A NEW SPECIES OF Ichthyosaurus FROM THE LOWER JURASSIC OF WEST DORSET, ENGLAND, U.K.

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ABSTRACT—We describe a new species of Lower Jurassic (Hettangian/Sinemurian–Pliensbachian) ichthyosaur, Ichthyosaurus anningae, sp. nov., from west Dorset, England, U.K. The holotype of I. anningae (DONMG:1983.98), at least a subadult, is from the lower Pliensbachian Stonebarrow Marl Member (Charmouth Mudstone Formation). It is the most complete ichthyosaur known from this time interval worldwide. The species is assigned to Ichthyosaurus on the basis of humerus, forefin, and pectoral girdle morphologies. Diagnostic features of the species include a short, robust humerus with prominent processes; a femur in which the proximal width is almost as large as the distal width; and a very small femur relative to the humerus (humerus/femur ratio >1.7). Four other specimens, at least three of which are juveniles, are referred to this species. The new species may display sexual dimorphism in humeral morphology, but this cannot be confirmed due to a lack of stratigraphic information. With the recognition of I. anningae, at least three and possibly as many as five ichthyosaur species, representing three genera, are known from the Pliensbachian.

http://zoobank.org/urn:lsid:zoobank.org:pub:A5778FB5-A116-480A-93CA-AFC932ACAB55

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The first genus of ichthyosaur to be recognized was Ichthyosaurus, and specimens collected during the 19th century were largely referred to that genus, with over 50 species described before 1900 (see list of taxonomic names in McGowan and Motani, 2003). Subsequent studies removed species from the genus and defined new ichthyosaurian genera, or synonymized names with those other species, or both. Today three species remain: I. communis, I. breviceps, and I. conybeari (McGowan and Motani, 2003), although Maisch and Matzke (2000) recognized a fourth, I. intermedius (but see discussion in McGowan and Motani, 2003). This paper describes a new species of Ichthyosaurus based on a partial skeleton, DONMG:1983.98, in the Doncaster Museum and Art Gallery, Doncaster, U.K.

Lomax (2010) placed DONMG:1983.98 in the genus Ichthyosaurus, the first specimen of the genus to be recognized from the Pliensbachian, and thus extended the range of the genus from Rhaetian to Pliensbachian. The specimen was probably exca- 
vated in the late 1970s or early 1980s and was originally owned by Hilary Corke Minerals, Surrey, U.K. According to Emma Corke, Hilary’s daughter, the specimen almost certainly came from the Charmouth area (N. Larkin, pers. comm. with D. R. L., 2012; Fig. 1). Purchased by the Doncaster Museum and Art Gal- 
lery in 1983, the specimen was on display in the main galleries until sometime in the later 1980s (Lomax, 2010). In 2008, the specimen was rediscovered in the collection by D.R.L. and was placed back on display in 2009. We have identified four additional specimens, some of which provide additional information on the species. Notably, the new species is represented by more than twice as many specimens as I. conybeari.

INSTITUTIONAL ABBREVIATIONS—ANSP, Academy of Natural Sciences, Philadelphia, U.S.A.; BGS, British Geological Survey, Nottingham, U.K.; BRSMG, Bristol City Museum and Art Gallery, Bristol, U.K.; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge, U.K.; DONMG, Doncaster Museum and Art Gallery, Doncaster, U.K.; LEICT, Leicester Arts and Museums Service (New Walk Museum and Art Gallery, Leicester, U.K.); MOS, Somerset Heritage Service (Museum of Somerset), Taunton, U.K.; NHMUK (formerly BMNH), Natural History Museum, London, U.K.; NMW, National Museum of Wales, Cardiff, U.K.; OUMNH, Oxford University Museum of Natural History, Oxford, U.K.

ICHTHYOSAURUS TAXONOMY

The genus Ichthyosaurus has an unusual history. The name was first used by König (1818), but the first ichthyosaur to be sci- entifically described was mentioned by Home (1819), who pro- posed the name Proteosaurus for a large skull and postcranial material (NHMUK R1158, now referred to Temnodontosaurus platyodon) collected by Joseph and Mary Anning in 1811 (McGowan and Motani, 2003). De la Beche and Conybear (1821), however, thought that König’s Ichthyosaurus had prece- dence over Proteosaurus, and their formal description of a differ- ent specimen (the holotype of Ichthyosaurus communis, which is lost; McGowan, 1974) used the former name. Ichthyosaurus has since prevailed in the literature.

Ichthyosaurus currently includes all Lower Jurassic forms with a wide forefin (five or more digits) in which a digital bifurcation occurs anteriorly (Motani, 1999; McGowan and Motani, 2003).
Differences among the Lower Jurassic genera are sufficiently distinct that isolated forefins, humeri, and coracoids can be assigned to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence. The arrangement of dermal skull elements is also diagnostic for Ichthyosaurus to a genus with a fairly high degree of confidence.

Not surprisingly, distinctions among species are more subtle, and thus perhaps more subjective, than generic distinctions. Within Ichthyosaurus, species are distinguished by overall size and skull proportions (snout ratio, orbit ratio), the presacral and preflexural vertebral counts, the number of digits in the forefin, the number of phalanges in the longest digit, and the presence of notchting on the forefin, although the latter is used inconsistently. However, many of the morphometric characteristics overlap between species (pers. observ.) and the diagnoses need to be revised. In addition, authors do not agree as to whether Ichthyosaurus has three species (McGowan and Motani, 2003) or four (Maisch and Matzke, 2000). To add to the problem, two populations of I. communis have been postulated, one from Lyme Regis, Dorset, and another from Street, Somerset, which differ substantially in forefin morphology (McGowan, 1974; McGowan and Motani, 2003).

