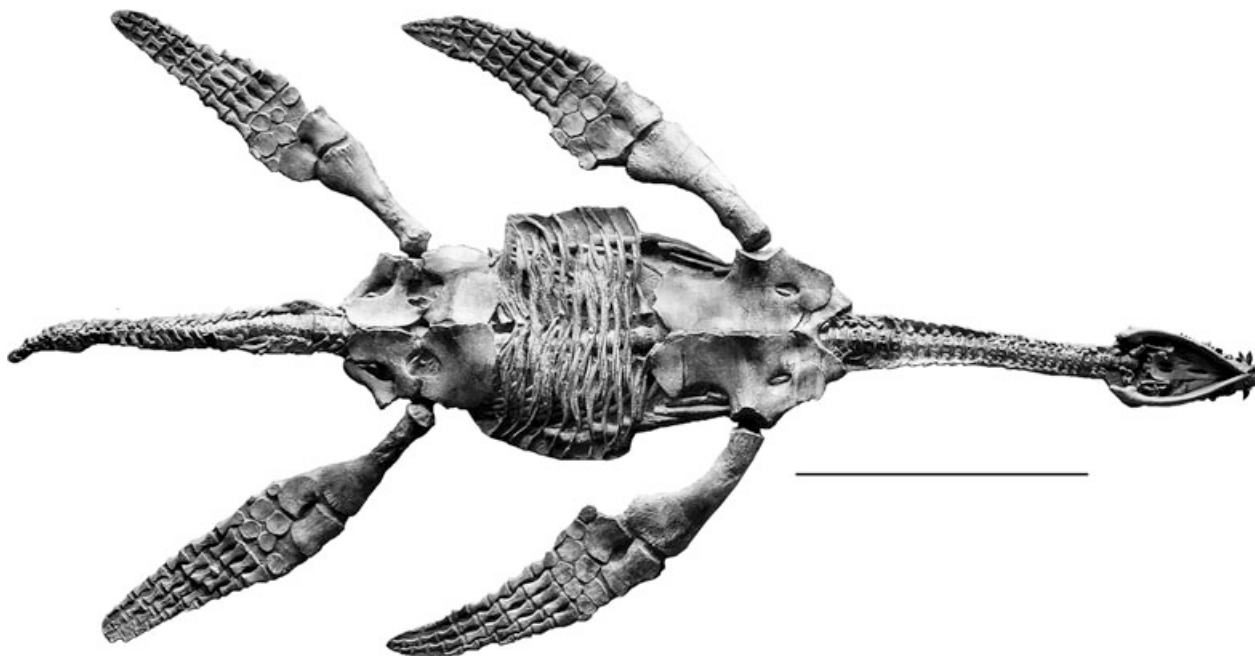
*Comment.* As explained by Tarlo (1960, p. 178) and expanded upon above, '*Thaumatosauros*' is an invalid taxon and cannot be reinstated for SMNS 12478.

### Description

*Skull.* SMNS 12478 is a complete articulated skeleton exposed in ventral view (Text-fig. 1). The animal is 3.35 m long in total with a skull length of 37 cm. A dorsal view of the postcranium was described by Fraas (1910) but is no longer visible due to the orientation of the specimen as mounted.

*Skull roof.* Most of the dorsal parts of the skull are missing, and only segments of the premaxillae, maxillae, squamosals and quadrates are visible (Text-fig. 2A, B). The palate and the mandible, however, are complete and extremely well preserved; the bone surface shows considerable detail (Text-fig. 2C, D). The jaws are fully occluded with most of the teeth located approximately *in situ*.

The premaxillae form a spatulate rostrum that is ornamented with numerous vascular foramina and radiating striations



**TEXT-FIG. 1.** SMNS 12478, *Meyerasaurus victor* (Fraas, 1910); Toarcian of Holzmaden (Germany). Skeleton in ventral view. Scale bar represents 100 cm.

(Text-fig. 2A, B), which correlate to the deep sockets for the implantation of the enlarged premaxillary teeth. The posterior-most parts of the premaxillae are not preserved, but they form a median posterior process, which extends between the external nares and contributes to their anterolateral margins. Anterior to the external nares the premaxillae form a rounded longitudinal midline crest. Each premaxilla-maxilla suture runs from the anterior border of the external nares to the lateral border of the rostrum, where it is marked by a constriction. It is unclear if there is a dorsomedian foramen between the external nares. The snout measures 10.5 cm from the external nares (anterior border) to the anterior tip of the rostrum. The premaxillae are obscured ventrally by the mandibular symphysis.

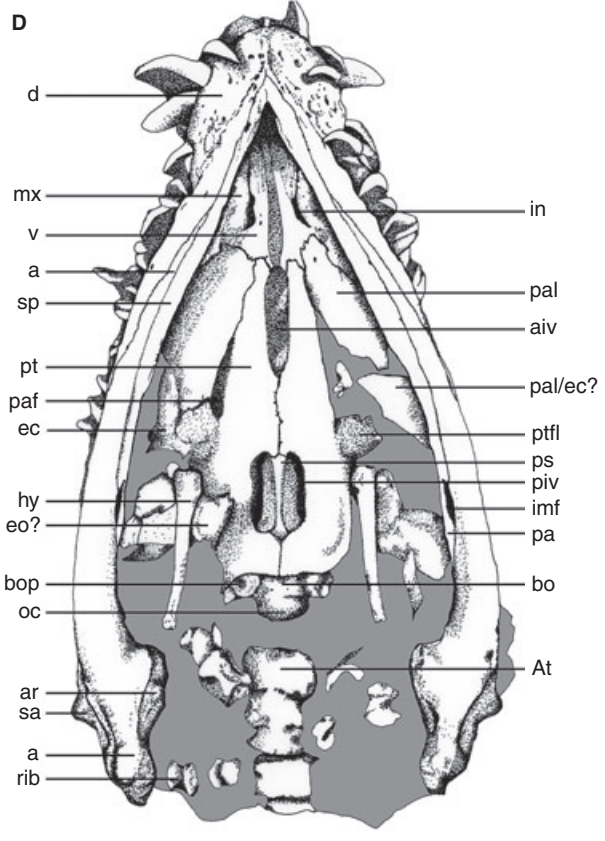
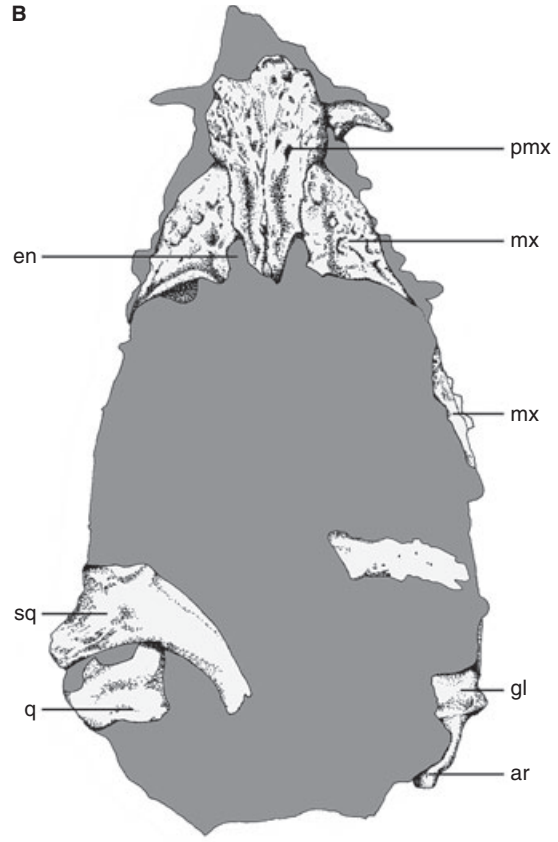
The maxillae appear to be very elongate, but their posterior extent cannot be determined. The maxilla contributes to the lateral margin of the external nares and the anterolateral margin of the orbits and contacts the lateral margin of the internal naris on the palate. The posteriormost portion of maxilla, preserved on the right side, extends as far as the coronoid eminence of the mandible, so the maxillae probably contributed to the lateral margins of the orbits and certainly extended posterior to them. The anterodorsal surfaces of the maxillae are broad and convex, with a prominent ornament consisting of numerous vascular foramina and striations. Broad furrows and ridges correspond to underlying sockets for the implantation of the large maxillary teeth. Ventrally the maxillae contact the vomers medial, anterior

