

# A redescription of *Plesiosaurus propinquus* Tate & Blake, 1876 (Reptilia, Plesiosauria), from the Lower Jurassic (Toarcian) of Yorkshire, England

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**SUMMARY:** The type specimen (WM 851.S, skull and post-cranial skeleton) of *Plesiosaurus propinquus* Tate & Blake, 1876, from the Toarcian (Upper Lias, Lower Jurassic) of Yorkshire, is re-examined. New observations permit a detailed understanding of the cranial anatomy of this specimen and hence its taxonomic affinity. The few differences between *Plesiosaurus propinquus* and *Rhomaleosaurus zetlandicus* cannot be considered diagnostic. Consequently, *Plesiosaurus propinquus* is here assigned to and considered a junior synonym of *Rhomaleosaurus zetlandicus*. Currently only three valid species of the genus *Rhomaleosaurus* are known; a complete revision of the specimens formerly attributed to *Rhomaleosaurus* must now be carried out.

Plesiosaur specimens described during the nineteenth century were most often attributed to *Plesiosaurus* (De la Beche & Conybeare 1821), even when they commonly displayed very different morphology. Therefore the genus *Plesiosaurus* has been considered as a waste-basket taxon (Storrs 1997, p. 146) and studies have been undertaken recently to clarify the taxonomic position of the many species referred to this genus (Storrs & Taylor 1996; Storrs 1997; Großmann 2007). As a result, *Plesiosaurus* is now considered a monospecific genus; the only currently recognized species of *Plesiosaurus* is *P. dolichodeirus* Conybeare, 1824.

The type specimen of *Plesiosaurus propinquus* Tate & Blake, 1876 (WM 851.S), comprises a partial skull and mandible and much of the postcranial skeleton of a pliosauroid plesiosaur (Cruikshank 1994). The specimen is still embedded in the matrix and the skull and skeleton would benefit from more complete preparation. Despite this, large portions of the anatomy are clearly visible and so it is important to describe this specimen to help elucidate the diversity and anatomy of Lower Jurassic pliosauroids.

Institutional abbreviations: BMNH, Natural History Museum, London, UK; YORYM, Yorkshire Museum, York, UK; WM, Whitby Museum, Whitby, UK; NMING, National Museum of Ireland (Natural History), Dublin, Ireland.

## 1. HISTORY OF SPECIMEN WM 851.S

The systematic status of specimen WM 851.S has changed many times since its discovery. Charlesworth (1845) first described it as *Plesiosaurus macrocephalus* on the basis of the relative proportions of its head and neck, a view followed by Carte & Baily (1863a) who noted the close similarity between WM 851.S and NMING F8785, the holotype of *Plesiosaurus cramptoni* (Carte & Baily 1863a, b). Later, WM 851.S was described and figured by Tate & Blake (1876), who introduced the new species name *Plesiosaurus propinquus* on the basis of

the shape of the cervical vertebrae, humerus and ulna. These authors also noted differences in the number of carpals and phalanges, which are irrelevant because the left front paddle is a composite of elements from several limbs and so the arrangement of elements is unreliable. Lydekker (1889) referred WM 851.S to *Thaumatosauros propinquus* and was, therefore, the first to formalize its pliosauroid affinity as *Thaumatosauros* is considered a junior synonym of the pliosaur *Rhomaleosaurus* (Tarlo 1960; Taylor 1992a).

Watson (1910) provided a more extensive description of specimen WM 851.S under the original name *Plesiosaurus propinquus*, but his description is insufficient to determine its taxonomic position clearly. More recently, Benton & Taylor (1984), Taylor (1992b), Cruikshank (1994) and Smith & Dyke (2008) all treated WM 851.S as *Rhomaleosaurus propinquus*. However, the specimen is in part a composite (Taylor 1992a), the significance of which is discussed below (see 'Description' and '3.1. Comparison and taxonomic identification' sections).

This paper re-examines the type specimen WM 851.S and provides an extensive description to contribute to the clarification of the taxonomy of Lower Jurassic plesiosauroids. Most parts of the skull and post-cranial skeleton are still obscured by matrix, thus we only attempt a revision sufficient to establish the taxonomic status of WM 851.S, here referred to *Rhomaleosaurus zetlandicus*.

### 1.1 Morphological abbreviations

a, angular; ar, articular; C, cervical vertebra; CA, caudal vertebra; cl, cleft; co, coracoid; d, dentary; D, dorsal vertebra; dmfo, dorso-median foramen; en, external naris; fr, frontal; g, gastralia; gl, glenoid fossa; il, ilium; is, ischium; mx, maxilla; orb, orbit; p, parietal; P, pectoral vertebra; pel bones, indeterminate bones of the pelvic girdle; pfo, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pu, pubis; S, sacral vertebra; sa, surangular; sq, squamosal.

## 2. SYSTEMATIC PALAEOLOGY

- Class **REPTILIA** Linnaeus, 1758  
 Superorder **SAUROPTERYGIA** Owen, 1860  
 Order **PLESIOSAURIA** de Blainville, 1835  
 Superfamily **PLIOSAUROIDEA** Seeley, 1874 (*sensu*  
 Welles, 1943)  
 Genus **RHOMALEOSAURUS** Seeley, 1874

*Rhomaleosaurus zetlandicus* (Phillips, 1854)

Chronology of taxonomic changes affecting WM 851.S

- 1845 *Plesiosaurus macrocephalus* Charlesworth, 49–50.  
 1863a *Plesiosaurus macrocephalus*; Carte & Baily, 169.  
 1876 *Plesiosaurus propinquus* Tate & Blake, 247.  
 1884 *Plesiosaurus propinquus* Tate & Blake, 1876; Simpson,  
 10.  
 1889 *Thaumatosaurus propinquus* (Tate & Blake)  
 Lydekker, 170.  
 1909 *Plesiosaurus propinquus* Tate & Blake; Watson, 2.  
 1910 *Plesiosaurus propinquus* Tate & Blake; Watson.  
 1984 *Rhomaleosaurus propinquus* (Tate & Blake) Benton  
 & Taylor, 415.  
 1992b *Rhomaleosaurus propinquus* (Tate & Blake); Taylor,  
 249.  
 1994 *Rhomaleosaurus propinquus* (Tate & Blake); Cruick-  
 shank, 257.