Relative rostrum length (snout ratio = preorbital length of rostrum divided by mandible length) figures prominently in the species diagnoses. As currently defined (McGowan and Motani, 2003), the species include one with a short rostrum (I. breviceps), one with a long, delicate rostrum (I. conybeari), and everything else (I. communis). I. conybeari has the longest, most slender snout, with a snout ratio of 0.65, compared with an average ratio of 0.63 for I. communis (McGowan, 1974). Whether a difference of 0.02 in the ratios has any significance is questionable, especially in light of the variation that can arise due to different amounts or directions of crushing of the skull. Moreover, the variation in snout ratio for I. communis specimens that we have measured can be as high as the ratio for I. conybeari. Only the short-snouted I. breviceps (snout ratio <0.57) seems to be distinctly different from the others. Snout ratio, however, has some value. A short-snouted species such as I. breviceps might capture different prey or capture prey in a different way than a long-snouted species such as I. conybeari; thus, snout ratio may have ecological significance. However, the utility of the snout ratio as a diagnostic taxonomic trait may need to be reevaluated. Similarly, the orbit ratio (length of the orbit divided by mandible length) is included in species diagnoses. The average ratios (from McGowan, 1973) are 0.23 for I. communis (27 specimens), 0.30 for I. breviceps (six specimens), and 0.23 for I. conybeari (two specimens). As with the snout ratio, there does not seem to be much difference among species except for I. breviceps, where the substantially larger orbit ratio is likely related to the relatively shorter jaw.

In addition to the overlap in ratios, the amount of intraspecific variation has not been addressed since McGowan (1973). Assessing variation has also been hampered by the variation in the number of individuals of each species. I. conybeari and I. breviceps are relatively rare, the former known from only two specimens, whereas most of the fairly complete skeletons in museum collections have been identified as I. communis or the supposedly equivalent I. intermedius (pers. observ.). As currently defined, I. communis is extremely variable. Whether the many specimens represent one extremely variable species or two or more distinct species needs to be examined. To avoid having to resolve the existing taxonomic problems here, we have followed the taxonomy of the most recent compilation (McGowan and Motani, 2003) in our comparisons. We also include a few key morphological ratios in our diagnosis, although with reservations as explained above.

**MATERIALS AND METHODS**

For features with dimensions less than 15 cm, measurements were made with dial calipers and recorded to the nearest 0.01 cm. For larger features, a measuring tape was used, and measurements were recorded to the nearest 0.1 cm. We follow the convention of McGowan (1973) in using the orbit and snout ratios to describe the skull (see also McGowan and Milner, 1999).

The presacral and preflexural vertebral counts were determined from a provisionally referred specimen (NHMUK OR 120), the only example with a complete, articulated vertebral column. Such counts are part of current species diagnoses, but they can be determined in more than one way. Presacral count can be determined by the position of the pelvis or femur relative to the vertebral column, the length of the ribs, or from where the diaphysis and parapophysis merge (Buchholz, 2001; Massare et al., 2006). We determined the presacral count by the position of the proximal end of the femur because rib articulations were not visible on the centra in the critical part of the vertebral column. Similarly, the preflexural count may be determined on a specimen by the midpoint of the bend of the vertebral column, anterior to the first wedge-shaped centrum, or anterior to the first fluke centrum. These counts could differ by three or more. Our preflexural count includes only centra anterior to the first wedge-shaped centrum and thus may be slightly lower than for other Ichthyosaurus species.
Taphonomy

The holotype specimen, DONMG:1983.98, is a skull and partial anterior skeleton, which is mediolaterally flattened and lying on its right side (Fig. 2). The skull is well preserved, but the tip of the rostrum is missing and the bones of the temporal and posterior regions are broken and displaced. The pectoral girdle is fully exposed, with paired, articulated coracoids in ventral aspect. The coracoids overlay the interclavicle and parts of the clavicle. The clavicle is exposed in several sections, the largest of which articulates with the left scapula. Both scapulae are present, but the right one is displaced anteriorly.

Twenty-five presacral vertebrae are associated with the skeleton, although only 15 are articulated. Posterior to the articulated vertebrae are two sets of displaced neural spines. Two isolated presacral vertebrae, articulated with each other, are at the distal end of the matrix. The posterior trunk and tail stock of DONMG:1983.98 is missing. A complete left femur (dorsal view) and a portion of the right one (ventral view), as well as a nearly complete ilium, are preserved posterior to the articulated vertebral column.

A gastric mass, containing numerous cephalopod hooklets, is preserved between the ribs. Lomax (2010) noted similarities to gastric contents described by Pollard (1968) and suggested that the hooklets belong to belemnite coleoids. The material described by Pollard (1968), however, has been reassessed as belonging to phragmoteuthid coleoids (Valente et al., 2010), which suggest that the hooklets in the gastric contents of DONMG:1983.98 probably belonged to phragmoteuthids also. At least two elongated masses, one with a single cephalopod hooklet, are preserved posterior to the specimen and could possibly be braomalites from this individual.

Reconstructed Forefin

The right humerus, with the ventral surface exposed, and most of a forefin are set in a tough, plaster-like filler (Fig. 3). Preparation revealed that the dorsal surface of the right humerus is weathered, suggesting that it was exposed at the surface when collected. Prior to purchase by the museum, the right humerus was reset oriented in ventral view, with the weathered surface facing down into the plaster. Along with the humerus, the radius, ulna, and many fin elements are also lying in plaster, and the wide spacing of the proximal fin elements is not original. Thus, the authenticity of the humerus, radius, and ulna, as well as the anterior and middle fin elements is questionable. A second humerus, however, was firmly imbedded in the original matrix, posterior to the right humerus (Fig. 3). It was rotated and positioned in anterior view with the distal articular surfaces, the head, and a portion of the shaft exposed.

