Paludicola 10(2):119-135 May 2015

A LARGE FOREFIN OF *ICHTHYOSAURUS* FROM THE U.K., AND ESTIMATES OF THE SIZE RANGE OF THE GENUS

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ABSTRACT

A large partial forefin (YORYM 2005.2411) from the Lower Jurassic of Yorkshire is assigned to *Ichthyosaurus* on the basis of the humerus shape, two digits originating from the intermedium, and an anterior digital bifurcation. The humerus is 11.7 cm long and the forefin is 38.5 cm long, but incomplete, probably missing more than 1/3 of its length. Regression analyses suggest that the individual had a jaw length of 56 cm and a total length to the tail bend of almost 3 m. This individual represents the largest *Ichthyosaurus* reported from the U.K. Although interest in the reptiles of the Yorkshire coast dates back to the early 1800s, specimens of *Ichthyosaurus* from the area are rare.

INTRODUCTION

The Lower Jurassic parvipelvian ichthyosaur genus *Ichthyosaurus* is common in museums throughout the U.K., especially in historical collections. Many specimens have been recovered from west Dorset and Somerset, but the genus has also been identified from Barrow-upon-Soar, Nottinghamshire, Warwickshire, and Yorkshire (Martin et al., 1986; Maisch, 1997; Smith and Radley, 2007; pers. obs. DRL). Large, fragmentary specimens from elsewhere in Europe have been assigned to *Ichthyosaurus* (Godefroit 1996; Maisch et al., 2008), but see discussion below.

Ichthyosaurus is the only Lower Jurassic genus that has a wide forefin with an anterior digital bifurcation (Motani, 1999a), so even isolated forefins are easily distinguished from other genera of the same age. This paper reports on an unusually large partial forefin (YORYM 2005.2411) of a Lower Jurassic ichthyosaur in the collection of the Yorkshire Museum, York, U.K. The specimen was set into a plaster-like filler and surrounded by a wooden frame, with both the plaster and frame painted. This style of mount was common during the 19th century (pers. obs. DRL, JAM), and so the specimen may have been collected then, but the date of acquisition is not recorded. The specimen has recently been conserved and removed from the original wooden frame (pers. comm. N. Larkin, 2015 DRL). YORYM 2005.2411 probably represents the largest *Ichthyosaurus* individual known from the U.K., although the rest of the skeleton is not preserved. The humerus and individual forefin elements are larger than in any other *Ichthyosaurus* forefin that we have observed.

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, Drexel University, Philadelphia, USA; **BGS** British Geological Survey, Keyworth, Nottingham, UK; **BRSMG** Bristol Museum and Art Gallery, Bristol, UK; **BRSUG** Bristol University Geology Department, Bristol, UK; **CAMSM** Sedgwick Museum, Cambridge University, Cambridge, UK; **DONMG** Doncaster Museum and Art Gallery, Doncaster, South Yorkshire, UK; **LEICT** Leicester Arts and Museums Service, New Walk Museum and Art Gallery, New Walk, Leicester, UK; **LYMPH** Philpot Museum, Lyme Regis, UK; **MAN** Manchester Museum, The University of Manchester, Manchester, UK; **MOS** Museum of Somerset, Taunton, Somerset, UK; **NHMUK** (formerly BMNH) Natural History Museum, London, UK; **NMS** National Museum of Scotland, Edinburgh, UK; **NMW** National Museum of Wales, Cardiff, UK; **OUMNH** Oxford University Museum of Natural History, Oxford, UK; **ROM** Royal Ontario Museum, Toronto, CA; and **YORYM** Yorkshire Museum, York, UK.

GEOLOGICAL SETTING

YORYM 2005.2411 was collected from the Lias of Yorkshire, with no further locality information recorded. ‘Lias’ is an old, informal stratigraphic term that referred to the entire Early Jurassic, and was commonly subdivided into the Lower Lias and Upper

Lias. The term is now restricted to the Lias Group, which spans the uppermost Triassic and the entire Lower Jurassic (Rhaetian-Toarcian; Cox et al., 1999; Hobbs et al., 2012). We follow the current usage as much as possible, but revert to the informal usage of 'Lias' for specific references to older literature.