*Range and distribution.* WM 851.S was originally excavated from the Kettlewell Alum Quarry (Simpson 1884), from the Cement Shales or the upper part of the Main Alum Shales, Middle Toarcian (Benton & Taylor 1984). A sample from the sedimentary matrix surrounding specimen WM 851.S was analysed for nanofossil content in order to determine the precise biostratigraphical age of the specimen (by G. Suan, Université Lyon 1, France). Unfortunately, the sample yielded only a single identifiable specimen, referable to the genus *Schizosphaerella* spp. (incertae sedis), which has a range from Hettangian to Kimmeridgian and thus brings no precision to the age of the specimen (G. Suan, pers. comm.). It is noteworthy that nanofossils are usually scarce or sometimes completely absent in Toarcian strata of North Yorkshire (Bucefalo Palliani *et al.* 2002).

*Remarks.* The species *Rhomaleosaurus zetlandicus* is known only from the Lower Jurassic (Toarcian) of NE Yorkshire. The holotype specimen of *R. zetlandicus*, YORYM G503, came from Loftus Alum Quarry (Phillips 1854), from the Cement Shales of the upper part of the Main Alum Shales, Middle Toarcian (Benton & Taylor 1984).

### 2.1 Description

*General preservation.* WM 851.S is a partially disarticulated, well-preserved skeleton (Fig. 1). It includes the skull and mandible in dental occlusion, most of the vertebral column and parts of the disarticulated paddles. The length of the animal is estimated to be about 4.50 m.

The skull is triangular in shape in dorsal view and approximately 60 cm long (from the tip of the snout to the posterior border of the medial part of the squamosal). The cranium is reasonably well preserved, and despite Watson's (1910, p. 1) comment that "no sutures are visible", there are many visible sutures on the cranium. The orbits are situated near the middle of the skull antero-posteriorly, and are followed by

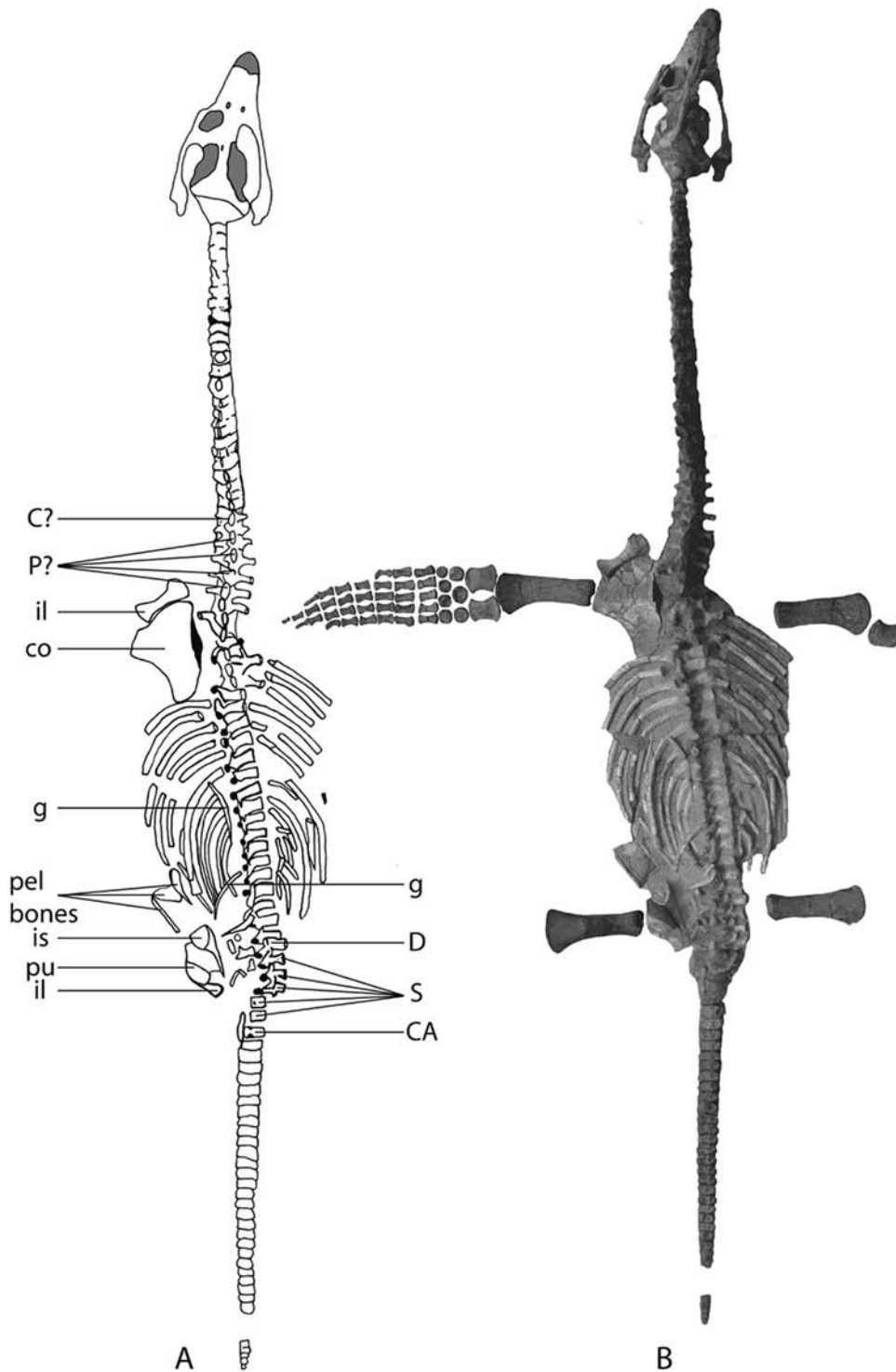
much larger temporal fenestrae. The tip of the snout is missing, having been broken off just posterior to the premaxilla-maxilla suture. This missing portion must have been removed some time after Watson's (1910) examination of the specimen, as he figures the specimen with the premaxillary rostrum intact. The missing portion cannot be located in the Whitby Museum (R. Osborne, pers. comm., 2005), and no reference can be found to when the snout was removed or where it may be. It must therefore be considered lost. The mandible is damaged and incompletely exposed; only parts of it are visible in dorsal aspect because the specimen is still embedded in the matrix. The vertebral column is almost entirely preserved. A total of eighty-four vertebrae are preserved, including between 48 and 56 presacral, 4 or 5 sacral and 31 caudal vertebrae. Most of the vertebrae are still partially covered by matrix. The articular facets of the centra are not visible, so identifying the exact transition between vertebral types is difficult. The girdles are only partially preserved; part of the pelvic girdle is obscured by the matrix. The pectoral girdle is partially visible. The left front paddle is an artificial reconstruction of the bones for display (Fig. 4b, and see below).