In order to verify that the right humerus belonged to DONMG:1983.98, both humeri were removed for comparison. The imbedded humerus was a left humerus, and it mirrored the size, shape, and morphology of the right humerus, strongly suggesting that both humeri belong to the same individual. In order to confirm which fin elements were in situ, a large portion of the forefin was removed from the plaster-like filler, revealing that only the distal-most phalanges, which are fairly closely spaced, retained their original position (Fig. 3). Further preparation underneath the forefin indicated that no other fin elements were present. The humeri and the removed portion of the forefin were then reset on the slab in their previous orientations after jesmonite acrylic resin casts were made of the humeri. We cannot verify, however, the natural arrangement and position of the radius, ulna, and anterior and middle fin elements.

SYSTEMATIC PALEONTOLOGY

ICHTHYOSAURIA de Blainville, 1835
ICHTHYOSAURIIDAE Bonaparte, 1841
ICHTHYOSAURUS de la Beche and Conybeare, 1821
ICHTHYOSAURUS ANNINGAE, sp. nov. (Figs. 2–6, 8)
Holotype—DONMG:1983.98, an incomplete skeleton comprising the skull, pectoral girdle, two humeri, anterior trunk, and scattered portions of the posterior skeleton, including two femora and an ilium. It is larger than any of the referred specimens and has more precisely known stratigraphic information.

Referred Specimens—NMW G.1597, a partial skull with anterior centra and a partial forefin (location unknown, although likely Dorset; pers. observ.), and NHMUK OR 35566, a complete left forefin from Lyme Regis, are referred to the species on the basis of the humerus morphology. NHMUK OR 120, collected by Mary Anning from the Lyme Regis area, Dorset (Chapman and Milner, 2010), and NHMUK OR 10028 (?Lyme Regis) are provisionally referred to the species on the basis of the femur morphology and a very small femur relative to the humerus, but both lack the diagnostic features of the humerus.

Locality and Horizon—Based on the identification of a belemnite, *Bairstowius junceus*, that lay in the matrix adjacent to the specimen, Lomax (2010) determined that the holotype derived from the lower Pliensbachian Stonebarrow Marl Member of the Charmouth Mudstone Formation, specifically Bed 110, the *polymorphus* subzone of the *jamesoni* Zone (lower Pliensbachian).

The exact locality of DONMG:1983.98 is uncertain. Bed 110 crops out at three locations in the Charmouth area: Black Ven, Westhay Cliff, and on the foreshore west of Seatown (Lomax 2010; Fig. 1). At the two latter locations, Bed 110 crops out at beach level. Recent archival information recovered at DONMG suggests that the specimen may have been collected from Kimmeridge, Dorset. However, exposures near Kimmeridge are Upper Jurassic (Kimmeridgian) in age and no outcrop of Pliensbachian age is present.

The stratigraphic positions and localities of the referred specimens are uncertain because they are from historical collections. For such specimens, the Lyme Regis locality encompasses several localities from the west Dorset coast (Fig. 1) and has been assigned a range of upper Hettangian–lower Sinemurian (McGowan 1974; Chapman and Milner, 2010), although Pliensbachian strata are also exposed in the area (Lomax, 2010). One provisionally referred specimen, NHMUK OR 120, has external molds of two ammonites preserved above and slightly anterior to the tail bend. They have been identified as the scho lithoimid, *Angulaticeras* (M. Munt and M. Howarth, pers. comm. with D. R. L., 2012). The genus has a stratigraphic range of upper Hettangian, *angulata* Chronozone–upper Sinemurian, *oxynotum* Chronozone (Page, 2010). Thus, the stratigraphic range of *I. anningae* is at least upper Sinemurian–Pliensbachian but may be as early as upper Hettangian.

Etymology—In honor of early paleontologist and fossil collector Mary Anning, whose hard work and dedication brought, among many other fossils, the ichthyosaurs from Lyme Regis, Dorset, to the attention of the scientific community.

Diagnosis—Total length to tail bend probably less than 1.5 m (comparable in length to *I. breviceps* and *I. conybeari*, but smaller than *I. communis*); long, fairly robust snout and mandible, snout ratio 0.60 or more, but probably $<0.65$ (longer than *I. breviceps*, within the range of *I. communis*, but shorter than *I. conybeari*); $\sim43$ presacral centra ($\sim41$ in *I. communis*, 42–43 in *I. breviceps*, $\sim42$ in *I. conybeari*; McGowan and Motani, 2003);
~74 preflexural centra (75–79 in *I. communis*, >74 in *I. conybeari*, and <74 in *I. breviceps*; McGowan and Motani, 2003).

**Autapomorphic characters:** short, robust humerus with prominent deltopectoral crest much larger than the dorsal process, and covering more than half the length of the shaft; anterior edge of humerus shaft much shorter than posterior in ventral view; circular depression on the articular surface anterior to the dorsal process of humerus; dorsoventral constriction in the humeral head; humerus length more than 1.7 times the length of the femur; femur almost as wide proximally as distally with a relatively short shaft (femur is much wider distally than proximally in all other *Ichthyosaurus* species).

