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# The first known neonate *Ichthyosaurus communis* skeleton: a rediscovered specimen from the Lower Jurassic, UK

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## ABSTRACT

Numerous specimens of *lchthyosaurus* are known, but only very few small examples (total body length of < 1 m) have been assigned beyond *lchthyosaurus* sp. Here, we report on a very small specimen (preflexural length of 560 mm) that can be unequivocally assigned to *lchthyosaurus communis* due to possessing a unique combination of diagnostic skull and postcranial characters that are found in larger examples of the species. Furthermore, the specimen is identified as a neonate because of the small size, large sclerotic ring relative to the orbital region, and poorly ossified (highly cancellous) bones of the skull and postcranium. It is not an embryo as it is not preserved within an adult specimen and stomach contents are clearly evident. This is therefore the first neonate *lchthyosaurus communis* skeleton to be described. The specimen, in the Lapworth Museum of Geology, University of Birmingham, has no provenance data associated with it. A microfossil analysis of the matrix in which the ichthyosaur skeleton is preserved strongly suggests a stratigraphic range of uppermost Hettangian to lowermost Sinemurian age (Lower Jurassic), but does not provide any geographical information.

## **KEYWORDS**

Ichthyosaurus; Ichthyosauria; microfossil; neonate; Lower Jurassic; United Kingdom

## Introduction

*Ichthyosaurus* is the most common genus of Lower Jurassic ichthyosaur to be found in the UK and was the first to be recognised by science (De la Beche and Conybeare 1821). Over a thousand specimens, ranging from isolated elements to complete skeletons, are known and are held in numerous institutional collections across the world. Most are from historical collections. The genus is almost exclusively from the UK, with the majority of specimens having been collected from exposures along the west Dorset coast between Charmouth and Lyme Regis or from the quarries of Street and surrounding areas in Somerset. Few specimens have been found outside the UK (Massare and Lomax 2017a). There are six valid species of the genus, *Ichthyosaurus communis, I. breviceps, I. conybeari, I. anningae, I. larkini,* and *I. somersetensis* (McGowan 1974; Lomax and Massare 2015, 2017). A revised diagnosis for the genus and a reassessment of the historically significant type species (*I. communis*) was provided by Massare and Lomax (2017a).

The smallest species of *lchthyosaurus* is *l. conybeari*, which has a total length estimate of < 1.5 m (Lomax and Sachs 2017). However, Massare and Lomax (2016) noted that, based on other specimens that may be referable to the species, the species was probably larger. The largest species of *lchthyosaurus* is *l. somersetensis*, with a total length of over 3 m (Lomax and Sachs 2017). Other unequivocal examples of the genus have also been reported at around 3 m in total length (Massare et al. 2015; but see Massare and Lomax 2017b).

There are in excess of 30 *Ichthyosaurus* specimens with a total length (or length estimate) of < 1 m (DRL pers. obs). They comprise complete and partial skeletons held in a variety of institutions. The small size suggest they are probably juveniles, but a detailed study of *lchthyosaurus* ontogeny is beyond the scope of this paper. Due to the incompleteness or poor preservation of such small specimens, only a few have been confidently assigned to species, including: BGS 956, I. convbeari (McGowan 1974); NHMUK PV OR10028, I. anningae (Lomax and Massare 2015); and an embryo preserved with NLMH 106234, *I. somersetensis* (Lomax and Sachs 2017). There are two other examples of an *Ichthyosaurus* skeleton containing an embryo (Pearce 1846; Deeming et al. 1993), but neither specimen has been positively identified beyond *lchthyosaurus* sp., although both specimens are probably referable to *I. somersetensis* (Lomax and Sachs 2017). The referral of a specimen to species, large or small, often requires a nearly complete skeleton or a well-preserved skull. Here, we report the smallest known specimen positively identified as Ichthyosaurus communis (Figure 1). Unfortunately, no provenance or stratigraphic information was known for the specimen, therefore an analysis of the matrix was undertaken.