and posterior to the internal nares. The maxillae also contact the palatines posteriorly. It is difficult to count the number of maxillary teeth, but there are at least 13 alveoli in the right maxilla.

The external nares are large, longitudinally ovate openings, but their posterior parts are not preserved. They are situated close to each other (2 cm apart) and are separated by the narrow facial processes of the premaxillae. They are retracted close to the anterior margin of the orbits. The preserved part of the left squamosal and quadrate are not very informative. The partially preserved squamosal is thick and arc-shaped. The articular surface of the quadrate forms a very wide and transversely concave trochlea.

*Palate and occiput.* The elongate vomers form the anterior part of the palate (Text-fig. 2C, D). Anterior to the internal nares they expand in width, but the anteriormost regions are obscured by the occluded mandibular symphysis. The vomers occupy a position between the internal nares, and each contacts the maxilla anteriorly and the pterygoid and palatine posteriorly. Each vomer wraps around the posterior margin of the internal naris to contact the maxilla along a short lateral suture that excludes the palatine from the margin of the internal naris. The vomers do not appear to be co-ossified although this apparent separation might be a preservational artefact. The internal nares are positioned slightly anteriorly relative to the external nares: the openings are narrower than the external nares and are 1.9 cm

**TEXT-FIG. 2.** SMNS 12478, *Meyerasaurus victor* (Fraas, 1910); Toarcian of Holzmaden (Germany). A, B, skull in dorsal view. A, photograph. B, interpretative drawing. C, D, skull in ventral view; C, photograph; D, interpretative drawing. See text of abbreviations. Scale bar represents 10 cm.





**TEXT-FIG. 3.** SMNS 12478, *Meyerasaurus victor* (Fraas, 1910); Toarcian of Holzmaden (Germany). A, photograph of skull in right lateral view. B, C, skull in left lateral view. B, photograph. C, interpretative drawing. D, photograph of mandible in oblique view showing medial surface of right ramus. See text of abbreviations. Scale bars represent 10 cm.

long. The openings face laterally so that in ventral view the maxilla forms a flat sunken plate at the base of each internal naris.

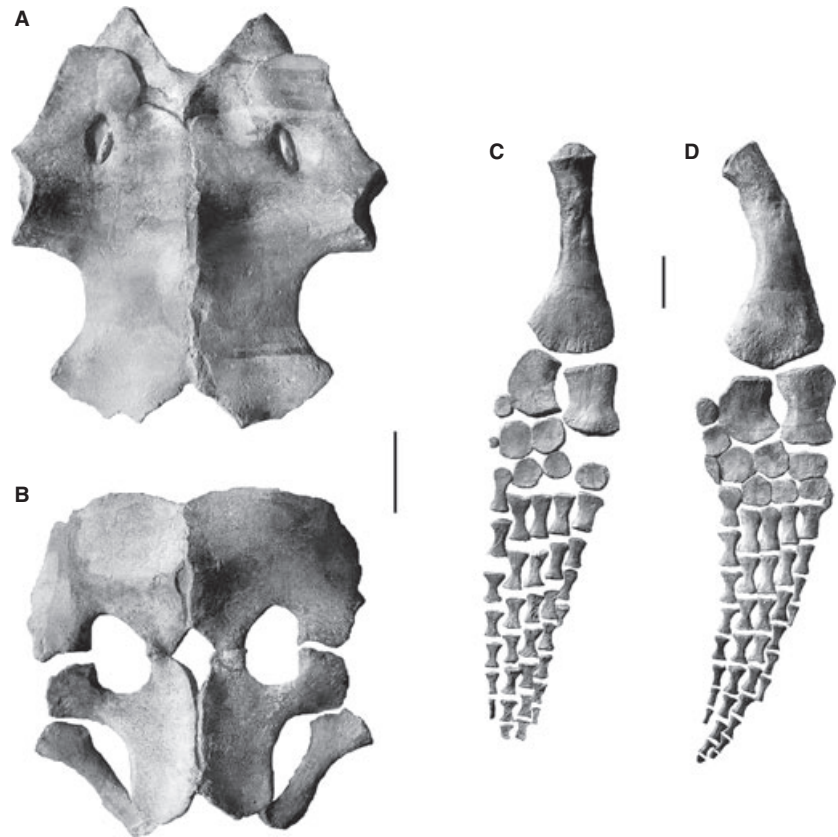
The palatines are large elongate bones that extend from the vomers to the lateral flange of the pterygoids. The right palatine is complete, but the left one is damaged posteriorly. Right and left palatines are separated along their entire length. Laterally, the palatine contacts the maxilla, and medially it contacts the pterygoid for half of its length; there is an elongate lateral palatine vacuity separating them posteriorly (Text-fig. 2C, D). Each lateral palatine vacuity is 4.5 cm long with a maximum diameter of 0.8 cm and represents an absence of fusion between the pterygoid and the palatine. The left lateral palatine vacuity is poorly visible due to *post mortem* displacement of the palatine, but the right opening is clear and forms a tear-drop shape that narrows anteriorly. Posteriorly the palatine contacts the pterygoid again medial to lateral palatine vacuity and contacts the ectopterygoid posterolaterally.