*Cranium.* The skull is large in proportion to the body, the ratio of cranium length to body length being 0.13 (Fig. 2). The premaxillae consist of massive bones forming the anterior part of the snout. The anteriormost part of the premaxillae is not preserved (see above) so the rostrum morphology cannot be verified. However, based on Watson (1910, fig. 1), this taxon appears to be unique, with a particularly deep lateral notch and a triangular-shaped premaxillary rostrum. On the other hand, in Tate and Blake (1876, plate II, fig. 1) the rostrum as reconstructed is foreshortened: it appears that the anterior border of the skull has been drawn truncated at the end of the maxillae. The premaxillae form a long, strongly developed facial process that extends between the frontals and contacts the parietal in an interdigitating suture located above the middle of the orbital opening. In dorsal view, the premaxillae unite in a closed median suture, forming a low median crest. A dorsomedian foramen lies between the premaxillae and extends from the posterior margin of the external nares to the anterior margin of the orbit. The premaxilla-maxilla sutures are well-marked and run posteromedially from the tooth row margin to the nares. These sutures are parallel for much of their length. Posterolaterally, the premaxillae contact the frontals.

The maxillae are elongate and massive triangular elements. They constitute the lateral margin of the external nares and form most of the anterior and ventral border of the orbit. Medially they contact the frontals, but their posterior extension along the cheek is not known because the posterior part is not preserved. A posteriorly projecting triangular process of the maxilla extends between the frontal and the prefrontal.

The external nares are distinct oval openings bordered by the premaxillae anteriorly, the maxillae laterally, and the frontals medially and posteriorly. Their maximum antero-posterior length is between 3 and 3.5 cm. They are retracted close to the anterior border of the orbital openings and separated on the midline by the facial processes of the premaxillae and anterior ramus of the frontals.

The prefrontals form the antero-medial margin of each orbital opening, bounded by the maxillae anteriorly and the



**Fig. 1.**  
WM 851.S, *Rhomaleosaurus zetlandicus*, Toarcian of Whitby, UK. Skeleton remains in dorsal view.

frontals medially. The left prefrontal is most obvious. The circum-orbital bones are damaged, however, so the posterior extent of the prefrontals cannot be determined.

The frontals are long thin bones separated by the premaxillae anteriorly and the parietal posteriorly so that they do not meet on the midline. The frontals form the medial margins of the external nares and orbits. Anterolaterally they contact the maxillae, and posteriorly they unite with the postfrontals.

The orbits are circular openings. The posterior border of the right orbital opening is not preserved, but the left one is

complete. There is a slight displacement affecting the post-orbital bar, which has shifted anteriorly by about 1 cm. The left orbit is approximately 10 cm long and 7.5 cm wide.

The postfrontals are almost totally preserved on the left side and partially on the right. They form the dorsoposterior edges of the orbits anteriorly, and contact the frontals and the parietals medially. Unfortunately their lateral extensions are unknown as no sutures are visible to delineate the post-orbitals. The left postfrontal is thin and presents a transverse crest, which extends laterally along the postorbital bar before becoming the anterior margin of the temporal fenestra.

The postorbitals cannot be identified with confidence because no clear sutures are visible on the postorbital bars.

The parietals form a plate of joined bones anteriorly, continuing in a slightly elevated parietal crest between the temporal fossae. This crest continues up to the posterior margin of the parietals, where it merges into a high transverse crest forming the posterior parietal margin. Posteriorly, they unite with the squamosals along a well-marked transverse suture situated on the expanded squamosal-parietal plate.

The pineal foramen is entirely enclosed by the parietals. It is 3.6 cm long and 1 cm wide.

The dorsal rami of the squamosals are completely preserved and join on the midline, forming the posterior part of the cranium dorsally and a very shallow posterior bulb. The anterior and lateral rami of the squamosals are not entirely preserved. The squamosal unites with the posterior process of the parietal, prolonging the crest that is formed by the parietal and overhangs the braincase roof.

**Mandible.** The length of the mandible is 69.5 cm, although the mandibular rami have been slightly displaced (Fig. 2). Some measurements can be made (without correction for the displacement): the width between the posterior extremities of the mandible is 34 cm and the maximum width is 40 cm, located at the level of the glenoid fossae.