## Institutional abbreviations

BU: Lapworth Museum of Geology, University of Birmingham, UK; NHMUK (formerly BMNH): The Natural History Museum, London, UK; NLMH: Niedersächsisches Landesmuseum (Lower Saxony State Museum), Hannover, Germany; OUMNH: Oxford University Museum of Natural History, UK; PETMG: Peterborough Museum and Art Gallery, UK; SMNS: Staatliches Museum für Naturkunde (Stuttgart State Museum of Natural History), Stuttgart, Germany.

## Determination of age and provenance

In an attempt to determine the age of specimen BU 5289, permission was granted to extract a small (~12 g) sample of the matrix from the rear of the specimen to be analysed for microfossils. This sample was disaggregated in ~1% solution of  $H_2O_2$  (hydrogen peroxide) for 30 minutes, rinsed, dried and sorted under a binocular microscope. Analysis revealed a relatively abundant and diverse assemblage of calcareous microfossils, including ostracods and foraminifera (Table 1).

The occurrence of the particular foraminifera species and subspecies (Table 1; Figure 2), strongly indicates the JF3 Foraminifera Biozone (after Copestake and Johnson 2014) spanning a range from the base of the Complanata-Depressa ammonite Subchronozone to the top of the Conybeari ammonite Subchronozone.

Furthermore, the co-occurrence of the foraminifera subspecies *Marginulina prima insignis* and *M. prima incisa* together with the ostracod species *Ogmoconcha hagenowi* and *Ogmoconchella nasuta*, indicates the age of the specimen must be restricted to the very latest Hettangian to very earliest Sinemurian of the Lower Jurassic (Figure 3).

Sediments of this age occur from southwest England and South Wales, through the English Midlands to the coasts of North Yorkshire and Humberside and are generally assigned to the Blue Lias Formation of the Lias Group. Due to the relatively widespread occurrence of sediments that could be assigned to Foraminiferal Biozone JF3 across the UK, it is not possible to use the assemblage to provide any geographical control on the specimen. Initially, the matrix sample was suggested to contain the same microfauna identical to that known from Hock Cliff, Gloucestershire, which led Massare and Lomax (2017a) to record the specimen as originating from Gloucestershire.

#### **Micro-CT scanning**

To aid analysis and identification of the very small bones, some of which are partially or fully embedded in matrix with key features hidden, BU 5289 was Micro-CT scanned. A 3D digital model of the skeleton, along with models of the skull, forefins and an isolated vertebrae, were created from the data. The scanner used in the Department of Zoology at the University of Cambridge was a Nikon XTH 225 Micro-CT Scanner, on the following settings: X-ray power 165 kV; 160 uA; Filtration 0.5mm copper; Resolution 125um; Projections 1080.

The outputs of the scanning process were TIFF files of the cross-section projections through the specimen separated into three sets of images showing the skull, dorsal and caudal sections of the specimen. The TIFF files, being raw image files, are large which makes them difficult to process efficiently into threedimensional models even with high-end processing hardware (e.g. an Intel i7 processor, NVIDIA GPU). Therefore the TIFF files were cropped (to remove empty surround) and turned into greyscale JPG's, using 'Blender 3D' (v2.78) compositing tools. The more manageable cropped and converted files were then imported into '3D Slicer' (v4.6.2) for conversion into a 3D surface model and exported as an STL (STereoLithography) file. The greyscale model maker in 3D Slicer was used to do this conversion.

The resulting models showed both sides of the specimen but the matrix contained molluscs and other debris that created noise in the models and partially obscured the rear surface of the specimen. It was decided to manually remove this noise using software, including mesh editing tools in Blender 3D.

Lastly, the 3D models of each section were aligned and joined to create a single 3D model of the whole specimen. The model scale was checked using reference photos of the specimen (that showed a metric scale) and fine adjustments were made. Measurements could be taken using the digital model and measuring tools in Blender 3D, although measurements of the skeleton were also taken manually with digital callipers and a tape measure. The micro-CT scan data and the digital 3D models are available from the Lapworth Museum.

