

A revision of *Ichthyosaurus* (Reptilia, Ichthyosauria)

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Abstract

The first ichthyosaur to be scientifically recognized was the common Early Jurassic form, *Ichthyosaurus*. Ichthyosaur specimens collected during the 19th century were almost exclusively referred to that genus, resulting in numerous species assigned. Most recent work prior to this study considered four valid species: *Ichthyosaurus communis* De la Beche and Conybeare, 1821, *I. breviceps* Owen, 1881, *I. conybearei* Lydekker, 1888 and *I. anningae* Lomax and Massare, 2015, although a fifth, *I. intermedius* Conybeare, 1822, was recognised by some workers. The type species (*I. communis*) has for a substantially long time been considered highly variable and common. Practically every *Ichthyosaurus* specimen that could not be identified as one of the other species was regarded as *I. communis*, essentially making it a wastebasket taxon. The genus and species therein have received little study since the 1970s. The recent description of *I. anningae*, coupled with other studies undertaken by the author, has provided a foundation for a revision of the genus.

This study recognises two new species of *Ichthyosaurus* (*I. larkini* and *I. somersetensis*), and confirms the synonymy of *I. communis* and *I. intermedius*. Thus, six species of *Ichthyosaurus* are recognised as part of this work, each of which can be reliably distinguished on the basis of skull and humerus morphologies. In addition, a new specimen described herein represents the largest example of the genus and provides new information on the size range of the genus and species; it is also one of only a handful of pregnant specimens known from the UK. Furthermore, based on specific skull and postcranial characters defined in this study, the first neonate *I. communis* is recognised and formally described, which will assist in future studies on ichthyosaur ontogeny. This body of work also examines the morphological variation of the hindfin of *Ichthyosaurus*, a part of the skeleton that is often overlooked in ichthyosaur taxonomy. With a smaller sample size it would have appeared that the hindfin was taxonomically useful, but instead the large sample shows a continuum of variation across species.

The examination of *Ichthyosaurus* provided a basis for the assessment of the contemporaneous Early Jurassic ichthyosaur *Protoichthyosaurus* Appleby, 1979, a genus that was previously synonymised with the former. Based on the unique forefin structure and features of the skull, *Protoichthyosaurus* is here considered distinct from *Ichthyosaurus*. A new species is also formally described, *P. applebyi*, along with the description of a large, three-dimensionally preserved skull and postcranial skeleton that was CT-scanned. This research confirms the presence of two Early Jurassic ichthyosaur genera with a wide forefin and anterior digital bifurcations. A revised diagnosis of both taxa is presented herein.

Declaration

No portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

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Dedication

To those who have been told you can't – prove that you can.

Acknowledgements

There have been many people who have helped me on my journey in palaeontology, a journey that began when I was a young child. Although I took an unusual route into palaeontology, I have now been working in the field professionally for over a decade. During that time, I have had the privilege of collaborating with some of the most remarkable individuals who I am grateful to call my friends. To each of the following, without your help and support over the years, I would not be the person I am today, nor would I have achieved what I have.

Professor Judy Massare has been the greatest mentor I could ever have asked for. I met Judy serendipitously in 2008 whilst on a dig in Wyoming, USA, at the age of 18. We have since collaborated on numerous projects and have travelled together across the UK and US as part of several unforgettable research trips. Nigel Larkin and I first met at the SVPCA conference in Lyme Regis, 2011, where I apparently looked “severe” (in-joke). Since our chance meeting, we have worked together on various scientific (and popular) papers, museum projects, fieldwork and science communication work. From encouraging me to write books, to present my research at the House of Commons, and to lift heavy weights at the gym, Dr David Penney has helped to steer my career in various directions. To my friend, colleague and advisor, Dr John Nudds, thanks for having confidence in me and encouraging me at every step. Each of you have been there for me throughout my career, offering support, encouragement and help whenever I have needed it.

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Finally, I would like to give a special thanks to The University of Manchester for awarding me a PGR Dean's Doctoral Scholarship Award, without which I would have been unable to undertake and complete this PhD. Thank you.

Frontispiece



Awful Changes. Man Found only in a Fossil State.

A lecture. – “You will at once perceive,” continued Professor Ichthyosaurus, “that the skull before us belonged to some of the lower order of animals; the teeth are very insignificant, the power of the jaws trifling, and altogether it seems wonderful how the creature could have procured food.”

*By Henry De la Beche (AKA Prof. Ichthyosaurus) in 1830.
Featured in Curiosities of Natural History by Francis Trevelyan Buckland.*

Institutional abbreviations (in alphabetical order)

Each of the following institutions have specimens of *Ichthyosaurus* in their collections. Although specimens from some of these institutions are not discussed in this thesis, it seems appropriate that the author lists every institution that has *Ichthyosaurus* specimens so that future workers are aware of the existence of these collections.

AMNH, American Museum of Natural History, New York, USA; **ANSP**, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; **AUZH**, Aberdeen University Zoology Museum, Scotland; **BELUM**, National Museums Northern Ireland (Ulster Museum), Cultra, Northern Ireland; **BG**, Biddulph Grange (National Trust), Biddulph, England; **BGS**, British Geological Survey, Nottingham, England; **BM**, Berwick Museum, Berwick-upon-Tweed, England; **BMAG**, Birmingham Museums, including Thinktank Museum, Birmingham, England; **BRLSI**, Bath Royal Literary and Scientific Institute, Bath, England; **BRSMG**, Bristol City Museum and Art Gallery, England; **BRSUG**, Bristol University, England; **BTM**, Blandford Town Museum, Dorset, England; **BU**, Lapworth Museum of Geology, Birmingham, England; **CAMSM**, Sedgwick Museum, Cambridge University, England; **CC**, Cliffe Castle Museum, Keighley, England; **CHCC**, Charmouth Heritage Coast Centre, Dorset, England; **CLC**, Cheltenham Ladies College, Cheltenham, England; **CM**, Carnegie Museum of Natural History, Pittsburgh, USA; **CMNH**, Cleveland Museum of Natural History, Ohio, USA; **CSM**, Charterhouse School Museum, Godalming, England; **DBYMU**, Derby Museum and Art Gallery, England; **DONMG**, Doncaster Museum and Art Gallery, England; **DORCM**, Dorset County Museum, England; **FMNH**, Field Museum of Natural History, Chicago, USA; **GLAHM**, Hunterian Museum, Glasgow, Scotland; **GCM**, Gloucester City Museum, England; **GNM**, Great North Museum (Hancock), Newcastle, England; **GPIT**, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; **HAUFF**, Hauff Museum, Holzmaden, Germany; **HERM**, Hull and East Riding Museum, England; **HM**, Haslemere Museum, England; **HMG**, Horniman Museum and Gardens, London, England; **IM**, Ilfracombe Museum, Devon, England; **IPSMG**, Ipswich Museum, England; **IST**, Instituto Superior Técnico, Lisbon, Portugal; **LDUCZ**, Grant Museum of Zoology, London, England; **KLM**, Lynn Museum, King's Lynn, England; **LEICT**, Leicester Arts and Museums Service, New

Walk Museum and Art Gallery, England; **LM**, Leeds Museum, England; **LYMPH**,
 Lyme Regis Museum, Dorset, England; **LYM**, Lynn Museum, King's Lynn, England;
LWM, Liverpool World Museum, England; **MANCH**, Manchester Museum, England;
MCZ, Harvard Museum of Comparative Zoology, Massachusetts, USA; **MCNB**,
 Museu de les Ciències Naturals de Barcelona, Spain; **MM**, Maidstone Museum,
 Kent, England; **MPS**, Museum in the Park, Stroud, England; **NCMAG**, Norwich
 Castle Museum and Art Gallery, England; **NEWHM**, Hancock Museum, Newcastle,
 England; **NHMUK**, The Natural History Museum, London, England; **NLMH**,
 Niedersächsisches Landesmuseum (Lower Saxony State Museum), Hannover,
 Germany; **NHMOV**, Natural History Museum Vienna, Austria; **NMC**, National Museum
 of Canada, Ottawa, Canada; **NMI**, National Museum of Ireland, Ireland; **NMNS**,
 National Museum of Natural Sciences (Canadian Museum of Nature), Ottawa,
 Ontario, Canada; **NMS**, National Museum of Scotland, Edinburgh, Scotland; **NMV**,
 Museums Victoria, Melbourne; **NMW**, National Museum of Wales, Cardiff, Wales;
NOTNH, Nottingham Natural History Museum (Wollaton Hall), England; **OUMNH**,
 Oxford University Museum of Natural History, England; **PETMG**, Peterborough
 Museum, England; **QMU**, Queen Mary University of London, England; **RAMM**, Royal
 Albert Memorial Museum, Exeter, England; **RBINS (IRSNB)**, Royal Belgian Institute
 of Natural Sciences, Brussels, Belgium; **RNHM**, Reutlingen Natural History Museum,
 Germany; **ROM**, Royal Ontario Museum, Toronto, Canada; **SHEFFM**, Sheffield
 Museum, England; **SM**, Swansea Museum, Wales; **SMNS**, Staatliches Museum für
 Naturkunde (Stuttgart Natural History Museum), Germany; **SOMAG** (formerly AGC),
 Alfred Gillett Collection, cared for by the Alfred Gillett Trust (C & J Clark Ltd), Street,
 Somerset, England; **TM**, Teylers Museum, Haarlem, Netherlands; **TMP**, The Royal
 Tyrrell Museum of Palaeontology, Alberta, Canada; **TPM**, Te Papa Museum,
 Wellington, New Zealand; **TTNCM** (formerly MOS), Museum of Somerset, Taunton,
 England; **UHM**, Urweltmuseum Hauff Museum (Hauff Museum), Holzmaden,
 Germany; **UMZ**, University Museum of Zoology, Cambridge, England; **UNM**,
 University of Nottingham Museum, England; **UOD**, University of Derby, England;
UOL, University of Leicester, England; **UOM**, University of Manchester, England;
UON, University of Nottingham, England; **UOS**, University of Southampton, England;
UOZ, University of Zurich, Switzerland; **UORCMZ**, Cole Museum of Zoology,
 Reading University, England; **USNM**, Smithsonian Museum, Washington D.C., USA;
UWGM, University of Wisconsin Geological Museum, USA; **WARMS**, Warwick

Museum, England; **WFIS**, The Wagner Free Institute of Science, Pennsylvania, USA; **WHITM**, Whitby Museum, England; **WM**, Woodspring Museum, Weston-super-Mare, England; **WMHM**, Watchet Market House Museum, England; **WORCS**, Worcester Museum, England; **YPM**, Yale Peabody Museum of Natural History, Connecticut, USA; **YORYM**, Yorkshire Museum, York, England.

Chapter 1: Introduction

1.1 The Project – Aims and Importance

Ichthyosaurus is among the most widely known fossil reptiles and has historical significance in being the first ichthyosaur recognised by science (König, 1818) (Figure. 1.1). Yet, even considering the great number of known specimens, the genus and species has received little study since McGowan (1974b), who provided the first modern overview and synonymy. Since then, others have incorporated *Ichthyosaurus* within larger reviews of the Ichthyopterygia and in various phylogenetic analyses (e.g. Motani, 1999a; Maisch and Matzke, 2000; Sander, 2000; McGowan and Motani, 2003; Ji et al., 2016; Moon, 2017) and smaller subclade analyses (e.g. Maxwell et al. 2012; Fischer et al. 2013; Maxwell et al. 2016). However, most of these studies are based on the type species of the genus, *Ichthyosaurus communis*, which is shown in this body of work to represent at least three species within the genus and two species within a separate (resurrected) genus. As part of this work, I examined complete and partial skeletons, isolated skulls, forefins, and hindfins that were measured (where possible) and photographed. Specimens that were identified as composites were critically evaluated and the useful data was retained.

The first part of the thesis, chapters 3-7, focuses exclusively on *Ichthyosaurus*. The first major aim of the project was to determine what *I. communis* actually is and whether the variation represents a single species or more, which included examining numerous specimens such as the neotype and previously referred specimens of the species. Further, this allowed for the formal recognition of two new species that were removed from the variation of *I. communis* and a reassessment and revision to the genus and species diagnoses. Both new species were added to a phylogenetic analysis. In light of these studies, a small-bodied *Ichthyosaurus* specimen that had not formally been reported previously was identified and described as the only known neonate specimen of *I. communis*. Another part of the project included the identification and description of an almost complete skeleton that had also not previously been studied, and which provided new information on the size range of the genus and species. The last part of this work on *Ichthyosaurus* analysed whether hindfins are taxonomically useful. The decision to look at hindfins was made

because they are often neglected in taxonomic studies, so this analysis revealed their potential usefulness at genus and species level, and shed light on their phylogenetic importance.

Whilst reviewing *Ichthyosaurus* specimens, multiple examples were found to have additional differences in the skull and postcranium that were not typical of the genus and therefore warranted further assessment. For this reason, the second major focus of the work was to reassess the Early Jurassic ichthyosaur *Protoichthyosaurus* Appleby, 1979. This genus was synonymised with *Ichthyosaurus* (Maisch and Hungerbühler, 1997), but without much explanation. Based on a comparison of the two genera, along with a re-examination of the original type material of *Protoichthyosaurus*, and the identification of additional specimens located during the study, it was found that the two genera could be reliably distinguished on the basis of skull and forefin morphologies. Furthermore, to assess its relationships with *Ichthyosaurus* and other ichthyosaurs, *Protoichthyosaurus* was added to a phylogenetic analysis for the first time. In addition, a description of the largest known *Protoichthyosaurus* specimen was also undertaken, based on a previously undescribed three-dimensional skull and postcranial skeleton. Thus, this part of the project helped resolve the synonymy and emphasise further the importance of taxonomic studies. Specifically, the recognition of another Early Jurassic taxon provides a better picture of the radiation of ichthyosaurs following the end Triassic extinction event (Thorne et al. 2011).

With the large number of specimens identified in various collections, *Ichthyosaurus* is among the most common Early Jurassic reptile fossil held in museums, especially in the UK. I located many additional specimens that have never before been discussed in the scientific literature. Considering that these specimens have provided additional, important information about the genus and/or species therein, this highlights the value of visiting smaller, lesser known institutions that are often overlooked, but which can have important specimens.

1.2 Original research previously undertaken by the author

The research in this thesis is built upon the author's previous studies on the genus *Ichthyosaurus*, which provided a platform for a detailed revision. The author first

began studying the genus in 2008 and has since visited numerous institutions to gather data and subsequently publish research on *Ichthyosaurus* (Lomax, 2010; Lomax and Massare, 2015; Lomax and Larkin, 2015; Lomax and Gibson, 2015; Massare and Lomax, 2014a, 2014b, 2016a, 2016b; Massare et al. 2015). Naturally, these data have been utilised herein, but this work required re-examination of numerous specimens held in a variety of institutions, along with the examination of other collections that the author had not previously visited.



Figure. 1.1. Around 195 million years ago, during the Early Jurassic, a group of *Ichthyosaurus* feast on a fish bait ball. Artist reconstruction courtesy of Bob Nicholls (Paleocreations).

1.3 Thesis Layout

This thesis is submitted under the journal format for a PhD thesis, as outlined by the regulations of The University of Manchester. The thesis is formatted with an introduction to this body of research, followed by a literature review, a series of seven original research papers that are published in peer-reviewed, academic journals and ends with a discussion of the main conclusions of the research and implications for future work.

The first component of the PhD, comprising five research papers, focuses exclusively on *Ichthyosaurus*. Chapters 3 and 4 revolve around the taxonomy

including diagnoses of two new species, a revised diagnosis of the genus, and the evaluation of the synonymy of *I. communis* and *I. intermedius*. The following two chapters include the description of two new specimens that have not previously been described: the largest example of the genus (Chapter 5) and the first-known neonate *I. communis* (Chapter 6). Each study provides new information on the size-range of the genus/species and the latter provides the basis for future studies on ichthyosaur ontogeny. This section concludes with a study on hindfin variation in *Ichthyosaurus* (Chapter 7), which tests the potential taxonomic usefulness of this part of the skeleton. The second major component of this work, comprising two research papers, compares *Ichthyosaurus* with *Protoichthyosaurus* and includes a description and revised diagnosis of the latter (Chapter 8), and the description of a large, three-dimensionally preserved skull and partial skeleton (Chapter 9).

1.4 Co-author contributions to papers included in this work

Co-author contributions to Chapter 3.

This chapter was co-authored with Prof. Judy A. Massare (SUNY College at Brockport, NY, USA). We examined *Ichthyosaurus* specimens held in numerous collections, mainly in the UK and North America, which included taking measurements and photographs. I made return visits to multiple museums to examine additional specimens, take more photographs, verify observations, or make additional measurements, as needed. I wrote the first draft of the manuscript and subsequent editions were written in collaboration with the co-author. Additionally, I created the character matrix and performed the phylogenetic analysis, with some suggestions from my co-author. I created all of the figures, including line drawings of specimens.

Co-author contributions to Chapter 4.

Co-author contributions to the work were as for Chapter 3. However, together with my co-author, we each wrote parts of the first draft of the manuscript and edited subsequent versions. In addition, I visited the Staatliches Museum für Naturkunde, Stuttgart, Germany, to examine the so-called '*Ichthyosaurus intermedius*' specimen that was critical to this study. My co-author was unable to visit the museum. Moreover, I also visited National Museums Northern Ireland (Ulster Museum) and

the Field Museum, Chicago, IL, USA, to study several specimens. Again, my co-author was unable to visit these institutions.

Co-author contributions to Chapter 5.

This chapter was co-authored with Sven Sachs (Bielefeld Natural History Museum, Germany). The key specimen for this study was brought to my attention by Sachs. I examined, measured, identified and photographed the specimen. Sachs assisted with measurements, photographs, and translated text from museum records. I created all of the figures and wrote the manuscript, which was edited by the co-author.

Co-author contributions to Chapter 6.

This chapter was co-authored with Nigel R. Larkin (Cambridge University Museum of Zoology, Cambridge, UK), Dr Ian Boomer (University of Birmingham, Birmingham, UK), Steven Dey (ThinkSee3D Ltd, Eynsham, UK) and Dr Philip Copestake (Merlin Energy, Resources Ltd, Ledbury, UK). I examined, measured, and photographed the primary specimen of this study. No location information was recorded with the specimen. Based on comparison with other ichthyosaurs, I suggested that it was probably from the Lower Jurassic. However, to evaluate this possibility some matrix from the specimen was analysed by Boomer and Copestake at The University of Birmingham. Numerous microfossils in the matrix helped to shed light on the stratigraphic range of the specimen. Boomer and Copestake wrote a short section on the age and provenance of the ichthyosaur, which I edited; it also led to the creation of a figure and table. The specimen was micro-CT scanned and a short section was written largely by Larkin and Dey, which I edited. I also created the figures, except for figures 2 and 3, and wrote the rest of the manuscript, which was edited by Larkin.

Co-author contributions to Chapter 7.

Co-author contributions to the work were as for Chapter 4. In addition, I examined multiple specimens that my co-author did not at the Field Museum, Chicago; National Museum of Ireland, Dublin; National Museum of Northern Ireland; Staatliches Museum für Naturkunde, Stuttgart; Lower Saxony State Museum, Hannover, Germany. Plus, many smaller museums in the UK, including: Cliffe Castle Museum, Bradford; Cheltenham Ladies College; Gloucester City Museum;

Haslemere Educational Museum, Surrey; Leeds Museums and Galleries; Royal Albert Memorial Museum, Exeter; Weston Park Museum, Sheffield.

Co-author contributions to Chapter 8.

This chapter was co-authored with Prof. Judy A. Massare (SUNY College at Brockport, NY, USA) and Rashmiben T. Mistry (University of Reading, UK). Contributions from Massare were the same as in Chapter 4. Again, I took the lead in the phylogenetic analysis and created all of the figures, including line drawings of specimens. Whilst writing this manuscript, Mistry called my attention to a juvenile ichthyosaurus with an unusual forefin structure, held in the collections of the University of Reading. She had described the specimen in her undergraduate thesis. I subsequently examined the specimen with Mistry and identified it as the only known juvenile of *Protoichthyosaurus*.

Co-author contributions to Chapter 9.

This chapter was co-authored with Nigel R. Larkin (Cambridge University Museum of Zoology, Cambridge, UK) and Dr Laura B. Porro (University College London, UK and Cambridge University Museum of Zoology, Cambridge, UK). Working with Larkin, we disassembled the entire three-dimensional skull, which Larkin cleaned and conserved. This provided an opportunity to study individual bones of the skull in detail. The incomplete postcranial skeleton was also cleaned by Larkin. I identified the specimen, identified the bones, took measurements and photographs, and created several figures (figures 1, 5-7). Larkin provided specific details about the conservation, the geological setting, and location of discovery. As part of the work, elements of the braincase were also micro-CT scanned. Porro led on the scanning and collected, segmented, visualized, and interpreted the CT data and created several figures. I aided Porro with the interpretation of the scanned elements. The manuscript was written by me and edited by Porro and Larkin. In addition, I examined comparative specimens in several UK institutions, including: Bath Royal Literary and Scientific Institution; Leicester Arts and Museums Service, New Walk Museum and Art Gallery; Natural History Museum, London; Alfred Gillett Collection, Street, Somerset; University of Nottingham Museum. As part of this project, my co-authors did not study specimens in these collections.

Chapter 2: Literature Review

2.1 Introduction

Ichthyosaurs are a well-studied group of fully aquatic marine tetrapods that gave birth to live young and swam using their tails, whilst the fore and hind fins were used for manoeuvring and breaking (Massare, 1988; Martill, 1996; Buchholtz, 2001). They were a particularly successful group that flourished throughout the Triassic, Jurassic and early Late Cretaceous, for about 155 million years (McGowan and Motani, 2003; Ji et al. 2016) (Figure. 2.1). To clarify, 'ichthyosaur' is used as a common name for the group Ichthyopterygia, which contains the clade Ichthyosauria and the more basal ichthyopterygians (Motani, 2005).

The first documented occurrences of what can now be identified as ichthyosaurs are from the late 1600s and 1700s (e.g. Lhwyd, 1699), although their identity was not recognized at the time and most were regarded as 'fish', 'crocodiles' or 'alligators' (Delair, 1969; McGowan and Motani, 2003). It was not until the early 19th century that their origin was determined. During this time, various individuals brought specimens to the attention of science. In particular, many of these early specimens were collected by Mary Anning (1799-1847), a fossil collector and palaeontologist who lived in Lyme Regis, Dorset, on the south coast of England (Torrens, 1995). The first scientific account of an ichthyosaur was by Home (1814), based upon a specimen collected by Mary and her brother Joseph. That same specimen is now identified as the Early Jurassic ichthyosaur *Temnodontosaurus platyodon* (Conybeare, 1822) and is on display at the NHMUK (Figure. 2.2). Such early discoveries sparked major interest in the study of ichthyosaurs and thousands of specimens have since been discovered across the globe.

Species ranged from less than 1 m to more than 25 m long (Maisch and Matzke, 2000; McGowan and Motani, 2003; Lomax et al. 2018a) and were the first group of tetrapods to reach truly gigantic size. Their terrestrial ancestry remains a mystery (Maisch, 2010) but recent analysis of specimens from the earliest Triassic of China may eventually yield more information about their origins (Motani et al. 2015; Jiang et al. 2016). In particular, the discovery of the possibly amphibious basal ichthyosauriform (Ichthyosauromorpha) marine reptiles *Cartorhynchus* (Motani et al. 2015) and *Sclerocormus* (Jiang et al. 2016), together with another Early Triassic

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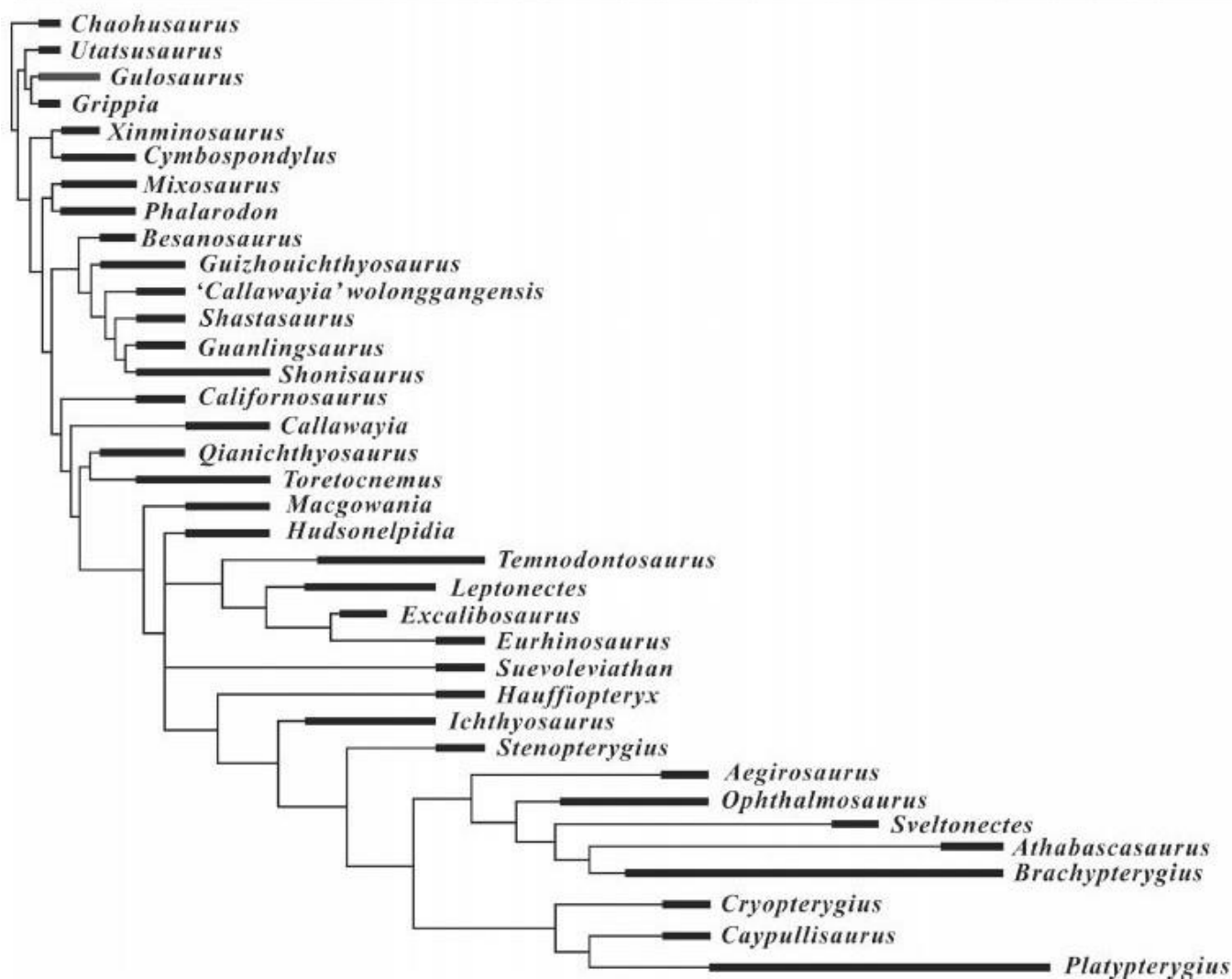


Figure. 2.1. Stratigraphic record of Ichthyopterygia from Ji et al. (2016, fig 6). Note that *Ichthyosaurus* is shown to be present in the Late Triassic (Rhaetian), but this has yet to be confirmed, as discussed in this thesis.

marine reptile group, the long-jawed Hupehsuchia, have helped to advance our understanding of the early evolution of ichthyosaurs and their relatives (Carroll and Dong, 1991; Motani et al. 2015; Jiang et al. 2016).

The earliest known ichthyosaurs such as *Chaohusaurus* from China lived during the Early Triassic (early-middle Spathian, a substage of the Olenekian),

alongside the basal ichthyosauriforms, and had the appearance of ‘lizards with flippers’, whereas later forms evolved the now iconic fish or cetacean-shaped bodies (Motani, 2005; Motani, 2009). One recently described *Chaohusaurus* specimen contained the remains of multiple embryos (Motani et al. 2014). Although the existence of viviparity in ichthyosaurs has been known since Channing Pearce (1846), with subsequent descriptions of Middle Triassic, Jurassic and Cretaceous aged ichthyosaurs with embryos (e.g. McGowan, 1979; Böttcher, 1990; Deeming et al. 1993; Dal Sasso and Pinna, 1996; Maxwell and Caldwell, 2003), this pregnant *Chaohusaurus* is significant as the geological age of the specimen suggests a likely terrestrial origin for live birth in the group (Motani et al. 2014).

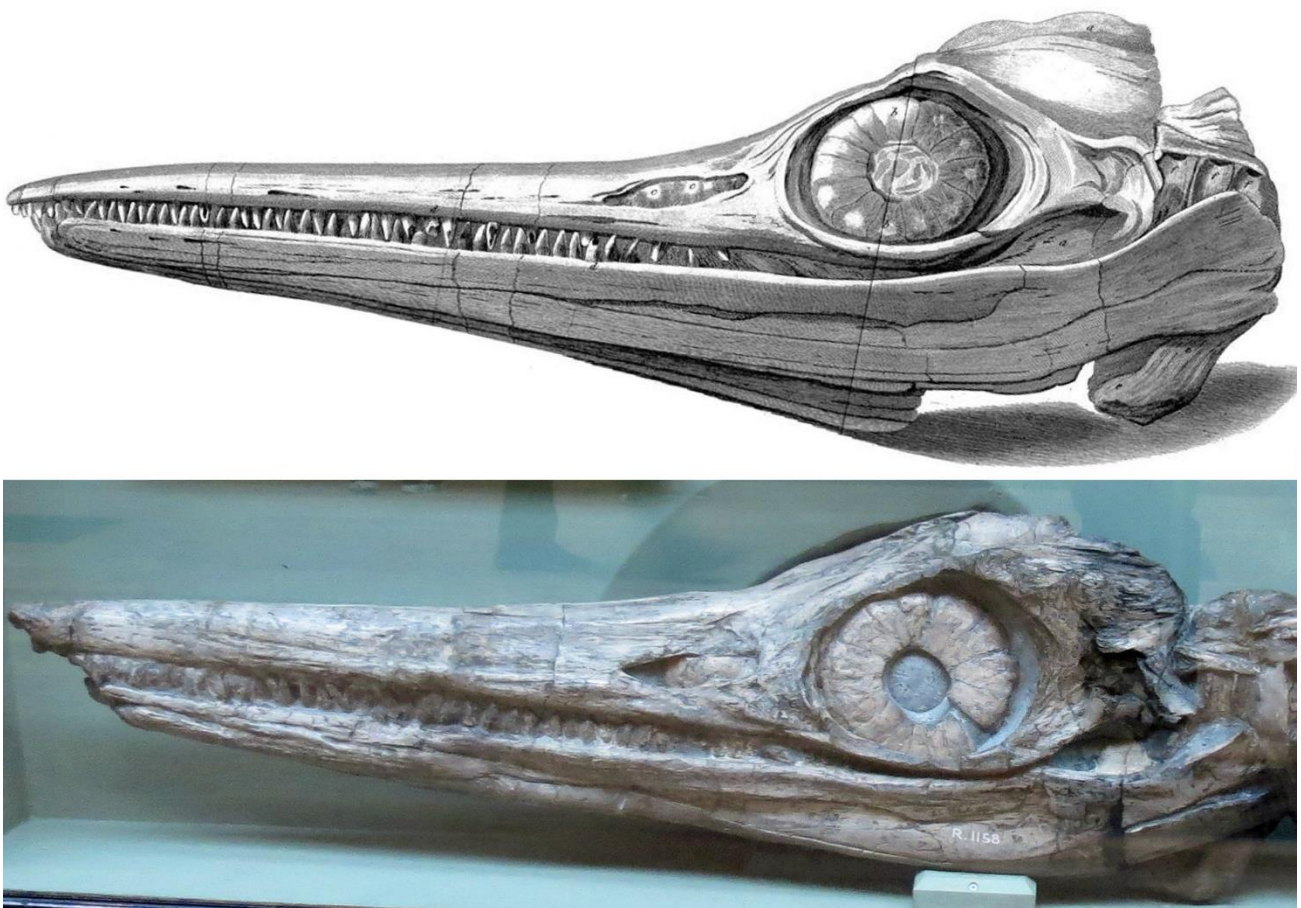


Figure. 2.2. NHMUK R1158, Joseph and Mary Anning’s ichthyosaur, now referred to as *Temnodontosaurus platyodon*. Original illustration from Home (1814) and photograph of same specimen on display at the NHMUK.

Ichthyosaurs were particularly well equipped predators. Tooth form varies among ichthyosaur species, with some bearing delicate teeth for piercing, and others possessing more robust teeth for cutting and grasping prey (Massare, 1987). Even

preserved stomach contents have been reported in several ichthyosaur genera and were first described over 180 years ago (see discussion in Pollard, 1968). They often comprise the tiny arm hooklets of squid-like cephalopods (Pollard, 1968; Massare and Young, 2005; Lomax, 2010; Valente et al. 2010; Dick et al. 2016), although remains of fish and even other ichthyosaurs have been recorded (Massare, 1987; Dick et al. 2016; see also the discussion in Pollard, 1968) and one Cretaceous specimen even contained the remains of hatchling-sized turtles and a bird (Kear et al. 2003), suggesting that ichthyosaurs fed upon a range of prey. Coprolites that may have been produced by ichthyosaurs sometimes contain fragments of bone, teeth and scales (Buckland, 1829).

In order to explore the evolutionary relationships among ichthyosaur taxa, in the last 40 years several cladistic analyses have been undertaken. The very first cladogram was presented by Mazin (1981), who examined relationships between basal ichthyopterygians outside of Ichthyosauria. A year later, Mazin (1982) expanded his analysis to include 54 taxa and 14 characters. This pioneering study provided the basis for several small-scale cladistic analyses undertaken on different ichthyosaur clades. Further, Callaway (1989) examined the relationships of the Triassic Shastasauridae and was the first person to use software for a cladistic analysis on ichthyosaurs. However, the first comprehensive phylogenetic analysis dedicated to ichthyosaurs was performed just 20 years ago by Motani (1999a) who provided a phylogenetic hypothesis for ichthyosaurs based on a cladistic analysis of 105 skull and postcranial characters for 32 taxa. For the first time, this work helped to determine the interrelationships between multiple ichthyosaur families. At about the same time as Motani's work, two other major phylogenetic studies were being undertaken and were published a year later (Sander, 2000; Maisch and Matzke, 2000). Sander (2000) compiled 120 characters for 31 taxa whereas Maisch and Matzke (2000) defined 128 characters for 33 taxa. Although there were some differences, all three phylogenies resulted in similar tree topologies. Subsequent large-scale ichthyosaur analyses are derivatives of these three major publications, although most have been based on or around Motani (1999b). Many later analyses focused on sub-groups within individual clades to attempt to uncover the relationships between taxa in the same family (e.g. Fernández, 2007; Chen and Cheng 2010; Druckenmiller and Maxwell 2010; Fischer et al. 2012, 2013; Maxwell et al. 2019). Ji et al. (2016) undertook an extensive phylogenetic analysis that

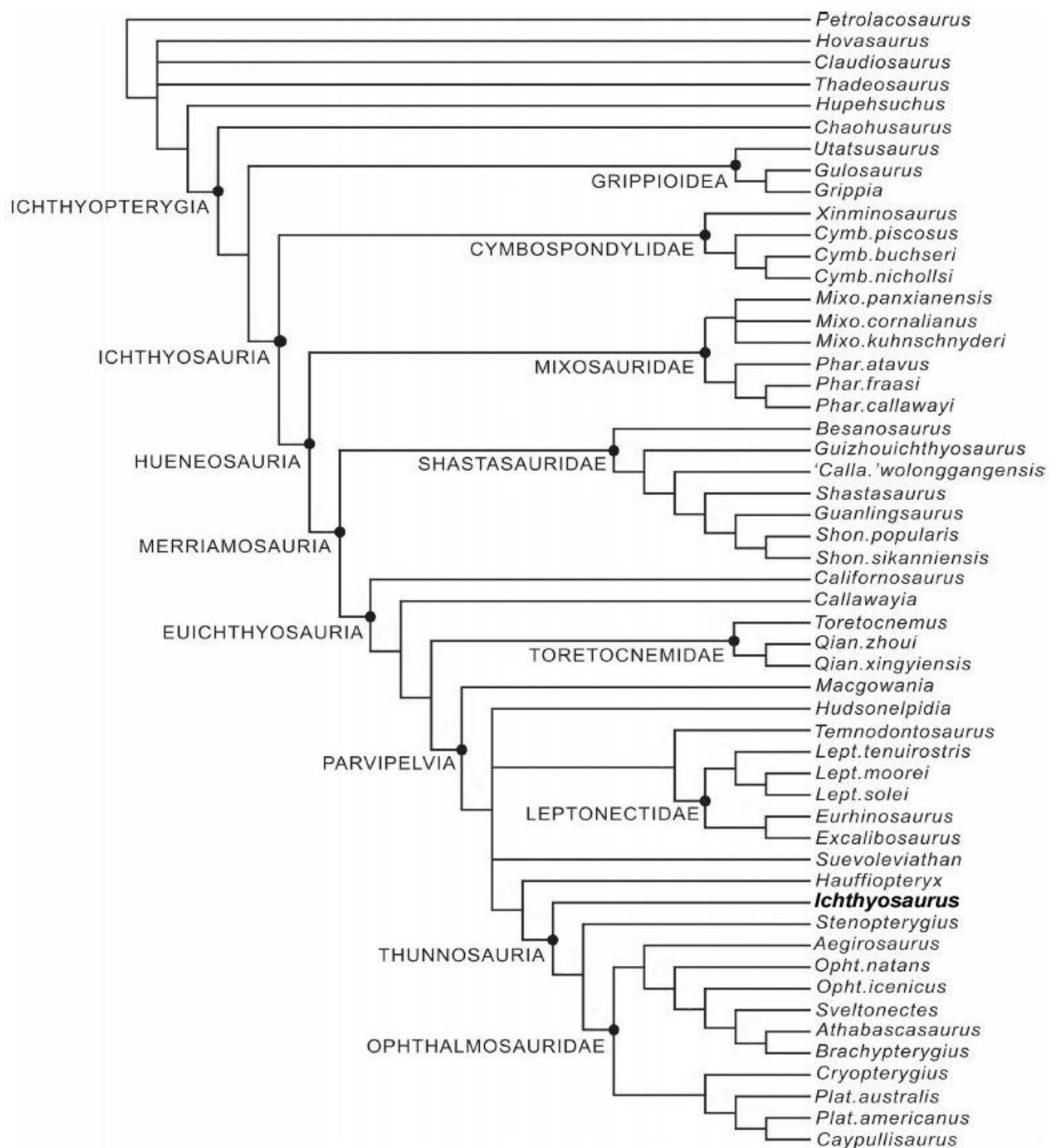


Figure. 2.3. Phylogenetic relationships among ichthyopterygians with removal of eleven poorly known taxa (from Ji et al. 2016, fig. 2). *Ichthyosaurus* is in bold to highlight its phylogenetic position.

incorporated newly described ichthyosaur taxa from the Triassic of China and the Upper Jurassic and Lower Cretaceous of Europe and South America (Figure. 2.3). In doing so, they provided a major update and created a list of 163 characters for a total of 59 taxa, representing nearly all known genera. Most recently, Moon (2017) performed a phylogenetic analysis based on 287 characters and 114 ingroup taxa

coded at species level. These recent analyses offer new interpretations about the evolutionary relationships of ichthyosaurs and their respective families, helping to resolve the affinities of certain taxa and groups.

According to the latest overviews, more than 100 species of ichthyosaur are currently recognised (Cleary et al. 2015; Ji et al. 2016; Moon, 2017), although new discoveries and descriptions have since increased this total. Ichthyosaurs were taxonomically diverse during the Triassic and Jurassic (Motani, 2009; Cleary et al. 2015; Ji et al. 2016). By comparison, Cretaceous ichthyosaurs were thought to be considerably less diverse, although recent work has shown that they were also taxonomically diverse well into the Cretaceous (e.g. Fischer et al. 2013, 2014; Fischer, 2016; Maxwell et al. 2016). The group became extinct during the early Late Cretaceous, specifically during the Cenomanian stage. Ichthyosaurs were drastically affected by several large-scale extinction events associated with global environmental changes, which ultimately led to their disappearance (Bardet, 1992, 1994; Fischer et al. 2016), but see discussion in Motani (2016).

2.2 Lower Jurassic ichthyosaurs

The great majority of Lower Jurassic ichthyosaur specimens have been recorded from the Posidonia Shale (Toarcian) in southern Germany (e.g. McGowan, 1979; Maisch, 1998; Maisch, 2008; Maxwell, 2012) and from the Blue Lias Formation at multiple locations in the UK. The wealth of specimens has significantly contributed to our understanding of ichthyosaurs from this time interval (McGowan and Motani, 2003). In the UK, the majority of Lower Jurassic ichthyosaur specimens are known from the historically important sites around the Lyme Regis-Charmouth area, along the Dorset coast (Milner and Walsh, 2010), historic quarries around Street, Somerset (Delair, 1969), from coastal and quarry exposures around Whitby, along the Yorkshire coast (Benton and Taylor, 1984), and to a lesser extent, from quarries in Barrow-upon-Soar, Leicestershire (Martin et al., 1986) and Barnstone and surrounding areas, Nottinghamshire (Lomax and Gibson, 2015).

Typically, ichthyosaurs from the Lower Jurassic can readily be identified to genus based on the morphology of the skull, rostrum or pectoral girdle (Maisch and Matzke, 2000; McGowan and Motani, 2003). Species identifications, however, are more difficult and require specific features of the skull and/or skeleton to be preserved. In some instances, the entire skeleton or exceptionally well-preserved

elements are required for a positive species identification. Thus, material can only be confidently referred to genus and species if critical portions of a specimen are present (Milner and Walsh, 2010).

Currently, Lower Jurassic ichthyosaurs are represented by ten valid genera and approximately 27 species. They include *Ichthyosaurus* De la Beche and Conybeare 1821, which contains the species: *I. communis* De la Beche and Conybeare 1821, *I. breviceps* Owen, 1881, *I. conybearei* Lydekker, 1888, *I. anningae* Lomax and Massare, 2015, *I. larkini* Lomax and Massare, 2017, and *I. somersetensis* Lomax and Massare 2017. The latter two species were described as part of the research undertaken herein (see Chapter 3); *Leptonectes* McGowan, 1996b, which contains the species: *L. tenuirostris* (Conybeare, 1822), *L. solei* (McGowan, 1993) and *L. moorei* McGowan and Milner, 1999; *Eurhinosaurus longirostris* (Mantell, 1851); *Excalibosaurus costini* McGowan, 1986; *Wahlisaurus massarae* Lomax, 2016; *Suevoleviathan* Maisch, 1998, which was originally split into two distinct species, but only the type is considered valid, *S. integer* (Bronn, 1844; von Huene, 1926; see synonymy in Maxwell, 2018); *Stenopterygius* Jaekel, 1904, which contains the species: *S. quadriscissus* (Quenstedt, 1856), *S. triscissus* (Quenstedt, 1856), *S. uniter* von Huene, 1931, and *S. aaleniensis* Maxwell et al. 2012; *Hauffiopteryx typicus* (von Huene, 1931); and *Temnodontosaurus* Lydekker, 1889, which contains the species: *T. platyodon* (Conybeare, 1822), *T. trigonodon* (Theodori, 1843), *T. crassimanus* (Blake, 1876), *T. eurycephalus* McGowan, 1974a, ?*T. acutirostris* (Owen, 1840), *T. ?nuertingensis* (von Huene, 1931), and *T. azerguensis* (Martin et al. 2012). In addition, as part of this work (Chapter 8), *Protoichthyosaurus* Appleby, 1979 is considered valid and includes two species: *P. prostaxalis* Appleby, 1979 and *P. applebyi* Lomax et al. 2017a. The latter species was recognised and described herein (Chapter 8). Except for *Suevoleviathan*, examples of each genus have been reported from the UK (Maisch and Matzke, 2000; McGowan and Motani, 2003; Williams et al. 2015; Lomax, 2016).

By far, the most common taxa known from thousands of specimens are *Stenopterygius*, recorded primarily from Germany, and *Ichthyosaurus* known largely from England. In particular, the former is one of the most well-studied ichthyosaur genera with numerous fossils known from Holzmaden, Germany. Many of these Holzmaden specimens show evidence of soft tissues, including skin and also the discovery of more than 100 pregnant specimens (McGowan, 1979).

2.2.1 Forefins of Lower Jurassic ichthyosaurs

The forefins of ichthyosaurs were for a long time separated into two groups, latipinnates and longipinnates (Kiprijanoff, 1881), but see Lydekker (1889) and McGowan (1969, 1972). The distinction was based largely on the number of primary digits in the forefin, which resulted in either a broad (latipinnate) or narrow (longipinnate) forefin. This terminology, however, was abandoned in light of new discoveries and further examination of specimens (McGowan, 1976; Appleby, 1979; Maisch and Matzke, 2000; McGowan and Motani, 2003). Forefins of Lower Jurassic ichthyosaurs are, however, easily distinguished among genera based on the number of digits, shape and number of phalanges, and the presence/absence of notching of anterior elements, among other features (Motani, 1999a; Figure. 2.4). The arrangement and number of elements in the mesopodium of the forefin does not change within a genus, and that determines the number of primary digits in the forefin, unless a digital bifurcation is present (Motani, 1999a). The Lower Jurassic taxa with a digital bifurcation and five or more digits in the forefin are *Ichthyosaurus*, *Stenopterygius* and *Suevoleviathan*, although it is not always the case in the latter two taxa. Furthermore, the digital bifurcation is always posterior to the primary axis in the forefins of *Stenopterygius* and *Suevoleviathan*, whereas it is always anterior to the primary axis in *Ichthyosaurus* (Motani, 1999a) and *Protoichthyosaurus* (see Chapter 8). All other Lower Jurassic genera have three or four primary digits and lack a bifurcation (Motani, 1999a; Maisch and Matzke, 2000; McGowan and Motani, 2003). The forefin morphology is unknown for *Wahlisaurus* (Lomax, 2016).

The presence of an anterior digital bifurcation in the forefin was considered unique to *Ichthyosaurus* (Motani, 1999a). This led to the notion that all Lower Jurassic ichthyosaurs with five or more primary digits and an anterior digital bifurcation could be assigned to *Ichthyosaurus*. However, Appleby (1979) described a new genus of Lower Jurassic ichthyosaur, *Protoichthyosaurus*, which possessed an anterior digital bifurcation, as in *Ichthyosaurus*, but had differences in the mesopodium. The two genera were subsequently synonymised (Maisch and Hungerbühler, 1997), which was followed by all later workers (e.g. Maisch, 1997; Maisch and Matzke, 2000a; McGowan and Motani, 2003). However, research undertaken in this thesis shows that the synonymy was not warranted (Chapter 8).

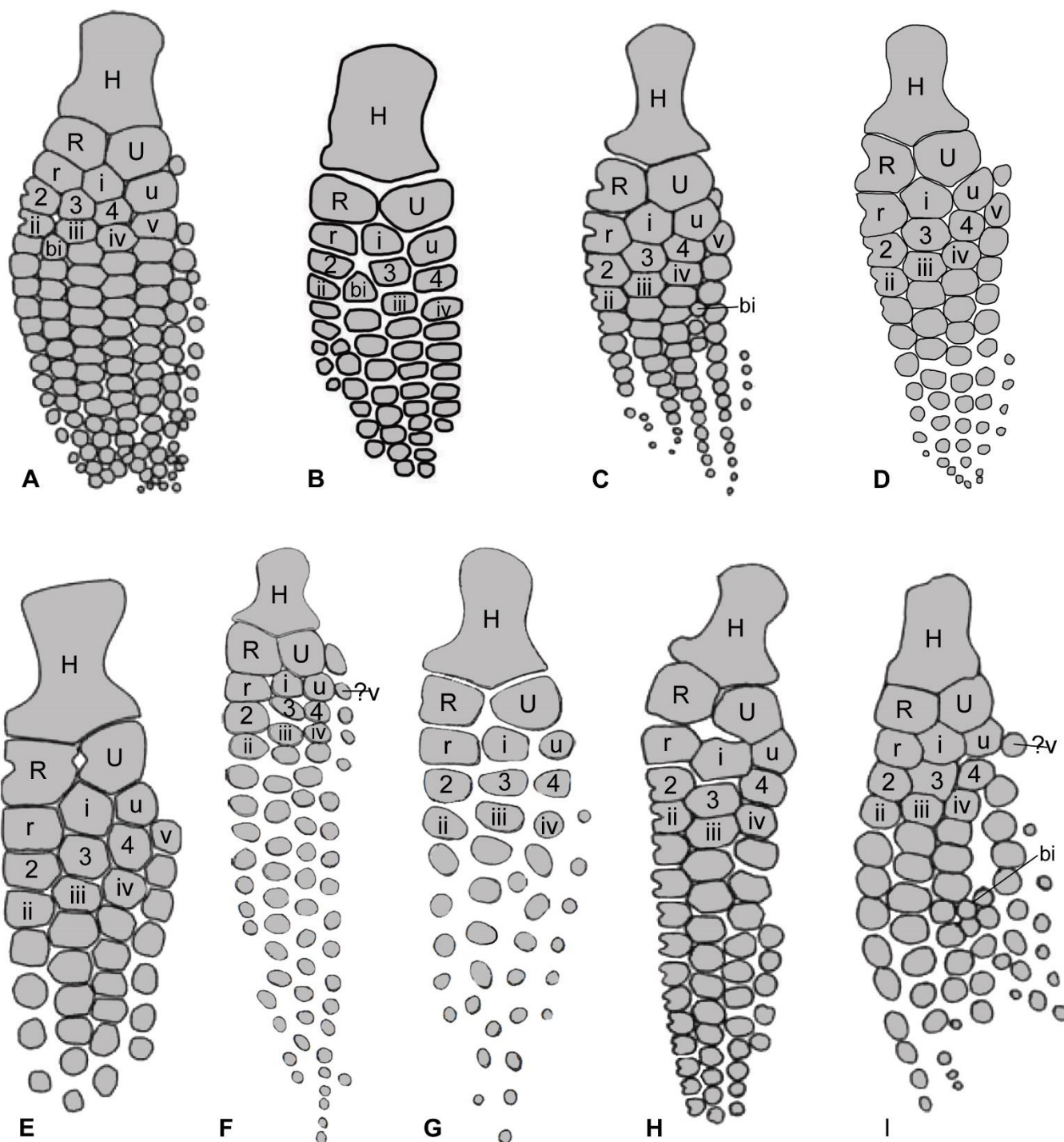


Figure. 2.4. Forefin morphology of Lower Jurassic ichthyosaurs. Anterior to the left in all forefins. A. *Ichthyosaurus*, after McGowan and Motani (2003, fig 70). B. *Protoichthyosaurus*, after Chapter 8 (Figure 8.9). C. *Stenopterygius*, after McGowan and Motani (2003, fig 70). D. *Hauffiopteryx*, illustration based on lectotype (pers. obs. GPIT 1491/4). E. *Leptonectes*, after McGowan and Motani (2003, fig 70). F. *Eurhinosaurus*, after McGowan and Motani (2003, fig 76B). G. *Excalibosaurus*, after McGowan and Motani (2003, fig 75B). H. *Temnodontosaurus*, after McGowan and Motani (2003, fig 70). I. *Suevoleviathan*, after McGowan and Motani (2003, fig 70). The forefin of *Wahlisaurus* is unknown (Lomax, 2016). Abbreviations. 2, distal carpal two; 3, distal carpal three; 4, distal carpal four; bi, indicates digital bifurcation; h, humerus; i, intermedium; ii, metacarpal two; iii, metacarpal three; iv, metacarpal four; R, radius; r, radiale; U, ulna; u, ulnare; V, metacarpal five.

2.3 *Ichthyosaurus*

The first ichthyosaur genus to be scientifically recognised was *Ichthyosaurus*, from Lyme Regis, Dorset (De la Beche and Conybeare, 1821). The name *Proteosaurus* (Home, 1819) was the first generic name given to a specific ichthyosaur specimen, but König (1818) had previously mentioned the name *Ichthyosaurus* and therefore that name took priority (see discussion in McGowan and Motani, 2003, pg. 1). The type species for the genus was named *Ichthyosaurus communis*, described briefly in a note appended to the paper by De la Beche and Conybeare (1821, p. 594). A year later, Conybeare (1822) further described the genus and identified three new species: *I. platyodon* (now *Temnodontosaurus*), *I. tenuirostris* (now *Leptonectes*) and *I. intermedius*; these original diagnoses were based on teeth. The latter species has been considered a synonym of *I. communis* by various authors (e.g. McGowan, 1974b; McGowan and Motani, 2003), although some have considered it a distinct species on the basis of multiple cranial characters (e.g. Appleby, 1979; Maisch, 1997; Maisch and Matzke, 2000). To complicate this issue further, the type specimens of both *I. communis* and *I. intermedius* are lost and presumed destroyed (McGowan 1974; Maisch and Matzke 2000a; McGowan and Motani 2003). This synonymy is addressed within this body of work (Chapter 4).

Of the species described during the 1800s and 1900s, McGowan (1974b) considered only four species valid (*I. communis*, *I. breviceps*, *I. conybeari*, and *I. tenuirostris*), although *I. tenuirostris* was later referred to *Leptonectes* (McGowan, 1989, but see McGowan, 1996b). With hundreds to thousands of *Ichthyosaurus* specimens in museum collections, McGowan (1974b) focused on a smaller group of well-preserved specimens, and assigned them to species on the basis of morphometrics. It was through McGowan's work that some form of taxonomic resolution was achieved. Specifically, he referred all of the short-snouted examples to *I. breviceps* (seven specimens), a species first described by Owen (1881) almost 60 years after the original description of *I. communis*. All specimens with a long, delicate snout and forefin notching (in Dorset specimens) were regarded as *I. conybeari* (two specimens). *I. conybeari* was originally described by Lydekker (1888) on the basis of a single, poorly preserved partial skeleton, which is on display at the NHMUK; McGowan (1974b) assigned a second specimen to the species. Everything else that was neither *I. breviceps* nor *I. conybeari* was identified as the type species, *I. communis* (39 specimens). McGowan (1974b) proposed that there were two

‘populations’ of *I. communis*, one from Dorset and one from Somerset (McGowan, 1974b); he also synonymised *I. communis* with *I. intermedius*. Although McGowan’s study addressed some of the issues regarding differences among species, it still resulted in many poorly defined and unquantifiable characters that could not be used with confidence to refer specimens to species. McGowan (1996a) later identified a new species of *Ichthyosaurus* (*I. janiceps*) from the Late Triassic of British Columbia, but this was later assigned to a separate genus (*Macgowania*; Motani, 1999a).

Recently there has been a major resurgence of interest in studying the genus *Ichthyosaurus*. This has challenged the previous taxonomy and led to a re-examination of the genus, which forms the basis of this thesis. This has been led by the author, largely in collaboration with Prof. Judy A. Massare. The first of these publications was provided by Lomax (2010), who described a specimen of *Ichthyosaurus* with stomach contents that also happened to be the first known example of the genus from the Pliensbachian Stage of the Early Jurassic. Subsequently, a full account of this specimen was presented by Lomax and Massare (2015), who recognised it as a new species of the genus, *Ichthyosaurus anningae*; they also identified five specimens. *I. anningae* differs from all other species of the genus in skull, humerus, and femur morphologies, and the humerus is more than 1.7 times the length of the femur. Since McGowan’s (1974b) review, this was the first new species identified from the variation that currently encompasses *I. communis*. Larkin and Lomax (2015) provided additional information on the history, discovery, conservation, and public engagement of the holotype specimen.

Massare and Lomax (2016a) reported on a new specimen of *I. conybeari* from Watchet, Somerset, and re-examined the species. This resulted in the first documented occurrence of *I. conybeari* from Somerset, a revised diagnosis of the species, and the referral of additional specimens to the species, including the skeleton from the Pliensbachian of Dorset described by Bennett et al. (2011), which had erroneously been assigned to *I. communis*. Massare and Lomax (2016a) identified several discrete characters of the skull and humerus that distinguishes *I. conybeari* from other species of the genus. Massare and Lomax (2016a) provided the first phylogenetic analysis that explored relationships between species of *Ichthyosaurus*, which is further expanded upon in this body of work (Chapter 3). Similarly, Massare and Lomax (2014b) described a specimen of *I. breviceps* collected by Mary Anning (CAMSMX.50187). They assigned the specimen to *I.*

breviceps on the basis of skull characters and ratios (short snout – snout length [ratio of preorbital length/jaw length] = 0.53). This specimen has a complete pelvis, which was the first complete *I. breviceps* pelvis described.

As a final note, a recently collected specimen of *Ichthyosaurus* from Dorset, held in a private collection, was regarded as a ‘new species’ as part of a BBC television documentary. The specimen was placed on loan and displayed at the Charmouth Heritage Coast Centre (CHCC) where the author examined it. The specimen is missing the skull, but is otherwise complete, although some portions are disarticulated, notably the distal portion of the tail. Measured from the preserved atlas-axis to where the tail begins to bend, it measures 193 cm. The forefin most closely resembles *I. longimannus* Owen 1884, which was deemed a species *inquerindae* by McGowan and Motani (2003). Moreover, they also likened the forefin morphology of *I. longimannus* to *I. breviceps*, with which I would agree, and which may suggest that the two species are synonymous. Thus, although this specimen is not discussed any further here, the humerus, forefin, hindfin, neural spine, and pelvis morphologies indicate that the specimen is most likely an example of *I. breviceps*. If correct, it would be the largest known specimen of that species and potentially provide information on the synonymy of *I. breviceps* and *I. longimannus*.

2.3.1 Geographic and stratigraphic range of *Ichthyosaurus*

The genus was first reported from the Dorset coast of the UK (De la Beche and Conybeare, 1821). Specimens of the genus are very common from the west Dorset coast, around the Charmouth-Lyme Regis area, and from historical quarry sites in Somerset, although coastal locations in Somerset have also yielded specimens (e.g. Deeming et al. 1993; Parsons, 2003; Massare and Lomax, 2016a). Other unequivocal occurrences of the genus, comprising fragments to complete skeletons, include various historical sites in: Leicestershire, such as Barrow-upon-Soar (Martin et al. 1986), Nottinghamshire, such as in the district of Rushcliffe (Lomax and Gibson, 2015), several isolated occurrences in Gloucestershire (pers. obs.), from quarries in Warwickshire (Smith and Radley, 2007), and from coastal and quarry exposures in Yorkshire (Maisch, 1997; Massare et al. 2015), England; from the Lavernock coast, Penarth, Glamorgan (pers. obs.), Wales; and from County Antrim, Northern Ireland (pers. obs.). Brusatte et al. (2015) reported isolated remains from

Scotland, but contrary to their study, these specimens, which consist of teeth and an impression of a lower jaw, are too fragmentary for positive identification.

Unequivocal occurrences of *Ichthyosaurus* from outside the UK include: isolated forefins from central Portugal (Zbyszewski and Moitinho de Almeida, 1952; Bardet et al. 2008); and an isolated forefin from Alberta, Canada (McGowan, 1978). The genus has also been reported from an incomplete skull from Bonnert, Belgium (Godefroit, 1996) and an incomplete skull from Frick, Switzerland (Maisch et al. 2008), but these specimens cannot be unequivocally assigned to *Ichthyosaurus* (Massare et al. 2015). Specimens described from the Queen Charlotte Islands, British Columbia (Dennison et al. 1990) were identified as *Ichthyosaurus*, but they show no diagnostic characters of the genus.

The majority of UK specimens come from historical collections, and unfortunately, most have poorly constrained geological and stratigraphical information, with often a general location (e.g. 'Dorset' or 'Somerset') listed. This presents a problem when attempting to decipher age and location differences among specimens and species. For a long time, it was thought that the genus was present in the Rhaetian Stage of the Late Triassic (McGowan, 1974b; McGowan and Motani, 2003). Yet, recent studies on the plesiosaur specimens from the same ichthyosaur-yielding deposits in Somerset found that they probably originated from the 'Pre-*planorbis* beds', most probably from the earliest Hettangian *P. tilmanni* Chronozone (Benson et al. 2012, 2015), the lowest chronozone of the Jurassic (Hillebrandt and Krystyn, 2009). Therefore, specimens of *Ichthyosaurus* from the Pre-*planorbis* beds (= *tilmanni* Zone) are probably Hettangian. However, the author has examined several Somerset specimens collected *in situ* from the base of the Blue Lias Formation, which suggests that some historical specimens are indeed Rhaetian (stratigraphy after Weedon et al. 2017). Although it is beyond the scope of this project, a study of the matrix of the specimens collected from the base of the Blue Lias Formation could yield important information regarding their stratigraphic position and confirm whether the genus is present in the latest Triassic. Additionally, some isolated ichthyosaur fragments from Aust Cliff, Gloucestershire, comprising largely of teeth and vertebrae, have been found in rocks of Rhaetian age, but none of these can be unequivocally referred to *Ichthyosaurus* (Storrs, 1999). Regardless, the genus is definitely known from the Lower Jurassic, Hettangian–Pliensbachian (Lomax and Massare, 2015; Figure. 2.5). Presently, the oldest confirmed occurrence

is from the Hettangian of Somerset and Leicestershire (McGowan, 1974b; Martin et al. 1986) and the youngest occurrence is from the lower Pliensbachian of Dorset (Lomax, 2010; Lomax and Massare, 2015).

Period	Group	Sub-group	Formation	Member	Traditional terms	Stage	Sub-stage
Lower Jurassic (in part)	Lias (in part)	Lower Lias	Charmouth Mudstone	Seatown Marl	'Green Ammonite Beds'	Pliensbachian (part)	Upper (part)
				Stonebarrow Marl	'Belemnite Marls'		Lower Pliensbachian
				Black Ven Mudstone	'Black Ven Marls'	Sinemurian	Upper Sinemurian
					U/C		
					U/C		
			Blue Lias		'Shales-with-Beef'		Lower Sinemurian
							Upper
						Hettangian	Middle
							Lower

Figure. 2.5. Stratigraphical framework of the British Lower Jurassic (in part), modified from Page (2010). Indicated by the silhouettes, *Ichthyosaurus* is known from the lower Hettangian ('Pre-Planorbis Beds' = Tilmanni Zone; McGowan, 1974b; Chapter 3 herein) through to the lower Pliensbachian (Polymorphus Subzone of the Jamesoni Zone; Lomax, 2010; Lomax and Massare, 2015). Silhouette from PhyloPic.org.

2.3.2 *Ichthyosaurus* size

McGowan (1974b) provided an estimate of the maximum size for each of the species. Prior to this, and especially during the early 19th century, the size estimates of *Ichthyosaurus* were based upon large ichthyosaur specimens (up to <10 m) that were later assigned to different genera with the very largest specimens being referred to *Temnodontosaurus*. McGowan (1974b) described *Ichthyosaurus communis* as a medium-sized species, reaching a total length of about 2.5 m, with a maximum jaw length of 54 cm. *I. breviceps* was described as a small species with a maximum length of about 1.5 m and a jaw length of about 25 cm. Massare and Lomax (2014b), however, reported the largest known specimen of *I. breviceps* that has a jaw length of 33.5 cm and an estimated preflexural length of 1.6 m. McGowan (1974b) also referred to *I. conybeari* as a small species, with one specimen having a total length of 87 cm, although he noted that this specimen might be an immature individual. Massare and Lomax (2016a) estimated a length of less than 1.5 m based on the specimen (CAMSM X.50187) that they described. However, they also stated that some fragmentary remains of a much larger specimen may belong to that species, pending further study. Lomax and Massare (2015) estimated that *I. anningae* had a preflexural length of less than 1.5 m.

For the genus alone, McGowan and Motani (2003) stated that it reached total lengths of about 2.5 m, the top end for *I. communis* specimens. However, Massare et al. (2015) described an historical *Ichthyosaurus* specimen comprising an isolated large forefin from the Lower Lias of Yorkshire, which was probably from the Yorkshire coast. This forefin is incomplete, but the humerus has a length of 11.7 cm. A regression analysis suggested that the individual had a jaw length of at least 56 cm and a total length to the tail bend of almost 3 m. However, the linear regression analysis for this specimen was revised by Massare and Lomax (2017a) who concluded that the total length of the specimen, from tip of the snout to end of the tail was just over 3 m, which at the time was the largest known example. However, herein the size range of the genus is reassessed with the description of two new species (Chapter 3) and the description of a very large individual (Chapter 5).

Considering the wealth of ichthyosaur specimens known, it is surprising that there have not been more studies dedicated to ichthyosaur ontogeny and growth allometry, which can provide further information on the growth stages and size of a given taxon. Nevertheless, there is a body of work dedicated to ichthyosaur

ontogeny that mostly revolves around the common German Jurassic genus, *Stenopterygius* (e.g. von Huene, 1922; Johnson, 1977; Caldwell, 1997; Maxwell et al., 2014; McGowan, 1973; McGowan, 1995; Deeming et al., 1993; Motani and You, 1998; Fernández et al. 2005; Dick and Maxwell, 2015; Dick et al. 2016). Bennett (2015) investigated ichthyosaur ontogeny as part of an unpublished PhD, which included an account of research undertaken on ichthyosaur ontogeny. The major limitation with studying ichthyosaur ontogeny is, with the exception of a few taxa, the lack of well-preserved, sufficiently complete specimens of the same species that vary in size and can be compared. Additionally, specimens differ with respect to their preservation and can be exposed in lateral, dorsal, and ventral views, or in three-dimensions. Thus, in order to study ontogenetic changes in features of the skull and skeleton it requires that specimens are complete or nearly complete, are well-preserved so that sutures can be easily identified, and that specimens are preserved in the same general orientation. Only three studies have looked at some aspects of ontogeny in *Ichthyosaurus* (McGowan, 1973; Deeming et al., 1993; Massare et al., 2015), but each study focused on morphometrics rather than individual bone morphologies of the skull and postcranium. Although there are no studies dedicated specifically to *Ichthyosaurus* ontogeny included in this work, one chapter (Chapter 6) is deemed to provide a basis for future ontogenetic studies.

2.4 Composite ichthyosaurs

Fossil fakes, forgeries and composites have been a problem since the dawn of palaeontology. Various fossils have been, and still are, unscrupulously ‘enhanced’, or entirely forged, to increase commercial value, and in some cases specifically to deceive (Mateus et al. 2008; Ruffel et al. 2012). This is a major problem for palaeontologists who can sometimes be misled, which can result in a fake or partially reconstructed specimen unintentionally entering the published literature and leading to errors. For example, the then visually impaired von Huene (1966) described what he thought was a juvenile ichthyosaur skeleton, but which was later shown to be a total forgery (Wild, 1976). Fortunately, besides experience, several techniques can be used to distinguish real fossils from fakes (Mateus et al. 2008; Kaye et al. 2015).

A composite is a specimen that is comprised of real material from several individuals, arranged as if original. Ichthyosaur composites have been known since the early 19th century. Thomas Hawkins, who amassed a huge collection of fossils,

was notorious for creating composites (McGowan, 1990). Much of his collection of ichthyosaurs from Somerset was purchased by the NHMUK in 1834, whereas other portions of his collection are held in several museums, including CAMSM and OUMNH. He also sold specimens to other collectors who donated or sold them to museums (McGowan, 1990). Hawkins did not necessarily act to deceive others. Instead these specimens were essentially pieces of 'art'. Historical specimens were often mounted in large wooden frames held together by plaster or cement, which was then painted. This presents a problem for later workers who are unable to determine the authenticity of a specimen. In particular, the paint is a problem because you cannot see whether the matrix is the same everywhere, or how the blocks the specimen lies in are put together. This also means that it is almost impossible to determine what bones are set in plaster or original matrix. Bearing this in mind, if assessing an historical specimen, it can be difficult to verify whether it is a composite because museums are very unlikely to allow their historical collections to be taken apart (see also discussion in McGowan, 1990). For these reasons, even some of the most reputable museums in the UK can have composite specimens in part because of how Hawkins' collection was dispersed (McGowan, 1990; Massare and Lomax, 2016b).

In order to create a composite, individual parts of a skeleton or even a skull would be added to a specimen to give the appearance of a more complete ichthyosaur. This practice resulted in numerous ichthyosaur composites, which remained unnoticed in historical collections. Sometimes specimens are even 'improved' with the body and skin outlines carved into the matrix around the specimen (Martill, 1993, 1995).

The first major review of ichthyosaur composites was by McGowan (1990), who focused on specimens of *Leptonectes* from Somerset. He identified numerous composite ichthyosaurs and proposed techniques for how to spot them. Massare and Lomax (2014a, 2016b) recognised several composite and dubious specimens of *Ichthyosaurus*. They found that the most common elements added to *Ichthyosaurus* skeletons are whole or partial forefins, hindfins, or posterior portions of the vertebral column (i.e. tails). Some specimens were also enhanced by reconstruction or with elements rearranged, sometimes done so expertly that it is practically indiscernible.

Chapter 3: Two new species of *Ichthyosaurus* from the lowermost Jurassic (Hettangian) of Somerset, England

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Two new species of *Ichthyosaurus* from the lowermost Jurassic (Hettangian) of
Somerset, England

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Abstract

All specimens of *Ichthyosaurus* from the Lower Jurassic of Somerset were previously identified as *I. communis*, an abundant and extremely variable species. Here, two new species of *Ichthyosaurus* are recognised from multiple specimens. The species are assigned to *Ichthyosaurus* on the basis of the humerus, pectoral girdle, and forefin morphologies. *I. larkini* sp. nov., is distinguished by a broad jugal with a blunt anterior end that extends as far forward as the middle of the external naris, separating the maxilla and lacrimal; and a unique combination of other features. *I. somersetensis* sp. nov., is distinguished by a jugal with a nearly straight dorsal ramus that lacks a right-angle dorsal bend; a high, narrow, crescentic postorbital that forms almost all of the posterior margin of the orbit and separates the jugal dorsal ramus from the orbit; and an ilium that is wide relative to its length, more oblong than rib-like. The identifications are supported by a phylogenetic analysis which finds the new species more closely related to each other than to other species of the genus. We also identify a squamosal in both species, which confirms that it is present in the genus. This study suggests that hindfin morphology has some taxonomic utility, at least within the genus. The new species increases the diversity of *Ichthyosaurus* to six species, three of which are found in the Hettangian of Somerset.

Key words: Ichthyosauria, *Ichthyosaurus larkini*, *Ichthyosaurus somersetensis*, Somerset, Lower Jurassic, Hettangian.

Introduction

The majority of marine reptile specimens from Somerset were collected during the 1800s from quarries in the area around the town of Street (Hawkins 1834; Delair 1969; Storrs and Taylor 1996; McGowan and Motani 2003; Benson *et al.* 2012; Benson *et al.* 2015). These quarries are no longer accessible, and so the historic collections represent the only record of specimens from inland areas of Somerset. Portions of collections amassed during the 19th century by Thomas Hawkins, Joseph Channing Pearce, Charles Moore, Alfred Gillett, and others were acquired by museums including NHMUK, CAMSM, OUMNH, BRSMG, and BRLSI. More recently, ichthyosaurs from Somerset have been collected at coastal locations such as Watchet, Kilve and Lillstock (McGowan 1986; Deeming *et al.* 1993; McGowan 2003; Massare and Lomax 2016a).

The specimens in historic collections were excavated at a time when detailed stratigraphic and locality data were not recorded. Specimens from Somerset almost certainly derive from the Blue Lias Formation of the Lower Lias Group, probably from the *Pre-planorbis* beds, which occur below the first documented occurrence of the zonal ammonite *Psiloceras planorbis* (Arkell 1933; McGowan 1974; Benson, *et al.* 2012). Somerset material had been considered latest Triassic (e.g., McGowan and Motani 2003), but recent work indicates that it is younger (Benson *et al.* 2012, 2015). Benson *et al.* (2012) determined that most of the Street plesiosaur specimens likely originated from the *Pre-planorbis* beds, and further suggested that they most probably derived from the earliest Hettangian *P. tilmanni* Chronozone, the lowest chronozone of the Jurassic (Hillebrandt and Krystyn 2009), although a review of the stratigraphy at Street will be needed to verify this. Arkell (1933, p. 123) and Storrs and Taylor (1996) however, had previously suggested that some specimens may be from slightly higher horizons. Recent discoveries of ichthyosaurs at coastal localities in Somerset have better stratigraphic information and have been collected *in situ* from the Hettangian (*I. ?communis*) and Sinemurian (*Excalibosaurus costini*, *I. conybeari*) strata of the Blue Lias (Deeming *et al.* 1993; McGowan 2003; Massare and Lomax 2016a). Lacking more detailed research on the stratigraphy of Somerset, and specifically Street, we consider the historic specimens to be lowermost Jurassic (Hettangian), not Rhaetian, as previously suggested (McGowan and Motani 2003; Lomax and Massare 2015).

In the most recent compilation of the Ichthyopterygia, all of the specimens of *Ichthyosaurus* from the lower Jurassic of Somerset were assigned to *I. communis* (McGowan and Motani 2003), although a single specimen of *I. conybeari* was recently identified (Massare and Lomax 2016a). Historically, another species, *I. intermedius*, was also recognized. In fact, based on the original museum identifications, at least half of the fairly complete skeletons of *Ichthyosaurus* from Somerset were originally referred to *I. intermedius* (pers. obs.). The validity of *I. intermedius*, however, has been debated. It is considered to be a synonym of *I. communis* by some authors (McGowan 1974; McGowan and Motani 2003), but a valid species by others (Maisch 1997; Maisch and Matzke 2000a). Further complicating the taxonomic issues, both species were originally defined on the basis of tooth form, and the holotypes are lost and perhaps destroyed (McGowan 1974; Maisch and Matzke 2000a; McGowan and Motani 2003). Resolving that debate is beyond the scope of this paper, and so we follow the most recent assessment of McGowan and Motani (2003). McGowan (1974) designated a neotype for *I. communis*, NHMUK PV R1162, a nearly complete skeleton collected from the Lyme Regis area in the 19th century. However, he also recognized that *I. communis* was an extremely variable species and that there were morphological differences between the Lyme Regis and Street ‘populations’ (McGowan 1974). We will demonstrate that the specimens described here differ substantially from *I. communis* and all other species of the genus, and should be considered new species.

Institutional abbreviations. AGC, Alfred Gillett Collection, cared for by the Alfred Gillett Trust, C & J Clark Ltd, Street, Somerset, UK; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BGS, British Geological Survey, Keyworth, Nottingham, UK; BRLSI, Bath Royal Literary and Scientific Institution, Bath, UK; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; BRSUG, University of Bristol, Bristol, UK; CAMSM, Sedgwick Museum, Cambridge University, Cambridge, UK; NHMUK, formerly BMNH, The Natural History Museum, London, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; ROM, Royal Ontario Museum, Toronto, Canada; UWGM, University of Wisconsin Geological Museum, Madison, WI, USA; WARMS, Warwickshire Museum, Warwick, UK.

Material

Historic collections, and in particular complete or nearly complete specimens, present the problem of evaluating their authenticity. All of the specimens in this study are part of historic collections, having been collected in the 19th century. Complete or nearly complete specimens need to be evaluated carefully because many historic specimens have been pieced together from separate individuals (McGowan 1989, 1990; Taylor 1989). In particular, forefins and hindfins are often added, but sometimes even portions of an articulated vertebral column may not be authentic (McGowan 1990; Lomax and Massare 2012; Massare and Lomax 2014*a, b*; Massare and Lomax 2016*b*). Differences in the matrix colour or texture, matrix covered by a plaster veneer, painted or patterned matrix (e.g. chisel-like marks), and an unusual positioning/orientation of the bones can further suggest a composite (McGowan 1990; Massare and Lomax 2014*b*). A composite specimen can provide valuable morphological information, however, once the added portions have been recognized. An evaluation of the key specimens in this analysis is presented below.

BRSUG 25300 is a practically complete, articulated skeleton, collected from a quarry in Walton, near Street, Somerset (Figure. 3.1). It was once part of the Channing Pearce collection (no. 356). According to the information with the specimen, it was purchased by the BRSMG in 1915 and was given to Bristol University in 1930, although the Channing Pearce collection was amassed well before then. A few portions of the skeleton are reconstructed, but the reconstructed elements are clearly shown, being carved from a darker material than the original bone. Most noticeably, most of the postorbital, a portion of the surangular, the proximal portion of the anterior digit in the forefin, and the distal half of each hindfin have been reconstructed.

AGC 11 is a nearly complete skeleton, with a complete, articulated vertebral column (Figure. 3.2A). The caudal centra and portions of the torso and forefin are at a higher level than the surrounding matrix, but this can be attributed to decisions made during preparation of the specimen. The specimen is comprised of two or three blocks of matrix: skull and pectoral girdle; torso and forefin; and hindfin and caudal centra, although the latter two might be a single block. The blocks fit together perfectly, and it appears that the specimen is entirely authentic.

CAMSM J59575 was donated to the museum by Thomas Hawkins, who amassed a huge collection of marine reptiles from Somerset in the first half of the 19th century. His collection is notorious for composite specimens (Taylor 1989; McGowan 1990). This specimen has at least four distinct types of ‘matrix’, including the clear use of plaster filler, a patchwork covering, and various colour distinctions, suggesting that it is a composite (Massare and Lomax 2016*b*). The skull and the dorsal skeleton, comprising the pectoral girdle, left forefin, articulated centra, and ribs seem to be from the same individual (Figure. 3.2B). The ribs, in particular, can be traced from one block to the adjacent one. The same can be said for the right forefin, which is on a separate block and is missing much of the proximal portion of the humerus. However, the blocks with the distal vertebral column and the hindfin and pelvis have been added to the specimen. The bones on both blocks have a darker colour than the anterior skeleton, and the hindfin morphology indicates that it is from a different species.

NHMUK PV R5595 is a nearly complete skeleton on display at the NHMUK (Figure. 3.2C). The skull, torso and tail seem entirely authentic, but the specimen is behind glass, so could not be examined closely. Most of the distal portion of the right forefin has been added to the specimen because elements do not line up across the crack in the forefin, and the distal portion is at a different level in the matrix. A clear difference in morphology between the right and left humeri indicates that the entire left forefin has been added to the specimen (Massare and Lomax 2016*b*). The forefin also appears to be entirely surrounded by plaster. The left hindfin is also suspicious. Digits II and III are distinctly offset, shifted anteroproximally from the other two rows of elements. The tarsal bones are arranged differently from those of the right hindfin and, in fact, differ from any other *Ichthyosaurus* hindfin that we have examined, although this could be due to displacement or pathology. It is also possible that the right hindfin does not belong to the skeleton, although it appears to be authentic.

ANSP 15766 is one of the most complete specimens of *Ichthyosaurus* known (Figure. 3.3). Museum records indicate that it is probably from Glastonbury, near Street. It was acquired by Dr. Thomas B. Wilson and donated to the ANSP in 1847 (E. Daeschler, pers. com. 2012). A cast of the specimen is in the Charles Moore Collection, housed at the NMW (BRLSI M3580). The specimen appears to be authentic, but the matrix is covered by a patterned plaster wash that makes it difficult

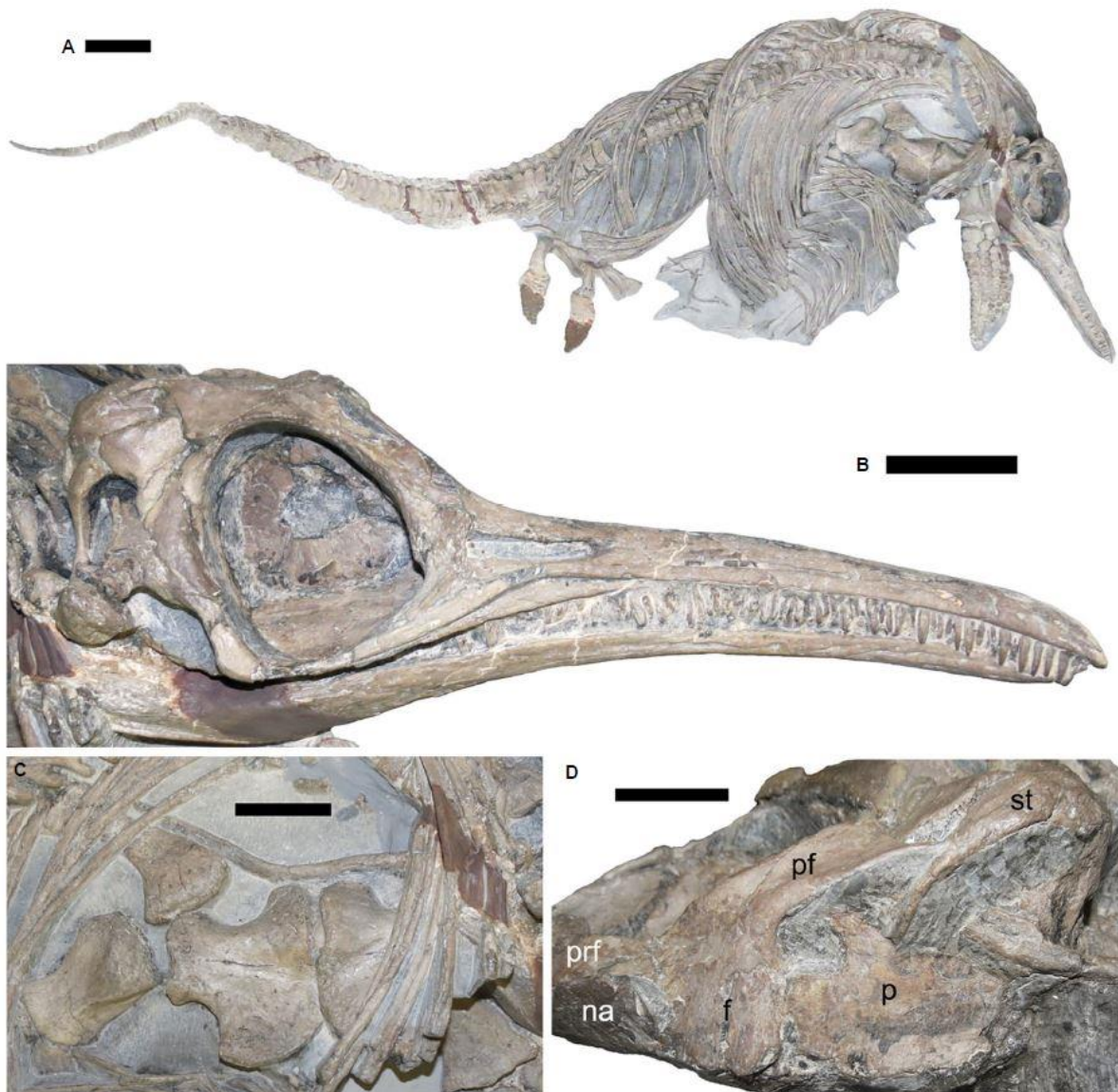


Figure. 3.1. BRSUG 25300, holotype specimen of *Ichthyosaurus larkini* sp. nov., from Walton, near Street, Somerset, UK. A. Practically complete skeleton lying on its left side, exposed in ventrolateral view. B. Close-up of the skull in right lateral view. C. Pectoral girdle and humeri in ventral view, right humerus to the left, left humerus at bottom right of image. D. Dorsal skull roof showing some of the elements including the unusual lateral process of the parietal. *Abbreviations:* f, frontal; na, nasal; p, parietal; pf, postfrontal; prf, prefrontal; st, supratemporal. Scale bars represent 10 cm (A); 5 cm (B–C); and 3 cm (D).

to see the original matrix. A filler substance has been added between pieces of several ribs and a few neural spines, and at the end of the scapula and clavicle. The specimen is so large that it could not have been collected in a single block, and despite the patterned matrix, it is clear that several blocks have been pieced together. The two forefins differ in the location of the digital bifurcation, which is unusual but not impossible as this occurs in other specimens (e.g. AGC 11, OUMNH J.13799). The right forefin is partially covered by ribs, but the left one is slightly separated from the main skeleton, and the proximal end of the humerus is surrounded by a plaster-like material, which could suggest that the left forefin has been added. An outline of a block of matrix surrounds the left forefin, although that in itself does not indicate that the forefin was added. The precaudal count is higher than is typical for *Ichthyosaurus*, but there is no obvious break in the column that would indicate a composite. Adjacent to the caudal centra, little matrix is visible and the patterned plaster contacts the centra, raising the question of whether centra have been added, but no breaks in the vertebral column occur. Bone orientation, preservation, and colour, also match the rest of the skeleton. The specimen is in excellent condition, with no deterioration of the plaster that would make it easier to identify added elements.

BRSMG Cb4997 is a fairly complete skeleton exposed in right lateral view (Figure. 3.4A). It is mounted behind glass at BRSMG, so it cannot be examined closely. The distal portion of the ?left forefin is set in a filler material, but elements line up well and it appears authentic. Elements of the hindfins, pelvic girdle, and posterior dorsal and anterior caudal vertebrae and ribs are also set into filler, but the preservation, colour, and size are consistent with the anterior skeleton; however, the authenticity of the arrangement of elements in the hindfins can be questioned.

Figure. 3.2. Referred specimens of *Ichthyosaurus larkini* sp. nov. A. AGC 11, nearly complete skeleton lying on its left side. B. CAMSM J59575, anterior skeleton lying on its left side. The hindfin, pelvis and the posterior portion of the vertebral column have been added. Note the large crack in the centre filled with plaster. C. NHMUK PV R5595, practically complete skeleton exposed in dorsal view on display at the NHMUK, photographed through glass. Note that the left forefin (upper in the image) and the distal half of the right forefin have been added. All specimens are from Somerset, UK. Scale bars represent 10 cm. The scale bar for C is estimated as the specimen is inaccessible for measurement.





Figure. 3.3. ANSP 15766, holotype specimen of *Ichthyosaurus somersetensis* sp. nov., a practically complete skeleton lying on its right side, from Glastonbury, near Street, Somerset, UK. Scale bar represents 10 cm. Image courtesy of E. Daeschler, © Academy of Natural Sciences of Drexel University, Philadelphia.

NHMUK PV OR2013* is a large, complete skeleton exposed in right lateral view, one of the most complete specimens of the genus (Figure. 3.4B). Although it was part of the Thomas Hawkins collection, there is no indication that it is a composite, but it is mounted behind glass at the NHMUK and cannot be examined closely. Because of its size, it was collected in several blocks that are put together within the wooden frame. Bones are continuous from one block to the next, and the colour and quality of preservation is consistent throughout the mount. Casts of the specimen were produced and distributed by Wards Scientific Inc., Rochester, NY, as early as the mid-1800s (Ward, 1866), and are in the collections of the Cincinnati Museum of Natural History and Science, UWGM, University of California Museum of Paleontology, NHMUK, and probably others.

AGC 16 is a skull and partial vertebral column from the posterior torso and anterior caudal region (Figure. 3.4C). An articulated forefin is isolated from the rest of the skeleton and may not belong to the specimen, but the remainder of the specimen seems authentic. The centra have an odd sequence in the pelvic region, where the diapophyses merge into one elongate articulation on two centra, then separate on the next one, then merge again. All of the centra are in matrix, and no cracks appear between them to suggest that pieces of matrix were put together, so this is likely an abnormality. A similar abnormality occurs in at least one other specimen (WARMS G2811). Just distal to these centra, the two blocks of matrix around the caudal centra

have a slightly different colour and texture from the rest of the specimen and may have been added.

ROM 26029 is a partial skeleton comprising a crushed skull in which only the rostrum is intact, anterior disarticulated skeleton, and articulated posterior caudal centra (Figure. 3.4D). The posterior caudal region is separated from the rest of the skeleton by approximately 25 cm. However, the preservation and colour of the centra, and the colour of the surrounding matrix is similar to the rest of the specimen. A written label on the matrix gives the location as 'Lias, Lyme Regis, Dorset', although the preservation of the specimen, the matrix the specimen is lying in and the colour of the bones suggest that it is more likely from Somerset (pers. obs.). The museum label suggests that others have also questioned the locality information.

Figure. 3.4. Referred specimens of *Ichthyosaurus somersetensis* sp. nov. A. BRSMG 4997, a nearly complete skeleton lying on its left side. B. NHMUK PV OR2013*, a complete skeleton exposed in dorsolateral view. C. AGC 16, skull and partial postcranial skeleton lying on its right side. D. ROM 26029, a partial skeleton lying on its left side. All specimens are from Street, Somerset, UK, except possibly ROM 26029, see text for more details. A and B are on display and photographed through glass. Scale bars represent 10 cm. The scale bar for B is based on measurements from a cast. There is no scale for A because the specimen is mounted behind glass, at a slant.



Systematic Palaeontology

This published work and the nomenclatural acts it contains have been registered in ZooBank: <http://zoobank.org/References/FE230EF8-1C34-4BD0-86D5-FDC1FD870A11>

Order **Ichthyosauria** de Blainville, 1835

Family **Ichthyosauridae** Bonaparte, 1841

Genus **Ichthyosaurus** De la Beche and Conybeare, 1821

Ichthyosaurus larkini sp. nov.

Figures 1, 2, 5A–B, 6A, 7A

LSID. urn:lsid:zoobank.org:pub:FE230EF8-1C34-4BD0-86D5-FDC1FD870A11

Synonymy.

Ichthyosaurus communis; McGowan, 1974: 9 [referred specimen].

Ichthyosaurus communis; Fischer *et al.*, 2013: 2.

Derivation of name. In honour of Nigel Larkin who has made substantial contributions to palaeontology, especially through his conservation work on marine reptiles. Our work has greatly benefited from his skills and attention to detail.

Holotype. BRSUG 25300, a practically complete skeleton comprising the skull, pectoral girdle, elements of both forefins, proximal hindfins, pelvic girdle, ribs, gastralia and the vertebral column.

Referred Specimens. AGC 11, a nearly complete skeleton; CAMSM J59575, a skull and anterior skeleton only, see text; and NHMUK PV OR5595, a nearly complete skeleton, but not all of the limbs are authentic, see above.

Diagnosis. *Ichthyosaurus larkini* is a medium-sized species (2.0–2.5 m) diagnosed relative to other species of *Ichthyosaurus* by the following unique characters: broad jugal with blunt anterior end, extending as far forward as middle of external naris, separating maxilla and lacrimal; jugal dorsal ramus bends dorsally at a right angle and bends posteriorly at about half its length, making up a small portion of the orbit;

wide dorsal process of triradiate lacrimal makes minor contribution to orbit margin. Three other characters might also be unique within the genus: hindfin with elements of three digits contacting astragalus, element of digit III nearly separating astragalus from tibiale, and elongated, narrow external naris.

The species is further diagnosed relative to other species of *Ichthyosaurus* by the following unique combination of characters: slender rostrum (not as slender as *I. conybeari*; more slender than *I. anningae*, *I. communis*, *I. breviceps*, and *I. somersetensis*); snout ratio > 0.60 but probably less than 0.65 (as in *I. anningae* and *I. communis*); high crowned skull (as in *I. conybeari*); large prefrontal forms at least half of anterior border of orbit, excluding dorsal process of lacrimal from orbit margin (as in *I. somersetensis*); premaxilla supranarial and subnarial processes about equal length, extending about half way across the dorsal and ventral margins of the external naris, with nasal about half of dorsal margin (as in all species of *Ichthyosaurus* except *I. breviceps*); low maxilla, height no more than the dorsoventral distance between the maxilla and external naris (similar to *I. communis*); humerus long relative to width, with prominent dorsal process that extends less than half way down the shaft (similar to *I. communis*); irregular depression on articular surface (as in *I. communis* and *I. somersetensis*); four elements in the third row of the hindfin (as in *I. communis* and *I. anningae*); precaudal vertebral count >45 but <50 (shared with *I. somersetensis*).

Locality and stratigraphical information. All of the specimens were collected in the 19th century, when locality and stratigraphic data were not recorded in detail. The holotype is from Walton, near Street, Somerset. CAMSM J59575 and NHMUK PV R5595 are from Street according to museum records. AGC 11 is probably from the Street area as well. Specimens are most likely from the lowermost Jurassic (Hettangian), Pre-*planorbis* beds of the Blue Lias Formation (McGowan 1974; Benson *et al.* 2012, 2015).

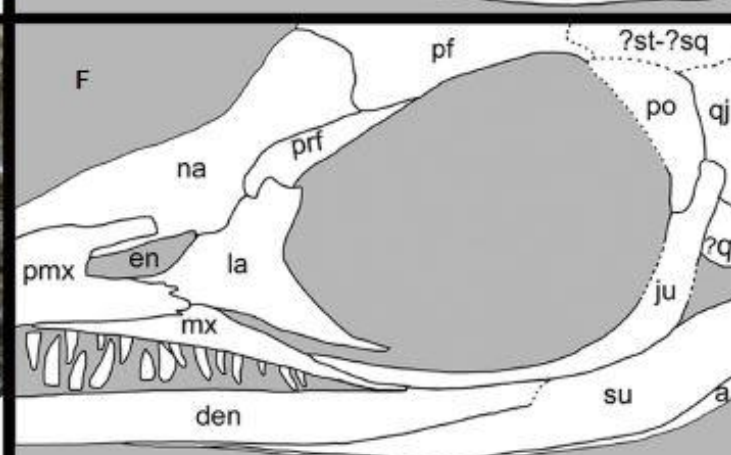
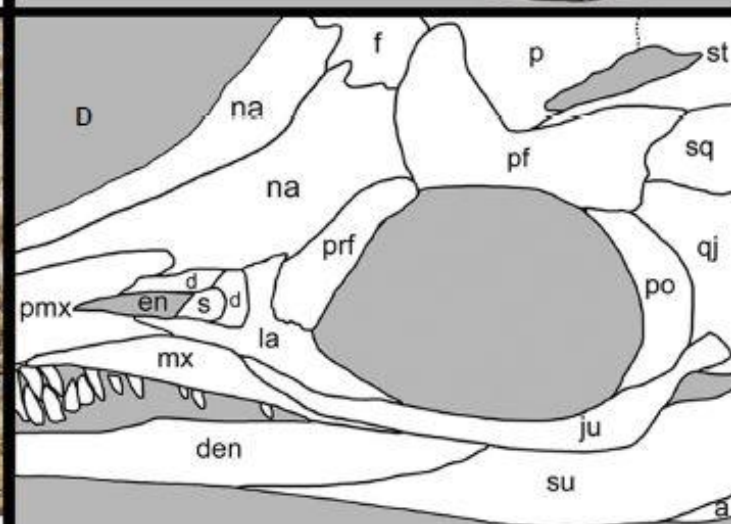
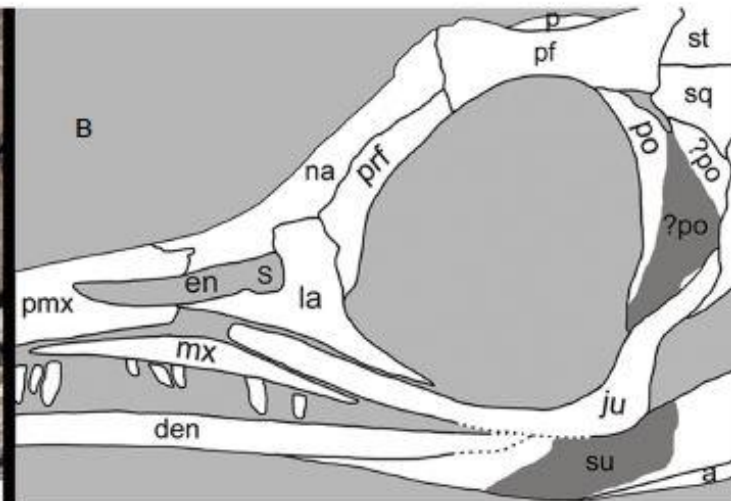
Description of holotype

The specimen is an articulated skeleton lying on its left side, with reconstructed portions shown in a darker colour (Figures. 3.1A–C, 3.5A–B, 3.6A). It is about 2.2

metres long from the tip of the snout to the tip of the tail, measured along the vertebral column. It is assigned to the genus *Ichthyosaurus* because of a tripartite pelvis with an unfused pubis and ischium, a coracoid with well-developed anterior and posterior notches, and a forefin with at least five digits, two digits originating from the intermedium, and an anterior digital bifurcation in the forefin (Motani 1999a; McGowan and Motani 2003).

Skull and mandible. The skull and mandible are in right lateral view, but a posterior segment of the mandible has been reconstructed (Figures. 3.1B, 3.5A–B). The skull has a slender rostrum, and is approximately 36 cm long (Table. 3.1). The skull is high-crowned, perhaps due to a large orbit that is higher than long, although it is slightly deformed. A large, robust prefrontal makes up most of the dorsal and at least half of the anterior margin of the orbit, and extends ventrally to the level of the external naris, similar to *I. somersetensis*. It is a larger, more robust bone and extends farther anteroventrally than in *I. communis* (Figure. 3.5E–F)

Figure. 3.5. Photograph and interpretive illustration showing the morphological differences in the preorbital and orbital regions of the skulls of *Ichthyosaurus larkini* sp. nov., *Ichthyosaurus somersetensis* sp. nov., and *I. communis*. A, B. BRSUG 25300, holotype of *I. larkini*; C, D. ANSP 15766, holotype of *I. somersetensis*; E, F. NHMUK PV R1162, neotype of *I. communis*. *Abbreviations:* a, angular; d, displaced bone from right side of skull; den, dentary; en, external naris; f, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; p, parietal; po, postorbital; pmx, premaxilla; pf, postfrontal; prf, prefrontal; q, quadrate; qj, quadratojugal; s, salt gland; sq, squamosal; st, supratemporal; su, surangular. Light grey denotes matrix and openings in skull. Dashed line indicates broken edge and possible suture line. Dark grey indicates reconstructed portions. Scale bars represent 5 cm. The scale bar for E is estimated as the specimen is behind glass and is inaccessible for measurement.



The lacrimal is triradiate, with a tall, wide dorsal process that contacts the nasal and prefrontal. The base of the dorsal process makes up a small portion of the orbit margin and the entire posterior margin of the external naris. The slender anterior process makes up about half of the ventral margin of the external naris. About half way along its length is a triangular protrusion, which probably defines the position of a salt gland at the posterior end of the external naris (Figure. 3.5A–B; Wahl 2012). The ventroposterior process of the lacrimal makes up less than half of the anterior margin of the orbit, and contacts the jugal ventrally.

The large, broad jugal extends almost as far anteriorly as the middle of the external naris, separating the lacrimal from the maxilla (Figure. 3.5A–B). It does not taper to a point anteriorly, unlike all other species of the genus. It also extends well beyond the anterior inner edge of the orbit, as in *I. somersetensis*, but unlike *I. communis*, *I. breviceps*, and *I. conybeari*, where the anterior process of the jugal is about even with the anterior edge of the orbit. The jugal dorsal ramus bends dorsally at a right angle, and then bends posteriorly, although some of it is damaged. The jugal makes up 1/4 to 1/3 of the posterior margin of the orbit. Most of the postorbital has been reconstructed, but its dorsal contact with the postfrontal is preserved as is a sliver of bone along the orbit margin, so it makes up most of the posterior margin of the orbit (Figure. 3.5A–B).

The quadratojugal is preserved in lateral view, although it is damaged ventrally and the dorsal margin is buried beneath the squamosal. Dorsally, the element is narrow and it widens ventrally in a somewhat triangular shape. It is positioned dorsally so that only the posteriormost portion of the jugal dorsal ramus contacts the anteroventral portion of the quadratojugal, which creates an embayment. An embayment is found in most non-baracromian neoichthyosaurians and a similar embayment was described in a specimen of *Ichthyosaurus* (Vincent *et al.* 2014).

The quadrate is exposed in lateral view but is rotated from life position. The articular condyle is large and bulbous. The dorsal ramus is thick and curved inward. Portions of the supratemporal and parietal are exposed in right lateral view, but they are incomplete. A rectangular squamosal contacts the supratemporal dorsally, the quadratojugal and possibly the postorbital ventrally, and the postfrontal and possibly the postorbital anteriorly (Figure. 3.5A–B). Some of the skull roof is exposed in dorsal view and a portion of what is probably the right parietal has a lateral process that extends more than half way across the anterior portion of the temporal fenestra

(Figure. 3.1D). The postfrontal is a large element that makes up almost all of the dorsal margin of the orbit and at least half of the anterior margin of the temporal fenestra (Figures. 3.1D, 3.5A–B).

The external naris is longer (5.2 cm) and narrower than in other species of *Ichthyosaurus*, although the salt gland opening at the posterior end makes it look even longer (Figure. 3.5A–B). The shape of the external naris is most similar to *Leptonectes tenuirostris* (McGowan 2003, fig. 1C). The supranarial and subnarial processes of the premaxilla are fairly long extending about half way across the dorsal and ventral margins of the external naris. The nasal is exposed along about half of the dorsal margin. The subnarial process contacts the anterior process of the lacrimal along the ventral edge of the naris, excluding the maxilla from contact with the external naris.

The maxilla is low and symmetric in lateral view. The anterior process is long and narrow, and extends beyond the anterior edge of the external naris. The posterior process is approximately the same length as the anterior process, and does not extend very far under the orbit in lateral view; however, in ventral view, it extends well under the orbit. The height of the maxilla appears to be less than the dorsoventral distance from the maxilla to the naris.

The mandible is approximately 36 cm long (Table. 3.1), but the posterior end is damaged, and a section below the orbit has been reconstructed (Figure. 3.5A–B). The mandible is slender, especially in the prenarial portion of the rostrum. The snout ratio (preorbital length/mandible length) is 0.64, but that is a very rough estimate because of the damaged mandible. In lateral view, the dentary tapers to a point approximately ventral to the middle of the orbit. The surangular does not extend anteriorly as far as the external naris. Only a small portion of the angular is exposed in lateral view, and it extends anteriorly to even with the posterior end of the orbit.

Premaxillary teeth have very slender, striated crowns with fairly acute tips. Roots are narrow but not ‘waisted’ (see Maisch 1997), and longitudinal striations are not evident, although they cannot be ruled out because of poor preservation. Some maxillary teeth are present, but are poorly preserved.



Figure. 3.6. Comparison of the hindfins and pelvis of *Ichthyosaurus larkini* sp. nov., *Ichthyosaurus somersetensis* sp. nov., and *I. communis*. A. BRSUG 25300, holotype of *I. larkini*, both hindfins are in dorsal view and the right one is the right hindfin; B. ANSP 15766, holotype of *I. somersetensis*, both hind fins are in dorsal view with the uppermost fin being the right; C. NHMUK PV R1162, neotype of *I. communis*, left hindfin in dorsal view. *Abbreviations:* il, ilium; is, ischium; pub, pubis. Scale bars represent 5 cm. The scale bar for C is estimated as the specimen is behind glass and is inaccessible for measurement.