During the 19th century, many coastal and inland quarries in Yorkshire exposed Lower Jurassic strata that yielded rare fossils, including marine reptiles and the first pterosaur from the county (Newton, 1888; Benton and Spencer, 1995; O'Sullivan et al., 2013). The area of the Yorkshire coast around Whitby, however, is famous for a wide range of Lower Jurassic fossils (Lomax, 2011). Specimens have been collected for over 200 years, making the Whitby coast one of the earliest localities in Britain to be exploited for its fossil reptiles (Benton and Taylor, 1984; Benton and Spencer, 1995). Perhaps the most notable finds are the exceptionally well preserved marine reptiles, including ichthyosaurs, plesiosaurs and thalattosuchian crocodylomorphs (Benton and Taylor, 1984; Benton and Spencer, 1995). The Whitby coast includes locations from Staithes in the north to Ravenscar in the south (Lomax, 2011), a distance of about 9-10 km (15-16 miles), with Whitby about midway (Figure 1). Historically, many specimens collected from this stretch of coastline were simply recorded as 'from Whitby', even if the original location may have been several miles from the town itself (Benton and Taylor, 1984; Benton and Spencer, 1995; pers. obs. DRL). Unfortunately, dozens of ichthyosaur specimens collected from the Whitby area in the early 19th century were collected or purchased by private collectors at the time and cannot currently be located (Benton and Spencer, 1995). However, many ichthyosaurs from the Lower Jurassic of the Whitby coast are in many museum collections (see Benton and Spencer, 1995), but they require a taxonomic review beyond the scope of this paper.

The majority of Lower Jurassic rocks in the Whitby area are from the upper Lias Group. Most marine reptile specimens are from the Toarcian Whitby Mudstone Formation (Benton and Spencer, 1995; Rawson and Wright, 2000; Lomax, 2011). Much rarer specimens of ichthyosaurs and isolated plesiosaur and crocodilian bones have been recorded from lower in the Lias Group (Benton and Taylor, 1984). The Redcar Mudstone Formation (Hettangian-Pliensbachian) underlies the Whitby Mudstone Formation, and is extensively exposed at Robin Hood's Bay. Outcrops of the lower Lias Group also occur near Staithes (Howarth, 2002). Further up the coast, to the north of Staithes, both Saltburn and Redcar also have excellent exposures (Rawson and Wright, 2000). It is also likely that some of the old inland quarries had exposures of the lower Lias Group as well. The genus *Ichthyosaurus*, to which YORYM 2005.2411 is here referred, has never been reported from the Toarcian, so the specimen is most likely from the Redcar Mudstone Formation.

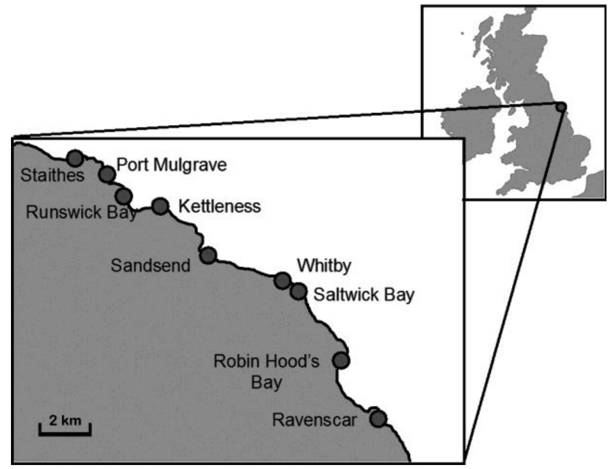

FIGURE 1. Map of the Whitby coast, with an inset map showing its location along the Yorkshire coast of England. Scale = 2 km.

Only a few ichthyosaurs from the lower Lias Group of Yorkshire have been reported in the literature. Owen (1840, p. 112) listed the Lias of "different parts of Yorkshire", and "near Whitby and Scarborough" among the locations for *Ichthyosaurus intermedius*. Benton and Taylor (1984), however, thought that the Scarborough locality referred to the museum that housed the specimens because the lower Lias Group is not exposed at Scarborough. Blake (1876, p. 254) mentioned other Lower Lias specimens probably belonging to the same species, and briefly described one poorly preserved specimen from Robin Hood's Bay. More recently, Maisch (1997) described a nearly complete skull housed in the Staatliches Museum für Naturkunde, Stuttgart (SMNS 13111), with the provenance given only as the Lower Lias of Whitby. He referred the specimen to *I. intermedius* based on cranial features and tooth morphology. The skull belongs to *Ichthyosaurus*, but currently, *I. intermedius* is considered a junior synonym of *I. communis* (McGowan and Motani, 2003; but see Maisch and Matzke, 2000). Unfortunately, no other stratigraphic information was recorded for SMNS 13111, and Maisch (1997) assumed that the specimen was from the Lower Lias based on its identification as *Ichthyosaurus*, as we do with the specimen described below.