## Description

#### Introduction

Specimen BU 5289 is a practically complete skeleton lying on its left side, exposed in lateral view (Figure 1). The preserved total length is 590 mm and the preflexural length is 560 mm; most of the postflexural region is missing. It comprises a wellpreserved skull, portions of both forefins, pectoral girdle elements, portions of both hindfins, pelvic elements, ribs, gastralia, and a largely articulated vertebral column. It can be assigned to the genus Ichthyosaurus because of the following combination of characters: maxilla excluded from margin of the external naris by subnarial process of premaxilla and anterior process of lacrimal; forefin with at least five primary digits; hindfin with at least four primary digits with a bifurcation in the third row; coracoid with prominent anterior and posterior notches; and a tripartite pelvis with an unfused pubis and ischium (although all elements are not preserved it is clear the ischium was not fused to the pubis). The specimen can be further assigned to *lchthyosaurus communis* because it shares the following unique combination of characters, as redefined by Massare and Lomax (2017a): a symmetric, triangular maxilla with an anterior process that extends beyond the external naris, and a posterior process that extends well under the orbit; the premaxilla supra- and subnarial processes are about equal in length, and extend about half way across the dorsal and ventral margins of the external naris, with the nasal contributing to about half of the dorsal margin; the anterior process of the jugal extends only slightly beyond the orbit, and the jugal dorsal ramus has a right angle dorsal bend; the humerus is much longer than wide, with a prominent dorsal process; and four elements are in the third row of the hindfin, owing to a bifurcation of tarsal 2. This specimen was designated a referred specimen of *I. communis* by Massare and Lomax (2017a).

## Maturity

Ichthyosaurus communis is known from multiple specimens, mostly from the Charmouth-Lyme Regis area, Dorset (Massare and Lomax 2017a). Specimen PETMG R174 was assigned to I. communis by Massare and Lomax (2017a). It is a practically complete, unequivocal example of *I. communis*, and has a jaw length of approximately 35.5 cm and a preflexural length (including the skull) of around 130 cm. The small size of BU 5289, with a preflexural length less than half that of PETMG R174, suggests a young individual, and probably even a neonate. Confirming the neonate status, however, is difficult because there is no published record of a growth series of Ichthyosaurus specimens. Furthermore, only three studies have examined some aspects of ontogeny of the genus (McGowan 1973; Deeming et al. 1993; Massare et al. 2015), all three taking a morphometric approach. Other studies of ichthyosaur ontogeny in Lower Jurassic ichthyosaurs have been published on the numerous embryos and neonates known from the Posidonia Shale of Holzmaden and surrounding areas in Germany (e.g. Stenoptervalus McGowan 1973; Johnson 1977; Dick and Maxwell 2015), although this material is younger (Toarcian) and belongs to other taxa.

The tip of the snout and much of the postcranial skeleton of BU 5289, especially the vertebrae, humerus, femur, and phalanges of the fore and hind fins

are highly cancellous/spongious (Figure 4). Similar preservation was reported in an embryo of the Cretaceous ichthyosaur Platypterygius australis (Kear and Zammit 2014, fig. 2). This suggests the elements were not fully ossified at the time of death and are probably representative of poorly ossified endochondral bone, or perhaps calcified cartilage. This porous texture is also present in various Stenopterygius embryos held in the collections of SMNS (DRL pers. obs.). The phalanges of the fore and hind fins of BU 5289 are very cancellous with the elements possessing somewhat scalloped edges (Figure 4D). This 'bottle-cap' like morphology was also reported by Lomax and Sachs (2017) in an embryo of Ichthyosaurus somersetensis. The atlas-axis is not fused, which is another indicator of the young age. The vertebral centra, including the rib articulations, are very cancellous and the centre of those that can be examined appear to be filled with matrix, which may suggest the centre still had a relatively large opening for the notochord (Figure 4C). The spongious texture of the centra has also been reported in a late-term embryo of the British Lower Jurassic ichthyosaur Leptonectes (Lomax and Massare 2012). That specimen, however, has an estimated preflexural length of 81.0 cm, about 30% larger than BU 5289, which suggests that Leptonectes gave birth to larger individuals than Ichthyosaurus communis.