Axial skeleton. Some sections of the articulated vertebral column are partially covered by ribs but the majority of the vertebrae are exposed (Figure. 3.1A). Although there are large cracks across the vertebral column in the caudal region, broken centra line up well across them. A total of 128 articulated centra are preserved. Forty-nine precaudal centra can be identified as those with two articulations for the rib. Other species of *Ichthyosaurus* have less than 46, except for *I. somersetensis*. The first apical centrum is no. 74, identified by rounded edges in lateral view. Centrum no. 83 or 84 is the last apical centrum, making the tail stock about 34 or 35 centra.

Neural spines are higher than the centrum height anteriorly, and the height is progressively lower going posteriorly along the vertebral column. Between centra nos. 30 and 35, the neural spines become shorter than the centra. Many ribs widen at the distal end, and seem to have a square, rather than round, cross-section. Some disarticulated, anterior gastralia are present, and they consist of three elements. The lateral elements are straight, slender, and taper to a point at each end, although some isolated elements appear blunt at one end, but this could be due to deformation. The medial element is slender and curved, somewhat boomerang shaped, and tapers to a point at each end. The lateral elements are about $\frac{3}{4}$ of the length of the medial element.

Pectoral girdle and forefin. The coracoid has both anterior and posterior notches, as is typical of the genus. The notches have different shapes however, with the anterior one being a very large and open C-shape, and the posterior one being open, but smaller, more of a J-shape. As a result of this asymmetry in notches, the coracoid is much narrower anteriorly than posteriorly (Figure. 3.1C). The glenoid facet is larger than the scapular facet, but not twice as large.

The right humerus, in ventral view, is associated with the pectoral girdle, but it is worn and is damaged distally (Figure. 3.1C). Although the humerus is rotated, it is clear that the deltopectoral crest is large. The left humerus, in ventral view, is preserved with an articulated forefin, but the proximal portion of the humerus is covered by ribs. A bifurcation occurs in the fifth phalangeal row of digit II, but there could have been a more proximal bifurcation because digit II has been reconstructed between the radius and the fourth phalangeal row. A single phalange is placed into plaster at the third phalangeal row making it look like a bifurcation, but the element is

entirely in plaster and the placement is speculative. There are thus at least five primary digits in the forefin; no accessory digits are preserved.

Pelvic girdle and hindfin. The pelvis is tripartite, as in all species of *Ichthyosaurus*, as well as most Lower Jurassic genera (Figure. 3.6A). The ilium is slightly curved and narrow, only a bit longer than the femur. The pubis and ischium are more than 10% longer than the ilium (Table. 3.1). The ischium is oblong, with a thick central ridge extending along the distal third of the element. The proximal and distal ends are slightly expanded relative to the middle of the element. The pubis is slightly expanded proximally, has a narrow shaft, and is very broad and somewhat asymmetric at the distal end. This morphology occurs on many specimens of *Ichthyosaurus* (e.g., ANSP 17429, BRSMG Ce16611, NHMUK PV R3372). BRSMG Ce 16611 and NHMUK PV R3372 are clearly female because they are each associated with an embryo (Pearce 1846; Deeming *et al.* 1993), which may mean that this character is sexually dimorphic. The pubis and ischium are about 15% longer than the femur (Table. 3.1).

Both hindfins are incomplete and are exposed in dorsal view. The femora are long relative to their distal width. The anterior segment of the shaft is expanded in the distal half, and then narrows just before the distal end, producing a noticeable expansion on the anterior edge of the femur (Figure. 3.6A). The proximal four or five rows of elements are articulated, but the distal portion of both hindfins has been reconstructed. The fibula is slightly larger than the tibia, but not more than 10% larger. Digit IV originates from the astragalus along a broad contact, but elements of two other digits contact the astragalus, seen best in the right hindfin (anterior one on specimen), an arrangement that does not occur in other species of *Ichthyosaurus* (Figure. 3.6A). The element of digit III nearly separates the astragalus from the tibiale (terminology as defined in McGowan and Motani 2003, fig. 67) and there is a facet on the astragalus for the contact. The contact with the element of digit V is small. The distal tarsal is notched on both hindfins and the metatarsal may be notched on the right one. There are four digits, but not enough of the fin is preserved to confirm that a distal bifurcation does not occur.



Figure. 3.7. Comparison of the humeri of all species of *Ichthyosaurus*. All of the humeri are the left in dorsal view, anterior to the left, except A, which is the right humerus reversed to show the same orientation. A. AGC 11, referred specimen of *Ichthyosaurus larkini* sp. nov.; B. ANSP 15766, holotype of *Ichthyosaurus somersetensis* sp. nov.; C. NHMUK PV R1162, neotype of *Ichthyosaurus communis*, rotated slightly; D. NHMUK PV OR43006, holotype of *Ichthyosaurus breviceps*, a small portion of the anterodistal side of the shaft is damaged; E. NMW 93.5G.2, a referred specimen of *Ichthyosaurus conybeari*; F. holotype of *Ichthyosaurus anningae*. Both *I. communis* and *I. breviceps* are behind glass at the NHMUK, so the scales are estimates. Scale bars represent 3 cm (A, F); 5 cm (B); and 2 cm (C–E). Scale bars for C and D are estimates because specimens are mounted behind glass and inaccessible for measurement.

Table. 3.1. Measurements, in centimetres, of specimens of *Ichthyosaurus larkini*. 'Width' for fin elements refers to the anteroposterior dimension, perpendicular to the long axis of the fin. L and R denote measurement of left or right skeletal elements. Asterisk denotes an estimate because the bone is damaged, rotated, or partially buried.

	BRSUG		CAMSM
	25300	AGC 11	59575
Skull length	35.5	32.0	
Preorbital length	23.3	20.0	27.8
Prenarial length	16.9	15.4	
Premaxillary length	15.4	14	19.8
Maxilla length	9.8	8.2*	7.4*
Jaw length	36.6*	32.0	43.9
Orbit height	8.3	7.6	
Orbit length	7.2	7.2*	
Scapula length	9.9L	6.5R 7.4L	
Coracoid ant-post length	9.9L	7.1R	
Coracoid med-lat length	7.4L	5.1R	
Humerus length	7.7L 4.8L	5.4L 5.4R	8.0L *
Humerus distal width	5.4R	3.7L 3.6R*	5.6L
Humerus proximal width	5.3L	3.5L 3.9R*	
Radius width	2.8R	1.9L 2.1R	3.3L
Ulna width	3.1R 5.6L	1.9L 2.1R	3.2L
Femur length	5.5R 2.9L	3.5R*	
Femur distal width	3.1R 2.4L		
Femur proximal width	2.9R* 1.6L	1.6R*	
Tibia width	1.6R		

	1.6L	
Fibula width	1.7R	
	6.5L	
Ischium length	6.3R	
	6.5L	
Pubis length	6.4R	
Ilium length	6.0L	
Precaudal length	139	87
Preflexural length	186	126
Skull length/precaudal		
length	0.26	0.37
Preorbital ratio	0.64*	0.63
Humerus/Femur ratio	1.4L	1.5R*

Description of referred specimens

AGC 11 is a nearly complete skeleton that is less than 3/4 the length of the holotype (Table 3.1; Figure. 3.2A). It is referred to *Ichthyosaurus larkini* on the basis of a high-crowned skull; a slender mandible and rostrum, especially in the prenasal portion (snout ratio = 0.63); a large, robust prefrontal that extends ventrally to the level of the external naris and excludes the dorsal process of the lacrimal from the anterior margin of the orbit; and an asymmetric coracoid with the glenoid facet longer but less than twice as long as the scapular facet. Although it is somewhat disarticulated, the hindfin clearly has an element of digit III nearly separating the astragalus and tibiale, and probably has elements of three digits in contact with the astragalus, as in the holotype. Two articulated forefins are preserved in dorsal and ventral view, providing additional information on the species. The humerus is long relative to its width, and has a prominent dorsal process that extends less than half way down the shaft. The articular surface ventral to the dorsal process has an irregular depression that forms a distinct ridge, similar to that seen in *I. communis* (Figure. 3.7A, C). In ventral view, the deltopectoral crest is large. The forefins might have two anterior bifurcations, one in the metacarpal (right fin) or p1 (left fin) rows; and probably a second, distal bifurcation in the p6 (right fin) or ?p4 (left fin) rows. However, the distal 'bifurcations' could be anterior accessory digits, but because there is only a single element, it is

uncertain. The bifurcation preserved on the forefin of BRSUG 25300 might be the distal bifurcation.

CAMSM J59575 is larger than the holotype (Figure. 3.2B; Table. 3.1). The skull is slightly distorted posteriorly and is preserved in ventrolateral view, unlike the other specimens of the species. It is referred to *I. larkini* because it has a broad jugal that extends almost to the ventral margin of the external naris, and does not taper to a point anteriorly, a morphology that is unique for the species. The maxilla is also similar if the ventral orientation is taken into account. The pectoral girdle is partially articulated in ventral view and provides additional information about the species. The notches on the coracoid are similar to those of BRSUG 25300, although the asymmetry of the coracoid is not as pronounced. The relative size of the glenoid and scapular facets is also similar, but the facets are somewhat more prominent and at a sharp angle to one another. This may be an indication of a more mature individual. The interclavicle has very long and slender anterior processes that lie along the ventral surface of the clavicles, together being well over twice the length of the medial process of the interclavicle. The medial process is short and almost hour-glass shaped, being broad where it contacts the anterior processes and at the posterior end, and very narrow in the middle. It probably extends a third of the anteroposterior length of the coracoids, although it is disarticulated and may be broken. The interclavicle is not preserved on any other specimen of the species.

NHMUK PV R5595 is assigned to *I. larkini* on the basis of the slender rostrum, although the skull is crushed and in dorsal view; and the morphology of the right humerus, showing a large, centrally located dorsal process and an irregular depression on the articular surface that forms a distinct ridge, as in AGC 11. Furthermore, the right hindfin, the only fin on the specimen that may be entirely authentic (Figure. 3.2C), has elements of three digits contacting the astragalus, and the astragalus and tibiale are nearly separated by the element of digit III, similar to the holotype. It is a more complete, better articulated hindfin than on the other specimens of this species. It is the only specimen that shows a second bifurcation, of digit III in the p2 row, bringing the total number of primary digits in the hindfin to five. *I. communis* also has five digits in the hindfin, but elements of two digits, not three, contact the astragalus and five elements are in the fifth row, not four (Figure. 3.6C). *I. conybeari* also has five digits in the hindfin, but only one digit contacts the astragalus and only three elements are in the third (distal tarsal) row.

Ichthyosaurus somersetensis, sp. nov.

Figures 3, 4, 5C–D, 6B, 7B

LSID. urn:lsid:zoobank.org:pub:FE230EF8-1C34-4BD0-86D5-FDC1FD870A11

Synonymy.

Paramecostinus; Hawkins 1840: pl.17.

Ichthyosaurus intermedius; Owen 1881: p1. XXX, fig. 1.

Ichthyosaurus intermedius; Lydekker 1889: 56, fig. 23.

Ichthyosaurus communis; McGowan, 1974: 9 [referred specimen].

Ichthyosaurus communis; Spamer et al. 1995: 12.

Ichthyosaurus communis; Lomax and Massare 2015: fig. 7C.

Derivation of name. Named for the county of Somerset in SW England, where numerous specimens of *Ichthyosaurus*, including the holotype and referred specimen of *I. somersetensis* sp. nov., were discovered.

Holotype. ANSP 15766, a practically complete skeleton comprising the skull, portions of the pectoral girdle, both forefins, portions of the pelvic girdle, both hindfins, ribs, gastralia, and an articulated vertebral column. The matrix is covered by a layer of painted plaster with a pattern imitating an irregular rock surface and/or chisel marks.

Referred Specimens. BRSMG Cb4997, a fairly complete skeleton; NHMUK PV OR2013*, a complete skeleton; AGC 16, a fragmentary skeleton; and ROM 26029 a fragmentary skeleton.

Diagnosis. *Ichthyosaurus somersetensis* is a medium-sized species (2-3 m long) diagnosed relative to other species of *Ichthyosaurus* by the following unique characters: broad, asymmetric maxilla with fairly long anterior process, and delicate, very long, and slender posterior process in lateral view; triradiate lacrimal with posterior shelf at base of dorsal process; jugal dorsal ramus only slightly curved, lacking a right angle dorsal bend; high, narrow postorbital forming almost all of the posterior margin of orbit, excluding the jugal dorsal ramus from the orbit; ilium wide relative to length, more oblong than rib-like.

The species is further diagnosed relative to other species of *Ichthyosaurus* by the following unique combination of characters: large prefrontal forms at least half of anterior border of orbit, excluding dorsal process of lacrimal from orbit margin (similar to *I. larkini*); anterior process of jugal relatively narrow and tapers to a point (as in all species of *Ichthyosaurus*, except *I. larkini*), and extends beyond anterior inner edge of the orbit, sometimes as far forward as the external naris (as in *I. larkini*, and to a lesser extent in *I. anningae*); premaxilla supranarial and subnarial processes about equal length, extending about half way across the dorsal and ventral margins of the external naris, with nasal about half of dorsal margin (as in all species of *Ichthyosaurus* except *I. breviceps*); humerus long relative to width, with small dorsal process (as in *I. breviceps*), that does not extend far down the shaft; presence of an irregular depression on the articular surface (as in *I. communis* and *I. larkini*); one digit in broad contact with astragalus, with a total of three elements in that row (as in *I. conybeari*, *I. breviceps*); 46 precaudal centra (about the same as *I. larkini* but more than other species of *Ichthyosaurus*).

Locality and stratigraphical information. Specimens were collected in the 19th century, when locality and stratigraphic data were not recorded in detail. The holotype is from Somerset, possibly Glastonbury. The referred specimens are from Street, Somerset. However, ROM 26029 is supposedly from Lyme Regis, Dorset, but the preservation of the specimen suggests it too is from Somerset. Specimens are most likely from the lowermost Jurassic (Hettangian), Pre-*planorbis* beds of the Blue Lias Formation (McGowan 1974; Benson *et al.* 2012, 2015).

Table. 3.2. Measurements, in centimetres, of specimens of *Ichthyosaurus somersetensis*. NHMUK PV OR2013* and BRSMG Cb4997 are on display behind glass and not accessible for measurements. ‘Width’ for fin elements refers to the anteroposterior dimension, perpendicular to the long axis of the fin. L and R denote measurement of left or right skeletal elements. Asterisk denotes a measurement that was estimated because the bone was damaged, rotated, or partially buried.

	ANSP 15766	AGC 16	ROM 26029
Skull length	43.8	44*	
Preorbital length	28.0	26.5*	25*
Prenarial length	21.0		
Maxilla length	11.8	7.2	
Jaw length	47.0		
Orbit height	6.7		
Orbit length	9.6		
Scapula length			8.3R
Humerus length	8.8L 8.2R*		5.6R*
Humerus distal width	6.7L 5.4R		5.6R
Humerus proximal width	6.2L		
Radius width	3.6L 3.8R		2.9R
Ulna width	3.9L 3.1R		3.3R*
Femur length	6.0L 6.3R	6.3L	5.2R
Femur distal width	3.3L 3.5R	4.0L	
Femur proximal width	2.7L 3.1 R	2.9R	
Tibia width	1.8L		1.8R
Fibula width	1.6L* 1.9R		
Ischium length		6.1R	
Pubis length		6.3R	
Ilium length		5.5R*	
Precaudal length	146		
Preflexural length			
(includes apical centra)	201		
Skull length/precaudal length	0.30		
Preorbital ratio	0.59		
Humerus/Femur ratio	1.5L		

Description of holotype

ANSP 15766 is an articulated skeleton lying on its right side, one of the most complete skeletons of the genus known (Figure. 3.3). It is 2.3 m long from the tip of the snout to the tip of the tail, measured along the vertebral column, although the fluke is incomplete. The precaudal length is almost 1.5 m, and the preflexural length is about 2.0 m. It is assigned to the genus *Ichthyosaurus* on the basis of a humerus with nearly equal width distally and proximally, with slight constriction in the shaft; and a forefin with five or more digits, two digits with broad contacts with the intermedium, and an anterior digital bifurcation (Motani 1999a, McGowan and Motani 2003).

Skull and mandible. The skull is 44 cm long, and is preserved in dorsolateral view (Figures. 3.3, 3.5C–D; Table. 3.2). Some portions of the skull roof such as the supratemporal, parietals and frontals are exposed but somewhat taphonomically deformed. The parietals form a low medial ridge and posterior shelf. The pineal foramen appears to be within the frontals as in other species of the genus (Motani 2005). A small, roughly square squamosal contacts the supratemporal dorsally, the postfrontal anteriorly, and the quadratojugal ventrally. The quadratojugal is much longer than wide in lateral view. The quadrate is in lateral view, showing a robust articular condyle and thin medial portion, but the dorsal end is broken.

The postfrontal is a large, robust, hour-glass shaped element that forms almost all of the dorsal margin of the orbit, similar to that seen in *I. conybeari* (BGS 956); the postfrontal is much more slender in the *I. communis* neotype, *I. breviceps*, and *I. larkini*, but is unknown in *I. anningae*. A large prefrontal makes up a small portion of the dorsal and at least half of the anterior margins of the orbit, and extends ventrally to the level of the external naris (Figure. 3.5C–D), similar to *I. larkini*. It is a much larger, more robust bone and extends farther anteroventrally than in *I. communis*, *I. breviceps*, *I. conybeari* and *I. anningae*.

The nasal is wide and robust posteriorly, and narrows anteriorly, with the anterior-most portion extending as far forward as the anterior process of the maxilla. The posterior portion of the nasal contacts the anterior portion of the postfrontal along a broad contact. In lateral view, the nasal contacts the external naris, the dorsal process of the lacrimal, the supranarial process of the premaxilla, and the

prefrontal. The supranarial and subnarial processes of the premaxilla make up at least half of the external naris borders.

The lacrimal has a long dorsal process that contacts the prefrontal and the nasal and is excluded from the anterior margin of the orbit (Figure. 3.5C–D). The anterior process of the lacrimal makes up the posterior margin and about half of the ventral margin of the naris. At the posterior end of the naris is what might be a damaged salt gland support structure (Wahl 2012) which has been pushed through the external naris from the other side. Other bones and teeth fill some of the external narial opening, possibly due to the dislocation of the right side of the skull (Figure. 3.5C–D). The ventroposterior process of the lacrimal makes up less than half of the anterior margin of the orbit.

The anterior process of the jugal is fairly narrow and tapers to a point, as in *I. communis*, but it extends farther forward, slightly beyond the anterior edge of the orbit. The posterior process of the jugal lacks a dorsal bend, and is separated from the posterior margin of the orbit by a high, narrow crescentic postorbital (Figure. 3.5C–D). This is somewhat similar to *Stenopterygius quadriscissus* and *S. longifrons* (Maisch and Matzke 2000a, fig. 7), the latter now considered a synonym *S. triscissus* (Maisch 2008). The postorbital is higher and narrower than that of *I. communis*, *I. breviceps* and *I. anningae*, but not as slender as in *I. conybeari*.

The maxilla is very large, with its maximum (dorsoventral) height about even with the posterior edge of the external naris. It is asymmetric in lateral view, with a fairly long and abruptly narrowing anterior process that extends beyond the external naris; and a delicate, very long, and slender posterior process that extends well under the orbit. The height of the maxilla is greater than the dorsoventral distance from the maxilla to the external naris.

The mandible is 47 cm long and the snout ratio (preorbital length/mandible length) is 0.59 (Table. 3.2), which is low, but not as low as *I. breviceps*. The right side of the rostrum is partially exposed and pushed forward relative to the left side, making the rostrum look longer than it actually is. In lateral view, the angular makes up a small portion of the posterior section of the mandible, and does not extend anteriorly beyond the posterior edge of the orbit; whereas the surangular extends as far anteriorly as the highest point of the maxilla. The dentary tapers abruptly to a point about half-way across the ventral edge of the orbit. The teeth possess relatively

slender crowns with longitudinal striations and subtly striated roots. The maxillary teeth are much smaller than the premaxillary teeth.

Axial skeleton. The atlas-axis are fused, but the border between the centra is still evident. There are 46 precaudal centra, identified by the presence of two rib articulations on the centrum. The first wedge-shaped centrum, indicating the beginning of the tail bend, is centrum no. 75. At least three other centra are noticeably wedge-shaped in lateral view, making the preflexural count 78.

Centra increase in length and height from the atlas-axis to about centrum no. 30. They decrease in length and height from about centrum no. 40 to the fluke (Supp. Materials, Fig. S1). In general, the centra are about twice as high as they are long in the trunk and anterior tail stock. The neural spines of the cervical and anterior dorsal vertebrae are taller, but not twice as tall, as the respective centra.

Pectoral girdle and forefin. The left forefin is articulated and completely exposed, but a portion of the right forefin is covered by the vertebral column (Figure. 3.3). The humerus is longer than wide, with a very small dorsal process. The proximal and distal widths are about equal. The left humerus has an irregular depression on the head, ventral and slightly anterior to the dorsal process. It does not form a prominent ridge as in *I. larkini* and *I. communis*; nor is it an oval depression with smooth, finished bone as on *I. anningae* (Figure. 3.7B, F).

The left forefin, in dorsal view, has five primary digits and one posterior accessory digit. The accessory digit begins between mc5 and p1 of digit V. The radius and ulna meet along a broad contact, although the radius is a rounded rectangle whereas the ulna is more pentagonal. The ulna is only slightly larger than the radius. Metacarpal 2 is much shorter than mc3, and there is an extra element distal to it in the metacarpal row (i.e., two short elements in the mc2 position). Assuming the extra element is an anomaly, the bifurcation occurs in the p3 row, although two co-ossified elements can be discerned in the p2 row. A similar co-ossification has been reported in other specimens of *Ichthyosaurus* (e.g. OUMNH J.13799, in Motani 1999a, fig. 6). The anterior branch of the bifurcation has much smaller, more circular elements than the posterior branch, a morphology that occurs in many specimens of *Ichthyosaurus* (e.g., OUMNH J.13799, OUMNH J.10343/p, BRSMG Ce 16611, CAMSM J35186), so it is unlikely to be a diagnostic

characteristic. Furthermore, although the right forefin has a similar morphology in other respects, the digital bifurcation occurs in the p2 row of digit II. This asymmetry may be due to pathology, although asymmetry in the location of a digital bifurcation occurs in other specimens of *Ichthyosaurus* (e.g. AGC 11). Portions of a scapula and clavicle are preserved, but they cover the edges of the coracoid so that its morphology cannot be seen.

Pelvic girdle and hindfin. The ?right ilium is the only pelvic element clearly preserved. It is fairly wide relative to its length, more oblong than rib-like (Figure. 3.6B). It is about the same length as the femur, even accounting for a small portion of the distal end that is covered by ribs. Both hindfins are preserved in dorsal view, and we identify the one nearest the vertebral column, partly covered by caudal ribs, as the right (Figure. 3.6B). The femur is long relative to the distal width, and the distal width is greater than the proximal width. Its proximal portion is thick and bulbous with no prominent dorsal process, and the shaft is relatively slender. The fibula is slightly larger than the tibia. One digit is in broad contact with the astragalus, and three elements are in that row. A bifurcation of digit II occurs in the fourth (metatarsal) row, and so four digits are present to at least the p3 row. The tibiale and metatarsal are notched.

Description of referred specimens

BRSMG Cb4997 is a large specimen but its total length cannot be estimated because it is on display, behind glass, positioned at a slant (Figure. 3.4A). It is referred to *I. somersetensis* on the basis of the large prefrontal, slightly curved jugal dorsal ramus, dorsal process of the lacrimal with a posterior shelf, high asymmetric maxilla, humerus morphology, and the shape of the ilium. The specimen provides additional information on the species. The coracoid has well-developed anterior and posterior notches, as in all species of the genus. The anterior notch is wide and shallow, whereas the posterior notch is smaller and more tightly curved, so the coracoid is much broader posteriorly than anteriorly. The scapula is wide proximally, has a narrow shaft, and is slightly flared distally, similar to all species of the genus. Elements of the pubis and ischium are preserved, but the morphology is better illustrated in AGC 16, described below.

NHMUK PV OR2013* is larger than the holotype (Figure. 3.4B; Table. 3.2). It is referred to *I. somersetensis* on the basis of the large prefrontal, shape and extent of the postorbital, slightly curved jugal dorsal ramus, dorsal process of the lacrimal with a posterior shelf, shape of the maxilla, and the morphology of the hindfin. It differs from the holotype in three features. The humerus appears to have a more prominent dorsal process than on the holotype, but the proximal end of the humerus is missing. The teeth have more prominent striations on the roots. The ilium is more slender, but this is probably related to the angle of view.

AGC 16 is about the same size as the holotype (Figure. 3.4C; Table. 3.2), but both the anterior and posterior ends of the mandible are broken, and the back of the skull is missing. It is referred to *I. somersetensis* on the basis of an oblong, rather than rib-like, ilium and the morphology of the hindfin, with one element in broad contact with the astragalus and three elements in the third row. The pubis and ischium are well preserved, and provide additional information on the species. They are approximately equal in length. The proximal portion and shaft of the pubis are slender, but the distal end is more than twice as wide as the proximal. Both the proximal and distal portions of the ischium are wide, whereas the shaft is slender (Figure. 3.4C). The morphologies of the pubis and ischium are similar to *I. communis*.

ROM 26029 is smaller than the holotype (Figure. 3.4D; Table. 3.2), but the specimen is incomplete. It is referred to *I. somersetensis* on the basis of a robust humerus with a small dorsal process and a hindfin, with one element in broad contact with the astragalus and three elements in the third row.

Phylogenetic Analysis

In order to demonstrate that the two new species are morphologically distinct from other species of *Ichthyosaurus*, a phylogenetic analysis was undertaken. The analysis was performed using the cladistics program TNT, selecting the implicit enumeration for the search as recommended by Goloboff *et al.* (2008) for small data sets. *Temnodontosaurus* was used as the outgroup taxon. Recent phylogenetic studies have focused on relationships among genera or on Upper Jurassic species (e.g. Maxwell *et al.* 2012; Fischer *et al.* 2011, 2013; Ji *et al.* 2016). They generally do not capture the range of variation among species of *Ichthyosaurus*, so we have

developed a new character matrix. The majority of characters were taken or modified from Massare and Lomax (2016a), and these were supplemented with additional characters from Motani (1999b); Fernández (2007); Maxwell (2010); Druckenmiller and Maxwell (2010); Fischer *et al.* (2011); Maxwell *et al.* (2012); and Fischer *et al.* (2013). In addition, 17 characters were added in this study to include other differences in morphology among species of *Ichthyosaurus*, bringing the total to 58: 23 cranial and 35 postcranial characters (Appendix). Of these, 40 are parsimony informative and 32 are informative for the ingroup.

Species of *Ichthyosaurus* are represented by the following specimens: *I. communis* neotype (NHMUK PV R1162), *I. breviceps* holotype (NHMUK PV OR43006) and a referred specimen (CAMSM X50187; Massare and Lomax 2014a), *I. conybeari* holotype (NHMUK PV R1064) and two referred specimens (BGS 956 and NMW 93.5G.2; Massare and Lomax 2016a), *I. anningae* holotype (DONMG: 1983.98) and a referred specimen (NHMUK PV OR120; Lomax and Massare 2015), *I. larkini* holotype (BRSUG 25300) and two referred specimens (AGC 11 and CAMSM J59575) and *I. somersetensis* holotype (ANSP 15766) and a referred specimen (NHMUK PV OR2013*). The neotype of *I. communis* can be scored for 50 of 58 characters (87%) so a second specimen was not included (Supp. Materials 2).

Temnodontosaurus and *Suevoleviathan* were included for the analysis because the two genera appear more primitive than *Ichthyosaurus* in many cladistic analyses (e.g. McGowan and Motani 2003; Maxwell *et al.* 2012; Fischer *et al.* 2013; Ji *et al.* 2016). Character states for *Temnodontosaurus* were assessed from images taken through glass of *T. platyodon* (NHMUK PV OR2003), diagrams of skulls of *T. trigonodon* and *T. platyodon* in Maisch and Matzke (2000a, fig. 4), and photographs of the forefin of *T. trigonodon* in McGowan and Motani (2003, pl. 6). Character states for *Suevoleviathan* were assessed from skull diagrams in Maisch and Matzke (2000a, fig. 5) and postcranial drawings in McGowan and Motani (2003, fig. 70). Snout ratio for *Suevoleviathan* from Maisch (1998). Snout ratios for *T. trigonodon* and *T. platyodon* from McGowan and Motani (2003). *Malawania*, which appears as a sister taxon to *Ichthyosaurus* on recent phylogenies (Fischer *et al.* 2013; Maxwell *et al.* 2016) was not included in the outgroup because only forefin and scapula characters could be coded (however, see below).

specimens share several additional characters that unite them and distinguish them from other species of *Ichthyosaurus*.

The tree has several polytomies, which includes a relatively well supported (node bootstrap value, 31) polytomy comprising all three specimens of *I. conybeari*. Regarding this species, where the character could be assessed and coded, both referred specimens of *I. conybeari* differed only in one character. Similarly, the holotype, for which only postcranial characters could be assessed, shared the same coding as the two referred specimens. Considering that this is a specimen level analysis, and that only a single character is different (between two of the three specimens), it could be expected that this would result in a polytomy. However, this may also be due to the incompleteness of the holotype because only 26% of the characters could be coded for this specimen. The polytomy with node bootstrap value 3 is poorly supported, although specimens are grouped in their respective species. This suggests that it is not possible to resolve the relationships among these species, but that some species are more closely related to each other (e.g. *I. larkini* and *I. somersetensis*) than they are to others (e.g. *I. larkini* and *I. breviceps*). In order to evaluate the relationships further, additional characters and more complete specimens should be added to the analysis, which might help to resolve these issues.

We performed a second analysis replacing *Temnodontosaurus* and *Suevoleviathan* with *Macgowania* and *Malawania* as the outgroup taxa, using the literature, and personal observations of the former, to evaluate characters. The latter is a sister taxon to *Ichthyosaurus* (Fischer *et al.* 2013), but only forefin and scapula characters could be coded on our matrix (17% of the characters). *Macgowania*, although Late Triassic in age, had originally been assigned to the genus *Ichthyosaurus* (McGowan 1996). Only 33% of the characters could be coded, far fewer than for *Temnodontosaurus* (95%) and *Suevoleviathan* (88%). The analysis resulted in fourteen trees, and bootstrapping found exactly the same groupings of specimens, although the relationships among the species were different (Supp. Materials 3).

Discussion

Ichthyosaurus communis has for a long time been regarded as a highly variable and common species of the genus (e.g. McGowan 1974; McGowan and Motani 2003), however specimens previously assigned to this species have recently been recognized as different (*I. anningae* in Lomax and Massare 2015; new specimens of *I. conybeari* in Massare and Lomax 2016a), and this work recognizes two more species. These species can be separated from the range of variation of '*I. communis*' by focusing on characteristics of the skull, humerus, hindfin, and pelvis morphologies. The new species have notable differences in skull morphology, especially around the orbit (Figure. 3.5). Further differences probably exist in the morphology of the dorsal and posterior portions of the skull, but most of the specimens examined here are preserved in lateral view. The features that are most useful in lateral view are (1) the shape of the maxilla and the extent of the anterior and posterior processes, (2) the anterior and posterior extent and shape of the jugal, (3) extent and shape of the postorbital, (4) the anterior extent and robustness of the prefrontal, and (5) the extent and shape of the dorsal processes of the lacrimal. These features can distinguish the new species from *Ichthyosaurus communis*. Moreover, they seem to be useful in distinguishing other species as well, e.g. *I. conybeari* (Massare and Lomax 2016a).

The absence of a squamosal in *Ichthyosaurus* has been considered a characteristic of the genus (Motani 2005) and this has been incorporated into studies on ichthyosaur phylogeny (e.g. Motani 1999b; Ji *et al.* 2016). However, Maisch and Matzke (2000b), Maisch *et al.* (2008), and Vincent *et al.* (2014) reported it from specimens of *I. communis*. The excellent preservation of the skulls of the holotypes of the two new species supports their observations that the squamosal is present in *Ichthyosaurus*. It occurs not only in *I. larkini* and *I. somersetensis*, but also in *I. conybeari* and perhaps *I. anningae* (mistaken for part of the supratemporal in Lomax and Massare 2015). It is likely that it occurs on all species of the genus, although it cannot be seen in the holotype of *I. breviceps* nor the neotype of *I. communis* because the post-orbital portion of the skulls are damaged. Maisch and Matzke (2000b) and Maisch *et al.* (2008) suggested that because the squamosal is a thin plate of bone that is only loosely attached to the rest of the skull, it is often lost or damaged. Therefore, its occurrence in *Ichthyosaurus* can easily be missed unless

the specimen is well-preserved. A similar situation occurs in *Platypterygius* (Fischer 2012).

Hindfins have rarely been evaluated taxonomically. The two new species described here have distinct differences in hindfin morphology compared to *I. communis*, which suggests that it has taxonomic significance (Figure. 3.6). Given that the forefin morphology is extremely variable, an argument can be made that hindfin morphology is likely to be variable as well. However, in the forefin, the number and arrangement of elements in the proximal rows are identical in all specimens of *Ichthyosaurus*, independent of other non-pathological variations in the forefin, such as the number and position of bifurcations, relative size of various elements, number of digits, etc. Distal to the radius and ulna are the radiale, intermedium, and ulnare, with the intermedium in contact with both the radius and ulna, although the extent of the contact and shape of the intermedium varies. Distal carpal 2 contacts the radiale, distal carpals 3 and 4 broadly contact the intermedium, and mc5 contacts the ulnare (Motani 1999a). In fact, this arrangement of the forelimb zeugopodium and mesopodium, arranged as rows of two, three and four elements, is a non-varying feature in *Ichthyosaurus*, as also shown by Motani (1999a, fig. 6).

In the corresponding region of the hindfin, at least three morphologies exist among specimens previously identified as *I. communis*. In the discussion that follows, we follow, in part, the terminology of McGowan and Motani (2003, fig. 67) for the hindfin. The key features are the number of digits that contact the astragalus, which largely reflects the number of elements in the third row. *I. larkini* has a distinctive arrangement in the mesopodium in which digit IV has a broad contact with the astragalus and elements of digits III and V also contact the astragalus. The element of digit III nearly separates the tibiale and astragalus, and there are four elements in the row distal to the astragalus (third row). *I. somersetensis*, *I. conybeari*, and *I. breviceps*, have only digit III with a broad contact with the astragalus. *I. communis* shows a third pattern, in which digits III and IV have broad contacts with the astragalus, and four elements are in the third row. *I. anningae* (NHMUK PV OR120) seems to have a similar pattern to *I. communis*, although no completely articulated hindfins are known. It thus appears that the morphology of the proximal hindfin has some taxonomic utility within the genus.

Conclusion

Two new species of *Ichthyosaurus* from Somerset have been identified based on morphological characters of the skull and postcranium (Figures. 3.5–7), and a phylogenetic analysis confirms that they can be distinguished from *I. communis* and all existing species of the genus (Figure. 3.8). The combination of cranial and postcranial features for the new species will allow isolated skulls and fragmentary skeletons to be identified to species level with a high degree of confidence. Isolated hindfins, unlike forefins, seem to be useful taxonomically and certain morphologies can be identified to species.

With the identification of these new species, the total number of species of *Ichthyosaurus* increases to six. It could be argued that the number of autapomorphic features of the two new species and the unique combination of other characters are sufficient to define new genera. Features that are part of the diagnosis for the genus, however, are found in the two new species, including the shape of the humerus, a coracoid with well-developed anterior and posterior notches, a tripartite pelvis with an unfused pubis and ischium, and a forefin with at least five digits, two digits with broad contacts with the intermedium, a prominent digit V, and an anterior digital bifurcation. Thus, there is no justification for erecting a new genus for either of the new species.

With the recognition of these new species, three species of *Ichthyosaurus* (*I. communis*, *I. larkini* and *I. somersetensis*), *Leptonectes tenuirostris* (McGowan 1974), *Wahlisaurus massarae* (Lomax 2016) and a possible shastasaurid (Martin *et al.* 2015) are known from the Hettangian of the UK. It is possible that *I. conybeari* and *I. breviceps* are also from the Hettangian (McGowan, 1974), but the stratigraphy is too poorly known for historic specimens.

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Appendix. Description of characters used in the phylogenetic analysis. Characters are polarized using *Temnodontosaurus* and *Suevoleviathan* as outgroups. All characters are unordered. Lengths or widths of skeletal elements are evaluated as

'approximately equal' if the measurements are within 10% of each other. Characters that are not referenced were developed as part of this study.

Skull and dentition:

0. Premaxilla supranarial and subnarial processes: (0) well-developed supranarial process overlying approximately 1/3–1/2 of external nares, with long subnarial process making up at least 1/2 of ventral margin of external nares; (1) supranarial process short relative to subnarial process (Maxwell *et al.* 2012: character 1; modified Massare and Lomax 2016, character 0).

1. Premaxilla-lacrimar contact: (0) absent; (1) present.

2. Position of premaxilla-lacrimar contact: (0) ventral to middle external naris; (1) ventral to posterior end of external naris or more posterior.

3. Highest point (dorsoventrally) of maxilla: (0) posterior to external naris; (1) anterior to external naris; (2) approximately even with the middle of the external naris (Druckenmiller and Maxwell 2010: character 4; modified Massare and Lomax 2016: character 3).

4. Dorsoventral distance between maxilla and external naris: (0) less than the height of the maxilla; (1) greater than or equal to the height of the maxilla.

5. Maxilla posterior (jugal) process, lateral exposure: (0) does not reach the orbit; (1) extends just under orbit; (2) extends 1/3 to 1/2 orbit length under orbit (modified from Maxwell *et al.* 2012: character 3).

6. Extent of posterior (jugal) and anterior (premaxillary) processes of maxilla relative to maximum height (dorsoventral dimension): (0) posterior process long relative to anterior process; (1) posterior process about equal to anterior process; (2) posterior process short relative to anterior process (Massare and Lomax 2016: character 5).

7. Anterior extent of maxilla in lateral aspect: (0) anterior end of maxilla positioned posterior to anterior edge of external naris; (1) anterior end of maxilla even with or

slightly beyond anterior edge of external naris; (2) anterior end of maxilla extends well beyond anterior edge of the external naris (Maxwell *et al.* 2012: character 2; modified Massare and Lomax 2016: character 7).

8. Jugal anterior extent: (0) extends no farther than just beyond anterior inner edge of the orbit; (1) extends beyond anterior inner edge of the orbit, sometimes as far forward as external naris.

9. Anterior process of jugal: (0) narrows and tapers to pointed end; (1) remains broad, does not taper, end blunt.

10. Jugal, dorsal ramus angle: (0) strongly curved dorsally (almost 90 degree bend); (1) only a slight dorsal bend, contributing little to the posterior margin of the orbit (Maxwell *et al.* 2012: character 7; modified Massare and Lomax 2016: character 8).

11. Lacrimal dorsal process: (0) minimal contribution to anterior margin of orbit, sometimes excluded completely by prefrontal; (1) participates in at least half of the anterior margin of orbit.

12. Lacrimal external naris contact: (0) lacrimal forms posterior edge of external naris and at least a 1/3 of ventral border of external naris; (1) anterior process reduced, lacrimal forms posterior edge of external naris and only a slight portion of the ventral margin if at all.

13. Postorbital in lateral view: (0) narrow, crescentic shape; (1) broad, crescentic shape (modified from Fernández 2007: character7).

14. Extent of postorbital in lateral view: (0) contributes to half or less of the posterior margin of orbit; (1) forming almost all of posterior margin of orbit.

15. Prefrontal, lateral view: (0) narrow, with a minor contribution to anterior border of orbit, does not reach the level of external naris; (1) large and robust, extending ventrally to at least level of external naris and forming at least half of the anterior

border of the orbit; (2) short and wide, contributing less than 1/2 of anterior margin of orbit but does not reach the level of external naris.

16. Postnarial region of skull: (0) high-crowned; (1) streamlined. Note that crushing and displacement can sometimes deform the shape of the orbit and this should be taken into account.

17. Extent of nasals relative to anterior process of maxilla, lateral view: (0) maxilla extends anteriorly as far as nasals or further anteriorly; (1) nasals extend farther anteriorly than the maxilla (modified from Fischer *et al.* 2011).

18. Separation of external naris from orbit: (0) narrow, anteroposterior constriction at base of dorsal process of lacrimal; (1) broad, no anteroposterior constriction in lacrimal (Massare and Lomax 2016: character 14).

19. Squamosal: (0) absent (1) present.

20. Rostrum relative length (snout ratio = preorbital length/jaw length [McGowan 1974]): (0) short rostrum <0.60; (1) moderate to long rostrum, snout ratio >0.60.

21. Angular lateral exposure: (0) much smaller than surangular exposure; (1) extensive, almost completely concealing surangular (Fischer *et al.* 2013: character 25).

22. Tooth root striations: (0) present and prominent; (1) absent or subtle (modified from Fischer *et al.* 2013: character 4).

Forefin:

23. Humerus distal and proximal ends in dorsal view: (0) distal end wider than proximal end; (1) nearly equal or proximal end slightly wider than distal end (modified from Fischer *et al.* 2011: character 32).

24. Deltopectoral crest of humerus: (0) present and large; (1) reduced, present and small (modified from Maxwell 2010: character 20).

25. Humerus in dorsal view: (0) relatively short, almost as distally wide as it is long; (1) long relative to width (modified from Massare and Lomax 2016: character 24).
26. Humerus, depression on articular surface, anterior to dorsal process: (0) absent; (1) irregular depression; (2) oval depression on smooth bone surface (modified from Massare and Lomax, 2016: character 26).
27. Humerus dorsal process: (0) small; (1) prominent (modified from Massare and Lomax, 2016: character 27).
28. Humerus dorsal process position: (0) centrally located; (1) offset anteriorly.
29. Primary digits in forefin: (0) three; (1) four; (2) five or more (Massare and Lomax, 2016: character 28). Note that the fin must be complete to at least p4 row to be certain that the count is correct.
30. Intermedium: (0) distal edge flattened, contacting digit III; (1) distal edge angular, contacting digits III and IV (modified from Druckenmiller and Maxwell 2010: character 40).
31. Anterior digital bifurcation: (0) absent; (1) present (modified from Massare and Lomax 2016: character 34). Note that fin must be complete to at least p4 row to verify absence.
32. Anterior edge of radius notched: (0) absent; (1) present (modified from Maxwell *et al.* 2012: character 38, coding reversed).
33. Preaxial accessory digit on forefin: (0) absent (1) present (Maisch and Matzke 2000: character 91; modified Massare and Lomax 2016: character 36).
34. Postaxial accessory digit on forefin: (0) absent; (1) present (Maisch and Matzke 2000: character 89; modified Massare and Lomax 2016: character 37).

35. Humerus/femur ratio (humerus length divided by femur length): (0) humerus \leq 1.4 times femur, (1) humerus > 1.4 but < 1.7 times as large as femur; (2) humerus > 1.7 times as large as femur (Massare and Lomax 2016: character 38).

36. Prominence of digit V: (0) smaller than digit IV; (1) as large or larger than digit IV.

Hindfin:

37. Femur distal and proximal ends, in dorsal view: (0) distal end wider than proximal end; (1) nearly equal or proximal end slightly wider than distal end (modified from Massare and Lomax 2016: character 39).

38. Primary digits in hindfin: (0) three; (1) four; (2) five or more. Note that the fin must be complete to at least p3 row to ascertain that the digit count is correct (Massare and Lomax 2016: character 41).

39. Tibia, fibula relative size: (0) approximately equal; (1) fibula anteroposteriorly and proximodistally larger than tibia; (2) fibula proximodistally larger than tibia but anteroposteriorly approximately equal, (Maxwell *et al.* 2012: character 56; modified Massare and Lomax 2016: character 42).

40. Number of digits with a broad contact with the astragalus: (0) one; (1) two (Massare and Lomax 2016: character 43).

41. Number of elements in third row of hindfin: (0) three; (1) four.

42. Anterior digital bifurcation: (0) absent; (1) present (modified from Massare and Lomax 2016: character 44).

43. Preaxial accessory digit on hindfin: (0) absent (1) present (Massare and Lomax 2016: character 45).

44. Postaxial accessory digit on hindfin: (0) absent; (1) present (Fischer *et al.* 2011: character 50; modified Massare and Lomax 2016: character 46).

45. Anterior edge of tibia notched: (0) absent; (1) present (modified from Maxwell *et al.* 2012: character 58, coding reversed).

Pectoral girdle:

46. Scapula: (0) with prominent acromion process; (1) large acromion process absent but anterior expansion of proximal scapula present; (2) proximal expansion absent, scapula strap-shaped (Maxwell *et al.* 2012: character 31).

47. Coracoid symmetry: (0) anterior and posterior medial expansions approximately equal; (1) anterior expansion much narrower than posterior expansion.

48. Relative size of coracoid facets: (0) glenoid facet at least twice as large as scapula facet; (1) glenoid facet larger than scapular facet but not twice as large (2) approximately equal.

49. Coracoid with well-developed anterior notch: (0) absent; (1) present (modified from Maxwell *et al.* 2012: character 33).

50. Coracoid with well-developed posterior notch: (0) absent; (1) present (modified from Maxwell *et al.* 2012: character 34).

Pelvic girdle:

51. Ilium shape: (0) narrow with expanded proximal region; (1) narrow proximally and distally, rib-like; (2) fairly wide relative to its length, oblong and curved, rather than rib-like (Maxwell *et al.* 2012: character 47; modified Massare and Lomax 2016: character 55).

52. Pubis shape: (0) long and rod-like, not expanded distally; (1) long shaft with moderate expansion distally, 'spatulate' shape; (2) long shaft with wide expansion distally, 'fan' shape, can be asymmetric (Massare and Lomax 2016: character 56).

53. Ischium shape: (0) much longer than wide, can appear oblong or slender depending on orientation; (1) relatively short compared to width, robust and

rectangular (Motani 1999b: character 87; modified Massare and Lomax 2016: character 57).

54. Pubis, ischium relative length: (0) nearly equal; (1) pubis longer than ischium (modified from Motani 1999b: character 86).

55. Ischium, femur relative length: (0) nearly equal; (1) ischium longer than femur; (2) femur longer than ischium (Massare and Lomax 2016: character 63).

Vertebral column:

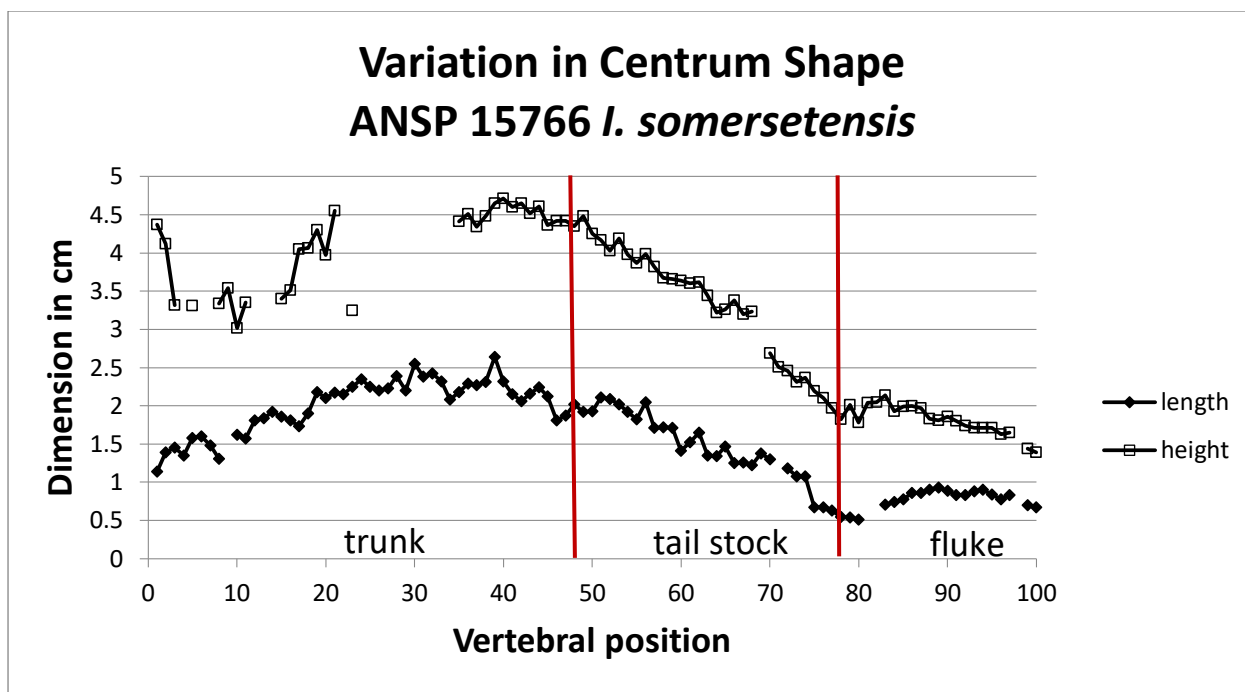
56. Preflexural vertebral count: (0) less than 80; (1) 80 or more (Massare and Lomax 2016: character 65).

57. Precaudal vertebral count: (0) < 40; (1) 40-46; (2) > 46 (Massare and Lomax 2016: character 66).

Supplementary Information

Two new species of *Ichthyosaurus* from the lowermost Jurassic (Hettangian) of Somerset, England

Fig. S1: Change in centrum dimensions along the vertebral column in ANSP 15766, *Ichthyosaurus somersetensis* sp. nov. Data are from Table S1. Vertical lines denote the approximate positions of the transition from dorsal to caudal centra and from caudal to fluke centra.



Note that centrum height and length decrease from about centrum no. 40 to the tail fluke.

Table S1: Centrum dimensions for ANSP 15766, *Ichthyosaurus somersetensis* sp. nov.

Centrum length (LEN), centrum height (HT), and the HT/LEN ratio are given in the table below. The last double-headed rib is on centrum no. 47, which marks the last dorsal centrum, making centrum no. 48 the first caudal centrum. The apical centra begin with centrum no. 75 and continue to no. 83 or 84.

Asterisk denotes a measurement that is estimated because the centrum was rotated, damaged, or partially buried.

CENTRUM NUMBER	CENTRUM LEN (CM)	CENTRUM HT (CM)	HT/LEN RATIO
1	1.14	4.37*	3.83
2	1.39	4.12	2.96
3	1.45	3.32	2.29
4	1.35		
5	1.58*	3.31	2.09

6	1.60		
7	1.48		
8	1.31	3.34	2.55
9		3.54	
10	1.62	3.02	1.86
11	1.57	3.35	2.13
12	1.81		
13	1.84		
14	1.92		
15	1.86	3.40	1.83
16	1.81	3.51	1.94
17	1.73	4.05	2.34
18	1.90	4.06	2.14
19	2.18	4.30	1.97
20	2.10	3.97	1.89
21	2.17	4.55	2.10
22	2.15		
23	2.25	3.25	1.44
24	2.35		
25	2.25		
26	2.20		
27	2.23		
28	2.39		
29	2.20		
CENTRUM NUMBER	CENTRUM LEN (CM)	CENTRUM HT (CM)	HT/LEN RATIO
30	2.55		
31	2.38		
32	2.42		
33	2.32		
34	2.08		
35	2.18	4.41	2.02
36	2.29	4.51	1.97

37	2.27	4.34	1.91
38	2.31	4.48	1.94
39	2.64	4.65	1.76
40	2.32*	4.71	2.03
41	2.15*	4.60	2.14
42	2.06	4.65	2.26
43	2.16	4.52	2.09
44	2.24*	4.61	2.06
45	2.12*	4.36	2.06
46	1.81*	4.42	2.44
47	1.87	4.42	2.36
48	2.02	4.35	2.15
49	1.92	4.48	2.33
50	1.93	4.25	2.20
51	2.11	4.17	1.98
52	2.09	4.03	1.93
53	2.02	4.19	2.07
54	1.92	3.98	2.07
55	1.82	3.87	2.13
56	2.05	3.99*	1.95
57	1.71	3.82	2.23
58	1.72	3.67	2.13
59	1.71	3.66	2.14
60	1.41*	3.64	2.58
61	1.52*	3.60	2.37
62	1.65	3.62	2.19
63	1.35	3.44	2.55
64	1.34	3.22	2.40
65	1.47	3.26	2.22
66	1.25	3.38	2.70
67	1.26*	3.20	2.54
CENTRUM NUMBER	CENTRUM LEN (CM)	CENTRUM HT (CM)	HT/LEN RATIO

68	1.22*	3.23	2.65
69	1.38*		
70	1.30	2.69	2.07
71		2.51*	
72	1.18	2.46	2.08
73	1.08	2.31	2.14
74	1.08	2.37	2.19
75	0.67*	2.19	3.27
76	0.67*	2.10	3.13
77	0.63*	1.97	3.13
78	0.55*	1.82	3.34
79	0.54	2.01	3.72
80	0.51	1.78	3.49
81		2.04	
82		2.05	
83	0.71	2.14	3.01
84	0.74	1.93	2.61
85	0.78	1.99	2.55
86	0.86	2.00	2.33
87	0.86	1.97	2.29
88	0.90	1.83	2.03
89	0.93	1.81	1.95
90	0.89	1.86	2.09
91	0.83	1.80	2.17
92	0.83	1.74	2.10
93	0.88	1.71	1.94
94	0.90	1.71	1.90
95	0.84	1.71	2.04
96	0.78	1.63	2.09
97	0.83	1.65	1.99
98			
99	0.70	1.44	2.06
100	0.67	1.39	2.07

Supplementary Material 2

#NEXUS

Temnodontosaurus

0102{01}0221{01}1{01}0{01}1{01}10111000?000000010{01}0?000000011?1110{01}
200211

Suevoleviathan

0{01}0{02}0{01}2{12}{01}011{01}11201111000?1???0000010?00?00001121?10021
0211

I_communis_neotype

0100121100010100111?1011?111021100101022111??01????1100101

I_breviceps_holotype

1110120000011100111?0000?1000211011110120011?01?????????01

breviceps_CAMSMX_50187

???2?????????????1?1?0000?101021101?110100111101???1?11011?1

I_anningae_holotype

?1010?021001?0101?1?101100211??????2?1?????????100111??????

anningae_NHMUK_120

?10???20?00?1???011???1011?0000211001211???11???0?0111?????01

I_conybeari_NMW_93_5G_2

11021???2000100100101?000?000121100101021???1???11?????1?1?201

I_conybeari_BGS_956

?1001222000100100?0?1000?0001211001010210010111?????1?????01

I_conybeari_holotype

????????????????????????010001211001?1??????????1???1??????????

I_larkini_holotype

0102?11111000?110011101?0?????211?????10?001???0111111200102

I_larkini_CAM_J59575

?????????11??????0???101?0?????211001?1??????????11111????????

I_larkini_AGC_11

0102?????????00??10?1?1011011102110???110?201???011111??????02

I_somersetensis_holotype

010002111010001111110011?110021100111010001000??????2?????02

I_somersetensis_NHM_2013

010202111010001111110001?1??0211001110110010101??1?2????12

;

end;

Supplementary Material 3

A second phylogenetic analysis was performed, with *Macgowania* and *Malawania* included in place of *Temnodontosaurus* and *Suevoleviathan*. The coding for the two genera is shown below. The taxa are substantially incomplete, especially when compared with *Temnodontosaurus* and *Suevoleviathan*.

Macgowania

?1?????0??11?010??11?00???????110101?0?????????1?????????????

Malawania

????????????????????????101???110000?0?????????1?????????????

The analysis was run using implicit enumeration. It recovered fourteen most parsimonious trees of 84 steps, with CI = 0.691 and RI = 0.688. The strict consensus tree is shown below (Fig. SA). Note that it shows similar groupings of specimens into species as the analysis with *Temnodontosaurus* and *Suevoleviathan* as outgroups, although the relationships among species are different. Bootstrapping the matrix with 1000 replicates again found similar results to the bootstrap tree presented in the paper (Fig. SB).

Fig. SA. Strict consensus of 14 trees.

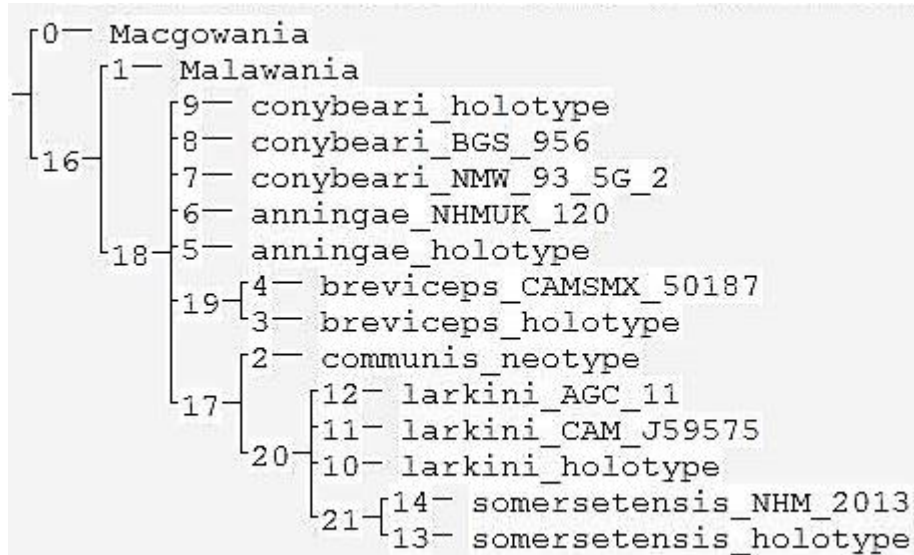
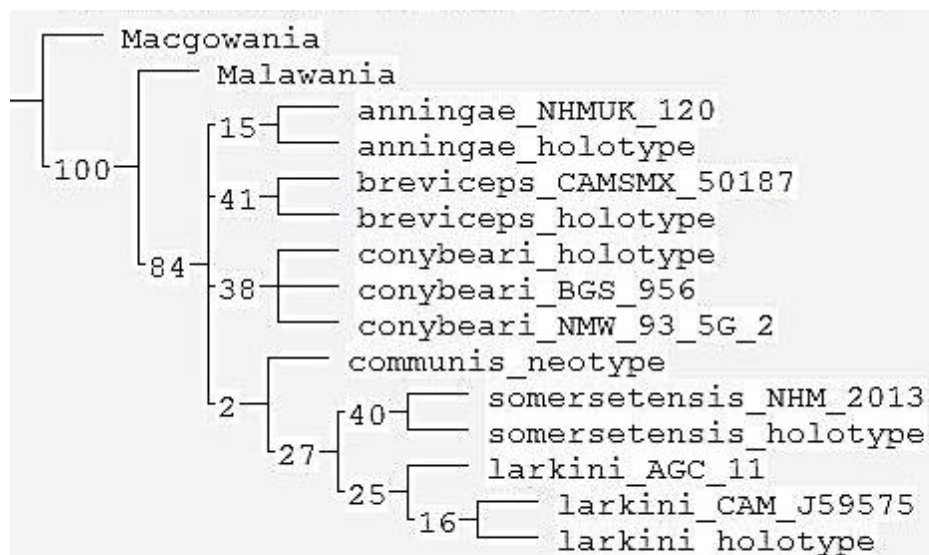


Fig. SB. Standard bootstrap tree, 1000 replicates.



Chapter 4: A taxonomic reassessment of *Ichthyosaurus communis* and *I. intermedius* and a revised diagnosis for the genus

The paper is presented in its final accepted form, prior to format by the journal. It was published in the peer reviewed journal: *Journal of Systematic Palaeontology*.

Reference:

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A taxonomic reassessment of *Ichthyosaurus communis* and *I. intermedius* and a revised diagnosis for the genus

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Abstract

Ichthyosaurus communis De la Beche and Conybeare, 1821 and *I. intermedius* Conybeare, 1822 have been considered synonymous by some researchers, but distinct species by others. The distinction between the two species was originally based on tooth morphology, which has been shown to vary ontogenetically as well as within an individual. Subsequent literature of the 19th century did not propose adequate diagnostic features to distinguish the two species. In addition, illustrations suggest that both species were confused with *I. breviceps*, which was defined over 50 years later. The type specimens of both species are missing, making the problem unresolvable. However, a neotype was previously designated for *I. communis* to retain the widely used species name and to stabilize the taxonomy. The species can be recognised by a symmetric, triangular maxilla with long processes and a large, broad, triradiate lacrimal, as well as a unique combination of other characters. The neotype shares numerous features with the *I. intermedius* 'type figure' including the morphologies of the maxilla, prefrontal, lacrimal, jugal and postorbital, such that the two are nearly indistinguishable. Thus *I. intermedius* must be considered a synonym of *I. communis*. *I. communis* can be identified from the Lyme Regis-Charmouth coast, west Dorset; the ?Whitby coast of Yorkshire; and from Street, Somerset. The stratigraphic range of *I. communis* is at least lower Hettangian to lower Sinemurian.

Key words: *Ichthyosaurus communis*, *Ichthyosaurus intermedius*, Lower Jurassic, Dorset, Somerset

Introduction

Arguably, the first modern, scientific palaeontological study of an extinct marine reptile was of a large ichthyosaur (NHMUK PV R 1158) collected by Mary and Joseph Anning from Lyme Regis, Dorset (Home 1814; Torrens 1995), although no name was proposed for it. A few years later, Home (1819a) proposed the name *Proteosaurus* to encompass all ichthyosaurs known at that time, however König (1818) had previously mentioned the name *Ichthyosaurus*, and that was the genus name accepted by subsequent workers. Home's (1814, 1819a, b) work and the new fossils coming from the Dorset and Yorkshire coasts, the limestone quarries of Somerset, and elsewhere paved the way for the identification and scientific study of ichthyosaurs and plesiosaurs. De la Beche and Conybeare (1821) provided the first detailed account of *Ichthyosaurus*, based on several specimens. However, the skull illustrations (De la Beche and Conybeare 1821, figs. 9-12) were composite sketches of several specimens (Conybeare 1822, p. 105). The type species for the genus, *I. communis*, was introduced by De la Beche and Conybeare (1821, p. 594). A year later, Conybeare (1822) further described the genus *Ichthyosaurus* and recognised four species from the UK: *I. communis*, *I. platyodon* (now *Temnodontosaurus*), *I. tenuirostris* (now *Leptonectes*) and *I. intermedius*. Subsequently, most new species of ichthyosaur from the Lower Jurassic were assigned to the genus *Ichthyosaurus*. Almost two decades later, Owen (1840) recognised ten species of the genus, and later included an additional two (Owen 1881).

By 1900, over 50 species of *Ichthyosaurus* had been described (McGowan and Motani 2003), although subsequent studies synonymised some and assigned other species to new genera, e.g., *Leptonectes* and *Temnodontosaurus*. McGowan and Motani (2003) recognised three valid species: *I. communis*, *I. breviceps*, and *I. conybearei* (McGowan and Motani 2003). *I. communis* is by far the most common species of the three, and it is extremely variable (McGowan 1974; McGowan and Motani 2003). However, recent work (Lomax and Massare 2015, 2016) has recognised three new species, *I. anningae*, *I. larkini* and *I. somersetensis*, based on specimens that were previously considered within the range of variation of *I. communis*.

Ichthyosaurus intermedius was described shortly after *I. communis* (Conybeare 1822), based largely on tooth morphology. Neither species was

sufficiently described when the names were proposed, and the locations of what would have been the type specimens are unknown. However, some teeth assigned to *I. communis* by Conybeare (1822, pl. XV, fig. 4, 8) may be those held at BGS (Geol. Soc. Coll. 4476, Geol. Soc. Coll. 4477). Many, if not most, of the fairly complete skeletons in museum collections were originally identified as *I. intermedius*. The species was recognised at more localities than *I. communis* (Owen 1840, p. 112), and was more common than *I. communis* at Somerset locations, whereas the reverse occurred at Dorset locations (Owen 1840; Lydekker 1889). McGowan (1974) synonymised *I. intermedius* with *I. communis*, although Appleby (1979), Maisch (1997) and Maisch and Matzke (2000a) disagreed. McGowan and Motani (2003) argued that the characters proposed to distinguish the species were too variable to be useful. The research presented here examines the original, 19th century diagnoses of the two species in more detail than previously published. It supports the synonymy of McGowan (1974).

Institutional abbreviations. AGC, Alfred Gillett Collection, cared for by the Alfred Gillett Trust (C & J Clark Ltd), Street, U.K.; ANSP, Academy of Natural Science of Drexel University, Philadelphia, PA, USA; BELUM, National Museums Northern Ireland (Ulster Museum), Cultra, Northern Ireland; BGS, British Geological Survey, Keyworth, Nottingham, UK; BU (BIRUG), Lapworth Museum of Geology, University of Birmingham, Birmingham, UK; CAMSM, Sedgwick Museum, Cambridge University, Cambridge, UK; CHMUS, Charterhouse School Museum, Surrey, UK; FMNH, Field Museum, Chicago, USA; GSL, Geological Society of London, UK; MANCH, Manchester Museum, University of Manchester, Manchester UK; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; NHMUK, formerly BMNH, The Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; PETMG, Peterborough Museum and Art Gallery, Peterborough, UK; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; WOSMG, Worcester City Art Gallery and Museum, Worcester, UK; YORYM, Yorkshire Museum, York, UK.

Original diagnoses

The name *I. communis* first appeared in the literature as a note at the end of De la Beche and Conybeare (1821) that briefly described a fairly complete specimen from Lyme Regis. Aside from providing measurements of certain features of the skeleton, the account did not specify any diagnostic characters. The specimen has been regarded as the holotype of *I. communis*, but it was reported lost by McGowan (1974), and we have not located it. The following year, Conybeare (1822) provided descriptions of *I. communis* and *I. intermedius*, and distinguished four species on the basis of tooth morphology, although he might not have intended that to be the sole criterion:

“Mr. De la Beche, however, long since believed himself able, from the examination of the teeth, combined with some other characters, to establish three species, to which he has applied the names *communis*, *platyodon*, and *tenuirostris*: and to these our joint observations have recently added a fourth, *Ichthyosaurus intermedius*.” (Conybeare 1822, p. 108).

I. intermedius has “more acutely conical” teeth (presumably meaning that the tooth crowns were more slender) with less prominent longitudinal striations than *I. communis* (Conybeare 1822, p. 108). Teeth representing these species were illustrated, although, as was common at the time, neither the tooth of *I. intermedius* nor any other material was formally designated a type specimen (Conybeare 1822, pl. XV, figs 8, 9; Figure. 4.1). The figures also suggest that the longitudinal striations of the root were more prominent in *I. communis* than in *I. intermedius*, although this was not mentioned in the text. The figure of the tooth of *I. intermedius* (Figure. 4.1B) shows a slender crown, with a base that is much narrower than the root, a form which Maisch (1997) called ‘waisted’; but again, the original diagnosis did not mention such a difference. Maxillary teeth often have crowns that are narrower than the root. Instead, we would argue that Conybeare (1822) was distinguishing between wider conical teeth with strong longitudinal striations (Smash guild of Massare 1987), and slender, more acute conical teeth with finer striations (Pierce I guild of Massare 1987). The former would include the teeth figured for *I. communis*, whereas the latter would include the teeth figured for *I. intermedius*.

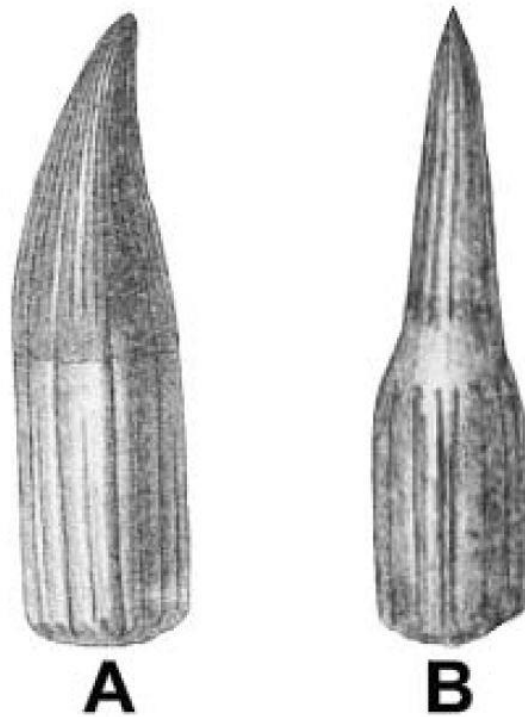


Figure. 4.1. Original figures of teeth of A: *Ichthyosaurus communis* (Conybeare, 1822, Pl. XV. fig. 8); and B: *I. intermedius* (Conybeare, 1822, Pl. XV. fig. 9). No size information given in the original publication, so a scale bar cannot be provided.

Conybeare (1822, p.112) also noted that *Ichthyosaurus intermedius* was distinguished from other species by differences in the lateral exposure of the angular and ‘coronoid’ (surangular) bones of the lower jaw. He contended that in *I. communis*, the surangular is partially-hidden by the dentary such that the angular is visible further anteriorly than the surangular; whereas in *I. intermedius*, the surangular extends further anteriorly than the angular. However, the figured morphology of a skull of *I. intermedius* contradicts the description in the text (Conybeare 1822, pl. XVII). Specifically, the angular extends slightly more anteriorly than the surangular (Figure. 4.2A).

Conybeare (1822, pl. XVI, fig. 8) also included a drawing of a partial skull identified as *I. communis* (Figure. 4.3A), which belonged to the Oxford Museum according to the caption, but we could not locate it at OUMNH. Thus Conybeare provided the first illustrations of specimens assigned to *I. communis* and *I. intermedius*, in the form of drawings of skulls showing the details of sutures, mainly in the post-narial portion of the skull. The *I. communis* figure, however, is problematic. The large maxillary teeth with prominent grooves in the roots, the lack

of an anterior process of the lacrimal, and especially the long subnarial process that makes up almost all of the ventral margin of the external naris, all suggest that this is a sketch of *I. breviceps* (Figure. 4.3) recognised as a distinct species more than 50 years later by Owen (1881). Given the emphasis on tooth morphology at the time, it is not surprising that an *I. breviceps* specimen would have initially been assigned to *I. communis*, especially if the entire rostrum was not preserved. Furthermore, both *I. communis* and *I. breviceps* have broad forefins with numerous phalanges. Adding to the uncertainty, the skull diagrams are interpretations. Without the actual specimens, it is impossible to determine their accuracy. But it appears that, apart from the probable *I. breviceps* skull, *I. communis* was not actually illustrated except for some teeth that might or might not be the same as those of the holotype. Thus, *I. intermedius* was initially better defined, or at least better illustrated, than *I. communis*.

Another figure, of a fairly complete forefin, was identified only as *Ichthyosaurus* (Conybeare 1822, pl. XX, fig. 1). It shows a bifurcation of digit II in the metacarpal row, and a second bifurcation between the p3 and p4 rows, for a total of six primary digits. Two posterior accessory digits are also present. It is certainly a specimen of what is presently considered *Ichthyosaurus* (Motani 1999; McGowan and Motani 2003), and it might be an *I. communis*. We could not locate this forefin.

What is *Ichthyosaurus communis*?

The first published figure of a practically complete specimen identified as *I. communis* was the skeleton of a small specimen (jaw length ~25 cm) in Buckland (1836, vol.2, pl.8, fig. 1). This could not have been the type specimen, because it is much smaller than the specimen mentioned in De la Beche and Conybeare (1821; jaw length ~47 cm). The figured specimen was described as the “Skeleton of a young *Ichthyosaurus communis*, in the collection of the Geological Society of London, found in the Lias at Lyme Regis” (Buckland 1836, p. 21). Most of the GSL collection was transferred to BGS (Taylor and Clark in press), but we could not locate the specimen. However, OUMNH J.10341 and CAMSM X.50259 are plaster casts of the figured skeleton, which must have been considered an important specimen at the time. Interestingly, on the same plate, Buckland (1836, pl. 8, fig. 2) identifies a specimen of *I. breviceps* (NHMUK PV R8437; McGowan 1974; Taylor

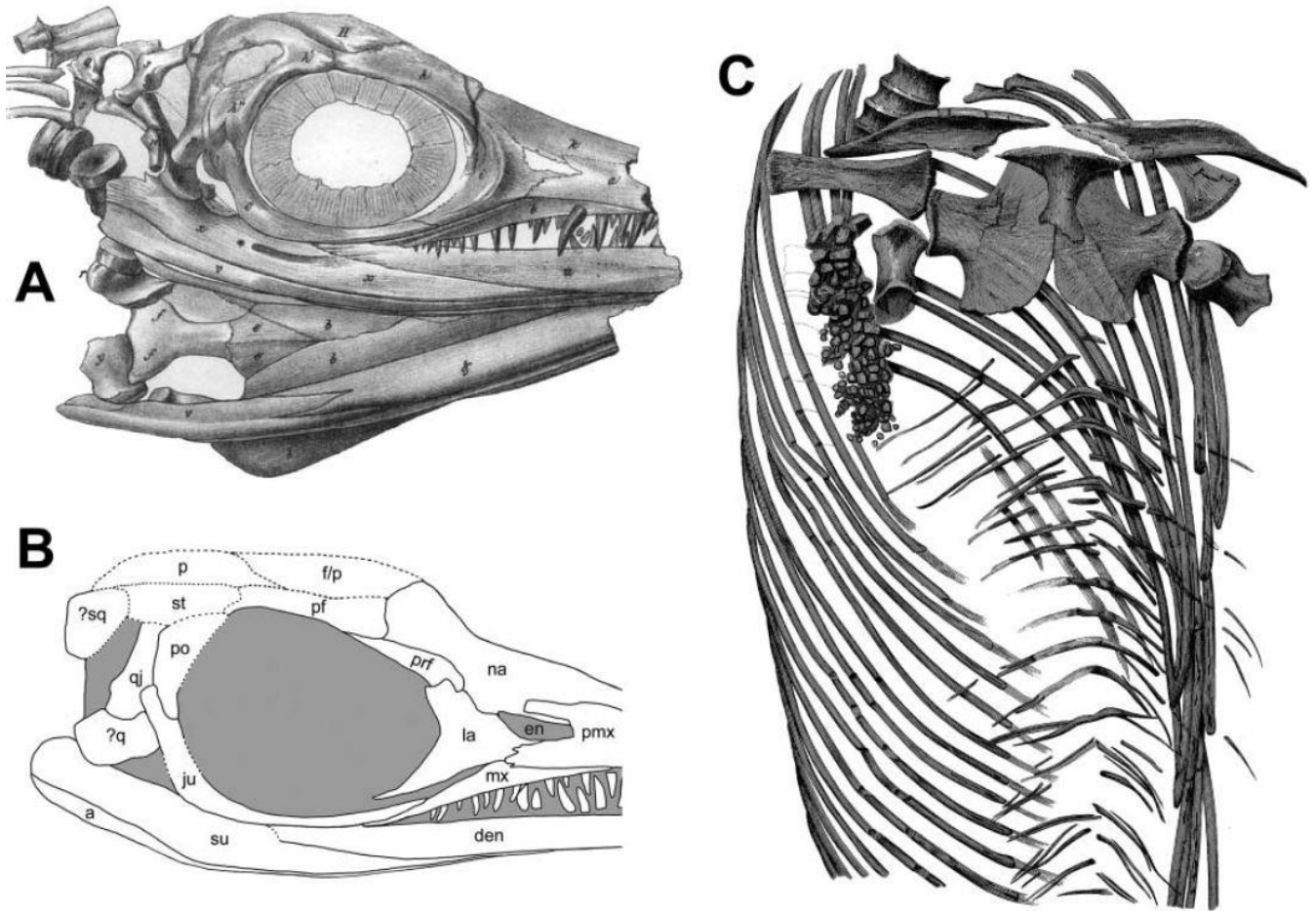


Figure. 4.2. A. The type skull of *Ichthyosaurus intermedius* as figured by Conybeare (1822, Pl. XVII). No size information given in the original publication, so a scale bar cannot be provided; B. Interpretive skull illustration of the neotype of *I. communis* (NHMUK PV R1162), reversed to show the same orientation. The dorsal skull roof of the neotype is poorly preserved due to crushing, so sutures and openings in the skull could not be determined with certainty; C. Postcranial skeleton of the type specimen (A) of *I. intermedius* as figured by Home (1819b). No size information in the original publication, so a scale bar cannot be provided. *Abbreviations:* a, angular; den, dentary; en, external naris; f, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; p, parietal; po, postorbital; pmx, premaxilla; pf, postfrontal; prf, prefrontal; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal; su, surangular. Light grey denotes matrix or openings in skull. Dashed lines indicate broken edge and possible sutures.

2014) as *I. intermedius*, again showing inconsistency or confusion in the early literature.

Owen (1840) expanded the diagnosis of *Ichthyosaurus communis*, but again emphasized tooth form. He described the conical, slightly curved crown “with longitudinal furrows” and noted the expanded roots with coarse, deep grooves that Conybeare (1822) figured but did not describe. Owen noted features of *I. communis* that are also characteristic of other parvipelvian ichthyosaurs (jugal forms entire ventral margin of the orbit; prefrontal and postfrontal only forming the dorsal margin of the orbit); features that eventually became characters of the genus (small frontals enclosing the pineal foramen; short, stout humerus relative to its length; broader forefins than are found in any of the other ‘species’, here encompassing all of the Lower Jurassic genera; phalanges “transversely oblong”, i.e. rectangular), and features of uncertain taxonomic utility (shallow depression on ventral basioccipital; basioccipital longer than wide; tooth count; number of sclerotic plates; mandibular symphysis about ¼ of the length of the mandible). Characters that might be interpreted as diagnostic for the species itself include: (1) 18 maxillary teeth, (2) external naris straight dorsally and curved ventrally; and (3) about 40 presacral centra, based on the position of the ilium. Thus even this emended diagnosis did not provide many characteristics that are not also characteristics of the genus, perhaps not surprising considering that *I. communis* is the type species for the genus.

Owen (1881) reviewed the species of *Ichthyosaurus* from the ‘Liassic Formations’, and-again noted that the main distinguishing features of *I. communis* were the morphologies of the teeth and forefin. His description of tooth morphology was essentially the same as Owen (1840), except that he pointed out that the teeth were proportionally larger than in most species. He also pointed out that the forefin has five primary digits and both an anterior and posterior accessory digit, for a total of seven (Owen 1881, p.105). We have found that an anterior accessory digit occur frequently on specimens of *I. breviceps*, but very rarely on other *Ichthyosaurus* species.

The early literature, however, sometimes confused a second digital bifurcation with an anterior accessory digit.

Owen (1881) also provided new information on other aspects of the morphology of *I. communis*. An important observation was that the external naris is bordered by the nasal dorsally, and by the lacrimal and premaxilla ventrally,

excluding the maxilla from contact with the external naris. We take this to mean that the supranarial process of the premaxilla is short, if present at all. Of all of the species of *Ichthyosaurus*, only *I. breviceps* has a reduced supranarial process such that the nasal makes up practically the entire dorsal margin of the external naris (Figure. 4.3B). This again suggests confusion between *I. communis* and *I. breviceps* in the early literature. On all other species of *Ichthyosaurus*, the supranarial process extends 1/3 to 1/2 of the length of the external naris (Lomax and Massare 2016). Owen (1881) also indicated that the mandibular symphysis was composed mainly of the dentaries, with only a small contribution from the splenials. He also provided the first description of a tripartite pelvis in *I. communis*, noting that the ischium and pubis were about the same length (~7.0 cm), and slightly longer than the moderately curved ilium (~6.4 cm). Finally, he described the hindfin as having five primary digits, owing to a bifurcation of the anterior digit in the “fifth bone from the femur” (Owen 1881, p. 112; presumably the first phalangeal row) and a posterior accessory digit (Owen 1881, p. 105, pl. XXVIII, fig. 5), although in the figure, the latter is represented by only a single element. He further noted that four elements were in the third (distal tarsal) row of the hindfin.

Lydekker (1889) relied heavily on tooth form and forefin width to assign specimens at NHMUK to *I. communis*. He introduced four new characters for the species (1) the rostrum length equal to or slightly less than three times the maximum orbit dimension; (2) cervical and dorsal centra with neural spines more than twice the centrum height; (3) small, indistinct vascular foramina on fin elements; and (4) lack of notching on the anterior digit of the fins. Fin notching, however, has only limited taxonomic utility (Maxwell *et al.* 2014; Massare and Lomax 2016a).

McGowan (1974) argued that the descriptions of *I. communis* in De la Beche and Conybeare (1821) and Conybeare (1822) were inadequate to erect a species. He synonymised *I. intermedius* and *I. latimanus* with *I. communis* because those species were also based on unreliable characters, although McGowan also considered *I. communis* to be a *nomen dubium*. However, because the name had been in use for so long, and had priority, McGowan (1974) retained the name *I. communis* by selecting a neotype (NHMUK PV R1162) that was consistent with the original definition and subsequent definitions in the early literature (Owen 1840, 1881). He emended the diagnosis of *I. communis* to include a presacral vertebral count of 41-47 (but usually <46), preflexural vertebral count of 75-79, several ratios

of skull elements, four or more primary digits with 17 or more elements in the longest digit, and up to 18 maxillary teeth. Interestingly, the latter two are somewhat similar to what Owen (1840) proposed.

McGowan (1974) also noted ‘two populations’ of *I. communis*, one from Lyme Regis, Dorset and the other from Street, Somerset, that vary in forefin structure. The Somerset ‘population’ often has only five primary digits, has notching in one or two elements of the anterior digit, and has less than 20 elements in the longest digit; whereas the Dorset ‘population’ usually has six or seven primary digits, lacks notching of the anterior digit, and has more than 20 elements in the longest digit. McGowan (1974) further pointed out that forefin morphology is quite variable, and these differences could be within the normal range of variation within a species. He also noted that the Somerset ‘population’ has a larger maxilla, smaller orbit, and relatively smaller skull, but the differences are not statistically significant. McGowan (1974) concluded that these differences are too small to warrant a taxonomic distinction. Appleby (1979), however, disagreed, and argued that the high variation in relative skull size and the differences in the forefins were too great to be considered a single species. Recent work (Lomax and Massare 2016) has demonstrated that many of the Somerset specimens are a new species, *I. somersetensis*.

What is *Ichthyosaurus intermedius*?

Owen (1840) agreed with the assessment of *I. intermedius* as a distinct species (Conybeare 1822). He pointed out that the surangular is exposed further forwards than the angular in *I. intermedius*, but not as far forward as in *I. communis*, correcting the description of Conybeare (1822). He further stated that the fore and hind fins are not very broad in proportion to their length in *I. intermedius*.

Owen (1881) gave a more detailed account by expanding on previous characters of the species, stating that the teeth of *I. intermedius* are more numerous and relatively smaller and longer, which we interpret to mean narrower and longer. Specifically, the finely striated crown is acutely conical with a narrow base, and the root has longitudinal grooves that are not prominent (Owen 1881, p. 113). He also recognised differences in the pectoral girdle: the clavicles of *I. intermedius* are “long, and less strong than in *I. communis*”, and the humero-scapular articulation of the coracoid “is of less relative extent than in *I. communis*” (Owen 1881, p. 114); but

pectoral girdle morphology can vary within a species (Johnson 1979; Maxwell and Druckenmiller 2011). Owen (1881) again indicated that *I. intermedius* has a narrower forefin with fewer phalanges than *I. communis*, but that both species have five primary digits. He also noted notching on three anterior elements of the hindfin. Although providing the location of discovery and repository for other reptiles illustrated in his monograph, Owen (1881) did not specify which specimens his ichthyosaur descriptions were based upon, although he illustrated one skeleton that he identified as *I. intermedius* (Owen 1881, plate XXX, fig. 1), which is definitely NHMUK PV OR2013*. Although by the time of Owen's publication, many specimens had been identified in museum and private collections, this was only the second illustration of *I. intermedius* in the literature since Conybeare (1822) defined the species. However, this specimen differs from the illustrated 'type' of *I. intermedius* (Conybeare 1822, pl. XVII) in several significant features including: the height and asymmetry of the maxilla; the size and anterior extent of the prefrontal; the shape and dorsal extent of the lacrimal; the anterior extent of the jugal; the shape and position of the postfrontal; the relative height of the posterior portion of the angular and surangular; and the prominent grooves in the tooth root (Lomax and Massare 2016). This specimen has recently been referred to a new species, *I. somersetensis* (Lomax and Massare 2016). The aforementioned Buckland (1836, pl. 8, fig. 2) illustration of '*I. intermedius*', the first illustration in the literature after Conybeare (1822), was also incorrectly attributed to the species. This inconsistency in identifying specimens arguably occurred because the initial diagnoses were inadequate.

A brief but notable account of the species was provided by Lydekker (1889). He mentioned various features that had previously been considered distinct for the species, including the morphology of the paddles and clavicles, but did not discuss the tooth morphology. He proposed additional features of the species including a somewhat lower neural spine height on the cervical and dorsal vertebrae and the presence of notching on the anterior digit in the hindfin and sometimes the forefin. His emphasis on notching, especially in assigning specimens to the species, provided no clarification because nearly all specimens of *Ichthyosaurus* from Somerset have notched hindfins, and many have notched forefins as well (Massare and Lomax 2016a).

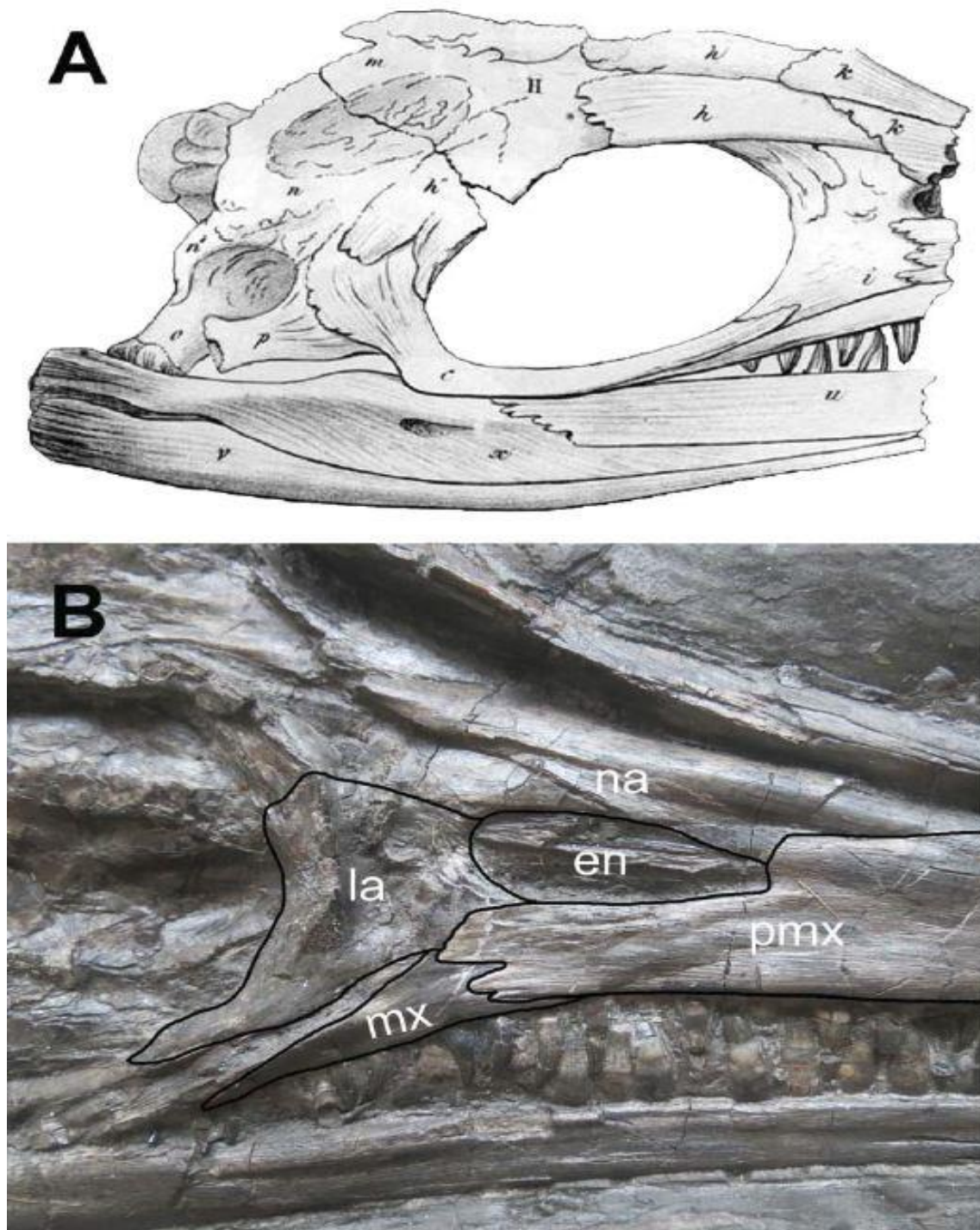


Figure. 4.3. A. Original figure by Conybeare (1822, Pl. XVI, fig. 8) of a specimen referred to as *Ichthyosaurus communis*. No size information in the original publication, so a scale bar cannot be provided. B. Holotype specimen of *I. breviceps* (NHMUK PV OR43006) with lines indicating key sutures of the skull. The skull has been reversed to show the same orientation. Note the similar extent of the subnarial process of the premaxilla and the reduced anterior process of the lacrimal. The medial portion of the lacrimal is damaged, and the dorsal extent is estimated. *Abbreviations:* en, external naris; la, lacrimal; mx, maxilla; na, nasal; pmx, premaxilla.

The most recent account of *I. intermedius* was by Maisch (1997), who identified the type specimen as the skull illustrated by Conybeare (1822, pl. XVII; Figure. 4.2A) and the postcranial skeleton figured by Home (1819b, pl. XIV; Figure. 4.2C), which is the same specimen, as noted in the plate explanations in Conybeare (1822). The skull was reported as specimen R7615 in the collection of the Geological Society of London by Blake (1902, p.1), donated by de la Beche who originally owned it (Conybeare 1822, explanation of pl. XVII). Although most of the GSL collection was transferred to BGS, this specimen probably was not (Taylor and Clark in press). The specimen was listed in the register when the collection was transferred, but its destination was listed as “Staircase”, presumably in the GSL rooms (P. Shepherd, pers. comm). We have not located the specimen at BGS, NHMUK, or GSL.

Maisch (1997) provided an emended diagnosis of the species, based on SMNS 13111, a well-preserved, isolated skull, apparently from the Lower Jurassic of Yorkshire. The additional features in his diagnosis included: only rudimentary fossae on the premaxilla and dentary; a very short fossa surangularis; a relatively high maxilla with a slightly concave ventral border and a delicate posterior process that extends to below the middle of the orbit; more than 20 maxillary teeth (possibly more than 25) that extend well below the orbit; distinctly curved posterior maxillary teeth; a dorsoventrally compressed dorsal ramus of the jugal, with a lateral ridge; a dorsoventrally shortened quadratojugal with a “well-developed and characteristically shaped processus quadratus”; and a delicately built quadrate with a narrow lateral edge (Maisch 1997, p.4).

Comparison of *I. communis* and *I. intermedius*

Although the original diagnoses were inadequate, many characters were subsequently proposed to distinguish *I. intermedius* from *I. communis* (Table. 4.1). Researchers of the 19th century (Conybeare 1822; Owen 1840, 1881; Lydekker 1889) agreed that *Ichthyosaurus communis* was much larger than *I. intermedius*, the former being up to 3.8 m (15 ft) long whereas the latter was 1.8 m (7 ft) or less. Thus the supposed maximum size of *I. intermedius* is only slightly larger than *I. breviceps*, which is generally regarded as a small species (~ 1.6 m preflexural length, Massare and Lomax 2014). The specimen of *I. communis* first mentioned in De la Beche and

Conybeare (1821), and presumed to be the holotype specimen, had a jaw length of 47 cm (18.5 in), which corresponds to an individual only about 2.4 m (7.9 ft) long, a rough estimate that assumes the skull length was about 20% of the total preflexural length. If the size difference is correct, one could argue that the two species are ontogenetic stages of a single species. The issue is complicated, however, by inconsistencies in species assignments based on size. One of the largest skeletons of *Ichthyosaurus*, NHMUK PV OR2013* (~2.7 m total length), was figured by Owen (1881) as an example of *I. intermedius*, although it is clearly within the supposed size range of *I. communis*, not *I. intermedius*. The basis for Owen's attribution is puzzling because the specimen also has little in common with Conybeare's (1822) 'type' figure. Another issue is that the maximum length given for *I. communis* in the early literature is too large, at least for specimens from the UK. The largest specimen measured by McGowan (1974, fig. 1) had a jaw length of about 55 cm, which corresponds to an individual about 2.8 m long, again assuming that the skull is about 20% of the preflexural length. Massare *et al.* (2015) estimated the maximum preflexural length for the genus in the UK as just under 3 m. Even allowing for a tail fluke, these estimates are quite a bit shorter than the size suggested for *I. communis* in the early literature; possibly other taxa were mixed up with *I. communis*, e.g. *Temnodontosaurus*. European specimens of the genus, however, are much larger (Godefroit 1996; Maisch 1997), although whether they represent *I. communis* cannot be determined. In any case, a difference in size between the two species does not seem to be a useful distinction.

Tooth form has been a major criterion for distinguishing the two species. The 'waisted' tooth form of *I. intermedius* has been a key argument for the retention of the species (Maisch 1997), although that feature was not in the original diagnosis (Conybeare 1822). We have seen individual specimens that have waisted teeth as well as those with a more gradual increase in the diameter of the root, i.e., not waisted (e.g. AGC 11; NMW 93.5G.2; CAMSM J35183). However, Conybeare (1822), and later Owen (1840), provided many other supposedly diagnostic features of the teeth: larger teeth with expanded roots; coarser, more prominent grooves in the roots; less slender, less acute crown; and fewer teeth in *I. communis* compared to *I. intermedius*. These differences are recognizable, but seemingly intermediate morphologies also exist (pers. obs.). Furthermore, tooth morphology varies within a species (McGowan 1974, 1994; Dick *et al.* 2016; Lomax 2016). Recent work

demonstrated that tooth size and morphology varies ontogenetically as well (Dick and Maxwell 2015; Dick *et al.* 2016), and that is certainly complicating the problem of recognizing distinct morphologies for a species. However, Lydekker (1889) recognised difference in tooth form between specimens of the same size, although he also pointed out that juveniles of the two species are difficult to distinguish. McGowan and Motani (2003, p. 92) argued that tooth morphology is not useful taxonomically, yet some general forms are clearly distinguishable among taxa (Massare 1987; Lomax 2016). Preservation, orientation and preparation can also complicate the recognition of distinct morphologies. So, although we recognise that different morphologies exist, we agree with McGowan and Motani (2003) that tooth morphology is not a reliable taxonomic character to distinguish these two species, at least with our current knowledge.

Owen (1840, p. 110) indicated that *I. communis* and *I. intermedius* can best be distinguished by the “form and relative size of the head and teeth”, with a shorter rostrum in *I. intermedius*. Lydekker (1889) quantified this somewhat by stating that the rostrum of *I. communis* was greater than or equal to three times the length (‘the maximum diameter’) of the orbit whereas the rostrum length of *I. intermedius* was less than three times the length of the orbit. However, the ratio is affected by preservation, specifically by the skull orientation and how much the orbit is distorted by compaction or crushing. McGowan (1974) used a similar metric, the snout ratio, which is the preorbital length divided by the length of the mandible, to characterize the relative size of the rostrum. He did not find a separation into two distinct morphologies, so if both species are valid, then their respective ranges for snout ratio must overlap.

Table. 4.1. An assessment of previously proposed characters to distinguish *Ichthyosaurus intermedius* from *I. communis*. Addition details are in the text. Neotype refers to NHMUK PV R1162, the neotype of *I. communis*.

Character	Author	Assessment
Body length	Conybeare 1822; Owen 1840, 1881;	Inconsistent with historic identifications of specimens.

Length of rostrum	Owen 1840; Lydekker 1889	Influenced by orientation and flattening; range overlaps among species. Intermediate forms exist;
Tooth crown morphology	Conybeare 1822; Owen 1840, 1881	ontogenetic in part; influenced by orientation. No obvious difference from
Lack expanded tooth root; grooves not prominent	Owen 1840, 1881	neotype.
'Waisted' tooth form	Maisch 1997	Varies within an individual.
Tooth count	Owen 1840	Uncertain taxonomic utility; depends on preparation and completeness in part.
Number of maxillary teeth	Owen 1840; Maisch 1997	Uncertain taxonomic utility; depends on preparation in part.
Curvature of maxillary teeth under orbit	Maisch 1997	Occurs in other species; depends on orientation.
Prominence of fossa on premaxilla, dentary, surangular	Maisch 1997	Uncertain taxonomic utility; range of variation has never been assessed. No obvious difference from
Extent of surangular vs angular, lateral view	Conybeare 1822; Owen 1840	neotype.
Relative length of mandibular symphysis	Owen 1840	Uncertain taxonomic utility; not commonly preserved so cannot be assessed.
Relative contributions of dentary and splenials to mandibular symphysis	Owen 1881	Uncertain taxonomic utility; not commonly preserved so cannot be assessed.
Morphology of maxilla	Maisch 1997	Noticeably lower, with shorter anterior process, on neotype.
Morphology of jugal dorsal ramus	Maisch 1997	No obvious difference from neotype.

Morphology of quadratojugal	Maisch 1997	No obvious difference from neotype.
Clavicle morphology	Owen 1881; Lydekker 1889	Highly variable within a species.
Extent of humero-scapular articulation of coracoid	Owen 1881	Highly variable within a species.
Forefin narrower with fewer phalanges	Owen 1881; Lydekker 1889	Highly variable; influenced by fin completeness and preparation.
Notching on anterior digit of hindfin/forefin	Lydekker 1889	Little taxonomic utility; ontogenetic in part.
Prominent vascular foramina in fin elements	Lydekker 1889	Little taxonomic utility; probably ontogenetic in part.
Neural spine height on cervical and dorsal centra	Lydekker 1889	Uncertain taxonomic utility; has never been assessed for most species.
Number of presacral centra	Owen 1840	Similar in all species of <i>Ichthyosaurus</i> .

Owen (1840) also proposed that forefin morphology could distinguish between *I. communis* and *I. intermedius*. The forefin of *I. communis* is broader, has an additional digit, and “about 50 additional phalangeal ossicles” (Owen 1840, p. 109), although exactly what is meant by the latter is unclear. It could mean that the fin had more numerous, smaller phalanges, which is a distinction between ‘populations’ noted by McGowan (1974); or that the fin was longer overall; or that it had more accessory digits. Moreover, the number of phalanges is related to the completeness of the fin. In reality, what is often seen as a typical ‘fairly complete’ forefin on specimens from Somerset (McGowan and Motani 2003, fig. 80D) is incomplete; the fin is considerably longer than what is normally preserved (compare Figure. 4.4A to Figure. 4.4B, C).

In a later monograph, Owen (1881) again indicated that *I. intermedius* had a narrower forefin, but the subjective criteria of ‘broad’ versus ‘narrow’ are not tied to the number of primary digits nor to the number of accessory digits in the forefin.

Owen (1881, p. 105, 115) described both species as having five primary digits and both an anterior and posterior accessory digit, although the anterior accessory digit illustrated for *I. intermedius* (Owen 1881, pl. XXXIII, fig. 1) is not an accessory, but a second distal bifurcation. This might have been the case for his interpretation of *I. communis* as well, but he did not figure the fin. Indeed, the fin width is not explicitly related to the number of primary digits. Fins with a proximal digital bifurcation (mc or p1 row) may be wider than one with a more distal bifurcation (p3 or p4) even though the number of primary digits is the same (compare Figure. 4.4B, C). Some fins that have five primary digits (a single digital bifurcation; Figure. 4.4B) can appear as wide or wider than fins with six primary digits (two digital bifurcations; Figure. 4.4D). The number of accessory digits and how proximally they originate also affects fin width. So Owen's distinction between 'broad' and 'narrow' fins is too poorly defined to apply consistently and objectively. Lydekker (1889) introduced fin notching as a character that distinguished the two species. However, Massare and Lomax (2016a) demonstrated that, although notching of the radius or tibia is useful in some taxa, notching has no taxonomic significance in more distal elements of either the forefin or hindfin in *Ichthyosaurus*. Furthermore, Maxwell *et al.* (2014) have shown that fin notching is, at least in part, ontogenetic in *Stenopterygius*.

Forefin morphology is extremely variable within and among species of *Ichthyosaurus*, differing in which digit bifurcates, the location of the bifurcation, the number of bifurcations, the relative size of the anterior and posterior branches of the bifurcation, and the number of accessory digits, among others. McGowan (1974) acknowledged that forefin morphology was different between specimens from Somerset and Dorset, but attributed it to intraspecific variation over time. Appleby (1979) argued that these were valid species differences. The problem is complicated by the frequent incompleteness of the forefin (Figure. 4.4), especially in recognizing a second or third digital bifurcation; and by unrecognised composites in historic collections (Massare and Lomax 2016b). Preparation can also be a factor. Some historic specimens have forefins that seem to be carved out of the matrix, so it is possible that some bone, such as isolated elements of accessory digits, could have been removed to make a cleaner, better defined fin, or even to make a more streamlined one, more aesthetically pleasing for display. Still other specimens have fins in which the elements were probably reset and rearranged (e.g. NHMUK PV R3372). The utility of forefin morphology for taxonomy will only become evident

when species of *Ichthyosaurus* are better defined on the basis of other characters. At that time, forefin morphology can be examined for features characteristic of each species. The number of digital bifurcations or the location of the first (proximal) digital bifurcation may eventually prove to be significant. For now, however, forefin morphology appears too variable to use in distinguishing species, although it is reliable in distinguishing *Ichthyosaurus* from other genera.

Owen (1881) contended that *I. communis* and *I. intermedius* could be distinguished by the extent of the contribution of the splenial to the mandibular symphysis. In ventral view, the dentaries form most of the mandibular symphysis in *I. communis*, with only a small contribution from the splenials; whereas the splenials comprise two thirds of the mandibular symphysis in *I. intermedius* (Owen 1881, pl. XXI, figs. 2, 4). Relatively few specimens of *Ichthyosaurus* with complete rostra are preserved in ventral view, so it is difficult to assess whether the range of variation is bimodal, as Owen (1881) suggested. Furthermore, it has not been evaluated in other species of the genus, which also raises the issue of reliability. An additional question arises in exactly which features, independent of the symphysis morphology, were used in the assignment of a specimen to *I. communis* or *I. intermedius*. If it was based on tooth morphology or forefin morphology, then Owen's (1881) distinguishing character is questionable.