The dentary is partially visible, but its anteromedial part is obscured by matrix. Its anterolateral portion is well exposed dorsally and displays several tooth sockets, some occupied by broken teeth. Between the fifth and the sixth tooth positions,

the mandible widens. At the level of the left orbit, part of the dentary has been pushed up and covers the surrounding bones around the left orbital opening.

The surangular is only partially visible and is missing in the region of the adductor fossa. Ventrally it unites with the angular and medially with the articular. A deep cleft beginning anterior to the glenoid separates the surangular from the articular. This cleft was interpreted as a posterior vestige of the Meckelian canal by Taylor (1992*b*) in his description of *Rhomaleosaurus zetlandicus*.

The angular forms the whole of the ventral part of the posterior portion of the mandible. Its dorsal part is visible at the level of the temporal fossa where the anterior part of the surangular is not preserved.

The articular is almost totally preserved, but not visible in its anteriormost part. It forms the glenoid fossa and the dorsal part of the retroarticular process. The right glenoid fossa is cracked; the left one is well preserved. Each glenoid fossa is expanded laterally, antero-posteriorly curved with lateral margins not bordered by any crest. The medial part of each glenoid fossa is more expanded than its lateral part. Medial to the cleft, the articular forms a raised rounded area. This feature was described as a 'knob' by Taylor (1992*a*) and Cruickshank (1994) (see '3.1. Comparison and taxonomic identification' section). Anteriorly, the glenoid fossa is bounded by a transverse crest, which has its highest elevation in the continuation of the cleft separating the surangular and the angular. Posteriorly, the glenoid fossa is also bounded by a transverse crest, which is lower and less curved than the

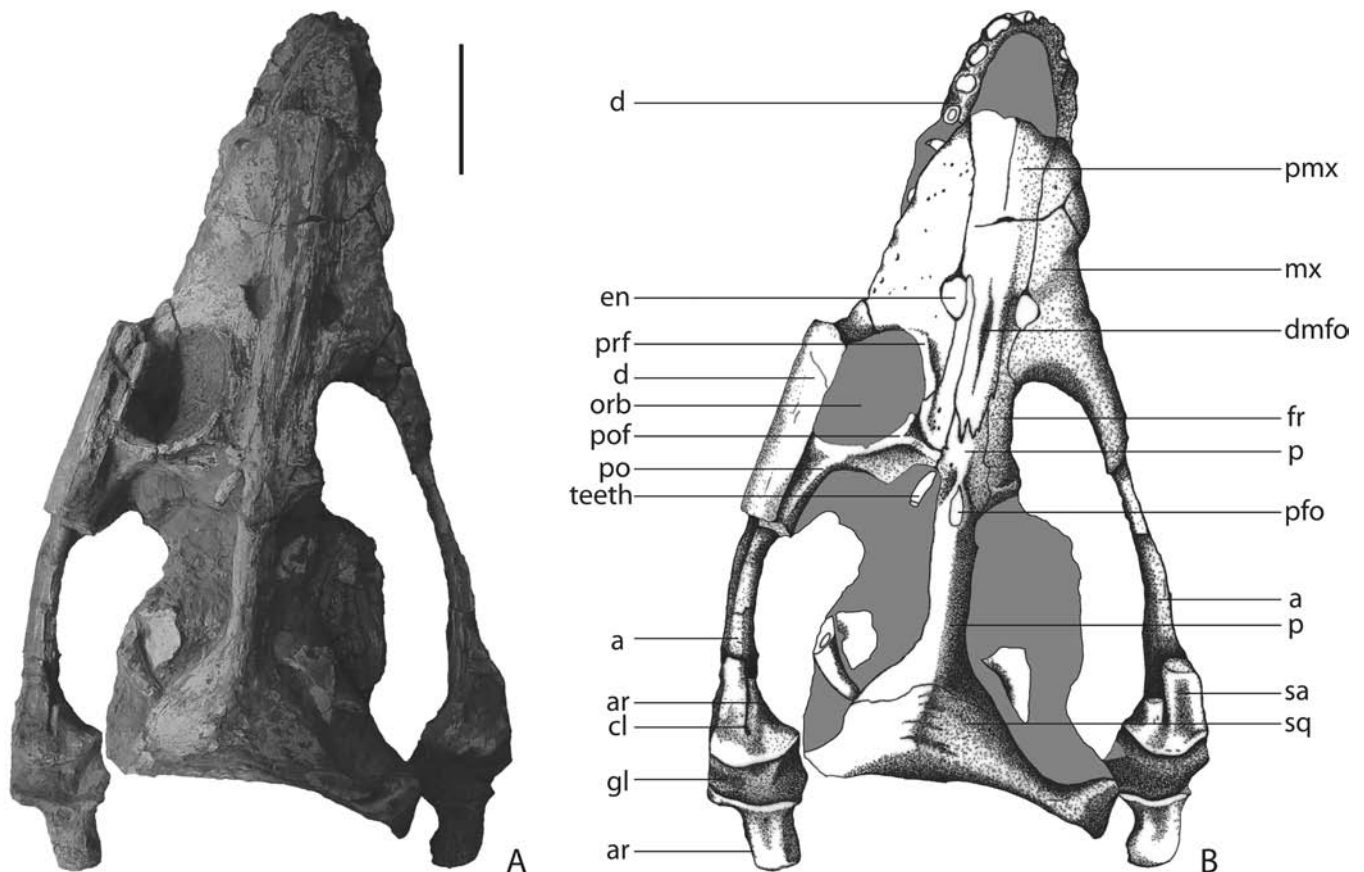


Fig. 2. WM 851.S, *Rhomaleosaurus zetlandicus*, Toarcian of Whitby, UK. Skull in dorsal view. Scale bar: 10 cm.

anterior crest. The retroarticular process is long, narrow, almost horizontally flat and postero-medially oriented. There is a weakly developed boss on the medial surface of the retroarticular process.

