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Brief report

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A mysterious giant ichthyosaur from the lowermost Jurassic of Wales

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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. 2011; 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-parvipelvians may challenge our understanding of their evolutionary history.

Here we describe a radius of exceptional size, collected at Penarth on the coast of south Wales near Cardiff, UK. This specimen is comparable in morphology and size to the radius of shastasaurids, and it is likely that it comes from a stratigraphic horizon considerably younger than the last definite occurrence of this family, the middle Norian (Motani 2005), although remains attributable to shastasaurid-like forms from the Rhaetian of France were mentioned by Bardet et al. (1999) and very recently by Fischer et al. (2014).

Institutional abbreviations.—BRLSI, Bath Royal Literary and Scientific Institution, Bath, UK; NHM, Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

Other abbreviations.—TBL, total body length.

Geological setting

Stratigraphic horizon of the specimen.—The Penarth-Lavernock Point coastal cliff section where the specimen was found as a loose block exposes strata from the upper beds of the Mercia Mudstone Group Blue Anchor Formation (?late Norian–Rhaetian), through Penarth Group Westbury and Lilstock formations (Rhaetian), to the lower beds of the Lias Group Blue Lias Formation (early Hettangian) at the top of the cliff (see Waters and Lawrence 1987; Lawrence and Waters 1989; Warrington and Ivimey-Cook 1995; Benton et al. 2002; Suan et al. 2012 for detailed descriptions).

The specimen NMW95.61G.1 preserves a patch of dark grey-bluish, non-fissile muddy limestone matrix. This excludes as a source the red mudstone and light grey dolomitic beds of the Blue Anchor Formation, the dark shales and sandy bonebeds of the Westbury Formation, and the pale limestone, sandstone and shale beds of the Cotham and Langport members of the Lilstock Formation. However, it could indicate that the specimen came from either the dark grey-bluish limestone beds of the Rhaetian Westbury Formation or the Hettangian Blue Lias Formation (Hodges 1994).

The matrix contains several invertebrate macrofossils, in varying states of preservation that constrain its likely age. Poorly preserved internal moulds of small (<5 mm) gastropods are attributed, based on whorl morphology, to *Allocosmia* sp.

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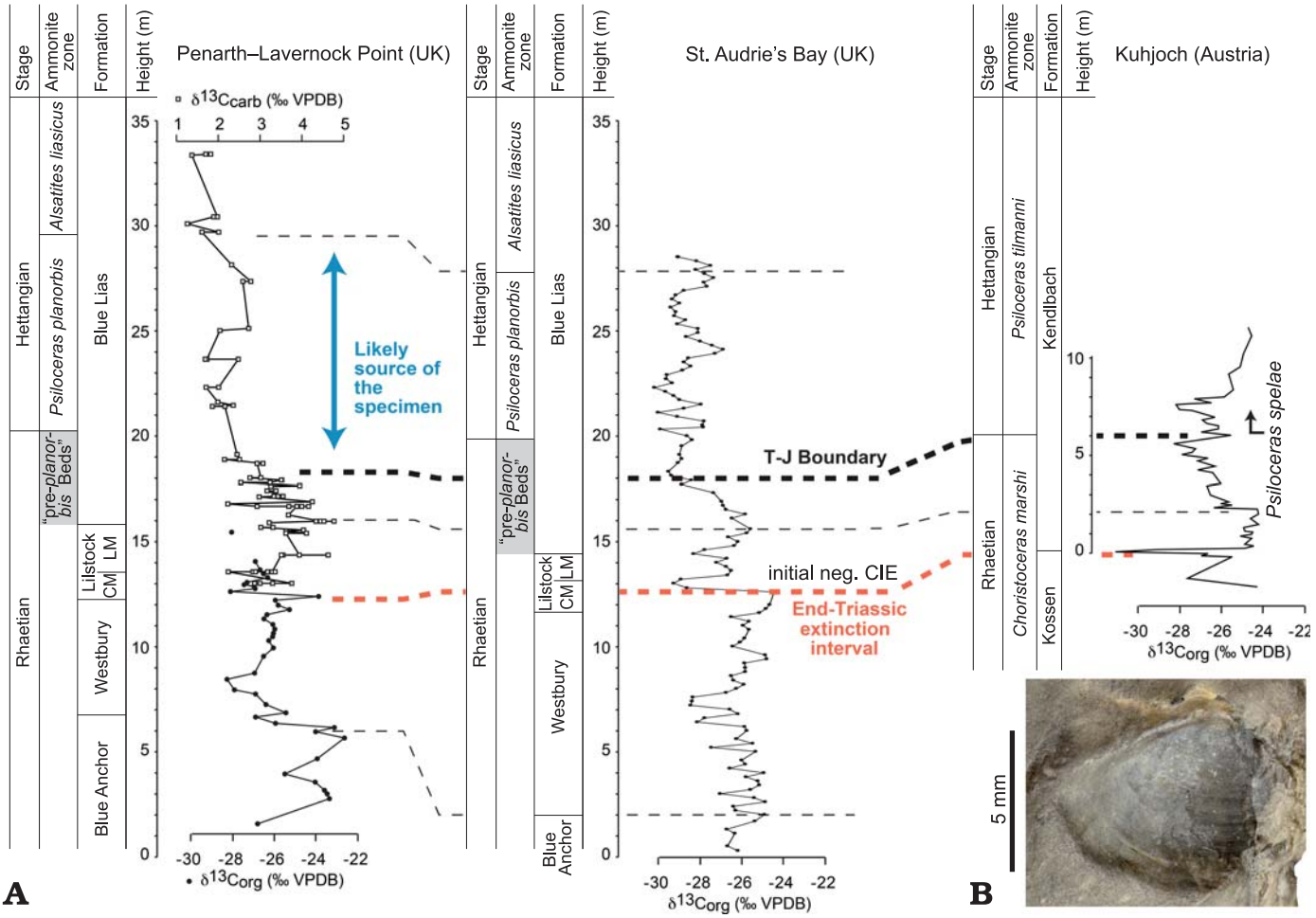