The pterygoids are the largest palatal bones, extending far posteriorly below and lateral to the braincase. Each pterygoid has anterior, posterior and lateral rami. The two anterior rami enclose an anterior interpterygoid vacuity and contact the vomers and palatines. The anterior interpterygoid vacuity is very large, elongate and broad (5.7 cm long with a maximum diameter of 1.3 cm) with curved anterior and posterior margins.

It is unclear whether the pterygoids contact each other anterior to the anterior interpterygoid vacuity. They appear to be separated, but this may be a taphonomic artefact; the separation is confluent with that described above for the vomers. The bones enclosing the anteriormost part of the anterior interpterygoid vacuity are also obscured by cracks concealing the suture between the vomers and the pterygoids. The lateral ramus of the pterygoid forms a squared projection contacting the ectopterygoid laterally and the palatine anteriorly, and the pterygoids reach their widest extent at this point. The pterygoids contact each other on the midline between the anterior interpterygoid vacuity and the anterior border of the parasphenoid. The posterior ramus of the pterygoid is very large and forms a square plate of bone surrounding the anterior, lateral and posterior borders of the posterior interpterygoid vacuity. The posterior interpterygoid vacuities (Text-fig. 2C, D) are kidney-shaped, deep and oriented anteroposteriorly (3.9–4.1 cm long and 1.4–1.3 cm wide). In this region, the pterygoid plate is ventrally concave from side to side so that the lateral edges of the plate are angled about 20 degrees from the horizontal. The pterygoids meet posterior to these vacuities along a long straight suture obscuring the relationship of the bones of the basicranium.

The ectopterygoid contacts the palatine anteriorly and the lateral rami of the pterygoid medially, but their lateral extension

**TEXT-FIG. 4.** SMNS 12478, *Meyerasaurus victor* (Fraas, 1910); Toarcian of Holzmaden (Germany). A, pectoral girdle. B, pelvic girdle. C, left hindlimb. D, left forelimb. Scale bar represents 10 cm.



cannot be determined because they are poorly preserved and obscured by the mandible. The right ectopterygoid is best preserved and extends anteriorly along the palate to form most of the medial border of the suborbital fenestra. The right ectopterygoid forms a downturned boss (dorsal projection) whereas the left one forms a domed boss (ventral projection).

The parasphenoid is very narrow and sharply keeled ventrally. The anterior extremity of the parasphenoid terminates at the anterior border of the posterior interpterygoid vacuities so there is no cultriform process. It is presumed that the parasphenoid is totally fused to the ventral surface of the basisphenoid (it cannot be demonstrated that they are separate elements). The parasphenoid contacts the pterygoid posterior and anterior to the interpterygoid vacuities, the anterior suture is transverse and the posterior one is 'V'-shaped, with the apex pointing posteriorly.

The basioccipital is partially exposed in ventral aspect, extending beyond the straight posterior margin of the pterygoid plate. The visible part of the basioccipital in ventral view is divided into two structures, the body of the basioccipital, which supports the basiptyergoid processes, and the occipital condyle. Two very small foramina are present on the base of the basioccipital. The anteroventral surface of the basioccipital is obscured by the pterygoids. The basioccipital basiptyergoid processes descend from the basioccipital, and each bears a concave rounded distal end. They are strongly developed and probably formed attachment sites for tendons (craniocervical flexor muscle tendon) stabilizing the skull on the neck and braced the base of the quadrate-ptyergoid flange. The occipital condyle is completely

visible in ventral view. It is prominent (slightly wider than deep) and slightly convex. A shallow ventral notch separates the condyle from the main body of the basioccipital.

A possible part of the right exoccipital opisthotic (eo?, Text-fig. 2D) is visible in palatal view between the hyoid element and the posterior ramus of the pterygoid. It is not particularly well preserved, and no useful features can be recorded. Two robust hyoid elements (hy, Text-fig. 2D) are preserved *in situ* in ventral view, each situated lateral to the posterior plate of the pterygoid. They are long, measuring 7.6 cm (left) and 7.9 cm (right), almost straight, and circular in cross-section. The anterior extremity is more strongly developed than the posterior one. They are both located in the same place and probably roughly occupy their natural position. This pair of rod-like bones probably represents the hyoid apparatus, corresponding to the *cornu branchiale 1* or branchial horns of extant reptiles (Romer 1956). Their shape is very similar to those present in *Crocodylus*; these elements usually lie on the floor of the mouth and pharynx in reptiles and are associated with the musculature of that region (Romer 1956).

**Mandible.** The mandible is complete and is preserved in life position (Text-fig. 3A–D). The dorsomedial parts of the jaws are not visible because the jaws are occluded. The mandibular rami are bowed in ventral view, and their widest part is situated anterior to the glenoid facet (Text-fig. 2C, D) (Druckenmiller and Russell 2008). Posteriorly, each ramus becomes increasingly compressed laterally and oriented vertically. The ramus is thinnest and totally

oriented vertically in the region of the coronoid eminence. The rami meet at an angle of approximately 30 degrees, forming an elongate (approximately 7 cm long), keeled, robust and slightly expanded spatulate symphysis.

The dentary comprises over two-thirds of total mandible length and forms the majority of the symphysis. In lateral view, the dentary rises slightly to form the anterolateral edge of the coronoid eminence (Text-fig. 3A–C). On the lateral surface of the dentary, level with the coronoid eminence, the dentary interdigitates with the surangular dorsally and the angular ventrally. The external surface of the dentary is roughened and pitted anteriorly. The splenial is a narrow blade of bone, which runs along the medial surface of the mandibular ramus and contributes to the mandibular symphysis anteriorly and contacts the anterior border of the internal mandibular fenestra posteriorly (Text-fig. 3A–D). The posterior part of the splenial is squeezed between the prearticular and the angular. The prearticular is only partially visible because of the occluded jaws, and its anterior and dorsal margins cannot be discerned. It contacts the angular posteriorly and forms the dorsal margin of the internal mandibular fenestra in medial view.