*Teeth.* Only a few teeth are preserved (Fig. 2). They are recurved and circular in cross-section and lack strong carinae. They are ornamented lingually and possibly buccally by sparse longitudinal ridges. The first tooth sockets of the dentary are clearly visible. The first one is smaller than the four following sockets, which all have a diameter of approximately 1.8 cm.

*Vertebral column* (Fig. 1, Table 1). The cervical vertebrae have been well described by Watson (1910), who counted 23 cervical vertebrae and figured the 4th and the 23rd. The number of cervical vertebrae is difficult to determine because of the matrix obscuring their lateral surfaces; we estimate between 23 and 28. The cervical vertebrae are exposed in dorsal aspect. Only the length of the cervical centra can be measured approximately (see Table 1). Their length seems to be less than their height. All of the preserved vertebrae bear neural arches attached to the centrum. Some show a closed suture between the two elements, although many of the cervical centra show distinct neurocentral sutures (see 'Ontogenetic status' section).

The neural spines are partially preserved; they are large and oval in cross-section, and situated far posterior relative to the centrum. The anterior edges of the neural spines are convex and the posterior ones slightly concave. The zygapophyses are poorly exposed, but very broad with circular margins and together form a 'butterfly-shape' in dorsal view, as figured by Watson (1910, fig. 3). The neural arches are extremely tall, roughly equal in height to their respective centra. The zygapophyses, especially the postzygapophyses, are situated high above the centrum and their articular faces are almost horizontal. In lateral view, 'V'-shape neurocentral sutures extend ventrally onto the lateral surfaces of the centrum. A passage of smooth bone extends dorsoventrally along the lateral surface of the centrum from the 'apex' of the neurocentral suture towards the cervical rib facet. This passage is bordered anteriorly and posteriorly by a distinct semi-circular vertical ridge. The margins of the articular faces of the centra are rounded. Only some cervical rib facets are visible and it is not possible to determine if they are single or double-headed. No cervical ribs are preserved.

Watson (1910) counted five pectoral vertebrae but this observation is uncertain as the matrix enclosing the vertebrae may lead to misidentification. The common number in plesiosaurs (Brown 1981) is four, but can vary between three and six.

We estimate the number of dorsal vertebrae to be between twenty-one and twenty-four, less than the estimate of twenty-eight by Watson (1910). The dorsal vertebrae are preserved in lateral aspect, exposing part of the neural spines and part of the left ribs. They are characterized by lateral apophyses located on the neural arch. Their articular facets are circular in shape and slightly amphicoelous. The dorsal neural spines are laterally broader than the cervical neural spines. The zygapophyses of the posterior dorsals are large and project considerably anteriorly and posteriorly of the centra. Their articular facets are well inclined latero-medially.

Four or five vertebrae are recognized as sacrals; this corresponds with *Rhomaleosaurus thorntoni*, which also has

**Table 1**

Axial skeleton measurements in centimetres. The vertebrae sequence is the natural one. C, cervical vertebrae; CA, caudal vertebrae; c., approximately

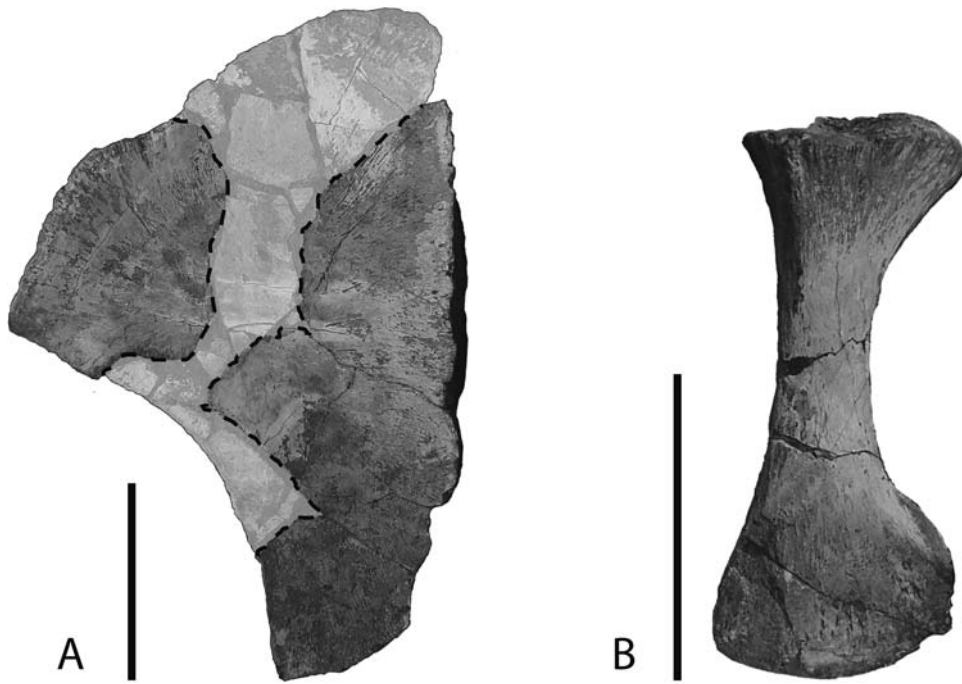
Length		Length	
C1	2.7	CA1	c.3.8
C2	?	CA2	c.3.7
C3	2.7	CA3	4
C4	c.3	CA4	c.3.8
C5	?	CA5	c.3.7
C6	c.3	CA6	3.6
C7	3.1	CA7	3.6
C8	2.9	CA8	c.3
C9	2.8	CA9	3.3
C10	3.4	CA10	3.3
C11	3.3	CA11	c.3
C12	3.7	CA12	3
C13	3.7	CA13	3
C14	?	CA14	c.2.8
C15	?	CA15	2.9
C16	3.5	CA16	3
C17	3.5	CA17	c.2.6
		CA18	c.2.6
		CA19	c.3
		CA20	c.2.7
		CA21	c.2.5

four or five sacral vertebrae (Andrews, 1922). They are morphologically intermediate between caudals and dorsals.