In BU 5289, the sclerotic ring is well preserved, complete, and fills the orbital region (Figure 5). Fernandez et al. (2005) found that the sclerotic ring fills the orbital region in juvenile ichthyosaurs, whereas the sclerotic ring does not fill the orbital region in adults. Thus, the size of the sclerotic ring relative to the orbit, small body size, and poor ossification of the various elements indicate that BU 5289 is a neonate.

#### Skull, mandible and dentition

The skull is well-preserved, although much of the posterior end and skull roof are damaged (Figure 5). There is a crack that runs through the mid-section of the premaxilla and anterior portion of the dentary which gives the appearance of a 'downturned' snout, similar to *I. breviceps* (McGowan 1974; Massare and Lomax 2014), but this downturn is not genuine and is due to the piece having been incorrectly realigned. The skull is 15.5 cm long with a slight overbite of the snout.

The orbit, although round, has been deformed due to crushing but it is clear that the sclerotic ring filled the orbital margin. As the skull is slightly displaced, the nasals are exposed in dorsal view. A portion of the right, however, is also partially exposed in lateral view. In dorsal view, the nasal is wide posteriorly. In lateral view, the nasal extends slightly beyond the anterior process of the maxilla. The supranarial process of the premaxilla extends at least half way across the external naris, and the subnarial process extends just beyond half way across the external naris. The maxilla is triangular with an anterior process that extends beyond the external naris and a posterior process that extends approximately a third under the orbit. The jugal anterior process does not extend beyond the anterior margin of the orbit and the dorsal ramus of the jugal has a right angle bend that makes up about half of the posterior margin of the orbit. The basioccipital is preserved in posterior view and possesses a broad extracondylar area.

The mandible length is 15.8 cm. The snout ratio (preorbital length divided by the length of the mandible) is 0.59 (Table 2), which is marginally lower than what is expected for the species (>0.60; McGowan 1974, but see revised diagnosis by Massare and Lomax 2017a), and is in the range of *I. somersetensis* (Lomax and Massare 2017). It is possible that this lower ratio could be due to the deformation of the orbit, or that perhaps small individuals of *I. communis* have proportionally shorter snouts than large individuals. That said, Lomax and Massare (2015) guestioned the validity of the snout ratio among species of *Ichthyosaurus*, noting that differences in crushing of the skull can affect the ratio. Furthermore, they noted that the snout ratio overlaps in all other species, including *I. conybeari*, which was thought to have been distinguished by a high snout ratio (McGowan 1974, but see revised diagnosis by Massare and Lomax 2016). Therefore, *I. breviceps* is the only species that can be distinguished by having a very low snout ratio (McGowan 1974; Massare and Lomax 2014). The angular has minimal exposure in lateral view and its anterior extent cannot be determined with confidence. The surangular, however, extends as far forward as the anterior margin of the orbit. The fossa surangularis is prominent, long and narrow. The posterior end of the dentary appears to meet the surangular at approximately level with the middle of the orbit.

As exposed, in right lateral view, the teeth are not well-preserved, although some complete crowns are present (Figure 5A). The crowns are finely striated and the roots do not appear to have longitudinal grooves. The left side of the snout, although embedded in matrix, can be examined using the micro-CT scan and displays numerous slender tooth crowns (Figure 5B).

#### Axial skeleton

The vertebral column is largely articulated but some portions are displaced in the precaudal region. This gives the appearance of a somewhat sinuous vertebral column, which is likely the result of taphonomic processes, especially as many of the neural spines are also displaced (Figure 1). Including the atlas-axis, there are at least 44 precaudal centra, identified as those with two rib articulations; the 45th centrum is where the two rib articulations have merged, accounting for vertebrae obscured by matrix or other elements. The precaudal length, including the skull (measured along the vertebral column) is 42.3 cm. From here, there are 23 vertebrae and three impressions, which suggests the tail stock count is at least 26. Another impression might be the first fluke vertebra, which is then followed by 8 additional fluke centra. Beyond here, the rest of the tail is missing. The neural spines of the mid-cervical and anterior dorsal vertebrae are almost twice as tall as the posterior dorsal neural spines. The longest rib measures 10.8 cm along its curvature. Few gastralia are preserved, which are very delicate and some appear to be spindle-shaped.

