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A mysterious giant ichthyosaur from the lowermost Jurassic of Wales

JEREMY E. MARTIN, PEGGY VINCENT, GUILLAUME SUAN, TOM SHARPE, PETER HODGES, MATT WILLIAMS, CINDY HOWELLS, and VALENTIN FISCHER

Ichthyosaurs rapidly diversified and colonised a wide range of ecological niches during the Early and Middle Triassic period, but experienced a major decline in diversity near the end of the Triassic. Timing and causes of this demise and the subsequent rapid radiation of the diverse, but less disparate, parvipelvian ichthyosaurs are still unknown, notably because of inadequate sampling in strata of latest Triassic age. Here, we describe an exceptionally large radius from Lower Jurassic deposits at Penarth near Cardiff, south Wales (UK) the morphology of which places it within the giant Triassic shastasaurids. A tentative total body size estimate, based on a regression analysis of various complete ichthyosaur skeletons, yields a value of 12–15 m. The specimen is substantially younger than any previously reported last known occurrences of shastasaurids and implies a Lazarus range in the lowermost Jurassic for this ichthyosaur morphotype.

Introduction

At the end of the Triassic, ichthyosaurs underwent a major diversity (Motani 2005) and disparity (Thorne et al. 2011) drop. From the latest Triassic (late Rhaetian) onward, lineages of the first ichthyosaurian radiation were replaced by the derived, “fish-like” parvipelvian ichthyosaurs, with the rapid successive appearances of several lineages during the latest Triassic (Fischer et al. 2013). Although Triassic ichthyosaurs filled various niches, as highlighted by tooth and mandibular morphology, with piercing, crushing (Massare 1987, 1997; Massare and Callaway 1990), giant gulping forms (the shastasaurids, Nicholls and Manabe 2004; Sander et al. 2007; but see Motani et al. 2013; Ji et al. 2013), and large macropredators (Motani et al. 1999; Fröbisch et al. 2006, 2013), the subsequent parvipelvian radiation comprised forms with less diverse diets (Sander 2000). In contrast to the first ichthyosaurian radiation, parvipelvians are not recognized to have included giant taxa (i.e., total body length over 15 m), the largest forms being represented by the genus Temnodontosaurus (e.g., McGowan 1996; Martin et al. 2012). The precise timing of the Late Triassic ichthyosaurian turnover (e.g., Thorne et al. 2011; Benson et al. 2012) is, however, unknown because of inadequate sampling in upper Norian–Rhaetian strata. The presence of a giant ichthyosaurian taxon in the Lower Jurassic of the UK has been suspected for some time, on the basis of large postcranial fragments (McGowan 1996), but such a giant form occurring after the demise of Triassic non-parvipel-
which ranges from Middle Triassic to Early Jurassic; a similar age range is indicated by a specimen of *Bakevellia* sp., identified based on hinge structure, and a poorly preserved ?pteriid bivalve. However, a possible immature ostreid is indicative of the lower part of the Blue Lias Formation “pre-planorbis Beds” and *Palaeonucula navis* (Piette, 1858) (Fig. 1), which is not known from beds older than the *Psiloceras planorbis* Biozone (PH personal observation; Mander and Twitchett 2008).

The Blue Lias Formation is exposed in the cliff section where the specimen was found. The lowermost beds of the Blue Lias Formation “pre-planorbis Beds” are immediately adjacent on the cliff top, but we would be inclined to dismiss these as they locally represent a very shallow subtidal to intertidal facies dominated by the bivalves *Liostrea hisingeri* (Nilsson, 1832) and *Modiolus minimus* (Sowerby, 1818). Further, the shallow waters of the pre-planorbis Beds could accommodate only strand-line type deposition of floating material, an unlikely scenario given the size and weight of NMW95.61G.1. The younger Hettangian *Psiloceras planorbis* Biozone strata crops out a short distance to the south, and cobbles and boulders of this are frequently carried northwards along the beach. As this is an offshore, deeper water facies, it is a stronger argument to suggest this as a source for specimen NMW95.61G.1. The Blue Lias Formation at Penarth has previously yielded well-preserved specimens of *Leptonectes* and *Ichthyosaurus*, now in the NMW.