DESCRIPTION OF YORYM 2005.2411

Throughout this paper, the term ‘length’ refers to the proximal-distal dimension, and the term ‘width’ refers to the anterior-posterior dimension of the forefin as well as individual forefin elements. YORYM 2005.2411 is an articulated but partial left forefin that is 38.5 cm long (Figure 2). The humerus is broad with a length of 11.7 cm, longer than its maximum width. It is wider distally than proximally (10.6 cm and 8.7 cm respectively). The radius and ulna are wider than long, with the radius slightly larger than the ulna. The radius is 3.9 cm long and 6.1 cm wide, whereas the ulna is 3.7 cm long and 5.8 cm wide. The intermedium is almost diamond-shaped, and smaller than the radiale and ulnare. Two metacarpals are in contact with it. The forefin can be assigned to *Ichthyosaurus* on the basis of (1) a humerus that is nearly as wide proximally as distally, (2) two digits originating from the intermedium, (3) a forefin with at least five digits, and (4) an anterior digital bifurcation (Motani, 1999a; McGowan and Motani, 2003). The digital bifurcation occurs in digit III in the metacarpal row (for terminology see Motani, 1999a). Both branches of the bifurcation have somewhat larger elements than digit II. The first element of the anterior branch is pentagonal and unusually large. Its proximal end extends between distal carpal 2 and 3, substantially restricting the contact between them. This is an unusual feature for *Ichthyosaurus*, but forefins are extremely variable (pers. obs. JAM, DRL), so this may not be of taxonomic significance. Only eleven phalanges are preserved in the longest digit (digit III), and the distal-most phalanges are fairly large and rectangular, suggesting that this forefin is very incomplete. By comparison, the neotype of *I. communis* (NHMUK R1162) has approximately twenty phalanges in the most complete digit (McGowan and Motani, 2003, pl 9). Furthermore, nearly complete forefins of *Ichthyosaurus* have small, rounded distal phalanges on the primary digits (Figure 3; pers. obs. JAM, DRL), which is not the case for YORYM 2005.2411. A posterior accessory digit is present, starting at the carpal row, but the first element is broken so it may have originated more proximally on the fin. Two small, round elements of a second posterior accessory digit are situated at about phalangeal row 5 of digit V, giving the forefin a total of seven digits.

METHODS FOR ESTIMATING SIZE

The specimens of *Ichthyosaurus* examined for this study included isolated forefins, partial skeletons with and without skulls, and nearly complete skeletons. Measurements were taken to the nearest 0.1 mm using digital calipers for lengths less than 15 cm, and to the nearest 1 mm using a measuring tape for greater lengths. We used a number of regression analyses to estimate the size of the individual represented by YORYM 2005.2411, which allows us to incorporate either isometric or allometric growth into the estimate of size.

To demonstrate that YORYM 2005.2411 is unusually large, humerus lengths for 99 *Ichthyosaurus* specimens, representing both isolated forefins and partial and nearly complete skeletons in museum collections were measured (Appendix 1). For specimens in which both humeri were preserved, only the larger measurement was used. Specimens on display at NHMUK, among the best preserved and most complete specimens of the genus *Ichthyosaurus*, were not accessible for measurements and so were not included.

Forefin length and humerus length were measured for 27 specimens of *Ichthyosaurus* (Appendix 2). On complete or nearly complete forefins, the distal phalanges of all of the digits are small and rounded, rather than rectangular. Moreover, the distal-most phalanges are not aligned in distinct digits as in the more proximal portion of the forefin (Figure 3). The specimens used in this analysis had a few to several rows of small, rounded phalanges at the distal end of the forefin, so were judged to be nearly complete. These data were used to estimate the complete forefin length of YORYM 2005.2411. An additional complication arises, however, because it is possible that the number of phalanges and the ossification of the distal-most phalanges may be related to ontogeny. Thus the relationship between forefin length and humerus length may not be linear; forefin length may be increasing faster with growth than humerus length. Therefore, an exponential growth in forefin length relative to humerus length was assumed. Forefin lengths were transformed using common logarithms before performing a linear regression with humerus length.