Thirty-one caudal vertebrae are preserved, a number congruent with the observations of Watson (1910). They are exposed in dorsal view. This portion of the vertebral column is probably incomplete. Some vertebrae seem to be missing anteriorly to the last preserved vertebrae and at the end of the tail. The caudal centra rapidly decrease in size towards the posterior end of the caudal region. None of the neural arches or ribs are preserved. The neural surface is narrow, particularly in the middle where it is encroached dorsally by the concave facets for the neural arch. The rib facets are located on the centrum just ventral to the suture for the neural arch.

*Ribs and gastralia.* Several partial dorsal ribs are exposed. They are strongly developed, single-headed, long, robust and curved, with flattened and enlarged articular heads. They are thicker at their axial ends than distally. From their axial ends distally, the ribs run first straight, then curve down. They seem to be circular in cross section. Very few gastralia are preserved. Their central part has a typical boomerang shape with a wide angle between the two branches. Four sacral ribs are preserved. They are short, massive and bear well-developed facets on their anterior and posterior ends for contact with the sacral vertebrae.

*Pectoral girdle.* Only a part of the left coracoid is observable in dorsal view (Fig. 3a). It was figured by Watson (1910) who noted that it had been reconstructed from several fragments of bone, which for the most part had been wrongly arranged. His observation is confirmed here. Figure 3 shows the parts of the coracoid that are considered to be dubious. The anterior and posterior borders of the coracoid are not preserved. The bone seems to be thin, except in the glenoid and symphyseal regions, giving these two parts of the bone a strong convexity. Antero-posteriorly, the symphyseal border is nearly straight.



**Fig. 3.** WM 851.S, *Rhomaleosaurus zetlandicus*, Toarcian of Whitby, UK. (A) part of the left coracoid. (B) right ilium. Scale bar: 10 cm.

*Pelvic girdle.* Both ilia are at least partially preserved. What is assumed to be the right ilium (Fig. 3b) has been displaced and inserted near the pectoral girdle (as observed by Watson 1910). This ilium is long and expanded at both extremities. The dorsal end (sacral) is more expanded anteroposteriorly than the ventral end (acetabular). It is slightly twisted with a constricted shaft. The dorso-medial margin, corresponding to the surface for the sacral ribs, is well rounded and passes by a rounded angle to the anterior border. The acetabular end corresponds to the facet of the ischium. Its shape differs radically from that of other species of *Rhomaleosaurus*, and given the composite nature of this specimen, leads us to interpret it as an ilium coming from another unknown specimen of plesiosaur (see '3.1. Comparison and taxonomic identification' section). The left ilium is almost totally hidden by the pubis and ischium. Part of the left ischium can be seen, probably corresponding to the anteromedial corner and the margin of the pelvic fenestration. A part of the pubis can also be observed and probably corresponds to the acetabular surface. Some other fragments of bones belonging to the pelvic girdle are partially preserved but cannot be identified.

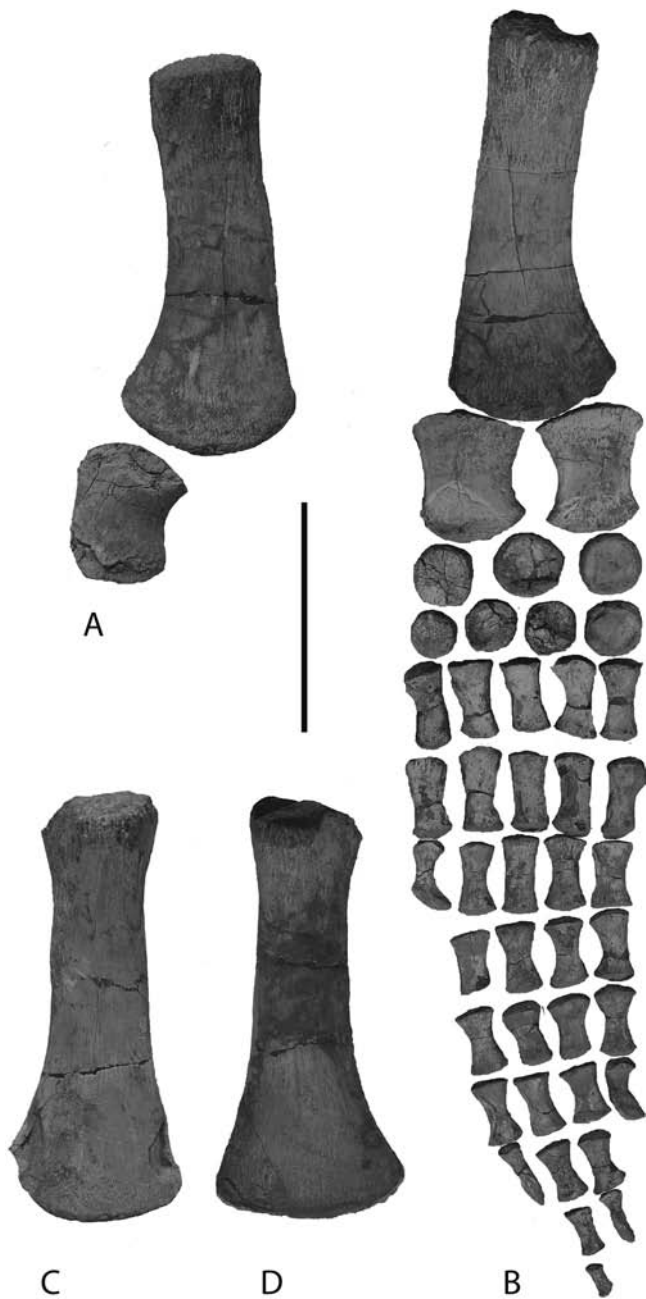
*Forelimbs.* The humeri (Fig. 4a–b) are well-preserved and exposed in dorsal aspect. Watson (1909, 1910) suggested that the right one might be the femur of another species, but examination does not confirm this idea. The humeri have approximately the same length, 33.5 cm for the right and 34.5 cm for the left, and they are identical in morphology. They are both markedly asymmetrical in dorsal view: the anterior border is nearly straight whereas the posterior one is concave because of the distinctive enlargement of its posterodistal part, as is typical of 'adult' plesiosaur humeri and unlike plesiosaur femora which have slightly concave margins (see Brown 1981, p. 276–280). The proximal portions of the humeri are raised and bear rugosities, marking the position of muscle insertions. A thick cartilage cap probably covered the humeral head in life. The distal extremity bears extensive areas of shallow ornamentation; it is well rounded and does not exhibit well-formed epipodial facets; the lack of well-formed epipodial