### DESCRIPTION

Lomax (2010) assigned DONMG:1983.98 to the genus *Ichthyosaurus* on the basis of the morphology of the pectoral elements and the humerus. The scapula and coracoid have the same morphology as illustrated for the genus by McGowan and Motani (2003:figs. 56, 70). The coracoid has both an anterior and a posterior notch (Maisch and Matzke, 2000). The humerus is short and robust (Maisch and Matzke, 2000), wider distally than proximally (McGowan and Motani, 2003), although only slightly. The shape is distinct from humeri of the other Plensbachian genera, *Leptonectes* and *Temnodontosaurus*, which have much wider distal ends relative to their proximal ends (McGowan and Motani, 2003). Those genera also differ from *Ichthyosaurus* in other attributes, including the shape of the coracoid and forefin morphology (McGowan and Motani, 2003).

**Maturity**

The preserved length of the articulated portion of DONMG:1983.98, including the skull, is approximately 74.7 cm, which includes only presacral vertebrae. We estimate that the individual would be 1.4 m long from the tip of the snout to the base of the fluke (see below for details). It is comparable in size to *I. breviceps* and *I. conybeari*, but the jaw length is larger than the largest specimen of either of those species (~32 cm for *I. conybeari*, McGowan, 1974:fig. 1; 33.5 cm for *I. breviceps*, Massare and Lomax, 2014a:table 1). This suggests that DONMG:1983.98 is either a juvenile or the species may have a proportionally larger skull. With 38.4 cm of the jaw preserved, that length falls near the median for the size range of *I. communis* (~12–54 cm; McGowan, 1974:fig. 1). It is unlikely, however, that DONMG:1983.98 is a juvenile *I. communis* based on the autapomorphic characters previously described. Assuming the same postcranial proportions for this species as for a typical *Ichthyosaurus* (Buchholz, 2001:fig. 5), the skull of DONMG:1983.98 is about 27% of the length measured to the tail bend. This proportion is in the range for a subadult *Stenopterygius* (see McGowan, 1973:fig. 4, reproduced from von Huene,
suggesting that DONMG:1983.98 is at least a subadult. Thus, *I. anningae* may have a proportionally larger skull than other species of *Ichthyosaurus*.

Johnson (1977) identified characteristics of the forelimb of *Stenopterygius* that distinguish mature and immature individuals. Immature individuals have more widely spaced proximal phalanges, whereas mature individuals have tightly articulating elements, but the forefin of DONMG:1983.98 does not retain the original spacing, so this criterion cannot be applied. In addition, immature individuals displayed a sandpaper-like surface texture on the shaft of the humerus, whereas mature individuals have a smooth surface. The latter is the case in DONMG:1983.98. In addition, the head of the humerus is flat on immature individuals but convex on mature individuals (Johnson, 1977), although this depends on how the humerus is viewed (McGowan, 1995). McGowan (1995) further suggested that the articular surface is rugose on immature individuals. The articular surface on DONMG:1983.98 appears somewhat rugose in places but smoother in others, suggesting that this is a fairly mature individual. Maxwell and Kear (2010) reviewed other criteria that have been suggested as indicators of maturity, but none of them can be applied to this specimen. Thus, current criteria make the determination of maturity of DONMG:1983.98 problematic. Our assessment is that it is at least a subadult, if not actually a fully mature individual.

**Skull**

The left side of the skull is exposed and laterally flattened, so very little of the skull roof can be seen (Fig. 4). The estimated snout ratio for DONMG:1983.98 is greater than 0.63, this ratio being calculated on only the preserved portion of the snout (Table 1). The distal ends of the premaxilla and dentary are broken, so the full length of the skull cannot be measured. However, the separation between the alveolar margins at the tip of the snout is about the same as the height of the tooth crowns. Based on the estimation method of McGowan (1996), this suggests that very little of the snout is missing, probably no more than 1 cm. The snout ratio is within the range of *I. communis*. However, in *I. anningae*, the robust, straight rostrum plus proportionally larger skull gives an appearance of a longer snout than on the other species. The orbit is slightly deformed and measures 7.25 cm long and 7.1 cm high. The orbit ratio is 0.19, but the actual value is probably slightly lower because the jaw is incomplete.

Most sutures are difficult to discern because of crushing, except in part of the preorbital region. The nasals appear short, but their anterior edge is damaged. They probably extend less than 40% of the preorbital length of the rostrum and comprise the entire dorsal edge of the external naris. The external naris is roughly triangular, although it is difficult to determine the exact border. The lacrimal appears unusually large, but the anterior...
The anterior end of the jugal is pointed, but the skull is crushed in that area, so it is difficult to distinguish. The posterior end of the maxilla extends under the orbit for less than one-fourth of the orbit length. Any maxillary teeth present were probably removed during preparation, because that portion of the tooth row appears to be cut more diagonally (Fig. 4). A somewhat similar ‘ridge and furrow’ ornamentation has been reported on the premaxillae of plesiosaurs (Maisch and Rücklin, 2000; Grossman, 2007) and was considered to have phylogenetic significance by Grossman (2007). None of the referred specimens, however, display this feature, so we have not included it as a diagnostic character. It may be related to ontogenetic stage or sexual dimorphism, but although lacking additional examples, it could also represent a pathology.

As for the braincase, a small bone, posterior to the supratemporal and isolated in the matrix, may be a partial exoccipital (Fig. 4B). One side (ventral) is curved, whereas the ?anterior edge has a narrow, squared edge.

**Mandible and Dentition**

The preserved jaw length is 38.4 cm, but the anterior end is missing a small amount. The posterior-most portion of the dentary extends to below the center of the orbit. From below the maxilla to the anterior end of the dentary, furrows are much more prevalent than on the premaxilla. The posterior ones are fairly short and difficult to discern, but they are longer and more prominent anteriorly (Fig. 4). The surangular extends anteriorly as far as the maximum height of the maxilla. The angular is exposed laterally as far anteriorly as the posterior edge of the orbit, contributing only a small portion to the mandible. When viewed ventrally, the angular extends as far anteriorly as the surangular. All of the teeth preserved are anterior to the maxilla, but this is likely because of preparation. The posterior ones are surrounded by what appears to be plaster but have a similar morphology and size as the anterior teeth. About 16 teeth are in the rostrum, four or five of which have become dislodged. Several isolated teeth are scattered in the matrix.