A second approach to the question of the size of YORYM 2005.2411 was to relate the humerus length to skull and jaw lengths. A regression analysis of humerus length vs skull length was performed using data from 25 partial to nearly complete skeletons of *Ichthyosaurus* (Appendix 3). Specimens identified as *I. breviceps*, however, were excluded from the analysis because *I. breviceps* has a very short rostrum compared to the other species (McGowan and Motani, 2003; Massare and Lomax, 2014). When both humeri were preserved, an average length was used. Skull size, however, displays negative allometry with growth (von Huene 1922; McGowan 1973), such that the relative size of the skull decreases with increasing body size. To account for allometric growth, a linear regression was performed on logarithmically transformed

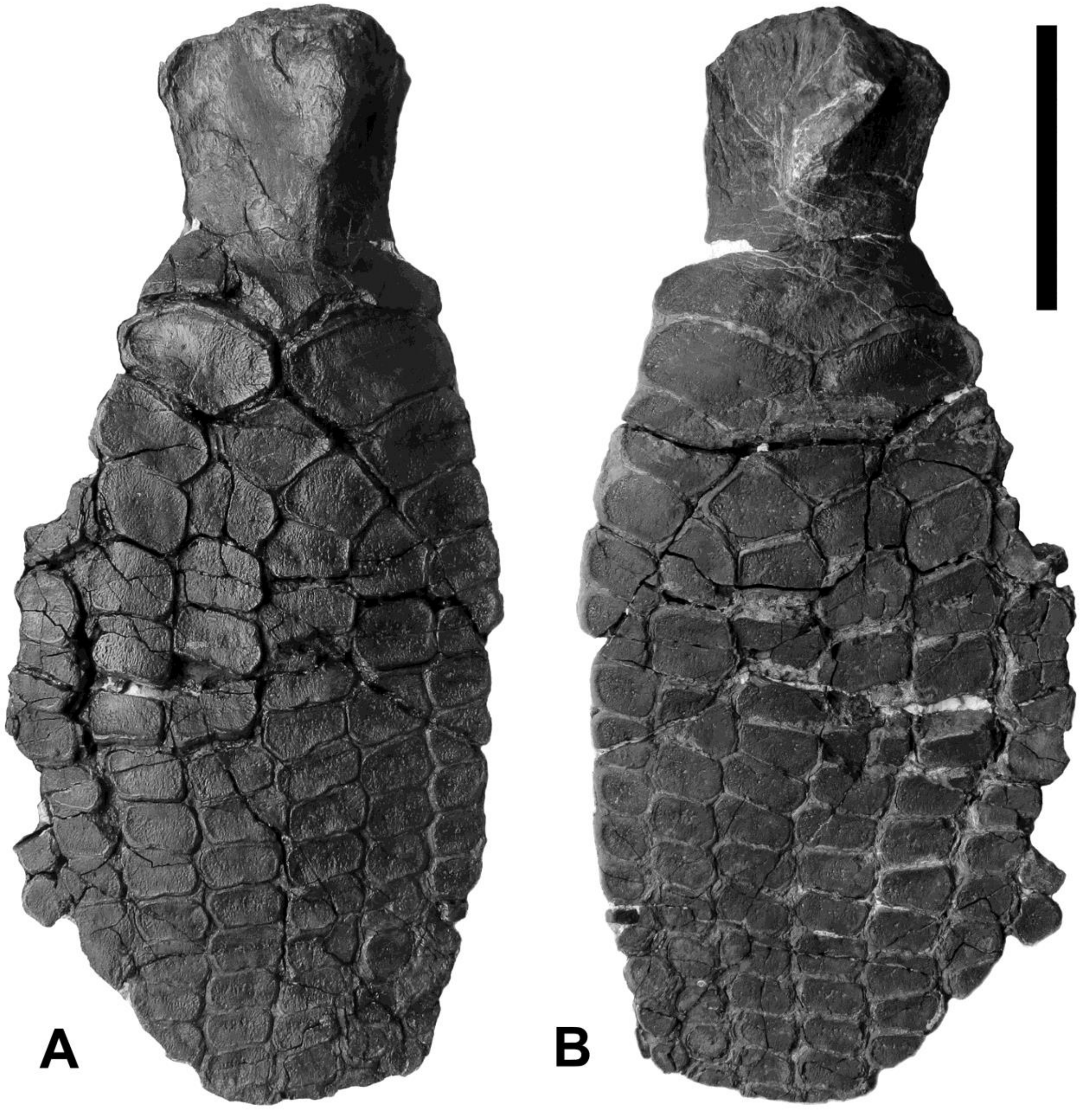

FIGURE 2. YORYM 2005.2411, an isolated, incomplete left forefin of a large *Ichthyosaurus* from the Lias of Yorkshire. A. Forefin in ventral view, anterior to the right; B. Forefin in dorsal view, anterior to the left. Scale = 10 cm