The coronoid is partially visible as a small fragment of bone in medial view, contacting the splenial ventrally (Text-fig. 3D). Its dorsal surface cannot be seen so its relationship to the dentary cannot be determined with certainty. The surangular is an extended wedge of bone, which contacts the dentary anteriorly in lateral view. A flange of the dentary overlaps the surangular resulting in a broadly digitating suture. The surangular forms the posterior part of the pronounced coronoid eminence and its dorsal margin descends posteroventrally towards the glenoid fossa. Ventrally the surangular contacts the angular along a straight suture for most of its length, but this suture becomes sinuous below the glenoid fossa. Several distinct foramina perforate the surangular close to this contact (five vascular foramina on the left ramus and three on the right).

The angular forms the entire ventral part of the mandible below the surangular. Anteriorly the angular forms a narrow wedge of bone between the dentary dorsally and the splenial ventrally, which closely approaches the mandibular symphysis in ventral view. Level with the coronoid eminence, the angular contacts the dentary and the surangular in lateral view. Posteriorly, the angular forms the ventral and ventrolateral portion of the retroarticular process. The articular is fused with the angular and surangular and forms the glenoid fossa and the dorsomedial portion of the retroarticular process. In lateral view, the dorsal surface of the retroarticular process is inclined posteriorly. The glenoid fossae are obscured by the matrix but are probably bicondylar as can be inferred from the shape of this region in ventral view (Text-fig. 2C, D), as is usual in plesiosaurs (Storrs and Taylor 1996). The medially opening lingual mandibular fenestra is longitudinally ovate (the right one is 2.5 cm long and 0.7 cm high). It is bordered by the splenial anterodorsally, the prearticular posterodorsally and the angular ventrally.

*Dentition.* Some teeth have been preserved: many have been slightly displaced, but some remain in their respective sockets (Text-figs 2C, D, 3). The premaxillary teeth cannot be counted accurately, but there appear to have been five. There are three

or four teeth situated on each side of the mandibular symphysis and about 25 teeth in each entire dentary. Tooth morphology is uniform throughout the jaws: only the diameter varies according to position. They form sharply recurved elongate cones, with a circular cross-section and bear enamel ridges but lack carinae. Only a few ridges extend to the tooth apex as most of them terminate halfway along the crown. The maximum diameter of maxillary teeth is 9 mm. No diastema is present in the tooth row between the premaxilla and the maxilla, but the first two teeth after the premaxilla–maxilla suture are notably smaller than the premaxillary teeth and the remaining maxillary teeth. The upper teeth are generally larger than those in the mandible.

*Postcranium.* The postcranium of SMNS 12478 is effectively complete and exposed in ventral view so that the girdles and gastralia are visible (Text-figs 1, 4A, B). Fraas (1910) described the postcrania in dorsal view, but this view of the specimen is no longer accessible due to the orientation of the specimen as mounted. The neck (approximately 82 cm) is shorter than the trunk (approximately 110 cm).

*Axial skeleton.* The preservation of the vertebral column is generally excellent: all of the vertebrae are preserved in articulation (Text-fig. 1). Measurements from the vertebral column are presented in Table 1. The cervical and caudal vertebrae are visible, but the pectoral, dorsal and sacral series are largely obscured by the girdles and dorsal ribs.

The atlas–axis complex is preserved on the skull block (Text-fig. 2C, D) (a cast of the skull block is associated with the postcranial specimen on display in the SMNS gallery). The cervical vertebrae C3, C4 and part of C5 are also preserved within this block. The atlas–axis is embedded in matrix and difficult to see. Although the atlas–axis complex is fused into a single unit, the sutures between the individual elements are visible. The third cervical is preserved in contact with the atlas–axis complex. The atlas appears larger than the axis, but no details can be ascertained. There are approximately 30 cervical vertebrae (including the atlas and axis): the exact number is difficult to determine, because the base of the neck and pectoral vertebrae are hidden by the pectoral girdle. Fraas (1910, p. 130) counted 27 cervical vertebrae but also noted six pectoral vertebrae. The common number of pectoral vertebrae is lower in plesiosaurs, although the number varies between species and the identification of pectorals can be subjective (Brown 1981).

The proportions of the cervical vertebrae are difficult to measure in SMNS 12478 because most of them are preserved articulated in ventral view: the only measurement that can confidently be ascertained is their length (see Table 1). On each centrum, there is a pair of small nutritive foramina in ventral view that are separated medially by a sharp longitudinal keel. Each nutritive foramen is situated in a squared depression. The paired foramina lie closer to each other in the anteriormost vertebrae and progressively migrate laterally, away from each other, in the posterior vertebrae. The number of cervical rib facets is unknown, but Fraas (1910, p. 131) stated that only one was present, which would be unusual for a Lower Jurassic plesiosaur (Brown 1981). Almost all of the cervical ribs are preserved: they are short in



**TABLE 1.** Axial skeleton measurements in centimetres.

	Length		Length
C4	2.1	CA1	?
C5	2	CA2	3.6
C6	2	CA3	3.5
C7	2.1	CA4	3.7
C8	2.1	CA5	3.5
C9	2.1	CA6	3.3
C10	2.3	CA7	3.4
C11	2.3	CA8	3.3
C12	2.3	CA9	3
C13	2.3	CA10	3.3
C14	2.5	CA11	3
C15	2.6	CA12	3
C16	2.7	CA13	3.1
C17	3		
C18	2.9		
C19	2.9		
C20	2.9		
C21	3		
C22	3.2		
C23	3		
C25	3.2		
C26	3.2		
C27	3.2		
C28	3.2		
C29	3.1		
C30	3.2		

The vertebrae sequence is as preserved in the specimen.

C, cervical vertebrae; CA, caudal vertebrae. Note that measurements are missing for the distalmost caudal vertebrae because they are partially covered by ribs and chevrons.

the anterior vertebrae and gradually increase in length posteriorly. The anteriormost cervical ribs possess similarly sized anterior and posterior distal flanges. The ribs become typically hatchet-shaped posteriorly with a prominent anterior flange and a long, hooked posterior flange.

The entire ventral part of one dorsal vertebra is exposed between the posterior part of the pectoral girdle (coracoids) and the first row of gastralia. It is rounded ventrally, but little detail can be deduced from this element. Small parts of several other dorsal vertebrae are also visible between the rows of gastralia, but no other details are apparent. Fraas (1910, p. 131) identified 25 dorsal vertebrae. The distal portions of the dorsal ribs are visible lateral to the pectoral girdle and underlying the gastralia.

The exact number of caudal vertebrae cannot be determined with precision: we have identified 36 vertebrae with chevron facets, but it is likely that a number of posterior vertebrae are missing. Fraas (1910, p. 130) recorded 39 caudal vertebrae. The caudal centra are subquadrate in shape, and their size decreases very rapidly towards the terminal end of the caudal region. The caudal vertebrae are obscured by chevrons and are difficult to observe. The caudal ribs are straight, dorsoventrally flattened, and decrease in size posteriorly. The chevrons are elongate and spatulate in shape: they do not present a well-defined recess.