Maisch (1997) has provided the most extensive and specific list of characters in the literature to diagnose *I. intermedius*. Most of the proposed diagnostic characters, however, can be seen on the neotype of *I. communis* (Figure. 4.5; Table. 4.1). In lateral view, the maxilla has the same, symmetric triangular shape, including the slightly concave ventral border, with the anterior process extending well beyond the edge of the external naris, and the posterior process extending under the orbit (Maisch 1997, figs. 1, 5). The maxilla is, however, noticeably higher in SMNS 13111. The lacrimal is large, but not as large as in the neotype. It has a similar triradiate shape, and the dorsal process makes up a large portion of the anterior margin of the orbit, as in the neotype. The dorsal ramus of the jugal of the neotype has a similar right-angle bend and the same dorsal extent as that of SMNS 13111, and like it, shows a lateral ridge. Only a portion of the quadrate is exposed in lateral view on the neotype, and it is similar to that of SMNS 13111. The well-developed processus quadratus of the quadratojugal and its extent are also very similar to those seen in the neotype. The neotype differs from SMNS 13111 in some characters that Maisch

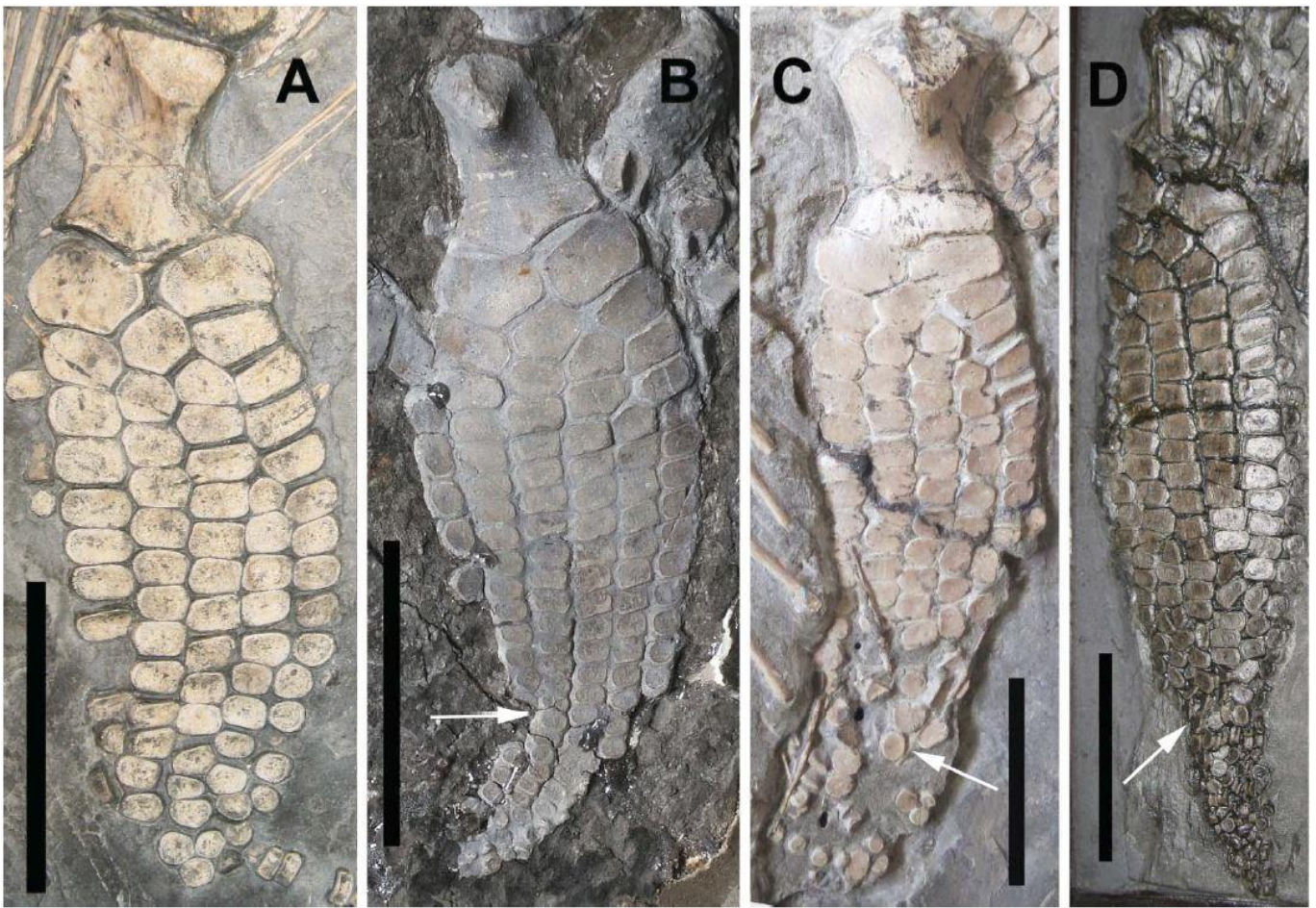


Figure. 4.4. Examples of forefin morphology of *Ichthyosaurus* A. CAMSM J35183 from Somerset, an example of what a ‘typical’ fin from Somerset looks like; B. CHMUS 2015.0102 possibly from Lyme Regis, an example of a wide, five-digit forefin; C. AGC 11 from Somerset, an example of a narrow, five digit forefin; D. YORYM 2006-3803 from Lyme Regis, an example of a narrow, six digit forefin. Specimens B–D are exceptionally complete. The arrows indicate the point at which specimens from Somerset (such as A) are usually considered to be complete. Scale bars = 5 cm.

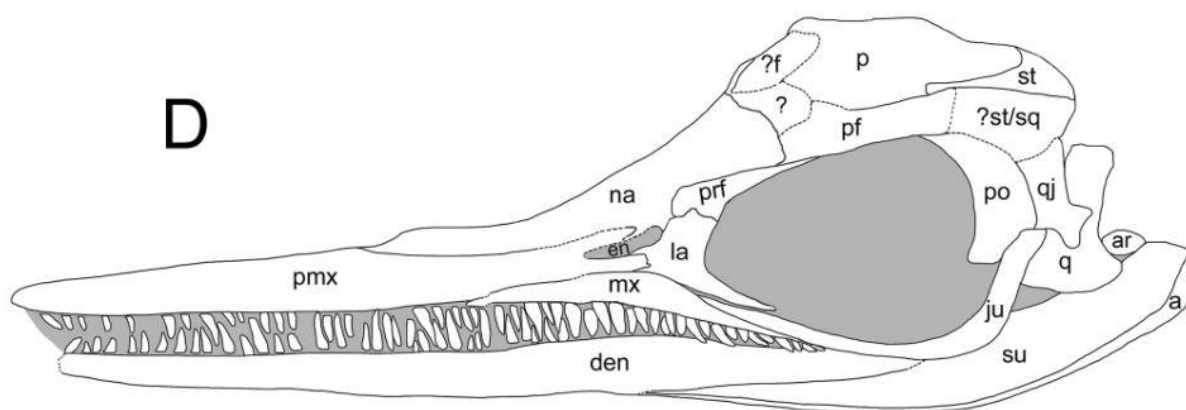
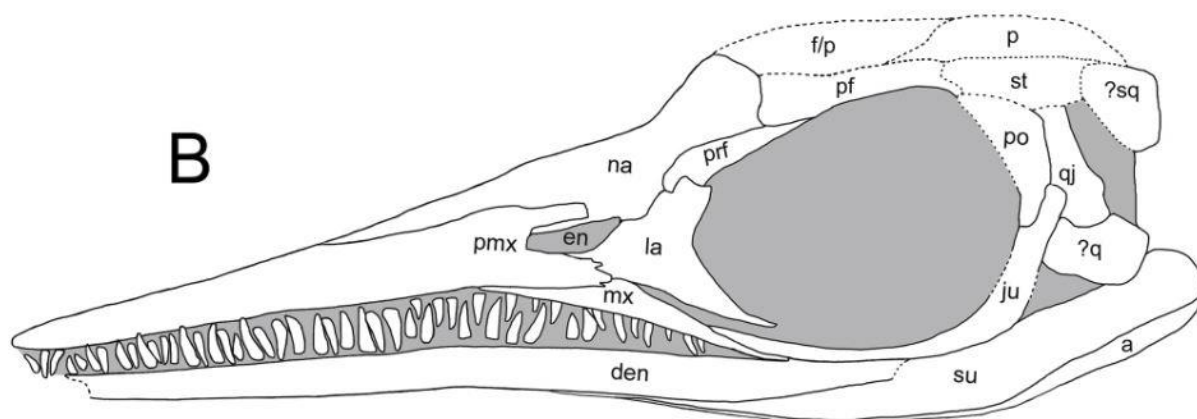
(1997) included in the emended diagnosis. The maxilla is lower and its anterior process does not extend as far anteriorly in the neotype as that of SMNS 13111. The neotype has only 12 maxillary teeth rather than 20+, although there is space for several more, and only three maxillary teeth are situated below the orbit. Furthermore, the posterior maxillary teeth lack curvature, but the latter could be because of the orientation in which they are preserved or due to displacement. In fact, curved maxillary teeth occur on many species of *Ichthyosaurus* (e.g., *I. breviceps*, CAMSM X50187; *I. larkini*, CAMSM J59575; *I. communis*, MCZ 1079; *I. somersetensis*, MANCH L.5666), and it is especially noticeable if a portion of the root

is also exposed. Finally, the premaxillary fossa are shorter, and the dentary fossa are longer and more continuous in the neotype than what is figured in Maisch (1997). However, intraspecific variation in fossa has never been assessed. The fossa surangularis, however, is similar on both.

In addition to the characters described by Maisch (1997) the neotype is similar to SMNS 13111 in a slender prefrontal that makes up less than half of the anterior border of the orbit; the subnarial process of the premaxilla that makes up half of the ventral margin of the naris; and an anterior process of the jugal that does not extend beyond the anterior margin of the orbit (Figure. 4.5). Our assessment is that SMNS 13111 has more similarities with the neotype of *I. communis* than differences, and we would assign it to that species.

The illustrated skull of *I. intermedius* (Conybeare 1822, pl. XVII; Figure. 4.2A) also shows features that are identical with the neotype specimen of *I. communis* (Figure. 4.2 A, B), including the shape and extent of the maxilla, the shape of the lacrimal, a slender prefrontal making up less than half of the anterior border of the orbit, the shape and extent of the anterior portion of the jugal, the dorsal ramus of the jugal with a right-angle bend, the extent of the bones surrounding the external naris, and the tooth shape. Therefore, because the type 'illustration' of *I. intermedius* displays features consistent with the neotype of *I. communis*, we agree with the synonymy of McGowan (1974) and McGowan and Motani (2003).

Figure. 4.5. A. Skull of *Ichthyosaurus communis* neotype (NHMUK PV R1162); B. Interpretive illustration of the neotype; C. Skull of SMNS 13111; D. Interpretive illustration of SMNS 13111. *Abbreviations:* a, angular; den, dentary; en, external naris; f, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; p, parietal; po, postorbital; pmx, premaxilla; pf, postfrontal; prf, prefrontal; q, quadrate; qj, quadratojugal; sq, squamosal; st, supratemporal; su, surangular. Light grey denotes matrix and openings in skull. Dashed lines indicate broken edge and possible sutures. The dorsal skull roof of the neotype is poorly preserved and the extent of the bones should be interpreted with caution as other bones and openings in the skull could not be identified. The parietal in SMNS 13111 is not well preserved and the shape and extent is deformed due to crushing. Scale bars = 5 cm. The scale bar for A is estimated because the specimen is behind glass and is inaccessible for measurement.



Systematic Palaeontology

Order **Ichthyosauria** de Blainville, 1835

Family **Ichthyosauridae** Bonaparte, 1841

Genus **Ichthyosaurus** De la Beche and Conybeare, 1821

Synonymy.

1818 *Ichthyosaurus* König: 54 [*nomen nudum*].

1819a *Proteosaurus* Home: 209.

1821 *Ichthyosaurus* De la Beche and Conybeare: 563.

1840 *Polyostinus* Hawkins: 12.

1840 *Paramecostinus* Hawkins: 15.

1904 *Eurypterygius* Jaekel: 32.

1979 *Protoichthyosaurus* Appleby: 492 [in part].

Emended diagnosis. Pineal enclosed within frontals at their posterior edge; large, wide nasals; maxilla excluded from margin of the external naris by subnarial process of premaxilla and anterior process of lacrimal; squamosal present; basioccipital with extensive extracondylar area and well-developed peg; angular with minimal exposure in lateral view; scapula with long shaft, slightly expanded distal end and expanded proximal end, but acromion process absent; coracoid with prominent anterior and posterior notches; humerus with nearly equal width distally and proximally, with slight constriction in the shaft; forefin with distal carpals 3 and 4 contacting the intermedium; metacarpal 5 in the distal carpal row, in contact with the ulnare; digit V as prominent or more prominent than digit IV; digital bifurcation anterior to the primary axis in forefin; forefin with at least five primary digits (although the fin must be preserved to at least p4 row to verify that a bifurcation is present); hindfin with at least four primary digits and an anterior digital bifurcation; rectangular, closely spaced phalanges on most of proximal to middle portion forefin; pelvic girdle tripartite, without fusion between pubis and ischium; femur longer than wide, with distal end wider than proximal end; preflexural vertebrae <80; (modified from McGowan and Motani 2003; Ji *et al.* 2016).

Occurrence. The genus is very common from Dorset and Somerset, England, but additional unequivocal occurrences of the genus include: Leicestershire (Martin *et al.* 1986), Nottinghamshire (Lomax and Gibson 2015), Warwickshire (Smith and Radley 2007), Gloucestershire (e.g. BU 5289, formerly BIRUG 4175), Worcestershire (WOSMG:1, WOSMG:2), Yorkshire (Maisch 1997; Massare *et al.* 2015), Devon (NHMUK PV R5787), England; Glamorgan, Wales (NMW 2009.35G.1); County Antrim, Northern Ireland (e.g. BELUM K1643, BELUM K28052); Belgium (Godefroit 1996); Switzerland (Maisch *et al.* 2008); Portugal (Zbyszewski and Moitinho de Almeida 1952; Bardet *et al.* 2008); and Alberta, Canada (McGowan 1978). The genus was also reported from Scotland, but contrary to Brusatte *et al.* (2015), those specimens (teeth and an impression of a lower jaw) are too fragmentary to be assigned to the genus. Similarly, a specimen from British Columbia, Canada (Dennison *et al.* 1990) shows no diagnostic characters of the genus, and the relative rostrum length would suggest that it is not *Ichthyosaurus*.

Ichthyosaurus has previously been reported from the uppermost Triassic (Rhaetian) of Somerset (McGowan 1974; McGowan and Motani 2003), but recent studies suggested that specimens from Somerset are probably from the lowermost Jurassic (Hettangian; Benson *et al.* 2012, 2015; Lomax and Massare 2016). However, DRL recently examined specimens of *Ichthyosaurus* currently held in a private collection that were collected *in situ* from the uppermost Triassic (Rhaetian) of northern Somerset (Carpenter 2001). Thus it is plausible that some specimens of *Ichthyosaurus* in historic collections are from the Rhaetian. The genus has definitively been reported from the lowermost Jurassic (Hettangian), Pre-*planorbis* beds of Somerset and Leicestershire (McGowan 1974; Martin *et al.* 1986; also see discussion in Lomax and Massare 2016). The youngest occurrence of the genus is from the lower Pliensbachian (Lomax 2010; Lomax and Massare 2015).

***Ichthyosaurus communis* De la Beche and Conybeare, 1821**

Synonymy.

1821 *Ichthyosaurus communis* De la Beche and Conybeare: 594.

1822 *Ichthyosaurus intermedius* Conybeare: 108.

Not 1834 *Ichthyosaurus chiropolyostinus* Hawkins: 25; pl. 7-12 [*nomen dubium*].

Not 1834 *Ichthyosaurus chiropamekostinus* Hawkins: 32; pl. 18-22 [*nomen dubium*].

Not 1840 *Ichthyosaurus latimanus* Owen: 123 [*nomen dubium*].

Not 1884 *Ichthyosaurus fortimanus* Owen: 176 [*nomen dubium*].

Not 1911 *Ichthyosaurus communis hyperdactyla* Jaekel: fig. 154 [*nomen dubium*].

1922 *Eurypterygius communis*; Huene: 5 [in part].

1922 *Eurypterygius intermedius*; Huene: 9 [in part].

1979 *Protoichthyosaurus prostaxalis* Appleby: 942 [in part].

*Note. 'Not' is with reference to these species not being synonymous with *I. communis* as previously suggested, e.g. by McGowan and Motani (2003).

Neotype. NHMUK PV R1162 (McGowan 1974), a practically complete skeleton comprising the skull, an articulated vertebral column extending into the tail fluke, ribs and gastralata, some pectoral elements, forefin, hindfin, and pelvic girdle.

Emended diagnosis. *Ichthyosaurus communis* is diagnosed relative to other species of *Ichthyosaurus* by the following unique characters: symmetric, triangular maxilla with long processes, extending anteriorly beyond external naris and posteriorly well under orbit; large, broad, triradiate lacrimal making up at least half of the anterior orbit margin.

The species is further diagnosed relative to other species of *Ichthyosaurus* by the following unique combination of characters: snout ratio >0.60 but probably less than 0.65 (as in *I. anningae* and *I. larkini*; in the lower range of *I. conybeari*); premaxilla supranarial and subnarial processes about equal length, extending about half way across the dorsal and ventral margins of the external naris, with nasal about half of dorsal margin (as in all species except *I. breviceps* and possibly *I. anningae*); pointed anterior process of jugal extends only slightly beyond the orbit, if at all (as in *I. breviceps*, *I. conybeari*); jugal dorsal ramus with a right angle bend (as in all species except *I. somersetensis*) makes up about half of posterior margin of orbit (as in *I. breviceps*); relatively short, wide, crescentic postorbital makes up about half of posterior margin of orbit (as in *I. breviceps*); lacrimal dorsal process participates in anterior orbit margin, with small prefrontal, contributing less than half of anterior orbit margin (as in *I. breviceps*, *I. conybeari* and *I. anningae*); humerus much longer than

wide (as in all species except *I. conybeari* and *I. anningae*); irregular depression on articular surface of humerus (as in *I. larkini* and *I. somersetensis*); humerus dorsal process large, central, extends less than half way down the shaft (similar to *I. larkini*); four elements in third (distal tarsal) row of hindfin, with two digits contacting the astragalus (as in *I. larkini* and *I. anningae*); hindfin with five primary digits (as in *I. conybeari*, *I. anningae*, unknown in *I. larkini*).

Material. Only two specimens referred to the species by McGowan (1974), both from Lyme Regis, can be unequivocally referred to *I. communis*: NHMUK PV R1073, NHMUK PV OR36256. The following substantially complete skeletons can also be referred to the species: BU 5289, CAMSM J35187, FMNH P 25027, MCZ 1079, MCZ 1493, OUMNH J.10341/P (cast of specimen figured by Buckland 1836, pl. 8, fig. 1), OUMNH J.13799, PETMG R174, and ROM 12805. SMNS 13111, a skull discussed above, is also referred to the species.

Occurrence. The geographic and stratigraphic ranges given here are based only on the neotype and referred specimens listed above. The neotype was collected from Lyme Regis, Dorset. Other referred specimens have been collected from the Lyme Regis-Charmouth area in Dorset, possibly from the Whitby coast of Yorkshire (Maisch 1997, as discussed above), and Gloucestershire (BU 5289). The species is probably also from Street and the surrounding area in Somerset (OUMNH J.13799; see ‘Discussion’ below). The species has been reported from Europe (Zbyszewski and Moitinho d’Almeida, 1952; Godefroit 1996; Maisch *et al.* 2008; Bardet *et al.* 2008) and the Isle of Skye, Scotland (Brusatte *et al.* 2015; as discussed above) but the remains are too incomplete for species assignment.

The Somerset specimens are most likely from the lowermost Jurassic (lower Hettangian), Pre-*planorbis* beds of the Blue Lias Formation (McGowan 1974; Benson *et al.* 2012, 2015; also see discussion above for genus). Specimens from the west Dorset coast are slightly younger, most likely from the Blue Lias and Charmouth Mudstone formations (Page 2010). Historically, the ‘Lyme Regis’ location was often recorded for ichthyosaurs from several localities along the west Dorset coast. The stratigraphic range usually given for Lyme Regis strata is upper Hettangian–lower Sinemurian (McGowan 1974), although upper Sinemurian–lower Pliensbachian strata are also exposed at nearby localities, such as Charmouth and

Seatown (Benton and Spencer 1995; Lomax 2010; Page 2010). It is likely that many historical specimens of *Ichthyosaurus* were collected from various localities along the west Dorset coast. However, *I. communis* has not been unequivocally reported from the upper Sinemurian or Pliensbachian (contrary to Bennett *et al.* 2011; Massare and Lomax 2016a). The uppermost Triassic (Rhaetian) White Lias Formation is also exposed along the coast, southwest of Lyme Regis (Gallois 2007), however, we have not seen any specimens of *I. communis* from the 'White Lias'. Thus the species range is at least lower Hettangian-lower Sinemurian.

Remarks. For most of the 19th century, all ichthyosaur specimens were identified as *Ichthyosaurus* so old museum identifications and identifications from historic literature should be considered carefully. However, even more recent identifications need to be checked against the criteria presented here. Previous diagnoses of the species allowed for so much variation that all large (>1.5 m) specimens of *Ichthyosaurus* were assigned to *I. communis*. The species has been treated as a catch-all for specimens that could not be assigned to *I. breviceps* or *I. conybeari*, two small species (<1.6 m) within the genus. But not all larger specimens are *I. communis*. In particular, the Somerset specimens NHMUK PV OR 2013*, NHMUK PV OR2013, NHMUK PV R44, CAMSM J59575, and probably CAMSM J35183, previously referred to the species by McGowan (1974), are not *I. communis* (Lomax and Massare 2016). In this analysis, we selected a few practically complete specimens that could be unequivocally assigned to the species based on the revised diagnosis. These were included in the geographic range summary above. Notably, *I. communis* is substantially more common from Dorset than from Somerset, as had been noted in the early literature (Owen 1840 1881). In fact, fairly complete skeletons of *I. communis* from Somerset seem to be rare.

Discussion

Because *I. communis* is herein diagnosed largely by a unique combination of characters, a substantial portion of a skeleton or a well-preserved skull is required to distinguish *I. communis* from other species in the genus. Therefore our synonymy for *Ichthyosaurus communis* differs from those previously published (e.g., McGowan and Motani 2003) in considering many species *nomina dubia* rather than synonyms.

I. chiropolyostinus (Hawkins 1834, pl. 7-12) and *I. chiropamecostinus* (Hawkins 1834, pl. 18-22) were not described in sufficient detail nor are the figured specimens sufficiently complete to assign them to *I. communis*. In fact, one of Hawkins' (1834, pl.7) figured specimens of *I. chiropolyostinus* is actually an example of *I. breviceps* (NHMUK PV OR2001*). The holotype of *I. latimanus* (Owen 1840) was fairly complete, but it was destroyed in 1940 during the bombing of Bristol (M. A. Taylor pers. comm.). Although 19th century casts of it exist (OUMNH J.10343/P, ANSP 17426, among others; Taylor and Clark in press), the quality is not sufficient to recognise features that can identify *I. latimanus* as *I. communis* or any other species of the genus. Moreover, the original published description of *I. latimanus* (Owen 1840) mixed the description of the holotype with that of another specimen (Taylor and Clark in press) and the validity of the species was questioned (Lydekker 1889; McGowan 1974). *I. fortimanus* (Owen 1884) and *I. communis hyperdactyla* (Jaekel 1911) were each defined on the basis of forefin morphology. Within *Ichthyosaurus*, forefin morphology is extremely variable and does not appear to be species specific, at least with our current knowledge. Thus these species are herein considered *nomina dubia* rather than synonyms of *I. communis*.

The absence of a squamosal in *Ichthyosaurus* has been considered a characteristic of the genus (Motani 2005; Ji *et al.* 2016), however, Maisch and Matzke (2000b), Maisch *et al.* (2008), and Vincent *et al.* (2014) reported it from specimens of *I. communis*. The squamosal is present in the holotypes of *I. larkini* and *I. somersetensis* (Lomax and Massare 2016), on the holotype of *I. anningae* (mistaken for part of the supratemporal in Lomax and Massare 2015) and on *I. conybeari* (NMW 93.5G.2). The postorbital portion of the skull is damaged in the neotype of *I. communis*, so the presence of a squamosal cannot be verified. Maisch and Matzke (2000b) and Maisch *et al.* (2008) suggested that a well-preserved post-orbital portion of the skull is required to recognise the squamosal because it is a thin plate of bone that is easily damaged or disarticulated. Well-preserved skulls of most of the species have a squamosal, so its presence should be considered a feature of the genus.

The morphology of the mesopodium of the hindfin has been suggested as a taxonomically useful feature (Lomax and Massare 2016). *Ichthyosaurus communis* has four elements in the third (distal tarsal) row, two of which contact the astragalus. In the neotype, the astragalus has an angular distal edge, and the contacts with digit

III and digit IV are equally broad. On some specimens, however, particularly those from Somerset, the astragalus has a flat distal edge and the contact with digit III is much narrower than the contact with digit IV. If the fin elements are displaced or poorly articulated, the contacts are sometimes difficult to discern, even in specimens from Dorset. However, four elements in the third row can identify a hindfin as belonging to either *I. communis*, *I. larkini*, or *I. anningae*. Additional information is required to determine to which of the three species a particular specimen should be assigned. One such example is OUMNH J.13799, from Somerset, a nearly complete specimen of an old individual that is preserved mainly in ventral view, although the skull is in dorsal view. The articulated left hindfin, missing the femur, has four elements in the distal tarsal row and two digits in contact with the astragalus. The astragalus has a straight distal edge, and the contact with digit IV is about twice as broad as the contact with digit III. There is a facet on the astragalus, however, for both of the contacts, so this is probably a variation on the pattern displayed on the neotype of *I. communis*. The humerus/femur ratio indicates that this is not a specimen of *I. anningae*. *I. larkini* also has a contact between digit V and the astragalus, which is absent on this specimen. Thus OUMNH J.13799 is assigned to *I. communis* solely on the basis of the hindfin morphology. It is the only substantially complete skeleton from Somerset that can, thus far, unequivocally be referred to *I. communis*.

Conclusion

As recognised by McGowan (1974), initial definitions and illustrations of *I. communis* and *I. intermedius* were insufficient to diagnose either species. Complicating the problem, the type specimen of *I. communis* was not illustrated, and the first illustration of the species (Conybeare 1822, pl. XVI, fig. 8), aside from some teeth that may or may not be the same as those of the holotype, was probably an example of *I. breviceps*. This raises the question of whether the differences described between *I. communis* and *I. intermedius* were actually differences between *I. breviceps* and *I. intermedius*. Specimens that would have been the holotypes cannot be located, making the problem unresolvable based on the original literature and illustrations. Subsequent 19th century descriptions of the species (Owen 1840, 1881; Lydekker 1889) did not propose suitable diagnostic characters nor adequately

distinguish between *I. intermedius* and *I. communis*. What had been considered the key character, namely tooth morphology, is part of a continuous spectrum of variation that is at least in part ontogenetic. Apparent variation in tooth morphology can also be due to the orientation of the tooth on specimens in lateral view, as well as the quality of preservation and care in preparation of the specimen. Other supposedly important characters were based on forefin morphology, which is also extremely variable.

The problems were more or less resolved by the designation of a neotype for *I. communis*, which provides the basis for redefining the species (McGowan 1974). Ironically though, the neotype displays most of the features originally associated with *I. intermedius*, based on our interpretation of the illustration of the type specimen (Conybeare 1822). In retrospect, when the neotype was assigned, *I. intermedius* would probably have been a better name to select, given that the skull of the species was figured. However, the name '*I. communis*' has been widely used in the literature and is historically significant. Changing the name at this point would only add confusion and destabilize the taxonomy. But regardless, *I. communis* has priority over *I. intermedius*, having been introduced a year earlier (De la Beche and Conybeare 1821). Because the neotype shares nearly all of the features originally proposed for *I. intermedius*, we agree with McGowan (1974) that the two species are the same.

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Chapter 5: On the largest *Ichthyosaurus*: A new specimen of *Ichthyosaurus somersetensis* containing an embryo

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On the largest *Ichthyosaurus*: A new specimen of *Ichthyosaurus somersetensis*
containing an embryo

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Abstract

A formerly undescribed *Ichthyosaurus* specimen from the collection of the Niedersächsisches Landesmuseum (Lower Saxony State Museum) in Hannover, Germany, provides valuable new information. The skeleton was collected from the Lower Jurassic strata (lower Hettangian, Blue Lias Formation) of Doniford Bay, Somerset, UK. However, the specimen is a composite as almost the entire tail has been added and other parts are reconstructed. Regardless of the incomplete preservation, the estimated total length of this individual, based on the skull and precaudal length, is between 300 and 330 cm and it is thus the largest unequivocal example of the genus *Ichthyosaurus*. Cranial and postcranial characters, specifically from the maxilla, lacrimal, jugal, the humerus, and the ilium justify a referral to *I. somersetensis*. A fork-like shape of the proximal end of the ilium is unusual and has not been reported for any species of *Ichthyosaurus*. Likewise the presence of four elements in the third row of the hindfin, indicated by the presence of a bifurcation is novel for the species and has wider implications for the taxonomic utility of hindfins within the genus. The specimen also bears an embryo, which is only the third embryo known for *Ichthyosaurus* and the first to be positively identified to species level.

Key words: Ichthyosauria, *Ichthyosaurus somersetensis*, embryo, Jurassic, Hettangian, UK, Somerset.

Introduction

During the mid-1990s, professional fossil collector Peter Langham found a large, well-preserved and mostly articulated ichthyosaur skeleton at Doniford Bay, Watchet, Somerset, UK (Figure. 5.1). The specimen was recovered from the Early Jurassic (lower Hettangian) Blue Lias Formation, specifically the *Caloceras johnstoni* Ammonite Subzone of the *Psiloceras planorbis* Ammonite Zone (Bed 36) and is now curated in the Niedersächsisches Landesmuseum (NLMH) in Hannover, Germany.

Numerous ichthyosaurs have been collected in Somerset. Most are historical specimens discovered in quarries around Street and surrounding areas during the early and middle 19th century, although several have been found on the Somerset coast more recently (Delair 1969; Deeming et al. 1993; McGowan 2003; Massare and Lomax 2016a). The majority of this material is referable to the genus *Ichthyosaurus*, which has been recorded from various locations in the UK, most notably the Lyme Regis-Charmouth location on the Dorset coast and from quarries in Street and surrounding areas in Somerset, but also outside the UK (Massare and Lomax 2017a).

There are six valid species of *Ichthyosaurus*: *I. communis* De la Beche and Conybeare, 1821; *I. breviceps* Owen, 1881; *I. conybeari* Lydekker, 1888; *I. anningae* Lomax and Massare, 2015; *I. larkini* Lomax and Massare, 2017; and *I. somersetensis* Lomax and Massare, 2017. The studied specimen (NLMH 106234) can be assigned to *Ichthyosaurus* because it possesses diagnostic traits for the genus, which are: a forefin with an anterior digital bifurcation, a humerus that is almost as wide proximally as distally, a hindfin with a bifurcation, and a tripartite pelvis (Massare and Lomax 2017a). A tripartite pelvis has been reported in the coeval *Temnodontosaurus* and *Leptonectes* specimens, but the morphology of those elements are distinctly different to those in *Ichthyosaurus* (McGowan and Motani 2003; Delsett et al. 2017). NLMH 106234 can further be assigned to *Ichthyosaurus somersetensis* based on the morphology of the skull, humerus, and ilium. *I. somersetensis* is known from multiple specimens, including complete to fairly complete skeletons (Lomax and Massare 2017). In fact most *Ichthyosaurus* specimens found in Somerset belong to this species (Lomax and Massare 2017; DRL personal observation). The studied specimen provides new information on the

morphology of the pelvis and hindfin of the species, along with the size range of the genus.

An embryo is also preserved with NLMH 106234, positioned between the ribs. The embryo comprises a portion of articulated vertebral column, fragments of ribs, a section of an articulated forefin, and probably a scapula. This is only the third embryo reported for *Ichthyosaurus* and the first to be positively identified to species level (Pearce 1846; Deeming et al. 1993).

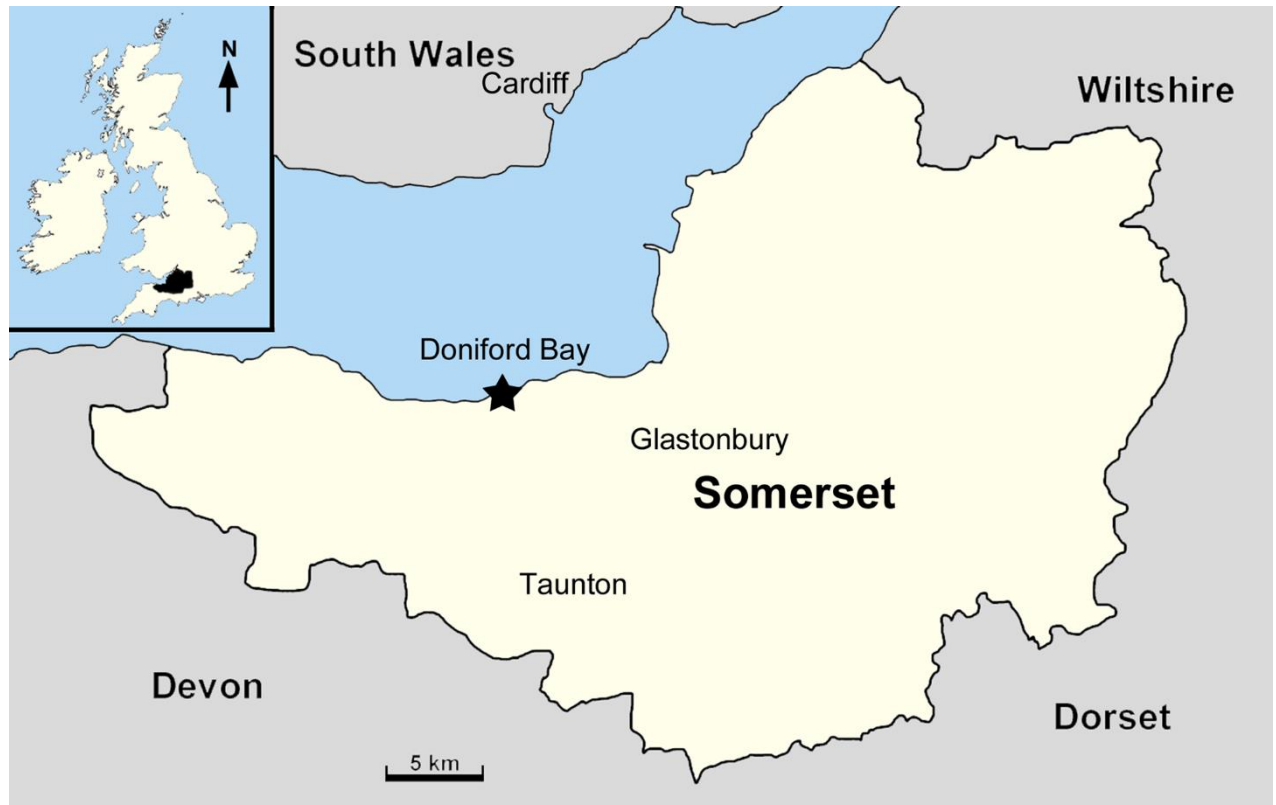


Figure. 5.1. Map of Somerset including the location of Doniford Bay (indicated by a star), Watchet, UK.

Institutional abbreviations. ANSP, Academy of Natural Sciences, Philadelphia, USA; BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; BU, Lapworth Museum of Geology, University of Birmingham, Birmingham, UK; NHMUK (formerly BMNH), The Natural History Museum, London, UK; NLMH, Niedersächsisches Landesmuseum (Lower Saxony State Museum), Hannover, Germany; PETMG, Peterborough Museum and Art Gallery, Peterborough, UK; SMF, Sauriermuseum, Frick, Switzerland; UWGM, University of Wisconsin Geological Museum, Madison, USA.

Material and methods

History and reconstruction of the specimen. The studied specimen, NLMH 106234, appears to be a complete skeleton, but is actually a composite (Figure. 5.2). When found, most of the caudal vertebrae could not be collected and the tail associated with NLMH 106234 comprises vertebrae from another individual as well as replica vertebrae (DRL and SS personal observation; personal communication Peter Langham, 2017). Composites of *Ichthyosaurus* have been reported, but most are from historical collections, although recently collected specimens are also known for composites or have modifications (Massare and Lomax 2014, 2016b), including specimens restored by Peter Langham (Deeming et al. 1993; Massare and Lomax 2016a).

NLMH 106234 was initially prepared by P. Langham who added a tail from a smaller ichthyosaur and various ammonites to create a better specimen for display. A large crack extends across the mid-dorsal region of the specimen where two adjacent blocks meet (Figure. 5.2). The vertebrae are disarticulated at this point and several centra are probably missing, as are several ribs. The neural spines appear consistent across the two blocks, although they are set in plaster. Parts of the skull, some neural spines and centra, and the forefin have also been reconstructed (Figures. 5.2B, 3, 4).

The forefin, however, requires some explanation. A portion of the radius, most of the radiale and distal carpal 3, all of distal carpal 2, metacarpal 2 and 3, and up to four phalanges of digits II and III, and several posterior phalanges of digit IV, are reconstructed from plaster (Figure. 5.4). The element that contacts the radiale anteriorly, along with the next four elements, are entirely reconstructed from plaster. Although, the sixth element is genuine and indicates the presence of an anterior bifurcation of digit II. Aside from the additions and reconstructions, the rest of the specimen, including several of the ammonites (*Caloceras johnstoni*) and a plant frond (probably an example of *Otozamites* or *Ptilophyllum*) are genuine (our observation; personal communication Peter Langham, 2017; Figure. 5.2).

The specimen was later sold to Siber + Siber, a Swiss company specializing in minerals, rocks and fossils. It was purchased from Siber + Siber by the Hannover-based art collector Ernst Schwitters who used it as a wall decoration in his living room. When Schwitters died the Kurt & Ernst Schwitters Foundation became the

owner. In 2005, the specimen was placed on loan to the NLMH, but was officially purchased by the museum in 2013. Initially, a wooden frame surrounded the skeleton, that was later removed when it was conserved for display in 2006 and 2007. Since December 2007 the specimen has been on display at NLMH, where one of us (SS) first became aware of it.

Length	ANSP 15766	NHMUK OR2013*	NLMH 106234
skull	43.8	47.0	57.5
preorbital	28.0	30.5	40.0
prenarial	21.0	31.1	33.3
maxilla	11.8		14.5
jaw	47.0	53.0	64.0–67.0 ¹
scapula		12 (R)	15.5 (R)
humerus	8.8 (L), 8.2 ^e (R)	9–10 ^e (R)	10.4 (R)
femur	6.0 (L) 6.3 (R)	7 (R)	7.7 (L), 7.8 (R)
ischium			8.6 (L), 8.4 (R)
pubis			8.3 ^e (L)
ilium			8.4 (L)
precaudal	102	118 ^e	122 ^e
preflexural (includes apical centra)	157	181 ^e	195 ^e
total length (from tip of snout to tip of tail)	230 (some posterior caudal vertebrae may be missing)	268	300–330 ^e

Table. 5.1. Measurements (in cm) of *Ichthyosaurus somersetensis* specimens, including the holotype (ANSP 15766) and a referred specimen, compared with NLMH 106234. (L/R), left/right skeletal elements; e, estimated measurement because the bone was damaged, rotated or partially buried; 1, see Materials and methods for details. The precaudal and preflexural lengths do not include the skull length. Note: NHMUK OR2013* is behind glass and not accessible for measurement, so a cast was measured instead. Some of the measurements are estimates because the cast does not display good enough detail.

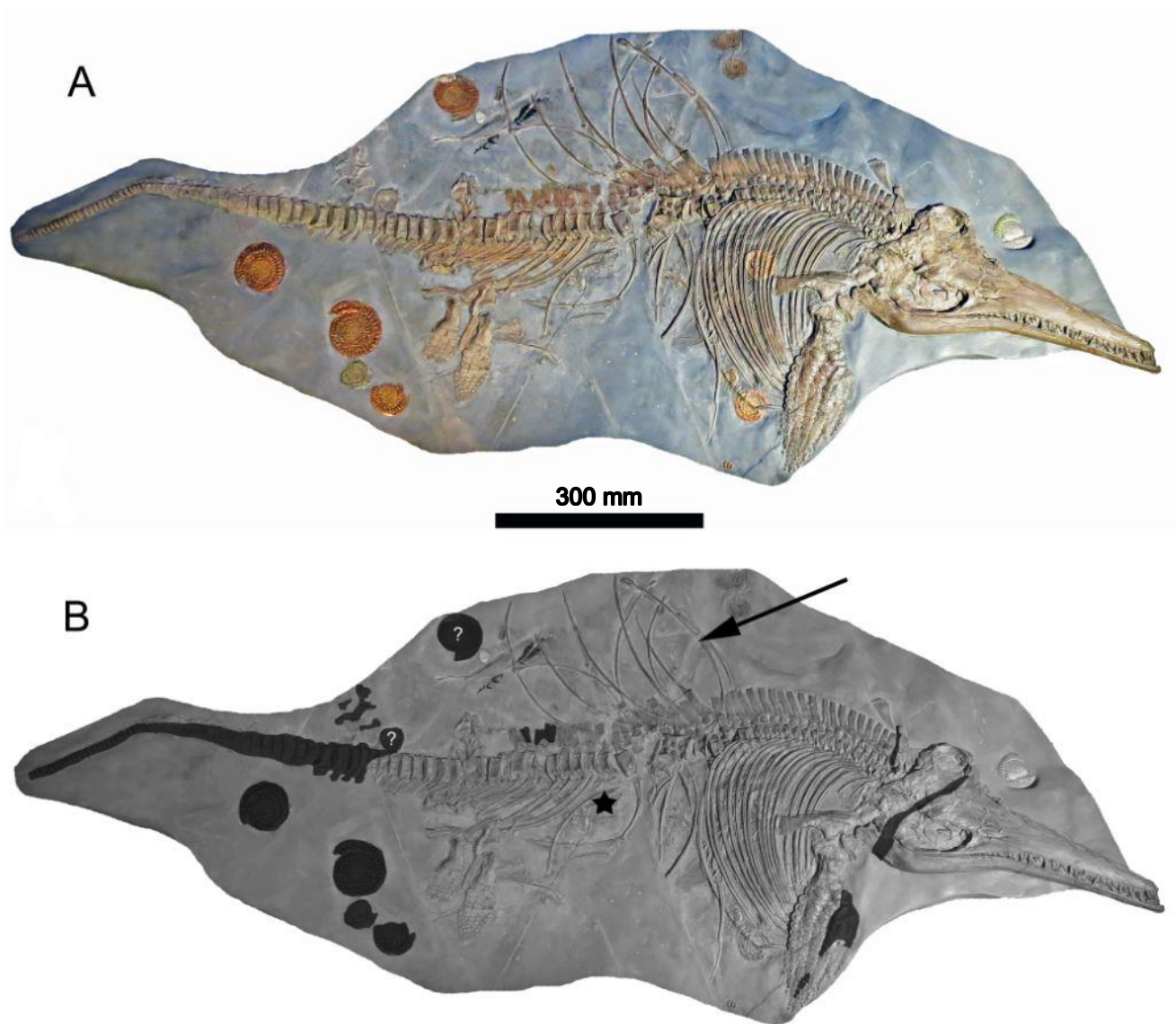


Figure. 5.2. **A.** Skeleton of *Ichthyosaurus somersetensis* Lomax and Massare, 2017 (NLMH 106234) from the Lower Jurassic (lower Hettangian) of Doniford Bay, Watchet, Somerset, UK. **B.** Explanatory photograph with the composite/reconstructed sections shown in black; the question marks indicate that the element may have been added to the specimen; arrow points to a large crack that extends across the specimen; star indicates the position of the embryo.

Methods for size estimation. Another issue that requires discussion is the skull, jaw, and precaudal lengths of NLMH 106234 (Table. 5.1). The skull length is 57.5 cm and the jaw length has a maximum of 67 cm and a minimum of 64 cm, accounting for some reconstruction (3 cm) in the posterior portion of the mandible. The precaudal vertebral column length, measured along the line of the vertebral column from the first vertebra at the back of the skull to the first definite single-headed rib, is approximately 107 cm. However, where the two adjacent blocks meet at the mid-dorsal region at least three vertebrae, and possibly a fragment of a fourth, are disarticulated and positioned adjacent to the rest of the vertebral column. At this position, the bones are all set in plaster. It is possible that the two large blocks were placed too close together and that some vertebrae are missing. Furthermore, the precaudal count for the studied specimen is 40, which is considerably less than for other examples of *Ichthyosaurus somersetensis*. The count should be greater than 46 (Lomax and Massare 2017), which suggests at least six vertebrae are missing in the mid-dorsal region. A mid-to-posterior dorsal centrum on this specimen measures approximately 2.5 cm long in lateral view, which, accounting for the missing centra, would add roughly 15 cm to the precaudal length, giving a total of 122 cm. Buchholtz (2001: fig. 5) showed that the tail stock (pelvis to bend in the tail) for *Ichthyosaurus* is about 60% of the precaudal length, which would suggest a tail stock length of approximately 73 cm for NLMH 106234 (i.e., a preflexural total length of 195 cm, not including the skull). For comparison, the tail stock is 56% of the precaudal length in the holotype of *I. somersetensis* (ANSP 15766). NHMUK OR2013*, a referred specimen of *I. somersetensis*, has a total length from tip of snout to tip of fluke of 268 cm, including a fluke length of ~ 40 cm. Considering the size of the studied specimen, it is probable that the fluke length may have been as much as 50 cm. Adding this fluke length and the skull length to the estimated preflexural length of NLMH 106234, suggests a total length of just over 300 cm (Table. 5.1).

Furthermore, using the equation between skull length and vertebral column length from Deeming et al. (1993) suggests that NLMH 106234 should have a vertebral column total length of 272 cm. Adding the skull length of 57.5 cm equates to a total body length of 329.5 cm, about 30 cm longer than the length suggested above, but that difference could probably be accounted for in the tail.



Figure. 5.3. Skull of *Ichthyosaurus somersetensis* Lomax and Massare, 2017 (NLMH 106234) from the Lower Jurassic (lower Hettangian) of Doniford Bay, Watchet, Somerset, UK; in dorsolateral view. Arrow points to the reconstruction that extends across the skull.

***Ichthyosaurus* size.** In the following discussion, the total length includes the skull length and the vertebral column length from the back of the skull to the tip of the tail. As currently defined, the smallest species of *Ichthyosaurus* is *I. conybeari*. The holotype of *I. conybeari* is the largest reported specimen, but it only comprises an anterior skeleton, including a damaged skull. This specimen probably has a total body length estimate of < 150 cm (Massare and Lomax 2016a; McGowan and Motani 2003). However, Massare and Lomax (2016a) noted that the species may be larger, in light of a fragmentary skeleton that may or may not belong to the species. Next in size is *I. anningae* which, based on the holotype, has a total length estimate of < 180 cm (Lomax and Massare 2015). Of similar size is *I. breviceps*. The largest specimen of *I. breviceps* has a total length estimate of < 190 cm (Massare and Lomax 2014). In comparison, *I. communis* is slightly larger, with a probable total length of around 200 cm (Massare and Lomax 2017a; DRL personal observation). *I. larkini* is the next largest species, with the holotype having a total length of 220 cm,

although Lomax and Massare (2017) indicated the species probably reached a total length of < 250 cm. *I. somersetensis* is the largest species, with the largest complete referred specimen (NHMUK OR2013*) having a total length of 270 cm. Lomax and Massare (2017), however, estimated the total length of the species as no greater than 300 cm.

McGowan and Motani (2003) gave the maximum length of the largest *Ichthyosaurus* as 250 cm. However, Massare et al. (2015) estimated a body length, from tip of the snout to the tail bend, of just under 300 cm for the genus based on an isolated forefin with a humerus length of 11.7 cm. The specimen was not assigned to a species of *Ichthyosaurus* because it was too incomplete. The total length of this individual was re-estimated as just over 300 cm from the tip of the snout to the end of the tail (Massare and Lomax 2017b), which still is the largest estimate for the genus until now.

However, some very large examples of *Ichthyosaurus* have been reported from Europe, including an incomplete ichthyosaur skull (SMF 46) from the lower Sinemurian of Frick, Switzerland (Maisch et al. 2008) and a fragmentary skull (IRSNB R145) from the upper Sinemurian of Bonnert, Belgium (Godefroit 1996). Massare et al. (2015) suggested that the Frick specimen could not be assigned to *Ichthyosaurus*, whereas the Bonnert specimen was identified as cf. *Ichthyosaurus*. This is contrary to Massare and Lomax (2017a), who erroneously referred both specimens to the genus. We agree with Massare et al. (2015), pending detailed examination of the European specimens. NLMH 106234 has a skull length of 57.5 cm, which is the largest skull of an *Ichthyosaurus* on record (compare McGowan 1974; Massare et al. 2015) and with an estimated total length of 300–330 cm, the specimen is the largest, unequivocal example of *Ichthyosaurus* known. Furthermore, it extends the total body length estimate for *I. somersetensis* to < 350 cm.

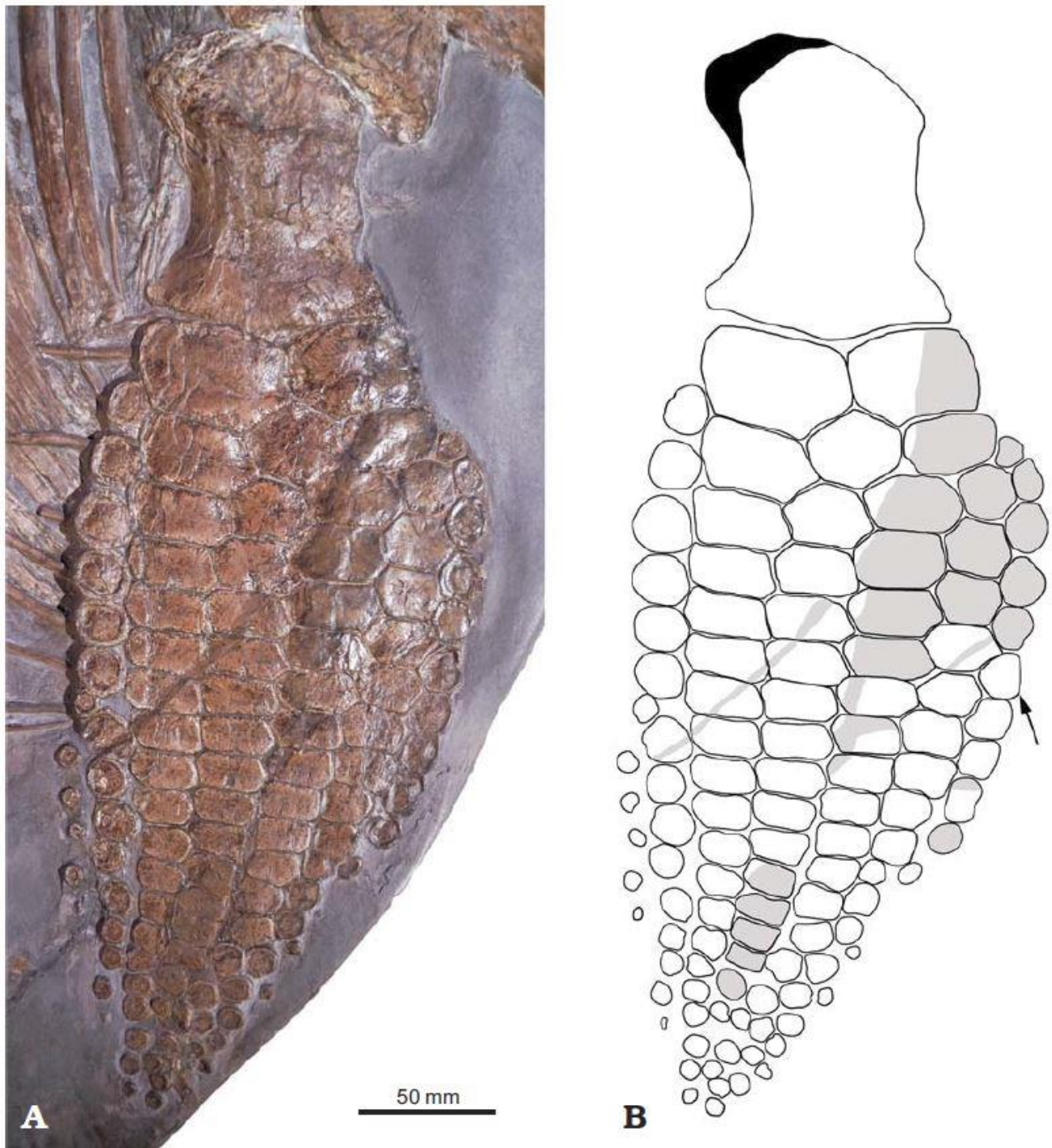


Figure. 5.4. Right forefin of *Ichthyosaurus somersetensis* Lomax and Massare, 2017 (NLMH 106234) from the Lower Jurassic (lower Hettangian) of Doniford Bay, Watchet, Somerset, UK; in dorsal view (anterior to the right). Grey indicates plaster filler (elements are not genuine); black indicates crushed and displaced portion of humerus. Arrow points to bifurcation. Photograph (**A**), explanatory drawing (**B**).

Systematic Palaeontology

Order **Ichthyosauria** de Blainville, 1835

Family **Ichthyosauridae** Bonaparte, 1841

Genus **Ichthyosaurus** De la Beche and Conybeare, 1821

Ichthyosaurus somersetensis Lomax and Massare, 2017

Referred material. NLMH 106234, a virtually complete, articulated skeleton lying on its left side, and missing almost the entire tail (see Material; Figure. 5.2).

Stratigraphic and geographic range. From Doniford Bay, Watchet, Somerset, UK. It was recovered from the Lower Jurassic (lower Hettangian) Blue Lias Formation, specifically the *Caloceras johnstoni* Ammonite Subzone of the *Psiloceras planorbis* Ammonite Zone (Bed 36).

Emended diagnosis. As in Lomax and Massare (2017) with the following changes: total length > 300 cm but < 350 cm; hindfin with three or four elements in third row, with one element (tarsal 3) in broad contact with astragalus; notching usually present in some elements of the leading edge of the hindfin, but absent in the tibia.

Description

The specimen can be assigned to *I. somersetensis*, because it possesses the following autapomorphies: a broad, asymmetric maxilla with a fairly long anterior process, and delicate, very long, and slender posterior process in lateral view; a triradiate lacrimal with a posterior shelf at the base of the dorsal process; a jugal dorsal ramus that is only slightly curved, lacking a right angle dorsal bend; and an ilium that is wide relative to its length and more oblong than rib-like (Lomax and Massare 2017). The specimen also possesses the unique combination of characters found in *I. somersetensis*, including: a prefrontal that excludes the dorsal process of the lacrimal from the orbit margin; the anterior process of the jugal extends slightly beyond the anterior inner edge of the orbit; the premaxilla supranarial and subnarial processes are about equal in length, extending about half way across the dorsal and

ventral margins of the external naris, with the nasal making up about half of the dorsal margin; and a humerus that is long relative to its width, with a small dorsal process that does not extend far down the shaft (Lomax and Massare 2017).

Skull, mandible, and dentition

The skull is 57.5 cm long, and is preserved in dorsolateral view (Figure. 5.3). It is complete, but damaged posteriorly and dorsoventrally crushed, with some bones missing and others difficult to identify. The skull has also been restored in the posterior region, where a crack extends across the skull and mandible (Figures. 5.2B, 3). The orbit is crushed and the shape is not original, although a complete sclerotic ring is preserved and does not fill the orbital margin. Unless otherwise stated, the skull morphology concurs with other specimens of the species.

The skull roof is damaged and crushed, but some information can be gleaned. A low medial ridge is formed by the parietals and the lateral border of the temporal opening is formed largely by the supratemporal. The contact of the latter with the parietal and postfrontal is indiscernible.

An element that is probably the squamosal is displaced posterior to the postorbital and separated by a large crack. This element is approximately rectangular and positioned ventral to the supratemporal. Irrespective of crushing, the prefrontal forms a small portion of the dorsal and at least half of the anterior margin of the orbit. The prefrontal extends ventrally to the level of the external naris, excluding the dorsal process of the lacrimal from the anterior margin of the orbit.

The lacrimal is triradiate, similar to the condition in the holotype of the species (ANSP 15766), but the dorsal process is larger and more robust in NLMH 106234. This difference may be due to the crushing or represent individual variation. There appears to be a shelf at the base of the lacrimal, which is found in all examples of the species (Lomax and Massare 2017), although this is somewhat obscured due to the crushing. The dorsal process of the lacrimal makes up the posterior margin of the external naris and the anterior process of the lacrimal, although broken, forms about half of the ventral border of the external naris. The posteroventral process of the lacrimal makes up less than half of the anterior margin of the orbit. A thickened anterior process of the jugal extends slightly beyond the anterior margin of the orbit (although some of it may be buried by the maxilla) and alongside the posteroventral process of the lacrimal. The dorsal ramus of the jugal is damaged, but has a robust

shape and clearly lacks a dorsal bend, as is characteristic for *I. somersetensis* (Lomax and Massare 2017).

In dorsal view, the nasal is wide posteriorly, with the anterior-most portion extending as far forward as the anterior process of the maxilla. In lateral view, the nasal forms about half of the dorsal border of the external naris. The supranarial and subnarial processes of the premaxilla make up at least half of the external naris borders. The maxilla is very large, as in all specimens of the species, and its maximum (dorsoventral) height is about even with the mid-posterior edge of the external naris. The maxilla is asymmetric in lateral view, with a long and abruptly narrowing anterior process that extends beyond the external naris. The posterior process of the maxilla is delicate, very long, slender, and extends well under the orbit.

In lateral view, the angular forms a small portion of the mandible and the anterior end extends forward to about even with the posterior edge of the orbit. The surangular, however, extends farther forward than the angular, as far anteriorly as the highest point of the maxilla. The posterior end of the dentary ends abruptly, about half-way across the orbit, where it overlaps the surangular.

The teeth have largely slender crowns with longitudinal striations. Most of the roots are continuous with the crown, although some of the roots are wider than the crown. The roots have coarse, longitudinal grooves. The posterior maxillary tooth crowns are much smaller than the premaxillary teeth.

Axial skeleton: There are at least 40 precaudal centra, including the atlas-axis, although six are probably missing (see Material and methods). At least one of the posterior dorsals or anterior caudals, probably the latter based on shape, is disarticulated and positioned beneath some of the caudal ribs. There are eight caudal vertebrae preserved in articulation, and an isolated caudal centrum in the matrix. The isolated caudal centrum may not belong with the specimen as it appears smaller than the preserved caudal vertebrae, although it could conceivably be from a more posterior section. In addition, the last two caudal vertebrae in articulation are partially reconstructed and all of the vertebrae beyond that point have been added to the specimen and are not discussed further (see Material and methods; Figure. 5.2).

The neural spine apices of most of the cervical through mid-dorsal neural spines appear to have been “carved” during preparation, as the tips are squared and differ in colour from the rest of the neural spine. However, it is difficult to confirm

whether this is an artefact of preparation or genuine. Regardless, the portions of the neural spines that are definitely genuine are at least twice as high as the centrum height. The posterior dorsal and anterior caudal neural spines are unusual in having a V-shape notch at the tip (Figure. 5.5), which is uncommon in *Ichthyosaurus*. This morphology is genuine, although some of the neural spines have been reconstructed to mirror the morphology (Figure. 5.5). The neural spines of the posterior dorsals and anterior caudals are also wider and about the same height as the centra.

The longest rib measures 49 cm along its curvature, but the distal end is buried.

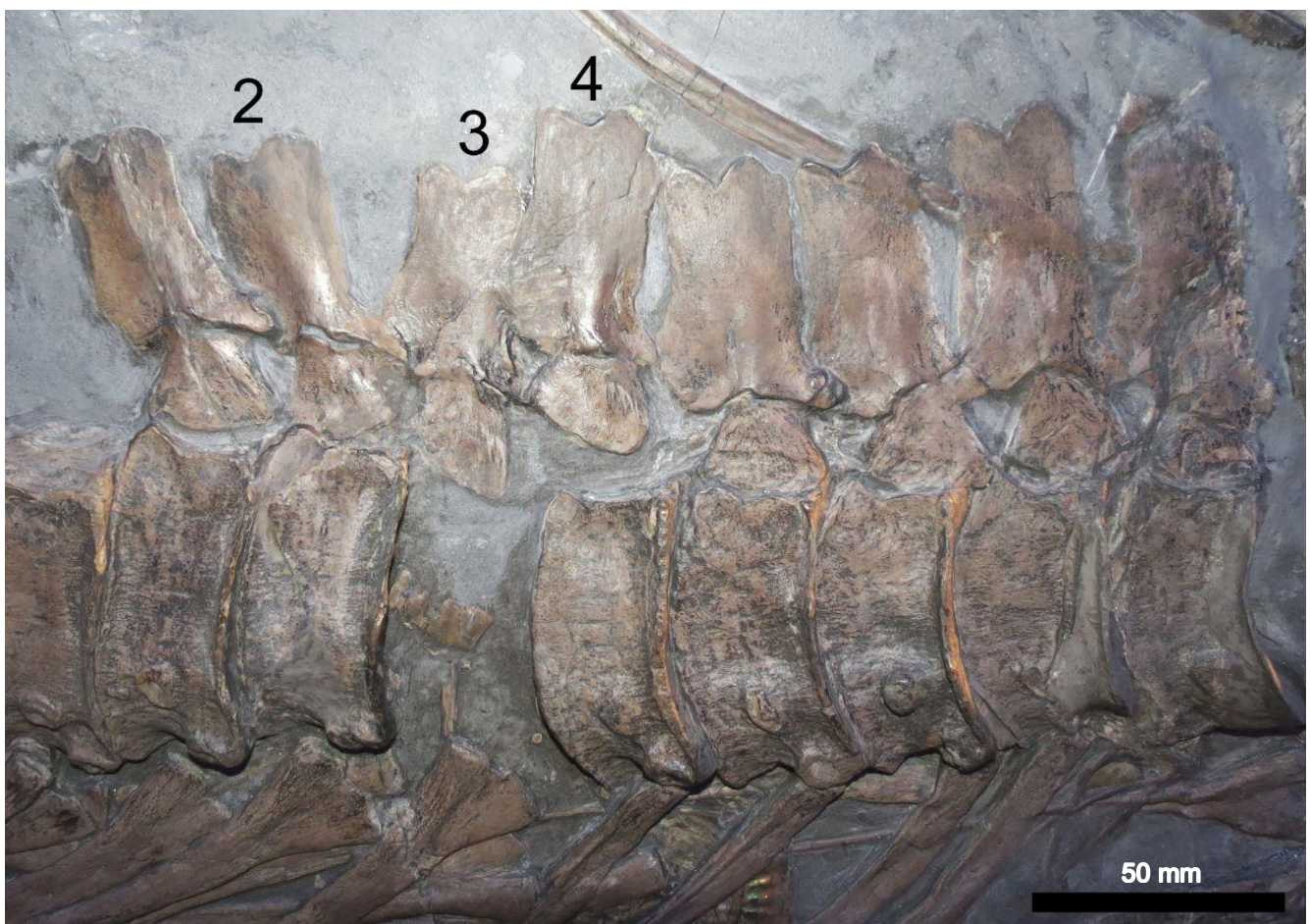


Figure. 5.5. Close-up of some mid-posterior dorsal vertebrae of *Ichthyosaurus somersetensis* Lomax and Massare, 2017 (NLMH 106234) from the Lower Jurassic (lower Hettangian) of Doniford Bay, Watchet, Somerset, UK; showing the unusual V-shape morphology of the neural spine apices. Note, the second, third, and fourth neural spine from the left are mostly reconstructed and the morphology is not genuine.

Pectoral girdle and forefin

Most of the pectoral girdle is obscured by matrix. However, the complete right scapula is preserved and visible in lateral view. It is a long, slender element, measuring 15.5 cm along the long-axis. The anterior end is wide and the shaft is narrow, whereas the posterior end is slightly flared, as is typical of all species of the genus (Massare and Lomax 2017a).

The right forefin is preserved in dorsal view, but has been partially reconstructed (see Material and methods; Figure. 5.4). The humerus is crushed, in that a portion of the proximal region has been displaced posteriorly and some of the shaft surface is missing. The proximodistal length of the humerus measures 10.4 cm, its proximal and distal widths are about equal and the dorsal process is small. There is an irregular depression on the head, ventral and slightly anterior to the dorsal process. The dorsal process does not form a prominent ridge. The depression appears deeper than is typical of *Ichthyosaurus somersetensis* (Lomax and Massare 2017: fig. 7B), but this could be due to crushing, which gives the appearance of a tall proximal region (Figure. 5.4). Alternatively it might be a pathological deformation (Rothschild and Storrs 2003). About midway down the shaft is a slight expansion of the anterior side. This may be an artefact of crushing. The anterodistal end of the humerus is expanded slightly, but there is no anterior facet.

There are at least five primary digits, identified by the presence of an anterior digital bifurcation (Figure. 5.4). Irrespective of the reconstruction, the bifurcation is present in digit II, at the third phalangeal row. The elements of the bifurcation are much smaller, more circular than the other digits, as is often seen in some specimens of *Ichthyosaurus*, including in the holotype of *I. somersetensis* (DRL personal observation of ANSP 15766). A posterior accessory digit contacts the ulna and extends to almost the distal end of the fin. A second posterior accessory digit is present at the fifth phalangeal row. Digit V is prominent, as in all specimens of the genus. Although a large portion of the forefin is reconstructed, it is clear that the intermedium contacts both distal carpals 3 and 4. This contact rules out any suggestion of the specimen being an example of *Protoichthyosaurus* (Appleby 1979; Lomax and Massare in press).



Figure. 5.6. Hindfins and pelvis of *Ichthyosaurus somersetensis* Lomax and Massare, 2017 (NLMH 106234) from the Lower Jurassic (lower Hettangian) of Doni ford Bay, Watchet, Somerset, UK. The right hindfin (**B**) is the more complete of the two, exposed in dorsal view. The left hindfin (**A**) is in ventral view. Abbreviations: 2, tarsal two; 3, tarsal three; 4, tarsal four; a, astragalus; bi, bifurcation; c, calcaneum; fi, fibula; ii, metatarsal 2; il, ilium; is, ischium; pu, pubis; ti, tibia.

Pelvic girdle and hindfin

The pelvis is tripartite, as in all species of *Ichthyosaurus* (Lomax and Massare 2017; Figure. 5.6). Both ilia are present and probably exposed in lateral view. The right ilium, identified as that closest to the skull, is damaged proximally, thus the description is based upon the left ilium (Figure. 5.6). The ilium is more oblong, than rib-like, as in other species of the genus (Lomax and Massare 2017). It is slightly curved, with the concave side presumably facing posteriorly, although the orientation of the element makes this difficult to confirm. It is marginally shorter than the ischium, but about the same length as the pubis. The ilium has a fork-like proximal end, which is an unusual trait that, to our knowledge, has not been reported in any other Lower Jurassic ichthyosaur. A lateral ridge runs from the middle of the ilium to the proximal end, where it is flared. This ridge is also present on the damaged right ilium. The central portion of the fork-like proximal end is separated from both lateral ridges and extends further proximally. This morphology has not previously been reported in any species of *Ichthyosaurus*, although the lateral ridge is reminiscent of the ilium in BRSMG Ce 16611, another *Ichthyosaurus* specimen with an embryo. It is possible that this morphology may be due to pathology. The ischium is the longest of the pelvic elements. It is elongate and robust, compared to either the ilium or pubis, and is only slightly flared proximally. The pubis has a very narrow shaft with a widely expanded, “fan” shaped, distal end. This pubis morphology is present in several examples of *Ichthyosaurus* spp., including BRSMG Ce16611 and NHMUK R3372, which both contain embryos.

Both hindfins are preserved. The more complete, preserved closest to the skull and identified as the right, is exposed in dorsal view, whereas the left hindfin is exposed in ventral view. The femur is long relative to its distal width. Its anterodistal end has an anterior facet and the posterodistal end is expanded posteriorly. The dorsal process is offset anteriorly. The ventral process is more centrally located, but is slightly offset anteriorly. The fibula is anteroposteriorly wider than the tibia but is proximodistally about the same length. Tarsal 2, the first element of the bifurcation, and the first two phalanges are notched, although the shape of the notch differs, as has been reported in some specimens of *Ichthyosaurus* (Massare and Lomax 2016a: fig 10). There is one element (tarsal 3) in broad contact with the astragalus. However, a bifurcation of tarsal 2 is present, which results in four elements in the third row. We identify the anterior branch of digit II as the bifurcation. A small portion

of metatarsal 2 contacts the astragalus. This differs from the condition described by Lomax and Massare (2017), who found that *I. somersetensis* had only one element (tarsal 3) directly in contact with the astragalus, with three elements in that row, and a bifurcation in a more distal row. In NLMH 106234, a distal bifurcation is present at the fourth phalangeal row, similar to that seen in NHMUK OR2013*. A posterior accessory digit is also present in the right hindfin, but is incomplete.

Embryo

The embryo is positioned between the ribs, near the mid-posterior dorsal vertebrae, on the block posterior to the crack (Figures. 5.2B, 7). There are 23 centra preserved in the embryo, although only 16 are articulated or associated. Of the articulated section, the 11th vertebra, counted from the left, is poorly preserved and/or partly missing; it may have been restored (Figure. 5.7A). The articulated vertebral column is 6.37 cm long. It is not possible to identify the exact portion within the column. However, some loose and isolated centra are very round and could belong to dorsal vertebrae. This may suggest that the articulated section also comprises dorsal centra, which would be consistent with the interpretation of the fin as a forefin. Numerous delicate ribs are preserved; some fragments are in articulation with the vertebral column whereas others are lying in the matrix. A very small partial fin is preserved, which is probably the forefin. The total length is 1.84 cm, but the humerus is missing or buried. Four primary digits are evident, although a fifth primary digit may be present, indicated by a possible distal bifurcation (Figure. 5.7B). It appears that the ?radiale, ?distal carpal, and ?metacarpal are notched. This may, however, be an artefact of preservation (Figure. 5.7). All of the forefin elements are highly cancellous, displaying a spongy texture. The rim of many of the phalanges possesses a “bottle-cap” like morphology, suggestive of poorly ossified bone, or perhaps calcified cartilage. Similar preservation is also present in very small examples of *Ichthyosaurus* (e.g., BU 5289). A large element, proximal to the fin, is too long to be the humerus and is probably the scapula, which is expanded proximally.



Figure. 5.7. Embryo of *Ichthyosaurus somersetensis* Lomax and Massare, 2017 (NLMH 106234) from the Lower Jurassic (lower Hettangian) of Doniford Bay, Watchet, Somerset, UK. **A.** Articulated vertebral column, isolated forefin, probable scapula (white arrow), ribs, and isolated centra. **B.** Close-up of the forefin. Arrows point to probable notching of the ?radiale, ?distal carpal, and ?metacarpal.

Discussion and conclusions

Despite NLMH 106234 being a composite, the specimen provides important new information on *Ichthyosaurus somersetensis*. In the diagnosis for *I. somersetensis*, Lomax and Massare (2017) stated that the species has one element (tarsal 3) in broad contact with the astragalus, with a total of three elements in that row (third row). In NLMH 106234, tarsal 3 is in broad contact with the astragalus but a bifurcation of tarsal 2 results in four elements in the third row (Figure. 5.6). Metatarsal 2 also contacts the astragalus. In addition, both the proximal element of the bifurcation and metatarsal 2 are smaller than tarsals 3 and 4. This has not been reported for the species so far, and shows that the hindfin of *I. somersetensis* is more variable than previously thought. This hindfin morphology, however, is present in other species of the genus as well (Lomax and Massare 2017; DRL personal observation) and so hindfin morphology must be used in conjunction with other features to assign a specimen to *I. somersetensis*.

The ilium morphology of NLMH 106234 is unusual and may reflect individual variation, pathology, or could be size related. It is possible that this morphology is

present in other specimens, but has gone unnoticed because the ilium must be well-preserved and exposed in a particular orientation in order to see the morphology. For example, in the holotype of *I. somersetensis* (ANSP 15766) the ilium is overlain by ribs and the proximal end cannot be examined in detail. Regardless, the morphology of the ilium in NLMH 106234 provides new information.

Only two other Lower Jurassic genera have been reported with embryos. *Stenopterygius*, which is known from multiple specimens from the Toarcian (McGowan 1979) and *Leptonectes*, which is known from a single specimen from the Hettangian (Lomax and Massare 2012). NLMH 106234 is the third *Ichthyosaurus* specimen from Somerset to be found with an embryo and the first to be positively identified to species level. However, the two other *Ichthyosaurus* specimens with embryos (NHMUK R3372 and BRSMG Ce16611) may also be *I. somersetensis*. Each of the three gravid females contain just one embryo. This may be because remains of other embryos have not been preserved or were unknowingly removed during preparation. Alternatively, the presence of a single embryo may suggest that *Ichthyosaurus* carried just one embryo. But without more specimens, it is not possible to confirm this observation.

Lomax and Massare (2015) discussed possible sexual dimorphism in the humerus morphology of *Ichthyosaurus anningae*. A feature that they recorded was the presence of an anterior facet on the humerus of some specimens, which they hypothesized could be because male *I. anningae* required additional musculature in the forefin to position themselves during mating. Lomax and Massare (2015) also noted that the anterior facet is seen in other species, but not on all specimens. Clearly, NLMH 106234, BRSMG Ce 16611 and NHMUK R3372 are females. All three specimens lack an anterior facet on the humerus. In addition, Lomax and Massare (2017) noted that some, but not all specimens of *Ichthyosaurus*, have a pubis with a very broad and asymmetric, almost “fan” shaped, distal end. They suggested that this may also be a sexually dimorphic character. All three gravid females of *Ichthyosaurus* have this pubis morphology. Thus, the lack of an anterior facet in the humerus and an identically shaped, distally broad pubis in all three specimens lends support for these characters being sexually dimorphic.

The length of the skull, jaw and estimated total body length of NLMH 106234 are the largest published records of an unequivocal example of *Ichthyosaurus*. It is also the hitherto largest example of *I. somersetensis* known.

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Chapter 6: The first known neonate *Ichthyosaurus communis* skeleton: a rediscovered specimen from the Lower Jurassic, UK

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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 *Ichthyosaurus* are known, but only very few small examples (total length of < 1 m) have been assigned to a species of *Ichthyosaurus*. Here, we report on a very small specimen (preflexural length of 560 mm) that can be unequivocally assigned to *Ichthyosaurus 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 *I. 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.

Key words: *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 *Ichthyosaurus* is *I. 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 *Ichthyosaurus* is *I. somersetensis*, with a total length of over 3 m (Lomax and Sachs 2017). Other unequivocal examples of the genus have also been reported with an estimated total length of around 3 m (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. Their small size suggests they are probably juveniles, but a detailed study of *Ichthyosaurus* 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. conybeari* (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 *Ichthyosaurus* sp., although both specimens are probably referable to *I. somersetensis* (Lomax and Sachs 2017). The referral of a specimen,

large or small, to species often requires a nearly complete skeleton or a well-preserved skull. Here, we report the smallest known specimen positively identified as *Ichthyosaurus communis* (Figure. 6.1). Unfortunately, no provenance or stratigraphic information was known for the specimen, therefore an analysis of the matrix was undertaken.



Figure. 6.1. Specimen BU 5289, an almost complete neonate skeleton of *Ichthyosaurus communis*. Scale equals 10 cm.

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 H₂O₂ (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. 6.1).

The occurrence of the particular foraminifera species and subspecies (Table. 6.1; Figure. 6.2), 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. 6.3).

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 noted to contain a microfaunal assemblage similar to that known from Hock Cliff, Gloucestershire, which led Massare and Lomax (2017a) to record the specimen as originating from Gloucestershire, from where Lower Jurassic ichthyosaurs have been recorded (Benton and Spencer 1995).

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 three-dimensional models even with high-end processing hardware (e.g. an Intel i7 Processor, NVIDIA GPU). Therefore the TIFF files were cropped and turned into greyscale JPGs, using 'Blender 3D' (v2.78) compositing tools. The more

Table. 6.1. Microfossils found during the matrix analysis of BU 5289. 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. 6.2.

FORAMINIFERA	OSTRACODA
<i>Marginulina prima incisa</i>	<i>Monoceratina frentzeni</i>
<i>Marginulina prima insignis</i>	<i>Ogmoconcha hagenowi</i>
<i>Marginulina prima praerugosa</i>	<i>Polycope pumicosa</i>
<i>Astacolus speciosus</i>	<i>Ogmoconchella nasuta</i>
<i>Planularia inaequistriata</i>	<i>Paracypris</i> sp.A
<i>Paralingulina tenera tenuistriata</i>	
<i>Mesodentalina matutina</i>	
<i>Nodosaria mitis</i>	
<i>Pseudonodosaria multicostata</i>	
<i>Nodosaria metensis</i>	
<i>Ichthyolaria terquemi sulcata</i> (6-ribbed variant)	
<i>Dentalina pseudocommunis</i>	
<i>Lenticulina</i> sp.	

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.

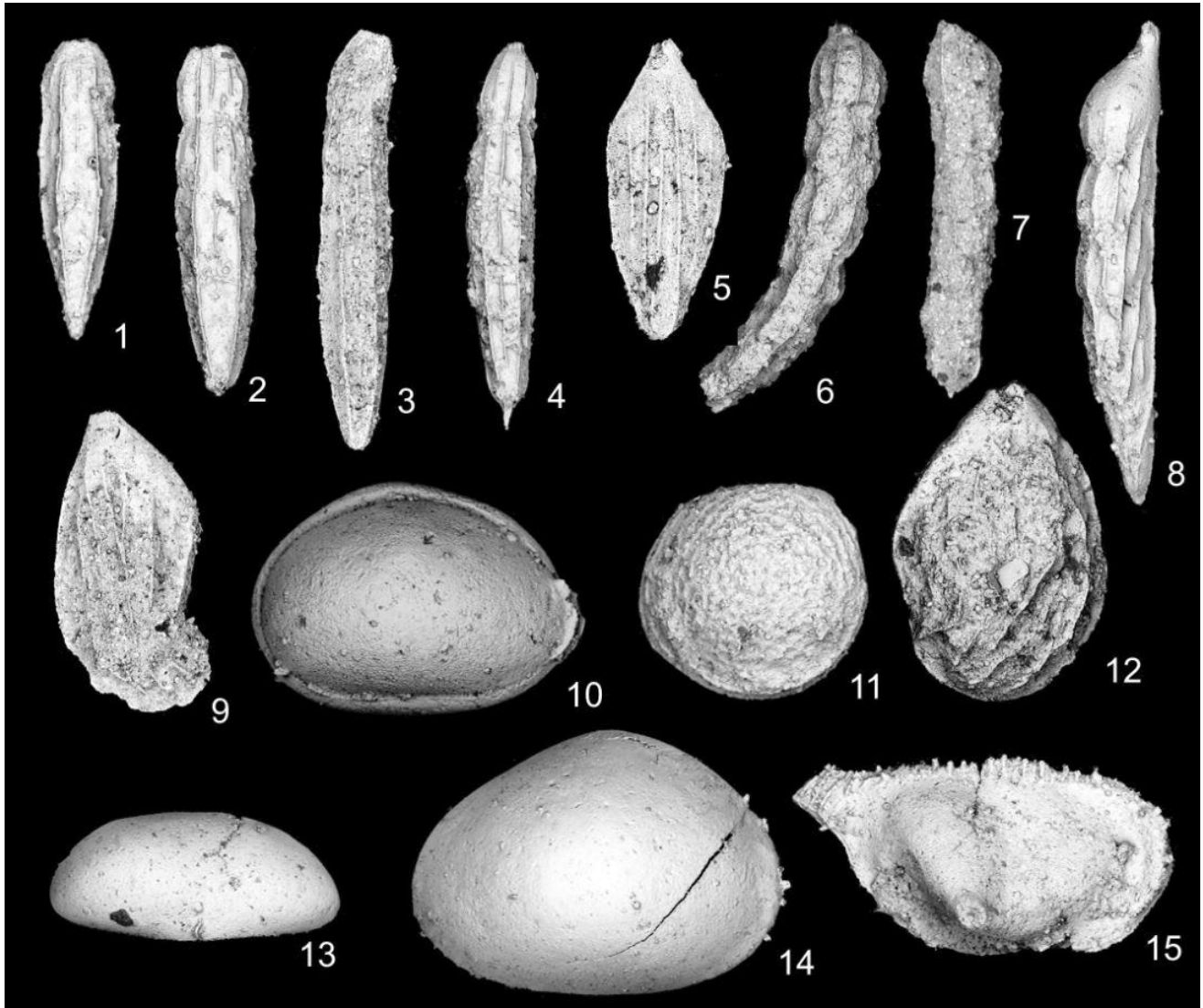


Figure. 6.2. Photomicrographs of the most abundant and/or stratigraphically important taxa from the sediment matrix of BU 5289. 1-3. *Paralingulina tenera tenera*. 1. 640 μm . 2. 790 μm . 3. 1075 μm . 4. *Nodosaria mitis*. 800 μm . 5. *Ichthyolaria terquemi* (4-ribbed type). 6. *Marginulina prima insignis*. 1290 μm . 7. *Marginulina prima incisa*, 925 μm . 8. *Mesodentolina 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 .

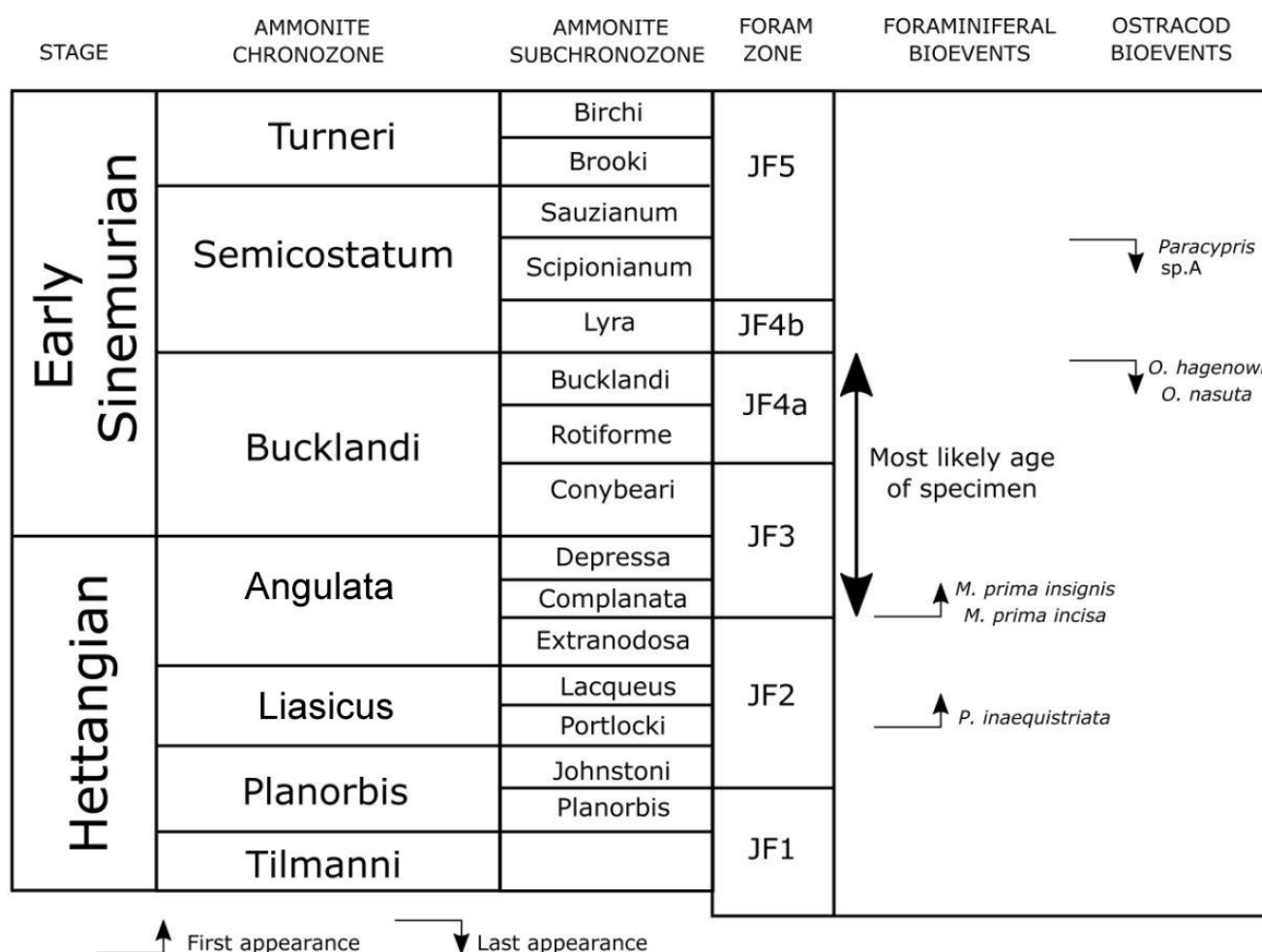


Figure. 6.3. Chronobiostratigraphy of the Early Jurassic interval with key biostratigraphic marker events noted. These confine the likely age of BU 5289 to the Liasicus Ammonite Chronozone or Bucklandi Ammonite Chronozone.

Description

Introduction

Specimen BU 5289 is a practically complete skeleton lying on its left side, exposed in lateral view (Figure. 6.1). The preserved total length (including the skull) is 590 mm and the preflexural length is 560 mm; most of the postflexural region is missing. It comprises a well-preserved 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 *Ichthyosaurus 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.

Stenopterygius 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/spongy (Figure. 6.4). 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. 6.4D). 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. 6.4C). The spongy 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. 6.5). 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. 6.5). 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



Figure. 6.4. 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.

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 nasal, 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. 6.2), 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 young individuals of *I. communis* have proportionally shorter snouts than older individuals. That said, Lomax and Massare (2015) questioned 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. 6.5A). 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. 6.5B).

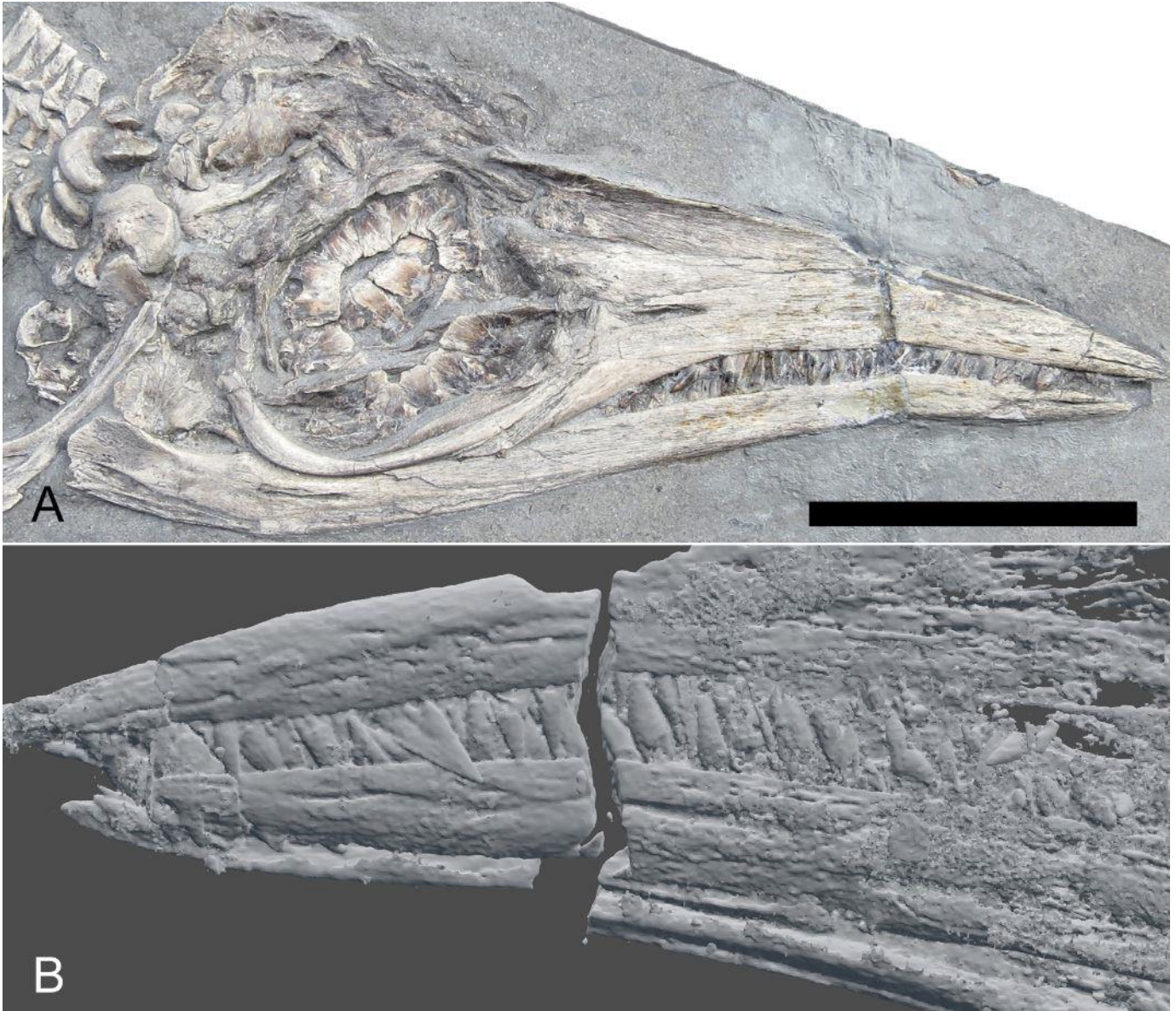


Figure. 6.5. A. Close-up of the skull and mandible of BU 5289. Note, the ‘downturn’ of the snout is not genuine and is a result of the crack across the premaxilla and dentary, which has not been realigned correctly. B. Micro-CT scan of snout with close-up of the reverse side (not exposed), showing well-preserved teeth with crowns. Scale equals 5 cm.

Table. 6.2. Measurements of BU 5289 (in centimetres), a neonate *Ichthyosaurus communis*. ‘Width’ for fin elements refers to the anteroposterior dimension, perpendicular to the long axis of the fin. L and R denote measurement of left or right skeletal elements. Asterisk denotes an estimate because the bone is damaged, rotated, or partially buried. The precaudal and preflexural length includes the skull.

Skull length	15.53
Preorbital length	*9.35
Mandible length	15.8
Orbit height	*3.81
Orbit length	*4.27
Coracoid ant-post length	2.59R 2.74L
Coracoid med-lat length	2.02R
Humerus length	*1.2?R
Femur length	1.17R 1.23L
Femur proximal width	0.68R 0.72L
Femur distal width	0.82R 0.8L
Ischium length	1.52
Precaudal length	42.3
Preflexural length	56
Total preserved length	59

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. 6.1). 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. 6.2). It has both well-developed anterior and posterior notches (Figure. 6.6). 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. 6.6-6.7). 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. 6.6). 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. 6.7). 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. 6.6-6.7). It appears to be roughly centrally located and there appears to be a rim that outlines a smooth articular surface (Figure. 6.7A). 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. 6.7B). 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. 6.7). 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. 6.4D, 6.7). There may be at least one posterior accessory digit.



Figure. 6.6. 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.

Pelvic Girdle and Hindfin

The pelvis, although incomplete, is tripartite, as in all species of *Ichthyosaurus* (Figure. 6.8). 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. 6.8). The femur is highly cancellous, especially in the proximal region and distal end; it is most noticeable on the left femur (Figures. 6.4F; 6.8). 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 and hindfin 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.

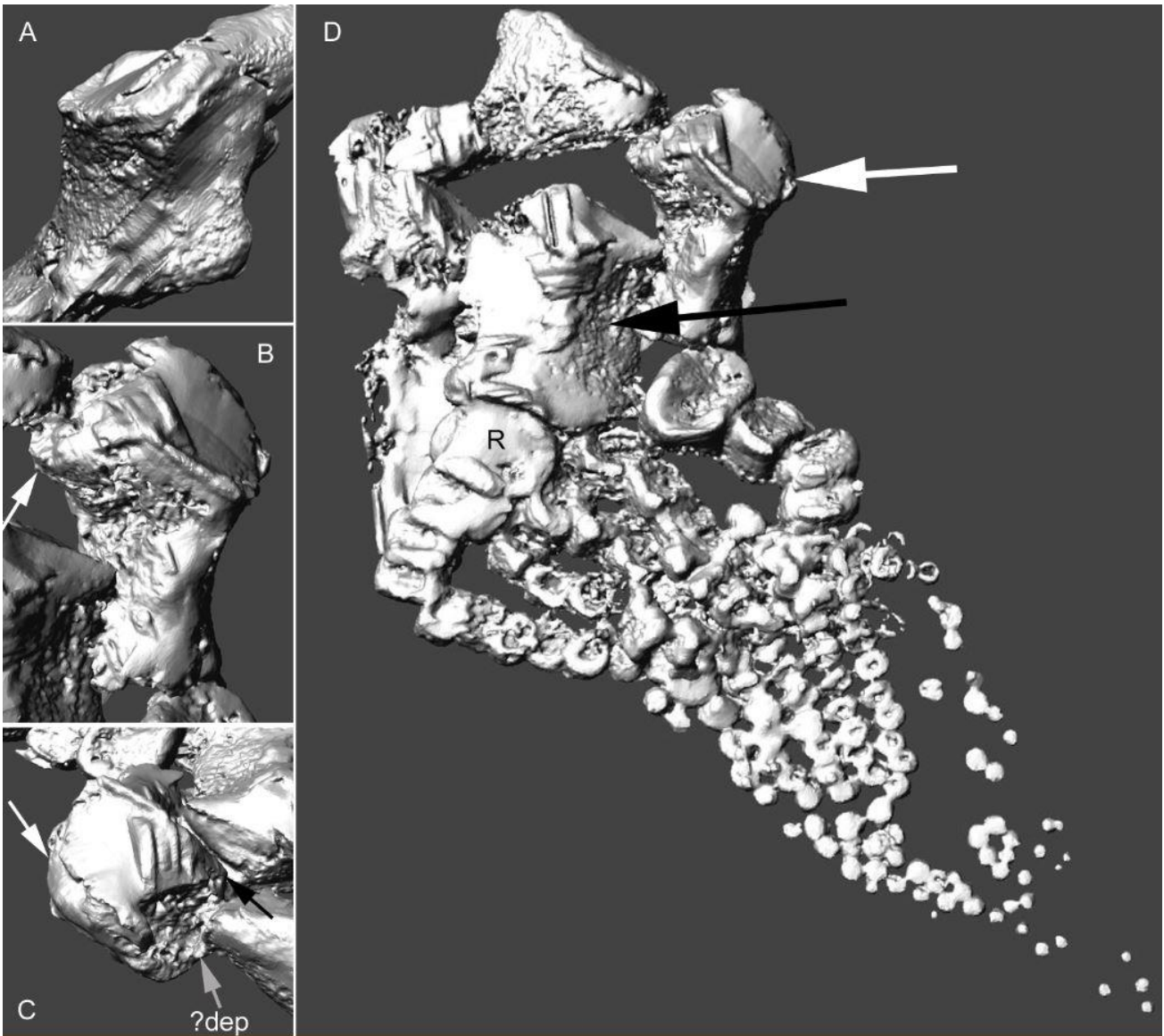


Figure. 6.7. Micro-CT scans of the forefin(s) of BU 5289. A. (?)Right humerus in ventral view, anterior to the left. The deltopectoral crest appears to be centrally located. B. (?)Right humerus in posterodorsal view; the arrow points to the dorsal process. C. Proximal surface of the (?)right humerus. 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. 6.8. 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.

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. 6.9). 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. 6.9). 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.

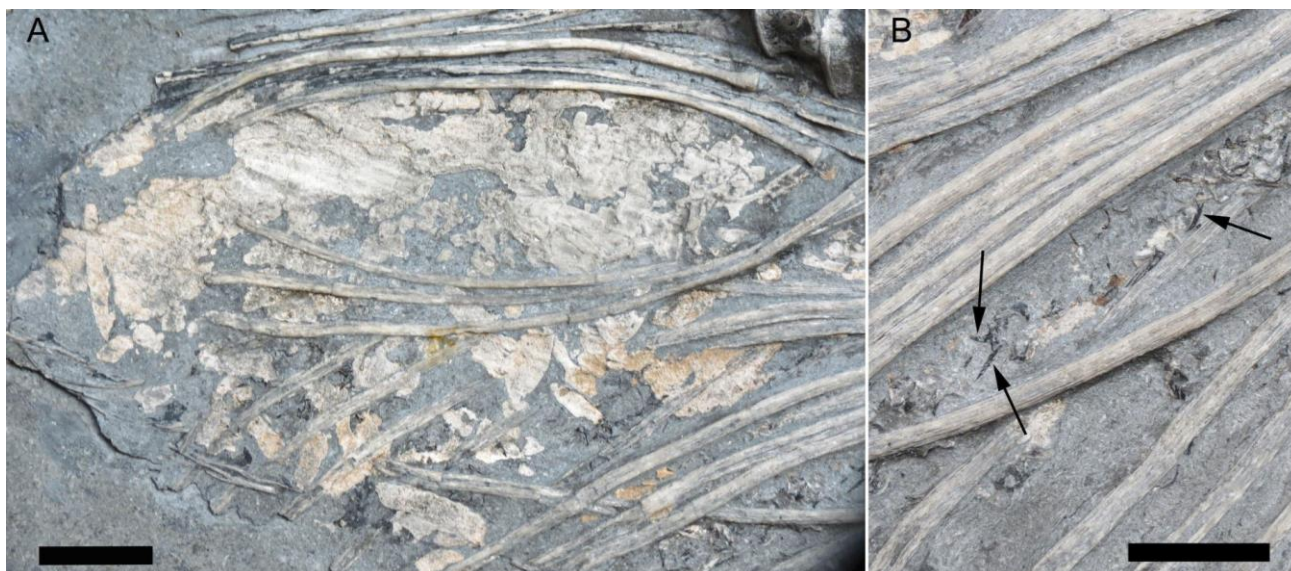


Figure. 6.9. A. Probable bromalitic material preserved between the ribs of BU 5289. B. Several black cephalopod hooklets preserved between the ribs of BU 5289. Note, arrows point to the more complete hooklets. Scale bars equal 1 cm.

This research highlights the significance of detailed, osteological comparison of small *Ichthyosaurus* examples with large examples in order to positively identify specimens beyond *Ichthyosaurus* sp. It is surprising, given the number of small *Ichthyosaurus* specimens known, that only a few small examples have been confidently assigned beyond *Ichthyosaurus* 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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Chapter 7: Hindfins of *Ichthyosaurus*: effects of large sample size on ‘distinct’ morphological characters

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Hindfins of *Ichthyosaurus*: effects of large sample size on 'distinct' morphological characters

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Abstract

The abundance of specimens of *Ichthyosaurus* provides an opportunity to assess morphological variation without the limits of a small sample size. This research evaluates the variation and taxonomic utility of hindfin morphology. Two seemingly distinct morphotypes of the mesopodium occur in the genus. Morphotype 1 has three elements in the third row: metatarsal two, distal tarsal three, and distal tarsal four. This is the common morphology in *Ichthyosaurus breviceps*, *I. conybeari*, and *I. somersetensis*. Morphotype 2 has four elements in the third row, owing to a bifurcation. This morphotype occurs in at least some specimens of each species, but it has several variations distinguished by the extent of contact of elements in the third row with the astragalus. Two specimens display a different morphotype in each fin, suggesting that the difference reflects individual variation. In *Ichthyosaurus*, the hindfin is taxonomically useful at the genus level, but species cannot be identified unequivocally from a well-preserved hindfin, although certain morphologies are more common in certain species than others. The large sample size filled in morphological gaps between what initially appeared to be taxonomically distinct characters. The full picture of variation would have been obscured with a small sample size. Furthermore, we have found several unusual morphologies which, in isolation, could have been mistaken for new taxa. Thus, one must be cautious when describing new species or genera on the basis of limited material, such as isolated fins and fragmentary specimens.

Key words: Lower Jurassic, Ichthyosauria, Ichthyosauridae, tarsus, intraspecific variation, pathology

Introduction

Lower Jurassic ichthyosaurs are known from thousands of specimens, although not all of them are sufficiently complete to assign to a species. Most Lower Jurassic genera can, however, be distinguished from one another by a few key postcranial elements, such as the forefin, humerus, coracoid, or pelvic girdle, in the absence of a skull. In fact, the genus *Ichthyosaurus* has an unusual forefin that easily distinguishes it from all other genera. The anterior digital bifurcation (shared only with *Protoichthyosaurus*, Lomax *et al.*, 2017a) and a prominent digit V gives the forefin a unique morphology (Motani, 1999). Forefins of *Ichthyosaurus* are extremely variable in the digit that bifurcates (digit II or III), the location of the bifurcation on the digit, the number of bifurcations in the fin, and the relative size of the branches of the bifurcation, even within a species. Although an isolated forefin can be identified as *Ichthyosaurus*, species assignment within the genus usually requires a well-preserved skull. Thus identification of postcranial features that are unique to a particular species of *Ichthyosaurus* can provide additional criteria for species identification that can be applied to partial skeletons or those with poorly preserved skulls.

Hindfins have been largely ignored in ichthyosaur taxonomy, probably in part because they are less frequently preserved than skulls and anterior portions of the postcranium. Hindfins are much smaller than forefins in some Jurassic ichthyosaurs, and so are more vulnerable to disarticulation and transport by currents before fossilization. When compared with the forefin, even comprehensive phylogenetic analyses incorporate relatively few hindfin characters (e.g. Ji *et al.*, 2016; Fischer *et al.* 2013; Maxwell *et al.* 2012). This research explores the potential for using hindfin morphology to distinguish species of the Lower Jurassic genus *Ichthyosaurus*.

The genus presently has six species: *Ichthyosaurus communis*, *I. breviceps*, *I. conybeari*, *I. anningae*, *I. larkini*, and *I. somersetensis*, distinguished largely by features of the skull (McGowan, 1974; Lomax and Massare, 2015, 2017; Massare and Lomax, 2017). *Ichthyosaurus* is thus one of the most speciose genera of parvipelvian ichthyosaurs. In fact, many of the genera recognised recently are monotypic, making *Ichthyosaurus* seem even more unusual for its large number of species. Moreover, several new genera of parvipelvian ichthyosaurs are presently known from just one specimen (e.g. *Malawania*, Fischer *et al.* 2013; *Muiscasaurus*,

Maxwell *et al.* 2016; *Keilhauia*, Delsett *et al.* 2017). In contrast, hundreds of well-preserved specimens of *Ichthyosaurus* are in museum collections worldwide, especially in the UK.