#### Pectoral Girdle and Forefin

Both coracoids are preserved, with the right being the more completely exposed. The coracoid is anteroposteriorly longer than mediolaterally wide (Table 2). It has both well-developed anterior and posterior notches (Figure 6). The glenoid facet is about twice the size of the scapular facet but without a prominent distinction between the two facets. In larger specimens, the two facets are roughly equal in size (e.g. NHMUK PV R1162 [neotype]). The lateral portion is expanded and extremely thin. The coracoids are rugose and show fibrolamellar bone that radiates towards the lateral edge of the coracoid.

Both forefins are intertwined and lying atop each other, which makes description difficult (Figures 6-7). Furthermore, the proximal end of the fins are disarticulated. Regardless, the partially exposed humerus, in (?)posterior view, is probably the right based on its association with the right coracoid (Figure 6). Although buried, it has an estimated length of 1.2 cm. It can be examined in further detail with the micro-CT scan data (Figure 7). The humerus is a fairly robust element that is longer than wide, with the distal end marginally wider than the proximal end. It has both a prominent dorsal process and deltopectoral crest, but unfortunately, as both the dorsal and ventral surfaces are buried, it is difficult to determine with confidence which side is dorsal and which is ventral. Considering, however, that the (?)right humerus is probably in posterior view, we identify the deltopectoral crest as the one that is positioned more distally (Figures 6-7). It appears to be roughly centrally located and there appears to be a rim that outlines a smooth articular surface (Figure 7A). Admittedly, this is difficult to confirm and could be an artefact of the scan. The dorsal process is centrally located and has a well-defined ridge. There may be a depression on the articular surface, ventral to the dorsal process (Figure 7B). However, this is difficult to confirm and may be an artefact of the scan. The left humerus is not exposed as it is buried beneath the coracoids, but one side of it can be seen in the CT-scan (Figure 7). It is probably the left in (?)dorsal view, although the morphology of the dorsal process cannot be described and the humerus is dorsoventrally flattened. There may also be an anterior facet. It is articulated with what is presumably the radius. As the two fins are intertwined, the proximal portion of the fin cannot be examined with confidence. Regardless, the exposed distal end of the forefin has at least five primary digits (Figures 4D, 7). There may be at least one posterior accessory digit.

#### Pelvic Girdle and Hindfin

The pelvis, although incomplete, is tripartite, as in all species of *Ichthyosaurus* (Figure 8). The only complete element is the ischium which is not fused to the pubis. It is a long, narrow element that is slightly flared both proximally and distally. It is much longer than the femur. A section of the other ischium is also preserved but does not provide additional information. A portion of what is probably the pubis is preserved, but is incomplete and partly buried by the ischium. Only a fragment of the ilium is present, but an impression in the matrix suggests it was originally preserved and was probably shorter than the ischium.

Both femora are present, although the left is isolated in the matrix and the right is articulated with a portion of hindfin (Figure 8). The femur is highly cancellous, especially in the proximal region and distal end; it is most noticeable on the left femur (Figures 4F; 8). It is longer than wide and the distal end is wider than the proximal end. The anterior margin of the femur is slight flared, but almost straight, whereas there is a noticeable expansion at the posterior end. This expansion is most apparent in the right femur, which is in dorsal view. The proximal end has a relatively