The lack of the latter character is characteristic of 'old adults' according to the criteria of Brown (1981) and indicates that they were probably fused to the centrum.

The gastral basket in SMNS 12478 is complete. Individual gastralia are thickened centrally and taper to slender points distally (Text-fig. 1). There are ten rows of gastralia: the first row is situated some distance from the coracoids, so there is a gap between these elements through which a single dorsal vertebra is visible. The gastralia are tightly packed and extend posteriorly to the pubes, which they contact closely. With the exception of the fourth row, each row of gastralia consists of a single median element and three pairs of lateral elements. The fourth row contains four pairs of lateral elements. The median element has a typical boomerang shape: this is especially prominent in the last (tenth) median element, and the lateral processes of this median element are confluent with a concavity in the anterior margin of each pubis.

*Appendicular skeleton.* Both limb girdles and all four limbs are completely preserved in ventral view (Text-fig. 4).

*Pectoral girdle.* The strongly developed interclavicle-clavicle complex is complete and preserved in natural position (Text-figs 1, 4A). It lies dorsal relative to the rest of the pectoral girdle so that it is only partially exposed in ventral view. There are no visible sutures on the complex indicating that the clavicle and interclavicles are strongly fused, and the anterior margin of the complex is punctuated by a deep and broad 'U'-shaped mesial notch. An anteroposteriorly orientated medial crest occurs just before the anterior border of the coracoid. The posterior border of the complex is hidden by the coracoids, so the extension of the crest and the shape of the posterior part of the interclavicles cannot be determined. The lateral extensions of the interclavicle-clavicle complex presumably correspond to the clavicles and terminate in triangular wings.

The scapulae are partially preserved, but the dorsal rami are not visible. The scapula contacts the coracoid laterally at the glenoid facet, but the sutures are unclear: the latter is a characteristic feature of 'old adults' *sensu* Brown (1981). The pectoral fenestrae are small, elliptical and diagonally oriented with rounded borders. The scapula also contacts the broad anterior process of the coracoid anteromedial to the pectoral fenestra. There is a notch marking the juncture between these two bones below the clavicle-interclavicle complex, with the suture extending diagonally towards the pectoral fenestra (Text-fig. 4A). The slightly expanded ventral (anterior) rami of the scapulae do not contact each other medially. The posterior rami are slightly less expanded and bear two facets; the lateral one forms the anterior part of the glenoid facet, and the posterior facet is fused with the coracoid. The glenoid is large and oval (11–12 cm long) but seems to be formed mainly from the coracoid.

The coracoids are large broad plates of bone (minimum distance between the glenoid facets is 40 cm). Anteriorly each broad square anterior process of the coracoid contacts the interclavicle-clavicle complex. Its medial border is straight in ventral view, the coracoids are united along almost their entire length (this suture measures 31.5 cm long), and there is a shallow 'V'-shaped posterior embayment. Between the glenoids there is a

reinforced ventral convexity on the coracoids. The lateral margins of the posterior processes are deeply concave (the minimal distance between the lateral border of the coracoid posterior to the glenoid facets is 28.5 cm) and terminate as posterior cornuae posterolaterally (the distance between the cornuae is 35.5 cm). The posterior borders are gently convex, but the right coracoid is notably crenulated (Text-fig. 4A).

*Pelvic girdle.* Both pubes are preserved and visible in ventral view (Text-fig. 4B). They are wider than long (45 cm wide and 19.5 long), and there is a deep semicircular notch on the posterior border of each pubis forming the anterior margins of the pelvic fenestrae. Each large ovate pelvic fenestra measures 10 cm long and 6.5 cm wide. The anterior border of the pubis is slightly convex and contacts the last row of gastralia (see above). The acetabular surface is posteromedially directed. The pubes unite along a median contact for most of their length (17 cm long), but they are interrupted by a small ovate aperture midway along the suture and diverge distally to form the anterior margins of a large (9-cm-long) diamond-shaped medial opening in the pelvic bar.

The ischium is hatchet-shaped as is typical in plesiosaurs (Text-fig. 4B). It is wider than long (37 cm wide and 21 cm long) and slightly shorter than the pubis. Its anterior margin is concave and forms the posterior margin of the large semicircular pelvic fenestra. The ischium contacts the pubis medial to the fenestrae forming a pectoral bar. Both ilia are preserved in ventral view and remain in near life position, in rough articulation with the ischia. The ilia are elongate (approximately 18 cm long) rod-like elements, twisted along their long axis, with a slightly constricted shaft. They are more expanded and thicker at their dorsal extremities (sacral end) and narrower at their ventral (acetabular) end. The sacral end forms two rough facets whereas the acetabular end is rounded and compressed.

*Forelimbs.* Both humeri are preserved and exposed in ventral aspect (Text-fig. 4D). They are both markedly asymmetrical in ventral view: the anterior border is nearly straight (slightly convex), whereas the posterior one is strongly concave so the humerus appears to be slightly kinked or recurved posteriorly. The left humerus is 42 cm long. Posterodistally the humerus expands to form a flange.

The proximal portions of the humeri are slightly raised and ornamented with rugosities, marking the position of muscle insertions, and the distal extremity also bears extensive areas of shallow ornamentation. A thick cartilage cap probably covered the humeral head in life. The humerus is slightly constricted immediately distal to the head. The facets for the epipodials are separate and distinct, and each is nearly straight. The proximal postaxial flange (deltopectoral crest) marking the insertion of the *M. coracobrachialis* is poorly developed.

Both the radius and ulna are longer (proximally to distally) than they are broad (preaxially to postaxially) (Text-fig. 4D). The left radius measures 13.5 cm long and the left ulna 11.5 cm long. The proximal and distal margins of the radius form long straight facets for contact with the humerus and radiale respectively, a markedly smaller posteromedial facet faces the intermedium. The preaxial and postaxial margins of the radius are

slightly concave giving an hourglass shape to the radius in ventral view. The preaxial margin of the ulna is concave enclosing a small spatium interosseum (epipodial foramen) between the epipodials. The ulna is lunate with a strongly convex posterior margin. It has a straight proximal margin for articulation with the humerus, two distinct distal facets for articulation with the intermedium and ulnare, and two additional facets for distal accessory ossicles on its postaxial margin.