Most of the fairly complete skeletons of *Ichthyosaurus* were collected in the 19th century, mainly from the west Dorset coast (Lyme Regis-Charmouth area) and quarries in Somerset (near the village of Street), although the genus is known from elsewhere (Massare and Lomax, 2017). This study examined nearly 100 specimens of *Ichthyosaurus* with hindfins that are sufficiently well-preserved to provide morphological information. The hindfins display two distinct morphologies of the mesopodium (tarsus), as a result of a bifurcation of digit II. The large number of specimens has resulted in a more complete picture of hindfin variation, which would not have been possible with a small sample size. What could have been interpreted as unique morphologies are actually end-members of a continuum of individual variation. This has implications for identifying unique diagnostic characters (autapomorphies) based on limited fossil material.

Institutional abbreviations. ANSP, Academy of Natural Science of Drexel University, Philadelphia, PA, USA; BGS, British Geological Survey, Keyworth, Nottingham, UK; BELUM, Ulster Museum, National Museum of Northern Ireland, Belfast, UK; BRLSI – Bath Royal Literary and Scientific Institution, UK; BRSMG, Bristol City Museum and Art Gallery, UK; BRSUG, University of Bristol, UK; BU, Lapworth Museum of Geology, University of Birmingham, UK; CAMSM – Sedgwick Museum, Cambridge University, UK; CC, Cliffe Castle Museum, Bradford, UK; CCHC, Charmouth Heritage Coast Centre, Dorset, UK; CLC, Cheltenham Ladies College, UK; CHMUS, Charterhouse School Museum, Surrey, UK; CMNH, Cleveland Museum of Natural History, Ohio, USA; DBYMU, Derby Museum and Art Gallery, UK; DORCM, Dorset County Museum, UK; FMNH, Field Museum, Chicago, IL, USA; GLAHM, Hunterian Museum, University of Glasgow, UK; GLRCM, Gloucester City Museum, UK; HEM, Haslemere Educational Museum, Surrey, UK; LEICT, Leicester Arts and Museums Service (New Walk Museum and Art Gallery), England; MANCH, Manchester Museum, The University of Manchester, UK; LMG, Leeds Museums and Galleries, UK; NHMUK (formerly BMNH), The Natural History Museum, London, UK; NLMH, Niedersächsisches Landesmuseum (Lower Saxony State Museum), Hannover, Germany; NMING, National Museum of Ireland, Dublin, Ireland; NMW, National

Museum of Wales, Cardiff, UK; NOTNH, Nottingham Natural History Museum (Wollaton Hall), UK; OUMNH, Oxford University Museum of Natural History, UK; PETMG, Peterborough Museum and Art Gallery, UK; RAMM, Royal Albert Memorial Museum, Exeter, UK; ROM, Royal Ontario Museum, Toronto, Canada; SHEFFM, Weston Park Museum, Sheffield, UK; SMNS, Staatliches Museum für Naturkunde (Stuttgart State Museum of Natural History), Germany; SOMAG (formerly AGC), Alfred Gillett Collection, cared for by the Alfred Gillett Trust (C & J Clark Ltd), Street, UK; TM, Teylers Museum, Haarlem, Netherlands; TTNCM, Somerset County Museum, Taunton, UK; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; WARMS, Warwickshire Museum, Warwick, UK; WFIS, Wagner Free Institute of Science, Philadelphia, PA, USA; WOSMG, Worcester City Art Gallery and Museum, UK; YPM, Peabody Museum, Yale University, New Haven, CT, USA.

Material

We examined 99 specimens of *Ichthyosaurus* with at least one hindfin that provided morphological information (Table. 7.1). Twenty-four specimens had two informative hindfins. Most hindfins were associated with a skeleton or significant portion of a skeleton, but some specimens were isolated or associated with pelvic bones and/or a few centra (ANSP 10123, BRLSI GP1870, GLAHM V1165, GLRCM 1987.45 [formerly GLRCM 938], MANCH L9664, NHMUK OR35567, NHMUK R5790, NHMUK R5918, NOTNH FS3450, OUMNH J.29351, OUMNH J.95338, and RAMM 124-2009). Other specimens with partial hindfins exist, but they are too incomplete and/or too disarticulated to provide morphological information. Many of the specimens examined, however, were not sufficiently complete to assign to species (Table. 7.1).

Table. 7.1. Specimens that were used in this study with at least one informative hindfin.

Specimen No.	Species	Morph	Location
ANSP 10123	<i>I. somersetensis</i>	2	possibly Dorset†
ANSP 15766		1	Somerset

ANSP 17429		?1	possibly Dorset†
BGS 955	<i>I. breviceps</i>	2	Dorset
BGS 956	<i>I. conybeari</i>	1	Dorset
BGS RGSCU1091		1	Somerset
	possible		
BRLSI GP1870	composite	1	
BRLSI M3559	<i>I. somersetensis</i>	1 & 2	possibly Somerset†
BRLSI M3572	composite	1	
BRSMG Ce16611	<i>I. somersetensis</i>	2	Somerset
BRSUG 25300	<i>I. larkini</i>	2	Somerset
BU 5289	<i>I. communis</i>	2	
CAMSM J35186		2	Leicestershire
CAMSM J35187	<i>I. communis</i>	np	Dorset
CAMSM J35188	<i>I. communis</i>	1	Dorset
CAMSM J35289	<i>I. ?communis</i>	2	Dorset
CAMSM J59574	<i>I. somersetensis</i>	2	Somerset
CAMSM J59575	composite	2	Somerset
CAMSM X50224	<i>I. conybeari</i>	np	Dorset
[formerly TN910]			
CAMSM X50187	<i>I. breviceps</i>	2	Dorset
CC BMT 03526		2	Dorset
CCHC2	<i>I. breviceps</i>	1	Dorset
CHMUS 2015.0102	<i>I. ?communis</i>	2	
			Cotswolds area,
CLC1	<i>I. somersetensis</i>	2	possibly
			Gloucestershire
CMNH 11088		2	Dorset
DBYMU 1877-16		2	Leicestershire
DORCM G1		2	Dorset
FMNH P25027	<i>I. communis</i>	2	Dorset
GLAHM V1030		2	possibly Somerset†
GLAHM V1032		2	Dorset
GLAHM V1165		1	Dorset
GLAHM V1179		2	Dorset
GLRCM 1987.45		1 & 2	
[formerly 938]			
HEM GF.6.3190		?1	Dorset
LEICT G125.1992		2	Leicestershire
			possibly
MANCH L.9664		2	Leicestershire†
NHUK OR120	<i>I. anningae</i>	2	Dorset
NHUK OR2001*	<i>I. ?breviceps</i>	2	Dorset
NHUK OR2013	<i>I. somersetensis</i>	1	Somerset
NHUK OR2013*	<i>I. somersetensis</i>	1	Somerset
NHUK OR2017		1	Somerset

NHМУK OR2024*		1	Somerset
NHМУK OR2025*		1	Somerset
NHМУK OR8165		2	Leicestershire
	<i>I.</i>		
NHМУK OR14563	<i>?somesetensis</i>	1	possibly Somerset†
NHМУK OR14565	<i>I. somesetensis</i>	2	Somerset
NHМУK OR14567	<i>I. somesetensis</i>	1	Somerset
NHМУK OR35567		2	Dorset
NHМУK OR36256	<i>I. communis</i>	2	Dorset
NHМУK OR41849		2	Dorset
NHМУK OR43006	<i>I. breviceps</i>	1	Dorset
NHМУK OR85791		2	Dorset
NHМУK R44	<i>I. somesetensis</i>	1	Somerset
NHМУK R1073	<i>I. communis</i>	2	Dorset
NHМУK R1162	<i>I. communis</i>	2	Dorset
NHМУK R1212		2	Dorset
[display specimen]			
NHМУK R1696		2	Dorset
NHМУK R3372	<i>I. somesetensis</i>	1	Somerset
NHМУK R5790	<i>I. conybeari</i>	2	Dorset
NHМУK R5918		2	Dorset
NHМУK R5595	<i>I. larkini</i>	2	Somerset
NHМУK R10028	<i>I. anningae</i>	np	?Dorset
NHМУK R11199		2	Dorset
NHМУK R11801	<i>I. ?conybeari</i>	2	possibly Dorset†
NHМУK R15907	<i>I. conybeari</i>	np	Dorset
NLMH 106234	<i>I. somesetensis</i>	2	Somerset
NMW 91.29G.1		2	Dorset
NMW 93.5G.1	<i>I. conybeari</i>	np	Somerset
NMW 33.401.G2		2	
NOTNH FS3450		2	probably Somerset†
NOTNH FS4940		2	Nottinghamshire
NOTNH FS13759		2	
OUMNH J.10325		2	Somerset
OUMNH J.10342/p		2	Somerset
OUMNH J.13592		2	Dorset
OUMNH J.13799	<i>I. somesetensis</i>	2	Somerset
OUMNH J.29351		2	Dorset
OUMNH J.29352		2	Dorset
OUMNH J.95338		2	Dorset
PETMG R174	<i>I. communis</i>	2	Dorset
RAMM 57/2009		2	
RAMM 124/2009	<i>I. conybeari</i>	2	Dorset
ROM 26029	<i>I. somesetensis</i>	2	probably Somerset†

SMNS 58275	<i>I. conybeari</i>	2	Dorset
SOMAG/GEO/11	<i>I. larkini</i>	2	Somerset
SOMAG/GEO/16	<i>I. somersetensis</i>	?1	Somerset
SOMAG/GEO/17	<i>I. somersetensis</i>	1	Somerset
TM F002727	<i>I. ?breviceps</i>	1	Dorset
	<i>I.</i>		
TTNCM 120-1996	<i>?somesetensis</i>	2	Somerset
TTNCM 166-1992		2	Somerset
TTNCM 8349		?1	Somerset
TTNCM 8359		2	probably Somerset†
TTNCM 8373	<i>I. somersetensis</i>	2	Somerset
USNM V4967	<i>I. ?conybeari</i>	2	Dorset
WFIS case 64		2	Dorset
	<i>I.</i>		
WARMS G6188	<i>?somesetensis</i>	1	Warwickshire
WOSMG No 3		2	Worcestershire
YPM 4198	<i>I. somersetensis</i>	1	
YPM 9204	<i>I. ?communis</i>	2	

Note: Two specimens display a different morphotype on each fin. Location is based on museum records or specimen labels, except as noted. Species identifications based on evaluations by authors.

Abbreviations: **Morph**, morphotype; **np**, mesopodium not preserved.

? species or morphotype identification is uncertain.

† assessment by the authors, based on preservation.

Six specimens were not included in the analysis because the authenticity of the arrangement of bones in the hindfins is questionable (Table. 7.2). BRSMG Cb4997 is a fairly complete skeleton of *I. somersetensis* with both the left and right hindfin preserved. All of the fin elements, however, are set in a filler material. We cannot assess whether the current position of the individual bones accurately reflects their original arrangement, so this specimen was not included in this analysis. Likewise, the hindfins of LMG.B.1843.4 have been rebuilt, and so the specimen was not included. A similar situation occurs in BRLSI M3551, a composite specimen in which both hindfins were probably added to the specimen (Massare and Lomax, 2016a). The hindfins themselves are on opposite sides of the vertebral column and surrounded by plaster. It is unclear whether the individual bones are in plaster or matrix. A proximal bone of one fin (?left) is too large to belong with the other elements and it is lying on the 'matrix' rather than within it. Furthermore, the femur is cracked across the shaft and the proximal portion is rotated relative to the distal

portion. Because of these issues, both fins of BRSLI M3551 were excluded from this analysis. A fourth questionable hindfin is NMING F8772, in which the posterior branch of digit II has some elements that are notched and oriented with the notches facing posteriorly rather than anteriorly. Considering that only elements of the leading edge can be notched, it is clear that these elements have been altered from their original orientation. This calls into question whether other elements have been reset into a different arrangement as well. Thus this specimen was also excluded from the analysis. Another specimen excluded is USNM 15152, a composite of probably three individuals. The entire fin is surrounded by plaster and it is unclear whether individual bones are in matrix. The femur is too large for the size of the tibia and fibula, and the elements of the distal half of the fin are probably from a forefin, or at least from a larger individual than the proximal fin. The last specimen excluded is an unnumbered skeleton on display at BELUM. Both hindfins are surrounded by plaster, and the portions distal to the femora appear to be forefins that were added to the specimen.

Three other specimens included in this research might be parts of composite specimens (Table. 7.2). BRSLI GP1870 comprises three blocks of matrix: one with a hindfin, another with a portion of forefin, and the third with some articulated caudal vertebrae, all of which are set in plaster within a wooden frame. The lack of direct association suggests that they might not belong to the same individual, but this is impossible to determine solely by visual examination. BRSLI M3572 is another suspicious specimen in which the skeleton appears to be pieced together from more than one individual (Massare and Lomax, 2016a). In particular, the caudal portion of the vertebral column and the hindfins might not belong to the same individual as the skull and pectoral region or the dorsal vertebral column. One hindfin is adjacent to articulated caudal centra whereas the other is on an isolated block of matrix, surrounded by plaster. The two hindfins have the same morphology and the matrix appears similar, so they probably belong to the same individual, although not necessarily the same individual as the anterior skeleton. In both BRSLI GP1870 and BRSLI M3572, the hindfins themselves are in blocks of matrix and appear to maintain the original arrangement of elements, so the specimens are included in the analysis. CAMSM J59575 is almost certainly a composite specimen in which the anterior and posterior portions of the skeleton do not belong to the same individual (Massare and Lomax, 2016a). The bone colour is different on the presacral skeleton

compared to the hindfin and caudal centra, and the blocks containing these bones are set in plaster and separated from the presacral portion of the skeleton. Although the hindfin of CAMSM J59575 is surrounded entirely by plaster, the hindfin might be at least partially in matrix. The arrangement of bones is consistent with what occurs in other specimens, and so this specimen was included in the analysis. Because of the issue of composites, these three specimens could not be assigned to a species.

Six other specimens were included in the study, but have been partially reconstructed, and require some explanation (Table. 7.2). SHEFFM: H93.188 has both hindfins preserved, but the left (upper) is disarticulated and does not provide any useful information, whereas the right (lower) has been incorrectly rebuilt, in part. The mesopodium is almost complete, with space for metatarsal two, which is missing. Distal to this, the fin is articulated, but set in plaster, with only portions of each digit preserved. The reset piece is, however, reversed relative to the rest of the fin, with the anterior edge facing posteriorly, identified by notching. Furthermore, the bone colour is different from the main specimen, so its authenticity can be questioned. We considered only the mesopodium morphology in this study. BRSUG 25300, the holotype of *I. larkini*, also has some reconstruction (Lomax and Massare, 2017). The distal portions of both fins have been reconstructed from plaster and have a much darker colour than the bone, but the proximal portion of each fin is authentic and provides useful morphological data. Similarly, some of the phalanges distal to the mesopodium of the left hindfin of SMNS 58275 have been restored and partially reset. NHMUK OR14567 is a practically complete skeleton that has the right hindfin preserved. The hindfin is surrounded by paint, which makes it suspicious. It is also on display, high on the wall and behind glass, so a close inspection is not possible. Nevertheless, the arrangement of bones appears to be authentic and so we include it here. The distal portion of each fin of WOSMG No. 3 has been painted to illustrate a complete hindfin. The mesopodium, however, is original bone imbedded in matrix, and so we have included the specimen in this study. Finally, in NHMUK R5790, an isolated hindfin, the femur is reversed relative to the rest of the hindfin, with the anterior end pointing posteriorly. The femur has probably been reset incorrectly.

Table. 7.2. Composite, unreliable, or reconstructed specimens. Some composite specimens were included in this study because hindfins were unaltered and preserved in matrix. See text for additional information.

Specimen No.	Comments
BELUM display specimen (no number)	Both hindfins surrounded by plaster. Fins appear to be forefins.
BRLSI GP1870	Hindfin block might not belong with associated material.
BRLSI M3551	Hindfins probably added to specimens; elements set in plaster so arrangement unreliable.
BRLSI M3572	Hindfins might not belong with anterior skeleton.
BRSMG Cb4997	Elements reset on both fins so arrangement unreliable.
BRSUG 23500	Distal portion of both fins are reconstructed using a modelling material for the elements, but proximal portions are in matrix.
CAMSM J59575	Hindfin probably does not belong with anterior skeleton.
LCM B.1843.4	Elements reset on both fins so arrangement unreliable.
NHМУK R5595	Left fin may have been reset into plaster incorrectly or has post-mortem displacement of digit II.
NHМУK R5790	Femur reversed relative to the rest of the fin.
NHМУK OR14567	Hindfin surrounded by painted plaster, but arrangement seems authentic; inaccessible for close examination.
NMING F8772	Some elements anteroposteriorly reversed and reset, so arrangement unreliable.
SHEFFM: H93.188	Section distal to astragalus/calcaneum set in plaster and orientation reversed, so distal arrangement unreliable.
SMNS 58275	Some elements distal to the mesopodium on left fin reconstructed and reset, so arrangement unreliable.

USNM 15152	Femur too large for tibia and fibula; distal fin does not belong with proximal fin.
WOSMG No. 3	Elements distal to mesopodium (right fin) or first phalangeal row (left fin) are painted on plaster.

Hindfin development and homology

The primitive ichthyosaurian hindfin has been greatly modified in parvipelvian ichthyosaurs. As in all other Merriamosauria, parvipelvians have lost digit I in the hindfin (Ji *et al.*, 2016). The tibia and fibula are polygonal bones that lack a shaft or even an anteroposterior constriction. Polygonal tarsal and metatarsals have broad contacts with adjacent bones, sometimes interlocking, and thus make the determination of homologies challenging. The problem is complicated by the presence of accessory digits (e.g. *Ophthalmosaurus*, *Platypterygius*) or digital bifurcations (e.g. *Ichthyosaurus*, *Protoichthyosaurus*). Additionally, *Ichthyosaurus* has lost digit V in the hindfin, as have other Lower Jurassic ichthyosaurs (e.g., *Leptonectes*, *Eurhinosaurus*), although Lomax and Massare (2017) incorrectly identified a digit V in *I. larkini* and *I. somersetensis*. In reptiles, digit I is the first to be lost when digit reduction occurs, and, if reduction continues, digit V is the next one to be lost (Bakker *et al.*, 2013). Because of digital bifurcations, however, *Ichthyosaurus* has more than just these three digits in the hindfin (see section 6b).

Because the limbs of ichthyosaurs are so derived compared to those of terrestrial reptiles, three terminologies have been used to identify elements of the mesopodium in parvipelvian hindfins. The three elements in the second row (immediately distal to the tibia and fibula) have been referred to as the centrale, astragalus, and calcaneum (Caldwell, 1997); tibiale, intermedium or astragalus, and fibulare (Zammit *et al.*, 2010; Massare and Lomax 2016b; Lomax and Massare, 2017); or distal tarsal two, astragalus, and calcaneum (Fernández, 2007; Maxwell, 2012). McGowan and Motani (2003, p. 57) noted the lack of consensus, and used two different terminologies in diagrams of hindfins (McGowan and Motani 2003, fig. 67, 70).

The important difference, however, is not merely in assigning names of bones. The identification of the anterior bone in the second row as the tibiale or distal tarsal two has implications for development of the fin because the process that forms

each bone is quite different. In embryonic development, the tibiale forms from segmentation of the tibia, whereas tarsal two would form in the digital arch from distal tarsal three (Shubin and Alberch, 1986). In extant reptiles (crocodiles, turtles, lizards), a condensation that will eventually become the femur segments distally and bifurcates to form condensations that will become the tibia and fibula. The fibula condensation similarly bifurcates into condensations for an intermedium and fibulare (Shubin and Alberch, 1986). Although Fabrezi *et al.* (2007) recognised a condensation for the radiale in the forefin, a similar condensation does not occur in the hindfin (Shubin and Alberch, 1986; Fabrezi *et al.* 2007). This contrasts with development in salamanders and birds, where a condensation that will eventually form the tibiale is present distal to the tibia (Shubin and Alberch, 1986). The interpretation of homology, and thus terminology, depends on the pattern of development that ichthyosaurs followed.

Phylogenetic analyses have placed the Ichthyopterygia with basal diapsids (Motani *et al.* 1998) or among the parareptiles (Maisch, 2010). The latter hypothesised an origin from a more plesiomorphic ancestral form than the former. Both studies hypothesised the origin of Ichthyopterygia before the divergence of archosauromorphs (which includes crocodiles) and lepidosauromorphs (which includes lizards). More recently, Scheyer *et al.* (2017, fig. 12b) proposed a phylogeny that supports this interpretation. All three phylogenetic hypotheses, however, place the group within the Reptilia. Key characteristics of the reptilian tarsus are recognised in many early reptiles (e.g., Rieppel, 1993; O’Keefe *et al.* 2006), suggesting that the reptilian developmental pattern was well established by the time the ichthyosaurs diverged. The hindfin of the Middle Triassic ichthyosaur *Mixosaurus* retains all five digits, and both distal tarsals one and two contact the tibia (Caldwell, 1997; Maxwell, 2012). Only two proximal tarsals (astragalus, calcaneum) occur in this primitive ichthyosaur, the typical reptilian pattern. Interestingly, Caldwell (1997) suggested that the most anterior, proximal tarsal in *Stenopterygius* could be a centrale that did not fuse with the intermedium to form the astragalus, although he acknowledged that it could also be distal tarsal two. Whether hindfin development in parvipelvians differed from the primitive reptilian pattern has yet to be established (but see Zverkov, 2017).

This work uses a conservative interpretation, which assumes that the ichthyosaurian tarsus developed in the primitive reptilian pattern and that the pattern

is retained even in derived taxa. Thus, in parvipelvian ichthyosaurs, the second row of the hindfin includes distal tarsal two, the astragalus and the calcaneum, and the third row typically includes metatarsal two, distal tarsal three and distal tarsal four. In *Ichthyosaurus*, however, a bifurcation in digit II commonly occurs, resulting in four elements in the third row (see section 5). An issue with this interpretation is that distal tarsals two and three do not contact one another in many specimens of *Ichthyosaurus*, as well as other parvipelvian taxa (McGowan and Motani, 2003, fig. 70; Maxwell, 2012, fig. 1). However, in *Mixosaurus*, the distal tarsals contact those of adjacent digits along a broad contact. Such a contact is expected considering how the distal tarsals develop from the digital arch (Shubin and Alberch, 1986). In *Ichthyosaurus*, and many parvipelvians, however, metatarsal two is often between distal tarsals two and three. Such changes in positions of distal tarsals could be related to the difference in shape of the tibia and fibula between *Mixosaurus* (elongated, with a distinct shaft) and *Ichthyosaurus* (polygonal). Alternately, a faster growth rate of metatarsal two relative to distal tarsal two could also result in separation of the two distal tarsals.

A clarification of the term ‘contact’ is also required. Ichthyosaurian fins often have gaps between elements either because of post-mortem disarticulation or because of the presence of uncalcified tissue in life. Juveniles, in particular, often lack an interlocking mosaic of fin elements (Johnson, 1977, but see Lomax *et al.* 2017b). In spite of gaps between bones, the presence of facets on adjacent elements often indicates that bones were in contact or have the potential to be in contact if the gaps were eliminated by additional growth or re-articulation. This work uses the term ‘contact’ in an imprecise sense to mean both physically touching and having the potential to physically touch an adjacent bone if gaps between elements are eliminated.

Femur morphology in *Ichthyosaurus*

In general, the femur of *Ichthyosaurus* is more elongated than the humerus, with a narrow shaft and a distal end that is flattened dorsoventrally and expanded anteroposteriorly (Figure. 7.1). The amount of anteroposterior expansion varies depending on the size and orientation of the facets for the tibia and fibula. Thus in dorsal or ventral view, the distal end is wider than the proximal end, but the difference in widths varies within a species. Minor differences in orientation of the



Figure. 7.1. Femora of the six species of *Ichthyosaurus*, anterior to the left. A. *I. larkini* (BRSUG 25300) right femur in ventral view. B. *I. somersetensis* (NLMH 106234, reversed) right femur in dorsal view. C. *I. somersetensis* (TTNCM 8373) left femur in dorsal view. D. *I. communis* neotype (NHMUK R1162) left femur in dorsal view. E. *I. breviceps* holotype (NHMUK OR43006) left femur in dorsal view. F. *I. conybeari* (NMW 93.5G.2, reversed), ?right femur in dorsal view. G. *I. anningae* holotype (DONMG:1983.98) ?left femur in dorsal view. Scales A-E equal 3 cm, Scale F equals 1 cm, Scale G equals 2 cm. Scale is estimated for D and E because specimens are on display behind glass.

femur also influences the assessment of relative widths. *Ichthyosaurus anningae* differs from the other species in having a much less elongated femur in which the distal and proximal ends are equally wide, making the femur shape similar to that of a humerus (Figure. 7.1G). This species can thus be distinguished from the others by femur morphology, as well as the relative size of the femur compared to the humerus (Lomax and Massare, 2015).

In *Ichthyosaurus larkini* and *I. somersetensis*, the anterior edge of the shaft is nearly straight, although some specimens have an expansion, or bulge, in at least the distal half of the shaft, that gives it a convex curvature (e.g., BRSUG 25300, *I. larkini*; BRSMG Cb4997, *I. somersetensis*; Figure. 7.1A-C). The posterior edge of the shaft is concavely curved, giving the femur a distinct, asymmetric shape in dorsal or ventral view. This asymmetry can distinguish *I. larkini* and *I. somersetensis* from the other species, although not from each other. In contrast, *I. communis*, *I. breviceps*, and *I. conybeari* have femora with more symmetric shapes in dorsal or ventral views, owing, in part, to a similar curvature of the anterior and posterior edges (Figure. 7.1D-F). *I. conybeari* usually has a distinctly narrow head and shaft, and a relatively broad expansion of the distal end in dorsal or ventral view (Figure. 7.1F). The distal end is much wider than the proximal end, more so than in other species, and this feature can sometimes distinguish *I. conybeari* from the other species.

In all species of *Ichthyosaurus*, the ventral process of the femur is centrally located and is more prominent than the dorsal process (Maxwell *et al.* 2012, fig. 1). The dorsal process, however, appears to be offset anteriorly in all species, although it can sometimes be slightly more centrally located, and its prominence also varies. For example, one specimen of *Ichthyosaurus somersetensis* (NHMUK OR2013*), has a dorsal process that is offset anteriorly; whereas another specimen (SOMAG/GEO/17), has a dorsal process that is slightly more centrally located, although still anteriorly offset. Such a minor difference could be the result of the femur orientation. Thus, the processes are not particularly useful in referring a specimen to species.

The relative size of the tibia and fibula are not useful in distinguishing species except for *I. conybeari*, which has a much larger fibula than tibia, both proximodistally and anteroposteriorly. *I. somersetensis* often has a fibula that is somewhat larger, at least anteroposteriorly, than the tibia (e.g., NHMUK OR2013*, NLMH 106234), but the difference is not of the magnitude seen in *I. conybeari*. In

general, the relative sizes of the tibia and fibula vary within a species, although in *I. anningae*, no sufficiently well-preserved specimens are known. The facets on the femur for the tibia and fibula are approximately the same length, even in *I. conybeari*. Variations in the size of facets arise mainly because of differences in the orientation of the femur. The angle between the facets also varies within species. The most striking example is in *I. somersetensis*, where in some specimens, a proximal deflection of the fibula facet occurs, with the angle between the facets nearly 90° in some specimens (e.g. BRSMG Cb4997, TTNCM 8373; Figure. 7.1C). This feature is not ontogenetic, because neither the smallest (NHMUK R44) nor the largest (NLMH 106234 [Figure. 7.1B], NHMUK 2013*) specimens of the species display this feature. Notably, in the holotype of *I. larkini*, one femur has facets at nearly a right angle (Figure. 7.1A) but the other femur does not, so the angle is likely related to differences in orientation.

Mesopodium morphology in *Ichthyosaurus*

The mesopodium of *Ichthyosaurus* has one of two morphotypes, distinguished by the number of elements in the third row. Morphotype 1 has three elements: metatarsal two, distal tarsal three, and distal tarsal four, which are immediately distal to distal tarsal two, the astragalus, and the calcaneum, respectively (Figure. 7.2A). Nearly all specimens showing Morphotype 1 have a bifurcation in the first phalangeal row of digit II. The exception is WARMS G6188, in which the right hindfin has the usual bifurcation in the first phalangeal row, but the left hindfin has the proximal bifurcation in the third phalangeal row. A bifurcation of phalanges that results in additional lines of elements is polyphalangy (Cooper and Dawson, 2009). Morphotype 2 has a bifurcation in the metatarsal row of digit II, resulting in four elements in the third row (Figure. 7.2B-D). Thus the third row has two metatarsal elements associated with digit II, distal tarsal three and distal tarsal four. A bifurcation in the metatarsal row resulting in an additional metatarsal is polydactyly (Cooper and Dawson, 2009). Our contention is that in *Ichthyosaurus*, the bifurcation process is essentially the same, but the position at which it occurs on digit II is the result of individual variation. Thus the distinction between polydactyly and polyphalangy is not useful for the unusual hindfin (and forefin) morphology found in *Ichthyosaurus*.

Should *Ichthyosaurus* be separated into two genera, one displaying polydactyly and the other not? This might have been the conclusion were fewer specimens available for examination, but in reality, the situation is more complex. Morphotype 1 is the common morphology in *I. breviceps*, *I. conybeari*, and *I. somersetensis*. However, all six species of *Ichthyosaurus* show Morphotype 2 in at least some specimens. *Ichthyosaurus communis* and *I. larkini* seem to show this morphotype exclusively, but the latter species is known from relatively few specimens. The only specimen of *I. anningae* with the proximal hindfin exposed also shows this morphology. Because three species show both morphotypes, we argue that the difference is the result of individual variation. Without the exceptionally large sample size, this might not have been recognised. Moreover, two of the 24 specimens that preserve both hindfins (BRLSI M3559, GLRCM 1987.45) show a different morphotype on each fin. Neither of these is a composite specimen, although composites occur in historic collections (Massare and Lomax, 2016a). This further suggests that the two morphotypes, although seemingly distinct, reflect individual variation. Thus the difference between Morphotype 1 and 2 is largely whether the bifurcation of digit II occurs in the first phalangeal row of digit II (Morphotype 1) or in the metatarsal row (Morphotype 2). Similarly, in the forefin of *Ichthyosaurus*, the proximal bifurcation can be in the metacarpal row or one of the phalangeal rows (not always the first) of either digit II or digit III (Motani, 1999, fig. 6). Moreover, the position of the bifurcation can vary between the left and right fin of an individual, although rarely (e.g. SOMAG/GEO11, ANSP 15766). So having a similar kind of variation in the hindfin is not unexpected.

In limb development, a bifurcation results in two equivalent branches, so in the hindfin, both branches of the bifurcation represent digit II (Oster *et al.*, 1988; Motani, 1999). In both the hindfin and forefin, however, one branch of the bifurcated digit can be oriented such that it appears to be a continuation of the original digit (Figure. 7.3A, D; Motani 1999, fig 6C,D; Lomax *et al.*, 2017a, fig. 11A, B), but this is not always the case (Figure. 7.3B, C; Lomax *et al.*, 2017a, fig. 11C, D). Furthermore, one branch can have smaller elements than the other (Figure. 7.3A; Motani 1999, fig 6E, F), although this is more common on distal bifurcations (Fig. 7.3B). Irrespective of size or orientation, this work considers the two branches to be equivalent subdigits of digit II. In Morphotype 2, due to the bifurcation, two metatarsals are associated with digit II, referred to herein as metatarsal two-a and two-b. This results in four

metatarsals in the hindfin. Neither metatarsal one nor five is present, as might have been inferred from four metatarsal elements if only a portion of the variation in the hindfins was examined. An alternate explanation, however, is that the posterior branch of the bifurcation is a continuation of digit II, whereas the anterior branch is a supernumerary digit. This interpretation is consistent with the posterior to anterior sequence of branching of the digital arch during limb development (Shubin & Alberch, 1986), so it also has some basis in development. However, there are a few cases where the anterior branch seems to be the continuation of digit II (e.g., Figure. 7.3D), which is why we favour interpreting the two subdigits as equal.

Three variations occur in Morphotype 2, mainly differing in the number and extent of contact of elements in the third row with the astragalus (Figure. 7.2B-D). Some specimens have two small metatarsals in digit II that are directly distal to distal tarsal two, with metatarsal two-b having little or no contact with the astragalus (Figure. 7.2C; 7.4A, B). Distal tarsal three has a broad contact with the astragalus similar to what occurs in Morphotype 1. In some specimens of *I. communis*, on the other hand, both metatarsal two-b and distal tarsal three have fairly broad contacts with the astragalus. The contacts are approximately the same length (Figure. 7.2B). These two variations seem to be distinct morphologies, and if only a specimen or two were known, one could conclude that each species had a diagnostic hindfin morphology. However, although many specimens of *I. somersetensis* have little or no contact between metatarsal two-b and the astragalus, others have contacts with the astragalus of varying amounts (Figure. 7.4 A-C). Similarly, although some specimens of *I. communis* have two equally large elements and broad, symmetric contacts of metatarsal two-b and distal tarsal three with the astragalus, other specimens of *I. communis* have a distal tarsal three contact that is somewhat longer than the metatarsal contact (e.g. Figure. 7.4D). The size of distal tarsal three relative to the adjacent metatarsal seems to be the controlling factor in the extent of contact with the astragalus, and could reflect individual variation in relative growth rates. Thus the seemingly distinct morphologies of *I. somersetensis* and *I. communis* are end members of a continuum of variation in the relative size of the contacts between metatarsal two-b, distal tarsal three, and the astragalus. In fact, two specimens of *Ichthyosaurus* (OUMNH J.29351, NHMUK OR41849) preserve two hindfins, each with a different variation of Morphotype 2. Neither is a composite specimen.

When Morphotype 2 occurs in *I. somersetensis*, typically distal tarsal three

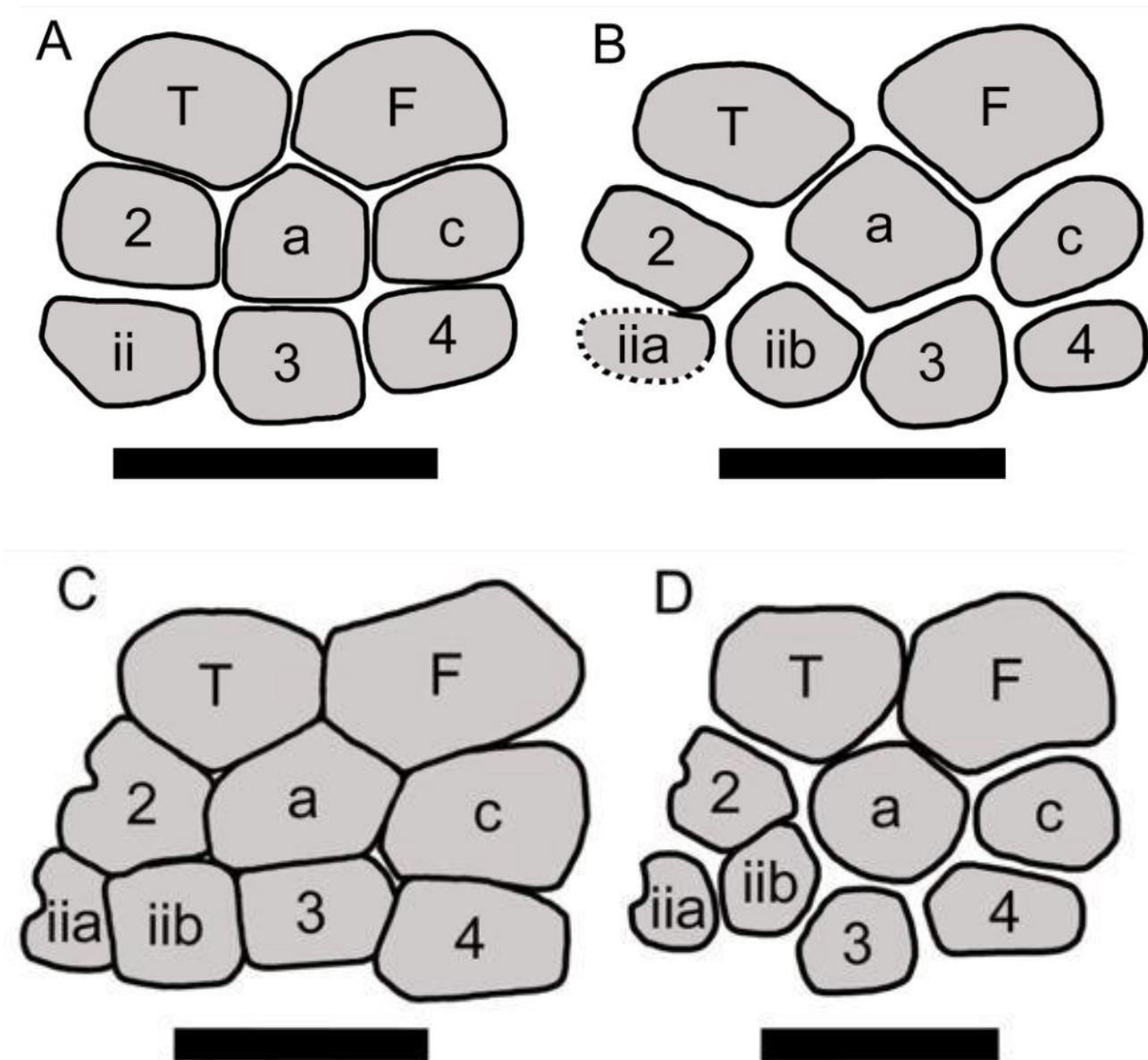


Figure. 7.2. *Ichthyosaurus* hindfin morphotypes. A. Morphotype 1 (NHMUK OR43006), with three elements in the third row. B. Morphotype 2 (NHMUK R1162), with four elements in third row. Metatarsal two-b and distal tarsal three have equal contact with the astragalus. Dashed line indicates inferred outline of metatarsal two-a that is partially overlain. C. Morphotype 2 variation (NLMH 106234, right hindfin, reversed), with distal tarsal three having broad contact with astragalus and metatarsal two-b having minor to no contact. D. Morphotype 2 variation (NHMUK R5595 right hindfin, reversed), with three elements in contact with the astragalus. Anterior is to the left in all specimens. Scales A, B, and C equal 2 cm. Scale C equals 3 cm, but A, B, and D scales are estimates because the specimens are on display behind glass. Abbreviations: 2, distal tarsal two; 3, distal tarsal three; 4, distal tarsal four; a, astragalus; c, calcaneum; F, fibula; iia, anterior metatarsal of digit II; iib, posterior metatarsal of digit II; T, tibia.

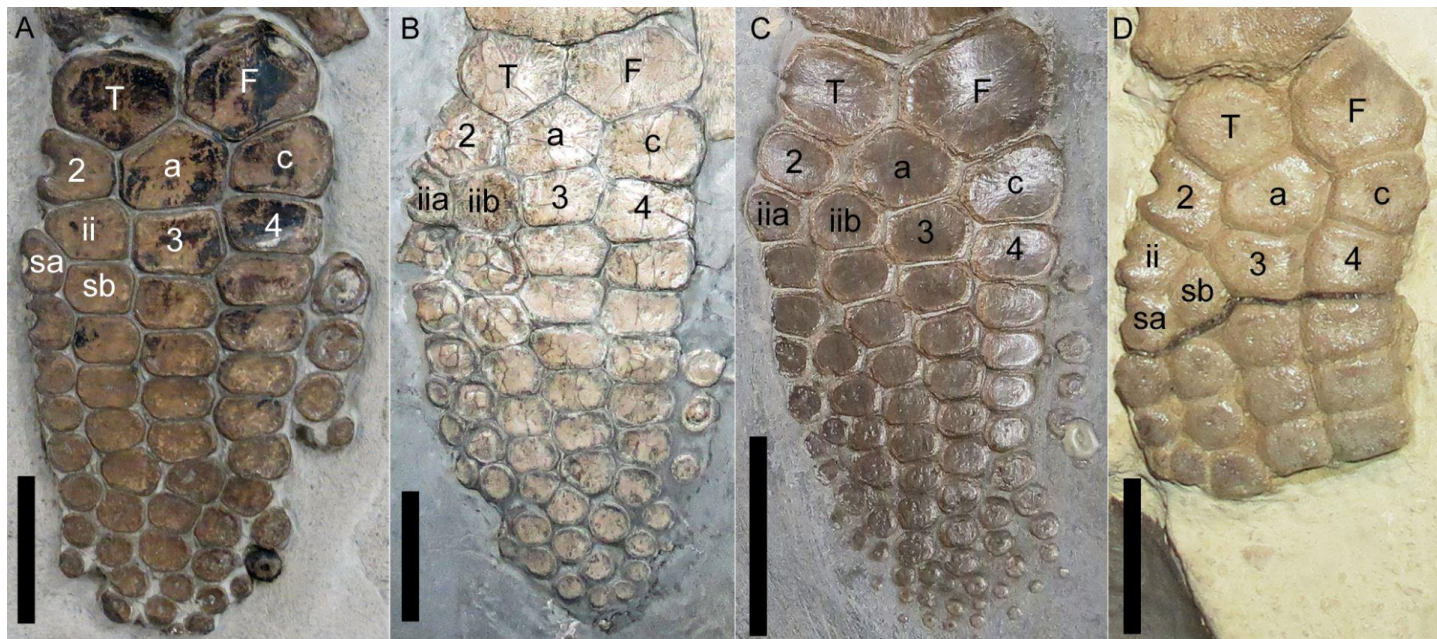


Figure. 7.3. Variation in the orientation and size of subdigits resulting from a bifurcation of digit II. Anterior to the left. A. WARMS G6188 (Morphotype 1), right hindfin (reversed) in which subdigit-b is more in line with proximal elements of digit II than is subdigit-a. Note that subdigit-a has somewhat smaller elements than subdigit-b. B. NLMH 106234 (Morphotype 2), right hindfin (reversed) showing the two subdigits of digit II symmetrically arranged with respect to distal tarsal two. Note the presence of a third subdigit in the fourth phalangeal row. C. SMNS 58275 (Morphotype 2), right hindfin, in which neither subdigit is in line with proximal elements of digit II. D. CLC1 (Morphotype 1), left hindfin in which subdigit-a is more in line with the proximal elements of digit II than is subdigit-b. A, C and D scales equal 2 cm. Scale B equals 3 cm. Scale for D is estimated because the specimen is on display behind glass. Abbreviations: 2, distal tarsal two; 3, distal tarsal three; 4, distal tarsal four; a, astragalus; c, calcaneum; F, fibula; iia, anterior metatarsal of digit II; iib, posterior metatarsal of digit II; sa, anterior subdigit of digit II; sb, posterior subdigit of digit II; T, tibia.

has a broad contact with the astragalus, with metatarsal two-b having only a minor contact, if any, with the astragalus (Figure. 7.2C; 7.4A, B). A similar morphology also occurs in *I. conybeari* (SMNS 58275, NHMUK R5790) and *I. breviceps* (CAMSM X50187, NHMUK OR2001*), although less commonly than Morphotype 1. Without several specimens of each species, the less common morphology would not have been evident, and mesopodium morphology might have been considered a species-specific character rather than a matter of individual variation.

In a third variation of Morphotype 2 metatarsal two-b, distal tarsal three, and distal tarsal four have fairly broad and nearly equal contacts with the astragalus, at least on well-articulated specimens (e.g. NHMUK R5595, NHMUK OR8165 left fin).

Metatarsal two-b is more proximally located such that it nearly separates distal tarsal two from the astragalus (Figure. 7.2D). It appears to be the common morphology of *I. larkini*, but only four specimens of the species are known, three of which preserve a hindfin. Lomax and Massare (2017, p. 12) misidentified the digit count in *I. larkini* and identified the element that almost separates tarsal 2 (their tibiale) from the astragalus as the proximal element of digit III, whereas it is actually metatarsal two-b. Two additional hindfins have this morphology (NOTNH: FS3450 and NOTNH: FS4940). They could be *I. larkini*, but additional diagnostic material is lacking, so they cannot be assigned unequivocally to the species. As in the other variations of Morphotype 2, the relative size of the contacts with the astragalus varies considerably. The contact between the astragalus and distal tarsal three is longer than the contact with metatarsal two-b and with distal tarsal four in NOTNH FS4940 and BRSUG 25300, compared to Figure. 7.2D. In fact, two variations of this morphology are preserved in BRSUG 25300 (the holotype of *I. larkini*): in one hindfin distal tarsal 4 has a significant contact with the astragalus, whereas in the other fin, tarsal 4 has only a slight, if any, contact with the astragalus, even accounting for taphonomic displacement. A slight contact between distal tarsal four and the astragalus occurs in Morphotype 1 and other variations of Morphotype 2, so it is not unique to the *I. larkini* variation of Morphotype 2. One specimen of *Ichthyosaurus* that preserves two hindfins (NHMUK OR8165; Figure. 7.5A, B) has the *I. larkini* variation in one hindfin and another variation of Morphotype 2 in the other fin; specifically, metatarsal two-b does not have a broad contact with the astragalus nor does it nearly separate it from distal tarsal two. This suggests that the morphology of *I. larkini* is another variation of Morphotype 2, but we have not yet identified specimens of other species with this variation. Although this variation seems to be unique to *I. larkini*, too few specimens are known to adequately evaluate it. To complicate the picture, another specimen with two hindfins (GLRCM 1987.45; Figure. 7.5C, D) has one fin with the '*I. larkini*' morphology but the other fin displays Morphotype 1, with three elements in the third row. Unfortunately, GLRCM 1987.45 is not sufficiently complete to assign to a species. Thus Morphotype 1 might occur in *I. larkini*, or equally likely, the *I. larkini* variation of Morphotype 2 might occur in another species. This suggests that this variation of Morphotype 2 cannot be used on its own to unequivocally refer a specimen to *I. larkini*.

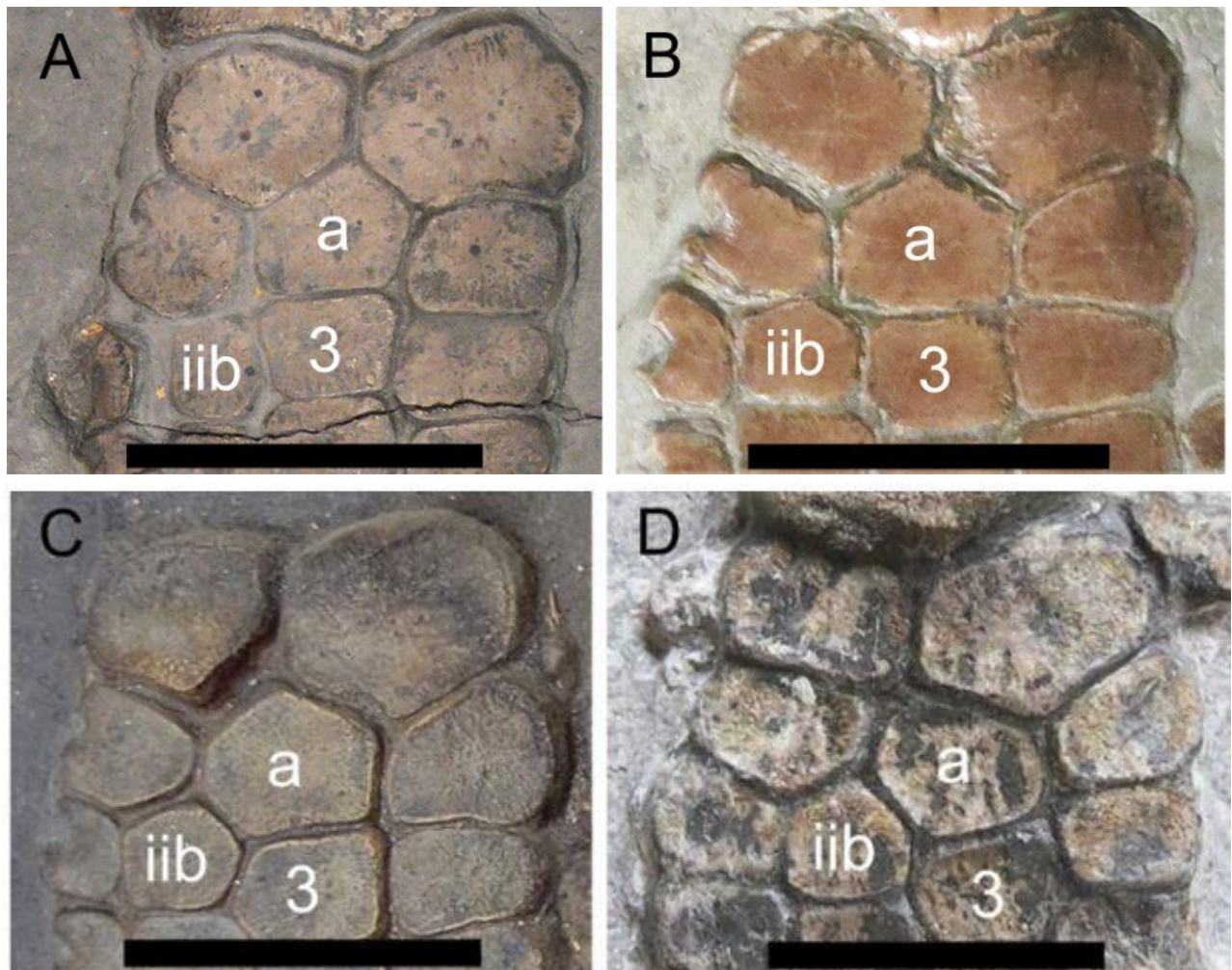


Figure. 7.4. The continuum of variation in Morphotype 2, all with four elements in the third row. A. CAMSM J59574, distal tarsal three with broad contact with astragalus and metatarsal two-b with no contact. B. BRSMG Ce16611, distal tarsal three with broad contact with astragalus and metatarsal two-b with minor contact. C. OUMNH J.13799 (reversed), distal tarsal three with broad contact with astragalus and metatarsal two-b with much shorter contact with astragalus. D. NHMUK R1073, distal tarsal three with slightly longer contact with astragalus than that of metatarsal two-b. Scales A and C equal 3 cm. Scale B equals 4 cm, based on a cast of the specimen at LEICT. Scale D equals 2 cm but is estimated because the specimen is on display behind glass. Abbreviations: 3, distal tarsal three; a, astragalus; iib, metatarsal of posterior subdigit of digit II.

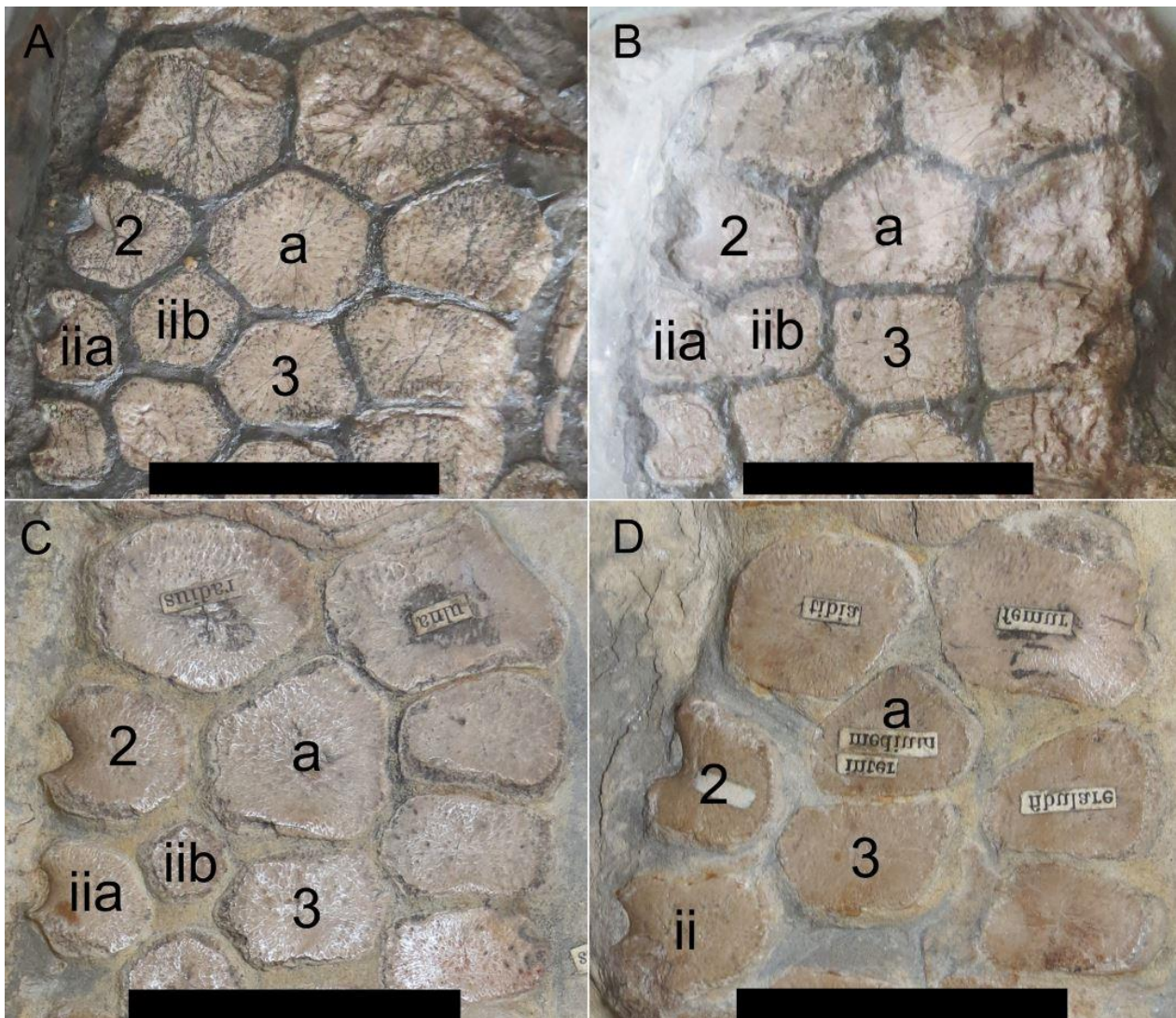


Figure. 7.5. Specimens with two different morphologies in the hindfins. A. NHMUK OR8165, left hindfin (reversed) showing one variation of Morphotype 2, with four elements in the third row and three elements in contact with the astragalus. B. NHMUK OR8165, right hindfin showing another variation of Morphotype 2, with four elements in the third row and one element (distal tarsal three) in broad contact with the astragalus. C. GLRCM 1987.45, ?left hindfin showing one variation of Morphotype 2, with four elements in the third row and three elements in contact with the astragalus. Specimen had previously been identified as a forefin, but the propodial shape and size indicate that it as a hindfin. D. GLRCM 1987.45, ?right hindfin (reversed) showing Morphotype 1, with three elements in the third row and distal tarsal three in broad contact with the astragalus. Scales equal 3 cm, but the scales for A and B are estimates because the specimens are on display behind glass. Abbreviations: 2, distal tarsal two; 3, distal tarsal three; a, astragalus; ii, metatarsal two; iia, metatarsal of the anterior subdigit of digit II; iib, metatarsal of posterior subdigit of digit II.

Other features of the hindfin

a. Notching of anterior elements

Notching on one or more elements in the anterior digit of the hindfin occurs in many Lower Jurassic ichthyosaurian genera including *Ichthyosaurus*. Notching has been interpreted as a retained primitive feature homologous to the shaft in long bones of the tetrapod limb (Motani, 1999) or as a structure to protect nerves or blood vessels (Johnson, 1979; Caldwell, 1997). Maxwell *et al.* (2014) found that periosteal bone is present at the anterior end of notched elements, whereas it is lacking at the posterior end. They suggested that this related to increased stresses on the leading edge of the forefin. Thus notching might be related to the way the fin was used during locomotion. The slight correlation between the number of notched elements and the size of the individual suggests an ontogenetic component of notching (Johnson, 1977; Maxwell *et al.* 2014) and supports the hypothesis that notching is related to fin use throughout life. In *Ichthyosaurus*, notching is more common in the hindfin than in the forefin (Massare and Lomax, 2016b). In *Stenopterygius*, notching is more variable in the hindfin than in the forefin (Maxwell *et al.* 2014).

Massare and Lomax (2016b) argued that notching in the fins of *Ichthyosaurus* probably had no taxonomic significance in elements other than the tibia, but this study has found that some species of *Ichthyosaurus* have notched elements whereas others do not. *Ichthyosaurus somersetensis* almost always has notching in the hindfin. Of 21 specimens of *I. somersetensis* recognised in this research (Table 7.1), only one (ROM 26029) might lack notching in the hindfin. Distal tarsal two lacks a notch, but the anterior element in the metatarsal row is probably missing, and the first phalanx is damaged. Most specimens of *I. somersetensis* have a notch in the distal tarsal or metatarsal or both, and sometimes in one or two phalanges as well. All known specimens of *I. larkini* with a hindfin show notching in at least one element, but with so few specimens, it is impossible to say whether this always occurs. On the other hand, no known specimens of *I. communis*, *I. breviceps*, or *I. anningae*, have notched elements in the hindfin (or the forefin). Only two specimens of *I. anningae*, however, preserve incomplete hindfins (NHMUK OR120 and NHMUK R10028), and although neither shows notching, with so few specimens, the variation in this feature cannot be assessed. *Ichthyosaurus somersetensis* is the common species from Somerset, whereas *I. communis* is the common species from Dorset (i.e., the Lyme

Regis-Charmouth area). *Ichthyosaurus larkini* is known only from Somerset, whereas *I. breviceps* and *I. anningae* are exclusively from Dorset. Consequently the difference in species abundances, notching of anterior elements of the hindfins is rare on specimens from Dorset, but occurs commonly on specimens from Somerset, as noted by McGowan (1974) and Massare and Lomax (2016b).

Ichthyosaurus conybeari, which is an uncommon species from both Somerset and Dorset (McGowan, 1974; Massare and Lomax, 2016b), almost always has a notched tibia, the only species of *Ichthyosaurus* to show notching in the zeugopodium. A notched tibia is present in very small specimens (CAMSM X50224, femur length = 1.3 cm), even in the absence of notching in the forefin. A larger specimen (BGS 956, femur length 1.9 cm) has a notched tibia and distal tarsal two, as well as forefin notching. A much larger specimen (SMNS 58275, femur length = 3.5 cm) also has a notched tibia and two notched elements in the right forefin. A notched tibia appears to be a unique character for the species, at least within *Ichthyosaurus*. If this is the case, then OUMNH J.10301 could also be referred to *I. conybeari*. This would be the largest example of the species known, with an estimated femur length greater than 6 cm. OUMNH J.10301 is an historic specimen in which the matrix block with the hindfin is isolated from at least two other blocks, all within a wooden frame. The entire specimen might be a composite (Massare and Lomax, 2016a). The picture is more complicated, however. Skull and humerus morphology suggest that NHMUK R11801 and USNM V4697 are probably *I. conybeari*, but both lack a notched tibia in the articulated hindfin that is preserved. The latter, however, has an odd morphology in the hindfin (see section 7). So although the presence of a notched tibia is indicative of *I. conybeari*, it would appear that the lack of a notched tibia does not completely exclude that possibility. Although both *I. somersetensis* and *I. larkini* have notched elements in the hindfin, the tibia is never notched in those species.

b. Number of digits

An issue arises in how to characterise the number of digits in the hindfin given that digit II can have a bifurcation in the metatarsal row. Applying the definition of digits as elements arising from a metatarsal/metacarpal (McGowan, 1972) creates complications in species diagnoses. For example, specimens of *I. conybeari* with Morphotype 1, would have three digits corresponding to metatarsals two, three, and

four; whereas specimens with Morphotype 2 would have four digits, corresponding to metatarsals two-a, two-b, three and four. Irrespective of the morphotype, all specimens of *I. conybeari* have similar hindfins, with five columns of elements (including a distal bifurcation of digit II). An additional complication is that the fourth digit arising from the metatarsal bifurcation is neither digit I nor digit V, making *Ichthyosaurus* distinctly different from a taxon with digit I or V in the hindfin (e.g. *Mixosaurus*). A strict application of the definition creates potential errors in phylogenetic analysis as well because the four digit hindfin in some species of *Ichthyosaurus* is not plesiomorphic. Cooper *et al.* (2007, fig.1) distinguished between digital rays (metatarsal plus phalanges) and digits (phalanges only), but those definitions create a similar issue in characterising hindfins of *Ichthyosaurus*.

Thus the standard terminology does not work well. All *Ichthyosaurus* species have three primary digits in the hindfin, digits II, III, and IV, with digit II having two subdigits resulting from a proximal bifurcation in either the first phalangeal row (Morphotype 1) or the metatarsal row (Morphotype 2). Most specimens have a third subdigit of digit II, resulting from a distal phalangeal bifurcation. Subdigits arise from bifurcations. They are distinct from pre- and post-axial accessory digits, which do not arise from the tarsus/carpus (McGowan, 1972) nor from a digital bifurcation. Previous workers have largely not distinguished between primary digits and subdigits, counting them together to describe the number of digits in the hindfin (e.g., Lomax and Massare, 2017) and forefin (e.g., McGowan and Motani, 2003; Ji *et al.*, 2016; Massare and Lomax 2017). Similarly, following Cooper *et al.* (2007) and Cooper and Dawson (2009), we use the term 'digits' here to include both primary digits and subdigits. We exclude accessory digits from the counts that follow.

Thus the common morphology of the hindfin of all species of *Ichthyosaurus*, for both morphotypes, has a total of five digits, the result of bifurcations in digit II. The two morphotypes are consistent in this context, but differ in the position of the proximal bifurcation, being either in the first phalangeal row (Morphotype 1) or in the metatarsal row (Morphotype 2). Usually a second bifurcation occurs distally, which results in five digits. However, the fin must be complete to the fifth phalangeal row in order to confirm the digit count because the distal bifurcation often occurs in the fourth or fifth phalangeal row of digit II (e.g., NHMUK R3372, NLMH 106234, OUMNH J.29351), especially in *I. somersetensis*.

Exceptions to this pattern occur. Two specimens of *Ichthyosaurus* have six digits. PETMG R174 (*I. communis*) and YPM 9204 (possibly *I. communis*) have bifurcations in the metatarsal, first or second phalanx, and fifth or sixth phalanx of digit II. A less unusual occurrence are specimens with fairly complete hindfins that have only four digits, although this could be a preservation issue. Collection or preparation could have missed a small distal bifurcation. In particular, the lack of a distal bifurcation on historic specimens needs to be evaluated carefully. The anterior edge of some hindfins is at the edge of the matrix, presenting the possibility that some fin elements, especially small ones, could have been accidentally overlooked or intentionally removed to show a better defined fin. Thus a distal bifurcation, especially one with small elements, cannot be entirely ruled out on historic specimens with only four digits, even in what appears to be a fairly complete hindfin. That being said, some specimens that are well-preserved and sufficiently complete have hindfins that lack the distal bifurcation (e.g. BRLSI GP1870, CAMSM J59574, NHMUK R11199, NHMUK OR43006, TTNCM 8359, and WARMS G6188; possibly also CAMSM J35188 and NHMUK OR2013 [not OR2013*]). Those that can be assigned to a species are either *I. breviceps* or *I. somersetensis*, but several specimens cannot be identified to species.

Although some forefins of *Ichthyosaurus* have a pre-axial (anterior) accessory digit (e.g., NHMUK OR43006), hindfins seem to lack them. Sometimes one subdigit of digit II has larger elements than the other, possibly as a result of unequal division of embryonic tissue or different growth rates. This does not change the developmental equivalence of the two subdigits. When this occurs, however, it is most often the anterior subdigit that is smaller (Figure. 7.3A). Poor preservation or disarticulation could make it difficult to distinguish a subdigit from a pre-axial accessory. This is especially problematic for distal bifurcations if one subdigit has small, rounded elements (Figure. 7.3B), if the proximally adjacent element lacks a distinct facet, or if only a few elements are present. It is often a judgement call as to whether small anterior elements belong to a subdigit or a pre-axial accessory digit. We have not been able to unequivocally identify a pre-axial accessory digit on any hindfin (contrary to Massare and Lomax, 2014), so we conclude that pre-axial accessory digits are absent or rare on hindfins of *Ichthyosaurus*.

In contrast, post-axial (posterior) accessory digits are easier to recognise. The elements are round or oval, whereas digit IV always has larger, rectangular

phalanges, at least in the proximal half of the fin. The presence of one post-axial accessory digit seems to be the typical condition in hindfins of *Ichthyosaurus*, although they are present on less than half of the specimens examined. A post-axial accessory digit occurs in all species, possibly even *I. anningae* (NHMUK R10028). Post-axial accessory digits are often poorly preserved, incomplete, or absent because of decisions made during preparation, especially on historic specimens. So, the lack of a post-axial accessory needs to be viewed initially with some scepticism.

Unusual hindfin morphologies in *Ichthyosaurus*

Several hindfins show unusual morphologies, some of which might be pathology (Table. 7.3). Had there been fewer or less complete specimens to examine, some of these morphologies could have been interpreted as sufficiently unique to be a new taxon. PETMG R174, a specimen of *Ichthyosaurus communis*, lacks a contact between the astragalus and the tibia (Figure. 7.6A). In addition, the calcaneum is proximodistally elongated and anteroposteriorly short. It is posterior to the fibula for much of its length. The hindfin otherwise has the Morphotype 2 arrangement of elements. A less aberrant, but similar, arrangement occurs in OUMNH J.29352. The astragalus has a minor contact with the tibia and the calcaneum is proximodistally elongated only in the posterior portion and it is not anteroposteriorly short (Figure. 7.6B). The calcaneum is, however, similarly posterior to most of the fibula. Another specimen, CHMUS 2015.0102, has a posteriorly expanded, but small, calcaneum and a posteriorly reduced fibula (Figure. 7.6C), but not to the extent displayed in OUMNH J.29352. The astragalus has a broader contact with the tibia and fibula. Thus the three specimens display a sequence of morphologies that grade from a highly unusual arrangement to one that is more similar to the typical morphology (compare Figure. 7.6C with Figure. 7.4B, C). It suggests that even the morphology of PETMG R174 is just an odd variation.

Another unusual hindfin morphology is that of RAMM 57/2009, which is clearly *Ichthyosaurus* based on the rest of the skeleton. The hindfin has four elements in the second row, with three elements in contact with the tibia (Figure. 7.7A). In addition to the facet for the astragalus, the tibia has two other facets, one more anteriorly oriented than the other. This arrangement could be interpreted as a bifurcation in the distal tarsal row. The matrix is darker around the fin than elsewhere on the block, so

it is possible that it was reset, but the facets on adjacent elements suggest that the arrangement is authentic. Taphonomic displacement is possible, but the facets and the lack of disarticulation suggest that this is not displacement. No other hindfin of *Ichthyosaurus* show this morphology in which the bifurcation of digit II seems to have occurred more proximally than usual. The anterior branch of digit II curves ‘outward’ as if displaced anteriorly by the posterior branch. Also, for a given position on the proximal half of the fin, there are more elements in the anterior branch than in the posterior branch of digit II (Fig. 7.7A). Both of these features also occur in DORCM G1, BGS 955, and NHMUK R11199 (Fig. 7.7B), although these specimens have the usual Morphotype 2 bifurcation in the metatarsal row. In all three specimens, the relative position of the proximal elements is the same: metatarsal two-a is slightly more proximally located than metatarsal two-b (Fig. 7.7A, B). The major difference is that the bifurcation apparently occurs in a more proximal row in RAMM 57/2009 than in the others. As with the previous example, the unusual morphology of RAMM 57/2009 shares similarities with fins having a more typical morphology.

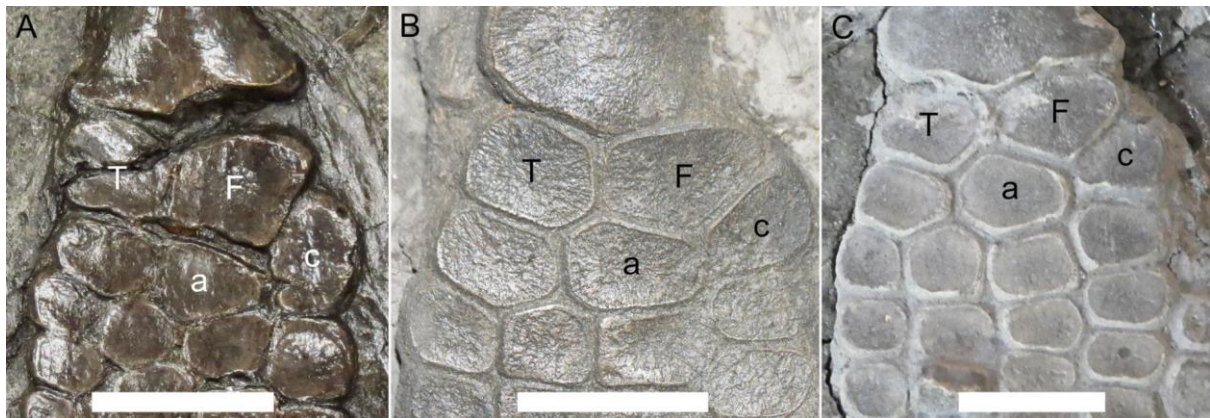


Figure. 7.6. An example of gradation in morphologies in proximal fin elements. Anterior to the left. A. The hindfin of PETMG R174 has an oval, proximodistally elongated calcaneum and the tibia and astragalus lack contact. B. The hindfin of OUMNH J.29352 has a similarly shaped astragalus, a short contact between the tibia and astragalus, and a calcaneum that is anteroposteriorly elongated only in the posterior portion. C. The hindfin of CHMUS 2015.0102 (reversed) has a calcaneum, astragalus, and fibula shaped similarly to B, but the relative sizes and arrangement of elements are more like that of a typical *Ichthyosaurus* hindfin. Image courtesy of Charterhouse School Archive. Scale A equals 3 cm. Scales B and C equal 1 cm. Abbreviations: a, astragalus; c, calcaneum; F, fibula; T, tibia.

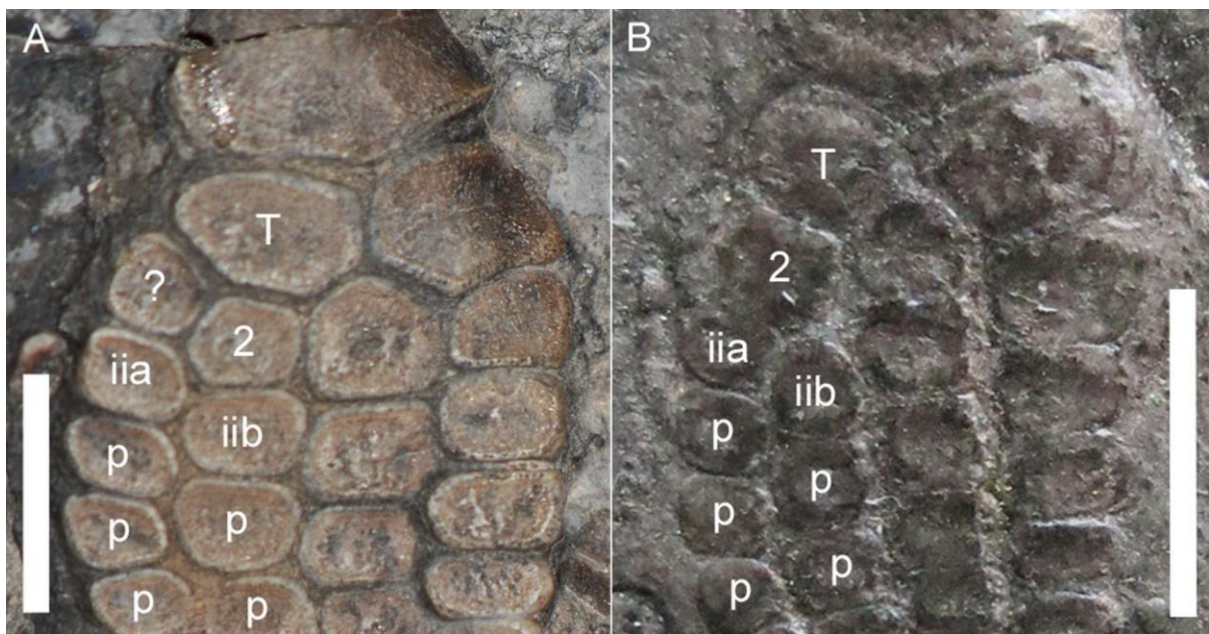


Figure. 7.7. Another unusual morphology of the hindfin. Anterior to the left. A. RAMM 57/2009, left hindfin showing two elements immediately distal to the tibia, possibly the result of a bifurcation in digit II. The anterior subdigit curves ‘outward’ (anteriorly) and metatarsal two-a is more proximally located than metatarsal two-b. B. NHMUK R11199, left hindfin, showing a bifurcation of digit II in the metatarsal row. The anterior subdigit curves ‘outward’ (anteriorly), and metatarsal two-a is more proximally located than metatarsal two-b. Scale A equals 2 cm. Scale B equals 1 cm but is estimated because the specimen is on display behind glass. Abbreviations: 2, distal tarsal two; iia, anterior metatarsal of digit II; iib, posterior metatarsal of digit II; p, phalanx; T, tibia; ?, homology unknown.

In NHMUK R11801, a small articulated skeleton, the astragalus is positioned so far proximally that it separates the tibia and fibula and almost contacts the femur. Distal tarsal two and the calcaneum seem to be pushed anteriorly and posteriorly, respectively, by metatarsal two-b and distal tarsal three (Figure. 7.8A). Disarticulation and displacement can produce this arrangement (e.g., BU 5289; Figure. 7.8B), but NHMUK R11801 is not disarticulated. In isolation, the arrangement of elements could be interpreted as having three elements in the first row and four elements in the second and third rows, thus an entirely new morphology. In fact, a contact between the astragalus and femur occurs in *Maiaspondylus* (Druckenmiller and Maxwell, 2010, table B1), and *Platypterygius hercynicus* (Kolb and Sander, 2009; Fischer, 2012). Other derived ichthyosaurs (*Aegirosaurus*, *Brachypterygius*, *Maiaspondylus*) have a comparable contact between the humerus and the

intermedium in the forefin (Bardet and Fernández, 2000; McGowan and Motani, 2003; Maxwell and Caldwell, 2006). However, the morphology of NHMUK R11801 is yet another ‘extreme’ variation of a common arrangement of Morphotype 2. NMW 91.29G.1 also has an astragalus that nearly contacts the femur, but metatarsal two-b is somewhat smaller than in NHMUK R11801, and so the calcaneum and tarsal 2 are closer to the astragalus (Figure. 7.8C). The second row of three elements is better defined, and distal tarsal two and the calcaneum are not displaced outward as much. This is also the case in one fin of NHMUK OR41849, where the astragalus practically contacts the femur, separating the tibia from the fibula. The other fin also shows the separation but the astragalus is not as proximally located. In NHMUK R1162 the astragalus is positioned slightly more distally (Figure. 7.2B), and the tibia and fibula are closer together, a more typical arrangement of elements.



Figure. 7.8. Hindfins in which the astragalus separates the tibia and fibula and almost contacts the femur. A. NHMUK R11801, left hindfin, showing digit III and the posterior subdigit of digit II more proximally positioned than usual. The fin appears to have three elements in the first row and four elements in the second row because tarsal 2 and the calcaneum are shifted anteriorly and posteriorly, respectively. B. BU5289, right hindfin (reversed), with a similar morphology as A. However, it is probably due to post-mortem displacement in this specimen. Note, that some elements are dorsoventrally rotated and partially buried. C. NMW 91.29G.1, ?left hindfin (reversed), showing the astragalus almost in contact with the femur, but digit III and the posterior subdigit of digit II do not displace distal tarsal two and the calcaneum as in A. Scales A and B equal 1 cm. Scale C equals 2 cm. Abbreviations: 2, distal tarsal two; 3, distal tarsal three; 4, distal tarsal four; a, astragalus; c, calcaneum; F, fibula; iia, anterior metatarsal of digit II; iib, posterior metatarsal of digit II; T, tibia.

USNM V4967 is another unusual morphology, where a fairly large, supernumerary element is anterior to the tibia and in contact with the femur (Figure. 7.9A). The tibia is smaller than usual relative to the fibula, so it is possible that the supernumerary bone restricted its growth. Maxwell (2012, p. 550) reported a somewhat similar, but more common, anomaly in *Stenopterygius quadriscissus*, in which a single element contacts the femur anterior to the tibia. USNM V4967 is otherwise a typical example of Morphotype 2, with a proximal bifurcation in the metatarsal row and a more distal bifurcation in the second phalangeal row. Other features of the skeleton identify this specimen as *Ichthyosaurus*, but as with PETMG R174, RAMM 57/2009, NMW 91.29G.1, and NHMUK R11801, the hindfin might have been considered a new taxon had it occurred in isolation. This makes it clear that fragmentary or isolated material does not usually provide sufficient information to justify a new taxon (e.g. as in Brusatte *et al.* 2015).

Several specimens have smaller, more distally located supernumerary elements in the fin, in the form of a small round bone between two of the digits (Figure. 7.9B-D). These elements are usually associated with digit II. BRSMG Ce16611 has a supernumerary element in digit II, between the first and second phalanges, and a second, smaller isolated element anterior to it (Figure. 7.9B). BGS 955 has a small, round supernumerary element in digit II between the first and second phalangeal rows and another anterior to the second phalanx of digit II (Figure. 7.9C). The right hindfin of SMNS 58275 has a supernumerary element between the fourth and fifth phalangeal rows of digit II. The left fin of WARMS G6188 has a supernumerary element anterior to and between phalanges one and two of digit II, proximal to where the distal bifurcation occurs (Figure. 7.9D). Similar supernumerary elements occur occasionally in the forefins of *Ichthyosaurus* (pers. obs.) and have been reported in forefins and hindfins of *Stenopterygius* (Maxwell, 2012), and in whales (Cooper and Dawson, 2009).

Another irregularity in a few hindfins is co-ossification of adjacent elements, which has also been reported in forefins of *Ichthyosaurus* (Motani, 1999; Lomax *et al.* 2017a), *Mixosaurus* (Maxwell, 2012), *Stenopterygius* (Johnson, 1979; Maxwell, 2012), *Undorosaurus* (Arkhangelsky and Zverkov, 2014, fig. 1C), and in the hindfin of *Suevoleviathan* (Maisch, 1998; pers. obs. SMNS 15390), as well as whales (Cooper and Dawson, 2009). In the hindfin of *Ichthyosaurus*, a co-ossification can be recognised as a large, anteroposteriorly elongated, irregular element. Thus in

TTNCM 8359 (Figure. 7.9F), the elongated bone in digit II, is probably a co-ossification of metatarsals two-a and two-b. So what was originally a bifurcation in the metatarsal row of Morphotype 2 mimics Morphotype 1 because of the co-ossification. ANSP 17429 (Figure. 7.9E) also shows two co-ossified elements between digits II and III, possibly metatarsal three and metatarsal two-b, but the fin is somewhat disarticulated and identification of elements is difficult. The proximal portion of the fin is missing in CAMSM J35187, but a co-ossification of phalanges of the two branches of digit II occurs in the third or fourth phalangeal row.

Post-mortem displacement of digits can also result in odd morphologies that could, in isolation, be mistaken for new taxa. Four specimens have a portion of the hindfin shifted proximally. In NHMUK R5918, an isolated hindfin, distal tarsal two has been rotated and moved anterior to the tibia and the two branches of digit II have also been shifted proximally (Figure. 7.10A), probably a taphonomic effect. Note that the space between the posterior branch of digit II and digit III is wider than between digit III and IV, suggesting post-mortem disarticulation. The left hindfin of NHMUK R5595 (Figure. 7.10C), a nearly complete skeleton of *I. larkini* (Lomax and Massare, 2017), shows a similar shift, but distal tarsal two has not been rotated and digit II is not shifted proximally as much as in NHMUK R5918. This, however, might not be taphonomic, but instead, the result of decisions made during preparation, because most of the fin appears to be set in a filler material. Unfortunately, the specimen is not accessible for close examination. BRSUG 25300, the holotype of *I. larkini*, also shows what might be post-mortem displacement on the right hindfin (posterior fin on specimen). Metatarsal two-b has been displaced proximally so that it is between distal tarsal two and the astragalus, resulting in what could be interpreted as four elements in the second row (Figure. 7.10B). Although metatarsal two-b in the left fin of the specimen partly separates the astragalus and distal tarsal two, it is more distally positioned and is clearly an element of the third row. Post-mortem displacement resulted in an odd morphology in one of the two fins. A similar displacement occurs in NHMUK R5790, a small, isolated hindfin. Metatarsal two-b is between the astragalus and distal tarsal two, allowing a similar interpretation of four elements in the second row. The wide separation between elements in NHMUK R5790 makes it clear that this odd arrangement is the result of post-mortem disarticulation and displacement.

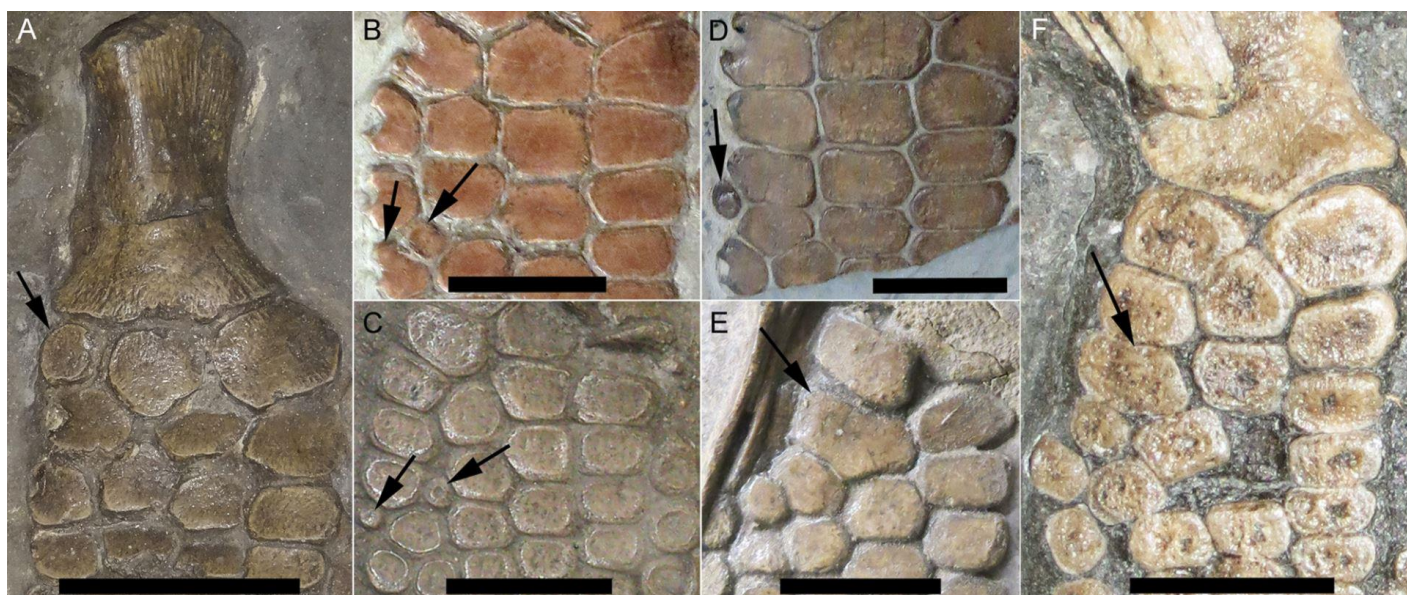


Figure. 7.9. Examples of supernumerary elements and co-ossifications. Anterior to the left. A. USNM V4967, showing a fairly large, supernumerary bone (arrow) that is anterior to the tibia and in contact with the distal end of the femur. B. BRSMG Ce16611, arrows point to two supernumerary elements in digit II. C. BGS 955, arrows point to two small supernumerary elements. D. WARMS G6188, arrow points to a supernumerary element anterior to digit II. E. ANSP 17429 (reversed), arrow points to a co-ossification of elements from digits II and III, possibly metatarsal three and metatarsal two-b. F. TTNCM 8359 (reversed), arrow points to a co-ossification of the proximal element of the two metatarsals of digit II. The other hindfin (not figured) shows Morphotype 2. Scales A and B equal 3 cm. Scales C and F equal 1 cm. Scales D and E equal 2 cm.

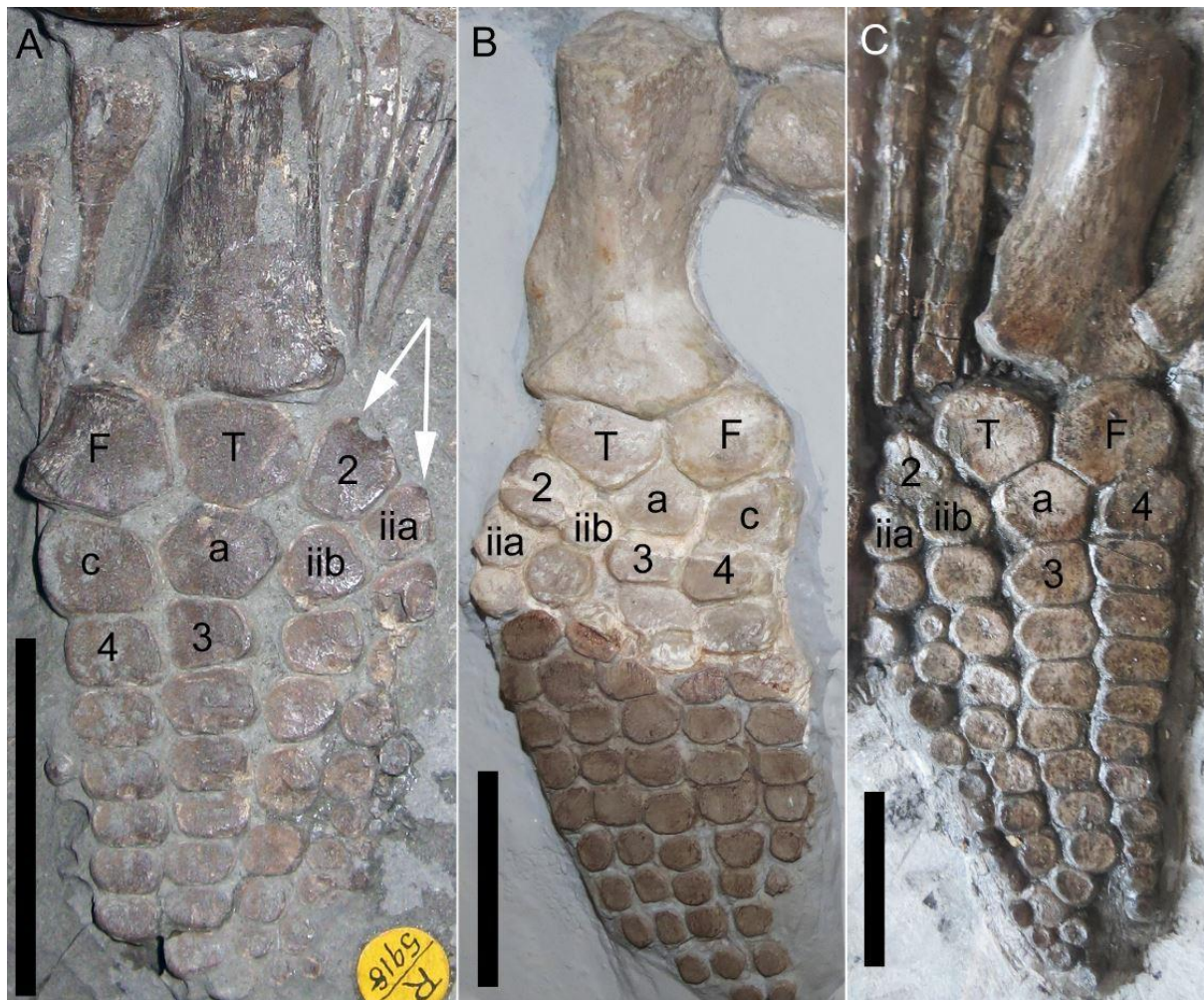


Figure. 7.10. Examples of post-mortem displacement that produces unusual morphologies. A. NHMUK R5918, an isolated hindfin, in which distal tarsal two has been rotated and moved proximally so that it is anterior to the tibia. This also shifts both branches of digit II proximally relative to digit III. B. BRSUG 25300, left hindfin, in which metatarsal two-b has been shifted so that it is almost in contact with the tibia. Darker elements of the distal portion of the fin are entirely reconstructed. C. NHMUK R5595, left hindfin, in which distal tarsal two and both branches of digit II have been moved proximally, similar to A. All scales equal 3 cm, but scale for C is an estimate because the specimen is on display behind glass. Abbreviations: 2, distal tarsal two; 3, distal tarsal three; 4, distal tarsal four; a, astragalus; c, calcaneum; F, fibula; iia, anterior metatarsal of digit II; iib, posterior metatarsal of digit II; T, tibia.

Table. 7.3. Hindfins with unusual morphologies.

Specimen	Morphotype	Unusual features
ANSP 17429	1	co-ossification occurs
BGS 955	2	supernumerary elements present
BRSMG Ce16611 left	2	supernumerary elements present
BRSUG 25300 right	2	bifurcation element displaced proximally; four elements in third row
BU 5289	2	middle two digits displaced proximally
CAMSM J35187	2	co-ossification occurs
NHМУK OR41849		
?right	2	astragalus separates tibia and fibula and almost contacts femur
NHМУK R5595 left	2	both branches of digit II displaced proximally
NHМУK R5790	2	middle two digits displaced proximally
NHМУK R5918	2	both branches of digit II displaced proximally
NHМУK R11801	2	astragalus separates tibia and fibula and almost contacts femur
NMW 91.29G.1	2	astragalus separates tibia and fibula; almost contacts femur
OUMNH J.29352	2	calcaneum enlarged posteriorly enlarged, proximodistally elongated
PETMG R174	2	calcaneum; astragalus does not contact tibia
RAMM 57/2009	2	three elements contact tibia; four elements in second row
SMNS 58275 right	2	supernumerary element present
TTNCM 8359	2	co-ossification occurs
USNM V4967	2	supernumerary element anterior to tibia; three elements contact femur
WARMS G6188 left	1	supernumerary element present

Note: 'left' and 'right' indicate the left or right hindfin on specimens that preserve both.

Discussion and conclusion

Ichthyosaurus has three primary digits (II, III, IV) in the hindfin, a feature it shares with *Temnodontosaurus*, *Suevoleviathan*, *Leptonectes*, *Eurhinosaurus*, *Stenopterygius*, and *Hauffiopteryx* (Maisch, 1998; McGowan and Motani, 2003; Maxwell 2012, fig.2). The hindfins of the other Lower Jurassic genera, *Excalibosaurus*, *Wahlisaurus*, and *Protoichthyosaurus*, are too incomplete to determine the total digit count. Only *Ichthyosaurus* is known to have an anterior digital bifurcation in the hindfin (but see below), which increases the digit count to as high as six, although five is more typical. The digital bifurcation can distinguish hindfins of *Ichthyosaurus* from most genera. However, incomplete hindfins present a problem in recognising *Ichthyosaurus*. Morphotype 1 is seen in other genera, so if only the first three rows of elements are preserved, *Ichthyosaurus* is not easily distinguished from other Lower Jurassic genera, although the femora might be distinctive. Thus the taxonomic usefulness of hindfin morphology has some limitations.

Another limitation is that the hindfin of *Protoichthyosaurus* shares similarities with that of *Ichthyosaurus*, a sister taxon (Lomax *et al.*, 2017a). Furthermore, both genera have an anterior digital bifurcation in the forefin, which suggests the possibility that *Protoichthyosaurus* also has a bifurcation in the hindfin. Only three specimens of *Protoichthyosaurus* with a hindfin or femur are known (Lomax *et al.*, 2017a). BRLSI M3555 is the only specimen to preserve a complete femur, which has a long shaft with a narrow proximal end and a very wide distal end. It is similar to that of *I. conybeari* but the shaft is more elongated and the distal expansion is broader. The femur on SOMAG/GEO/12 is not as elongated and the shaft is wider, although the proximal end is damaged and poorly preserved. With only two specimens the variation in the elongation cannot be assessed. Only SOMAG/GEO/12 preserves the mesopodium, which displays Morphotype 1. The more distal portion of the fin is partially disarticulated, and anterior elements are too scattered to ascertain the presence or absence of a bifurcation. A third specimen of *Protoichthyosaurus* (BRLSI M3563) preserves a hindfin, but the specimen is a composite. Only the right forefin and associated scapula and ribs definitely belong together and can be assigned to *Protoichthyosaurus*. The rest of the skeleton might not belong to the same individual or the same species (Massare and Lomax, 2016a; Lomax *et al.*,

2017a). Thus, based on currently recognised specimens, the hindfin of *Protoichthyosaurus* cannot be distinguished from that of *Ichthyosaurus*.

Within *Ichthyosaurus*, species cannot be identified unequivocally from a well-preserved hindfin, although certain morphologies are more common in some species than others (Table. 7.4). Morphotype 1 definitely occurs in *I. breviceps*, *I. conybeari*, and *I. somersetensis*, although *I. anningae* and *I. larkini* are known from few specimens, and so this morphotype could possibly occur in those species. Combined with the presence/absence of notching, *I. breviceps*, *I. conybeari*, and *I. somersetensis*, can be distinguished with some degree of confidence if a specimen displays Morphotype 1. A hindfin without notching is more likely *I. breviceps* than the others. A notched tibia almost certainly indicates *I. conybeari*. Any *Ichthyosaurus* hindfin with a notched tibia can be assigned to this species, at least based on currently known specimens. A notched distal tarsal two, metatarsal and/or phalanges is most likely *I. somersetensis*. Other features of the skull and postcranium, however, are needed to verify these preliminary identifications.

Table. 7.4. Morphologic characteristics of hindfins of species of *Ichthyosaurus*. Bifur = total number of bifurcations in digit II. Fins must be complete to at least the 5th phalangeal row to assess the presence or absence of a distal bifurcation.

Species	Morphotype	Notched tibia	Other notching	Bifur	Femur shape
<i>I. communis</i>	2	no	no	2 or 3	elongated, symmetric
<i>I. breviceps</i>	1 or 2	no	no	1 or 2	elongated, symmetric
<i>I. conybeari</i>	1 or 2	usually	sometimes	2	elongated, symmetric almost as wide as
<i>I. anningae</i>	2	no	no	2	long
<i>I. larkini</i>	2	no	yes	2	elongated, asymmetric
<i>I. somersetensis</i>	1 or 2	no	yes	1 or 2	elongated, asymmetric

The occurrence of Morphotype 2, in which the bifurcation is in the metatarsal row, presents more uncertainty in identifications based only on a hindfin. If metatarsal two-b nearly separates distal tarsal two from the astragalus, and three elements contact the astragalus (Figure. 7.2D), then the specimen could be *I. larkini*, the only species that has been unequivocally identified with this morphology. However, this variation might also occur in *I. somersetensis* because some specimens with this variation cannot be assigned to a species. *I. larkini* and *I. somersetensis* have similarly shaped femora as well. If distal tarsal three has a broad contact with the astragalus and metatarsal two-b has only a slight, if any, contact with the astragalus (Figure. 7.2C), then the specimen could be *I. somersetensis*, *I. conybeari* or *I. breviceps*. The presence of a notched distal tarsal two or more distal notching would most likely be *I. somersetensis*; a notched tibia would indicate *I. conybeari*, and a lack of notching would most likely be *I. breviceps*. A hindfin in which metatarsal two-b and distal tarsal three have broad, nearly equal contacts with the astragalus (Figure. 7.2B), indicates that the specimen is most likely *I. communis* or *I. anningae*, in the absence of notched elements. As with Morphotype 1, additional features of the skull or humerus shape are needed to confirm these preliminary identifications. Thus although morphotypes are not unique to a species, combinations of hindfin characters can suggest the most likely species assignment for a particular hindfin morphology. However, intermediate morphologies exist in the extent of contact of the astragalus and metatarsal two-b. In these cases, the hindfin morphology has no taxonomic utility; other features are required even for a preliminary species assignment.

This research has also shown the effect of large sample sizes on the identification of taxonomically distinct morphological characters. Without several fairly complete specimens of each species, the occurrence of both morphotypes in *I. somersetensis*, *I. breviceps*, and *I. conybeari* could not have been recognised. It would have appeared that the two morphotypes were diagnostic of two different sets of species within *Ichthyosaurus*. Hindfin morphology would have appeared much less variable and much more distinct with fewer specimens. The presence or absence of a bifurcation in the metatarsal row could be seen as a major difference among species or as individual variation, depending on how many specimens are known/examined. This raises doubts about the validity of new taxa based on limited material.

Gaps between morphologies are much larger when fewer specimens are available. With only one or two specimens, intermediate morphologies that grade from one form to another are unknown. More specimens result in more variation, and apparent gaps between morphologies are filled in, as is the case here with hindfin morphology. Distinct characters can be more easily defined if only one or two specimens are known because intermediate morphologies are missing. This raises the question of whether a particular morphology is distinct or only seems to be because of a small sample size.

One individual from a new location or an unusual horizon can be examined in such detail that often numerous 'unique' features can be identified. In fact, it is probably easier to identify such features on a single individual than on a dozen individuals, especially considering that multiple specimens will vary in orientation, preservation and completeness. To put it in a different context, a new specimen could look quite different from the type specimens of known species, but if one examines several specimens to get a better picture of variation, the new specimen might be within the variation of a known species. This is especially true of isolated elements, e.g. isolated hindfins that appear to have unique morphologies. Variation must be adequately assessed by comparing many specimens, rather than just examining type specimens or citing exclusively from the literature. Otherwise, the decision to erect a new taxon is not substantially different from what was largely done in the 19th century, when new species were erected on the basis of a single individual (often from a new location or horizon) if it showed a small difference in morphology from previously known specimens.

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Chapter 8: The taxonomic utility of forefin morphology in Lower Jurassic ichthyosaurs: *Protoichthyosaurus* and *Ichthyosaurus*

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The taxonomic utility of forefin morphology in Lower Jurassic ichthyosaurs:
Protoichthyosaurus and *Ichthyosaurus*

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Abstract

The validity of the parvipelvian ichthyosaur genus *Protoichthyosaurus* Appleby, 1979 was evaluated by examining the type material and recently recognized specimens. *Protoichthyosaurus* has a wide forefin with at least five primary digits, an anterior digital bifurcation in the forefin, a humerus that is nearly equal in width distally and proximally, and a coracoid with well-developed anterior and posterior notches, features it shares with the more common genus *Ichthyosaurus*. Previously, *Protoichthyosaurus* was synonymized with *Ichthyosaurus* because of an incomplete understanding of forefin variation in the latter taxon. However, *Protoichthyosaurus* has several features in the forefin that distinguishes it from *Ichthyosaurus*, including the presence of three elements in the distal carpal row, a contact between distal carpal 3 and the ulnare, a bifurcation of distal carpal 2 to form two elements in the metacarpal row, the proximal element of the bifurcation nearly separating distal carpal 2 from distal carpal 3, distal carpal 3 separating the intermedium from contact with distal carpal 4, and the absence of digit V. A phylogenetic analysis confirms that *Protoichthyosaurus* is the sister taxon of *Ichthyosaurus*, and is nested in Ichthyosauridae. We recognize two species, *P. prostaxalis* and *P. applebyi* sp. nov., but not *P. prosostealis*. *Protoichthyosaurus* is unequivocally from the Hettangian, but might be present in the Rhaetian to lower Sinemurian. The genus is geographically widespread across the U.K.

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Introduction

Appleby (1979) proposed a new Lower Jurassic genus of ichthyosaur, *Protoichthyosaurus*, based on an unusual forefin morphology that displayed both latipinnate and longipinnate characteristics, major subdivisions of the Ichthyosauria at the time (McGowan, 1972). The genus and family Protoichthyosauridae were diagnosed by forefins displaying one of two morphologies: (1) three distal carpals and an anterior digital bifurcation in the forefin, or (2) a supernumerary bone contacting the intermedium anteroproximally. The latter was described on the basis of a single specimen and the morphology is likely a pathology, as discussed below. The former, however, is distinctly different from *Ichthyosaurus*, with which *Protoichthyosaurus* has been synonymized (Maisch and Hungerbühler, 1997). Appleby (1979) noted that although both genera have a digital bifurcation anterior to the primary axis of the forefin, *Protoichthyosaurus* has only three elements in the distal carpal row, whereas *Ichthyosaurus* has four (Figure. 8.1).

Unrecognized composites and pathologies, however, made the distinction between the two genera difficult to justify. Many specimens of *Ichthyosaurus* in historic collections were altered, often with the addition of a fin or 'tail', probably to create a more attractive specimen for display (Massare and Lomax, 2016). Although not intended to be deceptive, this practice led to the notion that fins of *Ichthyosaurus* are more variable within an individual than is actually the case. Appleby (1979) must have been aware of the variation because his diagnosis specified that either the left or right fin have three distal carpals, the *Protoichthyosaurus* pattern, although he did not recognise the specimens as composites. The 'individual variation' caused by composite specimens with a forefin from each genus may have also led Maisch and Hungerbühler (1997) to synonymize the two genera because the forefins were too variable, and thus unreliable, to distinguish the genera. Subsequently, Maisch (1997), Maisch and Matzke (2000a), and McGowan and Motani (2003) agreed with the synonymy. However, with the recognition of composites and pathologic forefins in specimens from historic collections, the differences in the mesopodium described by Appleby (1979) are sufficient, at least in well preserved forefins, to separate specimens of *Protoichthyosaurus* from *Ichthyosaurus* and any other Lower Jurassic ichthyosaur genus. Additionally, we have identified other characters that distinguish *Protoichthyosaurus* from *Ichthyosaurus*. *Protoichthyosaurus prostaxalis* is a valid

taxon, whereas *P. prosostealis* is not. We also identify a new species, *P. applebyi* sp. nov.

Institutional Abbreviations. AGC, Alfred Gillett Collection, cared for by the Alfred Gillett Trust, C & J Clark Ltd, Street, Somerset, U.K.; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; BGS, British Geological Survey, Keyworth, Nottingham, U.K.; BRLSI, Bath Royal Literary and Scientific Institution, U.K.; BRSMG, Bristol City Museum and Art Gallery, U.K.; BU, formerly BIRUG, The Lapworth Museum of Geology, University of Birmingham, U.K.; CAMSM, Sedgwick Museum, Cambridge University, U.K.; GLAHM, Hunterian Museum, Glasgow, U.K.; LEICT, Leicester Arts and Museums Service, New Walk Museum and Art Gallery, U.K.; NHMUK, formerly BMNH, The Natural History Museum, London, U.K.; NMING, National Museum of Ireland, Dublin, Ireland; NMW National Museum of Wales, Cardiff, U.K.; NOTNH, Nottingham Natural History Museum (Wollaton Hall), U.K.; OUMNH, Oxford University Museum of Natural History, U.K.; ROM, Royal Ontario Museum, Toronto, Canada; TTNCM, Somerset County Museum, Taunton, U.K.; UOD, University of Derby, U.K.; UON, University of Nottingham, U.K.; UNM, University of Nottingham Museum, U.K.; UORCMZ, Cole Museum of Zoology, University of Reading, U.K.; WARMS, Warwickshire Museum, Warwick, U.K.; YORYM, Yorkshire Museum, York, U.K.