Fig. 1. **A**. Lithostratigraphy, biostratigraphy, and carbon-isotope stratigraphy of key Triassic–Jurassic sections illustrating the likely age of the specimen NMW95.61G.1 from Penarth, south Wales, UK. Organic and inorganic carbon isotope data of Penarth-Lavernock Point from Suan et al. (2012) and 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.

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 clifftop, 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 *Agassiceras scipionianum* Sub-biozone of the *Arnioceras semicostatum* 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 spelae tirolicum* 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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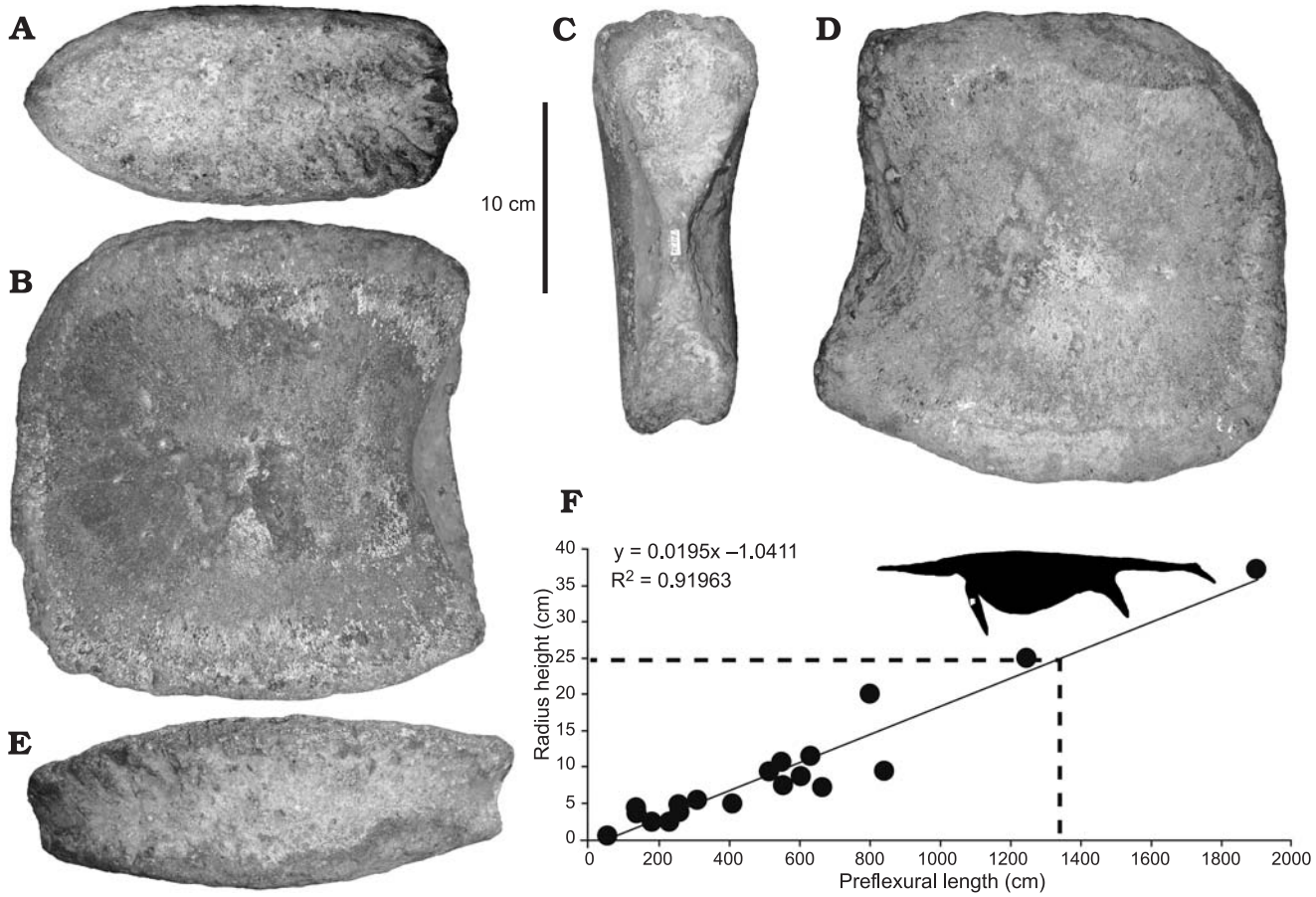