The teeth are slender and conical, and some have fairly coarse longitudinal striations. The roots show coarse inrolling and are continuous with the edge of the crown (i.e., the tooth is not ‘waisted’). The tips of the crowns are pointed, although some teeth have rounded, smooth tips, probably from wear against prey. Two anterior teeth were preserved well enough to measure: one has a crown height of 11.5 mm and a total height (including root) of 17 mm; a second has a crown height of 9 mm and a total height of 14 mm. The teeth of *I. anningae* are more similar to those of *I. conybeari* than to the more robust teeth of *I. communis* and *I. breviceps*. Tooth morphology, however, is not considered a useful taxonomic trait (McGowan and Motani, 2003; but see Maisch, 1997; Maisch and Matzke, 2000), and possible ontogenetic differences in tooth form have not been investigated. Thus, tooth morphology has not been established as a reliable taxonomic character.

**Axial Skeleton**

Eight disarticulated centra are anterior to 15 articulated dorsal centra. The average length of the latter is 1.55 cm, but there is an increase in length from the anterior to the posterior (see Supplementary Data: Table S1; Figs. S1, S2). The five anterior centra have an average length of 1.41 cm, whereas the three posterior centra have an average length of 1.72 cm, an increase of 22%. The centra have prominent anterior and posterior rims. The only complete neural spine, probably from the dorsal region, are

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**FIGURE 6.** Interpretive illustration of the right humerus of DONMG:1983.98, *Ichthyosaurus anningae*, sp. nov. A, dorsal view; B, anterior view; C, ventral view; D, proximal view; E, distal view (radial facet to the left, ulna facet to the right). **Abbreviations:** af, anterior facet; de, depression; dp, dorsal process; dpc, deltopectoral crest; dvc, dorsal process; z, ‘lump’ at the base of the deltopectoral crest. Scale bar equals 3 cm.
four that are displaced posterior to the articulated centra. They are rectangular, much higher than long, and have an average height of 4.3 cm. The ribs are relatively narrow and the longest rib, measured along the curvature, is 28 cm long. Only a few gastralia fragments are present.

### Pectoral Girdle and Forefin

The shaft of the scapula is straight, and the articular surface is expanded only posteriorly. The proximal peripheral edges of the scapulae are more squared than rounded, but this may be due to deformation (flattening). The coracoids are robust and have well-developed anterior and posterior notches. The anteroposterior length is much greater than the mediolateral length, a ratio of about 1.6 (Table 1). The anterior edge of the coracoid is exceptionally straight, which is unusual. However, considerable variation occurs in the shape of pectoral elements in Jurassic ichthyosaurs (Maxwell and Druckenmiller, 2011), so this may not be a consistent feature in this species.

The only in situ portion of the forefin is lying in the matrix at the distal end, slightly below and anterior to the larger, reset elements (Fig. 3). Because of the smaller size of these phalanges, they are likely from the mid-distal to distal region and do not indicate whether it is a left or right fin. They are closely packed polygons that lack notching and indicate that the forefin has at least four digits. Isolated, rotated phalanges show that they are as deep as they are long.

The humerus is short and robust, displaying prominent dorsal and ventral processes (Figs. 5, 6). The shaft is wide with barely a constriction. The distal end is only slightly wider than the proximal, as seen in other *Ichthyosaurus* species (Fig. 7A, C, E, G). A small anterior facet on the distal edge of the humerus is similar to that occurring in other *Ichthyosaurus* specimens (McGowan, 1974; Motani, 1999; pers. observ.), although it does not occur on all examples. The facets for the radius and ulna are roughly equal in size.

Within the articular surface and anterior to the dorsal process is a circular depression that is apparent in proximal, anterior, and dorsal views (Figs. 5D, E, F, 6A). In posterior view, the deltopectoral crest is much larger than the dorsal process. A small ‘lump’ is preserved on both humeri at the distal end of the ventral process (Fig. 6C), which may be a muscle attachment or a pathology.

The ratio is humerus length divided by femur length. Note that the ratios are 1.5 or less, whereas *Ichthyosaurus anningae*, sp. nov., has a ratio >1.7. *The rostrum is broken anterior to the external naris, so the actual length is greater.*

**The rostrum is broken anterior to the external naris, and may not have been attached in its original position.**
extends less than half way down the shaft. The difference between the posterior and the anterior length of the shaft is not as apparent in dorsal view, probably because the dorsal process is smaller and more centrally located than the deltopectoral crest.

Pelvic Girdle and Hindfin

The posterior part of the skeleton of DONMG:1983.98 is missing except for some scattered, isolated bones (Fig. 8). A complete left femur, in dorsal view, is about the same width proximally as distally. This is unusual compared with other *Ichthyosaurus* specimens, where the proximal end is much narrower than the distal, and the shaft is more elongated (Fig. 7B, D, F, H). The femur is exceptionally small in comparison to the humerus. The ratio of humerus length to femur length is 1.78 (Table 1) compared to ratios of 1.3–1.5 for other *Ichthyosaurus* species (Table 2). There is no overlap in the humerus length/femur length ratio between *I. anningae* and the three other species, and we suggest that this is an unequivocal character that distinguishes the new species. Relative limb length has been used similarly to distinguish between *Temnodontosaurus platyodon* and *T. crassimanus* (McGowan and Motani, 2003:87–88). The proximal portion of the right femur, seen in ventral view, displays a large head with a strong ventral process. An isolated, nearly complete ilium is closer to the right femur, so it may be a right ilium. It is rod-shaped with a slight curvature at the (?proximal end, which is damaged. It is much longer than the femur. The rest of the pelvis of *I. anningae* is unknown.