facets is a character of juvenile plesiosaur propodials (Brown 1981).

The two left epipodials show the same general outline, presenting concave preaxial and postaxial margins. This morphology is typical of the radius, but not of the ulna. Therefore, one of the two epipodials could be the radius while the second may be another radius or a tibia. The epipodials are followed by three rounded mesopodials; however, they do not necessarily represent the ulnare, intermedium and radiale. These are, in turn, followed by four well-rounded and slightly smaller discoidal bones representing the distal metapodials, which are usually three in number. Thirty-three phalanges are preserved but, as for the rest of the limb bones, these have been repositioned and may belong to one or more of the other limbs, or possibly even to another specimen. They are typically plesiosaurian, with an hourglass shape. The entire left paddle (Fig. 4b) is probably reconstructed from a mixture of elements from different paddles and is arbitrarily arranged.

The right front paddle preserves only the humerus and a single epipodial. The latter is slightly damaged, but has concave preaxial and postaxial margins so probably corresponds to the radius. Considering the relative length of the margins, it is possible that this element is reversed. The shape of the three epipodials preserved differs significantly from the morphologies observed by Watson (1910), and the possibility that at least one of them came from a different specimen cannot be excluded.

*Hindlimbs.* Both femora are exposed in dorsal aspect and are approximately the same size (36.4 cm long for the right and 36.5 for the left; Figs 1, 4). The femora are longer and larger than the associated humeri. Differences in propodial proportions are generally considered as an important taxonomic character (Welles 1943; Brown 1981) when considered in adult forms. The propodial proportions of WM 851.S are in accordance with the general trend in short-neck taxa that possess relatively longer femora (Andrews 1913; Brown 1981; O'Keefe 2002; O'Keefe & Carrano 2005). The femur expands



**Fig. 4.** WM 851.S, *Rhomaleosaurus zetlandicus*, Toarcian of Whitby, UK. (A) right humerus and epipodial. (B) left fore paddle. (C) right femur. (D) left femur. Scale bar: 10 cm.

nearly symmetrically, slightly more postaxially than preaxially. The head is moderately convex and rugose, and probably had a thick cap of cartilage in life. The trochanter is not well developed and this is a juvenile character (*sensu* Brown 1981). In outline, the distal articular surface forms a convex arc, with little development of epipodial facets.

## 2.2 Ontogenetic status

Some cervical centra in WM 851.S lack a distinct neurocentral suture and appear fused while others exhibit a distinct unfused neurocentral suture. Unfused neurocentral sutures are indicative of an immature ontogenetic stage (Brown 1981), but the additional presence of fused neurocentral sutures in WM

851.S indicate that the specimen was close to fully grown at the time of death (*sensu* Brown 1981). The distal extremities of the humeri and femora are rounded and lack well-formed epipodial facets. These characters also indicate that the specimen was not completely ontogenetically mature and it may be regarded as a young 'adult' (*sensu* Brown 1981). Nevertheless, O'Keefe (2001; p. 54) noted that the expression of facets varies phylogenetically in adults. The specimen is quite small when compared to closely related specimens (see below).

## 3. DISCUSSION

### 3.1. Comparison and taxonomic identification

The skull of WM 851.S is incompletely preserved and exposed, but the bone arrangement is very close to that of *Rhomaleosaurus zetlandicus* (YORYM G503) and *Rhomaleosaurus cramptoni* (NMING F8785), recently revised and described extensively by Taylor (1992a, b) and Smith & Dyke (2008), respectively.

In common with both *Rhomaleosaurus zetlandicus* (YORYM G503; Taylor 1992b) and *Rhomaleosaurus cramptoni* (NMING F8785), WM 851.S possesses a distinct dorsomedian foramen between the premaxillae, the frontals contact the external nares anteriorly and the orbit margins and postfrontal posteriorly and are separated from each other by the premaxillae and the parietal. All three taxa also possess robust teeth that are sparsely striated lingually and axially but not buccally. The post-cranial skeleton of WM 851.S presents many similarities to and some differences from *R. zetlandicus* and *R. cramptoni*. The number of cervical vertebrae in WM 851.S was estimated as between 23 and 28, and the higher estimate closely corresponds to the 28 cervical vertebrae present in both *R. zetlandicus* and *R. cramptoni* (Taylor 1992a; Smith 2007). Indeed, the skull block presents a mass of matrix posterior to the skull, where the anterior cervical vertebrae are probably present but not visible. WM 851.S possesses 21–24 dorsal, around 5 sacral and 31 caudal vertebrae, very closely matching *R. zetlandicus* and *R. cramptoni*. It is also noteworthy that all three specimens come from the same locality and stratigraphical level.