measurements for both humerus length and forefin length. As a check on this analysis, a similar regression of humerus length vs jaw length was performed using data from 55 partial to nearly complete skeletons (Appendix 3), again excluding *I. breviceps*. Jaw length is usually easier to measure than skull length, and can be accurately measured in many different orientations of a crushed skull.

Finally, we estimated the post-cranial length of YORYM 2005.2411 using a regression analysis of humerus length vs vertebral column length. The humerus grows isometrically with respect to body size (McGowan, 1973), so no data transformations were necessary for this analysis. The column length was measured along the articulated vertebrae from the anterior-most exposed cervical to the tail bend. Twenty-five nearly complete skeletons were included in the analysis (Appendix 4). The length estimated for YORYM 2005.2411 was added to the previous calculation of skull length to obtain an estimate of the pre-tail bend length of the individual represented by the partial forefin.

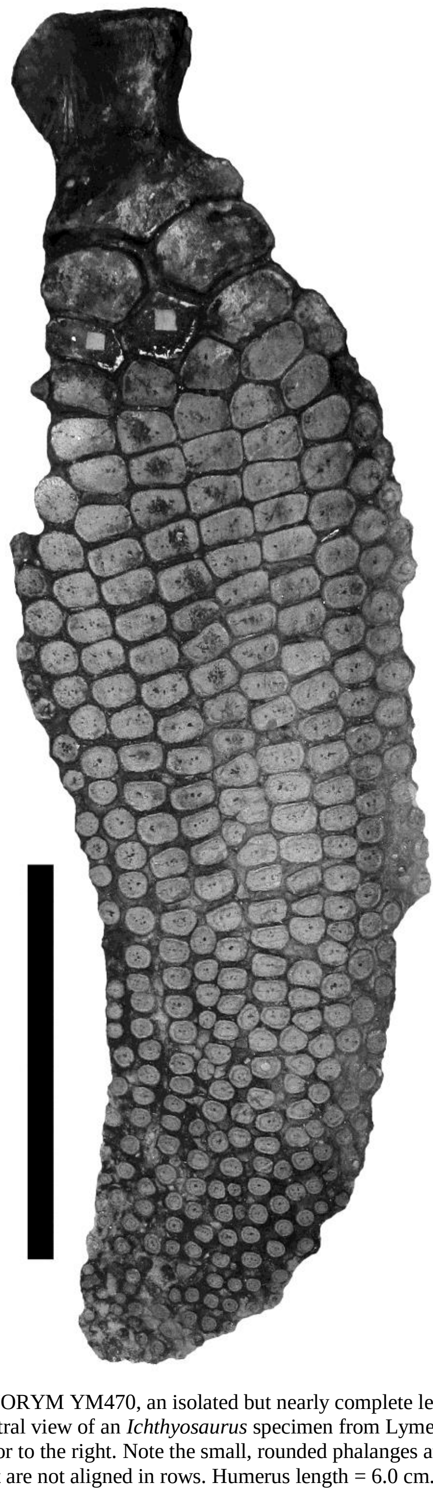

FIGURE 3. YORYM YM470, an isolated but nearly complete left forefin in ventral view of an *Ichthyosaurus* specimen from Lyme Regis. Anterior to the right. Note the small, rounded phalanges at the distal end that are not aligned in rows. Humerus length = 6.0 cm. The ulnare and intermedium are reconstructed. Scale bar = 10 cm.