Referred Specimens

**NMW G.1597**—This specimen is a small individual preserved on its left side comprising a partial skull, right forefin, pectoral elements, and 31 articulated centra (Fig. 9). An additional 42 centra added to the vertebral column belong to other individuals and are not figured here (Massare and Lomax, 2014b). NMW G.1597 is assigned to *I. anningae* on the basis of humerus morphology, specifically the depression behind the dorsal process that displays a strong ridge, and a dorsoventral constriction in the head.

The posterior part of the skull is completely fragmented, including the dorsal and posterior margins of the orbit. The jaw length measures 32 cm, about 85% the size of the holotype. The
skull is best preserved anterior to the orbit, although segments are broken, including portions of the premaxilla and dentary. The large lacrimal is roughly triangular and meets the premaxilla about halfway across the center of the external naris, in a ‘V’-shaped contact. It appears that the lacrimal and premaxilla exclude the maxilla from contact with the external naris, although the area is damaged. The nasals extend at least as far anteriorly as the break in the rostrum. The jugal is broken posteriorly but extends only as far anteriorly as the anterior edge of the orbit. The maxillary teeth have smooth roots and coarse striations on the crowns, and there were probably at least 10.

The specimen provides additional information on the anterior vertebral column and forefin of the species. The articulated centra have an average length of 0.99 cm and an average height of 1.95 cm. Both length and height increase from anterior to posterior (Table S1; Fig. S1). The average length of the five anterior centra (3–9) is 0.90 cm. The average length of the five posterior centra (27–31) is 1.09 cm, a 21% increase. Similarly, the average height of the five anterior centra is 1.72 cm, whereas the average height of the five posterior centra is 2.15 cm, a 25% increase. Thus, height is increasing slightly faster than length, resulting in somewhat higher height/length ratios posteriorly, at least for the anterior two-thirds of the trunk.

The humerus is oriented at a slight angle, with the posterior end buried slightly deeper in the matrix than the anterior end. It is 4.2 cm long when measured in dorsal view and shows an anterior facet. The forefin differs from NMW G.1597 in that the ulna is very wide compared with its length and is much wider than the radius. A similar bifurcation occurs in the metacarpal row of digit II(?) and, the two branches are equal in size, but NHMUK OR 35566 lacks the second bifurcation seen in NMW G.1597. There are three posterior accessory digits and possibly one anterior one. Twenty-two phalanges are preserved in the longest digit (IV).

**NHMUK OR 120**—This specimen is a nearly complete, small individual lying on its left side, exposed in right lateral aspect (Fig. 10). NHMUK OR 120 is provisionally referred to *Ichthyosaurus anningae* on the basis of femur morphology and a small femur relative to the humerus (humerus/femur ratio = 1.79), which is comparable to the proportions in the holotype. However, the humerus lacks the diagnostic features of the species.

**NHMUK OR 120** has a complete skull that is approximately 25.7 cm long, about 67% the size of the holotype. The dentary is not as deep as that of the holotype, especially towards the anterior, but it is preserved to the tip, with a length of 28.1 cm (Table 1). The snout ratio of 0.64 is slightly greater than the holotype and the average for *I. communis*, but below that of *I. conybeari* (0.65; McGowan, 1973). NHMUK OR 120 has an orbit ratio of 0.27, much larger than that of the holotype, and larger than both *I. communis* and *I. conybeari*. The maximum height of the maxilla is as far anterior as the external naris. The dorsal process of the premaxilla appears to contact the external naris, unlike the holotype. The maxilla extends posteriorly only a short distance under the orbit. Anteriorly it appears to extend beyond the external naris, although it is not possible to tell how much because the border of the external naris is broken. The rostrum is packed with numerous slender teeth, including about 15 maxillary teeth. However, there are gaps in the tooth row, and the number could have been 20 or more.

A complete vertebral column is preserved (Fig. 10; Table S1), including an unfused atlas-axis. There are about 43 presacral vertebrae, based on the position of the femur relative to the vertebral column, and a total of 74 vertebrae to the first wedge-shaped centrum that indicates the beginning of the tail bend. There may be as many as four wedge-shaped centra anterior to the fluke centra. An additional 59 vertebrae are in the tail fluke, although two gaps in the series may indicate there were at least two more. The average length and width of the dorsal centra are 0.76 cm (Table S1), increasing from an average of 0.60 cm for anterior centra 3–9 to 0.79 cm in centra 38–43, an increase of 32%. The average height of the dorsal centra is 1.41 cm (Table S1), increasing from an average of 1.30 cm for centra 3–9 to 1.53 cm for centra 38–43, an increase of 18%. The height increases more slowly than the length, which is the opposite of what occurs in the holotype and NMW G.1597, which could be
ontogenetic or phenotypic variation. There is a slight increase in length to around centrum 20, and then relatively little change in length until around centrum 55, where the length decreases sharply to the fluke (Table S1; Fig. S2). Centrum height is relatively constant until about centrum 35, after which it increases rapidly to centrum 50, then decreases sharply to the fluke (Table S1; Fig. S2). The neural spines on the anterior dorsal vertebrae are twice the height of the centra. The estimated length to the tail bend, measured from the tip of the rostrum along the vertebral column, is 85.5 cm, almost 30% of which is the skull. The total length to the last preserved centrum of the fluke is 102.0 cm (Table 1).