**Age and position relative to the end-Triassic extinction.**

The Blue Lias Formation, the probable source of the specimen NMW95.61G.1, includes the *Psiloceras planorbis* Biozone and passes through to the *Arnioceras semicostatum* Sub-biozone, making it Hettangian to Early Sinemurian in age. Nevertheless, the base of the Blue Lias Formation also includes the “pre-planorbis Beds”, the age of which is poorly biostratigraphically constrained. Indeed, the Triassic–Jurassic boundary has been defined at Kuhjoch in the Eiberg Basin in Austria in 2012 (Hillebrandt and Krystyn 2009) as the first occurrence of the ammonite *Psiloceras speleae* Hillebrandt and Krystyn, 2009, a species that does not occur in the UK. As such, the position of the base of the Jurassic is not readily identifiable in the field within the Blue Lias Formation on the Penarth-Lavernock Point cliff sec-

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**Fig. 1. A.** Lithostratigraphy, biostratigraphy, and carbon-isotope stratigraphy of key Triassic–Jurassic sections illustrating the likely age of the specimen NMW95.61G.1 from Penarth, south Wales, UK. Organic and inorganic carbon isotope data of Penarth-Lavernock Point from Suan et al. (2012) and Korte et al. (2009); organic carbon isotope data of St. Audrie’s Bay and Kuhjoch from Hesselbo et al. (2002) and Ruhl et al. (2009). The specimen was deposited several kyr after the end-Triassic mass extinction (initial neg. CIE = initial negative carbon-isotope excursion). Abbreviations: CM, Cotham Member; LM, Langport Member. **B.** Close-up photograph of the bivalve *Palaeonucula navis* (Piette, 1858) preserved in the embedding matrix of specimen NMW95.61G.1.
tion. Carbon isotope correlations suggest that the base of the Jurassic lies at or just below the base of a finely laminated shale unit (the “Paper Shales”) (Korte et al. 2009) indicating that the Blue Lias limestone beds (i.e., the likely source rock of the specimen NMW95.61G.1) were deposited several hundred thousand years (Ruhl et al. 2010) after the main end-Triassic extinction event (Fig. 1). Accordingly, the specimen postdates the main mass extinction event and associated carbon isotope excursion recorded at this locality (Mander et al. 2008; Suan et al. 2012). Most importantly, assignment to Triassic strata substantially older than the Rhaetian is precluded by their non-marine origin in the UK (Hounslow et al. 2004).

**Systematic palaeontology**

**Order Ichthyosauria Blainville, 1835**

**Family Shastasauridae? Merriam, 1902**

**Material.**—NMW95.61G.1 (radius) was collected in January 1995 as a fallen block on the beach about 1100 m south of the lifeboat station at Penarth in south Wales (Ordnance Survey National Grid Reference ST 18665 70107). We attribute the specimen, based on the appearance of the lithology and on the currently known ranges of the invertebrate assemblage preserved in the matrix, to the Blue Lias Formation and more precisely to the *Psiloceras planorbis* Biozone (Hettangian).

**Comparative description and affinities.**—NMW95.61G.1 is an exceptionally large radius; it is nearly as tall as wide with a quadratic outline (Fig. 2; Table 1). The anterior margin of the bone is slightly convex, whereas its posterior margin has a broad concavity, being emarginated at midshaft. Fragments of the fused ulna are restricted both proximally and distally from the emargination, implying the presence of a large interosseous opening positioned between the radius and the ulna and extending for most of their proximo-distal length, but excluded from the distal margin of the humerus. Such a large interosseous opening is not

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**Table 1.** Dimensions (in cm) of the shastasaurid radius (NMW95.61G.1) from the Lower Jurassic of Penarth, Wales.

<table>
<thead>
<tr>
<th>Dimension</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proximo-distal maximum length</td>
<td>24.8</td>
</tr>
<tr>
<td>Antero-posterior length at mid-shaft</td>
<td>22.2</td>
</tr>
<tr>
<td>Proximal articular facet length</td>
<td>22</td>
</tr>
<tr>
<td>Proximal articular facet maximum width</td>
<td>8</td>
</tr>
<tr>
<td>Distal articular facet length</td>
<td>24.5</td>
</tr>
<tr>
<td>Distal articular facet maximum width</td>
<td>6.5</td>
</tr>
</tbody>
</table>