WM 851.S also possesses an additional noteworthy character, as originally noted by Taylor (1992a, p. 52): 'the articular bears a strong anteriorly pointing boss along the dorsomesial side of the rear mandibular ramus, where *R. zetlandicus* [and *R. thornstoni*, A. Smith, pers. obs.] has a concave trough'. This feature was confirmed by Cruickshank (1994, p. 257), who described a 'prominent knob in the same position as the dorso-median trough described for *R. zetlandicus*...' and concluded that WM 851.S '... may therefore be a distinct species within the genus *Rhomaleosaurus*...'. Nevertheless, he noted that determining the affinities of WM 851.S would require further observations. This region is not visible in *R. cramptoni*. This raised 'knob' is interpreted in the present study as a part of the articular, lying medially to the cleft. *R. zetlandicus* also shows part of the articular lying medially to the cleft, although not as laterally prominent as WM 851.S. This anterior part of the articular terminates abruptly in WM851.S and possibly corresponds with a break. Whether this feature is a preservation artefact or not, it is considered too dubious to justify specific separation. If it is a genuine

feature then it could represent individual, ontogenetic or intraspecific variation. WM 851.S does not possess the robust ilium typical of *Rhomaleosaurus* (Smith 2007). However, this specimen is, in part, a composite (Taylor 1992a) so it is probable, given the many other shared synapomorphies, that the ilia mounted in this skeleton are not part of the same individual.

The humeri of *R. cramptoni*, *R. zetlandicus*, *R. thorntoni* and WM 851.S all differ from one another: those of *R. thorntoni* are greatly flared distally, one reason for the erection of a new species by Andrews (1922). In contrast, the humeri of WM 851.S are only gently flared distally, and the condition in *R. cramptoni* is intermediate between these two. This is likely related to the subadult ontogenetic status of this specimen and is therefore not a reliable taxonomic indicator.

Another difference observed between *R. cramptoni*, *R. zetlandicus* and WM 851.S is the size of the specimens. WM 851.S is the smallest (approximately 4.5 m), *R. zetlandicus* is longer (approximately 5.3 metres; Taylor 1992a), and the giant *R. cramptoni* is 7 m long (Smith & Dyke 2008). Again, this difference is also probably due to the different ontogenetic stage of development between the specimens.

The taxonomic status of WM 851.S has been discussed by previous authors working on *Rhomaleosaurus* (Taylor 1992a, b; Cruickshank 1994, 1996). All considered WM 851.S as belonging to a separate species, *R. propinquus*, on the basis of the mandibular difference described above, and based on the overall size. In the light of the new observations presented, these differences are considered too weak to justify the attribution of WM 851.S to a separate species of *Rhomaleosaurus*. The cladistic analysis performed by Smith & Dyke (2008) confirms this observation. WM 851.S shows greater similarity with *R. zetlandicus* than either *R. cramptoni* or specimen BMNH R4853, the holotype of *R. thorntoni*, most notably in the morphology of the frontals and its overall smaller size. WM 851.S is therefore reattributed to the species *Rhomaleosaurus zetlandicus*; the species *Rhomaleosaurus propinquus* is considered a junior synonym to the species *Rhomaleosaurus zetlandicus*.

### 3.2. Significance

This osteological study of WM 851.S adds corroborating information concerning particular aspects of cranial anatomy in *Rhomaleosaurus*. In *R. zetlandicus*, the presence of nasal elements is uncertain (Taylor 1992b); they are not observed in WM 851.S or in *R. cramptoni* (Smith & Dyke 2008), suggesting that this bone was absent in *Rhomaleosaurus*. The bone interpreted as the lacrimal in *R. zetlandicus* by Taylor (1992b) is also not observed in either WM 851.S or *R. cramptoni*. As WM 851.S presents a good state of preservation, the lacrimal is also probably absent in *Rhomaleosaurus*.

The pliosauroid species assigned to the genus *Rhomaleosaurus* Seeley, 1874, were listed by Cruickshank (1994). Some of these have been revised (Taylor 1992a, b; Cruickshank 1994, 1996; Smith & Dyke 2008), but others still need to be re-examined in order to clarify the taxonomy of the genus *Rhomaleosaurus* and its morphology (O'Keefe 2001). In a recent revision of the genus *Rhomaleosaurus* (Smith 2007), only three valid species of this genus were retained: *Rhomaleosaurus zetlandicus* (Phillips, 1854), *Rhomaleosaurus cramptoni* (Carte & Baily, 1863a), and *Rhomaleosaurus*

*thorntoni* Andrews, 1922, from the Toarcian of Kingsthorpe, Northamptonshire. *Rhomaleosaurus thorntoni* was reattributed to *R. zetlandicus* by Cruickshank (1996), but was considered valid by Smith (2007) based on unique characters of the humerus and proportions of the skull. '*Rhomaleosaurus propinquus*' Tate & Blake, 1876, is here re-examined and placed in synonymy with the species *Rhomaleosaurus zetlandicus*. This study corroborates the view that there are only three species of *Rhomaleosaurus* (*sensu* Smith & Dyke 2008); *Rhomaleosaurus cramptoni*, *Rhomaleosaurus thorntoni* and *Rhomaleosaurus zetlandicus*. The revision of the species '*R. longirostris* (Tate & Blake, 1876) and '*R. victor* (Fraas, 1910) (Smith & Vincent *in prep.*) is now necessary to understand the diversity and variation within the Rhomaleosauridae. The species *Macroplata tenuiceps* Swinton, 1930, another taxon regarded as a rhomaleosaurid (O'Keefe 2001; Smith 2007), is also undergoing revision (Ketchum & Smith *in prep.*).

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