flat head. The left femur is in ventral view and the ventral process is reduced and is roughly centrally located, offset closer to the anterior end. It is much more defined than the dorsal process of the right femur, which is barely discernible. The right hindfin is incomplete. Elements are largely spacious, although the spacing is probably due to post-mortem taphonomic displacement. This displacement can be identified by the position of the astragalus, which is located more proximally, separating the tibia and fibula. Additionally, the proximal element of the bifurcation and tarsal 3, which are directly distal to the astragalus, are located more proximally, in line with tarsal 2 and tarsal 4. Spacing between proximal fin elements has previously been used as a character to distinguish juveniles, as in Stenopterygius (Johnson 1977). But, the forefin elements are tightly packed in some other very small Ichthyosaurus specimens, including NHMUK PV OR10028, which is a specimen of I. anningae. This suggests that the spacing is not an indicator of age, at least in *Ichthyosaurus*. The fibula is anteroposteriorly longer than the tibia, but is roughly proximodistally the same. A bifurcation of digit II (distal tarsal 2) results in four elements in the third row, and tarsal 3 and the proximal element of the bifurcation are directly distal to and appear to have roughly equal contact with the astragalus. There are at least four primary digits, but the fin is incomplete so the total primary digit count is not possible to confirm. A posterior accessory digit is present at the level of the second phalangeal row.

#### Stomach contents

A large number of fragmented, black cephalopod hooklets are scattered between the ribs. Most are elongated, with a straight or slightly curved uncinus, whereas others are fragmented and lack any good 'hooks' (Figure 9). The elongated hooklets are similar to those described by Pollard (1968, fig 2B,C) and Lomax (2010, fig 11D). Hooklets have been reported in specimens of *Ichthyosaurus* (Pollard 1968; Lomax 2010) and although most were initially thought to have been from belemnites they also belong to phragmoteuthids (Valente et al. 2010; Lomax and Massare 2015). The presence of cephalopod hooklets in the stomach contents of the studied specimen differs from what was found by Dick et al (2016) for small juvenile specimens of *Stenopterygius*. They found that small juveniles had only fish scales in their stomach contents, whereas large adults had only cephalopod hooklets, therefore showing a size-related trophic niche shift through ontogeny. We have been unable to identify any fish scales in the studied specimen. Another juvenile specimen of *Ichthyosaurus* (DRL, pers. obs. OUMNH J.13593), however, has both cephalopod hooklets and fish scales in the stomach contents.

A dark mass also overlies several ribs, although no identifiable hooklets could be found in this material. It is possible that this could be soft tissue, similar to that preserved in other ichthyosaur specimens (see review by Martill 1993; Martill 1995). Another large, scattered, tan-coloured mass is positioned between the ribs, close to the pelvic region (Figure 9). Similarly, there are no hooklets preserved in this mass. The preservation and texture is comparable to coprolitic material so this may represent a bromalitic mass.

## Conclusions

BU 5289 displays several features that are consistent with *Ichthyosaurus communis*, which led Massare and Lomax (2017a) to refer it to the species, although a full description is provided here. It is the smallest known example of *I. communis* and is clearly not an embryo because it has stomach contents and was not preserved within an adult. Given the size of the specimen, the size of the sclerotic ring relative to the orbit, the porous nature of the bones, the early stage of ossification of some of the bones, and their similarity with the bones of embryos preserved in adults, the specimen can be considered a neonate.

This research highlights the significance of detailed, osteological comparison of small *lchthyosaurus* examples with large examples in order to positively identify specimens beyond *lchthyosaurus* sp. It is surprising, given the number of small *lchthyosaurus* specimens known, that only a few small examples have been confidently assigned beyond *lchthyosaurus* sp. Furthermore, microfossil analysis of the matrix has revealed an uppermost Hettangian to lowermost Sinemurian age for the specimen. This gives a geographical range within which the specimen must have been excavated, but does not provide a specific location. Therefore, this research also highlights the use of microfossil analyses to provide a more specific age for the many marine reptile specimens in museum collections that currently lack any stratigraphic data, thereby greatly increasing their research potential and scientific significance.

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#### **Disclosure statement**

No potential conflict of interest was reported by the authors.

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Table 1. Microfossils found during the matrix analysis of BU 5289.