The proximal row of carpals preserves (from the preaxial to postaxial margin of the limb) the radiale, the intermedium and the ulnare. The radiale is broader than long and smaller than the intermedium and ulnare, which are subequal in length and breadth and polygonal in outline. The distal row of carpals consists of distal carpal I, fused distal carpals II and III, and distal carpal IV. Distal carpal I is shorter and more rectangular than fused distal carpals II and III, the latter is more quadratic and distal carpal IV is polygonal. All of the distal carpals are slightly smaller than the elements in the proximal row.

The metacarpals and phalanges are hourglass shaped, but the midshaft constriction along the preaxial and postaxial margin is not well marked in metacarpal I. Metacarpal V is shifted proximally relative to the other metacarpals so it occupies a position partly within the distal carpal row. The bones of each digit are still in natural position. The phalanges decrease in size distally, and their extremities are flat to slightly convex. The phalangeal formula is (from the preaxial to postaxial margin of the limb) 3-5-8-8-7. It is probable that these counts represent the total number of phalanges as the more distal phalanges are tiny and subtriangular in shape.

Three additional bones form a row on the postaxial margin of the paddle, equivalent to the supernumerary (O'Keefe 2001) or accessory ossicles. They are large and well developed (the central element is slightly larger than the other two). The most proximal one is well rounded, whereas the central one is more pentagonal in shape and the distal element is triangular. The most proximal element is located halfway along, and in close articulation with, the posterior margin of the ulna. The central element is located in the notch between the distal margin of the ulna and the proximal margin of the ulnare, its positional relationship suggests that it may be homologous to the pisiform (see Caldwell 1997). The distal postaxial element is located close to the postaxial margin of the ulnare, in the line with the proximal carpal row. The positions of the three supernumerary ossicles can be accepted with confidence as they are present in the same positions in both forelimbs. The supernumerary and pisiform bones have fused in the right forelimb.

*Hindlimbs.* The femora are smaller than the humeri (approximately 38.5 cm long for the left) (Text-fig. 4C). The distal end of the femur expands preaxially and to a slightly greater degree postaxially. The capitulum of the femur is spherical and separated from the shaft by a sharp ridge. A large rugose area for muscle insertion is present on the ventral surface, situated approximately one-third of the distance from the proximal end. The distal articular surface of the femur forms a convex arc with little differentiation into separate epipodial facets. In general shape and proportions, the tibia and fibula mirror the radius and ulna respectively. The tibia is longer than wide with a slight

midshaft constriction. The proximal margin is almost straight, and the distal margin is slightly convex. The fibula is lunate with distal facets for the astragalus and calcaneum.

The centrale is missing from both hindlimbs indicating that the element had not yet ossified. The preserved proximal row of tarsals is composed (starting from the preaxial margin) of the astragalus and the calcaneum. The astragalus and the calcaneum are equal in size, polygonal in shape and contact each other closely. The distal row of tarsals is entirely preserved on both sides. The distal row consists of distal tarsal I, fused distal tarsals II and III, and distal tarsal IV. The general outline and organization of the metatarsals and phalanges is similar to that of the metacarpals and phalanges of the forelimbs. Again, the fifth metapodial has shifted to partly occupy the distal mesopodial row. The phalangeal formula (from the preaxial to postaxial margin of the limb) for the left paddle is 3-6-6-6-6 and for the right 2-6-7-7-6.

Two small bones occur along the postaxial margin of each hindlimb. They are rounded and markedly smaller than the equivalent supernumerary ossicles observed in a similar position in the forelimbs. They occupy approximately the same position as the two most distal supernumerary elements in the forelimbs.

## COMPARISONS

*Meyerasaurus* shares several characters with other Lower Jurassic pliosaurs but also exhibits a number of differences. *Meyerasaurus* and *Rhomaleosaurus* both have short and robust premaxillary rostra (length to width ratio *c.* 1.0), which contrasts sharply with the more elongate premaxillary rostra in *Macroplata* and 'R.' *megacephalus*. The premaxilla–maxilla sutures are parallel anterior to the nares in *Meyerasaurus* and *Rhomaleosaurus*, as is also the case in the Middle Jurassic *Maresaurus* (Smith and Dyke 2008). There is a large dorsomedian foramen with raised borders situated between the external nares in *Rhomaleosaurus* (Smith and Dyke 2008). Taylor (1992, p. 249) noted the presence of this feature in SMNS 12478 and a cleft was also figured between the external nares of this taxon by Fraas (1910, Taf. X); however, this area is not well preserved in SMNS 12478 and the presence of a dorsomedian foramen cannot be confirmed. The longitudinal midline crest on the premaxillae in *Meyerasaurus* is common in pliosaurs and is present in *Rhomaleosaurus* and 'R.' *megacephalus*, for example: it is most extremely developed in the Lower Cretaceous *Umoonasaurus* (Kear *et al.* 2006).

The vomers contact the maxillae posterior to the internal nares excluding the palatines from the margin of the internal naris, as is the case in *R. cramptoni* (Smith and Dyke 2008), *R. zetlandicus* (Taylor 1992a) and *R. thornntoni* (Smith 2007), but not in 'R.' *megacephalus* (Cruickshank 1994). *Meyerasaurus* has a broader anterior interpterygoid vacuity than the narrow vacuity present in 'R.' *megacephalus*. The open anterior interpterygoid vacu-

ity is absent in *R. cramptoni*, and the condition is uncertain in *R. zetlandicus* (Taylor 1992a). The cultriform process of the parasphenoid extends anterior to the posterior interpterygoid vacuities in *Rhomaleosaurus* and 'R.' *megacephalus* (Cruickshank 1994). *Meyerasaurus* is unique among rhomaleosaurids in lacking a cultriform process. The basioccipital of *Meyerasaurus* is exposed in ventral view extending beyond the pterygoid plates and the basipterygoid processes project posteroventrally. This contrasts with the condition in 'R.' *megacephalus* and *Rhomaleosaurus* in which only the posterior part of the occipital condyle is visible (AS, pers. obs). Lateral palatal vacuities between the pterygoids and palatines are common among pliosaurs and are found in *Meyerasaurus*, 'R.' *megacephalus* (Smith 2007) and *Rhomaleosaurus* (Smith and Dyke 2008), as well as many other pliosaurs (O'Keefe 2001).

The dorsal surface of the retroarticular process is inclined posteroventrally in *Meyerasaurus* whereas it is horizontally oriented in *Rhomaleosaurus zetlandicus* (Taylor 1992a) and in other plesiosaurs. A deep lateral trough occurs on the mandible at the level of the angular–surangular contact, a character that is not so strongly developed in 'R.' *megacephalus* or *Rhomaleosaurus*. The mandibular symphysis bears fewer than five pairs of teeth (although the exact number is not known, the symphysis is relatively short and probably bears a maximum of four pairs of teeth). *Rhomaleosaurus* and 'R.' *megacephalus* possess five pairs of symphyseal teeth. There are less than 30 teeth in each mandibular ramus of *Meyerasaurus*: this number is approximately the same for *Rhomaleosaurus* (Taylor 1992a) and 'R.' *megacephalus* (Cruickshank 1994).