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Fig. 2. **A**–**E.** Specimen NMW95.61G.1, radius of possible shastasaurid ichthyosaur from the Lower Jurassic of Penarth, South Wales, in proximal (**A**), posterior (**B**), ventral or dorsal (**C, D**), and distal (**E**) views. **F.** Regression graph shows the relation between preflexural length versus radius height (both in cm) in selected ichthyosaurian specimens (see Supplementary Online Material available at http://app.pan.pl/SOM/app60-Martin_etal_SOM.pdf). The stippled line corresponds to NMW95.61G.1. The outline is based on Kosch (1990) reconstruction of *Shonisaurus popularis.*
observed among parvipelvians, which possess adjoining radii and ulnae, but pierced by a small circular foramen in the earliest parvipelvians Hudonoplepida brevirostris (McGowan 1995) and Maccowania janiceps (McGowan 1996) and sometimes observed in the early neochitichyosaurs Leptonectes tenuirostris and Temnodontosaurus hurgundiae (Godefroit 1992; McGowan 1996). On the other hand, a large epipodial opening is a common feature of non-parvipelvian Triassic ichthyosaurs: the forms with tentative affinities Cymbaspodylulus buchseri (Sander 1989) and Californiosaurus perrottii (Merriam 1902); the mixosaurids Barracudasaurus maotaiensis (Jiang et al. 2005), Mixosaurus cornalianus (Morani 1998), M. panxianensis (Jiang et al. 2006), and Phalarodon atavus (Liu et al. 2013); and also among shastasaurids, Shonisaurus sikanniensis (Nicholls and Manabe 2004), Callaway neoscapularis (McGowan 1994), Shastasaurus spp. (Callaway and Massare 1989), and Shonisaurus popularis (Kosch 1990). The presence of such an epipodial opening was interpreted by Callaway and Massare (1989) and Maisch and Matzke (2000) as a primitive feature observed in all Triassic genera, although Besanosaurus leptorhynchus appears to be an exception (Dal Sasso and Pinna 1996).

However, the overall outline of NMW95.61G.1 is dissimilar to many of the Triassic forms cited above, in which the radius is longer than wide and the anterior margin is not convex but notched as in some mixosaurids (Jiang et al. 2006; Liu et al. 2013). On the other hand, NMW95.61G.1 is quadratic and presents an even convex anterior margin. In this regard, the genus Cymbaspodylulus also has a radius longer than wide with C. buchseri displaying an anterior notch (Sander 1989) or without in C. petrinius (Merriam 1908). In some other Triassic ichthyosaurs, the radius is about twice as wide as it is high (e.g., Shastasaurus osmondii [Morani 1998] = S. pacificus according to McGowan and Morani 2003). Nevertheless, the morphology of NMW95.61G.1 closely resembles that of the genus Shonisaurus as illustrated in McGowan and Morani (1999), and especially that of Shonisaurus sikanniensis (Nicholls and Manabe 2004), with the radius and ulna forming a single unit (as evidenced by the fused remains of the ulna) and in presenting an extensive epipodial opening and a convex leading edge. Another taxon with a similar shaped and sized radius is the shastasaurid Himalayasaurus tibetensis (Morani et al. 1999).

In light of its morphology, this radius is most like that of a shastasaurid ichthyosaur, especially the genus Shonisaurus. However, it should be noted that in the absence of further skeletal remains, this taxonomic attribution remains tentative.

Discussion

Body size.—We estimate a minimum preflexural length of 12–15 m for the Welsh animal (Fig. 2), therefore implying a slightly larger total body length (TBL). This estimate is based on the size of the radius. We compiled body measurements (TBL versus radius height and length) from 21 complete specimens belonging to 14 species in order to establish a linear regression (Fig. 2). This approach allows us to estimate allometric scaling of the radius in relation to TBL (see also Scheyer et al. 2014). That said, very few growth series can be measured for any given taxon; one of the few is Stenopterygius quadriscissus representing the best-sampled ichthyosaur species. This taxon is a parvipelvian ichthyosaur reaching a maximum size of 4 m, most certainly unrelated to the Welsh animal and therefore presumably with a different life history. Moreover, Stenopterygius and all thunnosaurians are characterized by a shortened tail compared to less derived ichthyosaurs (Maisch and Matzke 2000); for a given radius size, their TBL would therefore be shorter than for non-thunnosaurians. For these reasons, Stenopterygius is not the ideal candidate for comparison. Ideally, shastasaurids would provide the data for reliable estimates, but none of the numerous skeletons estimated at 15 m long is complete (Kosch 1990). Therefore, the best approach was to compile a linear relation based on as many taxa as possible, so as to cover the full spectrum of non-parvipelvian ichthyosaur body size and disparity. The correlated body measurements lie on lines with R² values of 0.908 and 0.919 for radius width versus preflexural length and radius height versus preflexural length, respectively.