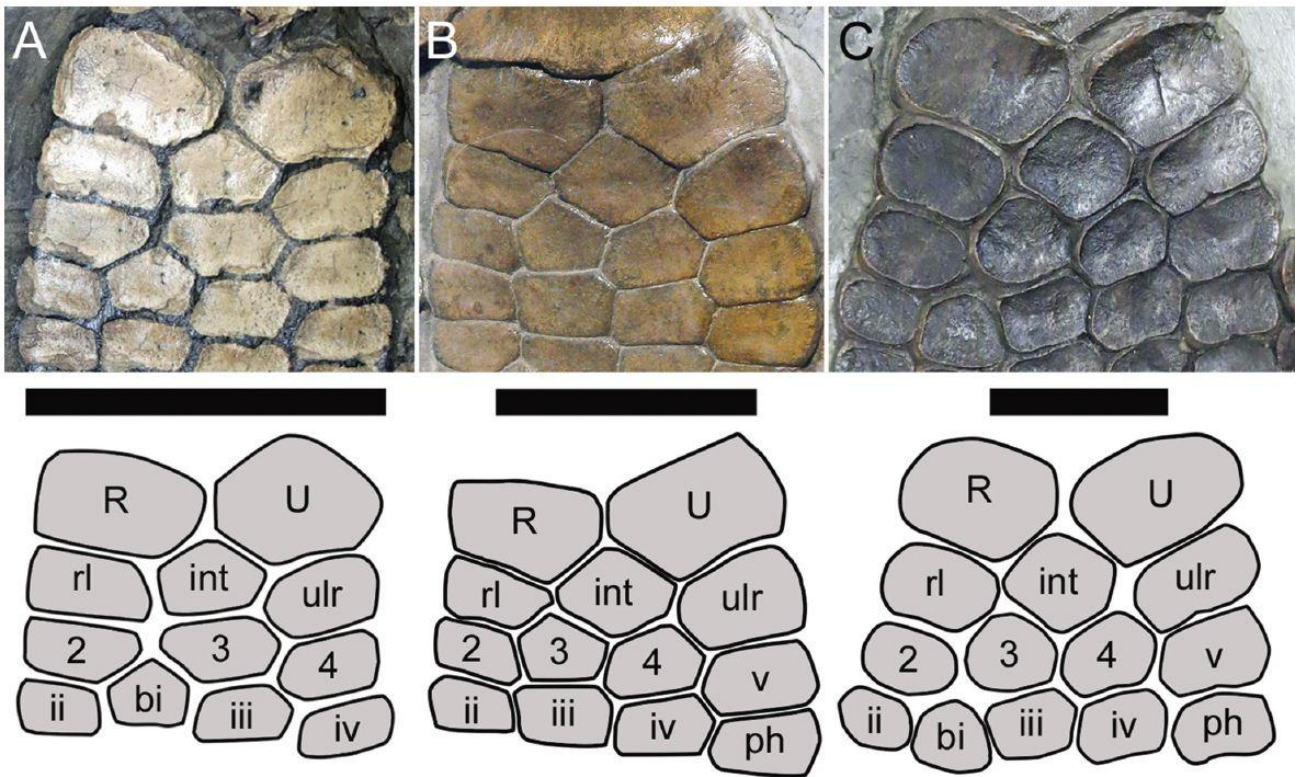


Figure. 8.1. Comparison of the proximal portion of the forefins of *Protoichthyosaurus* and *Ichthyosaurus*, showing the differences in arrangement of the carpal and metacarpal rows, anterior to the left. **A**, *Protoichthyosaurus applebyi* (UNM.G.2017.1). Note three elements in carpal row and four elements in metacarpal row. **B**, *Ichthyosaurus* sp. (ANSP 17429). Note four elements in carpal row and four elements in metacarpal row. **C**, *Ichthyosaurus* sp. (NHMUK R224). Note four elements in distal carpal row and five elements in metacarpal row. B and C are reversed to show same orientation. **Abbreviations:** **2**, distal carpal two; **3**, distal carpal three; **4**, distal carpal four; **bi**, bifurcation; **ii**, metacarpal two; **iii**, metacarpal three; **int**, intermedium; **iv**, metacarpal four; **ph**, phalanx; **R**, radius; **rl**, radiale; **U**, ulna; **ulr**, ulnare; **v**, metacarpal five. Scale bars equal 5 cm.

Material

The holotype and two of the paratypes of *Protoichthyosaurus prostaxalis* Appleby 1979 are part of the Charles Moore Collection housed at NMW, on long-term loan from BRLSI (Figure. 8.2). Another of the paratypes, an isolated forefin, is presently lost (LEICT G454.1951/164; M. Evans, pers. comm. 2016), but a line drawing exists (Appleby, 1979, fig. 1e). The fourth paratype (OUMNH J.13799), as well as the holotype of *Protoichthyosaurus prosostealis* Appleby, 1979 (BRLSI M3572) do not belong to the genus (see discussion below). Including the type and paratypes, 22

specimens of *Protoichthyosaurus* have been evaluated in this study, including articulated skeletons, as well as isolated skulls and forefins (Table. 8.1).

The question of possible composites arises in examining partial or fairly complete skeletons from historic collections. The holotype (BRLSI M3553) and one of the paratypes (BRLSI M3555) appear to be entirely authentic. BRLSI M3563, a partial skeleton also designated as a paratype by Appleby (1979), is a composite. The entire skeleton is in several blocks of matrix, placed into plaster and surrounded by a wooden frame. The left fin is set into and entirely surrounded by plaster, but the right fin, although a crack is present, is set in matrix and articulates with a portion of the skeleton (Massare and Lomax, 2016). The left forefin has been added to the specimen and is an example of *Ichthyosaurus*, whereas the right forefin is genuine and can be assigned to *Protoichthyosaurus*. The block that has the right forefin (*Protoichthyosaurus*) also has a portion of scapula and ribs, which probably belong together. However, the skull is separated from this block and entirely surrounded by plaster, as is the hindfin and pelvis. Therefore, although the skull, hindfin and pelvis may belong with the right forefin, they cannot be definitely identified as belonging to the same individual and should not be used in any phylogenetic study or description of the species. Conservation work may reveal what portions of this skeleton are authentic and what has been added, as was the case with another specimen from the NMW collection (Buttler and Howe, 2002; Buttler and Stooshnov, 2002).

AGC 12 was also identified as a composite by Massare and Lomax (2016). However, this was because the left forefin is almost entirely placed into plaster and reconstructed. This fin has the *Ichthyosaurus* forefin structure, whereas the right forefin has the *Protoichthyosaurus* pattern. It is possible that the left forefin belongs to the same specimen but was rebuilt incorrectly when it was placed into the plaster. Based on the morphologies of the right forefin and skull, however, we identify this specimen as an example of *Protoichthyosaurus*.

BU 5323 is an isolated, three-dimensional skull. Unfortunately, there is no geographic or stratigraphic information with the specimen, but it is clearly *Protoichthyosaurus* (see below). However, the skull has always been associated with at least five additional blocks of matrix that together form one block and contain a string of vertebrae, ribs and a hindfin (BIRUG 4176a–e). They might be the same individual, but no record exists (pers. comm. J. Clatworthy, 2017). The additional

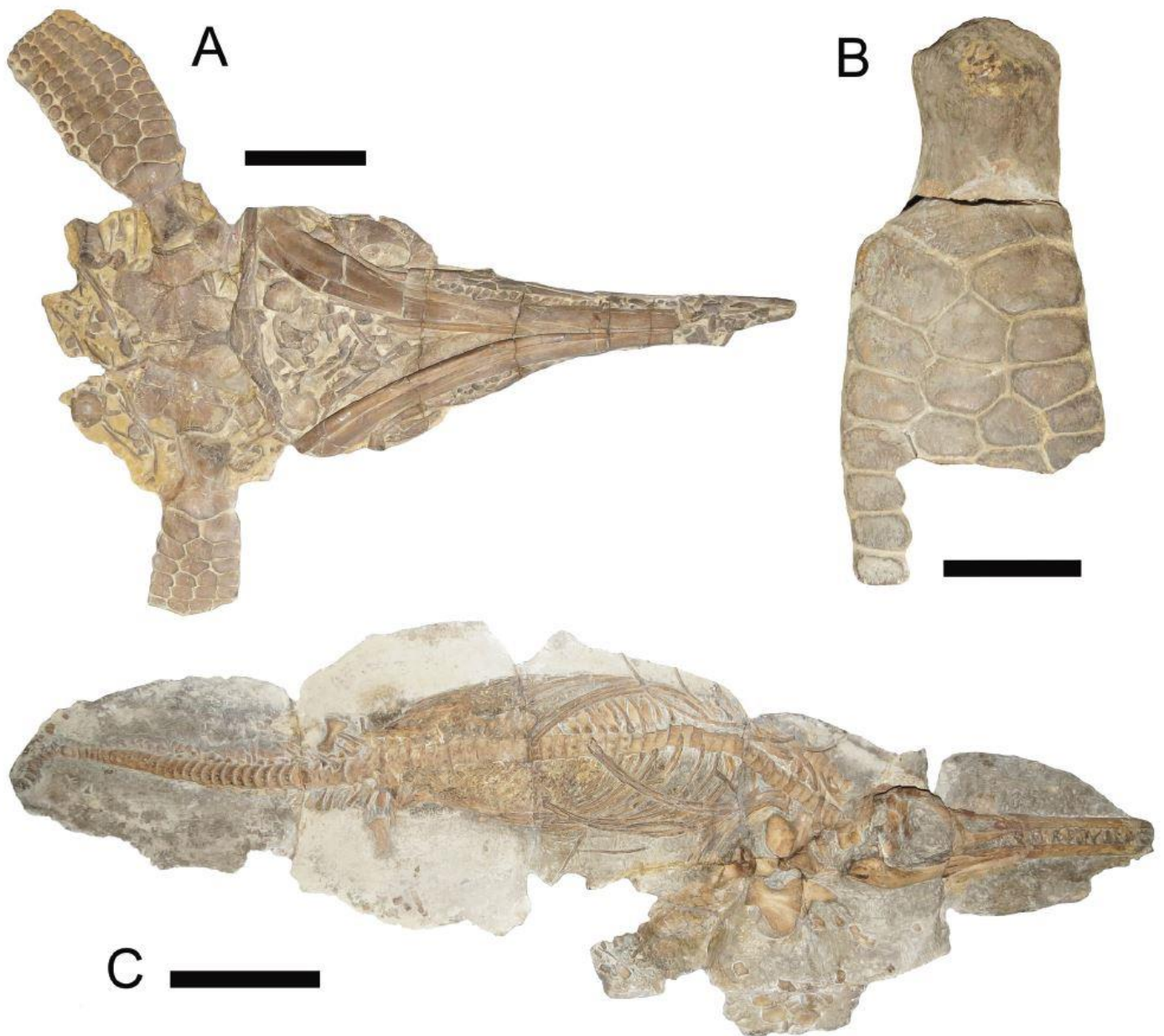


Figure. 8.2. Holotype and paratype specimens of *Protoichthyosaurus prostaaxalis*, all probably from the Lower Jurassic of Somerset, U.K. **A**, holotype, skull and pectoral girdle in ventral view (BRLSI M3553). **B**, paratype, right forefin in dorsal view, anterior to the right (BRLSI M3563). This specimen is a composite partial skeleton, so only the forefin is figured. **C**, paratype, partial skeleton lying on its left side, in lateral view (BRLSI M3555). The other paratype (LEICT G454.1951/164) is not figured because the specimen is presently missing. Scale bars equal 10 cm (A), 5 cm (B), and 20 cm (C).

blocks will not be discussed further. Another isolated skull in three dimensions is GLAHM V1180, which is a part and counterpart specimen. It is noteworthy for the preservation of soft tissue (Delair, 1966; Lingham-Soliar, 1999).

Massare and Lomax (2016) identified UNM.G.2017.1 (previously, UON VR159, UON TC3199) as a ‘suspicious’ specimen because the skull appears to be on a separate block of matrix and separated from the postcranial skeleton by about 3 cm of filler material. The skull is a darker color than the anterior centra, but those have been sheared off and the internal bone surface is exposed. Furthermore, the coloration varies in the precaudal region and the color of the skull matches some of the neural spines, as well as other elements. Furthermore, additional preparation has shown that the matrix is continuous between the skull and postcranium (N. Larkin, pers. comm., 2017). Thus, the skull, forefin, entire precaudal region, and the anterior caudal centra are from a single individual. Almost all of the caudal centra, however, have been set in plaster. The posterior, straight segment of articulated centra, making up about half of the tail, have most likely been added. Additionally, some of the very distal elements of the forefin have been set into plaster, but are consistent in size with the rest of the fin. The articulated skeleton is clearly *Protoichthyosaurus* based on forefin morphology.

Table. 8.1. Specimens of *Protoichthyosaurus* from the U.K. evaluated in this study.

Specimen no.	Material	Locality
AGC 12	Skull and articulated partial skeleton in left lateral view; anterior portion of rostrum missing	probably Street, Somerset
BU 5323 (formerly 27683)	Isolated three-dimensional skull; anterior portion of rostrum missing	unknown
BRLSI M0653	Composite; left forefin only	probably Street, Somerset
BRLSI M3553 holotype	Skull and anterior skeleton in ventral view	probably Street, Somerset
BRLSI M3555 paratype	Skull and articulated partial skeleton in right lateral view	probably Street, Somerset
BRLSI M3562	Composite; right forefin only	probably Street, Somerset

BRLSI M3563 paratype	Composite; right forefin only	probably Street, Somerset
GLAHM V1180	Part and counterpart of partial skull in concretion	Severn Valley, Gloucestershire
LEICT G454.1951/164 missing paratype	Isolated forefin but possibly a hindfin of <i>Ichthyosaurus</i> (see text)	probably Barrow-upon- Soar, Leicestershire
LEICT G729.1889.1	Partial skull that may be associated with caudal centra	Barrow-upon-Soar, Leicestershire
NMING F8747	Partial skeleton with skull in lateral view; poorly preserved	probably Street, Somerset
NHMUK OR29672	Isolated partial forefin with soft tissue preservation	Barrow-upon-Soar, Leicestershire
NHMUK R1063	Isolated forefin lacking humerus	?Lyme Regis, Dorset
NHMUK R36958	Isolated three-dimensional skull	Barrow-upon-Soar, Leicestershire
NMW 2012.23G.1	Isolated skull in left lateral view	Glamorgan, Wales
NOTNH: FS13770	Isolated partial skull	Barnstone, Nottinghamshire
OUMNH J.26971	Isolated proximal forefin	probably Lyme Regis area
TTNCM 41/2017 (formerly TV52)	Ventral skull and partial forefin; anterior portion of rostrum missing	probably Somerset
UOD D1	Isolated three-dimensional skull; anterior portion of rostrum missing	Barnstone, Nottinghamshire
UNM.2017.1	Skull and articulated partial skeleton in left lateral view	unknown (see text)
UORCMZ FE19-1	Partial anterior skeleton	unknown
WARMS G347	Isolated three-dimensional skull with complete rostrum	Binton, Warwickshire

Systematic Palaeontology

Order **Ichthyosauria** de Blainville, 1835

Family **Ichthyosauridae** Bonaparte, 1841

Genus **Protoichthyosaurus** Appleby, 1979

Type Species. *P. prostaxalis* Appleby 1979.

Referred Specimens. The following specimens are too incomplete to be referred to a species, but can be referred to the genus on the basis of the forefin morphology: TTNCM 41/2017 (formerly TV52), a fragmentary ventral skull and forefin; NHMUK R1063, a large forefin; NHMUK OR29672, a partial forefin with soft part preservation; UORCMZ FE19-1, a partial skeleton of a very small individual; OUMNH J.26971, an isolated proximal forefin. In addition, the right forefin of BRLSI M3562 and the left forefin of BRLSI M0653 can be referred to the genus, although both specimens are composites and the aforementioned fins probably do not belong to the main skeletons (Massare and Lomax, 2016). Other specimens that are sufficiently complete to assign to a species are listed below.

Locality and Horizon. NHMUK OR29672 is from Barrow-upon-Soar, Leicestershire, and LEICT G454.1951/164 might be as well; NHMUK R1063 is probably from the Lyme Regis area, west Dorset (Lydekker, 1889, p. 50), although the preservation is more similar to that of Street, Somerset; OUMNH J.26971 might also be from the Lyme Regis area according to museum records. TTNCM 41/2017 is probably from Somerset (D. Parsons, pers. comm. DRL, 2016). UORCMZ FE19-1 is from an unknown location. BRLSI M3562 and BRLSI M0653 are also from unknown locations, but because they are part of the Charles Moore Collection, they most likely come from Somerset (Copp et al. 1996). In addition, specimens of the type species are from Nottinghamshire, Somerset, Leicestershire, and Warwickshire (England); and Glamorgan (Wales). Thus *Protoichthyosaurus* is among the most geographically widespread genera of ichthyosaurs in the Lower Jurassic of the U.K.

The specimen from Barrow-upon-Soar is probably from the lowermost Jurassic (lower Hettangian), 'Pre-planorbis beds' (Tilmanni Zone; Martin et al., 1986). Similarly, specimens from Nottinghamshire, Somerset, and Warwickshire are

also Hettangian in age. The specimens that might be from Lyme Regis (NHMUK R1063, OUMNH J.26971) present the possibility that the genus continued at least into the lower Sinemurian. Historic specimens from 'Lyme Regis' are usually considered upper Hettangian–lower Sinemurian in age (McGowan, 1974b). However, areas along the coast near Lyme Regis, such as Charmouth and Seatown, have strata that are as young as lower Pliensbachian (Lomax, 2010; Page, 2010), and rare ichthyosaur specimens have been reported from the lowermost Hettangian in the area (Benton and Spencer, 1995; Page, 2010). Furthermore, Rhaetian (uppermost Triassic) strata are exposed in the Lyme Regis area, along Pinhay Bay (Benton and Spencer, 1995:fig. 5.3; Gallois, 2007). The basal beds of the Blue Lias Formation are also probably Rhaetian (Weedon et al. 2017). Thus the genus is definitively from the Hettangian but might extend from the Rhaetian to the lower Sinemurian.

Emended Diagnosis. *Protoichthyosaurus* is distinguished from other ichthyosaurian genera by the following autapomorphies of the forefin: distal carpal 3 contacts the ulnare; proximal element of bifurcation in metacarpal row nearly separating distal carpal 2 from distal carpal 3; intermedium separated from contact with distal carpal 4 by distal carpal 3. The combination of three elements in the distal carpal row and a bifurcation of distal carpal 2 producing four elements in the metacarpal row is unique for the genus.

Protoichthyosaurus is also characterized by the following unique combination of characters: pineal foramen probably between frontal and parietal (as in other Lower Jurassic taxa such as *Leptonectes*, *Temnodontosaurus* and *Stenopterygius*; McGowan and Motani, 2003; Motani, 2005); long internasal foramen (most similar to *Shastasaurus liangae*; also reported in some specimens of *Ichthyosaurus* and *Temnodontosaurus*, in *Platypterygius australis*, and other taxa; McGowan, 1974a; Maisch and Matzke, 2000b; Sander et al. 2011; Fischer, 2012); posteriorly wide nasals (as in *Ichthyosaurus* and *Stenopterygius*; Motani, 2005; Maxwell et al., 2012); triradiate lacrimal (shared with some species of *Ichthyosaurus*, *Temnodontosaurus*, and others); maxilla excluded from margin of the external naris by subnarial process of premaxilla and anterior process of lacrimal (shared with *Ichthyosaurus*, some species of *Stenopterygius*, *Temnodontosaurus* and others; Maisch and Matzke, 2000a); anterior process of jugal does not extend beyond anterior edge of orbit

(shared with some species of *Ichthyosaurus* and others); teeth with large roots having deep, prominent grooves (shared with some species of *Ichthyosaurus*, *Temnodontosaurus*, and others); coracoid with wide anterior and posterior notches (shared with *Ichthyosaurus*); scapula with long shaft, and slightly expanded anterior end, but without prominent acromion process (shared with *Ichthyosaurus*, *Temnodontosaurus*, *Suevoleviathan*; Maxwell et al., 2012; Lomax, 2016); humerus nearly equal in width distally and proximally, with slight constriction in the shaft (shared with *Ichthyosaurus*); presence of three elements in distal carpal row of forefin (shared with *Temnodontosaurus*, *Suevoleviathan*, *Eurhinosaurus*, and others; Motani, 1999a); one digit in broad contact with the intermedium (shared with *Temnodontosaurus*, *Suevoleviathan*, and others); digit V absent (shared with *Temnodontosaurus* and some Triassic genera; Motani, 1999a); five primary digits in forefin, although fin must be preserved to the fourth phalangeal row to verify number (shared with *Ichthyosaurus*, *Stenopterygius* and others; Motani, 1999a); bifurcation of digit II in phalangeal row of forefin (shared with *Ichthyosaurus*); forefin phalanges closely packed, mostly rectangular, but rounded at distal end (shared with *Ichthyosaurus*, *Platypterygius* and others).

Remarks. Appleby (1979) erected the genus *Protoichthyosaurus* to ‘unite’ two unusual forefin morphologies. This was reflected in two mutually exclusive diagnostic characters: (1) a forefin with three distal carpals and a fourth digit arising anteriorly in the metacarpal row, or (2) a forefin with a supernumerary bone in contact with the intermedium. The first character was diagnostic of *P. prostaxalis*, whereas the second was diagnostic of *P. prosostealis*.

Protoichthyosaurus prosostealis was based on a single specimen, BRLSI M3572 (formerly B. 1963’24/OS), in which a supernumerary element is positioned anteroproximally to the intermedium and surrounded by the radius, radiale, ulna and intermedium. This feature is present in both forefins of BRLSI M3572 (Figure. 8.3A, B). The same morphology occurs in one of the two forefins of NHMUK OR49204, but the supernumerary element is present only in the right fin; the left fin clearly shows the morphology of *Ichthyosaurus* (Figure. 8.3C). NHMUK OR49204 is not a composite, which suggests that this morphology is a pathology. The same morphology also occurs in the right forefin of NHMUK OR39844, but the left forefin is not preserved (Figure. 8.3D). In all other respects, the carpus of BRLSI M3572,

NHMUK OR49204 and NHMUK OR39844, is identical to that of *Ichthyosaurus*. Thus *P. prosostealis* is not a species of the genus *Protoichthyosaurus*.

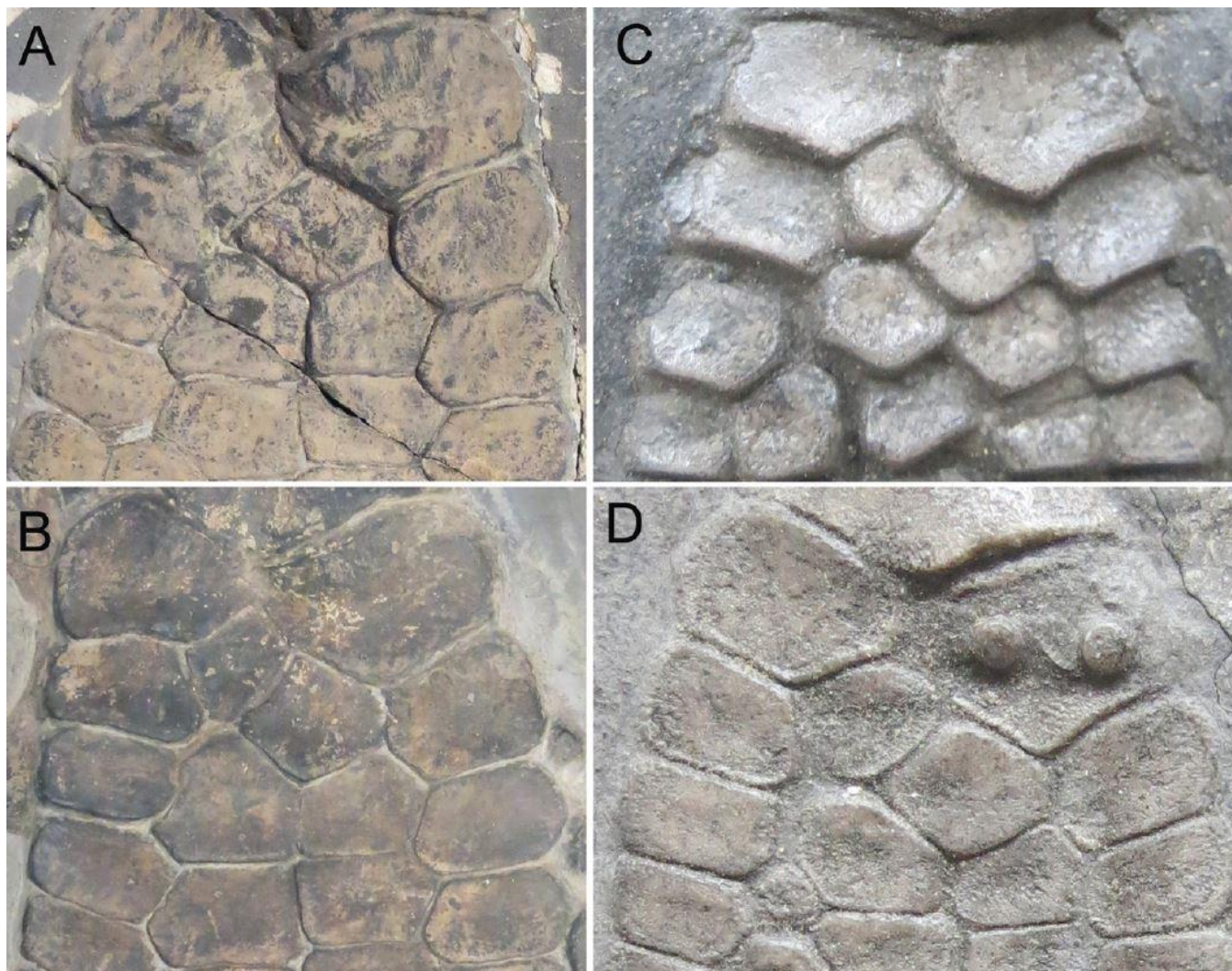


Figure. 8.3. Pathological forefins of *Ichthyosaurus*, showing a supernumerary element adjacent to the intermedium. Anterior is to the left in all specimens. **A**, left forefin (reversed) of the holotype of *Protoichthyosaurus prosostealis* (BRLSI M3572). **B**, right forefin of the holotype of *P. prosostealis* (BRLSI M3572). **C**, right forefin of NHMUK OR49204 showing the supernumerary bone. The left forefin (not figured) of this specimen displays the morphology typical of *Ichthyosaurus*. **D**, right forefin of NHMUK OR39844 showing the supernumerary bone as well as another small 'extra' element between distal carpals 2 and 3.

Protoichthyosaurus prostaxalis Appleby 1979

Figs. 2A–C, 4A–B, 5A

Holotype, BRLSI M3553 (formerly B.1963'5/OS), comprising a partial skull, pectoral girdle, and both forefins, preserved in ventral view.

Paratypes. BRLSI M3555 (formerly B. 1963'7/OS), a skull and partial skeleton, preserved in right lateral view; BRLSI M3563 (formerly B. 1963'15/OS), a composite partial skeleton; LEICT G454.1951/164 (formerly LM 454'1951/164), a partial forefin, presently missing (pers. comm., M. Evans, 2016), that might be a hindfin of a different genus (see text).

Referred Specimens. AGC 12, a skull and partial skeleton; BU 5323 (formerly BIRUG 27683), a skull preserved in three dimensions; GLAHM V1180, part and counterpart partial skull in nodule; LEICT G729.1889.1, a partial skull that might be associated with caudal centra; NHMUK R36958, a skull preserved in three dimensions; NMING F8747, a badly damaged skull and skeleton; NMW 2012.23G.1, a nearly complete skull; NOTNH: FS13770, a partial skull; UOD D1, a partial skull, preserved in three dimensions; and WARMS G347, a complete skull preserved in three dimensions.

Locality and Horizon. The type series of specimens and all except one of the referred specimens are from historic collections. Locality data are not recorded for some of them. BRLSI M3553, BRLSI M3555, and BRLSI M3563 are most likely from the area around Street, Somerset (Appleby, 1979), as is AGC 12 and probably NMING F874 (DRL, pers. obs.). GLAHM V1180 is from the Severn Valley area, Gloucestershire; NOTNH: FS13770 and UOD D1 are from Barnstone, Nottinghamshire; WARMS G347 is from Binton, Warwickshire. NHMUK R36958 and LEICT G729.1889.1 are from Barrow-upon-Soar, Leicestershire. NMW 2012.23G.1 is from Lavernock Point, Penarth, Glamorgan. BU 5323 is from an unknown location.

The Somerset specimens are most likely from the lowermost Jurassic (lower Hettangian), 'Pre-planorbis beds' (i.e., Tilmanni Zone) of the Blue Lias Formation (McGowan 1974b; Benson et al., 2012, 2015), although some might be Rhaetian (Gallois, 2007; Weedon et al. 2017). The Barrow-upon-Soar specimen is likely from

the Tilmanni Zone also (Martin et al., 1986). Museum records indicate that the Glamorgan specimen is Hettangian, from the Blue Lias Formation. The material from Nottinghamshire is from the Lower Lias Group, Hydraulic Limestones (lower Hettangian; Lomax and Gibson, 2015). The Warwickshire specimen is from the lowermost Jurassic (lower Hettangian), Wilmcote Limestone Member of the Blue Lias Formation (Smith and Radley, 2007). Thus, *Protoichthyosaurus prostaxalis* is definitely from the Hettangian, but might be as old as Rhaetian.

Emended Diagnosis. A medium-sized species, total length probably less than 2.5 m. It is distinguished by the following autapomorphies: large, dorsoventrally high, triangular maxilla with a long anterior process that extends at least half a naris length beyond the external naris, and beyond nasals in lateral view; dorsoventrally short, but anteroposteriorly wide, almost rectangular, postorbital; lacrimal dorsal process longer than anterior process.

Protoichthyosaurus prostaxalis is also characterized by a unique combination of features: prefrontal makes up less than half of orbit dorsal margin, but excludes dorsal process of lacrimal from orbit margin (shared with *Ichthyosaurus larkini* and *I. somersetensis*); prefrontal slender posteriorly but dorsoventrally wide anteriorly (shared with *I. larkini* and *I. somersetensis*); rectangular squamosal with triangular process extending ventrally from the posteroventral edge (shared with *I. somersetensis*); postorbital makes up no more than half of posterior orbit margin (similar to *I. communis*); robust humerus with small dorsal process that is centrally located and does not extend far down the shaft (similar to *I. somersetensis*); hindfin with three elements in distal tarsal (third) row (shared with some specimens of *I. breviceps*, *I. conybeari* and *I. somersetensis*); femur head robust, but with narrow shaft and distal end much wider than proximal (similar to *Excalibosaurus costini* and *Leptonectes tenuirostris*).

Remarks. Forefin morphology can distinguish *Protoichthyosaurus* from other genera, but does not distinguish species within the genus; a similar situation occurs in *Ichthyosaurus* (Lomax and Massare, 2017). This creates a problem in that the holotype (BRLSI M3553) and two of the paratypes (BRLSI M3563, LEICT G454.1951/164) display only traits of the genus (Figure. 8.2A, B). They would not be assigned to *P. prostaxalis* had they not been designated as the holotype and

paratypes by Appleby (1979). So, by definition, they are specimens of *P. prostaxalis*; but none of these specimens display the diagnostic characters of the species that are herein recognized on the other paratype, BRLSI M3555 (Figure. 8.2C), and referred specimens.

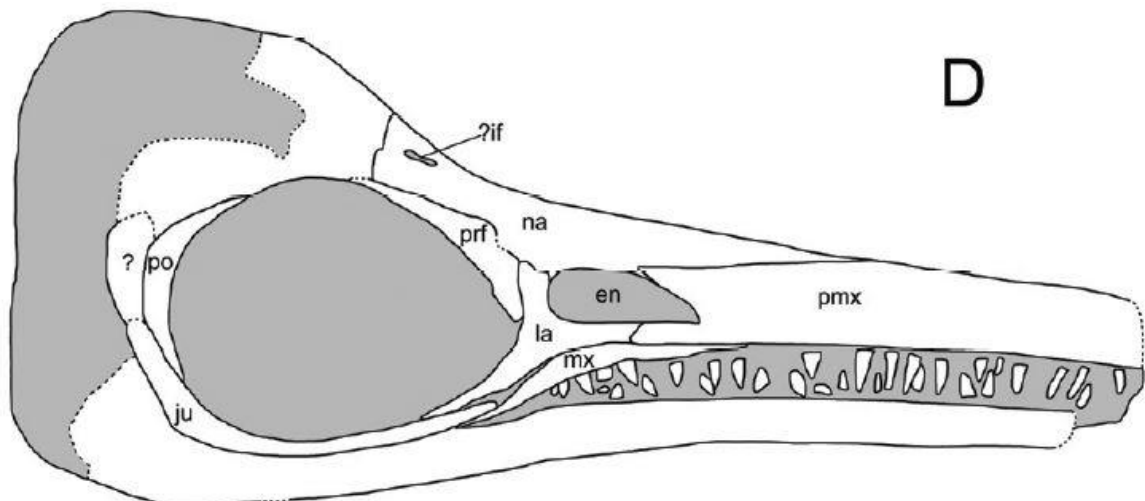
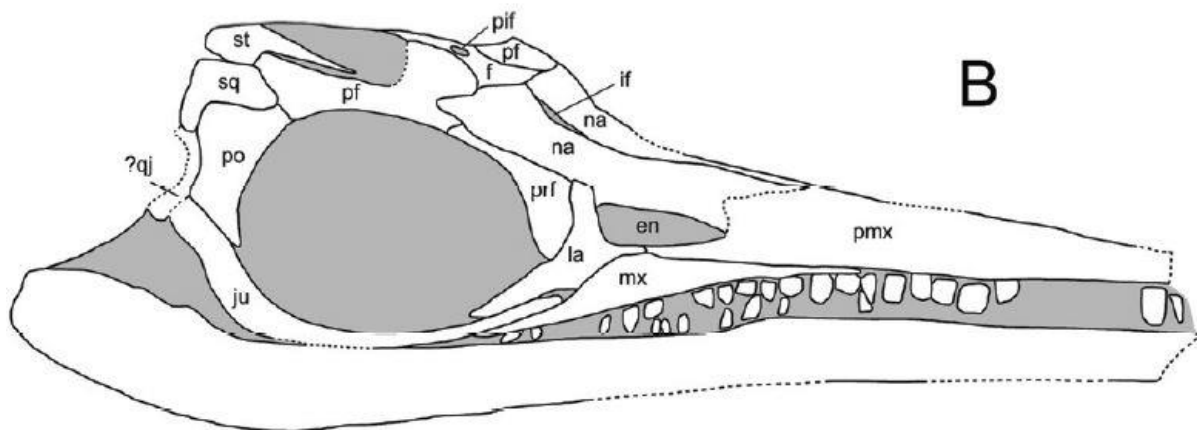
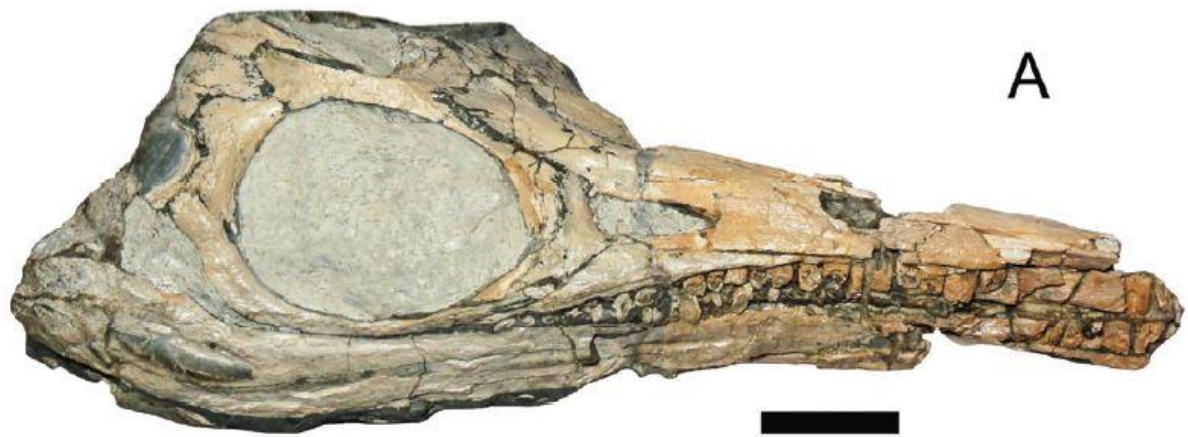
Description

The following description is based largely on the paratype specimen (BRLSI M3555), and some well-preserved referred specimens, as noted below. BRLSI M3555 is a partial, articulated skeleton with a skull, preserved in right lateral view. It includes a partial forefin, pectoral girdle elements, both femora, a vertebral column and ribs (Figure. 8.2C). The specimen is approximately 1.6 m long, from the tip of the rostrum to the bend in the tail, measured along the vertebral column (Table. 8.2). Only a small portion of the post-flexural vertebral column is preserved. The specimen can be referred to the genus on the basis of forefin morphology.

Skull

The description of the skull is largely based on BRLSI M3555 (Fig. 8.2C) and BU 5323, a well-preserved skull in three dimensions that clearly shows the sutures (Fig. 8.4AB). The description of elements, unless otherwise stated, are in lateral view. The

Figure. 8.4. Photograph and interpretive illustration showing the skull morphology of *Protoichthyosaurus prostaxalis* and *P. applebyi* sp. nov. **A, B**, BU 5323, referred specimen of *P. prostaxalis* in right lateral view. **C, D**, UNM.G.2017.1, holotype of *P. applebyi* in left lateral view, but reversed to show the same orientation as A and B. Light grey denotes matrix and openings in skull. Dashed line indicates broken edge. Much of the mandible in BU5323 is damaged and the full extent of the suture lines cannot be identified. Similarly, the sutures in the mandible of UNM.G.2017.1 cannot be identified and the posterior and dorsal skull roof are damaged and the sutures cannot be identified. **Abbreviations:** **en**, external naris; **f**, frontal; **if**, internasal foramen; **ju**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **pf**, postfrontal; **pif**, pineal foramen; **pmx**, premaxilla; **po**, postorbital; **prf**, prefrontal; **qj**, quadratojugal; **sq**, squamosal; **st**, supratemporal. Scale bars equal 5 cm.



skull is low and has a relatively long and slender rostrum. The orbit is anteroposteriorly wider than dorsoventrally tall, even in specimens that do not appear to be dorsoventrally crushed. In BU 5323 and NHMUK R36958, the frontals are damaged, but appear anteroposteriorly longer than mediolaterally wide. The pineal foramen is probably situated between the frontal and parietal, unlike in *Ichthyosaurus*, but more similar to other Lower Jurassic taxa such as *Leptonectes*, *Temnodontosaurus* and *Stenopterygius* (McGowan and Motani, 2003; Motani, 2005). The parietals are damaged in all specimens and most of the supratemporal is missing or poorly preserved. In dorsal view, the nasals are very wide posteriorly, comprising almost all of the anterior portion of the skull roof, similar to *Ichthyosaurus* and *Stenopterygius* (Motani, 2005; Maxwell et al., 2012). A long, prominent internasal foramen is present at the posterior end of the nasals in all specimens that expose the dorsal surface of the skull. In lateral view, the nasal makes up less than half of the dorsal border of the external naris (UOD D1, NHMUK R36958, NWM 2012.23G.1). The nasals do not extend beyond the anterior process of the maxilla in lateral view. In NHMUK R36958, however, the nasals appear to extend beyond the anterior process of the maxilla in right lateral view because the premaxilla is broken posteriorly, exposing the nasals. In left lateral view, the nasals do not extend beyond the maxilla on this specimen.

The prefrontal makes up less than half of the dorsal margin of the orbit, but contributes to more than half of the anterior margin of the orbit. Posteriorly it is slender, but the anterior process is dorsoventrally wide and extends ventrally to the level of the external naris. The anterior process is more than three times as dorsoventrally wide as the posterior portion. The anterior process of the prefrontal excludes the dorsal process of the lacrimal from the orbital margin, similar to *Ichthyosaurus somersetensis* and *I. larkini* (Lomax and Massare, 2017). The lacrimal is triradiate, as in *I. communis*, but with a narrow anterior process that extends half or less of the external naris length. The dorsal process of the lacrimal is tall and narrow, and is noticeably longer than the anterior process. It makes up the entire posterior margin of the external naris. The posteroventral process of the lacrimal is longer than the dorsal and anterior processes and contributes to less than a fourth of the ventral margin of the orbit. In NHMUK R36958, a small foramen is present at the posteroventral end of the anterior process of the lacrimal.

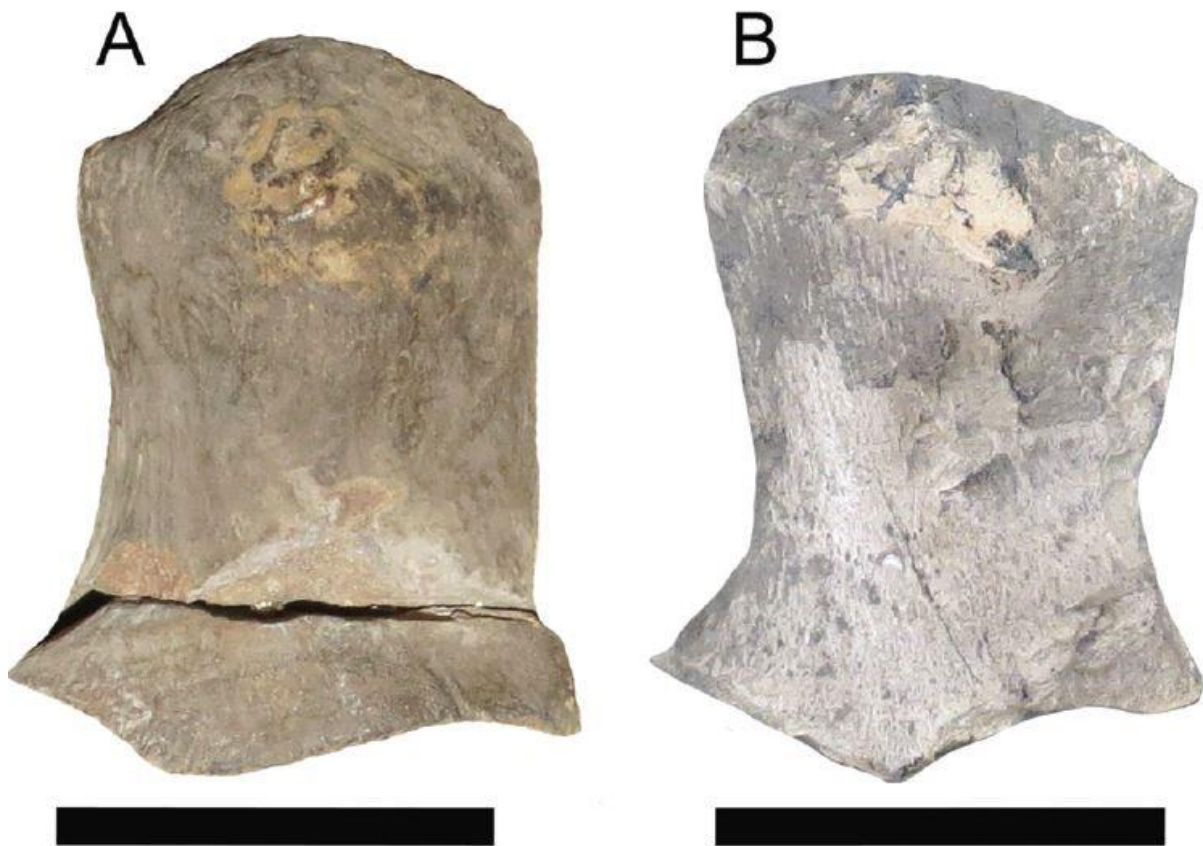


Figure. 8.5. A, *Protoichthyosaurus prostaxalis* paratype (BRLSI M3563), right humerus in dorsal view. At the crack, the distal portion is displaced slightly from the original position. **B,** *P. applebyi* sp. nov. holotype (UNM.G.2017.1), left humerus (reversed) in dorsal view. Note the distinct ridge at the proximal end of the dorsal process. Anterior is to the right in both specimens. Scale bars equal 5 cm (A) and 3 cm (B).

The maxilla is large, triangular, and very tall dorsoventrally, with its highest point positioned ventral and posterior to the center of the external naris. The anterior process is longer than the posterior process, when measured from the highest point of the maxilla. In lateral view, the posterior process extends to just under the orbit, whereas the anterior process extends well beyond the large external naris.

The external naris is a large, somewhat triangular opening that is wider posteriorly than anteriorly. The subnarial process of the premaxilla extends across at least half of the external naris length, whereas the supranarial process extends at least a fourth and as much as half (as in UOD D1) of the external naris length.

The anterior process of the jugal is slender, positioned between the lacrimal

Table. 8.2. Select measurements (in cm) for the most complete skeletons and skulls of *Protoichthyosaurus prostaxalis* and *P. applebyi* (UNM. G.2017.1 only). Precaudal and preflexural lengths are measured from the anterior-most centrum along the curvature of the vertebral column. Where anterior rostrum is broken, length is given as ‘>’ preserved length. **Abbreviations:** **a-p**, anteroposterior; **c**, crushed; **L**, left; **m-l**, mediolateral; **R**, right; **Vert col**, vertebral column. Asterisk indicates an estimated measurement.

Dimension	BRLSI M3553	BRLSI M3555	AGC 12	WARMS G347	BU 5323	UNM.G.2017.1
Skull length			>37	44.0	>40	>25
Jaw length	*46.9	43.7	>41	46.5		
Preorbital length		*29.2	>23	29.3		
Orbit length			9.6 c	10.6 c	10.4	7.6
Orbit height		7.9	7.9 c	6.4 c	7.7	5.5
External naris length		4.6		4.5	4.6	3.2
Maxilla length			>10	10.8	14.0	7.3
Coracoid a-p length	*9.7R	9.0	8.5			
Coracoid m-l width	7.2R 7.3 L	7.3	7.2			
Scapula length			8.2			6.4
Humerus length	6.5R 6.4 L		6.3			4.4
Proximal width	3.8R 4.2 L		*3.7			3.2
Distal width	5.4R 5.1 L		4.9			3.4
Femur length		4.9	*5.0			3.2
Femur proximal width		2.1				
Femur distal width		3.2	3.2			
Vert col precaudal length		66.0				
Vert col preflexural length		112.0	*119			

and the posterior process of the maxilla; it does not extend beyond the anterior margin of the orbit. The jugal dorsal ramus is dorsoventrally thickened, and bends at almost 90° in some specimens (AGC 12, NMW2012.23G.1), but at a wider angle in others (BU 5323). In all specimens, however, it makes up almost half of the posterior margin of the orbit. The posterior-most portion of the jugal articulates with the ventral border of the postorbital, along a broad contact. The postorbital is a short, anteroposteriorly wide element with a dorsoventrally elongated, almost rectangular shape, but both the anterodorsal and anteroventral edges taper to narrow processes. This is best seen in AGC 12 because the element is badly damaged in BRLSI M3555 and damaged posteriorly in BU 5323 (Figure. 8.4A, B).

The quadratojugal is incomplete in all specimens, although most complete in NMW 2012.23G.1. In lateral view, the dorsal end is flared and flattened, and somewhat fan-shaped; a cylindrical shaft widens ventrally into a bulbous end for the quadrate facet. The lower temporal arch between the jugal and quadratojugal is a shallow embayment, similar to that of *Ichthyosaurus*. The squamosal is positioned dorsal to the quadratojugal and postorbital. It is roughly rectangular, with a triangular process that extends ventrally at almost a right angle from the posteroventral edge,

similar to that of *I. somersetensis* (e.g., NHMUK OR2013*). It is best seen in BU 5323 (Figure. 8.4A, B), but is incomplete in the paratype BRLSI M3555. Anteriorly, the squamosal is wedged between the postfrontal and dorsal portion of the postorbital (Figure. 8.4A, B). The postfrontal is anteroposteriorly long, making up almost all of the dorsal margin of the orbit. It is slightly flared posteriorly, where it has minor contact with the postorbital. In dorsal view, the postfrontal is long, wide, and flared anteriorly, contacting the frontal laterally and nasal and prefrontal anteriorly, with a minor posteroventral contact with the parietal.

Mandible and Dentition

The mandible is long and slender, especially in the prenasal region. In BRLSI M3555 the snout ratio (preorbital length/mandible length) is estimated to be 0.66. The morphology of the posterior portion of the mandible is best seen in AGC 12 and NMW 2012.23G.1. The dentary extends as far posterior as the middle or just beyond the middle of the orbit. The surangular occupies most of the postorbital region of the mandible, but tapers to a point slightly posterior to the anterior end of the anterior process of the maxilla. The angular has only a minor exposure, but extends anteriorly beyond the anterior margin of the orbit, about as far as the surangular. In the holotype the surangular and angular extend to approximately the same point anteriorly in ventral view. The splenials are relatively robust elements, but become narrow anteriorly, although the splenials appear more robust in BU 5323. They extend much further than the angular and surangular, but their full extent cannot be determined because the anterior portion of the mandible is missing in the holotype.

The tooth morphology is best preserved in AGC 12. The teeth have large, relatively wide roots, but without an abrupt expansion of the root at the base of the crown. Tooth roots have deep longitudinal grooves that are clearly distinguished from the enamel of the crown. By comparison, the crowns are relatively short and not very slender, with longitudinal striations that do not reach the rounded tip (as observed in BU 5323). They fit the morphology of the 'crunch' guild of Massare (1987).

Axial Skeleton

There are at least 41 precaudal centra preserved in BRLSI M3555, but the first is mostly covered and it is unclear if it is the atlas-axis. Centrum number 42 appears to

be the first caudal, as identified by the short ribs and the position of the right femur (Figure. 8.2C). Similarly, NMING F8747 appears to have 40 or 41 precaudal centra. In both specimens, the centra are rotated so that rib articulations are not visible, and NMING F8747 is not well preserved, so the counts are estimates. The count is low in comparison to other Lower Jurassic ichthyosaurs, which is usually at least 43 (Buchholtz, 2001). Given the difficulty in recognizing the sacral region of the vertebral column, the difference is not large enough to be diagnostic. BRLSI M3555 has at least 74 preflexural centra, and an additional five wedge-shaped apical centra. AGC 12 has 77 preflexural centra, and 4–6 apical centra.

The neural spines are tall, wide, and rectangular, and some appear slightly higher on their posterior edge relative to the anterior edge. In NMING F8747, the neural spine height increases from the atlas-axis to about centrum number 20, and decreases posteriorly from there. Thus the maximum height is about midway across the trunk. The middle portion of the ribs has a circular or elliptical cross-section, seen best in AGC 12. The anterior caudal centra have short, spatulate ribs.

Pectoral Girdle and Forefin

The coracoid has both a well-developed anterior and posterior notch, as in *Ichthyosaurus* (McGowan and Motani, 2003). The anterior notch is wider than the posterior notch, which results in a much wider posterior than anterior end. The coracoids are anteroposteriorly longer than they are mediolaterally wide. The glenoid facet of the coracoid is longer than the scapular facet. The clavicles are mediolaterally long and robust. The interclavicle is well preserved on two specimens, the holotype and AGC 12, although the morphology is slightly different. In the holotype, the interclavicle is T-shaped, and the medial process extends under half the length of the coracoid, where it is forked. In AGC 12, it is also T-shaped, but the medial process extends at least half way down the coracoid but is not forked. The difference may be due to intraspecific variation or crushing. A complete scapula is not preserved in any of the referred specimens. However, the proximal end and part of the shaft is preserved in the holotype and BRLSI M3563 (paratype), which is a composite (although see above). The shaft and distal end is preserved in AGC 12. The scapula is long and slender, with a narrow shaft that is not markedly flared at the posterior end. The anterior end is widely flared but without a prominent acromion process. The coracoid facet of the scapula is twice as long as the glenoid facet.

However, the pectoral girdle is quite variable in some species (Johnson, 1979; Maxwell and Druckenmiller, 2011), so these features are probably not diagnostic, except perhaps at the genus level.

Both humeri are exposed in ventral view in the holotype. The humerus is robust, long, and is only slightly wider distally than proximally. The deltopectoral crest is large, slightly offset anteriorly, and extends less than half way down the shaft. The posterior end of the humerus is slightly flared. The distal end of the humerus has a small anterior facet, which is also present in AGC 12. The humerus is preserved in dorsal view in BRLSI M3563 (paratype) and probably in TTNCM 41/2017 (Figure. 8.2B, 8.5A). In dorsal view, the humerus has the same proportions as that of the holotype; robust, longer than wide, and slightly wider distally than proximally. The dorsal process is small, centrally located, and does not extend far down the shaft. The radius and ulna are roughly equal in size. Three elements are in the distal carpal row and digit V is absent, although at least one, and sometimes two, posterior accessory digits are present (Figure. 8.2A, B). Distal carpal 2 bifurcates, which results in four elements in the metacarpal row. The proximal element of the bifurcation nearly separates distal carpal 2 from distal carpal 3. In AGC 12, and in one fin of the holotype, the bifurcation separates the two carpals and almost contacts the intermedium, but this does not occur in any other specimens. A second bifurcation of digit II occurs distally, a feature that is shared only with *Ichthyosaurus* (Motani, 1999a). This results in five primary digits. Only one element in the third row, distal carpal 3, has a broad contact with the intermedium, and it contacts the ulnare proximally in all specimens. The intermedium is thus separated from contact with distal carpal 4 by distal carpal 3. The forefin elements are polygonal and proximal phalanges interlock in adults. The phalanges are rectangular and closely packed, but are mostly rounded at the distal end.

Pelvic Girdle and Hindfin

The pelvis and hindfin are preserved in BRLSI M3563, but that specimen is a composite (as discussed above) and they may not belong to the same individual as the forefin. The only other known pelvic bones are an isolated, poorly preserved partial ischium in BRLSI M3555 and poorly preserved, unidentifiable pelvic bones in NMING F8747 that provide no information on morphology.

The only well preserved hindfin is in AGC 12, although it is somewhat disarticulated. The proximal end of the femur is damaged, but the distal end is wide and slightly flared posteriorly. There are at least three primary digits, (tarsal 3) in broad contact with the astragalus, and the tibia and fibula are approximately equal in size. A single disarticulated phalanx is notched, but its placement within the fin cannot be determined. The only complete femur is preserved in BRLSI M3555. The femur head is robust but the shaft is narrow and the distal end is wider than the proximal (Figure. 8.2C), somewhat similar to the femora of *Excalibosaurus costini* (ROM 47697) and *Leptonectes tenuirostris* (ROM 47698) in being anteriorly and posteriorly flared.

Protoichthyosaurus applebyi sp. nov.

(Figs. 4C–D, 5B, 6)

Holotype. UNM.G.2017.1 (previously, UON VR159, UON TC3199), the only known specimen, a skull and articulated skeleton in left lateral view.

Locality and Horizon. No record. Possibly from Nottinghamshire or Leicestershire, based on preservation. Records indicate that fragmentary ichthyosaurian material in the UON geology collections are from Barnstone, Nottinghamshire, but this specimen is not mentioned (D. Large, pers. comm. 2017). The specimen is probably from the Lower Jurassic.

Etymology. In honor of paleontologist Robert M. Appleby, for his contributions to the study of ichthyosaurs. He first recognized the unique forefin structure of *Protoichthyosaurus* and erected the genus.

Diagnosis. *Protoichthyosaurus applebyi* is a small to medium-sized species, probably with a total length less than 2 m. It is distinguished from *P. prostaxalis* and all species of *Ichthyosaurus* by the following unique combination of characters: narrow, crescentic postorbital; dorsoventrally low maxilla that extends beyond external naris; nasal extends at least as far as anterior process of maxilla in lateral view; lacrimal anterior process as long or longer than dorsal process; humerus with centrally located and somewhat plate-like dorsal process, forming a narrow ridge

(similar to *Ichthyosaurus larkini*). Any one of these characters will distinguish *P. applebyi* from *P. prostaxalis*.

Description

UNM.G.2017.1 is referred to *Protoichthyosaurus* on the basis of forefin morphology. *P. applebyi* differs from *P. prostaxalis* in skull and humerus morphology, which warrants the erection of a new species (Figures. 8.4C, D, 8.5B, 8.6). The preserved length of UNM.G.2017.1 is about 135 cm, measured from the tip of the preserved rostrum and along the vertebral column to the last centrum of the tail (Table. 8.2), but the anterior portion of the rostrum is missing and some caudal centra probably do not belong with the specimen (see above).

Skull

The prefrontal appears to make up almost half of the dorsal margin and contributes to about half of the anterior margin of the orbit, although the posterior portion is poorly defined and might be damaged. Posteriorly, the prefrontal is slender, and the anterior process is expanded dorsoventrally and extends ventrally to the level of the external naris. The anterior process of the prefrontal is dorsoventrally wide but not as wide as in *P. prostaxalis*. The anterior process of the prefrontal excludes the dorsal process of the lacrimal from the orbital margin, but it does not extend as far ventrally nor is it as robust as in *P. prostaxalis*. The lacrimal is triradiate with an anterior process that extends across at least half of the external naris length. The anterior process is about as wide as but longer than the dorsal process of the lacrimal, and is much larger than in *P. prostaxalis*. The dorsal process makes up the entire posterior margin of the external naris. The posteroventral process of the lacrimal contributes to about a third of the ventral margin of the orbit.

The maxilla is dorsoventrally low and is more bar-like than triangular. The anterior process extends slightly anterior to the external naris. The posterior process extends slightly under the orbit. The maxilla is separated from the external naris by a broader contact of the anterior process of the lacrimal and subnarial process of the premaxilla than in *P. prostaxalis*. The supranarial and subnarial processes extend less than halfway across the margin of the external naris. The nasal makes up more than half of the dorsal margin of the external naris, and appears to extend much

farther anteriorly than the anterior process of the maxilla in lateral view. The external naris is large and roughly triangular, as in *P. prostaxalis*.

The anterior process of the jugal is slender, and does not extend beyond the anterior margin of the orbit, similar to *P. prostaxalis*. The jugal dorsal ramus bends at almost a 90° angle but is damaged dorsally so contact with the postorbital is difficult to discern. It makes up less than half of the posterior margin of the orbit. The postorbital is crescentic, high and narrow, and makes up most of the posterior margin and some of the dorsal margin of the orbit. The postfrontal is poorly preserved, but it makes up less of the dorsal margin of the orbit than in *P. prostaxalis* (Figure. 8.4C, D).

Much of the posterior portion of the skull and dorsal skull roof is missing or covered with plaster. Sutures in the mandible are unclear, and the posterior end of the mandible is missing (Figure. 8.4C, D).

Axial Skeleton

The atlas-axis is present but sheared in half so that the interior is exposed. The neural arches are fused into one broad element. Counting the atlas-axis as centra 1 and 2, the 38th centrum has two facets for rib attachment; the 41st centrum has a single rib facet. The rib articulations on the two centra in between are not clearly preserved. Thus *P. applebyi* has 38–40 precaudal centra, a low count for a Lower Jurassic ichthyosaur, but similar to *P. prostaxalis*.

The neural spines increase in height from the cervical to the mid-dorsal region, and then gradually decrease in height, but increase in width, into the posterior dorsal and anterior caudal regions. The posterior dorsal neural spines are unusually wide. The spines are higher than the centra until about centrum number 30, where the height is about equal. Posteriorly, the neural spines are progressively shorter relative to centrum height.

Black material on top of the distal ends of the first few anterior ribs and scattered around the posterior dorsal ribs is reminiscent of soft tissue described by Martill (1995). Stomach contents, comprising cephalopod hooklets, are preserved between the ribs. The longest rib measures 17.5 cm, although it is incomplete.



Figure. 8.6. UNM.G.2017.1, holotype specimen of *Protoichthyosaurus applebyi* sp. nov., a partial skeleton lying on its right side, in lateral view. Scale bar equals 20 cm.

Pectoral Girdle and Forefin

The complete left scapula has a long narrow shaft that is flared at the anterior end, but without a prominent acromion process, although it is slightly buried. The posterior end is only slightly flared. The left coracoid is partly exposed, showing an anterior notch and suggesting that the coracoid is almost as wide or wider mediolaterally than anteroposteriorly; however, half of the coracoid is covered.

The articulated forefin of UNM.G.2017.1 shows the typical *Protoichthyosaurus* pattern of the carpal rows, with only distal carpal 3 in contact with the intermedium, and a bifurcation of distal carpal 2 (Figure. 8.1A). Five primary digits are in the forefin, which includes a distal bifurcation that occurs in the fourth phalangeal row of the anterior branch of digit II. Only a single element is preserved and is partly overlain by matrix. In BRLSI M3553, the holotype of *P. prostaxalis*, the elements of the anteriormost branch of digit II are similarly reduced in size, although the digital bifurcation is on the posterior branch. In UNM.G.2017.1, one posterior accessory digit starts at the base of the ulna. The first phalanx of the accessory digit is smaller than most of the more distal elements of this digit. Some elements of the right forefin are preserved, but provide no additional information.

The humerus is 4.4 cm long, longer than wide, with the proximal and distal widths about equal (3.2 cm and 3.5 cm, respectively). The dorsal process is more prominent than in *P. prostaxalis*, and centrally located (Figure. 8.5). It forms a narrow ridge proximally that is offset anteriorly, similar to the ridge on *Ichthyosaurus larkini*,

but without a depression on the head. The dorsal process is more prominent in *I. larkini*.

Pelvic Girdle and Hindfin

Of the pelvic girdle, only a relatively narrow, rib-like ilium is preserved, 3.3 cm long. One end, possibly the anterior, is damaged, but it is wider and more robust than the narrow posterior end. However, this difference may be in part, due to damage. The femur is much longer than wide and about the same length as the ilium. It is sheared off, exposing the bone interior of the shaft and proximal end, and the distal end is broken. It appears to be robust proximally.

Phylogenetic Analysis

We added *Protoichthyosaurus* to the data matrix of Fischer et al. (2013) because this is the largest dataset that focuses on parvipelvian ichthyosaurs and includes most of the Lower Jurassic taxa. Due to the incompleteness of taxa and lack of characters that could be compared with more complete taxa, we modified the matrix by removing poorly known Upper Jurassic taxa that were less than 40% complete: *Arthropterygius*, *Maiaspondylus*, *Athabascasaurus*, *Chacaicosaurus*, and *Mollesaurus*. However, *Macgowania* and *Malawania*, which are also less than 40% complete, were retained because the former was originally identified as a species of *Ichthyosaurus* and the latter was recovered as a sister taxon to *Ichthyosaurus* by Fischer et al. (2013). We also removed *Ophthalmosaurus natans* and *Platypterygius hercynicus* and retained the better known species of each genus, *O. icenicus* and *P. australis*. We modified the character list by simplifying Fischer et al. (2013) characters 48, 49, 55 and 65 (characters 39, 40, 46, and 55 in our matrix) which resulted in recoding all of the taxa for each of these characters (Supplemental Data 1, 2). Three other characters were slightly modified but did not require recoding. We also removed 12 characters and added two new ones (Supplementary Data 1).

Ichthyosaurus communis, *Protoichthyosaurus prostaxalis*, and *P. applebyi* were coded based on our observations (Supplementary Data 1, 2). *I. communis* was selected because it is the type species for the genus. Coding was based mainly on the neotype NHMUK R1162, supplemented by referred specimens from Massare and Lomax (2017). Coding for *Protoichthyosaurus prostaxalis* was based mainly on

BRLSI M3555, BU 5323, and AGC 12 (see description above). Coding for *P. applebyi* was based on the holotype and only specimen, UNM.G.2017.1. *Ichthyosaurus communis* could be coded for 53 characters (95% complete). *Protoichthyosaurus prostaxalis* and *P. applebyi* could be coded for 44 (79% complete) and 27 (48% complete) characters, respectively. This is the first time that *Protoichthyosaurus* has been included in a phylogenetic analysis. Aside from the modifications mentioned above, the coding provided by Fischer et al. (2013) was retained for all other taxa.

The analysis was performed using TNT v.1.5, selecting the implicit enumeration option for the search, as recommended by Goloboff et al. (2008) for small data sets. Four trees of 104 steps (CI = 0.567 and RI = 0.775) were found, differing only in the relationships among ophthalmosaurids and other taxa more derived than *Stenopterygius quadriscissus*. The strict consensus tree was bootstrapped with 1000 replicates and the results show that *P. prostaxalis* and *P. applebyi* are sister taxa, and that *Protoichthyosaurus* is sister to *I. communis* (Figure 8.7). The tree topology is also consistent with the diagnosis of Ichthyosauridae by McGowan and Motani (2003), and includes *Protoichthyosaurus* within the family.

The analysis unites *Protoichthyosaurus* and *Ichthyosaurus* on the basis of three characters: presence of a square or rectangular squamosal (character 11:0); presence of a lower temporal arch between jugal and quadratojugal (character 13:0); and tightly packed rectangular phalanges (character 43:1). The two species of *Protoichthyosaurus* form a clade that can be distinguished from *Ichthyosaurus* on the basis of three characters: presence of three primary elements in the third (distal carpal) row (character 42:0); contact between distal carpal 3 and ulnare (character 45:1); and absence of manual digit V (character 46:0). The two species of *Protoichthyosaurus* differ in the extent of the nasals relative to the anterior process of the maxilla, in lateral view (character 2), which reflects differences in the morphology of the maxilla and nasal between the two species.

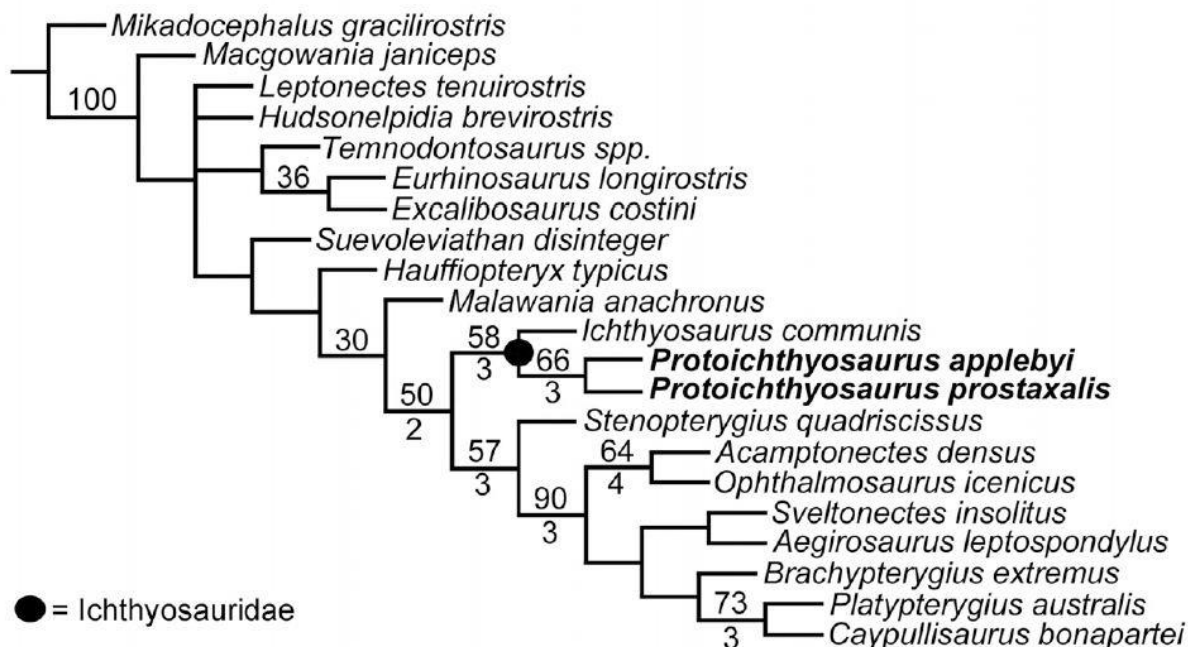


Figure. 8.7. Standard bootstrap (1000 replicates) of strict consensus of four trees of 104 steps (with CI = 0.567 and RI = 0.775). The results show that *Protoichthyosaurus prostaxalis* and *P. applebyi* are sister taxa to *Ichthyosaurus*. Bootstrap support values greater than 30 are shown above the branch and Bremer support values greater than 1 are given below the branch.

Forefin Morphology

In Lower Jurassic ichthyosaurs, the arrangement and number of elements in the mesopodium of the forefin is invariant within a genus, and that determines the number of primary digits in the forefin, unless a distal bifurcation is present, as in *Ichthyosaurus*, *Stenopterygius* and *Suevoleviathan* (Motani, 1999a). For example, all species of *Stenopterygius* display the same pattern in the mesopodium (Maxwell, 2012, fig. 1), as do all species of *Temnodontosaurus* for which the forefin is known (*T. platyodon*, NHMUK OR2003; *T. trigonodon*, McGowan and Motani 2003, pl. 6; *T. crassimanus*, YORYM: 497; ?*T. acutirostris*, NHMUK OR14553; *T. azerguensis*, Martin et al., 2012). In *Ichthyosaurus*, the distal carpal row consists of the three distal carpals and metacarpal five, which is in contact with the ulnare. This arrangement does not vary in the six species of *Ichthyosaurus*, even though the forefin is variable

in many other respects (e.g., number of primary digits, row of digital bifurcation, which digit bifurcates, relative size of branches of the bifurcation, etc).

The mesopodium of the forefin of *Protoichthyosaurus* can be interpreted in three possible ways (Figure. 8.8). One interpretation is that a short supernumerary bone is present between the radiale and distal carpal 2 (Figure. 8.8A). Four elements are in the distal carpal row, as occurs in *Ichthyosaurus*, *Leptonectes*, *Stenopterygius* and others (Motani, 1999a). Distal carpals 2 and 3 contact the supernumerary bone, distal carpal 4 contacts the intermedium, and metacarpal 5 contacts the ulnare as the first element of digit V. As in *Ichthyosaurus*, the fifth digit is as prominent as the fourth. The supernumerary bone, however, occurs in all specimens of *Protoichthyosaurus* in which the forefin is preserved, including a very small individual that is probably a neonate. It seems unlikely that a supernumerary bone would occur this frequently and occur in very young individuals, in exactly the same position.

A second interpretation is that only three carpals are in the second row of the mesopodium, with metacarpal 3 nearly separating distal carpal 2 and 3 (Figure. 8.8B). The problem with this interpretation is that distal carpals 3 and 4 do not contact their respective metacarpals distally. Distal carpal 3 has a broad contact with metacarpal 4, and distal carpal 4 has a broad contact with metacarpal 5. This lack of alignment is difficult to explain developmentally (Motani, 1999a). In this interpretation, digit V is present and it is as prominent as digit IV, as it is in *Ichthyosaurus*.

A third interpretation, which we contend is correct, is that distal carpal 2 bifurcates to form two elements in the metacarpal row, both representing digit II, for a total of four elements in that row (Figure. 8.8C). In this interpretation, distal carpals 3 and 4 align with their respective metacarpals along broad contacts. Digit V has been lost, unlike the condition in *Ichthyosaurus* and other genera (Motani, 1999a; McGowan and Motani, 2003:fig. 70). This is probably the interpretation that Appleby (1979) intended when he described the morphology as being neither latipinnate nor longipinnate, but an intermediate form.

The combination of three distal carpals, an anterior bifurcation from distal carpal 2, and four elements in the metacarpal row occurs in all specimens of *Protoichthyosaurus* that preserve a forefin. It can be difficult to tell which digit bifurcates because both distal carpal 2 and distal carpal 3 can have equally large facets that articulate with the first element of the bifurcation. In well preserved

forefins, however, digit III parallels digit IV, whereas digit II is displaced anteriorly by the bifurcation, indicating that distal carpal 2 bifurcates. This can be seen in the neonate specimen, UORCMZ FE19-1 (Figure. 8.9). In the largest specimen (NHMUK R1063) proximal elements of the bifurcation interlock with elements of digit III, whereas they abut with elements of digit II (Figure. 8.8C), again indicating that the bifurcation is in digit II. This also occurs in other large specimens (e.g. AGC 12 and BRLSI M3553), but is not evident on smaller forefins that have gaps between fin elements.

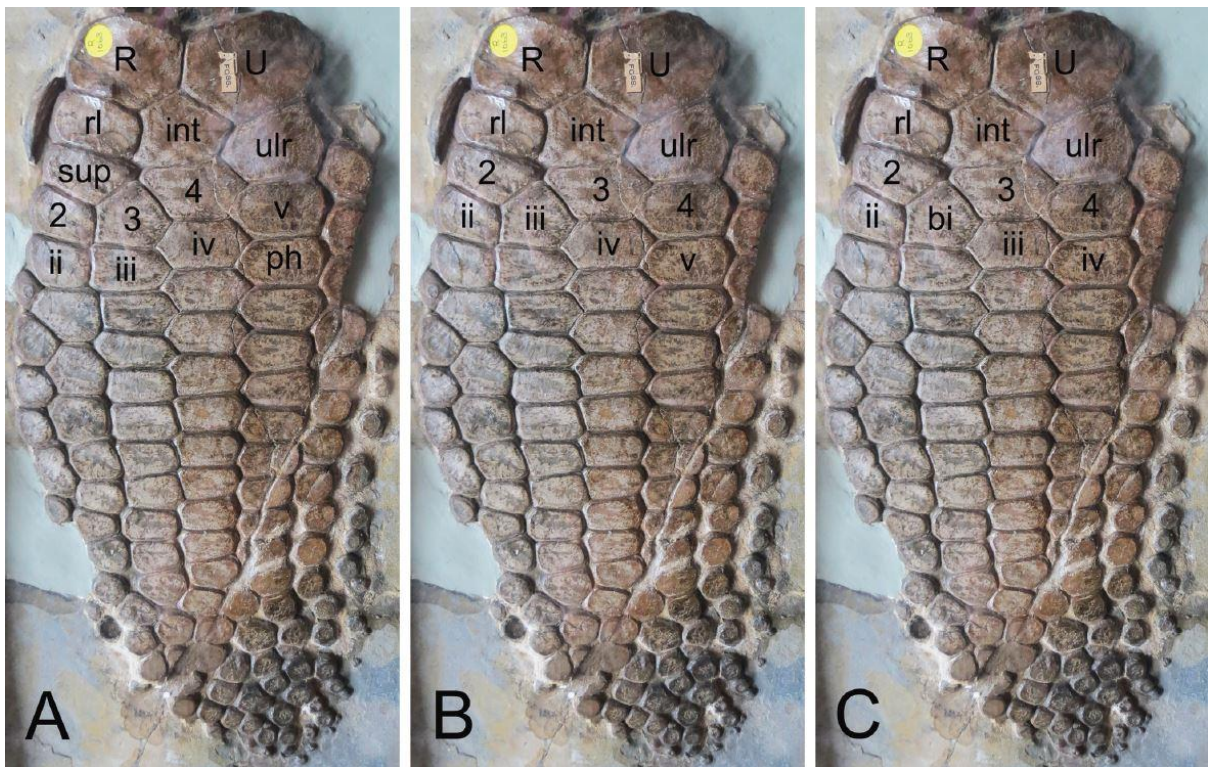


Figure. 8.8. Three interpretations of the forefin morphology of *Protoichthyosaurus*, based on NHMUK R1063, anterior to the left. **A**, this interpretation requires the addition of a supernumerary bone between the radiale and distal carpal 2. **B**, this interpretation results in distal carpals 3 and 4 not contacting their respective metacarpals distally. **C**, this interpretation, considered the correct one, results in the absence of digit V. **Abbreviations:** 2, distal carpal two; 3, distal carpal three; 4, distal carpal four; bi, bifurcation; ii, metacarpal two; iii, metacarpal three; int, intermedium; iv, metacarpal four; ph, phalanx; R, radius; rl, radiale; sup, supernumerary element; U, ulna; ulr, ulnare; v, metacarpal five.

At least one posterior accessory digit is always present in the forefin of *Protoichthyosaurus*, even in small individuals; some large specimens have two posterior accessory digits (e.g. BRLSI M3553, NHMUK R1063). The small accessory digit is not digit V because in some specimens, the elements are largest at about the first phalangeal row, and decrease in size both distally and proximally, unlike the elements in the primary digits that decrease in size from proximal to distal positions. Furthermore, the small, rounded elements of the accessory digits in *Protoichthyosaurus* are similar to those in *Ichthyosaurus*.

Protoichthyosaurus is not unique in having a bifurcation of a distal carpal. Some specimens of *Ichthyosaurus* have a bifurcation of a distal carpal to form five primary elements in the metacarpal (fourth) row (e.g., CAMSM X.50187, BRSMG Cb4997, NMW 91.29G.1; Figure. 8.1C), ignoring accessory digits. Motani (1999a:figs. 6c, d) argued that the bifurcation in *Ichthyosaurus* is always in distal carpal 3, although it is sometimes difficult to confirm. However, in *Protoichthyosaurus*, the bifurcation is always in distal carpal 2. Furthermore, in *Protoichthyosaurus*, the proximal element of the bifurcation is noticeably longer proximodistally than the other elements in the metacarpal row (Figures. 8.1A, 8.8C, 8.9), but that is not the case when a distal carpal bifurcation occurs in *Ichthyosaurus*.

A problem in distinguishing the forefins of *Protoichthyosaurus* and *Ichthyosaurus* is a rare co-ossification that occurs in the forefin of some specimens of *Ichthyosaurus*, which mimics the morphology of *Protoichthyosaurus*, and so the distinctions described above are not always clear (Figure. 8.10). Appleby (1979) referred OUMNH J.13799 to *Protoichthyosaurus prostaxalis*. This specimen is a practically complete skeleton in ventral view, with two well-preserved forefins. The forefins differ in the morphology of the mesopodium, with the left fin having the pattern of *Protoichthyosaurus* and the right showing the pattern of *Ichthyosaurus*. However, in the left fin of OUMNH J.13799, distal carpal 2 is co-ossified with distal carpal 3, with a faint line marking the boundary between the two (Figure. 8.10A). This is probably a pathology, as was also noted by Motani (1999a:fig. 6f). Only a subtle difference occurs in the pathological fin: the anterior element (distal carpal 2 + 3) in the third row has a broader contact with the intermedium than occurs on *Protoichthyosaurus*. It is difficult to quantify this difference and it would be difficult to recognize in a forefin that was not well preserved, completely articulated proximally, or from a juvenile. However, a similar pathology occurs in NHMUK R3372, where

again the two fins appear morphologically different, with the right fin having the morphology of *Protoichthyosaurus* (Figure. 8.10B) and the left of *Ichthyosaurus*. As in OUMNH J.13799, distal carpal 2 and distal carpal 3 of the right fin are co-ossified, and a faint outline distinguishing the two is situated in the centre of the element (Figure. 8.10B). However, portions of both fins of NHMUK R3372 have been reconstructed and that raises the possibility that one or both fins have been added to the specimen (Massare and Lomax, 2016). Another example of a similar co-ossification occurs on ANSP 15766, where the two anterior elements of the third phalangeal row of digit II are co-ossified at an odd angle on the left forefin (Figure. 8.10C). Again, a faint line outlining the two elements is evident. Thus, when looking at forefins with the *Protoichthyosaurus* morphology, special attention should be focused on possible pathology in the third row of elements, especially if the two forefins have different patterns in the carpal rows.

The forefin of *Protoichthyosaurus* shares only two features with that of *Ichthyosaurus*: at least five primary digits and a distal digital bifurcation anterior to the primary axis in the forefin (Figure. 8.8C; Table. 8.3). In *Protoichthyosaurus*, a distal bifurcation always occurs in a phalangeal row of one of the branches of digit II, whereas in *Ichthyosaurus*, it occurs in digit II or digit III (Motani, 1999a; pers. obs.). *Macgowania*, *Stenopterygius*, and probably *Malawania*, three other genera with forefins having at least four primary digits, lack this feature (Motani, 1999a; Fischer et al., 2013). *Macgowania janiceps* was assigned to *Ichthyosaurus* when it was first described (McGowan, 1996). *Malawania* is a sister taxon to *Ichthyosaurus* (Fischer et al., 2013). However, the forefin of *Ichthyosaurus* shares important features with *Macgowania*, *Malawania*, and *Stenopterygius*. Digit V is present and distal carpals 3 and 4 contact the intermedium in all four genera. In contrast, the forefin of *Protoichthyosaurus* lacks digit V and lacks contacts between the intermedium and distal carpal 4 (Table. 8.3). All of the forefin features of *Protoichthyosaurus* can be seen in a neonate (UORCMZ FE19-1; humerus length = 1.8 cm), as well as in adults (e.g., BRLSI M3553, left humerus length = 6.4 cm; BRLSI M3563, right humerus length 8.8 cm). For specimens with well-articulated forefins, these characteristics can be used to distinguish *Protoichthyosaurus* from *Ichthyosaurus* and other ichthyosaurian genera with a high degree of confidence.

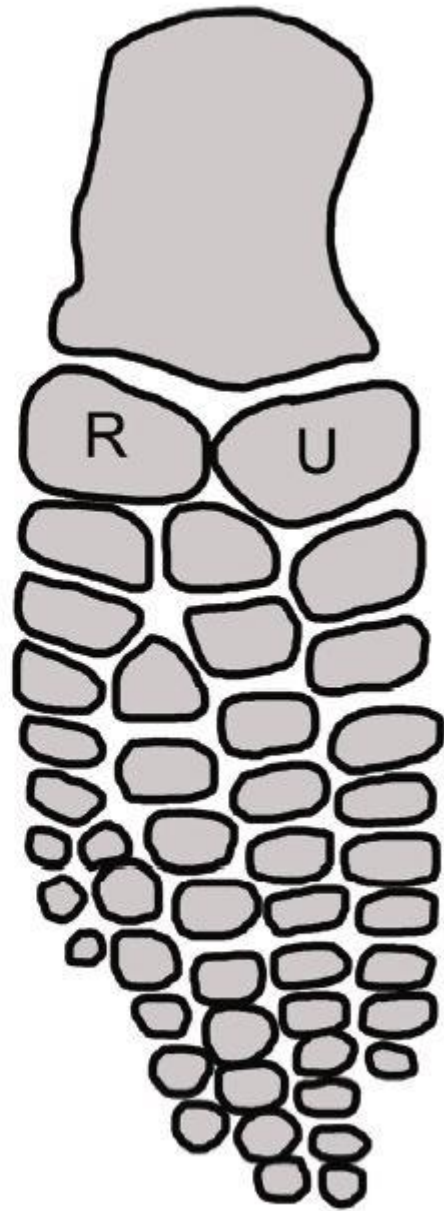


Figure. 8.9. Photograph and illustration of the right forefin of a neonate specimen of *Protoichthyosaurus* (UORCMZ FE19-1), ventral view, anterior to the left. Note that digit III parallels digit IV, whereas the two branches of the bifurcations in digit II do not. **Abbreviations:** **R**, radius; **U**, ulna. Scale bar equals 1 cm.

Identifying partial forefins and isolated skulls

Another issue that arises in recognizing specimens of *Protoichthyosaurus* is that small, isolated forefins superficially resemble hindfins of some species of *Ichthyosaurus*. Hindfins of *I. breviceps*, *I. somersetensis*, and *I. conybeari* frequently have just three elements in the third row, with tarsal three in broad contact with the astragalus. The fourth row has four elements, arising from a bifurcation of the anterior digit. Without a preserved femur, a hindfin with this morphology could be confused with a forefin of *Protoichthyosaurus*, which has the same number of elements in the third, and fourth rows. In hindfins of *I. breviceps*, the bifurcation seems to occur on the anterior side of the anterior digit (Figure. 8.11A). Neither branch of the bifurcation separates elements in the third row, as occurs in the forefin of *Protoichthyosaurus* (Figures. 8.1, 8.8C). In most hindfins of *I. somersetensis*, the two elements of the bifurcation are smaller than the other elements in the fourth row. In addition, the first element of the posterior branch of the bifurcation does not separate the elements in the third row (Figure. 8.11B). This contrasts with the large, pentagonal element that nearly separates the first two distal carpals in the forefin of *Protoichthyosaurus* (Figures. 8.1, 8.8C, 8.9). At least one specimen that is probably referable to *I. somersetensis*, however, has a hindfin with a pentagonal element in the posterior branch of the bifurcation and shows some separation between the two elements in the third row (Figure. 8.11C). Similar to *I. somersetensis*, the bifurcation in *I. conybeari* somewhat separates two anterior elements in the third row. The first element of the posterior branch is somewhat longer proximodistally than anteroposteriorly (Figure. 8.11D), but it lacks the distinct pentagonal shape seen in *Protoichthyosaurus* (Figure. 8.1). Furthermore, *I. conybeari* always has a notched tibia, whereas *Protoichthyosaurus* never has a notched radius. Similarly, most hindfins of *I. somersetensis* have at least one notched element (Lomax and Massare, 2017). However, Appleby (1979:fig. 1e) illustrated a small forefin, designated a paratype of *P. prostaxalis* (LEICT G454.1951/164), with what appears to be a notch in metacarpal two. None of the other specimens in this study have a notched element in the forefin. Because the specimen is missing, it is not possible to determine if it is a genuine notch or damage. Moreover, the fin, excluding the propodial, is less than 14 cm long (Appleby, 1979:fig.1 caption), within the size range of a hindfin of *I. somersetensis*. Until this specimen is found, we consider the lack of

notching sufficient to distinguish a forefin of *Protoichthyosaurus* from a hindfin of *I. somersetensis*.

Of all of the species of *Ichthyosaurus*, the skull of *I. somersetensis* is most similar to that of *Protoichthyosaurus prostaxalis*, mainly because both species have a large, tall maxilla. The maxilla of *P. prostaxalis* is distinctly triangular, coming to a point dorsally, whereas the maxilla of *I. somersetensis* has a rounded dorsal margin. However, preservation might obscure this difference. On both species, in lateral view, the posterior process of the maxilla tapers to a very slender bone, but the process extends much farther under the orbit in *I. somersetensis* than in *P. prostaxalis*. However, the posterior extent of the process is strongly influenced by the orientation of the skull: it appears longer if the skull is in lateroventral view and shorter if it is in dorsolateral view, making the difference difficult to assess in skulls that are crushed at different angles. A more reliable distinction is in the shape and extent of the anterior process of the maxilla. In lateral view, the posterior process is longer than the anterior process in *I. somersetensis* (measured from the highest point of the maxilla), but the anterior process is longer than the posterior process in *P. prostaxalis*. Additionally, in *I. somersetensis*, it is broad and tapers abruptly to a point, whereas in *P. prostaxalis*, it tapers more gradually and appears more slender. The lacrimal also differs between the two species in the presence of a 'shelf' at the base of the dorsal process in *I. somersetensis* (Lomax and Massare, 2017) that is probably absent in *P. prostaxalis*. Crushing, however, can obscure this feature. Less affected by crushing is the relative length of the dorsal and anterior processes of the lacrimal: the dorsal process is noticeably longer than the anterior process in *P. prostaxalis*, but the two processes are about the same length in *I. somersetensis*. The size and shape of the postorbital is also distinctly different between the two species. In *I. somersetensis*, the postorbital is a high, narrow crescent that makes up almost the entire posterior margin of the orbit. In *P. prostaxalis*, the postorbital is shorter and wider, making up only about half of the posterior margin of the orbit (similar to *I. communis*; Massare and Lomax, 2017). Thus, in *P. prostaxalis*, the jugal comprises about half of the orbit margin, whereas in *I. somersetensis*, it has only a minor contribution. Finally, *P. prostaxalis* has a large, prominent internasal foramen, whereas species of *Ichthyosaurus* typically do not. The latter suggests that the large, fragmentary skull from Frick, Switzerland, referred to *Ichthyosaurus* by Maisch et al. (2008) could possibly be an example of *Protoichthyosaurus*. This specimen also has

a pineal opening between the frontal and parietal, which might be the position in *Protoichthyosaurus* as well.

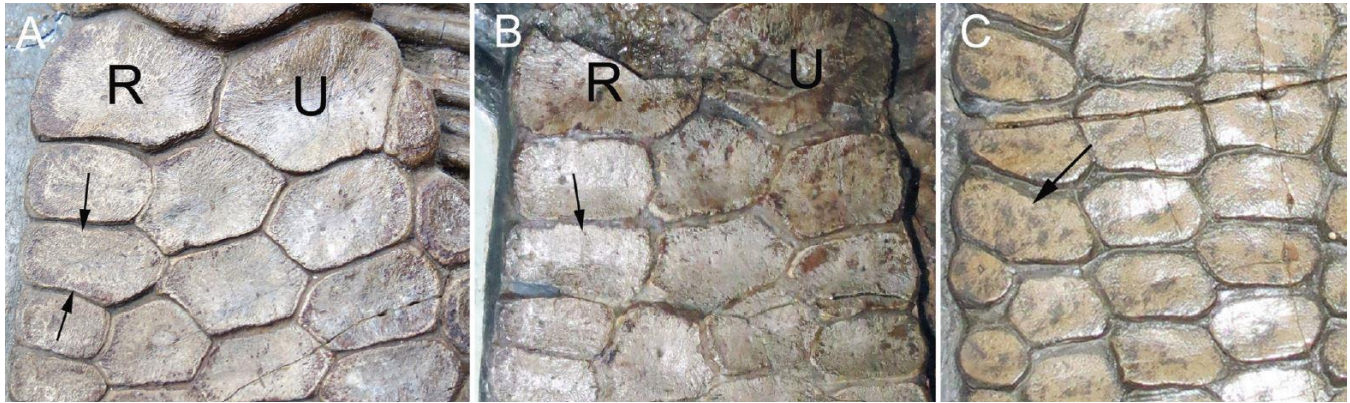


Figure. 8.10. Forefin pathology in *Ichthyosaurus* that mimics *Protoichthyosaurus* morphology. Anterior is to the left in all specimens. **A**, left forefin (reversed) of OUMNH J.13799, showing the co-ossification of distal carpal 2 with distal carpal 3. The arrows point to a faint line marking the boundary between the two elements. The right forefin (not figured) of the specimen shows the typical *Ichthyosaurus* morphology. **B**, right forefin of NHMUK R3372, showing the co-ossification of distal carpal 2 and distal carpal 3. Single arrow points to a faint line that distinguishes the two elements. The left forefin (not figured) of the specimen shows the typical *Ichthyosaurus* morphology. **C**, left forefin of ANSP 15766, showing the co-ossification of the two anterior elements of the third phalangeal row of digit II. The right forefin (not figured) of the specimen shows the typical *Ichthyosaurus* morphology. **Abbreviations:** R, radius; U, ulna.

Character	<i>Protoichthyosaurus</i>	<i>Ichthyosaurus</i>	<i>Macgowania</i>	<i>Malawania</i>	<i>Stenopterygius</i>	<i>Temnodontosaurus</i>
Elements in distal carpal row*	3	4	4	4	4	3
Elements in metacarpal row*	4	4 or 5	4	4	4	3
Radiale contacts dc3	No	Yes	Yes	Yes	Yes	Yes
Intermedium contacts dc4	No	Yes	Yes	Yes	Yes	Yes
Ulnare contacts dc3	Yes	No	No	No	No	No
Ulnare contacts mc5	n/a	Yes	Yes	Probably	Yes	n/a
mc4 contacts mc5	n/a	Yes	No	No	No	n/a
Number of primary digits	5	≥5	4	4	4/5	3
Digit V as prominent as digit IV	n/a	Yes	No	No	No	n/a
Anterior digital bifurcation	Yes	Yes	No	No	No	No

Table. 8.3. Comparison of the mesopodium and metapodium of the forefin of select ichthyosaurian genera. **Abbreviations:** dc, distal carpal; mc, metacarpal; n/a, not applicable. *Excluding accessory digits.

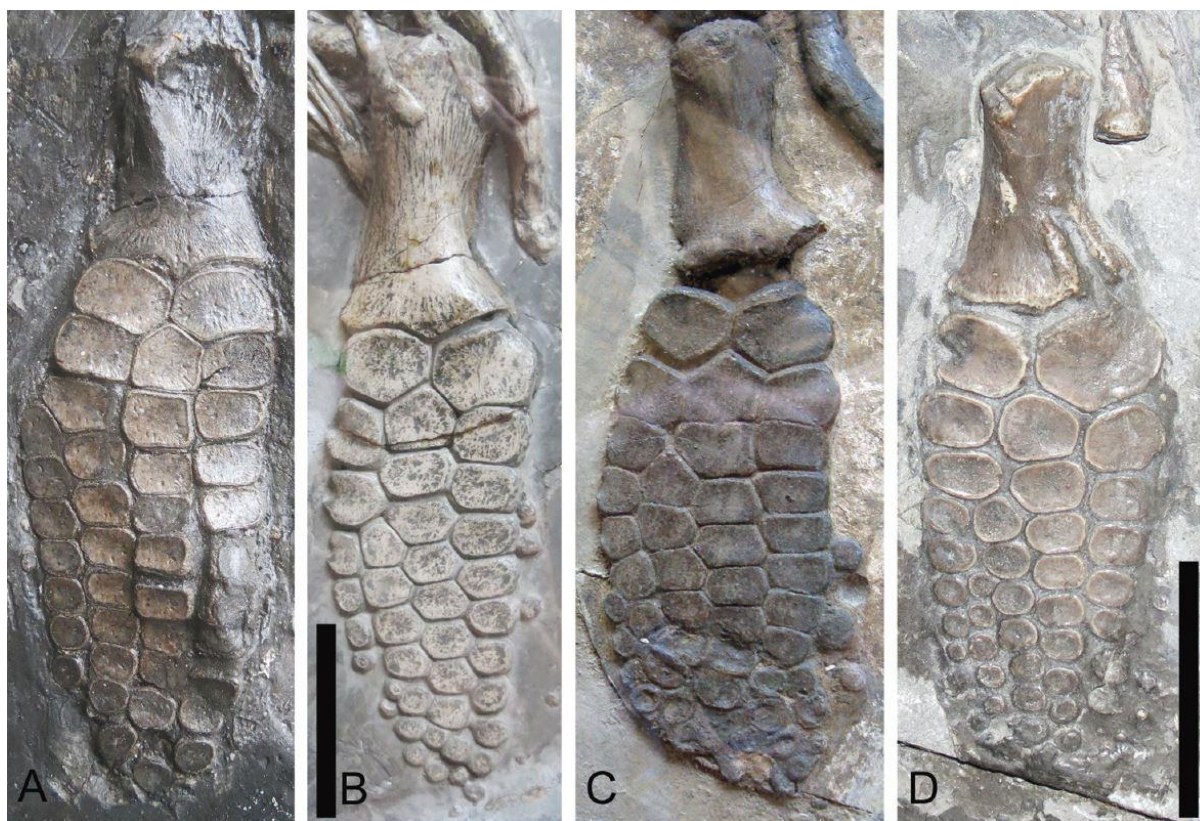


Figure. 8.11. Hindfins of some species of *Ichthyosaurus* are superficially similar to the forefin of *Protoichthyosaurus* in the presence of three elements in the third row and a bifurcation in the fourth row of the anterior digit. **A**, left hindfin of NHMUK OR43006, *I. breviceps* holotype. **B**, right hindfin (reversed) of NHMUK OR2013*, a referred specimen of *I. somersetensis*. **C**, left hindfin (reversed) of NHMUK R3372, probably an example of *I. somersetensis*. **D**, left hindfin of BGS 956, a referred specimen of *I. conybeari*. Anterior is to the left on all specimens. A scale bar could not be provided for A and C because they are on display, behind glass. Scale for B is from a cast of the specimen. Scale bars equal 5 cm (B) and 2 cm (D).

Conclusions

Unrecognized composite specimens and pathological forefins of specimens of *Ichthyosaurus* had given the impression that forefin morphology of individuals within *Ichthyosaurus* is more variable than it actually is. The forefin morphology was relied upon heavily in the initial diagnosis of *Protoichthyosaurus* (Appleby, 1979), and the misunderstanding of the variation resulted in the genus being synonymized with

Ichthyosaurus (Maisch and Hungerbühler, 1997; Maisch, 1997; Maisch and Matzke, 2000a; McGowan and Motani, 2003). *Protoichthyosaurus*, however, is a valid genus that is distinct from all other Lower Jurassic genera, including *Ichthyosaurus*. The forefin lacks digit V but has an anterior digital bifurcation. It has a unique combination of only three elements in the distal carpal row, and a bifurcation of distal carpal 2, resulting in four elements in the metacarpal row. In addition to the forefin differences first recognized by Appleby (1979), *Protoichthyosaurus* and *Ichthyosaurus* have differences in skull morphology as well. In lateral view, the skull of *Protoichthyosaurus prostaxalis* can be distinguished from all species of *Ichthyosaurus* in having a large, dorsoventrally tall, triangular maxilla with a longer anterior process than posterior process, extending well beyond the external naris, and a lacrimal with a dorsal process much longer than the anterior process. It also has a unique combination of skull characters shared with various species of *Ichthyosaurus*. The only known specimen of *P. applebyi* is incomplete and does not preserve unique skull characters that easily distinguish it from *Ichthyosaurus*. However, it possesses a unique combination of features in the skull that are shared with several species of *Ichthyosaurus*, including a narrow, crescentic postorbital (as in *I. conybeari*) and a low, symmetric maxilla (as in *I. communis* and *I. larkini*), and a prefrontal that extends to the level of the external naris, excluding the dorsal process of the lacrimal from the border of the orbit (as in *I. larkini* and *I. somersetensis*).

Recognition of the forefin morphology on at least 13 specimens, including a very small individual (Figure. 8.9), indicates that the unusual morphology is not a pathology. Thus two genera of wide-finned ichthyosaurs (five or more digits) with an anterior digital bifurcation are present in the Lower Jurassic of the U.K. This complicates the identification of fragmentary skeletons with a forefin or isolated forefins that had previously been identified as *Ichthyosaurus*. In the absence of an articulated skull (or at least the narial and orbital regions), the carpal portion of the forefin must be preserved in order to distinguish between the two genera. In addition, *Protoichthyosaurus* always has five primary digits, whereas *Ichthyosaurus* can have more. Accessory digits can be an issue, however, because in the distal portion of forefins of both genera, accessory digits are difficult to distinguish from primary digits because both have round elements.

Unlike other Lower Jurassic genera, *Protoichthyosaurus* cannot be distinguished from *Ichthyosaurus* solely on the basis of humerus morphology.

Ichthyosaurus conybeari and *I. anningae*, however, have much shorter humeri relative to their width compared to those of *Protoichthyosaurus*, so can be identified from an isolated humerus. In addition, *I. communis* and *I. larkini* can be distinguished from both species of *Protoichthyosaurus* by a more prominent dorsal process and a depression on the head of the humerus. The humerus of *Protoichthyosaurus prostaxalis*, however, is very similar to that of *I. somersetensis*, except that it lacks the depression on the head that occurs on all *I. somersetensis* specimens (Lomax and Massare, 2017).

Specimens of *Protoichthyosaurus* are not common, but they are fairly widespread geographically in the U.K. Aside from NMW 2012.23G.1, all other known specimens are from historic collections and so their stratigraphic position is not well known. Although most appear to be Hettangian in age, two specimens from Lyme Regis (NHMUK R1063, OUMNH J.26971) could be younger, and specimens from the 'Pre-planorbis Beds' could be older (Rhaetian). The recognition of *Protoichthyosaurus* as a valid genus increases the total number of Lower Jurassic ichthyosaurian genera from the U.K. to nine.

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Supplementary Data 1: Details of phylogenetic analysis

The phylogenetic analysis is largely based on the character list and coding developed by Fischer et al. (2013), with a few modifications that are enumerated below.

1. We have omitted taxa that were younger than Lower Jurassic and were less than 40% complete on the Fischer et al. (2013) matrix. This included *Arthropterygius* (33% complete), *Maiaspondylus* (36% complete), *Athabascasaurus* (35% complete), *Chacaicosaurus* (26% complete) and *Mollesaurus* (18% complete). We retained *Malawania* (27% complete), however, because it was recovered as a sister taxon to *Ichthyosaurus* by Fischer et al. (2013).

2. We omitted *Ophthalmosaurus natans* and *Platypterygius hercynicus* because the genus was represented by a better known species, *O. icenicus* and *P. australis*, respectively. As with the previously mentioned genera, these are more derived forms.

3. We used the character list and coding of Fischer et al. (2013), but modified seven characters:

Character 2 (Fischer et al. 2013, character 7). Extent of nasals relative to anterior process of maxilla, lateral view: maxilla extends anteriorly as far as nasals or further anteriorly (0); nasals extend farther anteriorly than the maxilla (1)

Character 11 (Fischer et al. 2013, character 16). Squamosal shape: square or rectangular (0); triangular (1); squamosal absent (2)

Character 39 (Fischer et al. 2013, character 48). Radius with anterior notch: present (0); absent (1).

Character 40 (Fischer et al. 2013, character 49). Postaxial accessory digits on forefin: absent (0); present (1).

Character 44 (Fischer et al. 2013, character 54). Digital bifurcation: absent (0); present (1).

Character 46 (Fischer et al. 2013, character 55). Manual digit V: absent (0); present (1).

Character 55 (Fischer et al. 2013, character 65). Tibia with anterior notch: present (0); absent (1).

These changes required recoding our characters 39, 40, 46 and 55 for all taxa.

4. We removed the following characters from Fischer et al. (2013): 1, 2, 6, 31, 32, 51 and 52 for reasons stated in Ji et al. (2016). We also eliminated character 3 because it does not specify where the cross section is taken and character 4 as it depends on preservation and how much of the root is exposed. Also, both characters are not always exposed in laterally compressed specimens of Lower Jurassic ichthyosaurs. Both 44 and 45 were removed because they were unclear and character 56 because it depends on how complete the fore and hind fins are.

5. We added two new characters to the matrix to capture differences in forefin morphology: 42 and 45.

6. We recoded *Ichthyosaurus communis* based on our own observations.

7. This is the first time that *Protoichthyosaurus* has been included in a phylogenetic analysis. The coding is based on our own observations.

Character list

The character list and coding was based largely on Fischer et al. (2013). Characters are polarized using *Mikadocephalus gracilirostris* as the outgroup. All characters are unordered. Characters that are not referenced were developed as part of this study.

1. Overbite: absent or slight (0); clearly present (1) (Motani 1999: character 33, Fischer et al. 2013: character 5).

2. Extent of nasals relative to anterior process of maxilla, lateral view: maxilla extends anteriorly as far as nasals or further anteriorly (0); nasals extend farther anteriorly than the maxilla (1) (rephrased from Fischer et al. 2013: character 7).