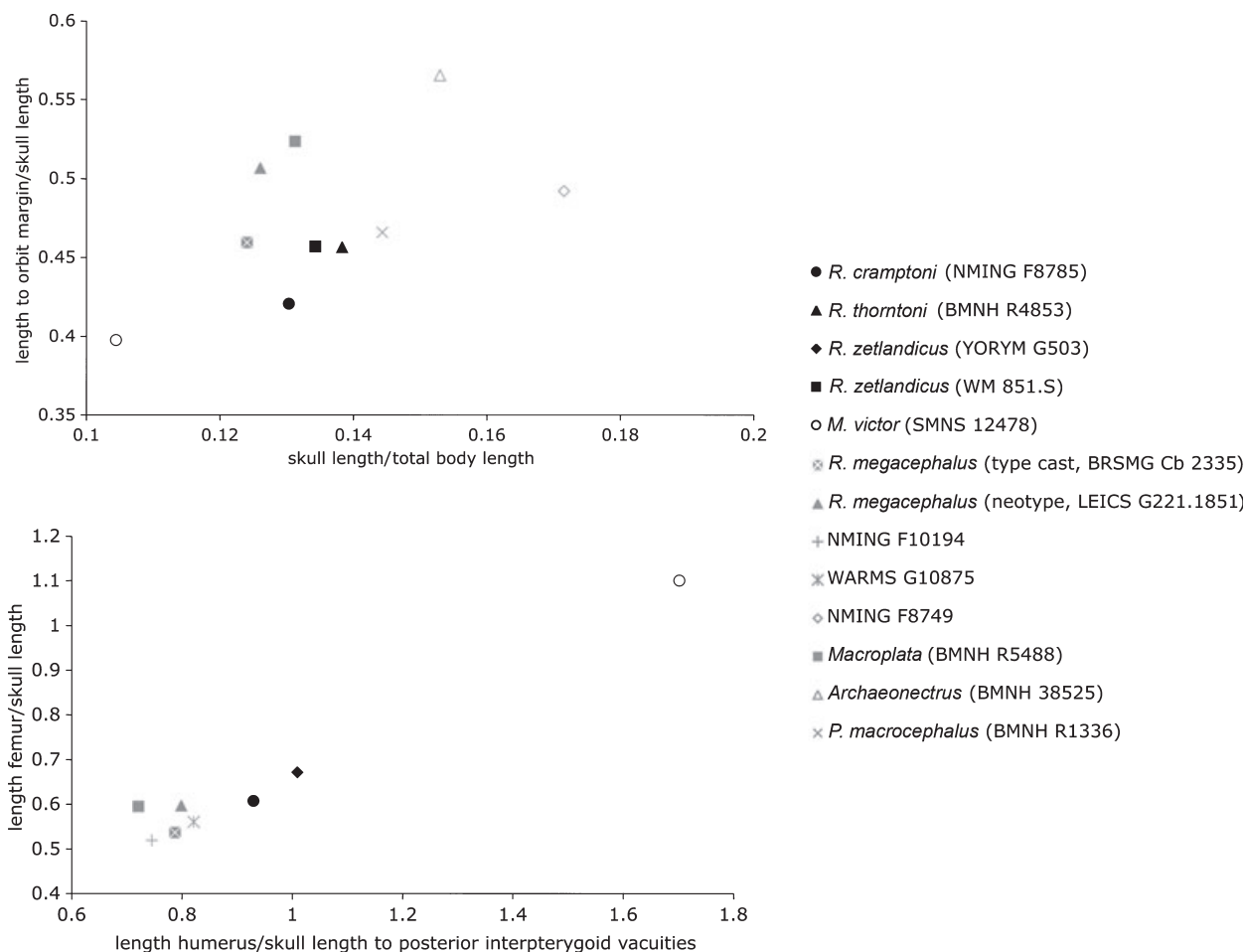
The number of cervical vertebrae, *c.* 28 minus the atlas–axis, is close to that observed in *Rhomaleosaurus cramptoni*, *R. zetlandicus* and 'R.' *megacephalus* (Smith 2007). Brown (1981) considered that 28–32 cervical vertebrae is the primitive number in plesiosaurs. *Meyerasaurus* has ten rows of gastralia, whereas *Macroplata tenuiceps* has seven, and the basal pliosauroid *Thalassiodracon* has eight. The coracoids unite along their entire length in *Meyerasaurus*, as is also the case in *Macroplata* (Swinton 1930). However, a posterior coracoid embayment is common in other Lower Jurassic pliosaurs: it is short and narrow in *R. thornntoni* (see Andrews 1922a) and forms a deep 'V'-shaped embayment in *Eurycleidus arcuatus* (see Andrews 1922b). Traditionally this character is regarded as an elasmosaurid feature among plesiosaurs (O'Keefe, 2001) but its presence in Lower Jurassic pliosaurs indicates that it is actually far more widespread. The scapula and coracoid meet medial to the pectoral fenestra in *Meyerasaurus* but not in *Macroplata* (Swinton 1930) or *Eurycleidus arcuatus* (Smith, 2007): this region is unclear in *Rhomaleosaurus*. The scapula–coracoid

suture lateral to the pectoral fenestra is unclear and could be closed, and this is rarely seen among plesiosaurs but could be indicative of an 'old adult' individual *sensu* Brown (1981).

Adult propodial proportions are generally considered to be an important taxonomic character (Welles 1943; Brown 1981). The humerus is typically equal to or longer than the femur in plesiosauroids whereas the femur is typically larger in pliosauroids (Brown 1981; O'Keefe 2002). However, the humerus is longer than the femur in *Meyerasaurus*. The centrale is absent from the proximal row of tarsals in *Meyerasaurus*. The preaxial elements of the limb are the last to ossify in the ontogenetic sequence of plesiosaurs (Caldwell 2002), and the centrale is therefore sometimes missing in plesiosaurs (e.g. BMNH 2018\* *Thalassiodracon hawkinsi*). This may indicate that *Meyerasaurus* is not fully grown or is exhibiting paedomorphosis. There are three supernumerary ossicles in the forelimb and two in the hindlimb, an unusual configuration for plesiosaurs. Supernumerary ossicles are rarely present in

plesiosaurs (this may represent an artefact of preservation) but where they have been preserved, there is usually a maximum of two. Usually, only one is present and recognized as the pisiform, but the true homology of the supernumerary ossicles is considered to be equivocal and is poorly known in Lower Jurassic pliosaurs (Caldwell 1997).