Fig. 2. **A**–**E**. Specimen NMW95.61G.1, radius of possible shastasaurid ichtyosaur from the Lower Jurassic of Penarth, South Wales, in proximal (**A**), posterior (**B**), ventral or dorsal (**C**, **D**), and distal (**E**) views. **F**. Regression graph shows the relation between preflexural length 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*.

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

Fig. 2.

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

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

Proximo-distal maximum length	24.8
Antero-posterior length at mid-shaft	22.2
Proximal articular facet length	22
Proximal articular facet maximum width	8
Distal articular facet length	24.5
Distal articular facet maximum width	6.5

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observed among parvipelvians, which possess adjoining radii and ulnae, but pierced by a small circular foramen in the earliest parvipelvians *Hudsonelpidia brevirostris* (McGowan 1995) and *Macgowania janiceps* (McGowan 1996) and sometimes observed in the early neoichthyosaurians *Leptonectes tenuirostris* and *Temnodontosaurus burgundiae* (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 *Cymbospondylus buchseri* (Sander 1989) and *Californosaurus perrini* (Merriam 1902); the mixosaurids *Barracudasaurus maotaiensis* (Jiang et al. 2005), *Mixosaurus cornalianus* (Motani 1998), *M. panxianensis* (Jiang et al. 2006), and *Phalarodon atavus* (Liu et al. 2013); and also among shastasaurids, *Shonisaurus sikanniensis* (Nicholls and Manabe 2004), *Callawaya 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 *Cymbospondylus* also has a radius longer than wide with *C. buchseri* displaying an anterior notch (Sander 1989) or without in *C. petrinus* (Merriam 1908). In some other Triassic ichthyosaurs, the radius is about twice as wide as it is high (e.g., *Shastasaurus osmonti* [Motani 1998] = *S. pacificus* according to McGowan and Motani 2003). Nevertheless, the morphology of NMW95.61G.1 closely resembles that of the genus *Shonisaurus* as illustrated in McGowan and Motani (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* (Motani 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 R^2 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 [BATGM] 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 *Cymbospondylus* (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* (Motani 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

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basal neoichthyosaurian *Leptonectes* and the basal thunnosaurian *Ichthyosaurus* from the "pre-*planorbis* Beds", were previously 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 parvipelvians *Hudsonelpidia brevirostris* and *Macgowania janiceps* are recorded much earlier, in lower and middle Norian strata, respectively, coexisting with shastasaurids (McGowan 1991, 1996, 1997; Jiang et al. 2006). The turnover between shastasaurid-dominated and parvipelvian-dominated ichthyosaur faunas, seemingly takes place in a stratigraphic interval with a poor fossil record: the upper Norian–Rhaetian interval. The present report indicates that a non-parvipelvian taxon occurs in lowermost Jurassic deposits, possibly representing one of the last members of the Shastasauridae. It substantially expands the stratigraphic range of non-parvipelvians and suggests that the replacement of the Triassic shastasaurids by the new parvipelvian radiation was more complex than previously appreciated and spread over several millions of years rather than being restricted to a single event, a view discussed by some authors (Benton 1986a, b; Mazin 1988; Bardet 1994, 1995). Consequently, further sampling 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 *Himalayasaurus tibetensis* (TBL 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 planktivorous 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 material, will help clarify the mechanisms of the end-Triassic ichthyosaurian faunal turnover.

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