3. Descending process of the nasal on the dorsal border of the nares: absent (0); present (1) (Fernández 2007: character 2, Fischer et al. 2013: character 8).
4. Processus narialis of the maxilla in lateral view: present (0); absent (1) (Fischer et al. 2011: character 9, inverted coding, Fischer et al. 2013: character 9).
5. Processus supranarialis of the premaxilla: present (0); absent (1) (Maisch and Matzke 2000: character 10, Fischer et al. 2013: character 10).
6. Processus narialis of prefrontal: absent (0); present (1) (Fischer et al. 2011: character 11, Fischer et al. 2013: character 11).
7. Anterior margin of the jugal: tapering, running between lacrimal and maxilla (0); broad and fan-like, covering large area of maxilla ventrolaterally (1) (Druckenmiller and Maxwell 2010: character 6, Fischer et al. 2013: character 12).
8. Sagittal eminence: present (0); absent (1) (Fernández 2007: character 5, inverted coding Fischer et al. 2011: character 13, Fischer et al. 2013: character 13).
9. Processus temporalis of the frontal: absent (0); present (1) (Fischer et al. 2011: character 14, Fischer et al. 2013: character 14).
10. Supratemporal-postorbital contact: absent (0); present (1) (Sander 2000: character 27, inverted coding Fischer et al. 2011: character 15, Fischer et al. 2013: character 15).
11. Squamosal shape: square or rectangular (0); triangular (1); squamosal absent (2) (Modified from Fischer et al. 2013: char. 16).
12. Quadratojugal exposure: extensive (0); small, largely covered by squamosal and postorbital (1) (Maisch and Matzke 2000: character 30, modified Fischer et al. 2011: character 17, Fischer et al. 2013: character 17).

13. Lower temporal arch between jugal and quadratojugal: present (0); absent (1) (Sander 2000: character 25, modified, Fischer et al. 2013: character 18).
14. Basipterygoid processes: short, giving basisphenoid a square outline in dorsal view (0); markedly expanded laterally, being wing-like, giving basisphenoid a marked pentagonal shape in dorsal view (1) (Fischer et al. 2011: character 18, Fischer et al. 2013: character 19).
15. Extracondylar area of basioccipital: wide (0); reduced but still present ventrally and laterally (1); extremely reduced, being nonexistent at least ventrally (2) (Fernández 2007: character 10, modified Fischer et al. 2011: character 19, Fischer et al. 2013: character 20).
16. Basioccipital peg: present (0); absent (1) (Motani 1999: character 29, modified Fischer et al. 2011: character 20, Fischer et al. 2013: character 21).
17. Ventral notch in the extracondylar area of the basioccipital: present (0); absent (1) (Fischer et al. 2012: character 19, Fischer et al. 2013: character 22).
18. Shape of the paroccipital process of the opisthotic: short and robust (0); elongated and slender (1) (Fischer et al. 2012: character 20, Fischer et al. 2013: character 23).
19. Stapes proximal head: slender, much smaller than opisthotic proximal head (0); massive, as large or larger than opisthotic (1) (Sander 2000: character 34, modified Fischer et al. 2011: character 21, Fischer et al. 2013: character 24).
20. Angular lateral exposure: much smaller than surangular exposure (0); extensive (1) (Motani 1999: character 32, inverted coding Fischer et al. 2011: character 22, Fischer et al. 2013: character 25).
21. Posterior dorsal/anterior caudal centra: 3.5 times or less as high as long (0); four times or more as high as long (1) (Maxwell 2010: character 15, inverted coding Fischer et al. 2011: character 24, Fischer et al. 2013: character 26).

22. Tail fluke centra: strongly laterally compressed (0); as wide as high (1) (rephrased from Maxwell 2010: character 16, Fischer et al. 2013: character 27).
23. Neural spines of atlas-axis: completely overlapping, may be fused (0); functionally separate, never fused (1) (Druckenmiller and Maxwell 2010: character 26, Fischer et al. 2013: character 28).
24. Chevrons in apical region: present (0); lost (1) (Sander 2000: character 72, modified, Fischer et al. 2013: character 29).
25. Rib articulation in thoracic region: predominantly unicipital (0); exclusively bicipital (1) (Maisch and Matzke 2000: character 53).
26. Tail as long or longer than the rest of the body (0); distinctly shorter (1) (Maisch and Matzke 2000: character 65, Fischer et al. 2013: character 33).
27. No lunate tailfin (0); well-developed lunate tailfin (1) (Maisch and Matzke 2000: character 66, Fischer et al. 2013: character 34).
28. Glenoid contribution of the scapula: extensive, being at least as large as the coracoid facet (0); reduced, being markedly smaller than the coracoid facet (1) (Fischer et al. 2012: character 27, Fischer et al. 2013: character 35).
29. Prominent acromion process of scapula: absent (0); present (1) (Fischer et al. 2011: character 28, Fischer et al. 2013: character 36).
30. Anteromedial process of coracoid and anterior notch: present (0); absent (1) (Fischer et al. 2011: character 29, modified, Fischer et al. 2013: character 37).
31. Plate-like dorsal ridge on humerus: absent (0); present (1) (Motani 1999: character 56, Fischer et al. 2013: character 38).

32. Protruding triangular deltopectoral crest on humerus: absent (0); present (1); present and very large, matching in height the trochanter dorsalis, and bordered by concave areas (2) (Fischer et al. 2011: character 31, modified, Fischer et al. 2013: character 39).
33. Humerus distal and proximal ends in dorsal view (thus regardless of the size of the dorsal and ventral processes): distal end wider than proximal end (0); nearly equal or proximal end slightly wider (1) (Fischer et al. 2013, character 40)
34. Humerus anterodistal facet for accessory zeugopodial element anterior to radius: absent (0); present (1) (Godefroit 1993: character 10, modified, Fischer et al. 2011: character 33, Fischer et al. 2013: character 41).
35. Humerus with posterodistally deflected ulnar facet and distally facing radial facet: absent (0); present (1) (Fischer et al. 2011: character 34, modified, Fischer et al. 2013: character 42).
36. Humerus/intermedium contact: absent (0); present (1) (Fernández 2007: character 16, Fischer et al. 2013: character 43).
37. Radio-ulnar foramen: present (0); absent (1) (Maisch and Matzke 2000: character 84, modified, Fischer et al. 2013: character 46).
38. Manual pisiform: absent (0); present (1) (Motani 1999: character 67, inverted coding Fischer et al. 2011: character 36, Fischer et al. 2013: character 47).
39. Radius with anterior notch: present (0); absent (1) (modified and recoded from Fischer et al. 2013: character 48).
40. Postaxial accessory digits on forefin: absent (0); present (1) (modified and recoded from Fischer et al. 2013: character 49).
41. Preaxial accessory digits on forefin: absent (0); present (1) (Maisch and Matzke 2000: character 91, modified, Fischer et al. 2013: character 50).

42. Primary elements, excluding accessory digits or pisiform, in third (distal carpal) row of forefin: three (0); four or more (1).

43. Tightly packed rectangular phalanges: absent, phalanges are mostly rounded (0); present (1) (Maisch and Matzke 2000: character 102, modified, Fischer et al. 2011: character 42, Fischer et al. 2013: character 53).

44. Digital bifurcation: absent (0); present (1) (Fischer et al. 2011: character 43 modified, Fischer et al. 2013: character 54).

45. Distal carpal 3 contacts the ulnare in forefin: absent (0); present (1).

46. Manual digit V (recognized by presence of metacarpal 5): absent (0); present (1) (modified and recoded from Motani 1999: character 73).

47. Ischium-pubis fusion in adults: absent or present only proximally (0); present with an obturator foramen (1); present with no obturator foramen (2) (Mazin 1982: character 13, modified Fischer et al. 2011: character 44, Fischer et al. 2013: character 57).

48. Ischium or ischiopubis shape: plate-like, flattened (0); rod-like (1) (Motani 1999: character 87, modified Fischer et al. 2011: character 45, Fischer et al. 2013: character 58).

49. Iliac antero-medial prominence: present (0); absent (1) (Motani 1999: character 81, Fischer et al. 2013: character 59).

50. Prominent, ridge-like dorsal and ventral processes demarcated from the head of the femur and extending up to mid-shaft: absent (0); present (1) (Fischer et al. 2011: character 46, Fischer et al. 2013: character 60).

51. Wide distal femur blade (distal end): present (0); absent, the proximal and distal extremity of the femur being sub-equal in dorsal view (1) (Fischer et al. 2013, character 61).

52. Astragalus/femoral contact: absent (0); present (1) (Maxwell 2010: character 33, Fischer et al. 2013: character 62).

53. Femur anterodistal facet for accessory zeugopodial element anterior to tibia: absent (0); present (1) (Fischer et al. 2011: character 48, Fischer et al. 2013: character 63).

54. Spatium interosseum between tibia and fibula: present (0); absent (1) (Maisch and Matzke 2000: character 114, modified, Fischer et al. 2013: character 64).

55. Tibia with anterior notch: present (0); absent (1) (modified and recoded from Fischer et al. 2013: character 65).

56. Postaxial accessory digit: absent (0); present (1) (Fischer et al. 2011: character 50, Fischer et al. 2013: character 66).

Table. 1S: Coding of all taxa in the matrix that was used for the phylogenetic analysis. Polymorphic states are denoted by A [01]; Missing data denoted by dashes.

	10	20	30
Mikadocephalus graciliros.	0000000--0	000-----0	-----000
Hudsonelpidia brevirostris	0-----	-----	-----
Macgowania janicep	0100-----	100-----0	-----
Leptonectes tenuirostris	0-00-00000	111-0-----	0---000000
Excalibosaurus costini	1-0-----	----00----	---0-00010
Eurhinosaurus longirostris	1100000000	111-0--000	0-10000000
Temnodontosaurus spp	0000000001	1010000000	0000000000
Suevoleviathan disinteger	0100000-00	101-----0	-----01-00
Hauffiopteryx typicus	0100---000	111-00--10	0---1110-0
Stenopterygius quadrissicus	0101000001	1110000010	1111111110

Ophthalmosaurus icenicus	0111101101	111A1A0111	1011111010
Acamptonectes densus	--1----1--	---1111111	00-1---010
Brachypterygius extremus	00110-1---	--11211--1	-----10
Caypullisaurus bonpartei	000100---0	001-----1	0-----111
Aegirosaurus leptospondylus	0111111-11	111-----1	-----11---
Platypterygius australensis	0000001011	2011211011	0111-1-011
Sveltonectes insolitus	011111111-	--10211-11	00-1---110
Malawania anachronus	-----	-----	-----00-
Ichthyosaurus communis	0101000000	010-000--0	0000111100
Protoichthyosaurus prostax.	0001000--0	010-----0	000-111100
Protoichthyosaurus applebyi	-101000---	-----	0-0-1--10-

TABLE 1S (cont.)

	40	50	
Mikadocephalus	0000000-0-	-----0000	0000--
Hudsonelpidia	0000000-10	010-010010	000000
Macgowania	--00000-00	010001----	-----
L. tenuirostris	0000000000	0100010000	000000
Excalibosaurus	0000001000	0000000000	000000
Eurhinosaurus	0-000011A0	0A000A0000	000000
Temnodontosaurus	0000001000	0000000000	000000
Suevoleviathan	0-00001-10	0001010010	000100
Hauffiopteryx	0-00001000	01000100-0	000100
S. quadrissicus	010000110A	01A101100-	100100
O. icenicus	1211101111	1100011001	100110
Acamptonectes	11111011--	1-0-----	-----
Brachypterygius	1-10011111	110001----	-----
Caypullisaurus	1211001111	1110-121-1	10-111
Aegirosaurus	1-10011111	11100121--	100111
P. australensis	1211001111	11100120-1	101111
Sveltonectes	1210001-11	11100121-1	101111
Malawania	-110001-10	010001----	-----
I. communis	0110001011	A111010110	100101
P. prostaxalis	0110001011	001110--10	A0011-

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Chapter 9: Descriptive anatomy of the largest known specimen of *Protoichthyosaurus prostaxalis* (Reptilia: Ichthyosauria) including computed tomography and digital reconstruction of a three-dimensional skull

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Descriptive anatomy of the largest known specimen of *Protoichthyosaurus prostaxalis* (Reptilia: Ichthyosauria) including computed tomography and digital reconstruction of a three-dimensional skull

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Abstract

Ichthyosaur fossils are abundant in Lower Jurassic sediments with nine genera found in the UK. In this paper, we describe the partial skeleton of a large ichthyosaur from the Lower Jurassic (lower Sinemurian) of Warwickshire, England, which was conserved and rearticulated to form the centrepiece of a new permanent gallery at the Thinktank, Birmingham Science Museum in 2015. The unusual three-dimensional preservation of the specimen permitted computed tomography scanning of individual braincase elements as well as the entire reassembled skull. This represents one of the first times that medical imaging and three-dimensional reconstruction methods have been applied to a large skull of a marine reptile. Data from these scans provide new anatomical information, such as the presence of branching vascular canals within the premaxilla and dentary, and an undescribed dorsal (quadrate) wing of the pterygoid hidden within matrix. Scanning also revealed areas of the skull that had been modelled in wood, clay and other materials after the specimen's initial discovery, highlighting the utility of applying advanced imaging techniques to historical specimens. Additionally, the CT data served as the basis for a new three-dimensional reconstruction of the skull, in which minor damage was repaired and the preserved bones digitally rearticulated. Thus, for the first time a digital reconstruction of the skull and mandible of a large marine reptile skull is available. Museum records show the specimen was originally identified as an example of *Ichthyosaurus communis* but we identify this specimen as *Protoichthyosaurus prostaxalis*. The specimen features a skull nearly twice as long

as any previously described specimen of *P. prostaxalis*, representing an individual with an estimated total body length between 3.2 and 4 meters.

Introduction

Ichthyosaurs were a highly successful group of predatory marine reptiles that appeared in the late Early Triassic and went extinct in the early Late Cretaceous (Fischer et al., 2016). Some of the earliest forms were ‘lizard-like’ in appearance, although later forms evolved fish-shaped bodies (Motani, 2009). Species ranged in size from small-bodied forms less than 1 m long to giants over 20 m in length (Motani, 2005; Nicholls and Manabe, 2004; Lomax et al., 2018). Numerous Lower Jurassic ichthyosaurs have been found in the UK, the majority being from the Lyme Regis-Charmouth area in west Dorset (Milner and Walsh, 2010), the village of Street and surrounding areas in Somerset (Delair, 1969), sites around the coastal town of Whitby, Yorkshire (Benton and Taylor, 1984) and Barrow-upon-Soar, Leicestershire (Martin et al., 1986). Notable specimens have also been recorded from Ilminster, Somerset (Williams et al., 2015), Nottinghamshire (Lomax and Gibson, 2015) and Warwickshire (Smith and Radley, 2007), with various isolated occurrences at other sites across the UK (Benton and Spencer, 1995).

A partial ichthyosaur skeleton (BMT 1955.G35.1 – Birmingham Museums Trust) was discovered in 1955 in Warwickshire, England. The specimen comprises a largely complete skull, portions of the pectoral girdle, pelvis, fore- and hindfins, and numerous vertebrae and ribs. Bones of the basicranium and palate were also found, which are rarely observed in association with Lower Jurassic ichthyosaur skulls (Marek et al., 2015). The skull bones were reassembled three-dimensionally on a wood and metal frame held together with alvar, jute and kaolin dough, with missing parts carved from wood; however, some aspects were not accurately reconstructed. Museum records indicate that BMT 1955.G35.1, which has never been formally described, was originally identified as an example of *Ichthyosaurus communis* De la Beche and Conybeare 1821.

In 2015, as part of the development of the new Marine Worlds Gallery at the Thinktank, Birmingham Science Museum, the skull was dismantled, conserved and reassembled to be more anatomically accurate. The skull and postcranial skeleton of BMT 1955.G35.1 were publicly displayed for the first time, forming the centrepiece of

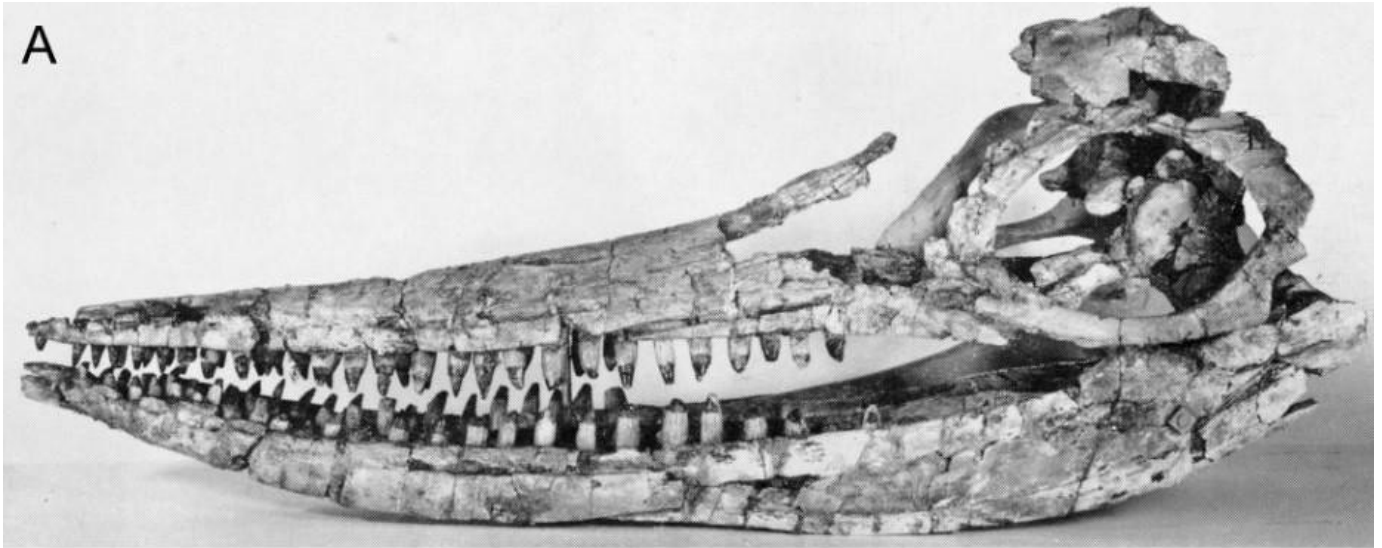
this permanent gallery. The skull of BMT 1955.G35.1 is preserved in 3D and is free of matrix; this contrasts with the majority of Lower Jurassic ichthyosaur skulls, which are often flattened or displaced and preserved in matrix, enabling a more detailed description than is typical. The large size of many marine reptile skulls has precluded attempts to visualize specimens using medical imaging (but see McGowan, 1989). Given the exceptional 3D preservation, the fact it is relatively free of matrix, and access to facilities capable of imaging large specimens, we took the opportunity to scan individual cranial elements as well as the entire skull of BMT 1955.G35.1 using computed tomography (CT) before and after reassembly. Computed tomography and 3D digital reconstruction are increasingly being applied to the skulls of fossil vertebrates, including early tetrapods (Porro et al., 2015a,b), dinosaurs (Rayfield et al., 2001; Lautenschlager et al., 2014, 2016; Porro et al., 2015c; Button et al., 2016) and extinct synapsids (Wroe, 2007; Jasinowski et al., 2009; Sharp, 2014; Cox et al., 2015; Lautenschlager et al., 2017). The first attempt to understand the internal anatomy of the ichthyosaur skull was carried out by Sollas (1916) using serial grinding; although this method produced excellent understanding of skull anatomy, it was time-consuming, labour intensive and resulted in the destruction of the specimen. In contrast, modern medical imaging methods have been applied only to isolated regions of fossil marine reptile skulls (Kear, 2005; Fernández et al., 2011; Sato et al., 2011; Neenan and Scheyer, 2012; Herrera et al., 2013), with the exception of one pliosaur (Foffa et al., 2014a), one small ichthyosaur (Marek et al., 2015), for which entire skulls were CT scanned, and the skeleton of a juvenile plesiosaur (Larkin et al., 2010).

In this paper, we use CT scanning of a large ichthyosaur skull along with careful examination of the original specimen to formally describe BMT 1955.G35.1. Based on this description we reassign the specimen to *Protoichthyosaurus prostaxalis* Appleby 1979, a genus recently shown to be distinct from *Ichthyosaurus* based on multiple characters (Lomax et al., 2017; Lomax and Massare, 2018). Furthermore, the studied specimen has an estimated maximum body length of 3.2 to 4 metres, greater than any other known specimen of *Protoichthyosaurus* or *Ichthyosaurus*.

Institutional abbreviations. BMT, Birmingham Museums Trust (encompasses BMAG, Birmingham Museum and Art Gallery and TSM, Thinktank, Birmingham Science

Museum), UK; BRLSI, Bath Royal Literary and Scientific Institution, Bath, UK; BU, Lapworth Museum of Geology, University of Birmingham, UK; LEICT, Leicester Arts and Museums Service, New Walk Museum and Art Gallery, Leicester, UK; NHMUK, Natural History Museum, London, UK; SOMAG (formerly AGC), Alfred Gillett Collection, cared for by the Alfred Gillett Trust (C & J Clark Ltd), Street, Somerset, UK; UNM, University of Nottingham Museum, UK.

Figure. 9.1. Three-dimensional skull of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*. A, original photograph of the first skull reconstruction (left lateral view) within a couple of years of the 1955 excavation. Note that the prefrontal and postorbital are present, which we have been unable to locate in our study. B, skull in left lateral view, as reconstructed in 2015. C, skull in right lateral view, as reconstructed in 2015. Note the distinctive asymmetric maxilla with long, narrow anterior process. Teeth are not in their original positions. Scale bar represents 20 cm.



Geological setting

BMT 1955.G35.1 was collected in situ from Fell Mill Farm, between Shipston-on-Stour and Honington, Warwickshire, England, grid reference NGR SP 277 415. The initial discovery was made by Mr Michael Bryan in May, 1955. A complete excavation, under the supervision of Assistant Keeper of Natural History at the City of Birmingham Museum, Mr Vincent Smith, subsequently took place. The specimen was found approximately 4 feet below the ground surface in a hard, blue-grey clay, lying directly on top of a brown grit layer containing numerous *Gryphaea* bivalves. Due to the fragmentary nature of the bones, they were removed embedded in clay.

Precise stratigraphic data associated with the discovery are not available but the remains were recorded as being from Liassic sediments, which conforms to the Early Jurassic age of the region's geology (Edmonds et al., 1965; Radley, 2003; Smith and Radley, 2007). In addition to the ichthyosaur skeleton, other fossils were collected alongside the specimen, including *Gryphaea* bivalves, a plesiosaur vertebra, and an isolated shark tooth identified as *Hybodus* cf. *H. cloacinus* Quenstedt 1858, which are also Early Jurassic in age, although this shark species ranges from the Rhaetic through Lower Lias (NRL pers. comm. D. Ward, 2015). Additionally, we found an ammonite fragment stored with the specimen, which is an example of *Euagassicerias sauzeanum* (d'Orbigny 1844), a species indicative of the *Semicostatum* Ammonite Zone, lower Sinemurian, Lower Jurassic (DRL pers. comm. M. Howarth, 2017). As there was no record stating whether this ammonite fragment was physically collected with BMT 1955.G35.1, NRL was given permission by the current owners of Fell Mill Farm to collect other fossils along with matrix from the original site at a depth of 2 m below the surface. This resulted in the collection of numerous ammonites identified as *Arnioceras semicostatum* (Young and Bird 1828), which is also indicative of the lower Sinemurian, *Semicostatum* Ammonite Zone (DRL pers. comm. M. Howarth, 2017). Thus, associated ammonites have provided the stratigraphic position of BMT 1955.G35.1.

Material and methods

BMT 1955.G35.1 is currently housed in the Thinktank Science Museum (TSM). It was originally accessioned into the collections of Birmingham Museum and Art Gallery (BMAG) and loaned to TSM. However, BMAG and TSM have since become part of the Birmingham Museums Trust (BMT). The postcranial skeleton, long

considered 'missing', was rediscovered in the collections of the Lapworth Museum of Geology (BU) and reunited with the skull as part of a funded project at the TSM. As BMT 1955.G35.1 was largely undeformed, the individual skull bones were assembled in 3D; however, several errors were made in this original reconstruction (Figure. 9.1A). As part of the funded project, the skull was disassembled and the individual bones cleaned, conserved, and remounted (Figure. 9.1B-C). Many of the preserved skull bones were disarticulated when discovered and several cranial bones are not represented. The teeth have been reset and are not in their original positions. Portions of some elements are poorly preserved and/or taphonomically distorted, which somewhat restricts our description; for example, the dentaries cannot be articulated at the symphysis or mounted in their correct anatomical position. The newly reassembled skull of BMT 1955.G35.1 is based on all the preserved elements robust enough to safely include, and we limit our description of sutural contacts to those between elements preserved in original articulation. Specific details of the reconstruction and conservation of the studied specimen will be dealt with in a separate paper.

Prior to remounting, several individual bones of the left side of the skull were scanned using microcomputed tomography (μ CT) in March 2015 at the Cambridge Biotomography Centre (Zoology Department, University of Cambridge) on an X-Tek H 225 μ CT scanner (Nikon Metrology, Tring, UK) at 135kV and 227 μ A with no filtering. Elements scanned individually include: the left articular, opisthotic, stapes, quadrate and pterygoid; the median supraoccipital and basisphenoid; and both parietals. Voltage, current and resolution (0.1 mm/voxel) were identical for all scans. Scan data were visualized in the software Avizo 8.0 (Thermo Fisher Scientific, Waltham, Massachusetts, USA) and the left-side elements mirrored across the sagittal midline. All 3D surfaces were exported as stereolithography (STL) files and 3D printed at life-size in gypsum on a 3DS x60 3D Printer; pieces were subsequently dipped in cyanoacrylate for strength (NRL pers. comm. S. Dey, 2016).

After remounting, the skull of BMT 1955.G35.1, including the 3D printouts previously described, was scanned in May 2015 at the Royal Veterinary College on a Lightspeed Pro 16 CT scanner (GE Medical Systems LTd., Pollards Wood, UK) at 120 kV and 200 μ A. Due to the size of the specimen, it was scanned in two parts – the front of the skull was scanned at 0.56x0.56x1.25 mm/voxel and the rear of the skull was scanned at 0.73x0.73x1.25 mm/voxel. Both scans produced a total of 2168

DICOM slices. Both scans used an exposure time of 2356 ms and a body filter. Density thresholding was used to separate higher-density fossil bone from lower-density matrix as well as areas of the skull historically modelled in wood, clay and jute, and portions newly modelled in gypsum. Scans were segmented to isolate individual bones and teeth, and to trace internal features. The two halves of the skull were overlain and merged using skeletal landmarks visible in both datasets (Figures 9.2-9.4). Three-dimensional surfaces were exported as wavefront (OBJ) files to create an interactive 3D PDF using Tetra4D Reviewer and Converter (Tech Soft 3D; Oregon, USA) and Adobe Acrobat Pro X (Adobe Systems, California, USA). This reconstruction is provided as supporting information (Appendix S1) and are the basis for the following description.

Surface models of individual bones were manipulated in 3D space using the Transform Editor within Avizo, allowing digital 3D reconstruction of the skull of BMT 1955.G35.1 following similar methods applied to early tetrapods (Porro et al. 2015a,b) and dinosaurs (Lautenschlager, 2016). Most of the bones in the digital reconstruction are from the left side of BMT 1955.G35.1 as this side is generally better preserved. Minor damage was manually repaired in the Segmentation Editor within Avizo using interpolation, including: minor breaks and missing alveolar margins in the left premaxilla, maxilla, dentary and splenial; minor breaks in the left nasal, lacrimal, jugal, quadrate, pterygoid, and parietal; the missing right margin of the supraoccipital; and gaps within the anterior half of the left surangular. Portions of bones preserved on the right but absent on the left – including the posterior tip of the right jugal and anterior tip of the right splenial – were duplicated, reflected across the sagittal midline, and merged with left side elements using anatomical landmarks. We did not attempt to reconstruct missing bones or preserved elements that could not be scanned due to their delicate nature (see Results). The disarticulated bones were then fitted together at sutural contacts; we also referred to known relationships between skull bones from other ichthyosaur skulls (Andrews, 1910; Sollas, 1916; McGowan, 1973; Kirton, 1983; McGowan and Motani, 2003; Marek et al., 2015; Moon and Kirton, 2016). Lastly, left side elements were duplicated and reflected to form the right side of the skull. Transformation matrices for all bones from the original data set to the final 3D reconstruction are available as supporting information (Appendix S2); a 3D PDF of the reconstructed skull is also available as supporting information (Appendix S3).

Systematic Palaeontology

Order **Ichthyosauria** de Blainville, 1835

Family **Ichthyosauridae** Bonaparte, 1841

Genus **Protoichthyosaurus** Appleby, 1979

Protoichthyosaurus prostaxalis Appleby, 1979

Type species. *P. prostaxalis* Appleby 1979. The type series of specimens are from historic collections. However, the holotype is most likely from the area around Street, Somerset and is most likely from the lowermost Jurassic (lower Hettangian) 'Pre-Planorbis Beds' (i.e., Tilmanni Ammonite Zone) of the Blue Lias Formation, although it could be latest Triassic (Rhaetian). See Lomax et al., (2017) for more details.

Holotype. BRLSI M3553, a partial skull, pectoral girdle, and both forefins, preserved in ventral view.

Paratypes. BRLSI M3555, a skull and partial skeleton, preserved in right lateral view; BRLSI M3563, a composite partial skeleton; LEICT G454.1951/164, a partial forefin, presently missing, which might be a hindfin of a different genus (see Lomax et al., 2017 for more details).

Referred specimen. BMT 1955.G35.1, an almost complete, three-dimensional skull and partial postcranial skeleton.

Emended diagnosis. As in Lomax et al., (2017), but with the following change: total length greater than 3.2 m but probably less than 4 m.

Occurrence. Fell Mill Farm, between Shipston-on-Stour and Honington, Warwickshire, England, grid reference NGR SP 277 415. The specimen was collected from blue-grey Liassic clay, and specifically from the Semicostatum Ammonite Zone, lower Sinemurian, Lower Jurassic.

Results

Anatomical description of the skull roof

Measurements of the skull are in Table 9.1. In lateral view, the upper jaw is shaped like a right-angle triangle, the ventral margin being nearly straight and dorsal surface of the snout being gently sloped (Figure. 9.1). In dorsal and ventral views, the anterior snout (formed by the premaxillae) is shaped like a finely pointed triangle (Figure. 9.2); the posterior portion of the skull is transversely expanded. Preserved bones of the skull roof (Figs. 9.1-2,5) include most of the premaxillae, both maxillae, partial nasals, partial left lacrimal, partial prefrontals and postfrontals, complete left and partial right jugals, nearly complete parietals, and partial supratemporals. Some of these elements (e.g. portions of nasal and postfrontals) were too fragmentary and/or poorly preserved to attach to the skull and are not part of the 3D model. The left postorbital was originally present (Figure. 9.1A), but we were unable to locate the element. The quadratojugals and squamosals are not preserved in BMT 1955.G35.1. The frontals are also missing with the exception of a small fragment attached to the left nasal. Unless otherwise stated, the morphology concurs with other specimens of the species (Lomax et al., 2017; Lomax and Massare, 2018).

Premaxilla. The premaxilla makes up two-thirds of the length of the cranium and most of the snout. The majority of both premaxillae are preserved, although portions of the posterior ends are missing including the margin of the external naris (Figs. 9.1-2). The left premaxilla is more complete than the right element. In lateral view, the anterior premaxilla is dorsoventrally low but becomes progressively taller posteriorly. A longitudinal groove exposing a series of foramina (see below) along the lateral surface represents the fossa praemaxillaris (Figs. 9.1B-C, 9.2). The right premaxilla preserves a long, tapering subnarial process that articulates with the maxilla and extends to the middle of the maxilla (Figs. 9.1B, 9.2A); the supranarial process is not preserved on either side. Laterally, the contact between the premaxilla and maxilla is clear and consists of an extensive scarf joint in which the ventral margin of the premaxilla laterally and dorsally overlaps the anterior process of the maxilla (Figs. 9.1-2). The contact between the premaxilla and maxilla on the palate is difficult to discern, although it appears that a maxillary shelf extends medially and replaces the

Table. 9.1. Measurements of some skull and postcranial elements of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*. 'Width' for fin elements refers to the anteroposterior dimension, perpendicular to the long axis of the fin. L and R denote measurement of left or right elements. Asterisk denotes an estimate because the bone is damaged or elements are missing.

Element	(cm)
Skull length	80*
	25.5R
Maxilla length	24.2L*
Lower jaw length	87*
Basisphenoid length	5.82
Basisphenoid width	9.95
Supraoccipital height	5.04
Supraoccipital width	6.11
Quadrate length	9.4
Quadrate max width	8.2
Hyoid length	18.5R 18.2L
Coracoid med-lat length	12.16
Coracoid ant-post	13.66
Scapula preserved length	12.9*
Scapula proximal end only	7.25
Humerus length	10.4
Humerus distal width	8.59*
Humerus proximal width	7.66
Femur length	8.7
Femur distal width	5.1
Femur proximal width	2.5*
Ilium length	9.38
Humerus/Femur ratio	1.2

premaxillary shelf at the level of the 18th preserved tooth on the right side. (The teeth, were reset during conservation and their positions in the jaw are not original. However, their reconstructed positions act as landmarks for our description.) Except at the anterior tip of the snout, the premaxillae do not meet at the ventral midline.

In dorsal view, the premaxillae would have contacted each other at a butt joint for much of their length, although they are largely separated due to deformation (Fig. 9.2E). Posteriorly, the nasals inserted between the premaxillae. The dorsal margin of the left premaxilla laterally and dorsally overlaps the nasal from approximately the level of the 13th premaxillary tooth to its broken posterior end. In dorsal view, a small, narrow portion of the anterior process of the nasal is exposed; the rest is overlapped by the premaxilla.

Anteriorly, the premaxilla is a laterally bowed sheet of bone in transverse cross-section; at the level of the seventh preserved tooth, it develops a medial shelf that roofs the alveolar groove. From this point until its articulation with the maxilla, the premaxilla consists of a ventral lamina that laterally overlaps the teeth, the medial shelf, and a dorsal lamina, which is deeply grooved along its margin (as preserved on the right premaxilla), presumably to receive the nasal. CT scans reveal that each premaxilla encloses a branching, longitudinal canal dorsal to the tooth row (Figure. 9.2G-J). This canal extends from the posterior end of the premaxillary tooth row to the third premaxillary tooth. Anteriorly, a series of short canals branch anterolaterally from the main conduit and open onto the fossa praemaxillaris, either immediately above the alveolar margin or on the dorsolateral aspect of the bone. The right premaxilla preserves five ventral and four dorsal foramina; the left premaxilla preserves four ventral and one dorsal foramina. The posterior half of each premaxilla contains two longer canals branching posteriorly from the main conduit, each of which opens onto posteriorly elongated grooves parallel to the alveolar margin of the premaxilla. The left premaxilla preserves two additional longitudinal grooves on the posterior half of its dorsolateral surface; however, these do not connect to the main canal within the premaxilla. These vascular canals within the premaxilla (as well as those within the dentary, see below) resemble canals in the facial bones of extant crocodilians and lepidosaurs, as well as those reported in theropod dinosaurs (Dal Sasso et al., 2009), pliosaurs (Ketchum and Benson, 2011; Foffa et al., 2014b), and plesiosaurs (Ketchum and Smith, 2010) and something similar in ichthyosaurs (Lomax and Massare, 2015). In extant taxa, these canals

carry neurovascular bundles consisting of the maxillary artery and maxillary branch of the trigeminal nerve (CN V₂) in the upper jaw, and the inferior alveolar artery and mandibular branch of the trigeminal nerve (CN V₃) (Witmer, 1997). The complex web of ramifications reported in the upper jaw of pliosaurs cannot be visualized in this specimen; this may be due to their absence, preservation or scan resolution. Nonetheless, it is possible these canals were also associated with pressure or electro-reception as seen in some extant taxa and as postulated for dinosaurs and pliosaurs (Foffa et al. 2014b).

Maxilla. Both maxillae are preserved, although the posterior portion of the left maxilla is missing and both are damaged. In lateral view, the maxilla is a triangular bone with slender anterior and posterior processes and is dorsoventrally tallest in its center (Figures. 9.1-2). The anterior process is longer and more delicate than the posterior process, which extends just under the orbit. Although the external naris is not preserved, it is clear the maxilla extended well beyond the anterior end of the external naris.

The alveolar groove of the maxilla is continuous with that of the premaxilla. In transverse section, the anterior maxilla has a ventral lamina that extends lateral to the tooth row, a ventrally curving medial shelf (forming the dorsal and medial walls of the alveolar groove) and a short dorsal lamina that contacts the medial surface of the premaxilla in a scarf joint. The dorsal lamina of the maxilla, which underlaps the premaxilla, is exposed slightly anterior to the middle of the left maxilla due to the damaged premaxilla. Posterior to the main body, the maxilla is triangular in transverse section with a ridge on its dorsomedial surface that appears to articulate with the short anterior process of the lacrimal, which is poorly preserved. An articulation surface on the dorsolateral surface of the posterior process of the maxilla meets the jugal in a scarf joint, separating the posterior process of the maxilla from the lacrimal.

Nasal. The anterolateral portion of the left nasal is preserved attached to the premaxilla (Figs. 9.1-2). It is best seen in ventral and posterior views, which reveals it is dorsoventrally thickened medially but becomes dorsoventrally thin laterally. The bone is laterally bowed in transverse section. The ventral margin of the nasal is laterally overlapped by the dorsal lamina of the premaxilla; the morphology of the

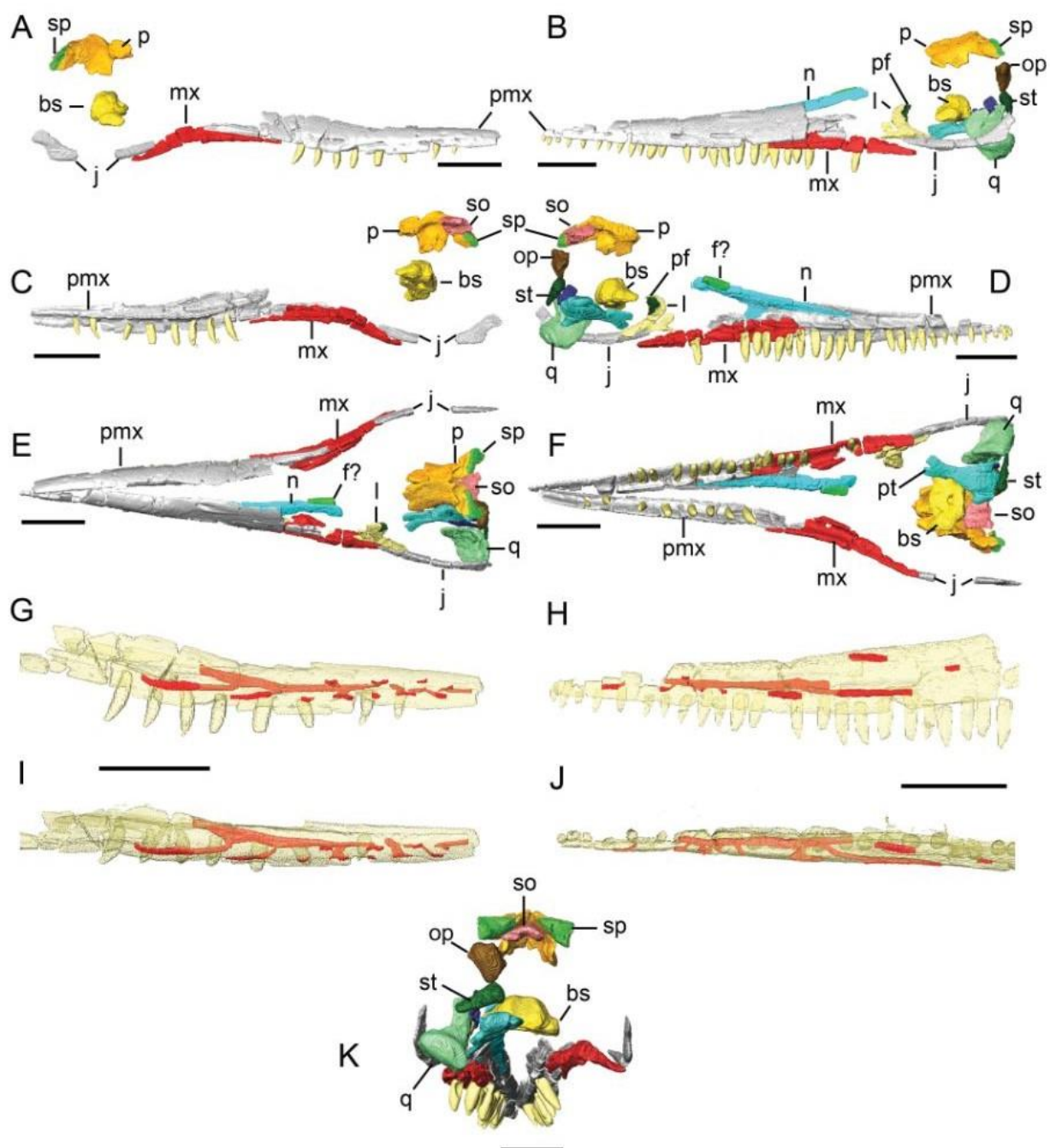


Figure. 9.2. Surface models (generated from CT scan data) of preserved bones from the upper jaw of BMT 1955.G35.1, *Protoichthyosaurus prostaialis*. Right (A) and left (B) lateral views of the cranium. Medial views of the right (C) and left (D) sides of the cranium. Dorsal (E) and ventral (F) views of the cranium. Lateral views of the right (G) and left (H) premaxillae. Dorsal views of the right (I) and left (J) premaxillae. Posterior (K) view of the upper jaw. Individual bones are shown in different colours. Bones in G–J are transparent to visualize internal canals (shown in red opaque). Teeth are not in their original positions. *Abbreviations:* bs, basisphenoid; f?, possible fragment of frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; o, opisthotic; p, parietal; pf, prefrontal; pmx, premaxilla; pt, pterygoid; q, quadrate; so, supraoccipital; sp, supratemporal; st, stapes. Scale bars equal 10 cm.

right premaxilla suggests this may have originally been a tongue-and-groove contact. Near the posterior end of the element is a small fragment featuring a grooved medial margin; it is unclear if this is a portion of the nasal or a fragment of the frontal. CT scans reveal a few short canals penetrating the nasal from its lateral surface.

Other fragments of the nasal were found with the specimen but not mounted on the skull due to their fragile nature. Although very fragmentary, much of the right nasal is preserved although the posterior end is missing and it is impossible to determine the presence of an internasal foramen. It is a long and delicate element that is wide posteriorly, and tapers to a point anteriorly (Figure. 9.5K-L). On the medial surface is a long groove that runs almost the entire length of the nasal. The slightly flared lateral wing is damaged. Two foramina are present posteriorly, positioned next to a portion of what may be the prefrontal.

Lacrima. The left lacrimal is poorly preserved. It appears to be triradiate with a short, but damaged anterior process and a longer posteroventral process. The dorsal process is tall and formed the posterior margin of the external naris. It was clearly excluded from the orbital margin by the anterior process of the prefrontal (Figures. 9.1B, 9.2B,D). The lateral surface of the dorsal process preserves external sculpting and several canals that penetrate the bone but cannot be traced. The short, tapering anterior process fits onto a shelf on the dorsomedial aspect of the maxilla. The posteroventral process, which is longer and mediolaterally wider than the anterior process, is complete and contributes to the anteroventral margin of the orbit. It meets the dorsal margin of the jugal in a curving contact. The lateral surface of the posteroventral process bears the remnant of a ridge from its posterior tip to the base of the dorsal process.

Prefrontal. Only a small portion of the anterior process of the left prefrontal is present, although original photographs of the mounted skull show that the element was once complete (Figures. 9.1B, 9.2B). The anterior process of the prefrontal medially and dorsally laps the lacrimal along a broad contact, where it is dorsoventrally tall and excludes the dorsal process of the lacrimal from the orbital margin.

Postfrontal. The anterior portions of both postfrontals are preserved but were not added to the mount. The right postfrontal is the more complete of the two elements (Figure. 9.5M). In dorsal view, the anterior end is mediolaterally broad and dorsoventrally thin. The postfrontal narrows posteriorly, where it is damaged. The medial surface exhibits a prominent ridge.

Jugal. The jugal is a long, slender bone forming the ventral margin of the orbit; the left is better preserved than the right (Figures. 9.1-2). Anteriorly it is oval-shaped in transverse section and tapers to a point, contacting the posteroventral margin of the lacrimal and dorsolateral aspect of the posterior process of the maxilla as previously described. Although damaged and perhaps missing a small portion, it is clear the anterior process extended to at least the level of the anterior margin of the orbit. Posteriorly, the dorsal ramus of the jugal gently curves dorsally, expands dorsoventrally and thins mediolaterally. Based on the original reconstruction (Figure. 9.1A), which featured a complete jugal and postorbital, the jugal contributed to about half of the posterior orbital margin.

Postorbital. An original photograph shows that the postorbital was complete, but we have been unable to locate the element (Figure. 9.1A). However, based on the photograph, it is clear that the postorbital is dorsoventrally short and anteroposteriorly wide, being almost rectangular in shape and making up half of the posterior orbital margin. The anterodorsal edge tapers to a narrow process.

Parietal. Both parietals are damaged and missing their anteroventral margins, the left element being better preserved (Figures. 9.3, 9.5A-D). In dorsal view, the parietals are hour-glass shaped and meet medially, diverging slightly anteriorly. CT scans reveal the dorsomedial margin of the anterior parietal is strongly dorsoventrally expanded in transverse section, the elements contacting each other at a tall midline butt joint; the parietal thins ventrolaterally in transverse section. The articulation of the parietals results in a well-defined sagittal crest (Figure. 9.5A, C); at its mid-section, the parietal is L-shaped in transverse section with the horizontal leg forming the roof of the braincase while the ventral leg forms the lateral wall of the braincase and medial wall of the supratemporal fenestra. Lateral to the crest, the dorsal surface of the parietal is convex and curves ventrally, widening posteriorly. Posteriorly, the

crest decreases in height to form an extensive shelf (parietal ridge) under which the supraoccipital articulates (Figure. 9.5A, C). Two elongate depressions, one on the posterior aspect of each parietal, may represent attachment sites for epaxial neck muscles (Figure. 9.5C).

In ventral view, the surface of the parietal is concave and bears impressions of structures that surrounded the brain (Figure. 9.5B, D). In the anterior region, impressions of the cerebral hemisphere and extra-encephalic depression are present (as in McGowan, 1973). McGowan (1973, fig. 48) showed that the cerebral hemisphere was present in both the parietal and frontal in a specimen of *Ichthyosaurus*. In BMT 1955.G35.1, there is no indication of the frontal at this position, suggesting the cerebral hemispheres were likely limited to the parietal. The descending parietal flange is present in both parietals, although the left is more complete (Figure. 9.5B, D). The anterior process is thick, short, and protrudes forwards, creating a ledge. Towards the centre of the parietal is the large, ovoid impression of the optic lobe, the most prominent of the cerebral structures, situated posterior to the parietal flange (Figure. 9.5B). The epiterygoid process is not preserved. Posteriorly, the parietal flares laterally to form the paraoccipital process; in posterior view, this process is shaped like a bowtie and ventrally deflected. In ventral view, there may be an impression of the cerebellum, although this is difficult to confirm because this portion is damaged.

Supratemporal. Portions of both supratemporals are preserved. The majority is exposed at the posterior margin of the skull, attached to the parietal (Figures. 9.3C, 9.5C). It is difficult to identify the parietal-supratemporal suture in the original specimen. In CT scans, the contact between the left parietal and supratemporal is visible as a very tight, sinuous butt joint; this contact cannot be discerned on the right and the two bones may have fused. In posterior view, the preserved supratemporal is large and triradiate; it is narrow medially and increases in width distolaterally, with a posteroventral process. In this view, it is roughened with numerous striae, probably for muscle attachment (Kirton, 1983) (Figure. 9.5C). There are also some foramina present, similar to those reported in this region of the supratemporal in ichthyosaurs such as the Cretaceous *Leninia stellans* (Fischer et al., 2014).

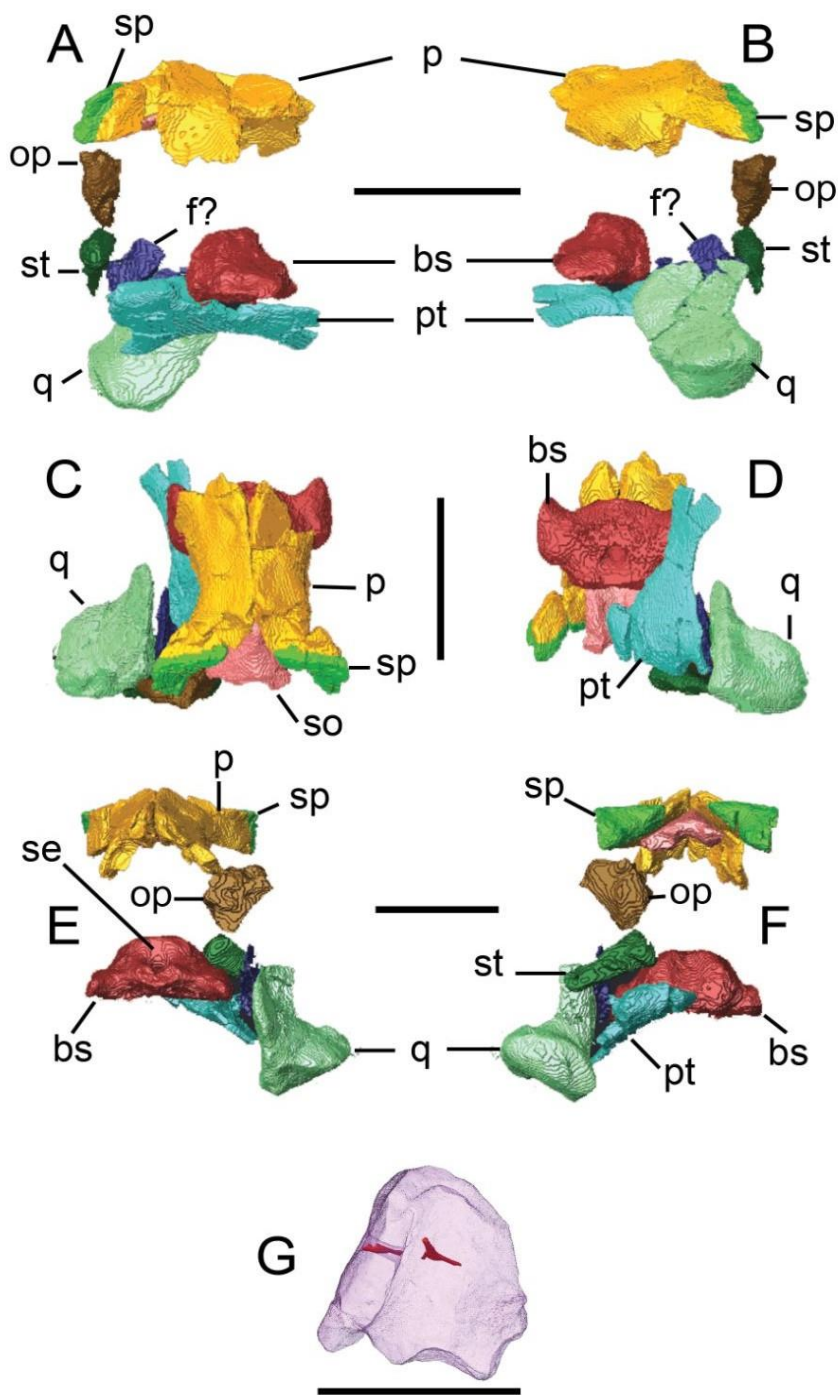


Figure. 9.3. Surface models (generated from micro-CT scan data) of preserved palatal and braincase bones from BMT 1955.G35.1, *Protoichthyosaurus prostaialis*. Right medial (A) and left lateral (B) views, dorsal (C) and ventral (D) views, and anterior (E) and posterior (F) views. Isolated supraoccipital in right anterolateral view (G). Individual bones are shown in different colours. Supraoccipital in G is transparent to visualize internal canals (shown in red opaque). *Abbreviations:* bs, basisphenoid; f?, probable fragment of upper pterygoid wing; op, opisthotic; p, parietal; pt, pterygoid; q, quadrate; se, sella turcica; so, supraoccipital; sp, supratemporal; st, stapes. Scale bars equal 10 cm, except for (G) which equals 5 cm.

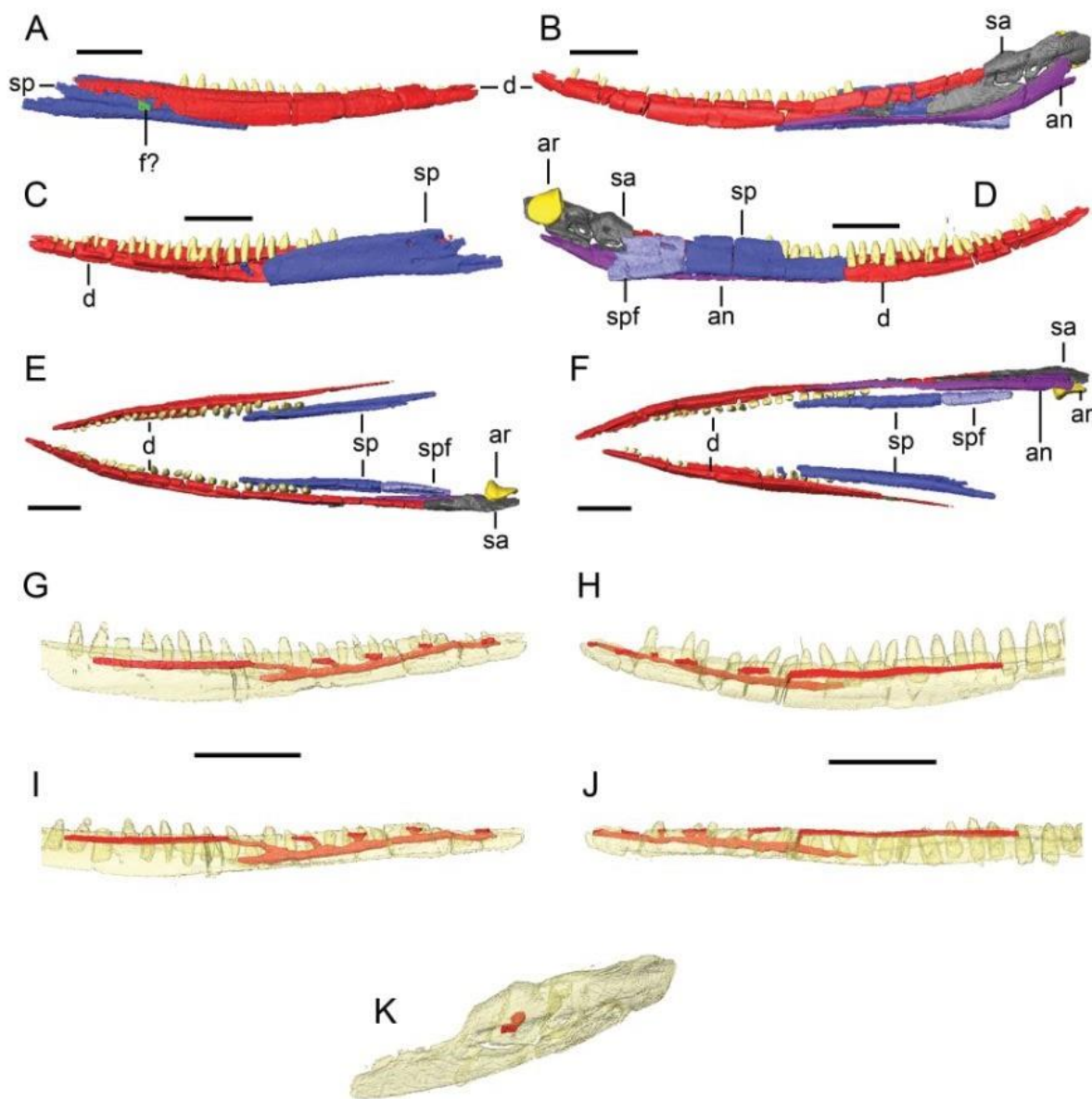


Figure. 9.4. Surface models (generated from CT scan data) of preserved bones from the lower jaw of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*. Lateral views of the right (A) and left (B) lower jaws. Medial views of the right (C) and left (D) lower jaws. Dorsal (E) and ventral (F) views of the both halves of the lower jaws. Lateral views of the right (G) and left (H) dentaries. Ventral views of the right (I) and left (J) dentaries. Lateral oblique (K) view of the left surangular. Individual bones are shown in different colors. Bones in G–K are transparent to visualize internal canals (shown in red opaque). Teeth are not in their original positions. *Abbreviations:* an, angular; ar, articular, d, dentary; f?, possible surangular fragment; sa, surangular; sp, splenial; spf, splenial fragment. Scale bars equal 10 cm.

Anatomical description of the palate

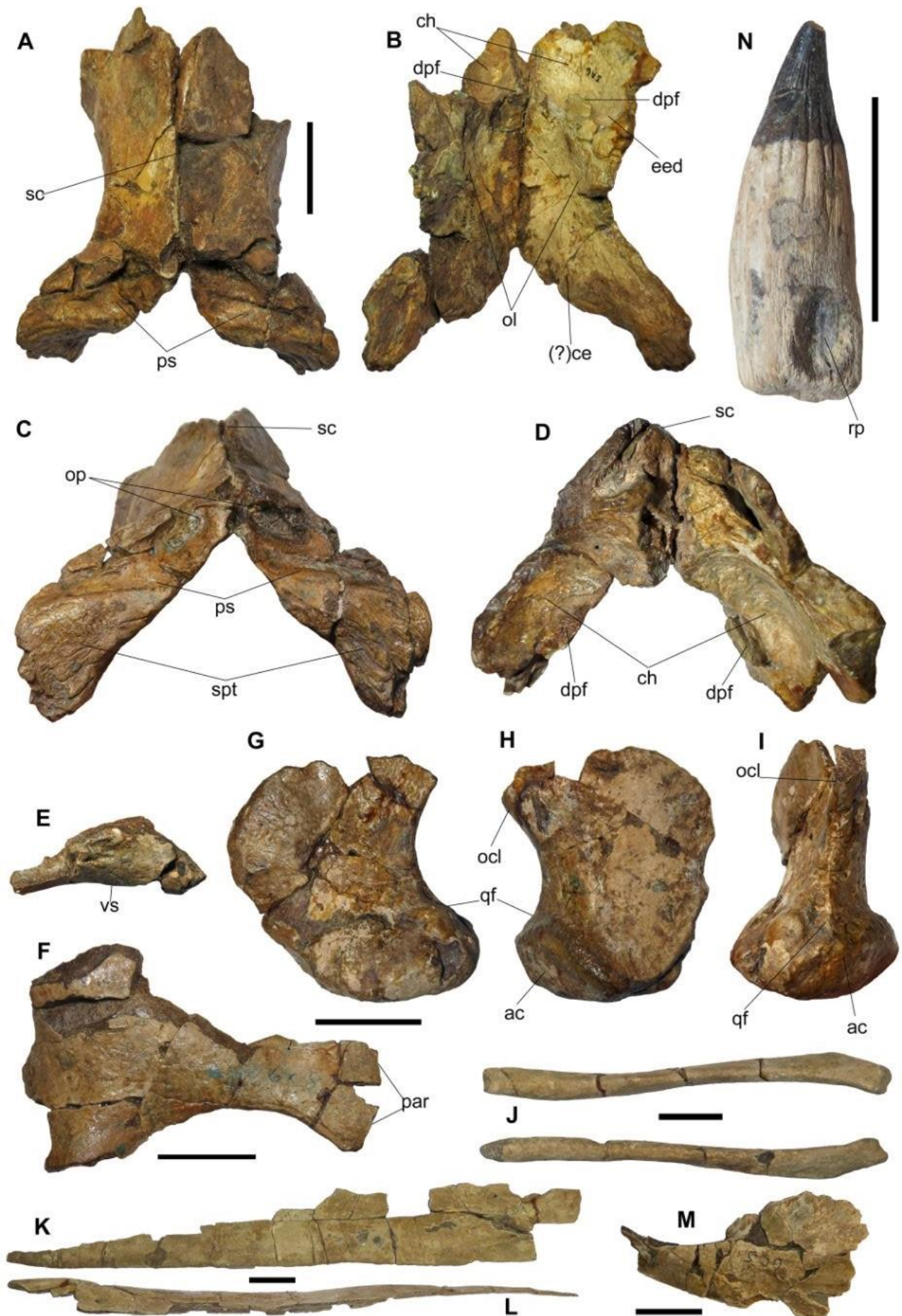
The left pterygoid, including a fragment representing the quadrate wing, and quadrate are preserved (Figure. 9.3).

Pterygoid. The left pterygoid can be positively identified, although it is damaged. It is an anteroposteriorly elongate element with a robust and mediolaterally wide posterior end and narrow anterior end (palatal ramus) (Figures. 9.3, 9.5E-F). The palatal ramus is dorsoventrally flattened and makes up over half the length of the pterygoid; it is narrowest at its mid-length and expands distally. Posteriorly, the pterygoid expands transversely and dorsoventrally to form the quadrate ramus; its dorsal surface rises in a ridge that would have been continuous with the quadrate wing (see below). Although damaged and incomplete, the overall morphology of this element, particularly how the shape changes from the posterior end to the narrow mid-shaft which then broadens anteriorly, is reminiscent to the pterygoid of *Sveltonectes* (Fischer et al., 2011, fig. 2G). This differs from *Ichthyosaurus*, which has a very narrow shaft posteriorly (McGowan, 1973, fig. 20), and from *Platypterygius longmani* Wade 1990 which has a mediolaterally wider shaft (Kear, 2005, fig. 8C-E) and even from *Ophthalmosaurus icenicus* Seeley 1874, in which the pterygoid has a distinctly different shape posteriorly (Moon and Kirton, 2016, plate. 6, figs 1, 2). In dorsal view, the posterior end has three wing-like projections. The medial projection, which is damaged and was originally more extensive, is the largest and most robust, whereas the lateral projection is slender and dorsoventrally flattened (Figure. 9.5E). The ventral surface is better preserved, although the edge of the interpterygoid vacuity is damaged (Figure. 9.5F). Regardless, the posterior end of the pterygoid is larger, wider, and narrows more gradually than that of *Ichthyosaurus* (McGowan, 1973, fig. 20B). The dorsal (quadrate) wing of the posterior ramus of the left pterygoid is almost certainly represented by a large but thin fragment of bone, the shape of which was obscured by a large amount of wood and plaster in the original reconstruction but is revealed in CT scans.

Quadrate. Only the left quadrate is preserved, which is a large and robust element (Figures. 9.3, 9.5G-I). In anterior and posterior views the quadrate is C-shaped, owing to strong curvature of the shaft (Figure. 9.5G-H); it is more of an L-shape in

Ichthyosaurus (McGowan, 1973, fig. 9). The articular condyle is massive and greatly expanded mediolaterally, whereas the dorsal end is mediolaterally thin. A well-defined ridge is present above the condyle and displays a long groove identified as the quadratojugal facet. A groove is present on the ventral surface of the condyle, which divides the jaw joint surface into two distinct faces as is common among ichthyosaurs.

Figure. 9.5. Elements of the skull, palate, lower jaw and dentition of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*. A-D, incomplete and damaged, articulated parietals in dorsal (A), ventral (B), posterior (C) and anterior (D) view. E-F, incomplete and damaged left pterygoid in posterior (E) and ventral (F) view. Note the three wing-like projections in posterior view. G-I, incomplete and damaged left quadrate in anterior (G), posterior (H) and lateral (I) view. J, hyoids in dorsal view. K-L, incomplete and damaged right nasal in dorsal (K) and (L) lateral view. M, incomplete and damaged right postfrontal in dorsal view. N, practically complete tooth missing the tip of the crown. Note that the root is large with prominent grooves that extend to the base of the crown and continue as longitudinal striations on the crown. *Abbreviations:* ac, articular condyle; (?)ce, impression of cerebellum; ch, impression of cerebral hemisphere; dpf, descending parietal flange; eed, extra-encephalic depression; ocl, occipital lamella; ol, impression of optic lobe; op, elongate openings in the posterior surface of the parietal; par, palatal ramus; ps, parietal shelf (ridge); qf, quadratojugal facet; rs, resorption pit; sc, sagittal crest; spt, supratemporal probably fused with parietals; vs, ventral surface. Scale bars represent 3 cm.



Anatomical description of the braincase

Preserved material includes the supraoccipital, left opisthotic, left stapes, and parabasisphenoid (Figure. 9.3). The anterior portion of the parasphenoid as well as the basioccipital, prootics, and exoccipitals are missing.

Supraoccipital. The median supraoccipital is triangular with its apex anterodorsally directed (Figure. 9.6A-C). CT scans revealed that the right margin of the supraoccipital had been reconstructed in plaster, obscuring the true shape of this element. In anterior and posterior views, the element is convex and arch-like, and is wider than it is tall, which is similar in *Ichthyosaurus* (McGowan, 1973, fig. 4). Of particular note, in this view, the dorsal portion of the opening for the foramen magnum is much more reduced than in either *Platypterygius longmani* (Kear, 2005, fig. 10D-E) or *Ophthalmosaurus icenicus* (Moon and Kirton, 2016, Plate 9, fig. 1-5). A median ridge is present on the posterior surface, which is sharpest anterodorsally and flattens as it approaches the foramen magnum (Figure. 9.6B-C). This ridge would have contacted the parietal, as shown in the 3D model (Figure. 9.3C, F) and separates two flat, posterolaterally-directed faces, each of which is pierced by a canal that opens onto its internal surface (Figure. 9.3B, G). These openings probably represent the foramen endolymphaticum (Andrews, 1910), which served for the passage of the endolymphatic ducts (McGowan, 1973; Maisch, 2002; Marek et al., 2015) or veins (Kirton, 1983; Moon and Kirton, 2016). The complete left half preserves two articulation facets along its ventral lateral margin – a larger, posteroventrally-directed facet that is deep and triangular-shaped (apex pointing forward) and a smaller, oval-shaped facet that is posterolaterally-directed.

In dorsal view, there is a well-defined ridge that is separated by a long, trenchant groove (Figure. 9.6B). For *Ichthyosaurus*, McGowan (1973, pg. 15) described the dorsal edge as having two shallow grooves. The groove marks the boundary between the ossified and cartilaginous portions of the neurocranium (McGowan, 1973). In ventral view, the element is arched with a smooth section for the roof of the foramen magnum (Fig. 9.6C). The exoccipital facet is roughly square.

Parabasisphenoid. The thin parasphenoid is broken with a small portion preserved fused to the basisphenoid (Figure. 9.6D). The basisphenoid is complete and is a large, robust element both mediolaterally wide and dorsoventrally tall (Figure. 9.6D-

E). There are deep grooves between the posterior corners of the bases of the basiptyergoid processes and the main body for the palatal ramus of the facial nerve (Kirton, 1983). In dorsal view, the midline of the anterior end is convex and, along with the protruding anterior ends of the basiptyergoid processes, gives the anterior margin of the basisphenoid a 'three-pronged' appearance, resembling a specimen of *Ichthyosaurus* referred to as the 'Evans Nodule' by McGowan (1973, plate 1a). The basiptyergoid processes are both complete, robust and oblong in ventral view (Fig. 9.6E). Their surfaces appear slightly roughened, probably due to a cartilaginous covering for contact with the pterygoid. The distal articular facet of the basiptyergoid process is defined by a depression with a rim. The anterior tip of the basiptyergoid process is tapered, whereas the posterior margin is thickened and rounded.

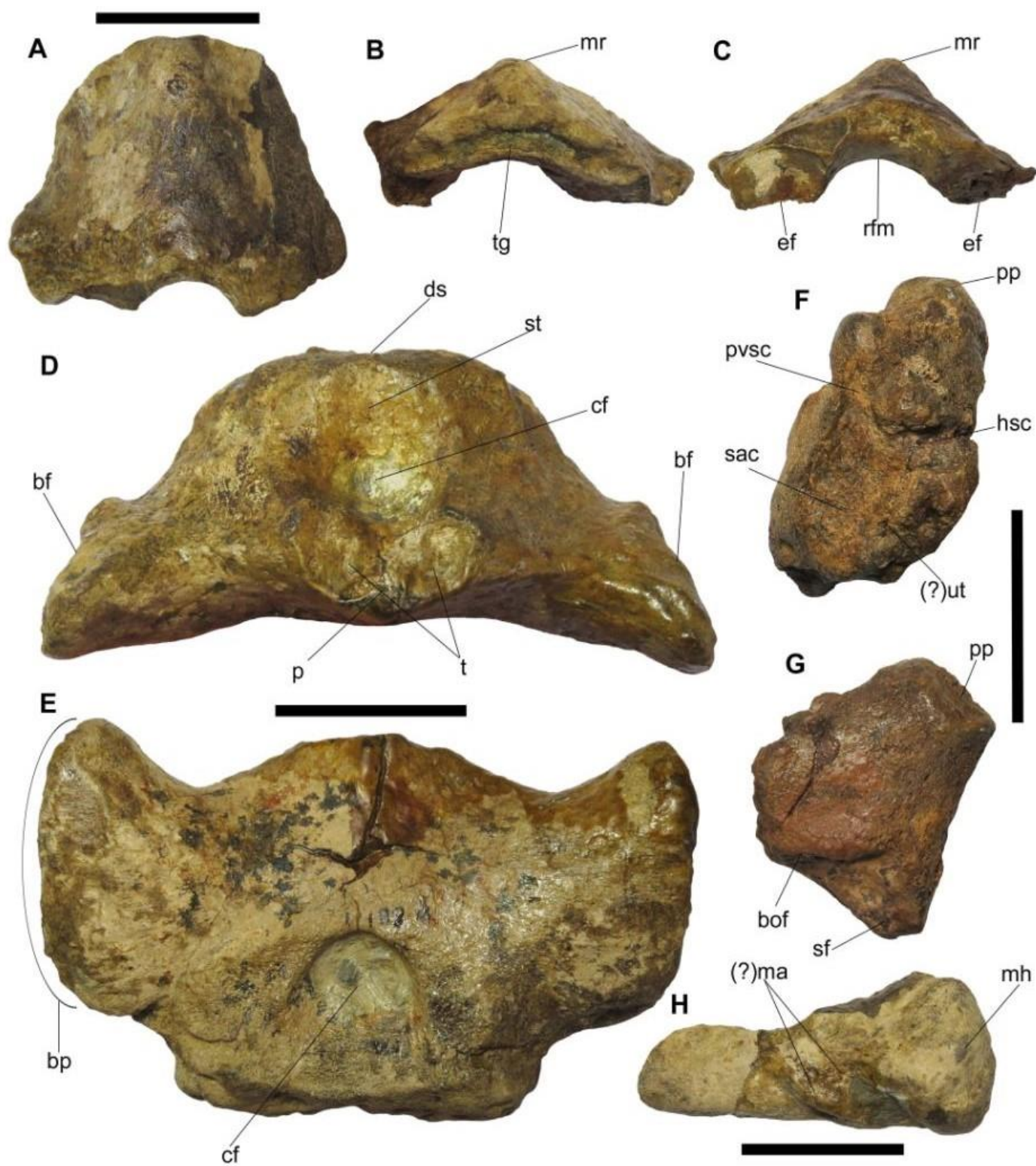
The anterodorsal aspect of the basisphenoid features a pair of robust protuberances separated by a slight midline depression – the sella turcica – that housed the pituitary gland (Figure. 9.6D). Below this is the median opening for the carotid artery, which courses posteroventrally through the bone and exits on its ventral surface as a rounded opening bounded proximally by an arch-like ridge (Figure. 9.6D-E). Ventral to this opening and dorsal to the parasphenoid is a kidney-shaped articulation facet, interpreted as the impressions of paired trabeculae (as in McGowan, 1973, fig. 1) (Figure. 9.6D). Immediately dorsal and posterior to the sella turcica, is a large, bulbous region that has the ossified dorsum sellae (dorsal crest). The posterior surface is a wide, rounded rectangle, indented for reception of the basioccipital.

Opisthotic. Only the left opisthotic could be identified (Figure. 9.6F-G). It is a robust and stout element that is roughly pentagonal in posterior view. Its ventrolateral margin is long and sharp. Ventrally the opisthotic tapers to a point that bears a small facet, which articulates with the stapes. The stapedia facet is large, but the lateral 'foot' (after Fischer et al., 2012) has minor exposure. The ventromedial margin is concave and bears a long, low groove that marks the basioccipital facet (Figure. 9.6G). The dorsolateral margin forms the prominent paroccipital process, the posterior surface of which bears a long, prominent ridge that ascends vertically from the ventral tip of the element, then turns medially. A deep groove, for either the glossopharyngeal or branch of the facial nerve (Kirton, 1983; Marek et al., 2015), separates this ridge from a pronounced protuberance on the dorsal margin of the

opisthotic. The dorsomedial margin is expanded into a rugose, subtriangular depression (apex pointing posterodorsally) surrounded by a raised lip and several small protuberances. Although poorly preserved, the membranous impressions of the posterior vertical semicircular canal, sacculus, the horizontal semicircular canal and possibly utriculus are represented by a somewhat 'V-shaped' impression, best observed in anteromedial aspect (Figure. 9.6F). The impression of the horizontal semicircular canal is damaged at the tip and the impression of the sacculus is wide and round. There are several grooves positioned adjacent to the impressions, which McGowan (1973, fig. 5) referred to as grooves in the margin circumscribing the membranous impression. Computed tomography reveals a great deal of trabecular bone within the opisthotic.

Stapes. Both stapes are preserved, with the left being more complete. The stapes is mediolaterally elongate with a bulbous occipital head and a tapered distal end (Fig. 9.6H). The proximodorsal region of the medial head bears a groove that marks the course of the stapedial artery. In anterior view, the medial head is laterally inclined and there is a shallow groove, which is probably the opisthotic facet. The posterior surface of the stapes bears a series of oblique ridges and grooves. This may have been an area for muscle attachment (McGowan, 1973, fig. 7a) (Figure. 9.6H). There are several small canals within the stapes; however, these are very difficult to trace.

Figure. 9.6. Braincase elements of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*. A-C, incomplete supraoccipital in posterior (A), dorsal (B) and ventral (C) view. D-E, parabasisphenoid with complete basisphenoid and broken parasphenoid in anterior (D) and ventral (E) view. F-G, left opisthotic in anteromedial (F) and ventrolateral (G) view. Note the 'V-shaped' membranous impression in F. H, incomplete left stapes in posterior view. *Abbreviations:* bf, facet for basiptyergoid facet; bof, basioccipital facet; bp, basiptyergoid process; cf, carotid foramen; ds, dorsum sellae; ef, exoccipital facet; hsc, horizontal semicircular canal; (?)ma, muscle attachment; mh, medial head; mr, median ridge; p, base of parasphenoid; pp, paroccipital process; pvsc, posterior vertical semicircular canal; rfm, roof of foramen magnum; sac, sacculus; sf, stapedial facet; st, sella turcica; t, paired trabeculae; tg, trenchant groove; (?)ut, utriculus. Scale bars represent 3 cm.



Anatomical description of the lower jaw

Nearly complete left and right dentaries are present, as are both incomplete splenials, the nearly complete left surangular, and the complete left articular and angular (Figure. 9.4).

Dentary. The dentary makes up over three-quarters the length of the lower jaw. It is elongate, tapering at its anterior and posterior ends (Figures. 9.1, 9.4). The ventral margin is convex while the dorsal margin is concave, and the entire element curves dorsally at its anterior end; the latter is likely the result of taphonomic distortion. As with the upper jaw, the lower teeth have been reset in a continuous groove, which we use as landmarks for our description. In transverse section, the anterior dentary is roughly oval-shaped with a convex lateral surface; a medial shelf forms the floor of the alveolar groove and a dorsal lamina laterally overlaps the dentary teeth. The medial shelf is separated from a longitudinal ridge that parallels the ventral margin of the bone by a shallow groove (lateral wall of the Meckelian canal); this ridge and groove dominate the internal face of the anterior half of the dentary. At the level of the 15th dentary tooth, the medial shelf disappears and the dentary becomes a laterally bowed sheet of bone with a thickened dorsal margin in transverse section.

The anterior tip of the right dentary is damaged and, as a result, the dentaries do not contact each other anteriorly to form the mandibular symphysis (Figures. 9.1, 9.4). As preserved, the dentary and splenial do not contact each other along their entire length but this is due to distortion. The anterior tip of the angular is level with the 17th preserved tooth on the right side; the angular laterally overlaps the ventral margin of the dentary in a very tight scarf joint. In contrast, the suture between the dentary and surangular, which reaches the level of the 22nd preserved dentary tooth, is a loose, horizontal butt joint except at its posterior end where the posterior tip of the dentary laterally overlaps the surangular.

As with the premaxilla, CT scans reveal that each dentary encloses an elongate, branching canal ventral and lateral to the tooth row that extends from the anterior tip of the bone to the 14th (right) and 9th (left) preserved dentary teeth, at which point the canal opens onto the internal surface (Meckelian canal) of the lower jaw ventral to the medial shelf of the dentary (Figure. 9.4C, G-J). Anteriorly, four small canals branch laterally from the main conduit and open onto short, posteriorly elongated grooves on the lateral face of the dentary. A posterior (fifth) canal opens

into a very long groove ventral and parallel to the tooth row that extends over a quarter the length of the dentary.

Splénial. The splénial is composed of a vertical sheet of bone that is medially concave, a slightly thickened dorsal margin that is turned medially, and a thickened, laterally deflected ventral margin. Thus, the element has a mild S-shape and is mediolaterally thin in transverse section anteriorly, becoming more robust with increasingly pronounced curvature posteriorly. The splénial forms the medial wall and part of the floor of the Meckelian canal for the posterior half of the lower jaw. Its contacts with other elements cannot be reliably interpreted as the bones were not in articulation; however, from their preserved ventral margins, it appears the splénial and angular met in a butt joint.

Angular. The angular extends over half the length of the lower jaw (Figures. 9.1, 9.4B). The anterior half of the angular is a long, straight rod while the posterior half is both dorsoventrally and mediolaterally expanded, curving dorsally and medially towards the jaw joint. In transverse section, the anterior half of the angular is diamond-shaped with a dorsomedial surface that contacts the ventral margin of the dentary in a tight scarf joint and a dorsolateral surface that meets the ventral margin of the surangular in a loose butt joint. The ventromedial surface of the anterior angular bears a shallow, longitudinal groove bounded dorsally and ventrally by low ridges that presumably articulated with the splénial. Posteriorly, the angular develops a robust tab or lamina that extends from its dorsomedial surface and medially laps the surangular. However, immediately ventral to the jaw joint, this lamina disappears and is replaced by taller, mediolaterally thin dorsolateral lamina that extensively overlaps the lateral aspect of the posterior surangular. Thus, the contact between the angular and surangular is morphologically simple and loose anteriorly but tighter and more complex posteriorly. In lateral view, the anterior end of the surangular is broken and it appears the angular extends further anteriorly than the surangular (Figure. 9.4B). This is similar to specimen SOMAG 12, a referred specimen of *Protoichthyosaurus prostaxalis* (Lomax et al., 2017).

Surangular. The surangular is a long, curved element forming the lateral aspect of the posterior third of the lower jaw (Figures. 9.1, 9.4B). The anterior half of the

surangular is poorly preserved as it is mediolaterally thin and is loosely joined to the dentary (dorsally) and angular (ventrally) via rounded butt joints. Posterior to the dentary, the dorsal margin of the surangular thickens dramatically to form the peaked coronoid process. A longitudinal lateral ridge, dorsally bounding the fossa surangularis, continues to the end of the surangular and separates the thickened dorsal margin from the thinner ventral lamina that articulates with the angular. The element expands dorsally and medially at its rounded posterior end to laterally cup the articular.

In medial view, the posterior surangular bears a ridge parallel to its ventral margin that articulates with the angular and forms the floor of the adductor fossa. There is another, more robust ridge on the medial surface originating at the coronoid process and widening posteriorly to contact the anterior surface of the articular. The medial face of the surangular between the two ridges is concave and forms the Meckelian groove and lateral wall of the adductor fossa. There is a large foramen clearly visible on the medial aspect ventral to the coronoid process; this foramen passes laterally through the surangular and exits ventral to the ridge on the lateral surface (Figure. 9.4D, K).

Articular. The preserved left articular has a triangular profile in dorsal and ventral views, with the apex posteriorly and medially directed, and a subcircular profile in medial and lateral views. The posterior margin is sharp while the anterior aspect is flat and broad where it contacts the quadrate to form the jaw joint. The medial aspect of the bone is smooth while the lateral aspect is pitted and porous. CT scans reveal several small, short canals that penetrate into the bone from its lateral surface.

Hyoid. Both hyoids are preserved and are large and complete, although some damage is apparent. The hyoid is a curved, rod-like bone (Figure. 9.5J). In dorsal view, the element is slightly bowed posterolaterally and the centre of the element is slightly mediolaterally narrower than either end. The anterior end is slightly flattened, rounded and pitted for reception of cartilage. In anterior view, the probable left hyoid is oval-shaped, with a defined rim.

Dentition. The teeth were implanted in an aulacodont fashion in continuous alveolar grooves as is typical in euichthyosaurs. As previously mentioned, the teeth were not

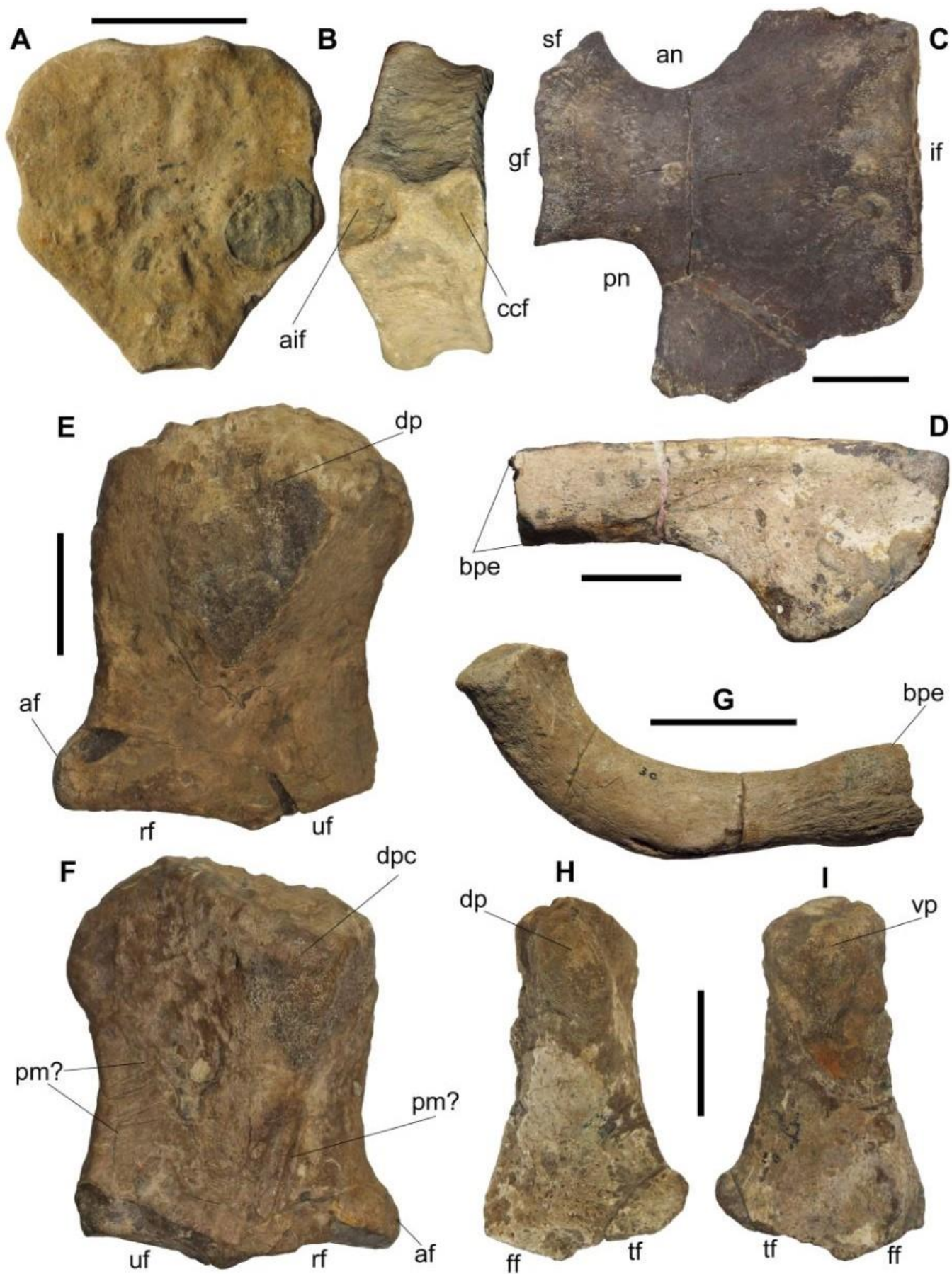
preserved in situ and were added to the grooves during reconstruction of the skull both in 1955 and in 2015; thus, they are not in their original positions. Furthermore, the dental groove is too poorly preserved to determine the exact number of teeth that would have originally been present. There are additional fragmentary and complete teeth associated with the specimen.

The teeth are lingually curved, large cones with short, robust crowns with fine striations and smooth apices (Figures. 9.1B-C, 9.5N). In complete teeth, the crown is much narrower than the root. The roots are large with prominent longitudinal grooves that extend to the base of the crown and continue as longitudinal striations on the crown (Figure. 9.5N). This morphology is found in all specimens of *Protoichthyosaurus* that have well-preserved teeth (Lomax et al., 2017; Lomax and Massare, 2018). Tooth morphology for each tooth is similar, with crowns ranging from 0.87 cm to 1.75 cm in height. As no teeth were preserved in situ, it is impossible to differentiate between the premaxillary, maxillary and dentary teeth. A resorption pit is present on the lingual surface in many teeth (e.g. Figure. 9.5N). CT scans reveal hollow pulp cavities within the teeth that open at the tooth bases and extend nearly the entire height of the tooth.

Anatomy of the postcranial skeleton.

Portions of the vertebral column, ribs, gastralia, forefin, pectoral girdle, pelvic girdle and the hindfin are preserved (Figure. 9.7). The forefin and hindfin phalangeal elements are entirely free of matrix and are not in their original context, so it is impossible to say whether elements are from the left or right fin.

Axial skeleton. A total of 37 vertebral centra are present, all of which are disarticulated. Most are poorly preserved but their positions in the column can be identified from their morphology. One centrum is unusual in possessing the following features: triangular in anterior and posterior views; being marginally anteroposteriorly longer than the preserved cervicals; diapophyses and parapophyses being high and positioned at the anterior end of the centrum in lateral view; two separate semi-circular facets for articulation with intercentra in ventral view (Figure. 9.7A-B). This morphology is indicative of an atlas-axis complex, but the centrum displays no fusion. This is unusual given that, with the possible exception of immature individuals



and some early Triassic taxa, the atlas-axis is always fused in ichthyosaurs (McGowan and Motani, 2003; VanBuren and Evans, 2017). The presence of two facets on the ventral surface might suggest that this element is the atlas, with the diagonally-oriented anterior facet being for the atlantal intercentrum and the posterior facet for the axial intercentrum (Figure. 9.7B). Alternatively, and more likely, this is the axis, with the anterior facet being for the axial intercentrum and the posterior facet being for the intercentrum of the third cervical vertebra (McGowan and Motani, 2003, fig. 5C). Interestingly, the anterior surface of the axis centrum is not well-defined, nor smooth and lacks the convexity typical of ichthyosaur centra (Figure. 9.7A). This might be pathological or it could be the surface that was fused with the atlas vertebra that is not usually preserved (or exposed). A second centrum features similar morphology but is slightly anteroposteriorly shorter and has only one small, anterior facet on the ventral surface, which articulates with the aforementioned vertebra. It is likely that this is the centrum of the third cervical vertebra. The remaining vertebral centra include 19 dorsals, including elements from the anterior, middle and posterior portions of the series as identified by their shape and position of the diapophyses

Figure. 9.7. Elements of the postcranial skeleton of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*. A-B, probable ‘unfused’ (see text for details) axis vertebra in anterior (A) and ventral (B) view. Note the unusual, almost rugose anterior surface. The dark, circular element to the right is a poorly preserved bivalve mollusc. C, left coracoid in dorsal view. D, incomplete left scapula in lateral view. E-F, left humerus in dorsal (E) and ventral (F) view. Note that the dorsal process (trochanter dorsalis) is damaged, as is the facet for the ulna. G, complete ilium in either lateral or medial view. Note that the posterior end (to the right) is bulbous, relative to the shaft. H-I, damaged (?) right femur in dorsal (H) and ventral (view). *Abbreviations:* af, anterior facet; aif, facet for the axial intercentrum; an, anterior notch; bpe, broken posterior end; bpe, bulbous posterior end; ccf, facet for the cervical centrum; dp, dorsal process; dpc, deltopectoral crest; ff, fibular facet; gf, glenoid facet; if, intercoracoid facet; pm?, predation marks; pn, posterior notch; rf, radial facet; sf, scapular facet; tf, tibial facet; uf, ulnar facet; vp, ventral process. Scale bars represent 3 cm.

and parapophyses, and 16 caudal vertebra, again including elements from the anterior, middle and posterior portions of the series as identified by their shape and the presence of a single rib facet.

One isolated and damaged neural spine, which is mediolaterally thin at its distal end, is preserved.

Numerous incomplete ribs and rib fragments are preserved. The cross-sectional geometry of the ribs varies, with some being rounded whereas others have a dumbbell-shaped cross section. A possible gastralia fragment is present, which is roughened at its anterior end where it presumably met its counterpart at the midline.

Pectoral girdle. The left coracoid is practically complete (Figure. 9.7C). It is a robust element that is slightly anteroposteriorly longer than mediolaterally wide (Table. 9.1). It has prominent and well-developed anterior and posterior notches. The anterior notch is wider than the posterior notch, resulting in the posterior end of the coracoid being mediolaterally wider than the anterior end. A prominent rim outlines the glenoid and scapular facets, the former being noticeably longer than the latter. In medial view, the intercoracoid facet is dorsoventrally thickened and bulbous at the anterior end but narrows posteriorly.

Only the left scapula is preserved and is missing its posterior end (Figure. 9.7D). The anterodorsal end is marked by a right angle, which extends to the ventral edge. This proximal end is twice as tall dorsoventrally as the mid shaft and is widely flared but without a prominent acromion process.

Forefin. As mentioned previously, none of the phalangeal elements were found in articulation. It is impossible to determine whether the elements are from the left or right fin or determine the morphology of the forefin in this specimen. The radius and ulna are missing and the preserved elements are polygonal. Of note, the forefin was reconstructed for display in 1955 and 2015 with the morphology typical of *Ichthyosaurus* (Motani, 1999). This was prior to the resurrection of *Protoichthyosaurus* (Lomax et al., 2017).

A single, nearly complete left humerus is robust, elongate, and slightly wider distally than proximally without a prominent constriction in the mid shaft (Fig. 9.7E-F). It is the largest humerus of *Protoichthyosaurus* described thus far (Table 9.1). The proximal end is large, bulky and the surface is rugose and roughened. In ventral

view, the deltopectoral crest is offset anteriorly and is large but does not extend far down the shaft. The base of the anterior end is slightly flared due to the presence of an anterior facet. The dorsal process is broken but appeared centrally located. There are several possible predation marks preserved on the ventral surface of the humerus (Figure. 9.7F). The facets for the radius and ulna are also damaged.

Pelvic girdle. A single ilium is well-preserved (Figure. 9.7G). It is a relatively thick and elongate element that is J-shaped in lateral and medial views, resembling the ilium of *Ichthyosaurus somersetensis* in being more oblong than rib-like (Lomax and Massare, 2017). The presumed posterior end is slightly bulbous, relative to the shaft, somewhat similar to the ilium of *Protoichthyosaurus applebyi* (Lomax et al., 2017, UNM.G.2017.1). The presumed anterior end is highly rugose. A possible ischium might also be preserved, but it is heavily damaged.

Hindfin. Like the forefin, some phalanges of the hindfin are preserved, which are largely polygonal, but none were found in articulation and all have lost their original context. Regardless, the single, incomplete femur provides information (Figure. 9.7H-I). As the proximal end is poorly preserved, it is difficult to identify the element as being from the left or right, but it is most likely a right femur, based on the following comments. It has a very slender shaft, narrow proximal end, and a flared distal end. Both the dorsal and ventral processes are damaged and worn, but the supposed dorsal process seems to be a prominent, narrow ridge and the supposed ventral process is large. There is a slight flare at the anterior end, but the posterior end is only slightly expanded, and is almost a right angle. The tibial facet is larger than the fibular facet.

Historically modelled regions of the skull of BMT 1955.G35.1

CT-scanning the skull of BMT 1955.G35.1 aided substantially in our anatomical description. Additionally, modelled areas of the skull can be clearly differentiated from fossil bone in scans by the differing densities of these materials (Figure. 9.8). Fossil bone is the densest material (appearing as bright areas within CT scans) followed by regions of the braincase that were 3D printed in gypsum (see Material and Methods). Areas of the skull modelled during its initial reassembly post-May 1955 are the least dense, as they are either composed of wood or a traditional mix of

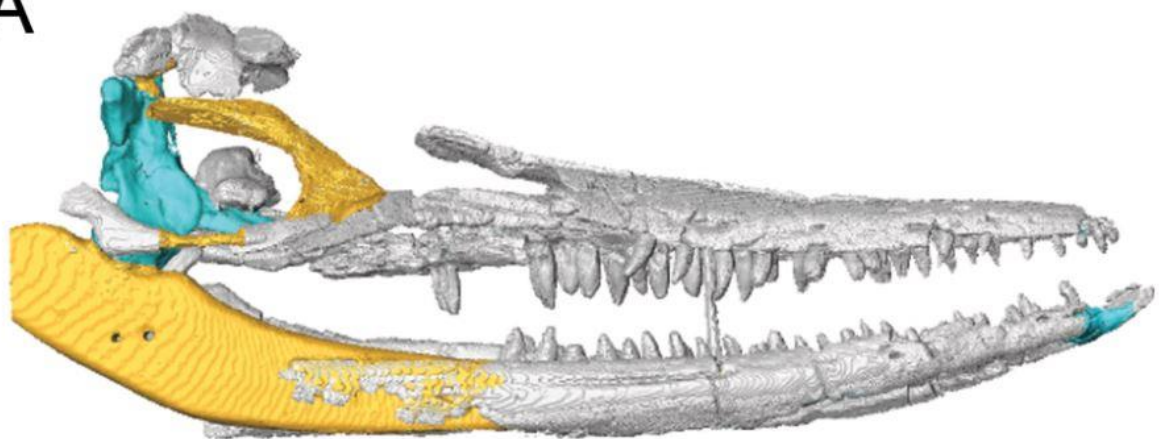
alvar, jute and kaolin (known as AJK dough). Some modelled areas – such as the posterior third of the right lower jaw, central portion of the right jugal, and “symphysis” between left and right dentaries – are immediately apparent. Other areas, including the right lacrimal and prefrontal, and various patches in the lower jaws, are less obvious. The skilfully modelled right margin of the supraoccipital is only evident in CT scans, as are portions of the braincase that were 3D printed and added to the newly reassembled skull. Thus, our work demonstrates the utility of applying CT scanning to older, potentially modified museum specimens to better understand both anatomy and specimen history.

3D digital reconstruction of the skull of BMT 1955.G35.1

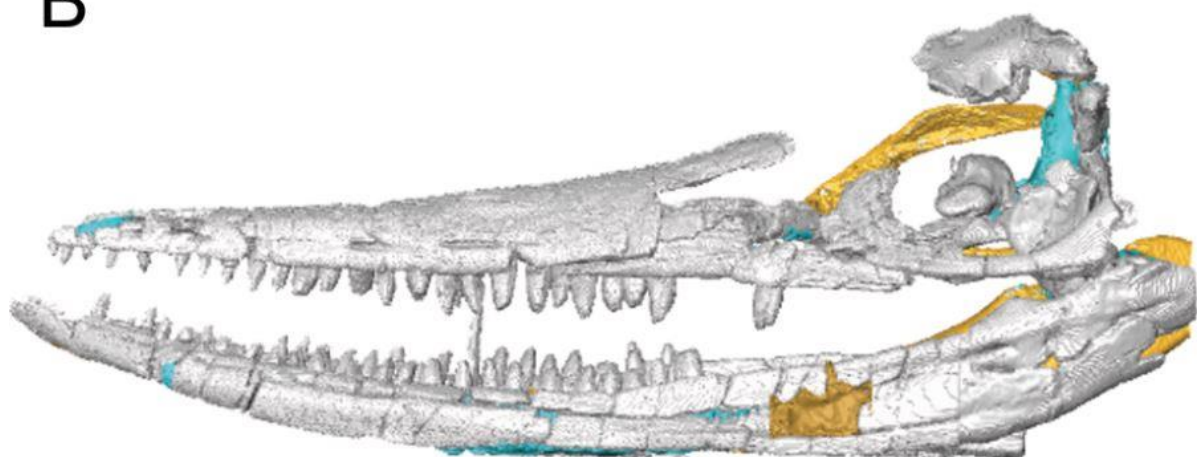
Limits to the data set used in the 3D digital reconstruction of the skull must be noted. Numerous bones are absent, fragmentary or were too delicate to scan, and some aspects of the 3D reconstruction are uncertain. For example, the width of the reconstructed skull is constrained by the articulation of the premaxillae (anteriorly) and contacts between the basisphenoid, pterygoids and quadrate (posteriorly). Bones of the skull roof and palate that determine width in the middle part of the skull are missing. Furthermore, the placement of the preserved bones of the posterior skull roof is an estimate based on 1) the predicted height of the missing exoccipitals relative to other braincase elements, and 2) the assumption of a smooth slope between the nasals and parietals, as observed in other large ichthyosaurs, including examples of the genus *Protoichthyosaurus* (Lomax et al., 2017; Lomax and Massare, 2018). We did not attempt to retrodeform elements that experienced plastic deformation, specifically the lower jaws. The exaggerated dorsal and lateral curvature of these elements prevents complete closure of the upper and lower jaws in our model. Similarly, the premaxilla and nasals could not be completely re-articulated due to their deformed nature. Thus, this 3D digital reconstruction is our

Figure 9.8. Surface models (generated from CT scan data) of the reassembled skull of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*, highlighting differences between fossil bone (grey), regions reconstructed during original reassembly in the 1950s (yellow), and regions reconstructed in the course of the current work (blue). Right (A) and left (B) lateral, and dorsal (C) and ventral (D) views of the upper and lower jaws.

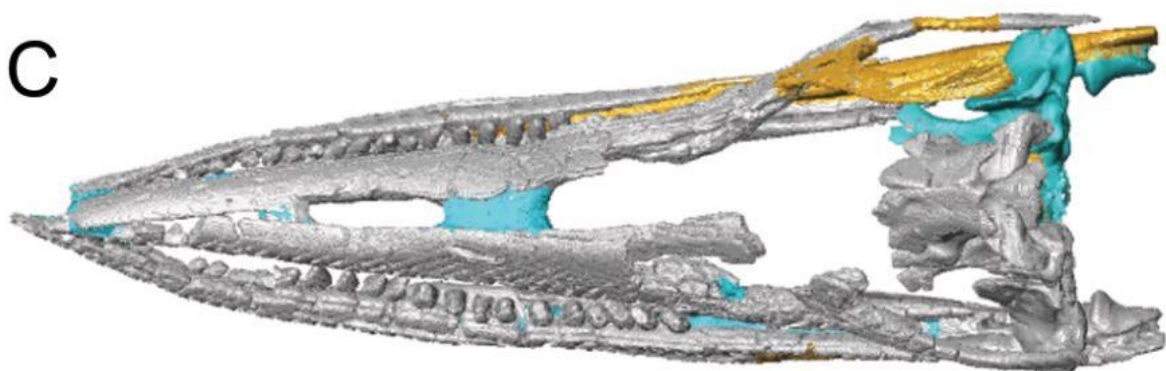
A



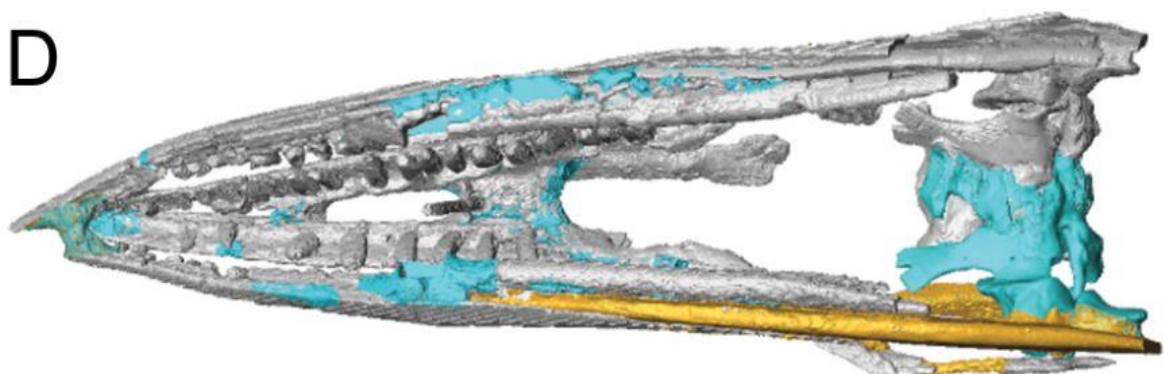
B



C



D



current best hypothesis of the original skull shape of BMT 1955.G35.1 based on preservation and personal interpretation. With these limitations in mind, the digital reconstruction nonetheless yields useful new information on overall skull shape in this taxon (Figure. 9.9; Appendix S3). This skull shape is typical of *Protoichthyosaurus prostaxalis* in lateral view (Figure. 9.9A), in having a low skull that is slightly inclined from the nasals to the posterior end of the skull and in possessing a relatively long and slender rostrum especially when compared with Lomax et al., (2017, figs. 2C, 4A-B) and Lomax and Massare (2018, figs. 2–3).