NHMUK OR 120 has a relatively short coracoid that is rounded anteriorly. It lacks the straight anterior edge of the holotype, suggesting that there is considerable variation within the species, which is perhaps ontogenetic. The scapula is nearly in articulation with the humerus and coracoid and, although flattened, has the typical shape for *Ichthyosaurus*. A complete right forefin is preserved in dorsal view. The humerus is relatively short and stout, almost as wide as it is long (Table 1), and does not have an anterior facet. However, the dorsal process is not prominent and the humerus lacks the unusual depression on the head, adjacent to the dorsal process, that is seen in the holotype and other referred specimens. The forefin of NHMUK OR 120 differs from that of NMW G.1597 in that the bifurcation takes place in the first row of phalanges and there is no second bifurcation. However, on both specimens, the bifurcation takes place on digit II and at least six digits are present, including a posterior accessory digit. The forefins of *Ichthyosaurus*, however, are extremely variable within species (McGowan, 1974; pers. observ.). There are at least 25 phalanges in the longest digit, and notching does not occur in any elements. The complete forefin is 13.3 cm long.

A hindfin with four digits is preserved in dorsal view, but it is not as complete as the forefin. As in the holotype, the proximal end of the femur is almost equal in width to the distal end. The tibia is smaller than the fibula. The complete hindfin is 4.2 cm long, and there are at least nine phalanges in the longest digit.

**NHMUK OR 10028**—This specimen consists of a partial vertebral column, pectoral elements, a partial left forefin, and portions of the hindfins and pelvis of a very small individual that has been acid prepared to show preserved skin(?). It is provisionally referred to *I. anningae* because of the femur morphology and a small femur relative to the humerus (humerus/femur ratio = 1.83). The partial forefin is completely free of matrix and can be viewed in three dimensions. The humerus is 2.2 cm long and does not have an anterior facet. It lacks the depression on the head and the dorsal process is barely noticeable. The deltopectoral crest is not as large as in the holotype, but it makes the anterior edge of the shaft look shorter than the posterior edge. Although the ventral aspect has some similarities, the humerus lacks the diagnostic characters and so this is a provisional assignment.

Portions of the hindfins and pelvic girdle are preserved on a single block that, like the forefin, has been completely freed of matrix. Both hindfins are preserved but are laid atop one another, with the uppermost (?right) femur in anterior view and the lower (?left) in dorsal view. They are almost as wide proximally as distally, displaying a relatively short shaft. Only the distal portion of one hindfin (?left) is articulated, displaying at least five digits, one more than for NHMUK OR 120, but it is unclear whether the extra digit is an accessory. A large, long, robust bone, with proximal and distal ends equal in width, possibly the ilium, is longer than the femur. A possible ilium is preserved. It is rod-shaped with a robust proximal end and becomes more slender towards the distal end. It is almost equal in length to the femur, which differs from the holotype, but this could be due to its very young age.

**DISCUSSION**

The estimated length of the vertebral column in DONMG.1983.98, from the first associated vertebra behind the skull to the end of the articulated section exposed, is 35.5 cm. In *Ichthyosaurus*, the presacral vertebral count is approximately 43 or 44 (Maisch and Matzke [2000] and Buchholtz [2001], respectively, although McGowan [1974] estimated it as 44 ± 3). Taking 43 as the presacral count, the 25 preserved centra in DONMG.1983.98 account for about 57% of the presacral centra, so 35.5 cm would represent about 57% of trunk length of this individual. The tail stock is approximately two-thirds the length of the trunk in *Ichthyosaurus* (Buchholtz, 2001:fig. 5). This would give a length of about 104 cm for the trunk and tail stock and a total length, from the tip of the snout to the base of the fluke, of about 1.4 m. Thus, *I. anningae* is considerably smaller in overall body length than *I. communis*, in the size range of *I. breviceps*, and larger than *I. conybeari* (McGowan and Motani, 2003).
Swimming style can be examined using the ratio between the centrum height and length (Massare et al., 2006). Although few centra are articulated on the holotype, the provisionally referred specimen, NHMUK OR 120, has a complete vertebral column. The specimen shows that the height/length ratio increases from the posterior dorsal region (centrum 37) to the anterior caudal region (centrum 59), attaining a maximum ratio of 3.1 (Table S1). This ratio is considerably less than for Stenopterygius and Ophthalmosaurus (Massare et al., 2006; fig. 5), taxa with highly regionalized vertebral columns and a more oscillatory mode of swimming that used mainly the tail fluke for propulsion. The ratios suggest that *I. anningae* had a less regionalized vertebral column and therefore a more flexible posterior trunk and tail stock, perhaps reflecting a more undulatory swimming style, at least in the juveniles. An undulatory style favors maneuverability over speed (Massare et al., 2006). The small hindfin would have had an opposite effect. In ichthyosaurs, fins are used for maneuvering and braking (Massare, 1988). The smaller hindfin suggests that the forefin performed most of that function, with the hindfin playing only a minor role. Because the forefin does not appear proportionally larger than in other *Ichthyosaurus* species, this could have made *I. anningae* less maneuverable. So perhaps the more flexible vertebral column compensated for the reduction in the hindfin.