Ostracoda
Ostracoda Monoceratina frentzeni Ogmoconcha hagenowi Polycope pumicosa Ogmoconchella nasuta Paracypris sp.A

Notes: In all, a total of about 110 calcareous microfossils were recovered from the small sample of matrix. These represented at least 13 species/subspecies of foraminifera (approximately 80 specimens) and 5 species (approximately 30 specimens) of ostracods. The most abundant and/or diagnostic taxa are illustrated in Figure 2.

# FIGURES



**Figure 1**. Specimen BU 5289, an almost complete neonate skeleton of *lchthyosaurus communis*. Scale equals 10 cm.



**Figure 2.** Photomicrographs of the most abundant and/or stratigraphically important taxa from the sediment matrix of BU 5289. 1-3. *Paralingulina tenera tenera*. 1. 640 μm. 2. 790 μm. 3. 1075 μm. 4. *Nodosaria mitis*. 800 μm. 5. *Ichthyolaria terquemi* (4-ribbed type). 6. *Marginulina prima insignis*. 1290 μm. 7. *Marginulina prima incisa*, 925 μm. 8. *Mesodentlina matutina*. 1015 μm. 9. *Planularia inaequistriata*. 790 μm. 10. *Ogmoconchella nasuta*, carapace, right lateral. 510 μm. 11. *Polycope pumicosa*, carapace, left lateral. 340 μm. 12. *Astacolus speciosus*. 660 μm. 13. *Paracypris* sp.,

right valve, external. 440 μm. 14. *Ogmoconcha hagenowi*, right valve, external. 590 μm. 15. *Monoceratina frentzeni*, right valve, external. 600 μm.



**Figure 3.** Chronobiostratigraphy of the Early Jurassic interval with key biostratigraphic marker events noted. These confine the likely age of BU 5289 to the Liasicus Ammonite Chronozone or Bucklandi Ammonite Chronozone.



**Figure 4.** Various portions of the skeleton of BU 5289 showing highly cancellous bones. A. Tip of the snout. B. Left coracoid; note the radiating fibrolamellar bone. C. Several caudal vertebrae; note the centre of the centrum appears to be filled with matrix, which may suggest that a large opening was present for the notochord. D. A portion of the ?left forefin showing the 'bottle-cap' like morphology of the phalanges that have somewhat scalloped edges. E. Distal end of the exposed ?right humerus. F. Left femur in ventral view.



**Figure 5.** A. Close-up of the skull and mandible of BU 5289. Note, the 'downturn' of the snout is not genuine and is a result of the crack running across the premaxilla and dentary, which has not been realigned correctly. B. Micro-CT scan of snout with close-up of the reverse side (not exposed), showing well-preserved teeth with crowns. Scale equals 5 cm.



**Figure 6.** Right (upper) and left (lower) coracoids, (?)right humerus and portions of a forefin of BU 5289. The humerus is possibly in posterior view and would suggest that

the deltopectoral crest is to the left (white arrow) and the dorsal process is to the right (black arrow). Scale equals 1 cm.



**Figure 7.** Micro-CT scans of the forefin(s) of BU 5289. A. (?)Right humerus in ventral view, anterior to the left. The deltopectoral crest appears to be centrally located. B. (?)Right humerus in posterodorsal view; the arrow points to the dorsal process. C. Proximal surface of the (?)right humerus. The white arrow points to the deltopectoral crest and the black arrow points to the dorsal process. Note: ?dep indicates possible depression ventral to dorsal process. D. Reverse side (not exposed), of intertwined forefins showing the (?)left humerus in dorsal view (black arrow), anterior to the left, and (?)right humerus in (?)posterior view. R means (?)radius.



**Figure 8.** Pelvic girdle and hindfins of BU 5289. The left femur (upper) is in ventral view, whereas the right (lower) is in dorsal view and is articulated with a portion of the hindfin. Anterior is to the right in both. The long element is the complete ischium. A fragment of ilium (arrow) is positioned proximal to the ischium. Scale equals 1 cm. Column width. Colour online only.



**Figure 9.** A. Probable bromalitic material preserved between the ribs of BU 5289. B. Several black cephalopod hooklets preserved between the ribs of BU 5289. Note, arrows point to the more complete hooklets. Scale bars equal 1 cm.