In order to assess the proportions of *Meyerasaurus* relative to *Rhomaleosaurus* and other Lower Jurassic pliosaurs, a morphometric analysis was performed. Key measurements including the total body length, skull length, preorbital skull length, length of the humerus and femur and ventral length of the skull to the posterior interpterygoid vacuities, were obtained for several specimens (see Smith 2007). This analysis differs from the broader morphometric analysis presented by O'Keefe and Carrano (2005), in that it expands the dataset for a more phylogenetically restricted set of taxa. The results are presented in Text-figure 5 and demonstrate a number of proportional differences between *Meyerasaurus* and other



**TEXT-FIG. 5.** Results of a morphometric analysis of several Lower Jurassic pliosaurs, illustrating the unique proportions present in *Meyerasaurus victor*.

pliosaur taxa. In *Meyerasaurus*, the skull length is much smaller in relation to the body length (10 per cent) compared with the larger headed *Rhomaleosaurus* (15 per cent) (Text-fig. 5). The rostrum of *Meyerasaurus* is also shorter than that of '*R.*' *megacephalus* (Cruikshank 1994) and *Rhomaleosaurus* (Taylor 1992a) (Text-fig. 5). In overall length, *Meyerasaurus* is much smaller (3.5 m) than *Rhomaleosaurus*, as specimens of *Rhomaleosaurus* range from 4.5 m (WM 851.S; Vincent and Smith 2009) to 7 m (NMING F8785; Smith and Dyke 2008).

## SYSTEMATIC POSITION

*Meyerasaurus* possesses a number of characters that place it within the pliosauroid superfamily (*sensu* O'Keefe 2001): a constricted snout at the premaxilla–maxilla suture, the premaxilla excluded from the internal naris, a scoop-like mandibular symphysis, the splenial included in the mandibular symphysis and a ventral keel on the cervical vertebrae. Furthermore, *Meyerasaurus* shares a number of characters with rhomaleosaurid pliosaurs (see above), and several recent cladistic analyses agree that SMNS 12478 belongs to a valid rhomaleosaurid clade (O'Keefe 2001; Smith and Dyke 2008; Ketchum and Benson 2010). Numerous other specimens have also been referred to the Rhomaleosauridae recently (Forrest 2000; Kear *et al.* 2006; Sato and Wu 2008; Smith 2008b). However, the cladistic analysis of Druckenmiller and Russell (2008) does not recognize a distinct rhomaleosaurid clade. In this alternative hypothesis, *Meyerasaurus* forms part of a paraphyletic sequence basal to pliosaurids. The following characters were considered diagnostic for the Rhomaleosauridae by O'Keefe (2001) and are present in *Meyerasaurus*: squared lappet of the pterygoid underlying the pterygoid quadrate ramus, presence of lateral palatine vacuities, a bowed mandible, premaxillary/dentary fangs and cervical centra length less than height. However, all of these characters are also present in other pliosauroids and cannot therefore be considered rhomaleosaurid synapomorphies. Because of the plesiomorphic nature of the group, synapomorphies for the Rhomaleosauridae are scarce, and the clade, if valid, is only poorly supported by a unique suite of plesiomorphic characters, as outlined by Smith and Dyke (2008). Given the current state of flux within pliosaur systematics, there is currently no consensus on the exact phylogenetic position of *Meyerasaurus* within the pliosaur family tree, but we follow the majority of workers and place it within the Rhomaleosauridae. All existing cladistic analyses (O'Keefe 2001; Druckenmiller and Russell 2008; Smith and Dyke 2008) agree that SMNS 12478 is phylogenetically separated from *Rhomaleosaurus*, and our observations herein confirm that there are sufficient discrete and proportional differences

to warrant generic separation of SMNS 12478 from *Rhomaleosaurus*.

## PALAEOBIOGEOGRAPHY

Studies of Toarcian marine reptile diversity have demonstrated the presence of separate palaeobiogeographical zones in Europe during this time, each containing a distinct fauna (Godefroit 1994; O'Keefe 2004; Maisch and Ansorge 2004; Grossmann 2007). As noted by these authors, the Toarcian is especially well suited for palaeobiogeographical studies on plesiosaurs as it has yielded high numbers of individuals and a wide diversity of well-preserved specimens. A simplified palaeobiogeographical system employed by Grossmann (2007) recognized two main zones, an English zone and a German zone. Fossils from deposits in Yorkshire, UK and Holzmaden, Germany, contribute substantially to the faunal composition within each zone (O'Keefe 2004). The zonation between the faunas appears high at a specific level and low at the familial level. Several species are unique to each zone, and none of them overlap, whereas the family composition is very similar, and the majority are present in both zones (depending on the classification used). According to Grossmann (2007), the Elasmosauridae and Pliosauridae are present in both zones whereas plesiosaurids (represented by indeterminate material) are unique to the German zone.

This specific and familial composition has remained stable following modern revisions of the component taxa; however, the generic composition is changing as a greater understanding of the faunas develops. Recent work on Toarcian plesiosauroids from Holzmaden has increased the generic diversity within the German zone: for example, O'Keefe (2004) erected the new genus *Plesiopterys* for a plesiosaur formerly referred to *Plesiosaurus*. Grossmann (2007) built on this work, erecting the new genus *Hydrorion* for the plesiosaur '*Plesiosaurus*' *brachypterygius* and reinstated the genus *Seeleyosaurus* for the plesiosaur '*Plesiosaurus*' *guillemiiimperatoris* (now including *Plesiopterys*).

Following revision of the plesiosauroids, Grossmann (2007) noted that *Rhomaleosaurus* was now the only Toarcian plesiosaur genus present in both the English and German palaeobiogeographic zones, represented in Germany by SMNS 12478. Our referral of SMNS 12478 to a new genus, *Meyerasaurus*, is therefore significant because it continues this trend of increasing generic separation between the German and English zones, while simultaneously increasing generic diversity within the German zone. Therefore, the known distribution of *Rhomaleosaurus* is reduced to the English zone. The resulting lack of any generic overlap between the respective plesiosaur faunas indicates that they are more distinct and phylogenetically separate than thought previously. The ages of the

Toarcian specimens from Yorkshire remain poorly constrained at the ammonite Zone level (Benton and Taylor 1984), and further investigation is required to determine how much of this generic divergence is the result of palaeogeographical isolation or temporal separation.

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