**Intraspecific Variation and Sexual Dimorphism**

The holotype is the largest of all known specimens, with a humerus length of 5.2 cm. If we assume that DONMG:1983.98 is an adult, then NMW G.1597 is a subadult (humerus length 4.2 cm). NHMUK OR 120, NHMUK OR 35566, and NHMUK OR 10028 (with humerus lengths of 2.8, 2.9, and 2.2 cm, respectively) are at least 30% smaller than the holotype, and probably juveniles. The atlas-axis is not fused in NHMUK OR 120, the only one of the three that preserves it. In addition, the dorsal surface of the humerus of NHMUK OR 120 has a sandpaper texture at the distal end, characteristic of juveniles (Johnson, 1977). The holotype and two referred specimens (NMW G.1597, NHMUK OR 35566) clearly show the diagnostic features of the humerus, although only the holotype preserves a femur to demonstrate the diagnostic morphology and the relatively small size. They also show an anterior facet on the humerus. The two provisionally referred specimens (NHMUK OR 120 and NHMUK OR 10028) display similar humeral morphologies that lack the depression on the head, have much less prominent processes (although only the dorsal side can be seen on NHMUK OR 120), and lack the anterior facet. So we have two groups of specimens, one showing all of the diagnostic features of the humerus and the other showing all of the autapomorphies except for the diagnostic features of the humerus.

Differences in morphology, in general, can be ecophenotypic, ontogenetic, taphonomic, taxonomic, or sexually dimorphic. We argue that the latter is most likely the situation here. Differences are unlikely to be due to ecophenotypic variation because all of the specimens derive from the Lyme Regis/Charmouth region of the Dorset coast. The differences are not ontogenetic because NHMUK OR 35566 is approximately the same size as NHMUK OR 120, yet the former shows the diagnostic features that the latter lacks. The differences are not due to taphonomic processes because the humeri are well preserved and display little crushing, damage, or deformation. No other species of *Ichthyosaurus* has a humerus to femur ratio as high as 1.7, so it is more likely that NHMUK OR 120 and NHMUK OR 10028 belong to *I. anningae* than to another species. The stratigraphy, however, is poorly known for all specimens except the holotype. Ammonites associated with NHMUK OR 120 indicate that it is stratigraphically older than DONMG:1983.98, so it is possible that the diagnostic morphology of the humerus developed late in the evolution of the species or that two chronospecies, both with unusually small hind limbs, are represented in these specimens. Equally likely, however, is that the difference reflects sexual dimorphism: the depression and larger processes on the humerus being associated with one gender. Notably, the specimens showing these features on the humerus also show an anterior facet at the distal end. The anterior facet occurs in other *Ichthyosaurus* species as well, but only on some of the specimens. It is possible that these features are associated with muscle attachments or soft tissue structures related to mating. It may be that *Ichthyosaurus anningae* males required additional musculature

![FIGURE 11. Strict consensus of five trees of length 143 steps (consistency index = 0.476; retention index = 0.615). The phylogenetic analysis used the matrix of Maxwell et al. (2012), and the consensus tree has a similar topology except for the addition of *I. anningae* as a sister taxon to *I. communis.*]
in the forefin to position themselves during mating. The holotype is the largest example of the species and may represent a male, but we do not intend to imply that males were larger than females.

Sexual dimorphism in limbs is not unheard of in reptiles. Males of the sauropodtygian *Keichousaurus hui* have more robust humeri that are wider distally and relatively larger than those of females or immature individuals (Cheng et al., 2009). The lizard *Psammodromus algerius* exhibits gender differences in hind limb size, probably related to chemical signaling (Iraeta et al., 2011). Katsura (2004) found differences in both humeral and femoral morphology in champsosaurs, with the female being more adapted to terrestrial locomotion because of the need to lay eggs on land.

**Phylogenetic Analysis**

We added *Ichthyosaurus anningae* to the data matrix of Maxwell et al. (2012; Table S2) to explore its relationship to other Lower Jurassic species. This matrix was selected because it incorporates Lower Jurassic taxa at the species level and does not assume generic monophyly. Only 33 of the 60 characters (55%) were preserved on the holotype and four referred specimens of *I. anningae*. A phylogenetic analysis was performed using the new technology search with default settings in TNT version 1.1 (Goloboff et al., 2008). The results generated five most parsimonious trees of length 143 steps (consistency index = 0.476; retention index = 0.615). The strict consensus tree topology did not differ from that of Maxwell et al. (2012) except that *I. anningae* was placed as a sister taxon to *I. communis* (Fig. 11; see also Fig. S3), supporting a close relationship between the two species.

*I. anningae* differs from *I. communis* in only three characters included in the matrix: the relative size of the supranarial and subnarial processes of the premaxilla (character 1), the extent of the jugal process of the maxilla (character 3), and whether the postorbital contacts the supratemporal in external view (character 6). The skulls of the holotype and referred specimens are not sufficiently well preserved to be certain of these character states (see Supplementary Data). Moreover, the matrix does not include propodial morphologies and their relative size, characters that distinguish *I. communis* from *I. anningae*.

**Pliensbachian Diversity**

Three ichthyosaur species with diagnostic material are now known from the Pliensbachian: *Ichthyosaurus anningae*, the most complete ichthyosaur from this time interval (described herein); a skull and fragmentary skeleton of *Leptocerites temnariostris* from Switzerland (Maisch and Reisdorf, 2006); and a skull and partial skeleton of *L. moorei* from Dorset, U.K. (McGowan and Milner, 1999). Bennett et al. (2012) reported that *Ichthyosaurus communis* occurred in the Pliensbachian, but the fragmentary specimen in question (NHMUK R15907) has no diagnostic features attributed to *I. communis*, and we therefore consider it *Ichthyosaurus sp*. Maisch and Hungerbuhl (1997) recognized *Temnodontosaurus nuertingensis* (von Huene, 1931) from the Pliensbachian of Germany, although McGowan and Motani (2003) consider the only specimen to be a species inquirendae. Thus, there may be as many as five Pliensbachian species of ichthyosaurs, three of which are known from Britain.

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