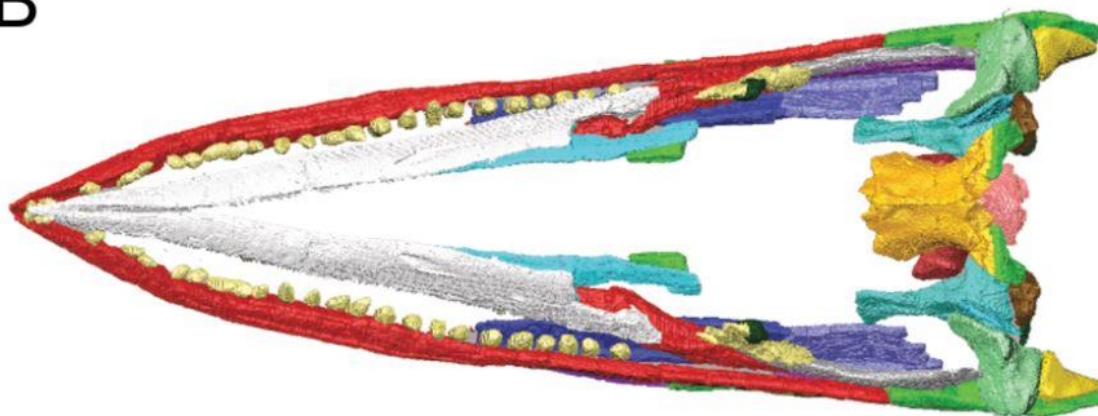
Due to the limitations of the fragile nature of the specimen some of the bones could not be articulated in life position in the physical model and there are differences between the digital and physical (Figures. 9.1, 9.2; Appendix S1) models. Of note, the rear of the skull is mediolaterally wider and dorsoventrally shorter in the digital reconstruction than in the physical model. This is due to placement of the basisphenoid dorsal and anterior to its true articulation with the pterygoids in the physical model, as well as midline contact between the pterygoids; the pterygoids are separated by the basisphenoid in ichthyosaurs (McGowan, 1973, Kirton, 1983; Kear, 2005). The stapes is dorsally displaced in the physical reassembly; in other ichthyosaurs, the stapes contacts the quadrate dorsal to its expanded base (Andrews, 1910; Kirton, 1983; McGowan and Motani, 2003). Lastly, the jugal extends posterior to the quadrate in the physical model, leaving no space for the posterior facial bones and resulting in the upper jaw being anteroposteriorly shorter than the lower jaw. Shifting premaxilla and contacting bones so that the anterior tips of the premaxillae and dentaries are level results in a gap between the jugal and quadrate large enough to accommodate the missing postorbital and quadratojugal. These

Figure. 9.9. Surface models (generated from CT scan data) of the skull of BMT 1955.G35.1, *Protoichthyosaurus prostaxalis*, after the removal of minor damage and duplication/mirroring of asymmetrically preserved elements, and digital articulation of individual bones to produce a more accurate digital 3D reconstruction. Displacement of the lower jaw and premaxillae and nasals are the result of deformation (see text). Left lateral (A), dorsal (B), ventral (C), anterior (D), and posterior (E) views of the upper and lower jaws. Individual bones labelled using the same colours as Figures 9.2–9.4.

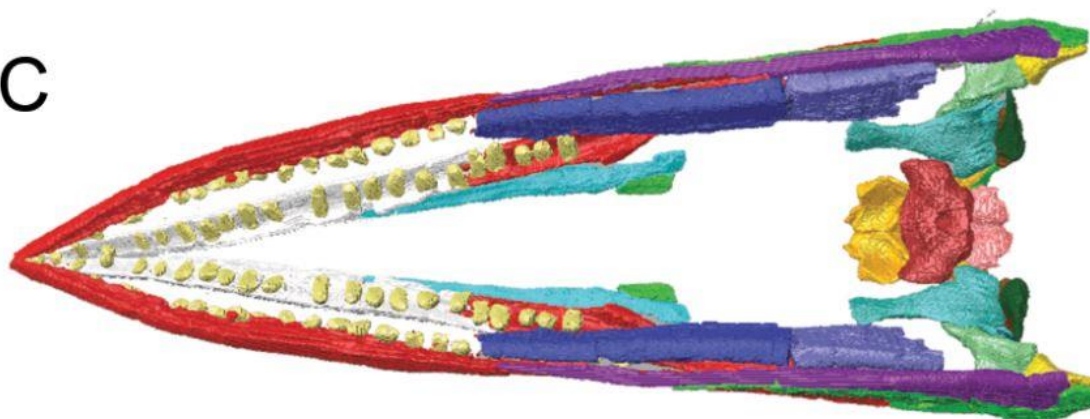
A



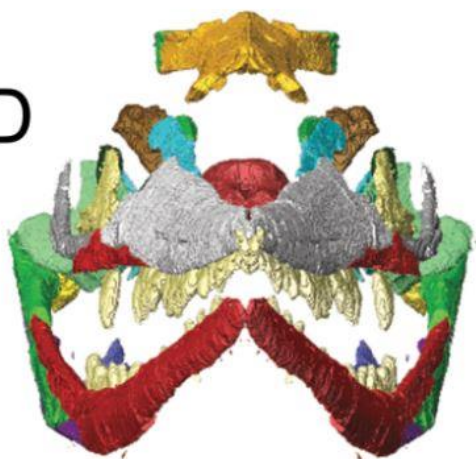
B



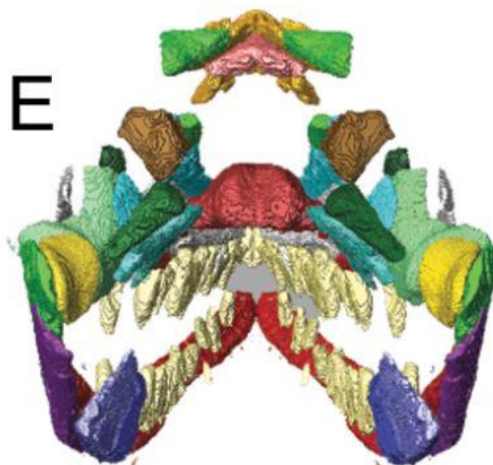
C



D



E



differences highlight another advantage of applying 3D imaging and visualization methods to large specimens. Large fossil bones are fragile and heavy, and there are practical limitations to how they can be physically manipulated and mounted when reassembling a skull or skeleton; digital manipulation of fossil bones reduces risk to the specimen and errors can be easily corrected.

Discussion

BMT 1955.G35.1 has never formally been described. The original museum record shows that it was initially identified as *Ichthyosaurus communis*, a species to which many ichthyosaur specimens were historically referred as it is among the most common ichthyosaurs in the UK (but see Massare and Lomax, 2017). In notes held at the Warwickshire Geological Records Service (pers. comm. J. Radley, 2015), a report by Dr Brian Seddon, stated: “It is believed that this animal is a new species lying somewhere between *communis* [*I. communis*] and *breviceps* [*I. breviceps*]”. A 1957 letter from Seddon states that it was ichthyosaur expert Robert Appleby who expressed the opinion that the specimen possibly represented a new species and requested photos be taken. More recently, Larkin et al. (2016) tentatively identified the specimen as *Ichthyosaurus*, based on available information at the time. Since then, a revised diagnosis of *Ichthyosaurus* has been published (Massare and Lomax, 2017), along with a redescription of *Protoichthyosaurus* (Lomax et al., 2017), a genus first described by Appleby (1979), which was later synonymized with *Ichthyosaurus* (Maisch and Hungerbühler, 1997).

Lomax et al. (2017) provided an emended diagnosis of *Protoichthyosaurus*, which included several autapomorphies of the forefin. Lomax and Massare (2018) provided additional information on the genus and species, including a revised diagnosis, and showed that the genus can also be distinguished from *Ichthyosaurus* by a combination of skull characters. They further noted that characters used to distinguish individual species of *Protoichthyosaurus* from individual species of *Ichthyosaurus* are more easily evaluated. The forefin of BMT 1955.G35.1 is entirely reconstructed and we have been unable to locate photographs or illustrations of how the freshly excavated forefin appeared. Thus, the forefin cannot be used to identify the specimen.

BMT 1955.G35.1 does possess features shared by both *Ichthyosaurus* and *Protoichthyosaurus*, including: a coracoid with both prominent anterior and posterior notches; scapula with a narrow shaft that is expanded at the anterior end, but without a prominent acromion process; a humerus with nearly equal width distally and proximally, with only a slight constriction in the shaft; and femur longer than wide, with distal end wider than proximal end. BMT 1955.G35.1 can, however, be assigned to *Protoichthyosaurus* on the basis of several characters. Some of these characters are also found in some species of *Ichthyosaurus* but not in the same combination (Lomax and Massare, 2018). They include: the prefrontal anterior process separates the lacrimal dorsal process from the orbit margin; strongly asymmetric maxilla with long, slender anterior process; teeth that have large roots with deep, prominent grooves that extend to the base of the crown and are continuous with the ornamentation of the crown itself; and a long, slender rostrum. In addition, the slightly diverging anterior end of the parietals in BMT 1955.G35.1, which leaves an opening at the anterior end, is indicative of the posterior opening for the pineal foramen between the parietals and frontals. Because the frontals are not preserved, it is not possible to confirm if this is correct, but it seems plausible as this is the position of the pineal in *Protoichthyosaurus* (Lomax and Massare, 2018). In *Ichthyosaurus* the pineal is between the frontals and parietals (Massare and Lomax, 2017).

Protoichthyosaurus prostaxalis and *P. applebyi* differ in skull and humeral morphologies (Lomax et al, 2017). A third questionable species, *P. fortimanus*, known only from an isolated forefin missing the humerus, displays only characters of the genus (see discussion in Lomax and Massare, 2018). The left humerus of BMT 1955.G35.1 is damaged on its dorsal surface. This restricts its usefulness in identification because the two species can be differentiated by the dorsal process, which is missing in this specimen. The humerus of BMT 1955.G35.1 is robust, more similar to *P. prostaxalis* than *P. applebyi*, but this may be due to the large size of BMT 1955.G35.1 (see Lomax et al, 2017, fig. 5). However, considering the size, Lomax and Massare (2018) recently described the second known specimen of *P. applebyi*, an isolated skull (NHMUK R1164), which is comparable in size with some smaller specimens of *P. prostaxalis*. They identified NHMUK R1164 as probably an adult and showed that the differences among the two species are not ontogenetic. BMT 1955.G35.1 is more than twice the size of NHMUK R1164 and is probably an

adult *P. prostaxalis*. Unfortunately, BMT 1955.G35.1 is missing some features of the skull that distinguish the two species. However, the maxilla of BMT 1955.G35.1 is large, triangular, dorsoventrally high, and possesses a long and narrow anterior process that is longer than the posterior process. In *P. applebyi*, the maxilla is dorsoventrally low. Furthermore, although the jugal is incomplete and the postorbital is missing, they were complete and part of the original mount (Figure. 9.1A). The morphology of the postorbital, although based on the interpretation of a photograph, in being dorsoventrally short but anteroposteriorly wide almost rectangular, and making up half of the posterior orbit margin are characters found in *P. prostaxalis* (Lomax et al, 2017; Lomax and Massare, 2018). In *P. applebyi*, the postorbital is dorsoventrally long, anteroposteriorly narrow, and makes up much more than half of the orbit posterior margin (Lomax and Massare, 2018). Consequently, even accounting for a misinterpretation of the postorbital morphology, its shape does not match what is found in *P. applebyi*. Thus, based on the morphology and extent of the maxilla and postorbital, we assign the studied specimen to *P. prostaxalis*. The difference in size between the studied specimen and the presumed adult specimen of *P. applebyi* (NHMUK R1164) is another indicator that the studied specimen belongs to *P. prostaxalis*.

It should also be noted that the maxilla of BMT 1955.G35.1, although dorsoventrally high, does not appear as tall as in some specimens of *P. prostaxalis* (e.g. BRLSI 3555, BU 5323), but this is due to damage to the dorsal lamina of the maxilla on both sides. It may also appear shorter due to the length of the studied skull, which is almost twice that of the largest reported specimen of *P. prostaxalis* (Lomax et al., 2017; Lomax and Massare, 2018), with an estimated total skull length of at least 80 cm and estimated mandible length of 87 cm. This is also much larger than the sister taxon *Ichthyosaurus*, with maximum skull and mandible lengths of 57.5 cm and 67 cm respectively (Lomax and Sachs, 2017). Considering that the skull length is approximately 20-25% of the total body length, based on a paratype specimen of *P. prostaxalis* (BRLSI M3555), we estimate BMT 1955.G35.1 would have been between 3.2 and 4 m in length. This is the largest example of the genus known, the previous total length estimate being 2.5 m (Lomax et al., 2017). The largest unequivocal example of *Ichthyosaurus* has a maximum total body length estimate of 3.3 m (Lomax and Sachs, 2017), thus the maximum length estimate of

the specimen described herein is also larger than all known examples of *Ichthyosaurus*.

Conclusions

In this study, we describe a large, partial ichthyosaur skeleton from the Early Jurassic of Warwickshire, England. In addition to examining the specimen, we carried out CT scanning of individual skull bones as well as the entire, reassembled skull, one of the first times the skull of a large marine reptile has been successfully CT-scanned, visualized and reconstructed in 3D (see McGowan, 1989; Foffa et al., 2014a). CT scanning contributed greatly to our anatomical description by revealing features not visible on original fossil material such as: branching, longitudinal vascular canals within the premaxilla and dentary; short canals penetrating the nasal, lacrimal, stapes, and articular; trabecular bone within the opisthotic; canals in the basisphenoid and supraoccipital; the presence of the quadrate process of the pterygoid; and the sutural morphology. We also demonstrate the utility of applying medical imaging techniques to historic specimens to differentiate between original fossil material and reconstructed regions, as well as the advantage of using digital visualization to accurately reconstruct large fossil specimens in 3D.

The detailed description of the three-dimensional skull and braincase presented herein also provides information that can be used in phylogenetic studies. Although incomplete, the skull and braincase preserve various elements that have not previously been reported or described in any specimen of *Protoichthyosaurus* and therefore it provides more information about this taxon so that its phylogenetic position can be explored in more detail. Furthermore, our study has found additional characters that may lend further support for the distinction of *Protoichthyosaurus* from its sister taxon *Ichthyosaurus*, such as the morphology of the pterygoid and anteroventral surface of the parietal, which differ from that described for *Ichthyosaurus* (McGowan, 1973). However, considering that only a couple of specimens preserve these elements, it is possible that the differences may be the result of individual variation; more three-dimensional specimens of both taxa are needed to test and clarify these findings.

Based on a unique combination of characters, we identify the specimen as *Protoichthyosaurus prostaxalis*. With a skull nearly twice as long as any previously

described specimen of *P. prostaxalis*, this specimen greatly increases the known size range of this genus. Compared with known, contemporaneous Sinemurian ichthyosaurs, the estimated size suggests it was larger than all species of *Ichthyosaurus* (Lomax and Sachs, 2017), and comparable with the largest known specimens of *Leptonectes tenuirostris* (McGowan, 1996a), but smaller than *Leptonectes solei* (McGowan, 1993), *Excalibosaurus costini* (McGowan, 2003) and *Temnodontosaurus platyodon* (McGowan, 1996b). Thus, our study also provides new information on ichthyosaur diversity and potential ecology in the Early Jurassic of the UK.

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Data and Materials

Original CT data of the full skull is available at MorphoSource, here:

https://www.morphosource.org/Detail/MediaDetail/Show/media_id/29156. Raw microCT data of individual braincase elements is not available as these data were lost; however, STLs and 3D PDFs of these elements are available (see here: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/33743) and all elements that were individually scanned were also scanned with the full skull.

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Supporting information

Additional Supporting Information can be found in the online version of this article:
<http://dx.doi.org/10.7717/peerj.6112#supplemental-information>.

Original CT data of the full skull is available at MorphoSource, here: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/29156. Raw microCT data of individual braincase elements is not available as these data were lost; however, STLs and 3D PDFs of these elements are available (see here: https://www.morphosource.org/Detail/MediaDetail/Show/media_id/33743) and all elements that were individually scanned were also scanned with the full skull.

Appendix S1. 3D PDF of segmented CT scans of the reassembled skull of *Protoichthyosaurus prostaxalis* (BMT 1955.G35.1). Download the PDF file and click once on the skull to activate. Left-click to rotate the model; right-click to zoom in or out; and hold both buttons to pan. Check or uncheck boxes in the model tree in the upper left corner of the viewer to display or hide individual parts.

Appendix S2. Transformation matrices for the 3D digital reconstruction of *Protoichthyosaurus prostaxalis* (BMT 1955.G35.1) from original CT data.

Appendix S3. 3D PDF of the reconstructed skull of *Protoichthyosaurus prostaxalis* (BMT 1955.G35.1).

Chapter 10: Discussion

10.1 Summary of preceding chapters and evaluation of findings

The preceding chapters (3-9) have provided a thorough assessment of *Ichthyosaurus*, which has led to the most up to date definition and diagnosis of that genus. This study is based on the examination of many *Ichthyosaurus* specimens held in various collections in the UK, Europe and North America. At large, this demonstrates the wider significance of contacting and visiting institutions that are not necessarily on the radar for researchers, but which may have specimens of scientific importance. Examining many specimens allows for a much greater understanding of issues surrounding taxonomy, morphology, ontogeny, variation etc., which cannot appropriately be assessed in a smaller sample size.

10.1.1 Variation of *Ichthyosaurus communis*: one species or more?

Having examined numerous well-preserved specimens of *Ichthyosaurus*, including those specifically assigned to the species by McGowan (1974b) and those identified as *I. communis* in museum collections, this research identified various differences in skull and humerus morphologies, which determined that *I. communis* represented at least three species, as seen in Chapter 3. Therefore two new species *Ichthyosaurus larkini* and *I. somersetensis* were formally described. Of note, *I. somersetensis* is as common as *I. communis* (see below, 10.1.2), although the former is mostly from Somerset whereas the latter is mostly from Dorset.

As there are multiple specimens of the two new species that vary in size, it demonstrates that their unique characters are not simply the result of an ontogenetic stage or intraspecific variation. The two new species were included in a specimen-level phylogenetic analysis that distinguished them from all other species of the genus. Moreover, this study shows that *I. communis* is rare from Somerset, which is the opposite of what was found previously (McGowan, 1974b; McGowan and Motani, 2003).

10.1.2 Synonymy of *Ichthyosaurus communis* and *I. intermedius*

Based upon the findings presented in Chapter 3, the description of two new species meant that there was now much less variation in *I. communis*, therefore an examination of that species was presented in Chapter 4. The first part of this work

was to evaluate *Ichthyosaurus intermedius* and its purported synonymy with *I. communis*. The species were initially synonymised by McGowan (1974b), but Appleby (1979), Maisch (1997) and Maisch and Matzke (2000) disagreed with this assessment. Most recently, McGowan and Motani (2003) considered *I. intermedius* a synonym of *I. communis*.

This work finds the synonymy to be justified because all of the original characters proposed to distinguish *I. intermedius* from *I. communis* are either found in the neotype of *I. communis* (and other specimens) or are of uncertain taxonomic utility, i.e. characters are infrequently preserved or vary considerably among specimens of the same species. This provided the basis for a revised diagnosis of *I. communis* that provides a unique combination of well-defined characters (Chapter 4).

10.1.3 The largest *Ichthyosaurus*: size implications for the genus and species

The discovery of an undescribed specimen of *Ichthyosaurus* held in the collections of the Lower Saxony State Museum in Hannover (NLMH), Germany, provided the basis for a reassessment of the size range of the genus, as described in Chapter 5.

Prior to this study, the largest size estimate of the genus was just over 3 metres, based on a regression analysis of a partial forefin described by Massare et al. (2015, 2017a). *I. communis* was previously considered the largest species of the genus (2.5 m: McGowan, 1974b; McGowan and Motani, 2003). This, however, was based on large specimens formally assigned to that species that are herein assigned to the two new species (*I. larkini* and *I. somersetensis*) described in Chapter 3. *I. communis* as discussed in that chapter is actually a small to medium-sized species with a possible maximum size of 2 m. Based upon the identification of unique skull and humerus morphologies, the NLMH specimen was identified as an example of *I. somersetensis*, one of the new species identified in Chapter 3. It has the largest skull and jaw length of any known *Ichthyosaurus* specimen. However, the tail of this individual did not belong with the rest of the specimen. Therefore, based on comparison with other large specimens of *I. somersetensis*, the total length of this new specimen was estimated at 3.3 metres. Thus, it is the largest example of *Ichthyosaurus* and shows that *I. somersetensis* is the largest species of the genus. Additionally, although not the primary focus of this study, this specimen is one of only

a few gravid ichthyosaurs from the UK (Boyd and Lomax, 2018), which further highlights the significance of the specimen.

10.1.4 A neonate *Ichthyosaurus communis*

There are a number of small bodied (<1 metre) *Ichthyosaurus* specimens (approx. 30) that might be deemed juveniles, neonates or ejected embryos, but only a couple of these specimens have been assigned to a species, and none of them to *I. communis*, until now (Chapter 6).

In this study, a previously undescribed, very small specimen of *Ichthyosaurus* (< 60 cm) in the collections of the Lapworth Museum, Birmingham, was examined. Based upon the new diagnosis of *I. communis* (Chapter 4), and specifically characters of the skull, this specimen could be assigned to *I. communis* with a high degree of confidence; the first unequivocal neonate specimen of this species. This shows that the unique character combinations defined for *I. communis* can be applied to smaller specimens of the genus that otherwise would have remained identified as *Ichthyosaurus* sp. This has potentially important bearings on future studies of ichthyosaur ontogeny because it might demonstrate that skull characters of this species, and perhaps other members of the genus, do not change with ontogeny. Thus, this research can be expanded upon further (see 11.2 below).

10.1.5 Testing the taxonomic usefulness of hindfins in *Ichthyosaurus*

Now that species of *Ichthyosaurus* can be distinguished from each other in skull and humerus morphologies, this provided the opportunity to evaluate the taxonomic usefulness of the hindfin (Chapter 7). The hindfin is often overlooked in species diagnoses and phylogenetic studies. Therefore, considering that *Ichthyosaurus* specimens are plentiful, it presented an ideal opportunity to examine variation.

A total of 99 *Ichthyosaurus* hind fins provided morphological information for this study. Two distinct morphotypes were identified, but variations within these morphotypes were found. With a small sample size, these variations could be mistaken for distinct, unique differences among species (Chapter 3). Gaps in hindfin variation are larger when fewer specimens are available. In reality, with a large sample size, the gaps in the supposedly 'unique' variations are filled in, showing that differences are simply the result of a continuum of individual variation and a lack of the full picture. It is thus easier to identify a 'new species' on the basis of a few

specimens than with many specimens. Therefore, the decision to name a new species on the basis of fragmentary or limited material should be considered very carefully. In isolation, a single hindfin could not be used to distinguish among species of *Ichthyosaurus*, but a particular variation was more common in certain species.

10.1.6 Are *Ichthyosaurus* and *Protoichthyosaurus* synonymous?

A re-examination of the Early Jurassic taxon, *Protoichthyosaurus* Appleby, 1979, was the focus of Chapter 8. This genus was synonymised with *Ichthyosaurus* by Maisch and Hungerbühler (1997) and dismissed by all later workers as simply representing variation in *Ichthyosaurus communis*. This work finds the synonymy to be unjustifiable.

The forefin of *Protoichthyosaurus*, in particular the morphology of the mesopodium, is unique among ichthyosaurs. In fact, even isolated forefins of this genus can be identified as *Protoichthyosaurus* with a high degree of confidence. More than 20 additional *Protoichthyosaurus* specimens were located. Only one of the two species that Appleby described is considered valid, the type species, *Protoichthyosaurus prostaxalis*. His second species, *P. prosostealis*, is synonymous with *Ichthyosaurus*, but this specimen does not have any diagnostic characters of any *Ichthyosaurus* species or possess features that warrant the distinction of a separate species. However, this work also recognises a new species, *P. applebyi*, which can be distinguished based on skull and humerus morphologies.

Protoichthyosaurus was also added to a phylogenetic analysis for the first time. Both *P. prostaxalis* and *P. applebyi* were added to the matrix of Fischer et al. (2013), and *Protoichthyosaurus* was found to be the sister taxon to *Ichthyosaurus*, in the family Ichthyosauridae. This study also recoded *I. communis* based on chapters 3 and 4. The resurrection of this genus means that there are two Lower Jurassic ichthyosaurs with wide forefins with at least five digits and anterior digital bifurcations. This body of work pertains to the revision of *Ichthyosaurus* because it helps to further reduce the variation in the genus.

10.1.7 A three-dimensional skull and partial skeleton of *Protoichthyosaurus*

The final section of research builds upon the previous work distinguishing *Ichthyosaurus* and *Protoichthyosaurus*. It focuses on a previously undescribed, originally identified as *I. communis*, in the collections of the Birmingham Museums

Trust (Chapter 9). The specimen is of particular interest because it is a three-dimensionally preserved partial skull and skeleton, which is unusual for a Lower Jurassic ichthyosaur.

Based largely on skull characters, this specimen was identified as *P. prostaxalis*. Of note, the skull and jaw are larger than any specimen of *Protoichthyosaurus* or indeed *Ichthyosaurus* and therefore provides information on the size range. The most important features, however, concern the anatomy of the skull. Given its three-dimensional braincase, the decision was made to CT scan the entire skull and micro-CT scan various individual skull and braincase elements. This provided new information for *Protoichthyosaurus*, including additional features of the braincase and palate that appear to be distinct from *Ichthyosaurus* that may potentially play a role in understanding the braincase evolution in ichthyosaurs.

Chapter 11: Conclusions

Two new species have been recognised and removed from the variation previously encapsulated in *Ichthyosaurus communis*. This led to an assessment of *I. communis*, which confirmed the synonymy of this species with *I. intermedius*. A revised diagnosis for the genus and *I. communis* have been presented. Based upon the identification of a suite of characters developed as part of the revision of *I. communis*, the first neonate skeleton of this species has been recognised and described. The previously undescribed specimen of *I. somersetensis* from Somerset, England, estimated at 3.3 metres long, held in a collection in Germany is the largest known *Ichthyosaurus*. This specimen is also one of only three known specimens of the genus with a preserved embryo. The study of 99 *Ichthyosaurus* hind fins assessed the taxonomic limitations of a small versus large sample size of specimens. With a smaller sample size, unique characters appear to be distinct, but with a larger sample size these characters are encompassed within the variation found among specimens. This demonstrates potential issues when describing new species based on limited or fragmentary material. In essence, having too few specimens to compare means that variation cannot be appropriately assessed. Combined with the recent reassessment of *I. breviceps* (Massare and Lomax, 2014b), *I. conybeari* (Massare and Lomax, 2016a) and *I. anningae* (Lomax and Massare, 2015), the revision of *I. communis* and the description of two new species (*I. larkini* and *I. somersetensis*) presented in this work means that all six species of the genus can now reliably be distinguished from each other on the basis of skull and postcranial characters.

Protoichthyosaurus was previously synonymised with *Ichthyosaurus*, but the synonymy is herein rejected and *Protoichthyosaurus* is resurrected. The forefin of *Protoichthyosaurus* is taxonomically useful and it can easily be distinguished from *Ichthyosaurus*. Furthermore, this work identifies a new species, *Protoichthyosaurus applebyi*. A phylogenetic analysis showed that *Protoichthyosaurus* and *Ichthyosaurus* were sister taxa in the same family, Ichthyosauridae. Additionally, the osteological description of a three-dimensional skull and postcranial skeleton, the former of which was CT-scanned, revealed new information on the braincase anatomy of *Protoichthyosaurus*. This is the largest known example of the genus, even larger than any known specimen of *Ichthyosaurus*.

11.1 Further Work

As *Ichthyosaurus* and *Protoichthyosaurus* have been revised in this study, this work will be a starting point for future research on both taxa and on the diversity of Lower Jurassic ichthyosaurs in general.

There is still further work that can be done with *Ichthyosaurus*. In particular, the recognition of the first neonate of *Ichthyosaurus communis* (Chapter 6) may aid with studies on ichthyosaur ontogeny. This is because the diagnostic characters found in this species do not change with ontogeny. It would be interesting to look at the existing small-bodied *Ichthyosaurus* specimens and evaluate whether any of these can be assigned to a particular species. Thus, given that several species of the genus are known from multiple specimens, it may be possible to identify a growth series, from neonate to adult.

Chapter 7 looked at the variation in the hindfin of *Ichthyosaurus*. Given that the forefin is one of the most readily preserved parts of an *Ichthyosaurus* skeleton, a study dedicated to the variation in the forefin could also be undertaken. Previous workers have shown that the forefin of *Ichthyosaurus* does not appear to be taxonomically useful at the species level (McGowan, 1974b; Motani, 1999b; McGowan and Motani, 2003). However, species of the genus have since been better defined, including as part of this work, and specifically *I. communis* is not as variable as it was previously thought to be (e.g. Chapters 3 and 4). Thus, this presents the possibility that there might be features of the forefin that are taxonomically useful. The logical starting point would be to compare the forefin morphology of specimens that have been assigned to a particular species.

Most of the specimens examined as part of this thesis are from historic collections, so the geological and stratigraphical information is often poorly constrained or lost. It would be beneficial to attempt to link specimens with their original context. One suggestion would be to examine the matrix of historic specimens to look for microfossils that may yield information on stratigraphy. This approach was applied to the neonate *I. communis* specimen described in this research (Chapter 6), which recovered some stratigraphic information. One problem with this, however, is that some museums may be unlikely to allow the removal of matrix for study. Nevertheless, only a fingernail-sized piece of matrix is usually required, so removal from the underside of a specimen, or from a portion of matrix situated away from any bones, could be the answer to unlocking this information.

This could be significant because it may prove that *Ichthyosaurus* and/or *Protoichthyosaurus* are present in the Late Triassic (Rhaetian).

There was a reduction in the taxonomic diversity of ichthyosaurs following a mass extinction event at the end of the Triassic (Kelley et al. 2014; Ji et al. 2016). Consequently, the latest Triassic-earliest Jurassic was a critical interval in the evolution of ichthyosaurs (Thorne et al. 2011). As a direct result of the research undertaken in this thesis, *I. communis* was shown to represent five different taxa, including a separate genus, *Protoichthyosaurus*. Therefore, this work demonstrates that there were more species of ichthyosaur in the earliest Jurassic than previously known and will thus aid in future studies on the radiation of ichthyosaurs and the recovery of marine life following the mass extinction event. Taxonomy has been ongoing for centuries and taxonomic studies such as those presented in this thesis are still a vital component in helping to not only determine the number of species and their differences, but also has the ability to reveal information that has wider implications for the evolution and diversification of life.

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Chapter 13: Supplementary Materials

The following published papers were written by the author during the PhD, but were not included in this thesis as they do not play a specific role in the revision of *Ichthyosaurus*. However, they are included here as supplementary materials because the work revolves primarily around Lower Jurassic ichthyosaurs and provides new information.

An ichthyosaur from the UK Triassic–Jurassic boundary: A second specimen of the leptonektid ichthyosaur *Wahlisaurus massarae* Lomax 2016

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The holotype of *Wahlisaurus massarae* is known only from a partial skull and postcranial skeleton from the Lower Jurassic, collected near Normanton on Soar, Nottinghamshire, UK. It is diagnosed relative to other ichthyosaurs on the basis of autapomorphies of the coracoid and a unique combination of characters. Here, we report a second specimen of *W. massarae*. The new specimen comprises a practically complete right coracoid that clearly shows the unique morphology of *W. massarae*. This specimen was collected in situ from a quarry in Somerset, from the base of the Blue Lias Formation, which corresponds to the Triassic–Jurassic boundary (uppermost Rhaetian or lowermost Hettangian), extending the geographic and stratigraphic range of the species. Furthermore, the coracoid of the new specimen is 20% anteroposteriorly longer than in the holotype, representing a larger individual. In light of preparation and the identification of additional fragments of the holotype, a redescription of the skull morphology of the holotype, as well as comparison with the skull roof of *Leptonectes tenuirostris*, is included.

KEYWORDS

Hettangian, Lower Jurassic, Rhaetian, Somerset, Triassic–Jurassic boundary, Upper Triassic, *Wahlisaurus massarae*

1 | INTRODUCTION

Thousands of ichthyosaurs have been collected from the Lower Jurassic deposits of the UK. Globally, Lower Jurassic ichthyosaurs are represented by ten genera, nine of which have been reported in the UK (Lomax, 2016; Maisch & Matzke, 2000; Williams, Benton, & Ross, 2015; Lomax, Massare, & Mistry, 2017). The most recently described, *Wahlisaurus massarae*, is known only from the holotype. The holotype comprises a partial skull and incomplete skeleton collected from Nottinghamshire (Lomax, 2016). *W. massarae* is diagnosed relative to other ichthyosaurs in possessing autapomorphies of the coracoid, along with a unique combination of characters. Lomax (2016) assigned it to the Leptonektidae, as defined by Maisch (1998). The defining features of the coracoid, which are not reported together in any other ichthyosaur, include a large, ovoid foramen; the presence of both a coracoid foramen and a scapular-coracoid foramen (the latter formed by articulation of the scapula and coracoid, which encompasses the anterior notch); and

a coracoid with a posterior notch that is much more developed than the anterior notch (Lomax, 2016). It was further demonstrated that the coracoid morphology of *W. massarae* was unique among ichthyosaurs and not a morphological variation of a currently recognized leptonektid and was therefore sufficiently different to be considered a new genus.

Here, we describe a second specimen of *W. massarae*, an isolated right coracoid, which possesses the diagnostic characters of *W. massarae*. The specimen provides new geographic, stratigraphic, and morphological information for the taxon. In addition to the new specimen, further preparation on the holotype, along with a re-examination, has enabled the identification of additional pieces of the skull, which help to interpret the skull morphology in greater detail.

Institutional abbreviations: BRSMG = Bristol Museum and Art Gallery, Bristol, UK; LEICT = Leicester Arts and Museums Service, New Walk Museum and Art Gallery, New Walk, Leicester, UK.

2 | GEOLOGICAL SETTING AND HISTORY OF THE SPECIMEN

The studied specimen (BRSMG Cg2405) was collected, with permission, by S. C. in 1996 and donated to BRSMG in December, 2016. It was found in situ at Sutton Hill Quarry (also called Stowey Quarry), Bishop Sutton, northern Somerset, grid reference ST597587 (Figure 1). The specimen was collected from immediately above the Sun Bed, the youngest bed of the Upper Triassic (Rhaetian) Penarth Group at this locality. The Sun Bed has been assigned to the White Lias of Gallois (2009), corresponding to the Langport Member, Lilstock Formation, of traditional usage (e.g., Hesselbo et al., 2004; Swift, 1995; Wignall, 2001).

When Sutton Hill Quarry was active, stone extraction exploited the thicker limestone layers exposed close to the quarry floor below the alternating layers of limestone and mudstone more typical of the Blue Lias Formation (Donovan & Kellaway, 1984). In the 1990s, the quarry expanded to cover an area of approximately 20 acres, and it was during this active phase of stone extraction that many of the vertebrates were found, including the studied specimen. Regular visits were made to the quarry by amateur collectors S. C. and Richard Wilkins. Over several years, a good relationship was made with the quarry owner so that the vertebrate-bearing horizon was left intact and undisturbed during normal quarrying. The material could then be examined and the fossils extracted in situ (Carpenter, 2001).

The base of the Jurassic System is now defined by the first appearance of the ammonite *Psiloceras spelae tirolicum*, with a Global Boundary Stratotype Section and Point (GSSP) at Kuhjoch in the Northern Calcareous Alps, Tyrol, Austria (Hillebrandt et al., 2013). Previously, in Britain, the base of the Jurassic had been defined by the first appearance of *P. planorbis* (Warrington et al., 1980), with a proposed GSSP at St. Audrie's Bay, Somerset (Warrington, Cope, & Ivimey-Cook, 1994). This is approximately 6 m above the base of the Blue Lias Formation,

so that the basal "Pre-planorbis beds" (the lowest subdivision of the Blue Lias Formation) were regarded as uppermost Triassic (e.g., Storrs & Taylor, 1996). Subsequent work identified the earliest British psiloceratid ammonites as *P. erugatum* at a lower horizon in nearby Doniford Bay, Somerset (Bloos & Page, 2000).

The basal ammonite faunas of the Tilmanni Chronozone now known from the GSSP in Austria are not present in Britain and north-western Europe (Hillebrandt et al., 2013), meaning that correlation of the Tr-J boundary is problematic. Benson, Evans, and Druckenmiller (2012), for example, regarded most of the plesiosaurs from the Pre-planorbis beds of the classic locality of Street, Somerset, as dating from the Tilmanni Chronozone. Similarly, Lomax and Massare (2017) surmised that many of the ichthyosaurs from this locality were also from the Pre-planorbis beds (= Tilmanni Zone), whereas Martill, Vidovic, Howells, and Nudds (2016) assigned a similar age to the theropod dinosaur *Dracoraptor*.

The Tr-J boundary can, however, be correlated through carbon-isotope stratigraphy. Based on the carbon isotope data of Hesselbo, Robinson, Surlyk, and Piasecki (2002), Hillebrandt et al. (2013) projected the boundary at St. Audrie's Bay to be within Bed 1 of the Blue Lias Formation of Warrington et al. (1994), that is, over 4 m below the first occurrence of *P. planorbis*. A similar assessment had been made by Clémence et al. (2010). The base of the Hettangian in Britain is currently taken as the base of the Tilmanni Zone (Page, 2010a, 2010b). In general, it appears that the basal few tens of centimetres of the Pre-planorbis beds of the Blue Lias correspond to the uppermost Triassic (Rhaetian; Weedon, Jenkyns, & Page, 2017).

At Sutton Hill Quarry, Donovan (1956) recorded approximately 1.5 m of Pre-planorbis beds above the top of the White Lias (i.e., the Sun Bed). Although this relationship might suggest that the basal Pre-planorbis beds are the latest Triassic, the condensed sequence (the "fossil bed" of Carpenter, 2001) with relatively abundant, isolated, and vertebrate elements such as BRSMG Cg2405 indicates a possible

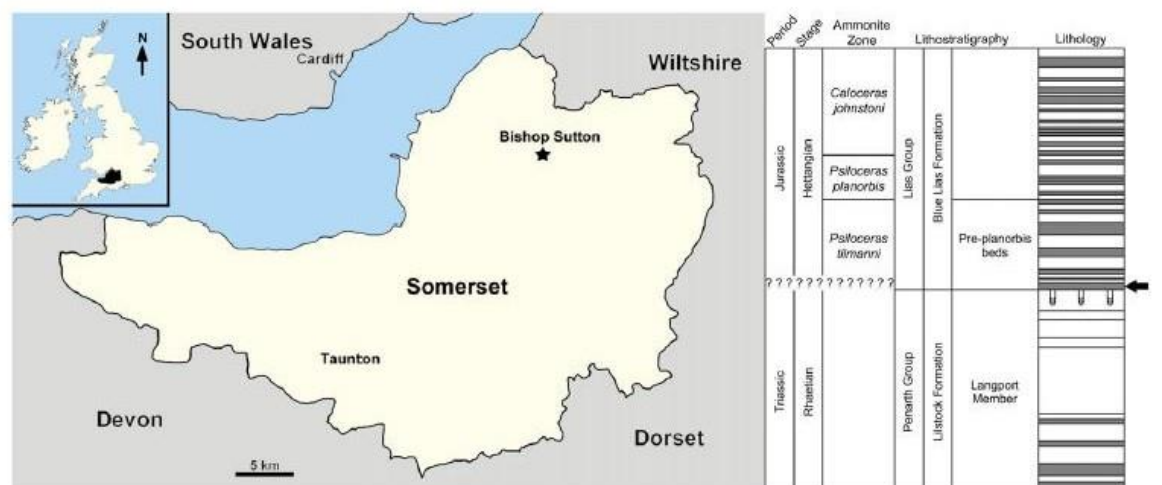


FIGURE 1 Map of Somerset including the location of Sutton Hill (Stowey) Quarry, in Bishop Sutton, indicated by a star. Stratigraphy across the Triassic-Jurassic boundary, after Hesselbo et al. (2004, figure 5) and Donovan (1956, figure 6). Arrow points to the stratigraphic position of BRSMG Cg2405. The dark beds in the section are the mudstones/shales and the white beds are limestones. Scale bar is 5 m [Colour figure can be viewed at wileyonlinelibrary.com]

disconformity. To test the possibility that a stratigraphic gap occurs between the White Lias and the Blue Lias at Sutton Hill Quarry, a sample of matrix from the new specimen was analysed at the University of Birmingham, UK. The lithology is not that of the usual Blue Lias mudstone facies, and no calcareous microfossils were found. The absence of these microfossils and the nature of the sediment (a poorly cemented, bioclastic-carbonate unit) is thought more likely to represent a transition between the Penarth Group and the Blue Lias Formation (I. Boomer, 2017 pers. comm.). Therefore, based on the in situ collection of BRSMG Cg2405 from directly above the Sun Bed, the specimen most likely dates from the latest Rhaetian, Triassic (K. Page, R. Gallois, G. Weedon, and I. Boomer, 2017 pers. comm.; Figure 1). Thus, this shows that the base of the Blue Lias at this locality is most likely latest Triassic rather than earliest Jurassic.

The holotype of *W. massarae* (LEICT G454.1951.5) was recorded as from the same locality and horizon as LEICT G378.1953.11, an unprepared ichthyosaur skull collected in 1953 from an old quarry at Normanton Hills, near Normanton on Soar, Nottinghamshire (grid reference SK538245). LEICT archives record the position of the specimen as from in a bed of rubbly limestone immediately below a "2-foot-thick" (0.6 m) bed of blue and yellow shale containing ammonites. These were identified as *P. planorbis*, although preservation of surviving specimens is poor (e.g., LEICT G378.1953.1). As no ammonites were recorded below the ichthyosaur specimen, it likely came from the top of the Pre-planorbis beds (Tilmanni Zone) and is earliest Hettangian in age. Intriguingly, Kent (1937, p. 168) recorded *Ichthyosaurus cf. tenuirostris* from a limestone bed immediately below a "2-foot" (0.6 m thick) shale bed that contained *Psiloceras* sp. from the same locality. It is possible that Kent was aware of the (now) holotype of *Wahlisaurus* before its acquisition by LEICT when it was in the collection of Mr. Percy Faulkes of Loughborough, Leicestershire. Certainly no other specimen matching this identification from this locality was recorded by Lomax and Gibson (2015) in their survey of Nottinghamshire ichthyosaurs. Although the holotype was recorded as being from the same quarry as LEICT G378.1953.11, the two specimens were collected several years apart. Lower Jurassic and Upper Triassic (Rhaetian) exposures are present in the vicinity of Normanton Hills (Swift, 1995). Therefore, there is a slim possibility that the holotype is also from the base of the Lias Group, although it is unlikely considering that all records suggest Jurassic.

3 | TRIASSIC ICHTHYOSAURS FROM THE UK

Triassic ichthyosaurs from the UK are known mostly from fragments collected from Rhaetian bone bed concentrations. Most specimens have come from the Westbury Formation (Penarth Group) of Gloucestershire. These include isolated vertebral centra, which are the most common finds, although other elements, such as ribs, limb bones, skull bones, and teeth, have been found, but can only be referred to *Ichthyosauria* indet (Benton & Spencer, 1995; Mears et al., 2016; Storrs, 1994, 1999). Other indeterminate, isolated specimens from the Westbury Formation, including teeth, phalangeal elements, and vertebrae, have been reported from quarries in Nottinghamshire

(Lomax & Gibson, 2015; Martill & Dawn, 1986; Sykes, Cargill, & Fryer, 1970) and Leicestershire (Harrison, 1876). A fragmentary, articulated ichthyosaur was collected from the Langport Member of the Lilstock Formation of the Antrim Coast, Northern Ireland, but this is also currently identified as *Ichthyosauria* indet. (Simms & Jeram, 2007; DRL, pers. obs.). A giant ichthyosaur radius, regarded as belonging to a possible shastasaurid ichthyosaur, was found at Penarth, South Wales (Martin et al., 2015). The specimen was found ex-situ, and Martin et al. (2015) discussed the possibility of the specimen having originated from the Westbury Formation (Rhaetian) or the lower part of the Blue Lias Formation (Hettangian). They opted for the latter, and indicated the Pre-planorbis beds or Planorbis Zone as the likely source of the specimen, based largely on the association of a poorly preserved possible immature ostreid bivalve and an associated *Palaeonucula navis* (Martin et al., 2015). Thus, pending further study, the specimen may turn out to be from the Westbury Formation or the base of the Blue Lias Formation. Other documented occurrences of Rhaetian ichthyosaurs, such as those from Somerset, were based on earlier stratigraphic studies of the age of the Pre-planorbis beds (e.g., McGowan & Motani, 2003, pp. 76 and 91), which were correct at the time. Pending a detailed, stratigraphic study of the ichthyosaurs from the Pre-planorbis beds, earlier studies suggesting a Rhaetian age may turn out to be correct.

Allard, Carpenter, Duffin, and Benton (2015) assigned some isolated ichthyosaur teeth to *Ichthyosaurus* sp., pending further research. The remains, however, are too incomplete for positive identification and should instead be regarded as *ichthyosauria* indet. The only generically determinate ichthyosaur definitely from the UK Upper Triassic was reported by Storrs (1994). Storrs cited a pers. comm. with C. McGowan, an authority on ichthyosaurs, who identified an isolated humerus from near Chipping Sodbury, Gloucestershire, as belonging to *Leptopterygius cf. L. tenuirostris* (now *Leptonectes*). Although McGowan's identification is almost certainly correct, given his extensive research on that genus (e.g., McGowan, 1989, 1996) that specimen is presently missing and was never figured. Additionally, the specimen number provided by Storrs (1994) does not correspond with the BRSMG accession register and the specimen cannot presently be located (DRL, pers. comm. D. Hutchinson, 2017).

A specimen of *Leptonectes tenuirostris* from Barrow-upon-Soar, Leicestershire (LEICT G491.1889), has a precise horizon recorded; "Slavin between Black Rummels and White Hurs." Using the quarry workers' terms (Fox-Strangways, 1903), this can be translated as the shale ("slavin") between the Rhaetian White Lias ("White Hurs") and the basal limestone bed of the Barnstone Member of the Scunthorpe Mudstone Formation ("Black Rummels"). This places the specimen in the Pre-planorbis beds. Teeth of the actinopterygian fish *Severnichthys* (Storrs, 1994) have been recorded from this shale (Martin, Frey, & Riess, 1986, as *Saurichthys acuminatus*), suggesting that it may well be Rhaetian in age and therefore that the *L. tenuirostris* is from the Triassic. It is possible that other examples of *Leptonectes*, but also *Ichthyosaurus* (Massare & Lomax, 2017) and *Protoichthyosaurus* (Lomax, Massare, & Mistry, 2017), may be present in the Rhaetian. This, however, requires detailed studies on the matrix of historical ichthyosaur specimens from the Pre-planorbis beds, which may yield important information about their stratigraphic position.

4 | SYSTEMATIC PALAEONTOLOGY

Order Ichthyosauria de Blainville, 1835

Minorder Parvipelvina Motani, 1999

Suborder Neoichthyosauria Sander, 2000

Family Leptonectidae Maisch, 1998

Genus *Wahlisaurus* Lomax, 2016

Type Species. *Wahlisaurus massaræ* Lomax, 2016.

Diagnosis. As for type and only species.

Wahlisaurus massaræ Lomax, 2016

Holotype. LEICT G454.1951.5, a partial skull and an associated incomplete skeleton comprising the pectoral girdle, humeri, pelvic elements, partial hind fins, vertebrae, and ribs.

Referred specimen. BRSMG Cg2405, a practically complete right coracoid.

Locality and horizon. The holotype was recorded from the Lower Jurassic, either the top of the Pre-planorbis beds (Tilmanni Zone) or the base of the Planorbis Zone, lowermost Hettangian; Lias Group, Scunthorpe Mudstone Formation, Barnstone Member, and was collected in Normanton Hills, near Normanton on Soar, Nottinghamshire,

England, UK. BRSMG Cg2405 is from the approximate position of the Triassic–Jurassic boundary, probably from the Upper Triassic (uppermost Rhaetian; Lias Group, Blue Lias Formation), and was collected from Sutton Hill (Stowey) Quarry, Bishop Sutton, northern Somerset, UK, grid reference ST597587.

4.1 | Description of new specimen

BRSMG Cg2405 is a nearly complete right coracoid (Figure 2). The coracoid is anteroposteriorly almost twice as long as mediolaterally wide (anteroposterior measurement = 15.2 cm; mediolateral measurement = 8.7 cm). A small portion of the anterior section is missing, and so it would have originally been slightly longer. The anteroposterior length of the coracoid of BRSMG Cg2405 is approximately 20% larger than in the holotype (holotype, anteroposterior measurement = 12.7 cm), and the mediolateral width is almost 15% larger than in the holotype (holotype, mediolateral measurement = 7.6 cm). Therefore, BRSMG Cg2405 clearly represents a larger animal than the holotype. A photogrammetry model of the coracoid was also created (Data S1).

The following description of features are all present in the holotype, unless otherwise stated. An anterior notch is present as a very small, incipient emargination. Although there is no scapula to confirm the presence of a scapular–coracoid foramen, which is identified only

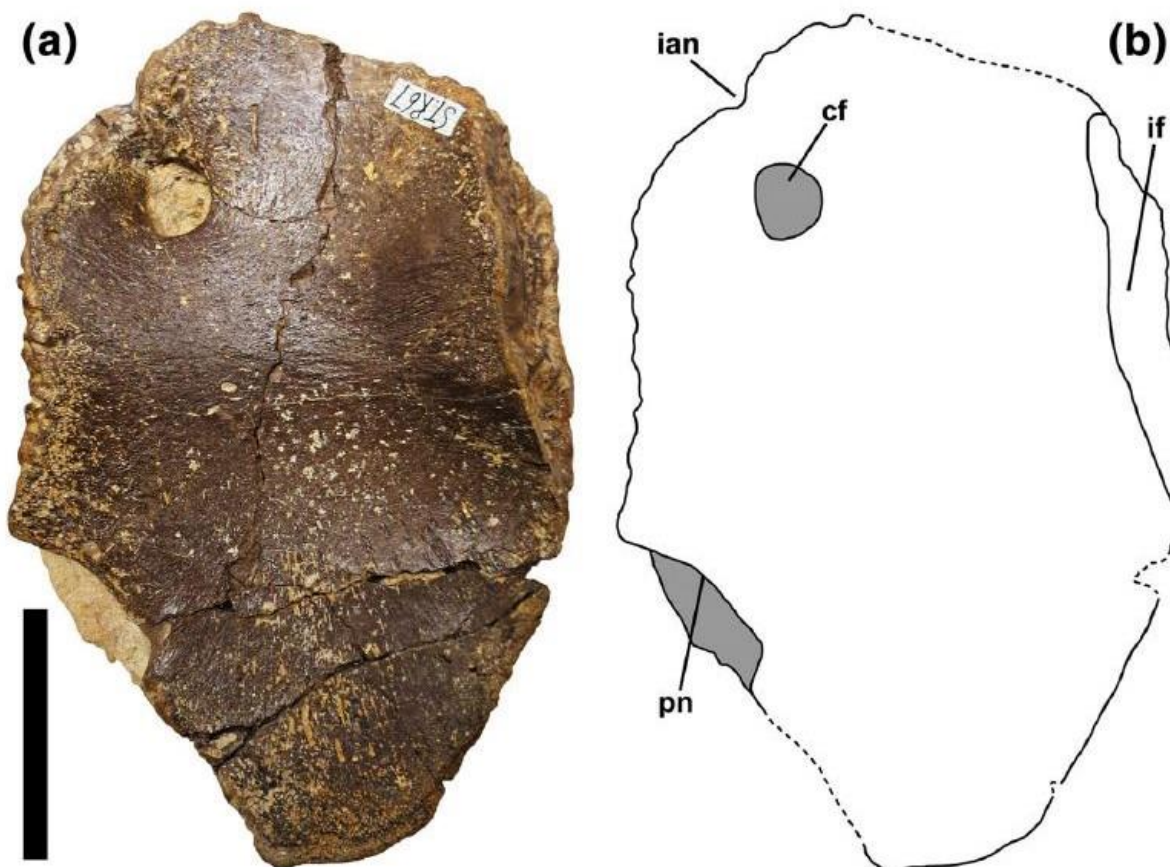


FIGURE 2 BRSMG Cg2405, right coracoid of the referred specimen of *Wahlisaurus massaræ* from the Triassic–Jurassic boundary of Somerset. (a) Photograph. (b) Interpretive illustration. Abbreviations: cf = coracoid foramen; ian = incipient anterior notch; if = intercoracoid facet; pn = posterior notch. Dotted line indicates broken edge; grey represents matrix. Scale bar = 5 cm [Colour figure can be viewed at wileyonlinelibrary.com]

when the scapula and coracoid are articulated, the presence of a long anterolateral edge for articulation with the scapula is present and suggests that the anterior notch would be enclosed by the contact of the scapula with the coracoid. The anterolateral edge is less than 1.5 times longer than the glenoid contribution of the coracoid, as in the holotype, although this may be due to the missing anterior portion, or may suggest the coracoid proportions changes with ontogeny. The glenoid contribution is robust, thickened and the articular surface, which cannot be seen in the holotype, is very rugose. Positioned posterior to the anterior notch, and entirely within the coracoid, is a large, well-defined ovoid foramen. Posteriorly, the coracoid is fan-shaped, and a well-developed posterior notch is much larger than the anterior notch.

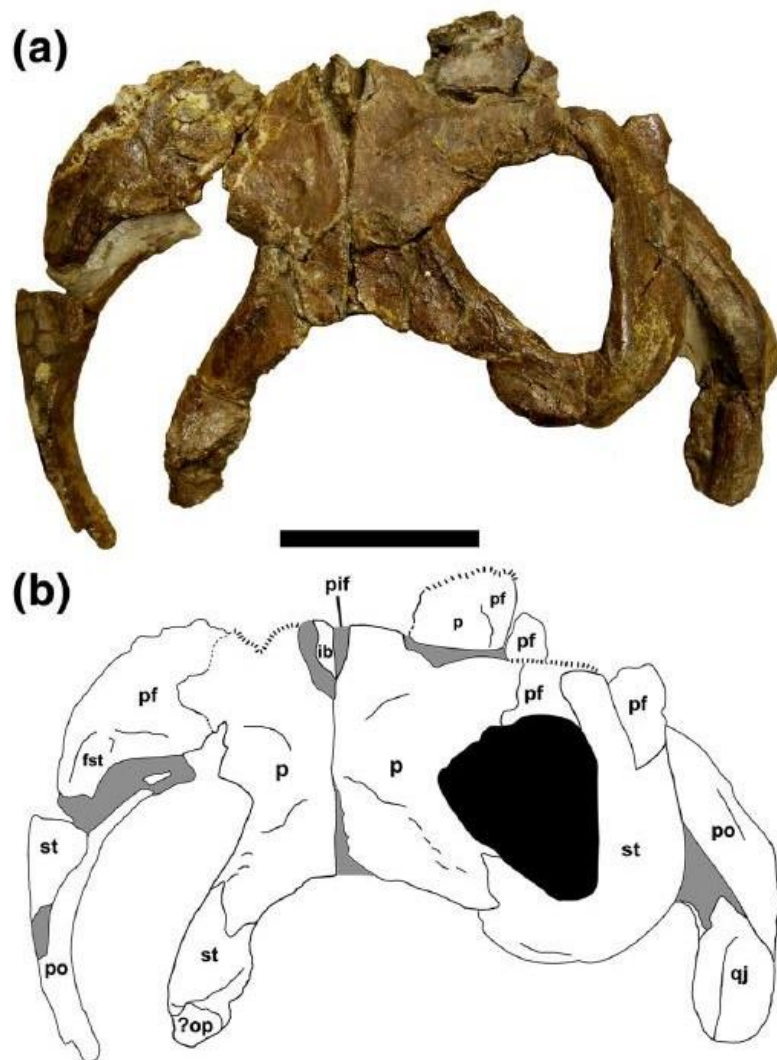
4.2 | Additional comments on skull morphology of the holotype

As discussed by Lomax (2016), the skull roof of the holotype (LEICT G454.1951.5) is poorly preserved and some of the skull sutures are difficult to discern. This was partly due to old glue and a thick layer of

consolidant that has now been removed in selected areas of interest, which has aided with this redescription. The left parietal is displaced posterolaterally by approximately 1 cm, which suggests that some of the skull elements may not have been fused, although it is more likely the result of taphonomy and the poor preservation, as discussed by Lomax (2016). In light of additional preparation, some of the morphology can be redescribed, including a reassessment of the contact and extent of some elements (Figure 3).

The posterolateral displacement of the left parietal created a gap between the anterior portions of both parietals. In this gap, Lomax (2016) identified a fragment of the left frontal and noted that the pineal foramen is situated within the frontals. However, when articulated with other fragments from the underside, the left "frontal" is a fragment of indeterminate smooth bone pushed through the gap from the underside. This bone actually contacts a portion of the parietal, which was previously obscured by discoloured consolidant. Furthermore, the shape, contact, and position led Lomax (2016) to erroneously identify this as a frontal, but in light of this reassessment, no frontal can be identified. Considering the displacement of the left parietal, if articulated

FIGURE 3 Skull roof of the holotype of *Wahlisaurus massarae* (LEICT G454.1951.5), with additional pieces articulated. (a) Photograph; (b) interpretive illustration based on the preserved skull elements. Due to crushing and displacement of the left parietal, the entire left side of the skull is posterolaterally offset. Note, as discussed in the text, the postfrontal is damaged but the anterior portion of the supratemporal overlaps the postfrontal. Dashed line indicates a possible suture; vertical lines indicate a broken edge; grey represents matrix exposed between the bones; black opening represents the upper temporal fenestra. Abbreviations: fst = facet for supratemporal; ib = isolated bone; j = jugal (indicating possible edge of underlying jugal); op = opisthotic; p = parietal; pf = postfrontal; pif = pineal foramen; po = postorbital; qj = quadratojugal; st = supratemporal. Scale bar = 5 cm [Colour figure can be viewed at wileyonlinelibrary.com]



correctly with the right parietal, and the isolated piece of bone removed, the opening probably forms the posterior margin of the pineal foramen. Thus, the pineal foramen would be at least partially situated in the parietals, but more complete remains are needed to verify if it is entirely within the parietals or between the parietals and frontals.

The right supratemporal is well preserved, but Lomax (2016) could not confidently identify the suture contact with the postfrontal. However, the identification of a portion of the left supratemporal and postfrontal has enabled positive identification of the sutures in the right supratemporal. The supratemporal comprises the entire lateral edge of the upper temporal fenestra and extends anterior to it. It also makes up the posterior margin of the upper temporal fenestra. The right postfrontal is largely damaged, although it wraps around the anterior portion of the supratemporal along a clear suture (see Figure 3). The anterolateral contact of the left parietal and postfrontal can be identified through a small piece of the parietal that overlaps the postfrontal, and this contact can also be identified in the right postfrontal and parietal.

A portion of the left postorbital has also been identified and enables a better interpretation of the right postorbital. The postorbital is a robust element that is roughly dorsoventrally rectangular. It contacts the postfrontal and possibly the supratemporal dorsally and there appears to be a slender anterodorsal process, but some of it is probably missing. The ventral edge is also missing. Additional posterior segments of the right jugal show that the element is delicate posteriorly as well as anteriorly, although its dorsal extent cannot be identified because it is broken and taphonomically distorted posteriorly.

As the new interpretation of the holotype skull differs from the original description by Lomax (2016), it requires some discussion and comparison. Lomax (2016) showed that *Wahlisaurus* could easily be distinguished from all members of the Leptonectidae, in possessing autapomorphic characters of the coracoid and other features of the skull and postcranium. For example, *Wahlisaurus* lacks a lower jaw that is greatly reduced relative to the upper jaw, as is the case in *Eurhinosaurus* and *Excalibosaurus*. Comparison of the skull roof of *Wahlisaurus* with *Leptonectes tenuirostris* is, however, necessary. The new skull interpretation is markedly different from that of *Leptonectes cf. tenuirostris* described by Maisch and Matzke (2003) and *L. tenuirostris* described by Maisch & Reisdorf (2006) in having a supratemporal that forms the entire lateral edge of the upper temporal fenestra, a postfrontal with minimal contribution to the upper temporal fenestra, and a robust postorbital. It is, however, more similar to the skull roof interpretation of *L. tenuirostris* given by McGowan & Motani (2003, figure 69). In that reconstruction, the postfrontal is a massive element that is greatly expanded posteriorly, which is not the case in *Wahlisaurus*. Furthermore, the supratemporal in *Wahlisaurus* extends much further forward than shown by McGowan & Motani (2003, figure 69) for *L. tenuirostris*. Our observations of specimens of *L. tenuirostris* from Barrow-upon-Soar (LEICT G491.1889, G122.1992, and G124.1992) indicate that an anteriorly extensive supratemporal excludes the postfrontal from the lateral margin of the upper temporal fenestra. Thus, as stated by Maisch & Reisdorf (2006) and Lomax (2016), *L. tenuirostris* is in need of detailed re-examination and revision. Regardless of a revision, *Wahlisaurus* can demonstrably be distinguished from *L. tenuirostris* on the basis of current knowledge.

5 | CONCLUSIONS

Wahlisaurus massarae was known only from the Lower Jurassic of Nottinghamshire. The discovery of a new specimen (BRSMG Cg2405) provides additional details on the stratigraphic and geographic distribution of the taxon. An analysis of the matrix and stratigraphic position of BRSMG Cg2405 shows that it is from the base of the Blue Lias Formation Tr-J boundary of Somerset, probably from the Triassic (Rhaetian), rather than Jurassic (Weedon et al., 2017). This extends both the geographic and stratigraphic range of the species. If definitely Triassic, this might be the first unequivocal occurrence of a generically determinate ichthyosaur from the Triassic of the UK. Furthermore, the coracoid of BRSMG Cg2405 is larger than in the holotype, which suggests a larger animal that might not be "small-bodied," as suggested by Lomax (2016). A re-examination of the holotype, after additional preparation and conservation has enabled a better interpretation of the skull morphology. This has allowed for comparison with the skull roof of *Leptonectes tenuirostris*, which is markedly different from *W. massarae*. Thus, *W. massarae* can be reliably distinguished from *L. tenuirostris* on the basis of skull and postcranial morphologies.

D. R. L. has examined many ichthyosaurs held in numerous museum and university collections and has yet to discover any additional examples of *W. massarae*. The discovery of BRSMG Cg2405 in a private collection is therefore significant. Responsible fossil collectors play an important role in discovering new material that is significant to science.

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The youngest occurrence of ichthyosaur embryos in the UK: A new specimen from the Early Jurassic (Toarcian) of Yorkshire



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Abstract: The remains of between six and eight ichthyosaur embryos, still situated within a fragment of the rib-cage of the parent animal, are described. Each is represented by a string of vertebral centra, some with associated ribs. Other skeletal elements, including possible skull material, are represented only by isolated bones, none identifiable with certainty. The small limestone boulder in which the ichthyosaur specimens are preserved was collected from the beach at Sandsend, near Whitby, North Yorkshire, and derives from the Whitby Mudstone Formation (*Hildoceras bifrons* Ammonite Biozone) of the Toarcian Stage of the Lower Jurassic. The specimen cannot be identified beyond Ichthyosauria indet. However, it represents the geologically-youngest occurrence of ichthyosaur embryos thus far recorded from the UK and the first such occurrence to be reported from Yorkshire.

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The existence of viviparity in ichthyosaurs was first reported by Chaning Pearce (1846), who noted the presence of an embryo within the pelvic region of a specimen of *Ichthyosaurus* from the Early Jurassic (probably Hettangian) Blue Lias Formation of Somerset. Woodward (1906) provided a further account of this specimen. Small ichthyosaur skeletons found inside larger individuals had previously been described (e.g. Jäger 1824), but only after Chaning Pearce (1846) had published his short paper did they become regarded as embryos and thus further evidence for viviparity. The argument, however, for cannibalism rather than embryos continued to persist until a detailed study was provided by Böttcher (1990). Seeley (1880) discussed the occurrence of small ichthyosaur skeletons associated with two further ichthyosaur specimens from the Early Jurassic of Britain and a number from the Early Jurassic of Germany. Noting that their positions within the adult skeletons did not suggest the small skeletons were stomach contents, Seeley came to the conclusion that they represented embryos. One of the two British specimens described by Seeley cannot presently be located. Over a century later, an important paper by Deeming *et al.* (1993) included a detailed description of what they concluded to be a 'mid-term' embryo associated with an Early Jurassic specimen of *Ichthyosaurus* from the Hettangian of Kilm in Somerset. They concluded that, not only were the ichthyosaur genera *Ichthyosaurus* and *Stenopterygius* viviparous (embryo-bearing specimens of the latter being well-known from the Toarcian of Germany), but that ichthyosaur young were typically born tail-first – like those of modern cetaceans – and this was thought to be an aquatic adaptation to minimize the possibility of their drowning during parturition. Lomax & Massare (2012) provided a further account of one of the British ichthyosaur specimens discussed by Seeley (1880, pl. 1, fig. 1). They

identified the specimen as an example of *Leptonectes* from either the Late Triassic (Rhaetian) or most likely the Early Jurassic (Hettangian–Sinemurian) of Street, Somerset and confirmed its embryo-bearing status. More recently, Lomax & Sachs (2017) described the largest known specimen of *Ichthyosaurus somersetensis* from the Early Jurassic (Hettangian) of England, which also contained an embryo.

Outside the UK, localities from which ichthyosaur embryos have been reported are few in number, but widespread in space and time. The best-known and most productive horizon and locality is the Early Jurassic (Toarcian) *Posidonienschiefer* of Holzmaden and the surrounding area in southern Germany, which has yielded over one hundred embryo-bearing examples of *Stenopterygius* (e.g. McGowan 1979). Embryos have also been recorded in the Middle Triassic (Anisian) genera *Mixosaurus* from Switzerland (Brinkmann 1996) and *Besanosaurus* from Italy (Dal Sasso & Pinna 1996). Camp (1980, p. 144) mentioned 'embryonic material' within a *Shonisaurus* from the Late Triassic (Carnian) of Nevada, USA, although he did not describe or figure it. An ichthyosaur embryo was found in the stomach contents of a plesiosaur from the Late Jurassic Sundance Formation (Oxfordian) of Wyoming, USA (O'Keefe *et al.* 2009). More recently, Stinnesbeck *et al.* (2014) described an Early Cretaceous (Valanginian–Hauterivian) ichthyosaur graveyard from southern Chile, which contained several ophthalmosaurid ichthyosaur embryos, including some inside a complete skeleton of *Platypterygius hauthali*. The geologically-youngest ichthyosaur embryos reported to date have been described by Maxwell & Caldwell (2003) in a skeleton of *Maiaespondylus* from the Albian (Early Cretaceous) of the Loon River Formation in the Northwest Territories of Canada and by Kear & Zammit (2014) in a specimen of *Platypterygius australis* from the late Albian of Australia.

Motani *et al.* (2014) recently described three embryos in a specimen of the Early Triassic ichthyopterygian *Chaohusaurus* from China. Interestingly, these embryos appear to exhibit head-first parturition, which may suggest that the tail-first procedure later seen in ichthyosaurs *sensu stricto* represents a fuller adaptation to aquatic life, although more specimens are required to confirm this. The presence of viviparity in an early ichthyopterygian also suggests, as Motani *et al.* (2014) pointed out, that live birth may have been characteristic of the terrestrial ancestors of ichthyosaurs.

It can thus be seen that embryos have been described, not only in an Early Triassic ichthyopterygian, but in eight genera of ichthyosaurs, ranging from the Middle Triassic to the upper part of the Early Cretaceous. In the UK, embryos have been reported in five ichthyosaur specimens, the four currently-identifiable examples of these being referable to two genera, *Ichthyosaurus* and *Leptonectes*. However, in no instance do these rare British examples of embryo-bearing ichthyosaurs post-date the Sinemurian stage of the Early Jurassic; indeed the genera *Ichthyosaurus* and *Leptonectes* have not been recorded later than the Pliensbachian (Maisch & Reisdorf 2006; Lomax & Massare 2015).

Description

Yorkshire Museum specimen YORYM: 2016.316 consists of the greater part of an externally-weathered boulder of grey, calcite-septarian, limestone (Fig. 1). It was discovered *ex situ* on the beach at Sandsend, near Whitby, and derives from the Whitby Mudstone Formation, *Hildoceras bifrons* Ammonite Biozone, Toarcian Stage, Lower Jurassic. The age was further confirmed by the identification of bivalves (*Meleagrinella substriata*) in the block (C. Little, pers. comm. 2017). After collection by Mark Hawkes in 2013, it was acquired by fossil collector Martin Rigby. Since Mr Hawkes considered the presence of the calcite septa to preclude normal preparation, he had the greater part of the boulder sawn in two, and the sawn surfaces polished. Suspecting the presence of ichthyosaurian embryos, Mr Rigby consulted one of the two present authors (DRL), who duly confirmed his suspicion.

The two halves of YORYM: 2016.316 are here referred to as blocks A and B (Fig. 1). These correspond to the two pieces accessioned as YORYM: 2016.316a and YORYM: 2016.316b respectively.

The shafts of at least seven ribs of an adult ichthyosaur traverse the specimen; they have been sectioned longitudinally in such a fashion that lengths of all seven appear on the polished surface of Block B and lengths of five on that of Block A (Fig. 1A and B). The truncated proximal ends of these ribs may be seen in transverse section on the edge of Block B. Although these display a distinct 'dumb-bell' shape, indicating that the shafts were longitudinally-grooved, this does not convey any useful information regarding the taxonomic identity of the gravid female ichthyosaur.

The polished surfaces of blocks A and B reveal a wealth of detail, much of it difficult to interpret because so many visible structures have clearly been sectioned in planes other than the precisely horizontal, transverse or sagittal. In addition, portions of the specimen are highly calcitised, which also makes interpretation and description difficult

(Figs 1 and 2). However, the most important structures that are clearly identifiable are six (or possibly seven) distinct lengths of vertebral column pertaining to ichthyosaur embryos. Some are visible only on the surface of Block A or that of Block B; others have been so sectioned that they appear on both blocks (Fig. 1). In places, on both blocks, embryonic ribs may be discerned, some still apparently in articulation with their vertebrae (Figs 1, 2E and 3C). Perhaps the most notable feature common to many of the centra in these 'strings' of vertebrae is that, where the centra are well-preserved and have been sectioned at the relevant levels, it can be seen that their notochordal foramina are still open (Figs 2 and 3), a very clear indication of their immaturity. A possible opening for the notochord was also reported in a neonate specimen of *Ichthyosaurus communis* (Lomax *et al.* 2017). Furthermore, the vertebrae are highly cancellous (Figs 2 and 3). It is also clear, due to the sectioning, that the centra are deeply amphicoelous in the manner characteristic of ichthyosaurs. For purposes (and ease) of description, we have numbered these lengths of vertebral column in sequence (Fig. 1).

Column 1 is represented on both blocks A and B, although it is best preserved on B (Figs 1, 2A, B and 3A–C). It is comprised of 38 centra, with visible diameters ranging from 5.6 mm to 5.8 mm, and measures 100 mm in overall length. In addition, at least six extremely delicate ribs, the longest being under 20 mm in length, are preserved in visible association with Column 1 (Fig. 3C).

Column 2 is mostly apparent on Block A, although a couple of centra may be present on Block B (Figs 1 and 2A, C). It is made up of 27 centra, having a maximum diameter of 6.4 mm and measures 80 mm in overall length. This length includes a gap that contains a fragmentary centrum and room for at least two further centra. The gap is occupied (in part) by rib fragments (Figs 1A and 2A).

Column 3 is visible only on Block A (Figs 1A and 2D). If allowance is made for a gap that would suffice to contain four centra, it would originally have comprised 14 centra with a maximum visible diameter of 5.5 mm. Two of the ten centra that are present are lying at an angle of 90° to the others. This has a preserved length of 33 mm.

Column 4 is also present only on Block A (Figs 1A and 2E). It is the least well-preserved of the columns present on Block A and is divided, by a rib of the adult, into two lengths, with a combined total of 48 mm (Fig. 2E). An accurate total count is impossible, although at least seven centra are present in one of the lengths. The centrum having the greatest visible diameter measures 6.7 mm. Of several isolated centra, lying at 90° to those of Column 4, the largest appears to be 6.8 mm in diameter; the opening for the notochord is clearly visible in one of the centra (Fig. 2E).

Column 5 is represented only on Block B (Figs 1B and 3D). It comprises 14 visible centra, although one is partially hidden, the largest of which has a diameter of 5.7 mm; this column has an overall length of 34 mm. Several fragmentary ribs are also associated with this column (Figs 1B and 3D).

Columns 6 and (?)7 is/are poorly-preserved. They form an inverted V-shaped feature on Block B only (Figs 1B and 3E), although some poorly preserved centra of column 6 may be present on Block A (Fig. 1A). Due to the preservation, it is unclear whether the two columns represent one or two individuals, although probably the latter. That labelled as

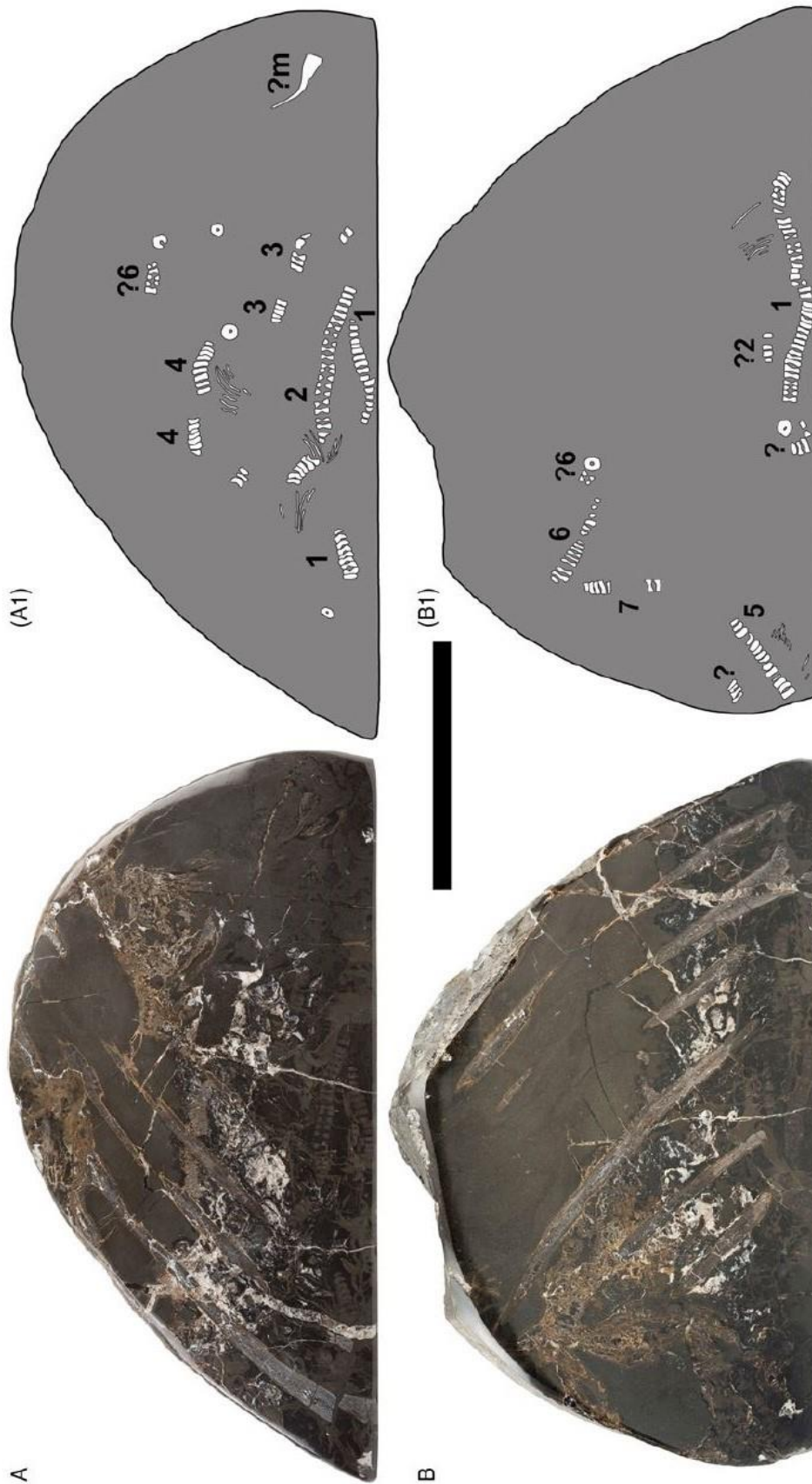


Fig. 1. Studied specimen: YORYM: 2016.316. A cut and polished boulder containing between six and eight ichthyosaur embryos, collected from Sandstead, near Whitby, Yorkshire. (A) Block A, showing ribs of the adult, at least five (or six) embryo vertebral columns, isolated centra, ribs and more. (B) Block B, showing ribs of the adult, at least four and perhaps five independent embryo vertebral columns, and ribs. (A1 and B1) Illustrations of the identifiable sections of embryos. Note that the number of centra illustrated for columns 4 and 6 are estimates. 1–7, indicates embryo vertebral column; ?, articulated vertebral centra that cannot be assigned to an identifiable column; ?m, possible mandible element (?suangular). Scale bar equals 100 mm.

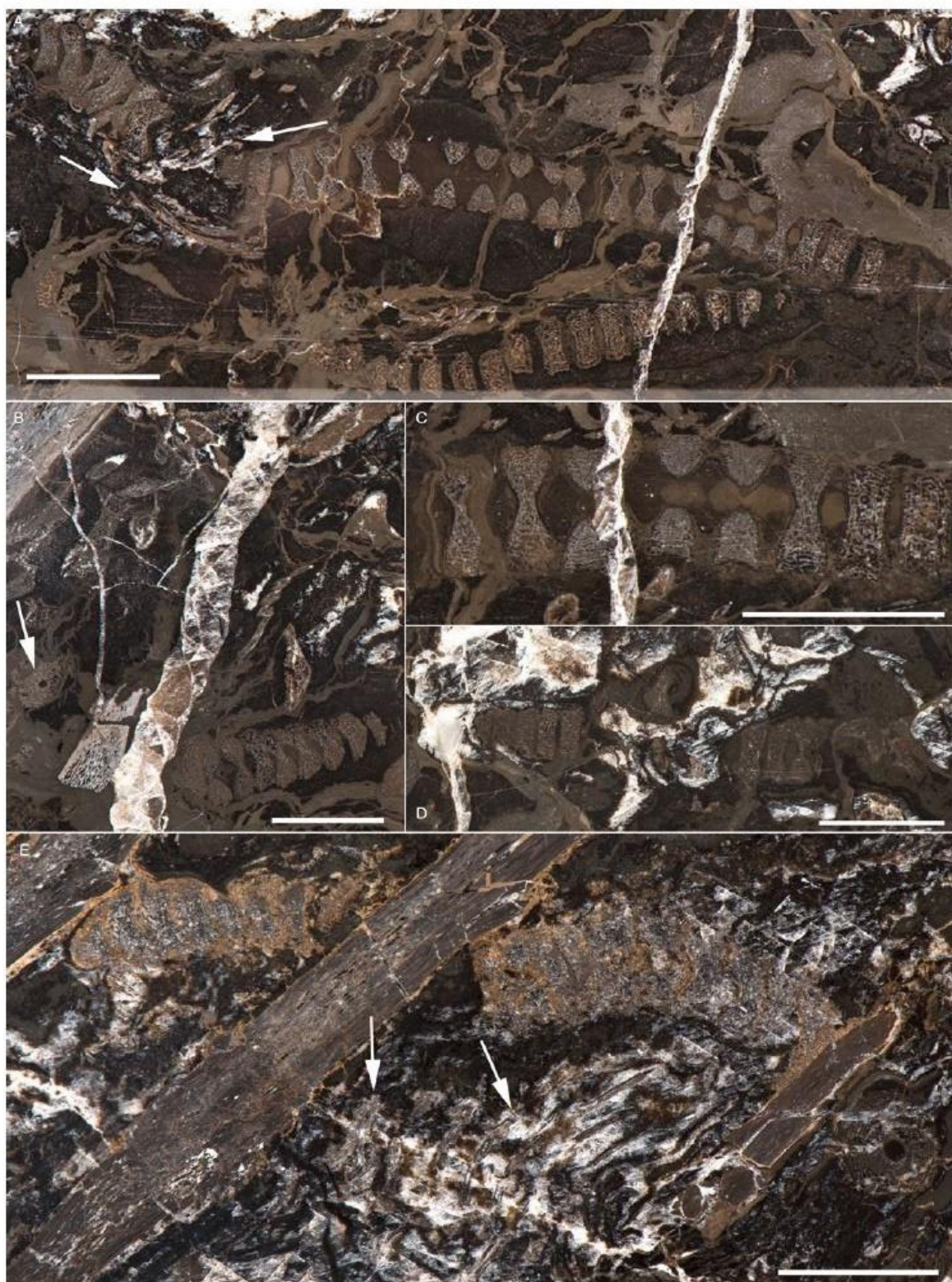


Fig. 2. Close-ups of Block A, YORYM: 2016.316a, showing ichthyosaur embryos. 'Column' refers to the individual embryo vertebral column described in the paper. (A) Column 1 (lower), column 2 (upper). Note the fragmentary ribs lying in a gap (to the left; arrows), separating portions of column 2. (B) Extension of column 1 with isolated centrum showing an opening for the notochord (arrow). (C) Close-up of column 2, showing variation due either to differences in centrum ossification or to the levels at which the centra have been sectioned. (D) Column 3 with a gap separating the centra. (E) The poorly preserved column 4, which is divided by a rib from the adult. Note the fragmentary ribs of an embryo, probably from column 4 or alternatively from an eighth embryo (two arrows indicate at least 9 delicate ribs), and an isolated centrum with an opening for the notochord. Scale bars equal 10 mm.

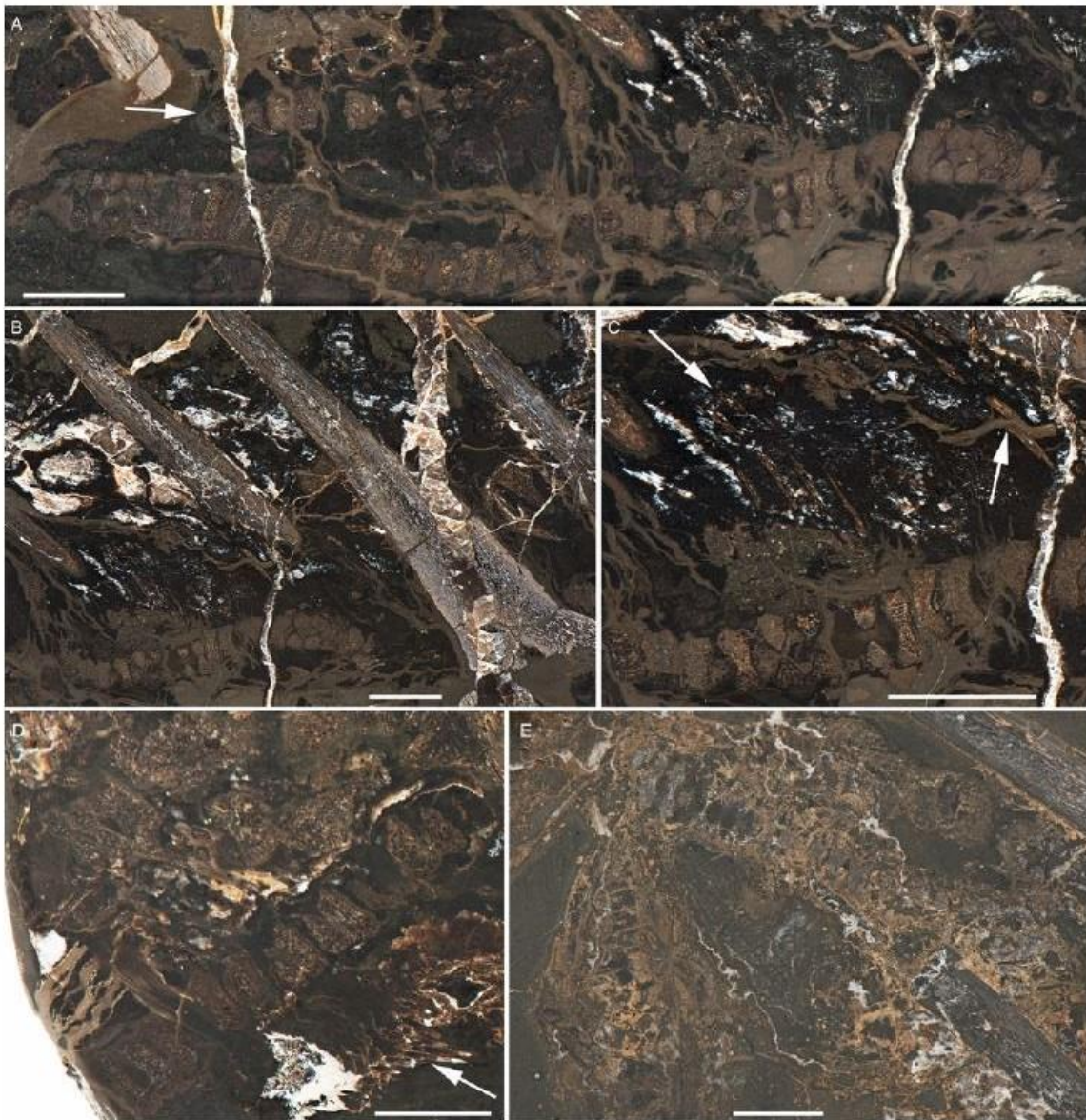


Fig. 3. Close-up of Block B, YORYM: 2016.3 16b, showing ichthyosaur embryos. 'Column' refers to the individual embryo vertebral column described in the paper. (A) Column 1, showing 38 articulated centra. Note a couple of articulated centra above (arrow), which may belong to column 2. (B) General cross section showing several ribs of the adult, with a portion of column 1. (C) Close-up of column 1 and associated ribs. At least six individual ribs are present. Left arrow indicates several, delicate ribs. Right arrow points to one of the larger, more complete ribs. (D) Column 5 showing 14 centra, fragmentary ribs and various indeterminate bones. Arrow points to the accumulation of fragmentary ribs. (E) The poorly preserved columns 6 and (?)7, preserved in a V-shape. The two columns probably do not belong together, but it is not possible to confirm this. Scale bars equal 10 mm.

Column 6 measures 38.8 mm in overall length; the putative 'Column 7' has a length of 30.3 mm, making allowance for a gap in the column.

In the centre of Block A, lying between vertebral 'columns' 2 and 4, but nearer to the latter, is a compact and confused mass of ribs (Figs 1A and 2E). These should possibly be associated with Column 4 or, alternatively, may be seen as representing a further (eighth) ichthyosaur embryo lying at an angle widely different to those which have been described from their lengths of vertebral column. Two features of these tiny ribs are of particular interest. First, their shafts can be seen, even at this stage of their development, to bear longitudinal grooves resembling those commonly seen

on the rib-shafts of adult ichthyosaurs. In addition to this, a thin, incomplete film of black mineral(s) covers some of the ribs. It is possible that this may represent degraded soft tissues, but further study is required. Similar material is also present in other areas of both blocks. As noted earlier, other bones are intermingled within both blocks, but it is near impossible to identify them. However, one bone might be a portion of a mandible (surangular) (Fig. 1).

Discussion

With respect to the studied specimen, we have also considered the potential counter-argument that the embryos

may actually be ingested prey, such as neonates or aborted embryos from another individual, thus meaning the specimen does not represent a gravid female. Due to the very incomplete nature of the adult specimen, it is impossible to argue their embryonic status merely from their positions within the body of the adult. However, we consider it inherently unlikely that an adult ichthyosaur would consume, at about the same time, at least six similarly-sized neonates (or, more likely, aborted embryos, based on their size and preservation) of its own or a distinct species – or of both. Other reasons for preferring to interpret these tiny ichthyosaurs as embryos include:

(1) The absence of any signs of physical damage to the vertebral columns and ribs of the specimens.

(2) The absence of any signs of chemical corrosion, such as that caused by digestive secretions.

(3) The total absence, in association with the tiny ichthyosaur skeletons, of any plausible stomach contents, such as the cephalopod hooklets so commonly and characteristically seen in the stomach regions of many ichthyosaur skeletons, especially those of Early Jurassic age (e.g. Pollard 1968).

While it might be argued that six (or eight) embryos is a large number to be borne by an individual ichthyosaur, it should be noted that McGowan (1979) mentioned a specimen with four or five embryos, whereas Böttcher (1990) recorded between one and eleven embryos within the body cavity of ichthyosaurs.

Finally, we would note that, not only do the specimens described here represent the first ichthyosaur embryos reported from the Lower Jurassic rocks of Yorkshire, but they are also the only undoubted reptile embryos of any kind so far described from these rocks, despite their historical and present richness in the fossils of marine crocodylomorphs, plesiosaurs and ichthyosaurs (e.g. Benton & Taylor 1984). Seeley (1887) described a group of supposed plesiosaur embryos (or juveniles) from the 'Lias of Whitby' but these were reinterpreted as crustacean burrows (*Thalassinoides*) around a concretion (Thulborn 1982). In addition, Melmore (1931) described a possible teleosaur (crocodylomorph) egg. This, along with the putative plesiosaur embryos, was reviewed by Benton & Taylor (1984), who suggested that both specimens were probably concretions and wholly inorganic in origin.

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Scientific editing by Stephen K. Donovan

Correction notice: After the online publication of this paper, it came to light that the original collector of the specimen was Mr Mark Hawkes of Edwinstowe, Nottinghamshire. The location of discovery has been updated to Sandsend (to the north of Whitby) rather than Saltwick Bay, which lies immediately south of the

town. The year that the specimen was collected has been updated to 2013. This minor revision of the find locality makes no difference to the stratigraphic data relating to the specimen.

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RESEARCH ARTICLE

A giant Late Triassic ichthyosaurus from the UK and a reinterpretation of the Aust Cliff 'dinosaurian' bones

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Abstract

The largest reported ichthyosaurs lived during the Late Triassic (~235–200 million years ago), and isolated, fragmentary bones could be easily mistaken for those of dinosaurs because of their size. We report the discovery of an isolated bone from the lower jaw of a giant ichthyosaur from the latest Triassic of Lillstock, Somerset, UK. It documents that giant ichthyosaurs persisted well into the Rhaetian Stage, and close to the time of the Late Triassic extinction event. This specimen has prompted the reinterpretation of several large, roughly cylindrical bones from the latest Triassic (Rhaetian Stage) Westbury Mudstone Formation from Aust Cliff, Gloucestershire, UK. We argue here that the Aust bones, previously identified as those of dinosaurs or large terrestrial archosaurs, are jaw fragments from giant ichthyosaurs. The Lillstock and Aust specimens might represent the largest ichthyosaurs currently known.

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Introduction

Ichthyosaurs were major components of Mesozoic marine ecosystems from the Early Triassic (Olenekian) until their extinction in the early Late Cretaceous (Cenomanian). Their wide geographic range in the Early Triassic suggests a very early Triassic radiation for the clade [1]. They reached their maximum disparity in feeding type, locomotory styles, and especially body size (1 m to >20 m) in the Late Triassic [1–3]. A major reduction in the morphospace occupied by ichthyosaurs occurred from the Late Triassic into the Early Jurassic [3,4]. A reduction in taxonomic diversity also occurred within that interval, with only the parvipelvian ichthyosaurs surviving into the Early Jurassic [4,5; but see 6]. Thus the latest Triassic-earliest Jurassic was a critical interval in the evolution of ichthyosaurs.

The largest ichthyosaurs of the Late Triassic were the shastasaurids (Family Shastasauridae), which ranged in size from about 6 m to more than 20 m [5,7]. Shastasauridae, as defined by Ji et al [5], includes six genera of large, long-bodied forms (precaudal centra count >55): *Shastasaurus*, *Besanosaurus*, *Guanlingsaurus*, *Guizhouichthyosaurus*, *Shonisaurus*, and 'Callawayia' *wolonggangensis*. *Himalayasaurus* was tentatively referred to the Shastasauridae [8,9], but the

genus has not been included in recent phylogenies [e.g., 5,10,11], so its affinities are unresolved. Shastasaurids appeared in the Ladinian (Middle Triassic) and persisted to at least the Rhaetian (Late Triassic), with their highest taxonomic diversity occurring in the Carnian (early Late Triassic) [5, 12]. The shastasaurids might even have survived into the early Jurassic [6], although this has been questioned [13]. The last of the shastasaurid taxa that can be assigned to genera are *Shonisaurus sikanniensis*, and, probably *Himalayasaurus tibetensis*, both of which occurred in the Norian (middle to late Late Triassic). The former species is the largest ichthyosaur previously known, with an estimated total length of 21 m [7]. No specimen that can be assigned to a genus is known from the Rhaetian (latest Triassic), but shastasaurids have been reported from France [12]. In addition, large ichthyosaur bones from the Rhaetian of the UK [14] could possibly be shastasaurids, based on their size.

This work reports the discovery of a large, isolated jaw fragment of a giant ichthyosaur from the UK, which estimates suggest was even larger than *S. sikanniensis*. Some ichthyosaurs were as large or larger than contemporaneous Late Triassic dinosaurs. Isolated bone fragments of giant ichthyosaurs could easily be mistaken for those of dinosaurs because of their size. For that reason, this discovery has prompted a reinterpretation of the 'dinosaur bone shafts' [15,16] from the historic Aust Cliff site in southwestern UK.

Material

Institutional abbreviations

BRSMG, Bristol Museum and Art Gallery, UK; BRSUG, University of Bristol, UK; TMP, The Royal Tyrrell Museum of Palaeontology, Alberta, Canada; NSMLV, Nevada State Museum, Las Vegas, USA.

Material examined in this study

The new specimen reported herein, BRSMG Cg2488, is a portion of an ichthyosaurian surangular from the Westbury Mudstone Formation of Lillstock, Somerset, UK. BRSMG Cb3869, BRSMG Cb3870 and BRSMG Cb4063, identified herein as ichthyosaurian, are from the Westbury Mudstone Formation of Aust Cliff, Gloucestershire, UK, as is BRSUG 7007, an isolated vertebra (20 cm diameter) of a very large ichthyosaur. TMP 1994.378.02, the holotype of *Shonisaurus sikanniensis*, is from the Upper Triassic (Norian) Pardonet Formation of northeastern British Columbia, Canada. Measurements were taken with digital callipers and a tape measure, and recorded to the nearest 1 mm.

Geological setting and taphonomy

The Lillstock specimen (BRSMG Cg2488) was collected *in situ* (by PDLs) from the lower part of the intertidal area [ST 185 457] near Lillstock, Somerset. The area lies within an extensive outcrop of Late Triassic and Early Jurassic rocks that are cut by numerous small faults (Fig 1). The specimen was found in the highest part of the Westbury Mudstone Formation (Upper Triassic), 0.8 m below the junction with the Cotham Formation (Fig 2). The almost complete exposures in the intertidal area allow the boundaries of the Westbury Mudstone, Cotham, and Blue Lias formations to be mapped with confidence notwithstanding the complex faulting (Fig 3). The sedimentology and palaeontology of the Westbury Mudstone are well documented [17]. The mudstones have been interpreted as having been deposited in a shallow, storm-dominated shelf sea [18]. The diverse fauna includes quasi marine and fully marine elements including bivalves, conodonts, gastropods, foraminifera and vertebrates that indicate that the whole of the formation is of Rhaetian age.

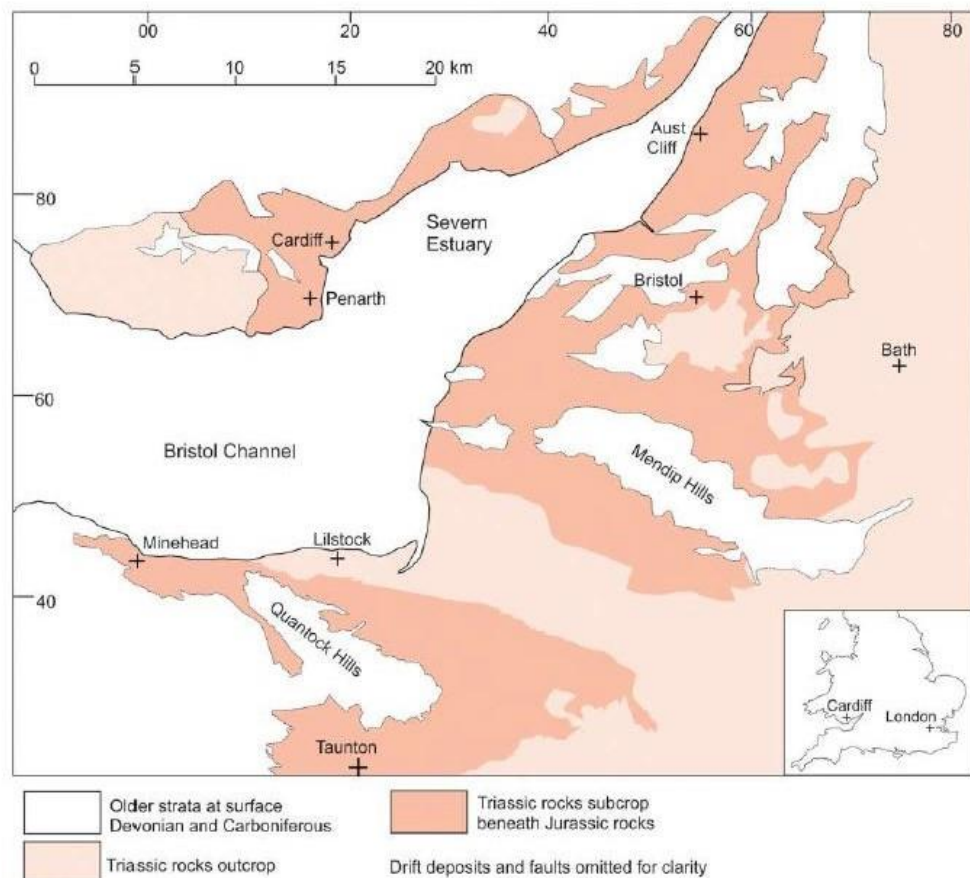


Fig 1. Distribution of the Triassic rocks in the Bristol channel area and the three ichthyosaur localities referred to in the text.

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The Lillstock specimen shows signs of abrasion and encrusting organisms, including bivalves (*Chlamys valoniensis*) and borings, along with probable scavenging marks (Fig 4), similar to what has been documented in other ichthyosaur bones (e.g. [19]). This suggests that the specimen was exposed on the sea floor for some time before burial. The absence of associated bones suggests that the specimen was disarticulated and washed in from a more open-water environment, possibly during a storm. The specimen has been broken into five pieces. It is fractured along its length, and shows displacement along some fractures, notably in the anterior three pieces, which results in some misalignment.

The stratigraphical position of the Late Triassic extinction event has not been identified with certainty in the Severn Estuary region, largely because of the low diversity of the faunas in the lagoonal to brackish-water environments in which the latest Triassic sediments were deposited. The extinction is thought to have occurred in the middle [20] or highest [21] part of the Cotham Formation. The Lillstock specimen thus predates the extinction event and is the latest Triassic occurrence of giant ichthyosaurs in the UK.

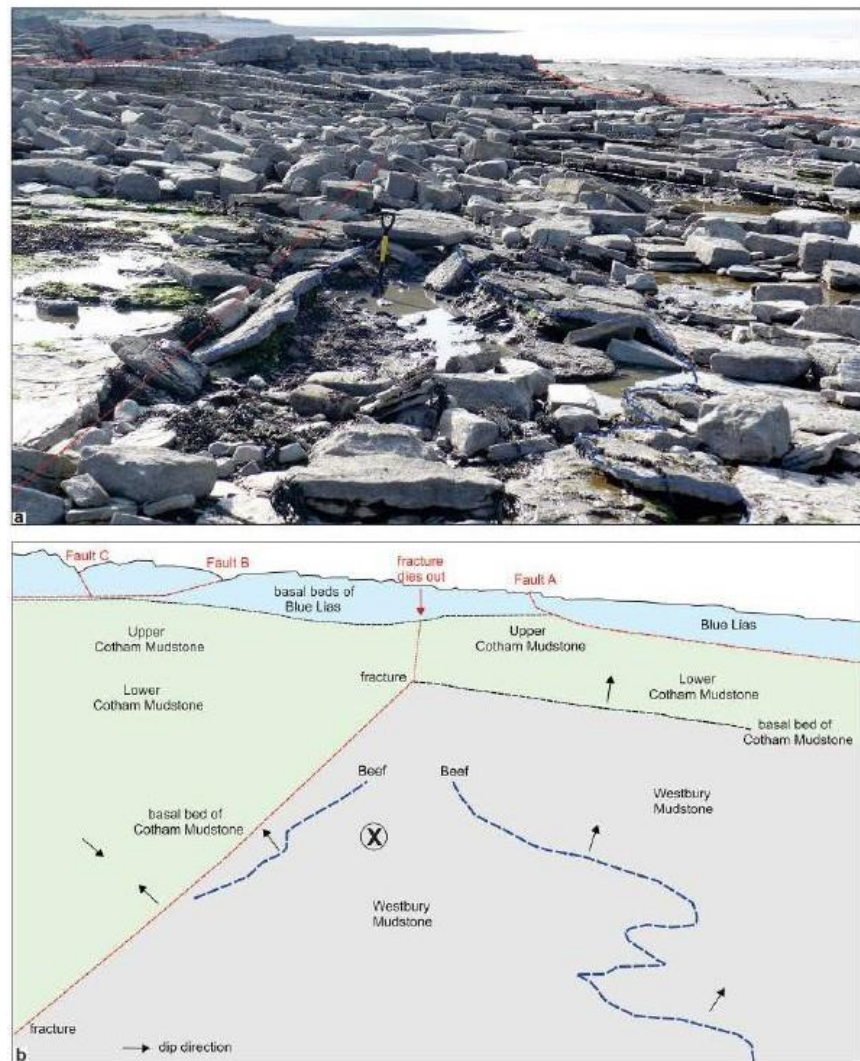


Fig 2. A. View EWE across the intertidal area at the Lilstock site, Somerset, 23rd August 2016. B. Geological sketch map of the site showing the location of the ichthyosaur occurrence in the highest part of the Westbury Mudstone.

<https://doi.org/10.1371/journal.pone.0194742.g002>

Description

The Lilstock specimen is a large, robust, but incomplete, left surangular, preserved in three dimensions and fractured into five articulating pieces that expose the cross-section (Fig 5; DOI: [10.6084/m9.figshare.5975440](https://doi.org/10.6084/m9.figshare.5975440)). The bone is 96 cm long, but an unknown length of the anterior portion is missing, and the bone surface has been heavily worn away in some places, notably on the medial surface. Relatively few surangulars from the largest Triassic ichthyosaurs are known and three-dimensional preservation of isolated ones is rare [7,22].