There may have been other large, possibly giant, ichthyosaurs in European Lower Jurassic deposits. Noteworthy are several bones of large size reported by McGowan (1996), including a large scapula (44.4 cm long) and a centrum (20.5 cm in diameter) both from Lyme Regis, Dorset, England, as well as a series of vertebrae from Banz, Germany (22 cm centrum in height). The largest complete skull reported from Lower Jurassic deposits so far is that of Temnodontosaurus platyodon, with a specimen (SMNS 50000) reported as more than 9 m long (McGowan 1996). However, our measurement of that SMNS 50000 specimen (see SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app60-Martin_etal_SOM.pdf) indicates this size has been overestimated (6 m instead). Other Lower Jurassic large forms from Europe include Temnodontosaurus azerguensis (Martin et al. 2012) and Leptonectes solei (McGowan 1993) with lengths of 8–10 m and 6 m, respectively. Temnodontosaurus platyodon may hold the record, with a skull length approaching 2 m (see measurements in McGowan 1996 for NHMUK PV R 51155 and BRLSI [BAGTM] M3577) therefore surpassing the 1.5 m long skull specimens for which a TBL does not exceed 7 m (SMNS 50000). Nevertheless, with a possible maximal TBL of 10 m, Temnodontosaurus cannot be considered as gigantic and is smaller than the Welsh animal.

Although an estimate of TBL for NMW95.61G.1 is shorter than Shonisaurus sikanniensis (TBL estimate of 21 m; Nicholls and Manabe 2004), it is substantially longer than Cymbaspodylulus (less than 10 m TBL; Sander 1989; Merriam 1908) and is more comparable in size to Shonisaurus popularis from Nevada (Kosch 1990) or to the radius of Himalayasaurus tibetensis (Morani et al. 1999). This size certainly exceeds that of any known Lower Jurassic ichthyosaurs from Europe or elsewhere in the world.

Faunal turnover at the Triassic–Jurassic transition.—Non-parvipelvian ichthyosaur taxa have never been reported with confidence in strata younger than the middle Norian. Both the
basal neoichthyosaurian Leptonecetes and the basal thunnosa- 
rian Ichthyosaurus from the “pre-planorbis Beds”, were pre-
viously considered as latest Rhaetian in age (Motani 2005), 
but a recent reassessment of the biostratigraphic marker of this 
unit regards it as basal-most Hettangian in age (Hillebrandt 
and Krystyn 2009; Benson et al. 2012). The basalmost par- 
velpovians Hudsonoselphida breviostris and Macgouvania janiceps 
are recorded much earlier, in lower and middle Norian strata, 
respectively, coexisting with sthastasaurids (McGowen 1991, 
1996, 1997; Jiang et al. 2006). The turnover between sthastasu-
rid-dominated and parvelpovian-dominated ichthyosaur faunas, 
seemingly takes place in a stratigraphic interval with a poor 
fossil record: the upper Norian–Rhaetian interval. The present re-
port indicates that a non-parvelpovian taxon occurs in lowermost 
Jurassic deposits, possibly representing one of the last members 
of the Sthastasauridae. It substantially expands the stratigraphic 
range of non-parvelpovians and suggests that the replacement 
of the Triassic sthastasaurids by the new parvelpovian radiation was 
more complex than previously appreciated and spread over several 
millions of years rather than being restricted to a sin-
gle event, a view discussed by some authors (Benton 1986a, b; 
Mazin 1988; Bardet 1994, 1995). Consequently, further sam-
pling is needed to precisely define the tempo and severity of 
this turnover. Notably, the lack of complete specimens hampers 
a full appraisal of the ecology of the previously last reported 
giant ichthyosaurs and the nature of their radiation/extinction. 
For instance, the predator Himalayasauria tibetensis (TL estimated 
over 10 m) from the Norian of Tibet (Motani et al. 1999) is 
known only from a fragmented skeleton and Shonisaurus 
sikanniensis Nicholls and Manabe, 2004, considered as a plank-
tivorous animal is more complete, but poorly preserved. Only a 
fresh look at ichthyosaurian material from strata spanning the 
Triassic–Jurassic boundary, even based on fragmentary mate-
rial, will help clarify the mechanisms of the end-Triassic ich-
thyosaurian faunal turnover.

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