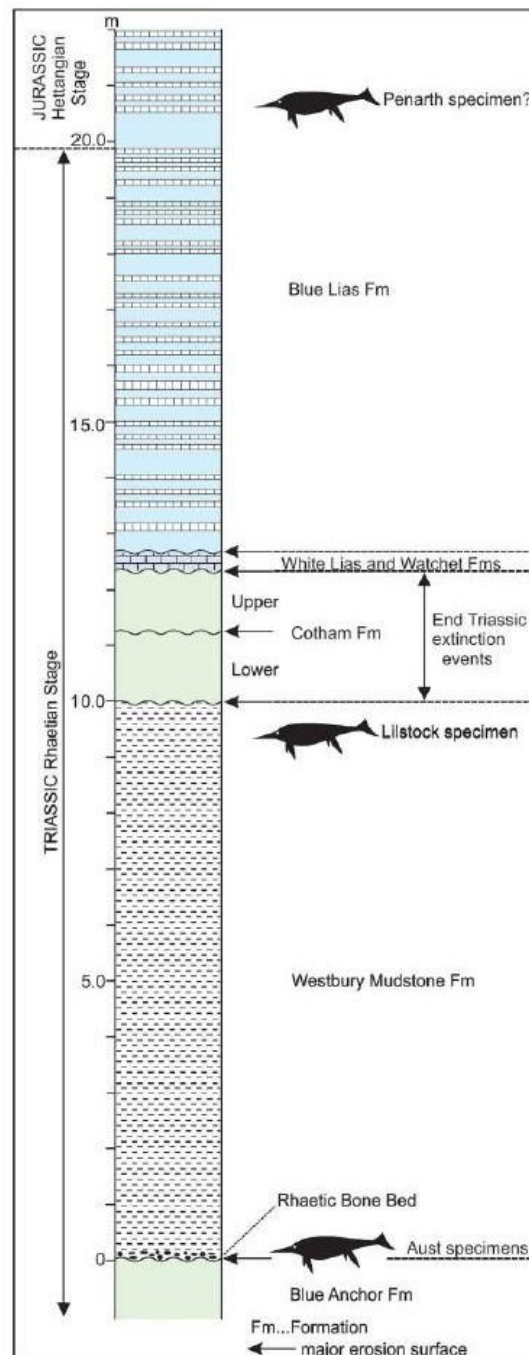


Fig 3. Stratigraphy. Generalised stratigraphy of the Upper Triassic and Lower Jurassic of the Severn Estuary area (after Gallois [53]) showing the positions of the three giant ichthyosaur localities. Stratigraphic position of the Penarth specimen estimated from Martin et al [6].

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BRSMG Cg2488 is similar in overall shape to the surangular of *Shonisaurus sikanniensis* (TMP 1994.378.02) and *S. popularis* [22: figs 19, 20]. The posterior end of the Lillstock surangular is thick and dorsoventrally tall (height 24 cm, but ventral edge is broken), more similar to *S. sikanniensis* than to *S. popularis*. A prominent, triangular M.A.M.E. process (terminology after Fischer et al. [23]) is present, as in *S. popularis*. Parts of both the medial and lateral surfaces of the posterior end are roughened, indicative of muscle attachments [24]. In medial view, the posteroventral portion is concave for articulation with the angular.

The cross section of the posterior end is oval and broad, mediolaterally wider dorsally and in the centre, but narrowing ventrally. This is similar to *S. popularis*, although the ventral edge is much narrower in *S. popularis* (compare Fig 6A with fig 19 in Camp [22]). Along its length, where the dorsoventral height decreases, the surangular is markedly curved, seen best in lateral view (Fig 5A). In part, some of this curvature might be the result of taphonomic distortion (bending) or misalignment along fractures. Similar curvature occurs in the surangular of *Shonisaurus sikanniensis* ([2]; DRL, JAM, pers. obs.) and a slight curvature can be seen in *S. popularis* ([22: fig 19]; Fig 7A). The degree of curvature appears to differ among taxa, but it is impossible to determine its significance with such a small sample size.

The coronoid process is marked by a dorsoventrally oriented ridge that extends ventrally to about the middle of the element, best observed in medial and dorsal views (Fig 5B and 5D). At

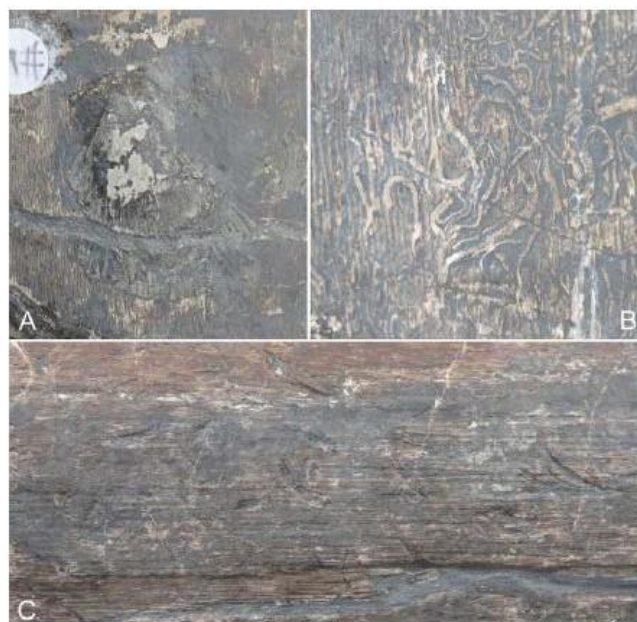


Fig 4. Invertebrate and trace fossils found on the bone surface of the Lillstock surangular (BRSMG Cg2488). A. Bivalve, *Chlamys valoniensis*. B. Numerous borings. C. Probable scavenging marks.

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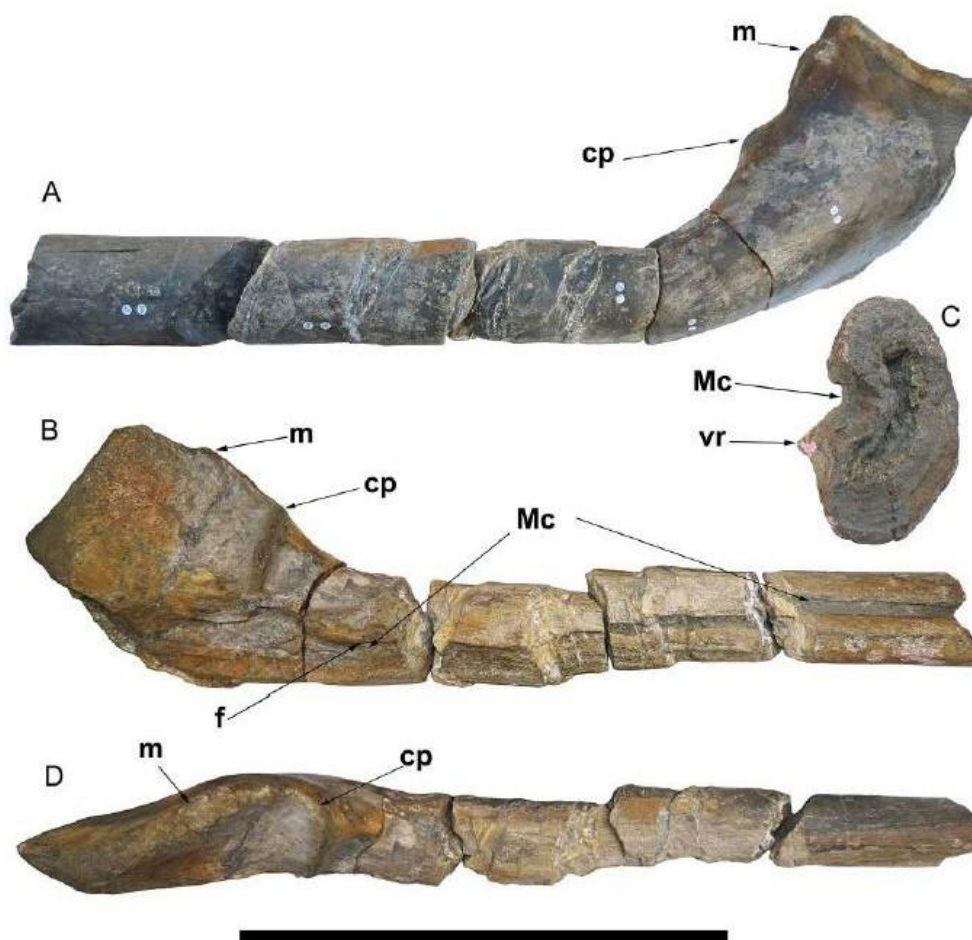


Fig 5. Lilstock ichthyosaur surangular (BRS MG Cg2488). A. Lateral view of Lilstock surangular. B. Medial view of the same, note the prominent groove for the Meckelian canal. C. Cross-section (anterior view, medial to the left) of the anterior-most portion of the surangular, showing the prominent ridge ventral to the Meckelian groove. D. Dorsal view of the Lilstock surangular. Abbreviations. cp, coronoid process; m, M.A.M. E. process; Mc, groove for Meckelian canal; vr, ventral ridge. Scale for the surangular equals 50 cm.

<https://doi.org/10.1371/journal.pone.0194742.g005>

the coronoid process, the dorsoventral height is 19 cm. Anteriorly from there, the height decreases rapidly to about 10 cm for the remainder of the bone. In lateral view, several grooves are about 10 cm anterior to the coronoid process. Anterior to these grooves, along its length, the bone is pierced by several well-defined foramina. We interpret these as part of the *fossa surangularis*, which penetrates through the bone, into the Meckelian canal on the medial surface [24]. A *fossa surangularis* is sometimes absent in ichthyosaurs and its prominence, extent and position varies among taxa [25,26,27]. In medial view, approximately 10 cm anterior to the coronoid process, is a prominent, well-preserved anteroposteriorly elongated foramen which leads into the groove for the Meckelian canal, for the passage of nerves and blood vessels [24, 25]. The groove for the Meckelian canal is poorly preserved posteriorly, but it is continuous to

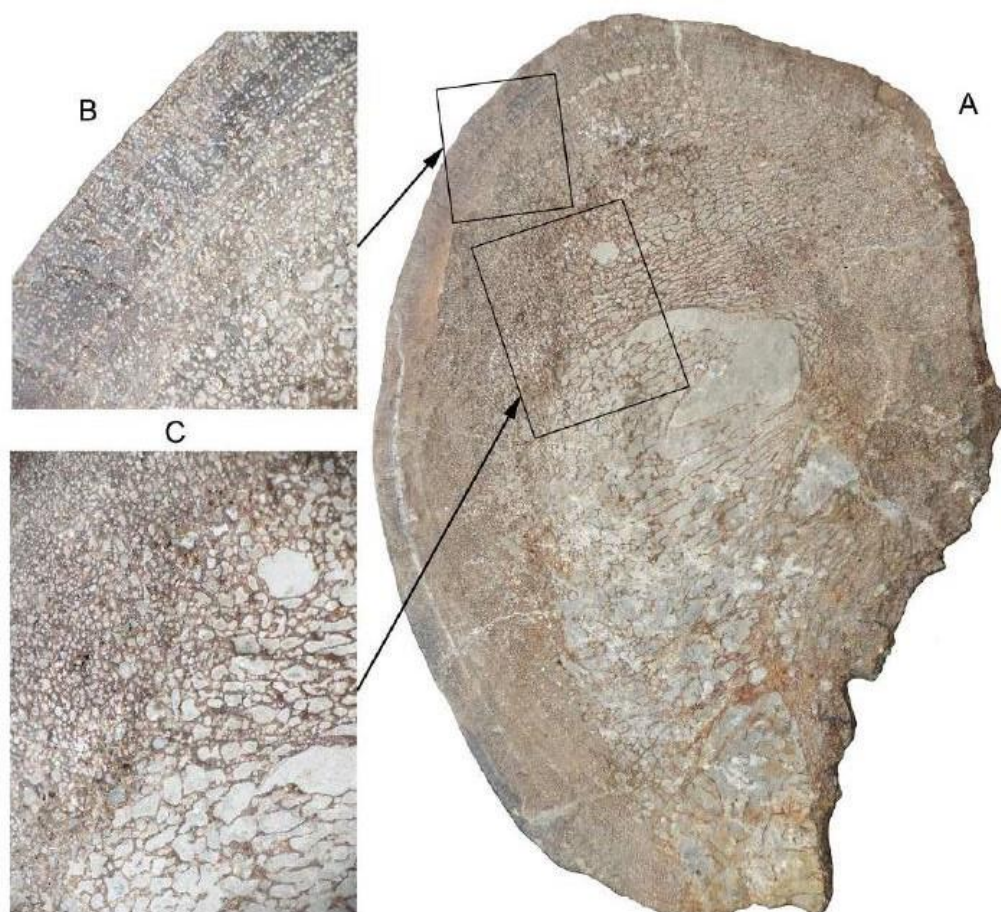


Fig 6. Cross-section of Lilstock surangular (BRSMG Cg2488). A. Cross-section of the second segment from the posterior end. The medial side (right in image) is highly eroded (maximum dimension equals 12.4 cm). B. Closer view of cortical bone and transition to spongy inner bone. Note aligned, longitudinal vascular canals in the cortical bone. C. Closer view of spongy bone, showing numerous, irregularly spaced vacuities, exterior towards the upper left corner. Note that the vacuities are larger towards the interior.

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the anterior end of the bone, where it is better preserved (Fig 5B and 5C). Posteriorly, the groove is more ventrally located but becomes more centrally located anteriorly. This change in position can also be seen in cross-section, where posteriorly the surangular is an elongate oval that becomes less elongate anteriorly. The most anterior segment has the best preserved medial surface, although the anterior end is slightly deformed by crushing. It has a deep, well-preserved channel for the Meckelian canal, made prominent by a sharp ridge, immediately ventral to the canal (Fig 5C). This ridge is present more posteriorly, but is eroded and thus less prominent. Due to the poor preservation, its full extent cannot be determined.

The same Meckelian groove morphology is present in the element identified as the surangular in *S. sikaniensis* ([7: fig 3]; DRL, JAM, pers. obs.; Fig 7B). A cast of the skull of *S. sikaniensis* (TMP 1994.378.02), in dorsal aspect, shows the surangular. One portion of the right

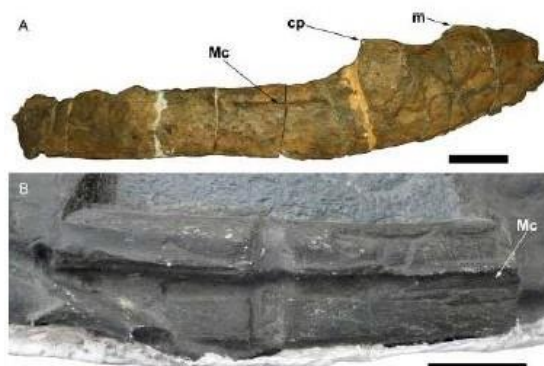


Fig 7. Giant shastasaurid ichthyosaur surangulars. A. Right surangular in medial view of *Shonisaurus popularis* (NSMLV VM-2014-057-C; specimen C-5 of Camp [22]), image courtesy of NSMLV. The specimen is worn and partially reconstructed, but part of the groove for the Meckelian canal is clearly visible. B. Exposed portion of the right surangular in medial view on a cast of the dorsal aspect of the skull of *Shonisaurus sikanniensis* (TMP 1994.378.02). Note the prominent groove for the Meckelian canal. Abbreviations. cp, coronoid process; m, M.A.M.E. process; Mc, groove for Meckelian canal. Scales equal 10 cm.

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surangular is rotated and exposed in medial view, which clearly shows the groove for the Meckelian canal, along with a prominent ridge (Fig 7B). The left surangular can also be examined on the original skull, which is exposed in ventral aspect. Here, the left surangular has been rotated and is exposed in medial view, but the Meckelian groove, although present, is largely obscured because bones are articulated with the surangular. In both instances, it is not possible to see how far the groove extends posteriorly or anteriorly.

The Meckelian groove is visible in other ichthyosaurs that expose a medial view of the surangular, although the prominence and extent of the groove differs. In *S. popularis*, a well-defined groove for the Meckelian is present, but only partly exposed ([22]; Fig 7A). Another example is *Platypterygius longmani*, where the Meckelian groove is very prominent and extends for much of the length of the bone [28; fig 14G]. Similarly, in *Ophthalmosaurus*, the groove for the Meckelian canal is prominent and is marked by a ridge dorsal to a channel [24].

The Cuers ichthyosaur

A very large 'fused mandible' of an ichthyosaur has been reported from the Late Triassic (Rhaetian) of France [12]. The fusion of a mandible is a unique condition among ichthyosaurs of any age. Even the very large shastasaurids, *Shonisaurus sikanniensis* ([7]; DRL, JAM pers. obs.) and *S. popularis* [22] have sutures in the mandible. A second unique feature of the Cuers specimen is what was identified as a narrow dental groove on the medial surface of the 'mandible' [12]. We argue that the Cuers specimen is not a jaw in which all of the bones are fused, but it is a single bone, another very large surangular. The overall shape is similar to the Lilstock specimen [12; fig 2]. The posterior end is markedly curved and dorsoventrally tall. No coronoid process can be confidently identified in the Cuers specimen, due to poor preservation, but the posterior end is high and it decreases fairly abruptly anteriorly, similar to the Lilstock specimen. The position of the groove on the medial surface and its extent along the bone in the Cuers specimen is also very similar to the groove for the Meckelian canal in the Lilstock specimen. The purported presence of a dental groove on the medial side of the mandible is not found in any other ichthyosaur, as noted by Fischer et al. [12], whereas the groove for the

Meckelian canal has been reported on the medial surface in many ichthyosaurs (e.g. [24,28,29]). In the Cuers specimen, the aligned foramina on the lateral surface were identified as part of the *fossa dentalis* [12], but they are similar to the foramina on the lateral surface of the Lilstock specimen and could be part of the *fossa surangularis*. Thus, the bone morphology of the Cuers specimen is consistent with that of a surangular and does not require calling on an unusual morphology for the specimen.

Fischer et al. [12] also provided a redescription of *Ichthyosaurus carinatus* [30], also from the French Rhaetian, which included another large mandible fragment, identified as a portion of dentary. They concluded that the morphology was similar to that of the Cuers specimen in having a continuous dental groove on the medial surface, but noted that the groove appeared much deeper in this specimen. The cross-section is also similar to the Lilstock specimen, especially with respect to a prominent ridge (wall), ventral to the groove [12: supp. S5 fig]. Although this specimen is not as complete as the Cuers ichthyosaur, we suspect that this is probably also a portion of a surangular, and the medial groove is the groove for the Meckelian canal, not the dental groove.

Fischer et al. [12] argued that the Cuers specimen and the remains of '*Ichthyosaurus carinatus*' should be regarded as Aff. Shastasauridae, although they could not be identified more precisely. The geological age and giant size of the Lilstock specimen also suggests possible shastasaurid affinities. Overall, the shape of the Lilstock and Cuers surangulars are more similar to *S. sikaniensis* than to *S. popularis*, especially in the posterior portion.

Implications for the Aust Cliff 'Bone Shafts'

Five large 'limb bone shafts' were collected from the Upper Triassic 'Rhaetic Bone Bed', at or close to the base of the Westbury Mudstone Formation at Aust Cliff, Gloucestershire (Fig 1), although two of the specimens were presumed destroyed in the 1940 bombing of Bristol [14,15,16]. A detailed account of their history has been provided elsewhere [15]. The first described specimen, which is now missing, was originally referred to the Labyrinthodontia [15,31]. This bone, along with two other specimens, was later identified as dinosaurian [15,32]. Recent work has suggested that one or more of the three surviving Aust bones are from stegosaurian dinosaurs [15], sauropod dinosaurs [15,33] (although this has been challenged [34]), indeterminate dinosaurs [14,15,16,35], archosaurian (pseudosuchian) reptiles [16] or indeterminate reptiles [36,37]. The surviving Aust bones have been illustrated elsewhere [15]. Large bones belonging to the sauropodomorph dinosaur *Camelotia borealis* are known from the Westbury Mudstone Formation of Somerset [15,38,39], thus the previous identifications of the Aust bones were consistent with those finds. In each interpretation, other than perhaps the very first description [31], the Aust bones were thought to be from a large terrestrial reptile, although one study noted that the bone microstructure was unusual [16].

This study identifies the Aust bones as ichthyosaurian because of similarities to the Lilstock specimen. The 'unusual foramen' on one of the Aust specimens (BRSMG Cb3869) identified as the nutrient foramen by Galton [15] is similar in morphology and extent to the *fossa surangularis* of the Lilstock specimen (e.g. see Fig 8). However, similar grooves and series of foramina are also found in the premaxilla (*fossa praemaxillaris*) and the dentary (*fossa dentalis*) of several ichthyosaurs (e.g. [23,26,40]). Galton [15] pointed out that a foramen is rarely preserved in the femoral shaft of sauropodomorphs. It is difficult to determine whether this specimen (BRSMG Cb3869) is a portion of surangular, dentary or premaxilla, although the cross-sectional shape of the specimen would suggest it is unlikely to be the latter. Unfortunately, the medial surface is crushed, damaged and partly eroded and thus a groove cannot be identified. The cylindrical shape of BRSMG Cb3869 [15: fig 4F and 4G] is comparable to the third or



Fig 8. Comparison of a portion of the Lilstock specimen to an Aust specimen. A. Anterior-most preserved portion of the Lilstock ichthyosaur surangular (BRSMG Cg2488), showing an elongated foramen on the lateral surface, part of the *fossa surangularis*. B. BRSMG Cb3869, the largest Aust specimen, displaying a similar foramen, interpreted here as most likely part of the *fossa surangularis*. Scales equal 5 cm.

<https://doi.org/10.1371/journal.pone.0194742.g008>

fourth anterior segment of the Lilstock surangular (Fig 5). Another Aust specimen (BRSMG Cb3870), considered the same species as the aforementioned specimen based on bone microstructure [16], lacks any identifiable foramina, but it has suffered significant surface erosion. It and the remaining Aust specimen (BRSMG Cb4063) could be portions of a surangular, another bone from the jaw, or possibly a ceratobranchial (hyoid). The latter is very long and robust in *S. sikamiensis* (120 cm long, with a max diameter of 11 cm [2]). Very large ichthyosaurian vertebrae (e.g., BRSUG 7007, 20 cm diameter) from Aust Cliff have been previously reported [14], so the presence of giant ichthyosaurs at this location has already been confirmed. By comparison, the size of BRSUG 7007 is within the range of centrum size of *S. popularis* and *S. sikamiensis*, although some of those reached diameters of 25 cm or more [7: Appendix 1; 22: tables 1–4; 41].

The posterior segments of the Lilstock specimen preserve a good view of the bone microstructure on the cross-sections (Fig 6A). An irregular vacuity is slightly offset from the centre. The rest of the interior bone is filled with thin trabeculae surrounding large, frequently elongated, vacuities. This texture grades outward into somewhat denser spongy bone with smaller, irregular vacuities (Fig 6B). Another gradual transition leads to the outer cortical bone, which has even smaller vacuities (Haversian canals) that are frequently aligned roughly parallel to the outer bone surface and might define growth lines (Fig 6C). The outer cortical bone layer is relatively thin, 0.8–1.3 cm on the lateral side, for a cross-section width of at least 8.5 cm (measured on the second segment from the posterior end), although the boundary with the spongy bone is not well defined. The more or less concentric pattern of the changes in microstructure suggest that there has not been fusion of two or more bones.

The microstructure of the Aust bones is similar to that of the Lilstock ichthyosaur in the large region of spongy bone that grades into a relatively thin, outer layer of cortical bone [16]. Both have longitudinally oriented vascular canals, although the canals are more numerous in

the Lilstock ichthyosaur. Both the Lilstock specimen and the Aust bones have abundant vacuities in their bones, resulting in a less dense bone that is more typical of aquatic tetrapods than terrestrial ones [42,43]. The details of the microstructure are beyond the scope of the paper. In any case, it is likely that different taxa of ichthyosaurs will differ in their bone microstructure, as is the case for mosasaurs, marine squamates of the Cretaceous [42]. The unusual microstructure of the Aust bones was interpreted as an indication that the animal was still growing, possibly a mechanism to attain a large size [16]. A similar mechanism was suggested for mosasaurs [43]. Mosasaurs retained characteristics of juvenile bone, indicating paedomorphosis, a mechanism that could have allowed mosasaurs to continue juvenile growth rates after sexual maturity and reach much larger sizes than terrestrial squamates [43]. Such mechanisms could also explain the giant size of ichthyosaurs.

Size estimation

Determining the size of an extinct animal, especially if it is known from isolated or poorly preserved remains, is a challenge. Large shastasaurid ichthyosaurs can provide a rough estimate for the total length of the Lilstock ichthyosaur by using a simple scaling factor. Such estimates, however, are not entirely realistic because of differences among taxa in bone morphology and overall body proportions, as well as effects of individual variation and allometric growth [44]. Nonetheless, simple scaling is commonly used to estimate size, especially when comparative material is scarce (e.g., [45,46]).

The largest shastasaurid, *Shonisaurus sikanniensis* has an estimated length of up to 21 m, based on length estimates of the specimen *in situ* [7]. The only specimen of the species (TMP 1994.378.02) preserves portions of the surangular, which has a maximum height at the posterior end of 19 cm ([7]; DRL, JAM pers. obs.). The maximum height of the posterior end of the surangular in the Lilstock specimen is at least 24 cm, ~25% larger than that. Simple scaling would suggest that the Lilstock ichthyosaur has an estimated total length of up to 26 m, approaching the size of a blue whale.

A smaller shastasaurid, *Besanosaurus leptorhynchus* has an estimated total length of 5.4 m [47]. Measurements of a drawing of the skull [47: fig 9] gives an estimate for the height of the surangular exposure as 4.5–4.7 cm at the coronoid process. The height of the Lilstock surangular at the coronoid process is 19 cm, suggesting that the Lilstock ichthyosaur is about four times larger than *Besanosaurus*, with a total length estimate of about 22 m.

It is difficult to provide an estimate for the skull length of the Lilstock specimen because the skull length of *S. sikanniensis* is itself an estimate, and relative skull length varies among shastasaurid taxa [22,47]. Furthermore, there are clear differences in snout length in shastasaurids, some with long snouts (e.g. *Shonisaurus popularis* [22], *Besanosaurus* [47]), and others with short snouts (*Guanlingsaurus liangae* [10,48]).

The same method has its limitations, but a comparison can be made to the Aust specimen (BRSMG Cb3869) that might be a portion of surangular. The maximum cross-sectional dimension of the Aust fragment is 13.8 cm ([15]; DRL, PDLS pers. obs.), which is similar in cross-sectional shape to a portion of the Lilstock surangular anterior to the coronoid, where the bone is roughly cylindrical. That region of the Lilstock specimen has a dorsoventral height of 10.6–9.2 cm, suggesting that the Aust ichthyosaur was a much larger animal, perhaps more than 30% larger. If the Aust specimen is a portion of the dentary or premaxilla, then the ichthyosaur was probably even larger. Of course, considering that the Lilstock and Aust bones represent only portions of the lower jaw, these estimates are very speculative. Nevertheless, it is reasonable to suggest that the Lilstock ichthyosaur was on the order of 20–25 m long. Previously, the largest ichthyosaur from the UK was estimated as about 15 m, based on isolated

elements of an unnamed ichthyosaur from the Early Jurassic [49]. Even accounting for the limitations in the size estimates, the Lilstock and Aust ichthyosaurs were much larger.

Conclusion

The discovery of a large ichthyosaur surangular from the Upper Triassic of England has documented that giant ichthyosaurs persisted well into the Rhaetian Stage. The Upper Triassic also records the appearance of the more advanced parvipelvian ichthyosaurs [50–52]. The Lilstock specimen confirms that giant shastasaurid-like ichthyosaurs overlapped temporally (before and possibly after the Late Triassic extinction) with the early parvipelvian ichthyosaurs [12]. A large, shastasaurid-like radius from Penarth has been reported from the lowest Jurassic [6] (Fig 3), indicating that the shastasaurids might have survived the Late Triassic extinction. However, the specimen was found loose on the beach and the stratigraphy of the specimen is not well constrained. It is possible that the specimen is actually from the Westbury Mudstone Formation [13], which would be more consistent with the occurrences of the Lilstock and Aust specimens.

The Lilstock surangular has also clarified the affinities of the historically important Aust Cliff 'dinosaurian bone shafts'. They are portions of giant ichthyosaurs and are not an example of an early experiment in gigantism in archosaurian reptiles as previously suggested [16]. Size estimates suggest that the Lilstock and Aust ichthyosaurs are the largest ichthyosaurs presently known.

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Writing – review & editing: Dean R. Lomax, Paul De la Salle, Judy A. Massare, Ramues Gallois.

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A SECOND SPECIMEN OF *PROTOICHTHYOSAURUS APPLEBYI* (REPTILIA: ICHTHYOSAURIA) AND
ADDITIONAL INFORMATION ON THE GENUS AND SPECIES

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ABSTRACT

Three isolated, partial skulls from historic collections, previously identified as *Ichthyosaurus communis* are herein assigned to *Protoichthyosaurus prostaxialis*. A fourth, nearly complete skull is referred to *Protoichthyosaurus applebyi*, only the second known specimen of the species. It provides additional information on the posterior portion of the skull and mandible. The diagnosis of *P. applebyi* is emended to include a postorbital that is dorsoventrally long but anteroposteriorly narrow relative to its length. It separates most of the jugal dorsal ramus from the orbit margin and makes up much more than half of the orbit posterior margin. The genus *Protoichthyosaurus* can be most easily distinguished from its sister taxon, *Ichthyosaurus*, by the forefin morphology, with three primary digits (II-IV) in the former and four primary digits (II-V) in the latter. In addition, the pineal in *Protoichthyosaurus* is bordered posteriorly by the parietals rather than being entirely enclosed by the frontals as in *Ichthyosaurus*. Many skull features, although not unique to *Protoichthyosaurus*, can together distinguish it from *Ichthyosaurus*. These include: a low-crowned skull with a long, slender rostrum; a large, posteriorly high, triangular external naris; an asymmetric maxilla with a long anterior process; a dorsoventrally long prefrontal anterior process that separates the dorsal process of the lacrimal from the orbit margin; and tooth roots with deep grooves that extend to the base of the crown. However, these characters vary among individuals and are often difficult to assess because of orientation, completeness, or preservation. Characters that distinguish individual species of *Protoichthyosaurus* from individual species of *Ichthyosaurus* are less subjective and often more easily evaluated.

INTRODUCTION

Recent work has shown that the Lower Jurassic genus *Protoichthyosaurus* Appleby, 1979, is valid and can be distinguished from the more common and better known genus *Ichthyosaurus* De la Beche and Conybeare, 1821, on the basis of a unique forefin (Lomax et al., 2017). Without the presence of a forefin, determining the identification of an isolated skull or other elements of the postcranial skeleton as either *Protoichthyosaurus* or *Ichthyosaurus* can be difficult. *Protoichthyosaurus*, however, possesses several skull characters that are not found together in any species of *Ichthyosaurus* (Lomax et al., 2017), although each species shares some characters. In this paper, we review the combination of features of the skull that distinguish the two genera and discuss the variation in those features.

The genus has two species: *Protoichthyosaurus prostaxialis*, first described by Appleby (1979), and *P. applebyi*, recently recognized by Lomax, et al. (2017). Differences in skull morphology can distinguish the two species from each other and from species of *Ichthyosaurus*. Here we report on four specimens, isolated partial skulls that had previously been identified as *Ichthyosaurus communis*, but can be assigned to species of *Protoichthyosaurus*. One skull is

only the second specimen known of *P. applebyi* and provides additional information on the skull morphology of the species. This paper also presents a summary of skull characters that can distinguish species of *Ichthyosaurus* from species of *Protoichthyosaurus*. Species identifications are often necessary to confirm the generic assignment if the proximal forefin is not preserved.

Institutional abbreviations—BRLSI, Bath Literary and Scientific Institution, UK; BU (formerly BIRUG), Lapworth Museum, University of Birmingham, UK; GPIT, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Germany; LEICT, Leicester Arts and Museums Service, New Walk Museum and Art Gallery, UK; NHMUK (formerly BMNH), The Natural History Museum, London, UK; NMING, National Museum of Ireland – Natural History, Dublin; NMW, National Museum of Wales, Cardiff, UK; SOMAG (formerly AGC), Alfred Gillett Collection, cared for by the Alfred Gillett Trust (C & J Clark Ltd), Street, Somerset, UK; TTNCM, Somerset County Museum, Taunton, UK; UNM, University of Nottingham Museum, UK.

MATERIALS

The specimens of *Protoichthyosaurus* described here are from historic collections, as are almost all referred specimens and the holotypes of the two species (Lomax et al., 2017). Although all four are preserved in three dimensions, only one or two aspects of the skull of each specimen are sufficiently well-preserved to provide information on morphology. None of the skulls are complete.

NMING:F16625 (Figure 1) was part of the William Lee Collection (acquired by the Royal Dublin Society by purchase in 1867, incorporated into the state-run Dublin Science and Art Museum, Ireland, in 1877, now the National Museum of Ireland), although the specimen and species list of the original acquisition is missing (Nigel Monaghan, pers. comm.). The present museum label suggests that it is probably specimen “o” cited by Lydekker (1891, p. 50) in his catalogue of specimens at the Dublin Science and Art Museum. Two old NMING labels affixed to the specimen indicate that it is from Barrow-upon-Soar, Leicestershire, which is also the location indicated by Lydekker (1891) for specimen “o”. The preservation and bone color of the specimen is consistent with the preservation style from that locality. The specimen is the middle portion of a skull and mandible, from about the middle of the orbit to several centimeters anterior to the external naris, preserved in three dimensions. Bones comprising the anterior, dorsal, and ventral margin of the orbit and those surrounding the external naris are well preserved in right lateral view, but the skull is broken posterior to that. In left lateral view, the bones are fragmented and portions of their surfaces have been sheared off, and so this side of the skull provides little information. The dorsal side preserves mainly the nasals and the anterior portions of the left prefrontal, parietal and frontal, but the same elements from the right side are damaged, displaced, or missing. The ventral side of the skull is poorly preserved and damaged, so does not provide any useful information.

NMING:F8756 (Figure 2) is a poorly preserved, isolated skull in three dimensions, but the anterior portion of the rostrum and some portions of the posterior part of the skull are missing. As with the previous specimen, it is from the William Lee Collection. Information with the specimen identify it as Lydekker’s (1891, p. 49-50) specimen “k” from Barrow-upon-Soar, Leicestershire. Lydekker’s (1891) comment on the “large size of the teeth” supports this attribution because the teeth are large and very prominent on the specimen. NMING:F8756 has a similar bone color and preservation style as NMING:F16625. The specimen was removed from plaster in 1988 and presently is in four pieces. The right lateral view provides the most information,

although the skull is broken across the lacrimal and maxilla anterior to the orbit. The second break is in the premaxillary portion of the rostrum, and the third break is at the anterior end of the rostrum forming a very small anterior piece. In right lateral view, a portion of the left mandible is exposed, which is presumably due to taphonomic distortion. In left lateral view, only the portion of the skull anterior to the orbit is present, but it is more poorly preserved than the right side. In dorsal view, the entire posterior half of the left side of the skull is missing, although the dorsal surface provides some information. In ventral view, the right mandible is preserved for the entire length of the specimen but the left mandible is absent on the posterior piece. Mediolateral crushing has moved the two sides of the mandible so that they touch for the entire rostrum length anterior to the maxilla.



FIGURE 1: NMING:F16625, *Protoichthyosaurus prostaialis* preorbital-narial region of skull, probably from Barrow-upon-Soar, Leicestershire, UK. Although the specimen is preserved in three dimensions, the other views are too poorly preserved to provide information. Anterior to the right. Scale = 10 cm.

GPIT 1796/1 (Figure 3) is an isolated skull from the Lyme Regis area, Dorset, one of only three specimens of *Protoichthyosaurus* from that location. The anterior portion of the rostrum is missing. The left side and dorsal surface are poorly preserved, but the right side and ventral surface preserve much of the original bone surface. This results in a clear difference in color, with the eroded surface being much lighter (tan) than the other (brown).

NHMUK R1164 (Figure 4) is another isolated skull from the Lyme Regis area, Dorset (Lydekker, 1889, p. 46). Interestingly, the specimen was mentioned and figured by Motani (2005, p. 341-342, fig. 3D-F), who suggested that it was not *Ichthyosaurus*, but probably represented a new genus or species. The skull is in three-dimensions but laterally compressed, and it is almost entirely removed from matrix. The anterior tip of the rostrum, probably



FIGURE 2: NMING:F8756, nearly complete skull of *Protoichthyosaurus prostaialis*, probably from Barrow-upon-Soar, Leicestershire, UK, in right lateral view. Anterior end of rostrum is missing. Although the specimen is preserved in three dimensions, the other views are too poorly preserved to provide information. Scale = 10 cm. Photo courtesy of National Museum of Ireland.

less than 5 mm, is missing. Five cervical centra and partial neural spines are articulated with the skull, one of which might be the atlas-axis, but it is poorly preserved and partially buried. The skull is best preserved in right lateral view, although the ventral portion of the lacrimal is missing (Figure 4), exposing the dorsal portion of the maxilla that is normally overlain by the lacrimal and subnarial process of the premaxilla. The left side preserves only the rostrum, with almost the entire post-narial portion of the skull missing. The dorsal side does not provide much information but shows the strong lateral compression of the rostrum. The portion of the skull posterior to the nasals is missing except for a few poorly preserved bones on the right side. In ventral view, the posterior half of the left mandible is missing, and the remaining bones provide little useful information.

In addition, as part of this study, we located an additional specimen of the genus, an isolated articulated forefin (TTNCM: 59/2000) collected from the shoreline at Lillstock, Somerset, U.K. The humerus is damaged, but the rest of the fin is nearly complete. The specimen has three primary digits (II-IV), a bifurcation of digit II in the metacarpal row, a second more distal bifurcation of digit II, and the posterior metacarpal of digit II nearly separates distal carpals two and three. These features are diagnostic for the genus. The specimen is not discussed further.

SYSTEMATIC PALEONTOLOGY

ICHTHYOSAURIA de Blainville, 1835
 ICHTHYOSAURIDAE Bonaparte, 1841
PROTOICHTHYOSAURUS Appleby, 1979

Revisions to the Diagnosis—Diagnosis as emended in Lomax et al. (2017), but with the following additions and corrections to the “unique combination of characters”: pineal bordered posteriorly by parietals;

prefrontal anterior process separates most, if not all, of dorsal process of lacrimal from anterior orbit margin (shared with *Ichthyosaurus larkini*, *I. somersetensis*); large external naris, usually somewhat triangular (much higher posteriorly than anteriorly); strongly asymmetric maxilla with long, slender anterior process; prominent grooves on tooth root extend to base of crown (shared with *Temnodontosaurus*, *I. somersetensis*); three primary digits (II, III, IV) in forefin (shared with *Stenopterygius*, *Temnodontosaurus*, and others, but not *Ichthyosaurus*); digital bifurcation of digit II results in five digits in forefin (shared with *Ichthyosaurus*).

Additional Referred Specimen—TTNCM: 59/2000, a left forefin and associated partial scapula, ribs, and vertebrae collected *ex situ* at Lillstock, Somerset, UK.

Remarks—The emended diagnosis in Lomax et al. (2017) stated that the jugal anterior process does not extend beyond the anterior edge of the orbit. This is incorrect. The anterior extent of the jugal anterior process varies among specimens of *P. prostaialis* and so it is not diagnostic for the genus. Additionally, Lomax et al. (2017) stated that a long internasal foramen was always present, but we have found that the presence and size varies among specimens and thus is likely the result of individual variation or preservation. The midline of the nasals is often filled with matrix, making it difficult to confirm the presence of a foramen. As also identified by Maisch and Matzke (2000), a depression along the midline of the nasals usually occurs in specimens that preserve the skull roof. The depression is usually broader and deeper posteriorly. The feature seems to be more common in *Protoichthyosaurus* than in *Ichthyosaurus*.

In addition, an error in the terminology used by Lomax et al. (2017) resulted in an error stating that the forefin of *Protoichthyosaurus* had five primary digits,

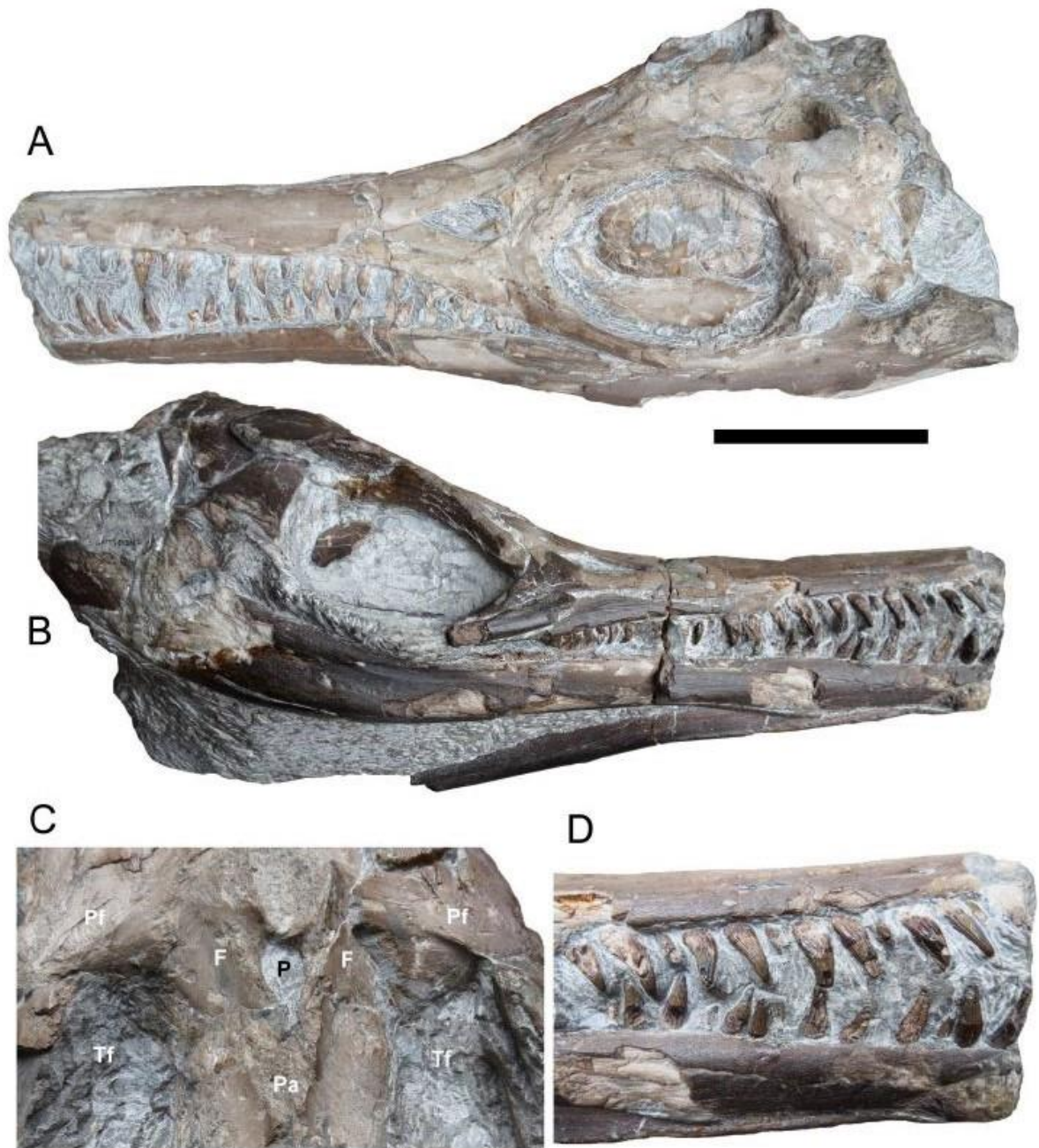


FIGURE 3: GPIT 1796/1, isolated skull of *Protoichthysaurus prostaialis* from the Lyme Regis area, Dorset, UK. A. Skull in left lateral view, but exposing some of the skull roof. B. Right lateral view of the same. C. Close-up of the skull roof, showing the pineal foramen between the frontals and parietal. D. Close-up of some of the teeth figured in 'B'. Abbreviations: F, frontal; P, pineal foramen; Pa, parietal; Pf, postfrontal; Tf, temporal fossa. Scale = 10 cm.

which it shared with *Ichthyosaurus*. Both genera have anterior digital bifurcations in the forefin, resulting in five digits (as defined by Cooper et al., 2007, fig.1). However, *Ichthyosaurus* has four primary digits (II, III, IV, V) whereas *Protoichthyosaurus* has only three (II, III, IV), regardless of the number of bifurcations. In *Protoichthyosaurus*, a proximal bifurcation results in two metacarpals associated with digit II. Thus four elements are in the metacarpal row (fourth row of the forefin), the same number that usually occurs in *Ichthyosaurus*. However in *Ichthyosaurus*, metacarpal five and distal carpal four contact the distal edge of the ulnare; whereas in *Protoichthyosaurus*, distal carpals three and four contact the ulnare, and metacarpal five is absent (Motani, 1999; Lomax et al., 2017). The combination of three primary digits (II-IV) and an anterior digital bifurcation in *Protoichthyosaurus* is unique among parvipelvic ichthyosaurs.

Finally, one of the specimens described here confirms that the pineal opening is between the frontal and parietal (Figure 3C), as suggested by Lomax et al. (2017), a feature shared by *Leptonectes*, *Stenopterygius*, *Temnodontosaurus* and others (McGowan & Motani, 2003, fig. 69; Motani, 2005). This is different from *Ichthyosaurus*, where the pineal is at the posterior edge of the frontal, but completely enclosed by it (Motani, 2005; Massare and Lomax, 2017). Preservation can often make this difficult to discern.

SKULL FEATURES OF *PROTOICHTHYOSAURUS*

In addition to the position of the pineal opening, which is not frequently preserved, several skull characters can distinguish *Protoichthyosaurus* from *Ichthyosaurus*, but only in combination: (1) *Protoichthyosaurus* has a low skull, with a low slope of the crown from the temporal region to the external naris. Skulls of *Ichthyosaurus* vary, but usually have a higher crown, especially *I. larkini* and *I. conybeari*. (2) *Protoichthyosaurus* has a long slender rostrum, similar to *I. larkini*, but not as robust as the long rostra in *I. anningae* and some specimens of *I. communis*. The difference is not easily quantified because the slenderness is not reflected in the snout ratio (as defined by McGowan, 1973). (3) In lateral view, the prefrontal of *Protoichthyosaurus* is dorsoventrally long anteriorly, and extends along part of the anterior orbit margin, separating most (if not all) of the dorsal process of the lacrimal from the orbit margin, as in *Ichthyosaurus larkini* and *I. somersetensis*. By itself, it cannot distinguish the genus from *Ichthyosaurus*. (4) Uncrushed skulls of *Protoichthyosaurus* usually have a large, triangular external naris that is distinct from that

of *Ichthyosaurus* because it is dorsoventrally very high posteriorly. Some specimens of *Ichthyosaurus*, notably *I. somersetensis*, have a triangular naris, but the difference in height between the posterior and anterior ends is not as great. The dorsoventral height of the naris in *Protoichthyosaurus* is greater than in *Ichthyosaurus*, making it appear much larger. *Ichthyosaurus conybeari* and *I. breviceps* also have dorsoventrally high nares, but they are shorter anteroposteriorly than in *Protoichthyosaurus*. The amount of flattening and the orientation of the skull, however, can distort the shape of the naris and its dorsoventral height, so the naris shape is not distinctive in all specimens. In some specimens, it is an elongated oval rather than triangular, so the lack of a triangular shape does not rule out the genus. (5) *Protoichthyosaurus* has an asymmetric maxilla with a long, slender anterior process in lateral view, measured from the maximum height of the maxilla, and extends well beyond the naris. This is similar to *I. conybeari*. Many specimens of other species of *Ichthyosaurus* have maxillae with anterior processes that extend beyond the external naris. The asymmetry is the important feature in recognizing *Protoichthyosaurus*, but even then, the difference from *I. conybeari* is subtle. The orientation of the skull, however, can affect the apparent lengths; a more ventral orientation can make processes appear longer; a more dorsal orientation can make processes look shorter. (6) *Protoichthyosaurus* and some species of *Ichthyosaurus* have prominent grooves and ridges in the tooth roots. In *Protoichthyosaurus* and *I. somersetensis*, the grooves extend to the base of the crown and are continuous with the ornamentation of the crown itself (Figure 4C). It does not occur on every tooth of every specimen, largely because of preservation. In other species of *Ichthyosaurus*, the root is usually smooth at the base of the crown. Because of the large roots and wide bases of the crowns, the teeth of *Protoichthyosaurus* often look massive in comparison to the slenderness of the snout.

Most of these characters are qualitative and difficult to assess. They are all variable, in part because of individual variation, but also the result of differences in completeness, orientation, and preservation. A given specimen might not display the typical morphology of every feature, making a generic assignment difficult, especially on poorly preserved skulls. Individual species of each genus, however, have unique combinations of characters that distinguish them from each other, and sometimes species can be more readily identified than the genus, thus allowing assignment to *Ichthyosaurus* or *Protoichthyosaurus* (see below).

PROTOICHTHYOSAURUS PROSTAXALIS Appleby, 1979

Holotype—BRLSI M3553 (formerly B. 1963'5/OS), a partial skull, pectoral girdle, and both forefins, preserved in ventral view.

Additional Referred Specimens—NMING:F16625, the middle portion of a skull preserved in three dimensions. NMING:F8756, a poorly preserved, isolated skull in three dimensions. GPIT 1796/1, an isolated skull in three dimensions, missing the anterior portion of the rostrum.

Locality and horizon—NMING:F16625 and NMING:F8756 are probably from Barrow-upon-Soar, Leicestershire, England, UK, as are some other referred specimens of *P. prostaxalis* (Lomax et al., 2017). Specimens from that locality might be from the Tilmanni Ammonite Zone (Martin et al., 1986; but see Page, 2010; Weedon et al., 2017), but as with most historical specimens, specific stratigraphic information is not available. GPIT 1796/1 is from Lyme Regis, specifically from the Bucklandi Ammonite Zone (lower Sinemurian) according to the label with the specimen. This confirms the occurrence of the genus and species in the lower Sinemurian.

Diagnosis—As emended in Lomax et al. (2017).

Remarks—Only fragmentary hind fins of *Protoichthyosaurus prostaxalis* are known, but they indicate that three primary digits (II, III, IV) are present. This feature is shared with *Ichthyosaurus* (note error in terminology in Massare and Lomax, 2017), and it might prove to be a genus characteristic for *Protoichthyosaurus* as well. Hindfins of *Ichthyosaurus* have a proximal bifurcation of digit II in the metacarpal or first phalangeal row (Massare and Lomax, 2018). Whether a similar bifurcation occurs in either species of *Protoichthyosaurus* is unknown.

DESCRIPTION

None of the specimens herein referred to *Protoichthyosaurus prostaxalis* preserves a forefin with the diagnostic features of the genus. NMING:F16625 (Figure 1) has a large, triangular external naris that is high posteriorly and tapers anteriorly. NMING:F16625 might also have an internasal foramen or at least a depression in the nasals at the midline of the skull, but the area is filled with matrix. The maxilla is dorsoventrally high and roughly triangular, although its dorsal edge is somewhat rounded and partially covered by matrix. The maxilla morphology is most similar to that of BU 5323, a referred specimen of *P. prostaxalis*. Furthermore, the narrow anterior process of the maxilla extends well beyond the external naris and is much longer than the posterior process, measuring from the maximum height of the maxilla. The high, asymmetric

maxilla in lateral view in NMING:F16625 is characteristic of *P. prostaxalis*. *Ichthyosaurus somersetensis* can have a long anterior process (e.g., ANSP 15766), but the very slender posterior process is even longer, resulting in the opposite sense of asymmetry as *P. prostaxalis*. *Ichthyosaurus communis* can also have a long anterior process of the maxilla (e.g., NHMUK R1162, SMNS 13111), but on such specimens, the posterior process is also long, making the maxilla nearly symmetric. In NMING:F16625, because of damage to the anterior ends of the maxilla and nasal, it is unclear whether the maxilla extends as far as the nasals in lateral view. The left maxilla is too poorly preserved to provide any useful information. The lacrimal is triradiate, as also occurs in most species of *Ichthyosaurus*, but the dorsal process is much longer than the anterior process, a diagnostic feature of *P. prostaxalis* (Lomax et al., 2017). The anterior process of the lacrimal would have contacted the damaged subnarial process of the premaxilla slightly posterior to the mid-point of the ventral margin of the external naris. The dorsal process of the lacrimal is dorsoventrally high and has a long contact with the prefrontal. The posteroventral process of the lacrimal is longer than both the dorsal and anterior processes, as in *P. prostaxalis* and some species of *Ichthyosaurus*. However, disarticulation or the orientation of the skull can affect the extent of exposure of the posteroventral process, and thus its perceived length relative to the other processes. The prefrontal has a dorsoventrally long anterior process that separates the dorsal process of the lacrimal from the anterior border of the orbit, as in *Protoichthyosaurus*, *I. somersetensis*, and *I. larkini* (Lomax and Massare, 2017; Lomax et al., 2017). The jugal extends anteriorly beyond the anterior edge of the orbit, as in NHMUK R36958, another specimen of *P. prostaxalis*, although it might be displaced anteriorly in NMING:F16625. In other specimens of *P. prostaxalis*, the jugal extends just to the anterior edge of the orbit or only slightly beyond (e.g., BU5323, BRLSI M3555, GPIT 1796/1). Thus the position of the anterior extent of the jugal is variable and is not diagnostic of the genus (contrary to Lomax et al., 2017). The anterior termination of the jugal in NMING:F16625 is blunt rather than pointed and does not look damaged, similar to the shape in NHMUK R36958. *Ichthyosaurus larkini* has a similar blunt termination of the jugal, but in that species, the jugal extends much farther anteriorly than in NMING:F16625 and it separates the lacrimal from the maxilla. The extent of the prefrontal, the asymmetric maxilla with a long anterior process, and the large, triangular external naris identifies the specimen as *Protoichthyosaurus*. The dorsoventrally high maxilla and relative size of the dorsal and anterior processes of lacrimal identifies NMING:F16625 as *P. prostaxalis*.

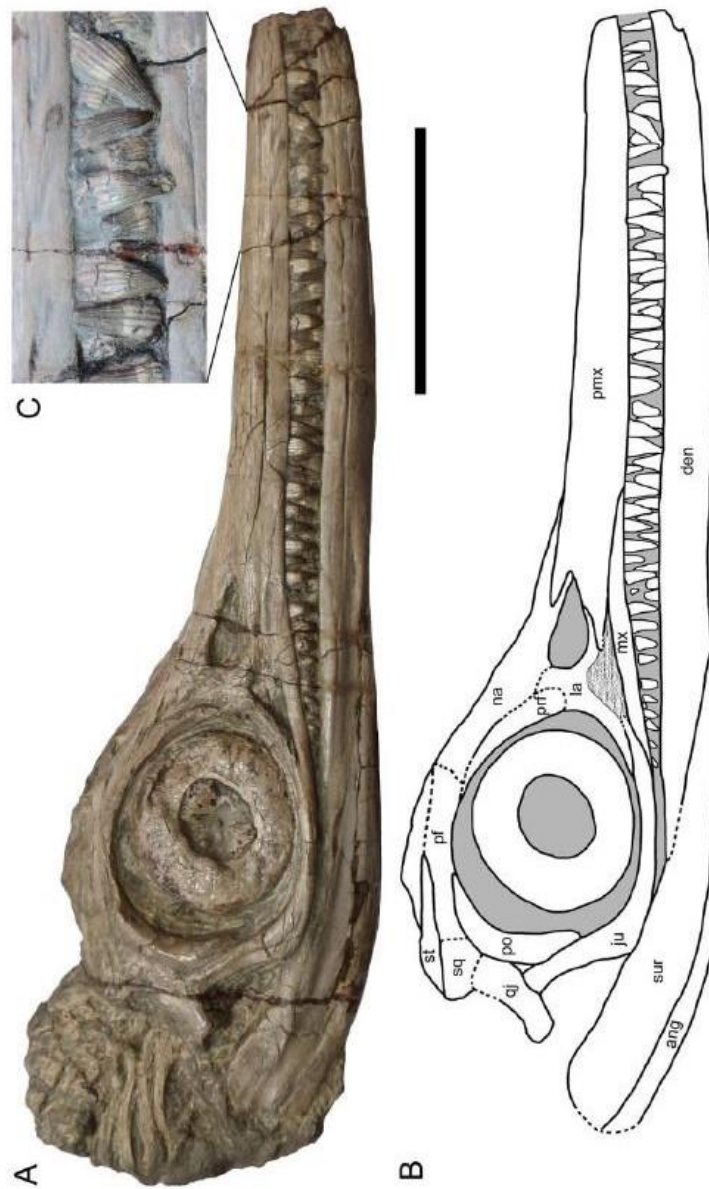


FIGURE 4: NHMUK R1164, nearly complete skull of *Protoichthyosaurus* appleyby from the Lyme Regis area, Dorset, UK. A. Right lateral view, anteriormost tip of rostrum is missing. Although the specimen is preserved in three dimensions the other views are too poorly preserved to provide information. B. Interpretive illustration of skull. Stippled region indicates where lacrimal is missing, exposing bones that were beneath it. Gray areas are matrix. C. Close-up of anterior premaxillary teeth. Abbreviations: ang, angular; den, dentary; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pf, postfrontal; po, postorbital; pmx, premaxilla; prf, prefrontal; qj, quadratojugal; sq, squamosal; st, supratemporal; sur, surangular. Scale = 10 cm.

NMING:F8756 (Figure 2) has a low skull with a long slender rostrum. The preserved length is 49 cm, with a preorbital length of 34.5 cm, although an unknown length of the anterior rostrum is missing. The preserved mandible length is 54 cm (snout ratio > 0.64). The external naris is triangular, but not as high posteriorly as is typical of *Protoichthysaurus*. The dorsoventrally high maxilla is asymmetric, with a long, slender anterior process that extends well beyond the external naris, as is diagnostic of *P. prostaxalis*. On the right side of the skull, the maxilla appears to contact the ventral margin of the external naris because the lacrimal process and subnarial process of the premaxilla are broken or worn off. On the left side, although damaged, it is clear that the anterior process of the lacrimal and subnarial process of the premaxilla separate the maxilla from the ventral margin of the external naris. On the left side of the skull, the dorsal process of the lacrimal is noticeably longer than the anterior process, a characteristic of *P. prostaxalis*, although the lacrimal processes and subnarial process of the premaxilla are poorly preserved. On the right side, the anterior process of the prefrontal is dorsoventrally high and separates the dorsal process of the lacrimal from the anterior margin of the orbit, a diagnostic feature of *Protoichthysaurus*, but also present in *Ichthysaurus larkini* and *I. somersetensis*. The sclerotic ring is complete (height=6.5 cm, length=7.0 cm) and fills just under 50% of the orbit (height=8.7 cm; length=11 cm). The anterior process of the jugal is broken. The jugal dorsal ramus makes up about half of the posterior orbit margin, and has a broad contact with the ventral edge of the postorbital as in BU 5323 and BRLSI M3555, referred specimens of *P. prostaxalis* (Lomax et al., 2017). The postorbital makes up no more than half of the posterior orbit margin, as in *P. prostaxalis*, *Ichthysaurus communis*, and *I. breviceps*. It is roughly rectangular, but slightly anteroposteriorly wider dorsally than ventrally, with both the anterodorsal and anteroventral edges tapering to narrow processes, as in BU 5323. In right lateral view, the surangular is exposed to just beyond the external naris. The angular makes up only a small portion of the posterior part of the mandible, and appears to extend anteriorly slightly beyond the surangular, although this could be due to the orientation or damage of the skull (Figure 2). No teeth are preserved well enough to describe, however, the diameters of the roots appear fairly large for the rostrum length. In dorsal view, only the right nasal is complete, articulated with part of the left nasal. It does not appear to have an internasal foramen, although that portion of the skull is damaged and most of the left side

is missing. Only the right temporal fenestra is present and is an anteroposteriorly elongated oval. The surrounding elements are poorly preserved and broken, and it is difficult to confidently interpret sutures. NMING F8756 can be referred to *Protoichthysaurus* on the basis of a long rostrum, a prefrontal that separates the dorsal process of the lacrimal from the orbit margin, and the asymmetric maxilla with a long slender anterior process. It is identified as *P. prostaxalis* because of the dorsoventrally high maxilla that extends well beyond the external naris, and a dorsoventrally short, but anteroposteriorly wide, postorbital that makes up no more than half of the posterior orbit margin.

GPIT 1796/1 (Figure 3) has a preserved skull length of 41 cm and jaw length of 43 cm. It has been described in detail by Maisch and Matzke (2000), but we disagree with some of their interpretations. The prefrontal anterior process is dorsoventrally wider and extends ventrally to at least the level of the ventral edge of the external naris, contrary to their illustration (Maisch and Matzke, 2000, fig. 3). They also suggested that the lacrimal anterior process makes up the entire ventral margin of the external naris and extends beyond it. However, the subnarial process of the premaxilla makes up most of the ventral margin and the anterior process of the lacrimal is short, although it is damaged on both sides of the skull. Maisch and Matzke (2000) also describe the presence of a septomaxilla in the posteroventral part of the external naris. This might be part of a salt gland structure (Wahl, 2012). Several features of this specimen clarify previously unknown morphology of the skull roof. The pineal opening is enclosed largely in the frontals but continues slightly posteriorly, beyond the posterior edge of the complete left frontal (as seen in LEICT G729.1889.1 and can be inferred in BU 5323 and NHMUK R36958). Thus, although the anterior parietals are damaged, it is clear that they made up the posterior border of the pineal, as noted by Maisch and Matzke (2000). The nasals lack an internasal foramen but there is a depression along the midline (Maisch and Matzke, 2000). GPIT 1796/1 is assigned to *Protoichthysaurus* on the basis of the slender rostrum, large triangular external naris, a prefrontal that separates most of the lacrimal dorsal process from the orbit margin, and large tooth roots with prominent grooves that extend to the base of the crown. It is assigned to *P. prostaxalis* because of the dorsoventrally high, asymmetric maxilla, a wide postorbital that makes up about half of the posterior border of the orbit, and a squamosal with a triangular posteroventral process (Figure 3).

PROTOICHTHYOSAURUS APPLEBYI Lomax,
Massare, and Mistry 2017

Holotype—UNM.G.2017.1 (formerly UON VR159), a nearly complete skull and skeleton, although the posterior portion of the tail has most likely been added (Lomax et al., 2017).

Referred Specimen—NHMUK R1164, a nearly complete, isolated skull with a few articulated cervical vertebrae.

Locality and Horizon—No locality or horizon information is known for the holotype, but the preservation style suggests that it might be from the Lower Jurassic of Nottinghamshire or Leicestershire (Lomax et al., 2017). NHMUK R1164 is from Lyme Regis, Dorset, England, UK, generally assumed to be Hettangian–Sinemurian in age, although strata from the Rhaetian–Pliensbachian are preserved in the area (Benton and Spencer, 1995, fig. 5.3; Gallois, 2007; Page, 2010). As with most historic specimens, the stratigraphic horizon is unknown.

Emended Diagnosis—*P. applebyi* is distinguished from *P. prostaxalis* and all species of *Ichthyosaurus* by a unique combination of characters listed in Lomax et al. (2017) to which is added: postorbital makes up much more than half of orbit posterior margin (as in *I. conybeari*, *I. amingae*, *I. larkini*, and *I. somersetensis*, but unlike *P. prostaxalis*); postorbital dorsoventrally long but anteroposteriorly narrow relative to its length (similar to *I. somersetensis* and *I. conybeari*).

DESCRIPTION OF NHMUK R1164

NHMUK R1164 (Figure 4) is a larger skull than that of the holotype (UNM.G.2017.1), and thus likely represents a more mature individual. Of particular note, this specimen is about the same size (mandible length 44.0 cm; Table 1) as several specimens assigned to *P. prostaxalis* (Lomax et al. 2017, table 2; and herein). This demonstrates that the morphological differences between the two species are not ontogenetic. *Protoichthyosaurus applebyi* is not a juvenile of *P. prostaxalis*.

The dorsal skull roof of NHMUK R1164 is poorly preserved. However, the most important feature of the dorsal surface is a depression along the midline of the nasals, made more prominent because the left side has been pushed upward with respect to the right. An internasal depression occurs on specimens of *Protoichthyosaurus prostaxalis* that preserve the dorsal skull, but this is the first specimen of *P. applebyi* on which it is preserved. The presence of an internasal foramen cannot be confirmed because of compression of the skull.

The remaining description is from the right lateral view, unless otherwise stated (Figures 4A, B). The post-orbital region of the skull and posterior portion of the mandible are much better preserved than on the holotype and provide new information.

The subnarial and supranarial processes of the premaxilla make up the anterior margin of the external naris. The subnarial process extends about half the external naris length, but makes up the anterior quarter of the naris ventral margin. For much of its length, it is separated from the naris by the thin anterior process of the lacrimal. The supranarial process extends less than half the external naris length and is separated from the dorsal margin of the naris by a thin sliver of the nasal. The supranarial process does not seem to be broken, and thus the nasal makes up all of the dorsal margin of the naris.

The low maxilla is more bar-like than triangular, a feature that distinguishes *P. applebyi* from *P. prostaxalis* (Lomax et al., 2017). However, a portion of the lacrimal is missing and the end of the subnarial process is broken, exposing a small length of the maxilla that is usually covered. This makes the maxilla appear higher and more triangular than it would be on an undamaged skull (compare Figures 4A and B). The maxilla is separated from the margin of the external naris by processes of the lacrimal and premaxilla. The posterior process of the maxilla narrows abruptly, and does not extend very far below the orbit. Its anterior process extends at least ½ naris length beyond the external naris, a much longer extent than in the holotype of *P. applebyi* and similar to that in *P. prostaxalis*. In lateral view, the maxilla appears to extend beyond the nasals, which is not the case in the holotype, but the skull is distorted and the nasals are pushed inward (seen in lateral and dorsal views).

The large, triangular external naris that tapers anteriorly is diagnostic of the genus (Lomax et al., 2017). The lacrimal is triradiate, and the anterior process extends more than half the length of the ventral margin of the external naris, although it is very slender in the anterior portion. The dorsal process of the lacrimal is damaged so its length relative to the anterior process, a feature that distinguishes *P. prostaxalis* from *P. applebyi*, is not evident. It probably makes up most of the posterior margin of the external naris, but a tiny process on the nasal makes up the posterodorsal edge, as is seen in other specimens of the genus (Lomax et al., 2017, fig. 4). The prefrontal makes up at least half of the dorsal margin of the orbit, which was also suggested in the holotype (Lomax et al., 2017). Anteriorly, it separates the dorsal process of the lacrimal from the anterior orbit margin.

The sclerotic ring in NHMUK R1164 is complete and undistorted, and fills 62% of the orbit. Fernández et al. (2005) suggested that the sclerotic ring nearly

filled the orbit in juveniles, but occupied less of the orbit in adults, at least in ophthalmosaurid ichthyosaurs. For comparison, in large *Caypullisaurus* specimens (skull length 1.0–1.5 m), presumably adults, the sclerotic ring was 54–60% of the area of the orbit (Fernández et al., 2005).

The jugal does not extend beyond the anterior margin of the orbit, but seems to be separated into two pieces by a groove that exposes matrix, so it might have been damaged. The dorsal ramus bends at nearly a right angle and is narrow for most of its length. Although it extends dorsally for about half of the orbit height, it is largely separated from the posterior margin of the orbit by the postorbital and makes up only a small portion of the posterior orbit margin. A long contact between the jugal and postorbital extends for almost half of the length of the jugal dorsal ramus.

The crescentic postorbital is tall and narrow, and makes up about three-quarters of the posterior margin of the orbit. The shape and extent of the postorbital is entirely different from that of *P. prostaxalis*, and distinguishes the two species (Lomax et al., 2017). The postorbital shape and extent is somewhat similar to that of *I. somersetensis*, but the jugal of that species has only a slight bend of the dorsal ramus and the postorbital makes up more of the posterior orbit margin (Lomax and Massare, 2017). The postorbital of *I. conybeari* is also high, but it is narrower relative to its height than that of *P. applebyi*.

Most of the quadratojugal is exposed, but the dorsal portion is crushed and damaged. The shaft narrows, forming a slightly bulbous ventral end for the quadrate facet. This is similar to the morphology in *P. prostaxalis* (NMW 2012.23G.1; Lomax et al., 2017). A deep embayment between the jugal dorsal ramus and quadratojugal results in a high lower temporal arch, which appears to be more prominent than what occurs in *P. prostaxalis* and *Ichthyosaurus*.

The angular makes up about one third of the posterior end of the mandible in lateral view, the remaining portion being the surangular. Both bones taper anteriorly, with the angular terminating at a position slightly anterior to the middle of the orbit, and the surangular extending to a position posterior to the middle of the external naris. The posterior end of the dentary extends at least to the middle of the orbit.

Many well-preserved teeth are present. The teeth have large roots with prominent longitudinal grooves that extend to the base of the crown in well preserved teeth (Figure 4C). The portion of the root between the grooves becomes the base of the longitudinal striations of the crown, suggesting that the crown striations are formed by folds in both the enamel and dentine layers in *Protoichthyosaurus*, rather than just in the enamel layer. The tooth crown itself has an acute but rounded apex, and the longitudinal striations do not extend all

the way to the apex. When the entire tooth is preserved, the crown is small relative to the root, even on premaxillary teeth.

NHMUK R1164 is assigned to *Protoichthyosaurus* because of a combination of features that include: a large, triangular external naris, a long slender rostrum, a strongly asymmetric maxilla with a long anterior process, the prefrontal anterior process separating the lacrimal dorsal process from the orbit margin, and tooth roots with prominent longitudinal grooves that extend to the base of the crown. It is assigned to *P. applebyi* because the maxilla is dorsoventrally low and the postorbital is high and narrow, making up more than half of the posterior margin of the orbit.

THE STATUS OF *ICHTHYOSAURUS FORTIMANUS*

Owen (1849–1884) described a new species of *Ichthyosaurus*, *I. fortimanus*, defined on the basis of a forefin that was missing the humerus. The main distinguishing characters were the number of digits, size of the elements, the angular shape of phalanges, and the width of the fin relative to its length. Almost a century later, McGowan (1974) synonymized *I. fortimanus* with *I. communis*.

The specimen figured by Owen (1849–1884, pl 30, fig. 1) is no doubt NHMUK R1063 (Figure 5). It possesses the diagnostic characters of *Protoichthyosaurus*: only digits II, III, and IV are present, with digit V missing, unlike in *Ichthyosaurus*; a bifurcation in the metacarpal row results in two metacarpals associated with digit II; the posterior metacarpal two is proximodistally long, nearly separating distal carpal two from distal carpal three; and a distal bifurcation of digit II results in a total of five digits in the forefin, the same number as in many specimens of *Ichthyosaurus*. Lomax et al. (2017) assigned the specimen to the genus without realizing that it was the holotype of *I. fortimanus*. Additionally, they expanded the diagnosis of *P. prostaxalis* to include additional characters of the paratypes and referred specimens. NHMUK R1063, however, possesses only features characteristic of the genus.

NHMUK R1063 is from Lyme Regis, Dorset, as is GPIT 1796/1, a specimen of *P. prostaxalis*, and the new specimen of *P. applebyi* (NHMUK R1164). The Lyme Regis location encompasses strata along the coast that range from Rhaetian (uppermost Triassic) to Pliensbachian (upper Lower Jurassic; Benton and Spencer, 1995). Although the stratigraphic horizon is known for GPIT 1796/1, the stratigraphic horizon is unknown for the other two specimens, as is common with historical specimens. Thus, we cannot confirm that either species occurs at the same stratigraphic horizon or location as *I. fortimanus*. On the other hand,

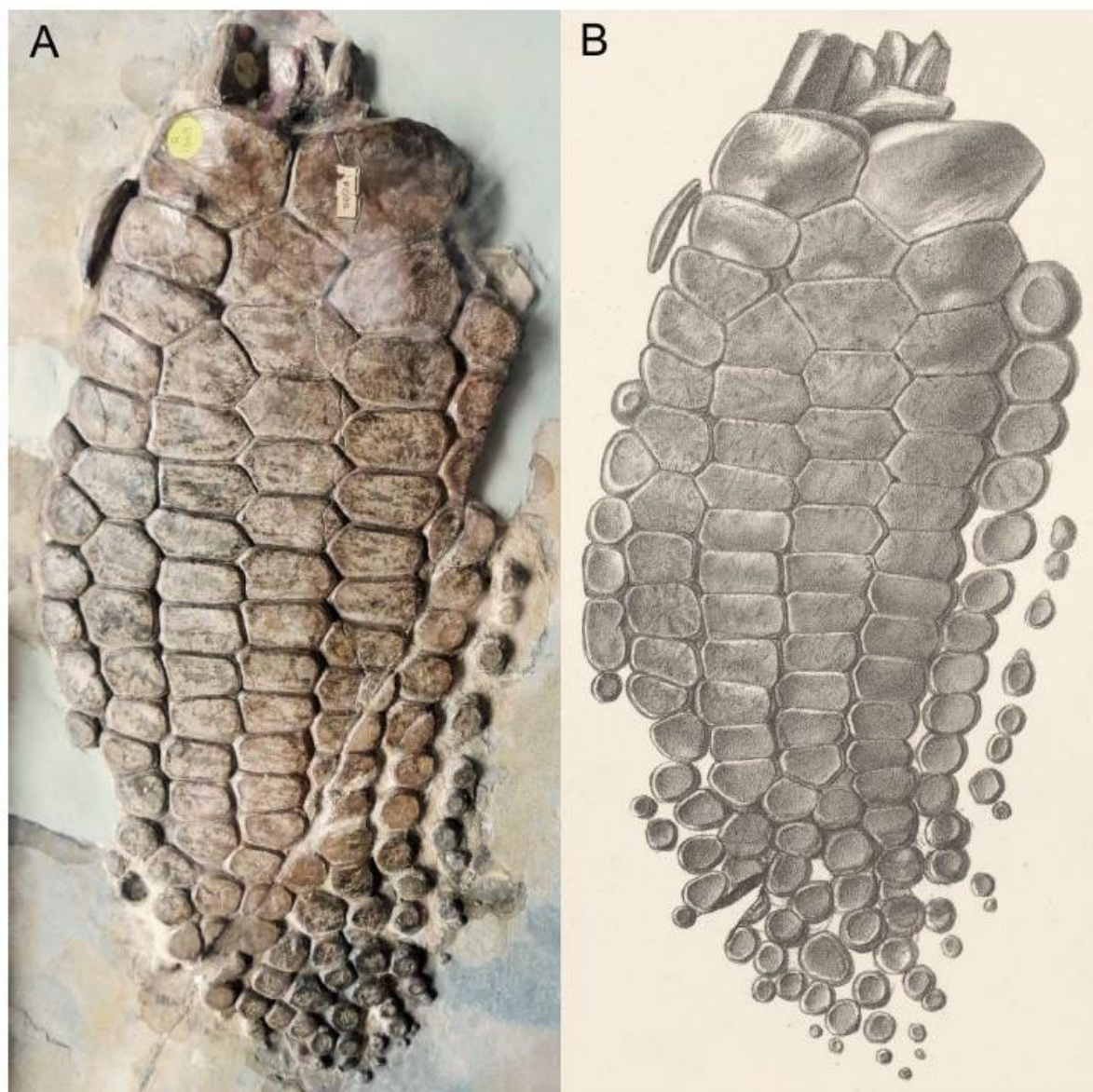


FIGURE 5: NHMUK R1063, isolated forefin of *Protoichthyosaurus fortimanus* (Owen, 1849-1884). A. Photograph of the specimen, on display and behind glass at the NHMUK. B. Illustration from Owen, 1849-1884, *Ichthyosaurus* plate 30, reversed from the original publication. The forefin displays only genus characters and cannot be distinguished from either *P. prostaxalis* or *P. applebyi*.

the size of NHMUK R1063 is more similar to *P. prostaxalis*, a seemingly larger species than *P. applebyi*. The isolated forefin, however, does not possess any diagnostic characters of either *P. prostaxalis* or *P. applebyi*. It is possible that *P. prostaxalis* or *P. applebyi* is a junior synonym of *P. fortimanus*, but it is impossible to determine with only a single forefin. Thus, pending the discovery of features of the forefin that can distinguish species of

Protoichthyosaurus, *P. fortimanus* must be retained as a separate species of the genus.

DISTINGUISHING SPECIES OF *PROTOICHTHYOSAURUS* AND *ICHTHYOSAURUS* FROM SKULL MORPHOLOGY

For Lower Jurassic taxa that are not monotypic (e.g., *Stenopterygius*, *Temnodontosaurus*), postcranial

characteristics, especially forefin morphology, identify the genera more readily than skull characteristics. In *Stenopterygius*, for example, few skull characteristics define the genus, whereas differences in skulls are useful to identify species (McGowan and Motani, 2003; Maisch, 2008; Maxwell, 2012). Of the characters selected for distinguishing species in this study, *Stenopterygius quadriscissus* shares six skull characters with some species of *Ichthyosaurus*, although four or less with species of *Protoichthyosaurus* (Table 1; Maxwell, 2012, fig. 1). *Protoichthyosaurus* is similar in that the skull features of the genus are not as objectively assessed as those that distinguish individual species of *Protoichthyosaurus* from individual species of *Ichthyosaurus*. Thus a species assignment can often be made with confidence, whereas assignment to a genus is more equivocal without a species assignment.

TABLE 1: Measurements of NHMUK R1164, *Protoichthyosaurus applebyi*. * Anteriormost tip of the rostrum is missing so these measurements might be slight underestimates.

Dimension	Measurement in cm
Skull length	39.7*
Preorbital length	26.7*
Prenarial length	22.9*
Premaxillary length	19.5*
Jaw length	44.0*
Maxilla length	10.7
Orbit length	8.5
Orbit height	7.3
Sclerotic ring length	6.3
Sclerotic ring height	6.1
Naris length	3.6
Naris maximum height	1.5

The species of *Protoichthyosaurus* can be distinguished from each other and from species of *Ichthyosaurus* by a combination of characters, but the portion of the skull around the external naris and orbit must be well preserved in lateral view so that several bone shapes and contacts can be evaluated (Table 2). For example, in *P. applebyi*, the postorbital is a dorsoventrally long element that makes up nearly all of the posterior margin of the orbit, similar to *I. conybeari*, *I. somersetensis*, *I. anningae*, and *I. larkini* (Lomax and Massare, 2015, 2017; Massare and Lomax, 2016). This is also similar to *Stenopterygius quadriscissus*, where the long, narrow postorbital makes up the entire posterior margin of the orbit (Maxwell, 2012, fig. 3). In *P. prostaxalis*, on the other

hand, the postorbital makes up no more than half of the posterior orbit margin, similar to *I. communis* and *I. breviceps* (Massare and Lomax, 2017), although the postorbital is roughly rectangular in *P. prostaxalis* rather than crescentic as it is in the other two. By examining additional characters, process of elimination will lead to a species identification. In this way, both species of *Protoichthyosaurus* can be distinguished from each other and all species of *Ichthyosaurus* (Table 2). Of course, identification becomes complicated if critical portions of the skull are missing or not well-preserved (see below). Furthermore, the extent of intraspecific variation has yet to be determined for individual skull bones.

Table 2 compares useful characters for distinguishing species for skulls preserved in lateral view. For these traits, *Protoichthyosaurus prostaxalis* is most similar to *Ichthyosaurus breviceps* sharing seven of nine characters. *Protoichthyosaurus prostaxalis* can easily be distinguished from *I. breviceps* by a much longer rostrum. In addition, the anterior process of the prefrontal is dorsoventrally long and separates the dorsal process of the lacrimal from the anterior margin of the orbit, and an asymmetric maxilla with a long anterior process that extends well beyond the external naris.

Based on the same characters (Table 2), the skull of *Protoichthyosaurus applebyi* is most similar to that of *I. larkini*, and *I. somersetensis*, sharing six and seven of nine characters, respectively. *P. applebyi* has a lower crowned skull compared to *I. larkini*, although both species have fairly long rostra. The teeth of *P. applebyi* have prominent longitudinal grooves on the roots that extend to the base of the crown. This is not the case for *I. larkini*. The species can also be distinguished in lateral view by the symmetry of the dorsoventrally low maxilla: in *P. applebyi*, the anterior process is much longer than the posterior process whereas in *I. larkini*, the two processes are about equal in length. *P. applebyi* has a dorsoventrally high external naris, whereas *I. larkini* has a dorsoventrally low external naris that is very elongated anteroposteriorly. Of course, naris shape is greatly influenced by orientation and taphonomic flattening of the skull. *P. applebyi* can be distinguished from *I. somersetensis* by a much longer rostrum and, as with *I. larkini*, by the shape of the maxilla. The maxilla of *P. applebyi* is dorsoventrally low, with a much longer anterior process compared to the posterior process; whereas the maxilla of *I. somersetensis* is dorsoventrally high, with a much longer and more slender posterior process compared to the anterior process.

Preservation can also affect how skull characters are evaluated. As the extent of crushing and orientation varies from specimen to specimen, it is inevitable, that skull features will also vary among specimens of the

TABLE 2: Skull characters that can, in combination, distinguish species of *Ichthyosaurus* from species of *Protoichthyosaurus*. Abbreviations: comm, *I. communis*; brev, *I. breviceps*; cony, *I. conybeari*; anni, *I. anningae*; lark, *I. larkini*; some, *I. somersetensis*; pros, *P. prostaxalis*; appl, *P. applebyi*; quad, *Stenopterygius quadrissicus*.

Skull character	comm	brev	cony	anni	lark	some	pros	appl	quad
Postorbital makes up more than half of posterior margin of orbit	no	no	yes	yes	yes	yes	no	yes	yes
Postorbital dorsoventrally long and much narrower anteroposteriorly	no	no	yes	yes	yes	yes	no	yes	yes
Prefrontal excludes all or most of lacrimal dorsal process from anterior orbit margin	no	no	no	no	yes	yes	yes	yes	no
Lacrimal dorsal process longer than anterior process	yes	yes	yes	?	no	no	yes	no	no
Maxilla taller than distance between dorsal edge of maxilla and external naris	rarely	rarely	no	yes	no	yes	yes	no	yes
Maxilla is approximately symmetric - processes are about the same height and length from tallest point of maxilla.	yes	no	no	yes	yes	no	no	no	no
Prominent grooves in tooth root	no	yes	no	no	no	yes	yes	yes	no
Grooves in tooth root extend to base of crown and merge with striations in enamel	no	no	no	no	no	no	yes	yes	no
Angular exposure much less than half of surangular exposure at posterior end of mandible	yes	yes	yes	yes	yes	yes	yes	yes	no

same species. For example, Lomax and Sachs (2017) reported a very large specimen of *Ichthyosaurus somersetensis* in which the lacrimal dorsal process was larger and more robust than in the holotype, and the characteristic shelf at the base of the lacrimal dorsal process was somewhat obscured due to crushing, especially if viewed directly in lateral view. However, the triradiate shape of the lacrimal, its dorsal extent, its exclusion from the orbital margin, and the extent of its anterior process were all consistent with *I. somersetensis*. A slight difference in view/orientation can easily distort an element so that it looks different than what is expected for the species. Individual variation can also result in slightly different morphologies of individual bones. Thus, for these reasons, a single character should not be used to refer a specimen to a specific species, and nor should a slight difference in a single feature be considered representative of something new.

CONCLUSIONS

Without the presence of a forefin, *Protoichthyosaurus* and *Ichthyosaurus* can be distinguished on the

basis of skull characters, but only in combination. Thus, in poorly preserved or incomplete skulls, generic identification can be especially difficult and often species identifications can be more readily discerned. The recognition of four new specimens of *Protoichthyosaurus* expands information on the genus. One specimen, GPIT 1976/1, extends the geographic range of *Protoichthyosaurus prostaxalis* to the Lyme Regis area, and more importantly, confirms that the genus/species persisted to the lower Sinemurian (Bucklandi Ammonite Zone). It also confirms that the pineal foramen is between the frontals and parietals, as suggested by Lomax et al. (2017). Another specimen, NHMUK R1164, is only the second known specimen of *P. applebyi*, and extends its geographic range to the Lyme Regis area, Dorset. Furthermore, it provides new information on the post-orbital region of the skull and posterior portion of the mandible that adds to the original species diagnosis. It also confirms Motani's (2005) suggestion that NHMUK R1164 represented something different from *Ichthyosaurus*. The specimens described herein bring the number of specimens assigned to *Protoichthyosaurus* to 27, including the missing paratype. Seventeen specimens

can be assigned to *P. prostaxalis*, and two can be assigned to *P. applebyi*.

This work further illustrates the importance of historic collections in the search for additional, unrecognized specimens of *Protoichthyosaurus*. Because *Protoichthyosaurus* was not recognized until 1979 (Appleby, 1979), isolated skulls of *Ichthyosaurus* and *Protoichthyosaurus* were confused with each other in the early literature and collections from the 19th century. In fact, Lydekker (1891, p. 49; 1889, p. 46) identified two specimens discussed here (NMG F8756, NHMUK R1164) as *I. communis*. It would not be surprising to find more '*I. communis*' specimens in historic collections that are actually *Protoichthyosaurus*.

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A forefin of *Leptonectes solei* from the Lower Jurassic (Pliensbachian) of Dorset, UK



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ABSTRACT

An incomplete forefin in the collections of the National Museum of Wales, Cardiff, is herein assigned to the rare leptonectid species, *Leptonectes solei*, known only from the west Dorset coast. It is only the third specimen of the species and is smaller than both the holotype and referred specimen. The new specimen is from the Lower Jurassic (lower Pliensbachian, Charmouth Mudstone Formation, *Tragophylloceras ibex* Ammonite Zone, *Acanthopleuroceras valdani* Ammonite Subzone) of Seatown, Dorset, UK. It confirms that all three species of *Leptonectes* were present in the Pliensbachian and expands the known diversity of ichthyosaurs for that time period. We show that isolated forefins of *Leptonectes* can be assigned to a species with a high degree of confidence.

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1. Introduction

The genus *Leptonectes* McGowan, 1996, is one of the common ichthyosaurian taxa from the Lower Jurassic of the UK and is known from many complete and partial skeletons. *Leptonectes* has a wide geographic distribution, with specimens recorded from various counties in the UK (Somerset, Dorset, Leicestershire, Gloucestershire, Warwickshire and possibly Nottinghamshire) (McGowan and Motani, 2003; Smith and Radley, 2007; Lomax and Gibson, 2015) and several occurrences from Europe, including specimens from Switzerland (Maisch and Reisdorf, 2006), Belgium (Godefroit, 1992), Germany (Maisch, 1999) and Spain (Fernández et al., 2018). The genus also has a long stratigraphic range with specimens recorded from the Upper Triassic (Rhaetian) to the Lower Jurassic (upper Pliensbachian) (Storrs, 1994; Maisch and Reisdorf, 2006; Lomax et al., 2018). However, specimens recorded from the Rhaetian of the UK are from historical collections and lack precise stratigraphic information and some might actually be from the Lower Jurassic (Hettangian).

Leptonectes belongs to the family Leptonectidae Maisch, 1998a, which also includes *Eurhinosaurus*, *Excalibosaurus* and *Wahlisaurus* (Abel, 1909; McGowan, 1986; Lomax, 2016). There are three species of *Leptonectes*. The type species, *Leptonectes tenuirostris*, is a moderately sized taxon (<4 m) recorded from the UK and Europe and has a long stratigraphic range from the (?)Rhaetian to

Pliensbachian (McGowan, 1996; McGowan and Motani, 2003; Maisch and Reisdorf, 2006). One specimen, probably referable to this species, has been found with embryos (Lomax and Massare, 2012). As noted by previous workers, considering the amount of variation in specimens currently identified as *L. tenuirostris*, the species requires a detailed revision that is beyond the scope of this study (Maisch and Reisdorf, 2006; Lomax, 2016; Lomax et al., 2018). The second species, *L. solei*, is a large taxon (>7 m) known from two specimens from the Sinemurian of Dorset, UK (McGowan, 1993). The third species, *L. moorei*, is known from a single anterior skeleton, including a fairly complete skull, from the Pliensbachian of Dorset (McGowan and Milner, 1999).

Here, we report on a large, incomplete isolated forefin (NMW 91.296.2.2) from the Pliensbachian (Lower Jurassic) of Seatown, Dorset. We assign the specimen to *Leptonectes solei*, only the third specimen of that species.

1.1. Institutional abbreviations

BRSMG, Bristol City Museum and Art Gallery, Bristol, UK; MHN, Museum, The Hague, Netherlands; NHMUK, The Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK.

2. Materials and geological setting

NMW 91.296.2.2 is a large, isolated and incomplete forefin lying mostly in matrix, but it can be viewed on both the dorsal

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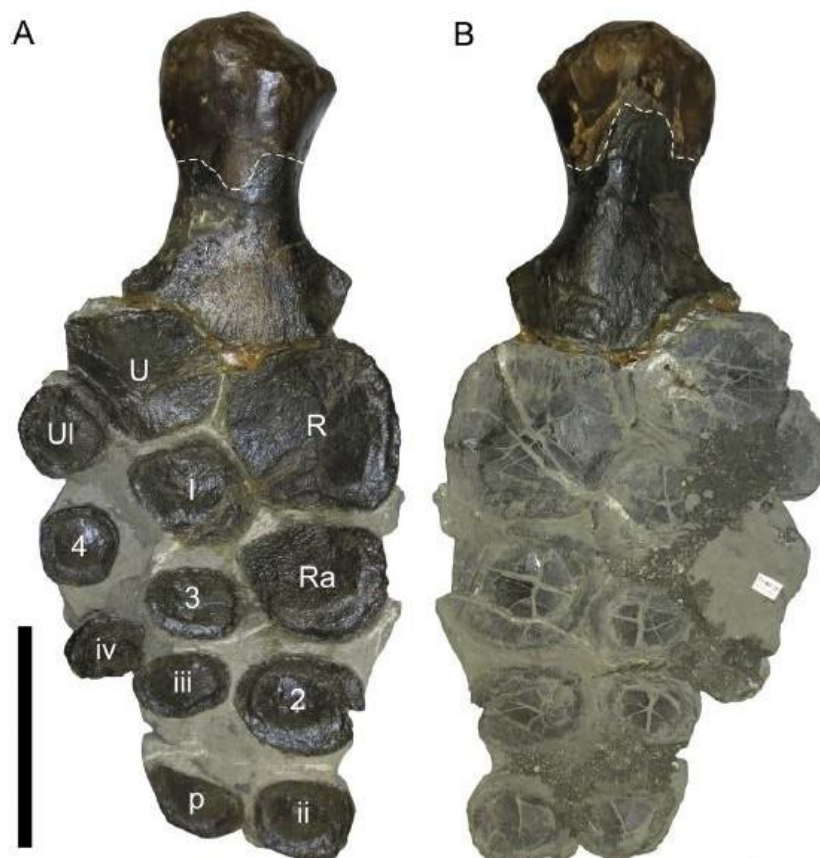


Fig. 1. NMW 91.296.2.2: An isolated forefin herein assigned to *Leptonectes solei*. A. Best preserved side, anterior to the right. B. Poorly preserved and unprepared underside, anterior to the left. The humerus probably does not belong with the rest of the fin and it is impossible to determine whether this is a left or right forefin, and thus which is ventral or dorsal view. Abbreviations: 2, distal carpal two; 3, distal carpal three; 4, distal carpal four; I, intermedium; ii, metacarpal two; iii, metacarpal three; iv, metacarpal four; p1, first phalange of digit two; R, radius; Ra, radiale; U, ulna; Ul, ulnare. Dashed line indicates proximal portion of humerus that is made from plaster. Scale measures 10 cm.

and ventral sides (Fig. 1). It is impossible to determine whether the fin is a left or right because the humerus has been restored and might not belong with the rest of the fin (see below). One side of the fin has been fully prepared and the bones coated with a preservative, which clearly distinguishes them from the matrix (Fig. 1A). The reverse side has not been prepared, although the humerus has been treated with preservative (Fig. 1B). This side exposes several of the same elements as the prepared side, but some are covered by matrix. Most are damaged, and the cracks have been filled.

The entire proximal region of the humerus is made of plaster, although most of the shaft and the distal end are original bone (Fig. 1). The humerus has been attached to the rest of the fin with glue or epoxy, which is clearly visible (Fig. 1). Although, the distal end of the humerus is expanded anteroposteriorly as is typical of the genus, it is not as wide as the radius and ulna, which are significantly wider anteroposteriorly than their respective facets on the humerus. The distal facets of the humerus are thus too small for the radius and ulna. This strongly suggests that the humerus does not belong with the specimen and thus it is a composite. Ichthyosaur composites are common in historic collections (McGowan, 1990; Maisch, 1998b; Massare and Lomax, 2014, 2016b) and even recently collected material can be composites

(e.g. Lomax and Sachs, 2017). The remainder of the forefin is authentic.

The specimen was collected in 1990 from Seatown, Dorset, and acquired by the NMW in 1991 from The Old Forge Fossil Company, Dorset. It is from the Lower Jurassic, recorded as “1 foot below the belemnite stone”. The term ‘belemnite stone’ refers to the top of the Stonebarrow Marl Member (‘Belemnite Marls’) of the Charmouth Mudstone Formation. It is lower Pliensbachian, from the *Tragophylloceras ibex* Ammonite Zone, *Acanthopleuroceras valdani* Ammonite Subzone according to museum records. The single specimen of *Leptonectes moorei*, also from Seatown, was from a horizon less than a metre below this.

3. Description of specimen

The humerus is not included in the description or species assignment because it probably does not belong with the rest of the forefin. See previous section for details.

Systematic Palaeontology

Order Ichthyosauria de Blainville, 1835

Family Leptonectidae Maisch, 1998a

Genus *Leptonectes* McGowan, 1996

Leptonectes solei (McGowan, 1993)

Emended diagnosis: As in McGowan (1993) with the addition of: forefin with three digits (II, III, IV); carpals, metacarpals, and phalanges rounded and widely spaced.

Specimen number: NMW 91.296.2.2.

Element: Incomplete forefin.

Locality: Seatown, Dorset, England, UK.

Stratigraphy: Lower Jurassic (lower Pliensbachian), *Acanthopleuroceras valdani* Ammonite Subzone, *Tragophylloceras ibex* Ammonite Zone, Charmouth Mudstone Formation.

3.1. Description

NMW 91.296.2.2 has three primary digits (II, III and IV; Motani, 1999) preserved up to metacarpal two of digit II, the first phalanx of digit III, and metacarpal four of digit IV (Fig. 1). Excluding the humerus, it has a preserved length of at least 24 cm and maximum width of 17 cm. Digit II has the largest elements of the three digits. Only the radius, ulna, and proximal carpals could have possibly interlocked, although even these are not in contact with one another as preserved in this specimen and in the referred specimen of *L. solei* (McGowan, 1993).

The radius is large, rounded and lacks a notch on the leading edge, as in *Leptonectes solei* and *L. moorei* (McGowan, 1993; McGowan and Milner, 1999), but unlike *L. tenuirostris*, which always has a notched radius, even in embryos (McGowan, 1993; McGowan and Milner, 1999; McGowan and Motani, 2003; Lomax and Massare, 2012). No elements are notched in NMW 91.296.2.2. Notching of other elements of the leading edge is common in specimens of *L. tenuirostris*. Only a single element is notched in the holotype of *L. solei*, but its position in the fin is unknown. The referred specimen (MHN 96270), which has a more complete forefin, has no notched elements. *L. moorei* also lacks notching (Fig. 2).

The ulna of NMW 91.296.2.2 is sub-rectangular and proximodistally slightly shorter than the radius, but anteroposteriorly approximately equal to it. There is no foramen between the radius and ulna. Many specimens of *L. tenuirostris* (McGowan and Motani, 2003) have a circular foramen between the radius and ulna (Fig. 2), although other specimens do not. *L. moorei* might have a very small, narrow, elliptical foramen between the radius and ulna (McGowan and Milner, 1999), but *L. solei* lacks a foramen (McGowan, 1993).

The radiale is anteroposteriorly elongate, but round; it is noticeably larger than the intermedium and ulnare. Similarly, the intermedium is rounded and is larger than the ulnare. The ulnare is small and circular. The distal carpals, metacarpals, and the one

preserved phalanx are oval, with the long axis oriented anteroposteriorly.

Leptonectes tenuirostris has a notched radius and a broad notch on the tibia as well, and so NMW 91.296.2.2 cannot be assigned to that species, the most common member of the genus. The forefin elements of NMW 91.296.2.2, and particularly the carpals, are not polygonal nor closely packed like those of *L. moorei* (McGowan and Milner, 1999, fig. 4), but are rounded and widely spaced, similar to those of the only referred specimen of *L. solei* (Fig. 2; McGowan, 1993, fig. 5C,D). The forefin of the holotype of *L. solei* (BRSMG Ce 9856) is disarticulated and incomplete (McGowan, 1993, fig. 3A), but the elements distal to the radius and ulna are oval, not polygonal. In addition to the spacing and shape of elements, the elements of digit II in *L. solei* (i.e., MHN 96270) are larger than those in digit IV, as in NMW 91.296.2.2, whereas *L. moorei* shows little size difference among the digits (Fig. 2). The studied specimen has three digits as in *L. solei*, whereas *L. moorei* has four digits. However, the fourth digit is either digit V or a posterior accessory digit. We suggest it is most likely the latter because the element contacts the ulnare posteriorly rather than distally. Therefore, based on all of the characters above, NMW 91.296.2.2 is assigned to *L. solei*. It is much smaller than the holotype but only slightly smaller than MHN 96270, based on the size of the radius. Note that the hindfin of *L. solei* might have only two digits (McGowan, 1993, fig. 5A), so the described specimen is not a hindfin.

3.2. Remarks

The rounded, widely spaced carpals and metacarpals of NMW 91.296.2.2 are distinctly different from the polygonal, closely packed elements in other Lower Jurassic genera (e.g., *Ichthyosaurus*, *Protoichthyosaurus*, *Temnodontosaurus*, *Stenopterygius*, *Hauffiopteryx*, *Suevoleiathan*) (Motani, 1999; McGowan and Motani, 2003; Lomax et al., 2017a, 2017b). Furthermore, many of the Lower Jurassic taxa have a notch on the anterior edge of the radius, carpal two, and/or metacarpal two (e.g., *Temnodontosaurus*, *Stenopterygius*, *Hauffiopteryx*) (Motani, 1999; McGowan and Motani, 2003; Maisch, 2008). Among the Leptonectidae, *Eurhinosaurus* and *Excalibosaurus* have closely packed, polygonal elements in the carpus (McGowan, 2003; McGowan and Motani, 2003). Both known specimens of *Excalibosaurus* have a notched radius (McGowan, 2003). *Eurhinosaurus* usually has notching in at least one element of the carpus (McGowan and Motani, 2003). The forefin of *Wahlsaurus*, another leptonectid, is unknown, but the tibia is notched in the hindfin (Lomax, 2016), suggesting that the forefin might also have notched elements. Similar arguments can

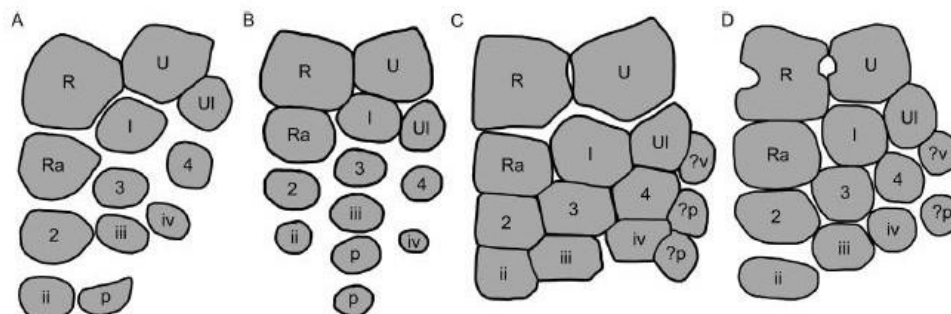


Fig. 2. Comparative illustrations of the forefins discussed in the text. A. NMW 91.296.2.2: Forefin specimen shown in Figure 1, reversed to show the same orientation as B, C and D. B. MHN 96270: Left forefin in dorsal view of referred specimen of *Leptonectes solei*, drawn from McGowan (1993, fig. 5). C. NHMUK R14370: Left forefin in dorsal view of only specimen of *Leptonectes moorei*. D. BRLSI M3575: Left forefin in dorsal view of a typical *Leptonectes tenuirostris* forefin. In C and D, the posterior digit is either digit V or an accessory digit. Anterior to the left for all specimens. Abbreviations: 2, distal carpal two; 3, distal carpal three; 4, distal carpal four; I, intermedium; ii, metacarpal two; iii, metacarpal three; iv, metacarpal four; p, phalanx; R, radius; Ra, radiale; U, ulna; UI, ulnare; v, metacarpal five.

be made for hindfins of these Lower Jurassic taxa. Only the genus *Leptonectes* includes species with rounded, widely spaced fin elements and a radius/tibia without an anterior notch. Thus NMW 91.296.2.2 can be assigned with confidence to *Leptonectes*.

4. Discussion

Johnson (1977) demonstrated that juveniles of *Stenopterygius* have rounder, more widely spaced fin elements than adults but this might not be the case for all genera (Lomax et al., 2017a, 2017b). The differences between *Leptonectes solei* and *L. moorei*, however, are not ontogenetic: the holotype and only specimen of *L. moorei* is much smaller than previously described specimens of *L. solei* (McGowan, 1993; McGowan and Milner, 1999), yet its fin elements are more tightly packed and polygonal. Thus Johnson's (1977) criteria for recognizing juveniles does not apply to *Leptonectes*. However, the shape, relative size, and spacing of fin elements seem to be valid characters for distinguishing the two species.

Pliensbachian ichthyosaurs are rare. Only a few substantially complete or well-preserved specimens have been reported. Many ichthyosaurs in historic collections lack detailed stratigraphic information, so some of those could be from the Pliensbachian. Nevertheless, ichthyosaurs previously recorded from the Pliensbachian include: *Leptonectes moorei*, *Ichthyosaurus anningae*, and *I. conybeari* from Dorset, UK (McGowan and Milner, 1999; Lomax and Massare, 2015; Massare and Lomax, 2016a), and *Leptonectes tenuirostris* from Switzerland (Maisch and Reisdorf, 2006). Hungerbühler and Sachs (1996) described an incomplete skull of *Temnodontosaurus* from Bielefeld, Germany. Maisch and Hungerbühler (1997) recognized *Temnodontosaurus nuertingensis* (von Huene, 1931) from Nürtingen, Germany, although the validity of the species has been questioned (McGowan and Motani, 2003). Additionally, '*Ichthyosaurus numismalis*' (Frass, 1892), possibly referable to the genus *Leptonectes* (Maisch, 2010), has also been reported from the lower Pliensbachian of Germany. Thus, the studied specimen, herein identified as *Leptonectes solei*, adds another species to the Pliensbachian diversity. Of particular note, this specimen demonstrates that all three species of *Leptonectes* were present in the Pliensbachian.

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