SIZE ESTIMATES FOR YORYM 2005.2411

With a proximal-distal length of 11.7 cm, the humerus of YORYM 2005.1411 is larger than that of any other specimen of *Ichthyosaurus* that we have seen (Figure 4). The next largest *Ichthyosaurus* humerus after YORYM 2005.2411 is 10.9 cm long (NHMUK R224). The specimen is a large, substantially complete, right forefin from Barrow-upon-Soar, with about 30 phalanges in the longest digit (Figure 5). NHMUK R224 is the holotype of *I. longimanus* (Owen, 1884), although McGowan and Motani (2003) consider the taxon a *species inquirendae*. The forefin elements of NHMUK R224 are smaller and less robust than those of YORYM 2005.2411, even taking into account that the latter is incomplete. The two forefins could belong to different species.

The relationship between forefin length and the humerus length for skeletons and isolated forefins of *Ichthyosaurus* that met the criteria for completeness is shown in Figure 6. The regression line was statistically significant ($p< 0.001$) with a goodness of fit of 88%. This model, however, assumes that all species of *Ichthyosaurus* are similar in the relative proportion of the humerus to total forefin length as an individual grows. The forefins of the holotype of *I. breviceps* (NHMUK 43006) and the neotype of *I. communis* (NHMUK R 1162) meet our criteria for completeness, but because they are on display at NHMUK, they could not be measured directly. We estimated the length of the humerus and forefin for each specimen based on illustrations (McGowan and Motani, 2003, p. 94-95, plate 9 for NHMUK R1162 and fig. 81b for NHMUK 43006). Both specimens plot along the regression line, close to the middle of the cluster of points (Figure 6, open squares), suggesting that the assumption of completeness is reasonable. Using the regression equation, $\log_{10}$ (forefin length) = 0.0773 (humerus length) + 0.8887, the total forefin length of YORYM 2005.2411 was estimated as 62 cm. This would suggest that the specimen is only about 60% complete.

The relationship between the skull length and the humerus length assumes allometric growth (Figure 7). The regression line is statistically significant ($p< 0.001$) with a goodness of fit of 88%. Note that the slope is less than one, showing the expected negative allometry of the skull relative to the humerus (McGowan, 1973). From the regression equation, $\log_{10}$ (skull length) = 0.5974 $\log_{10}$ (humerus length) + 1.095, the skull length of YORYM 2005.2411 was estimated as 54 cm. Similarly, a regression analysis of jaw length vs. humerus length yielded a statistically significant line ($p<0.001$) with a goodness of fit of 85% (Figure 8). From the regression equation, $\log_{10}$ (jaw length) = 0.5809 $\log_{10}$ (humerus length) + 1.1292, the jaw length of YORYM 2005.2411 was estimated as 56 cm, more or less consistent with the skull length estimate, even though many of the specimens used were different from the previous analysis (Appendix 3). McGowan (1974, fig. 1) reported a maximum jaw length of about 54 cm for the largest species of *Ichthyosaurus*, *I. communis*, so this individual was not much larger. This seems counter-intuitive given that the humerus length is so much larger than that of any other *Ichthyosaurus* specimen (Figure 4). Of course, the analysis assumes that the size of the humerus relative to the jaw/skull is similar for all *Ichthyosaurus* species, and that the large forefin described here can be assigned to one of the currently recognized species, neither of which can be tested with the data used in this study.

TABLE 1. Large partial skeletons (humerus length > 7.5 cm) examined in this study. Ratio of jaw length to humerus length for each specimen can be used to estimate the jaw length of YORYM 2005.2411 (humerus length = 11.7 cm) by simple scaling, which assumes isometric growth. The wide variation in estimated size may be due to the variation in the relative length of the snout. The rostrum of OUMNH J.10330 may be a composite. Although all of the specimens are currently considered *I. communis*, these specimens may include more than one species.

Specimen	Humerus length	Jaw length	Jaw length YORYM 2005.2411
AGC No 8	8.9 cm	45.5 cm	59.8 cm
OUMNH J.10330	8.2 cm	58.5 cm	83.5 cm
CAMSM J59575	8.1 cm	43.9 cm	63.4 cm
CAMSM J69477	8.1 cm	45.0 cm	65.0 cm
CAMSM J59574	7.9 cm	46.6 cm	69.0 cm
BRSUG 25300	7.7 cm	36.6 cm	55.6 cm
ANSP 15766	7.7 cm	50.2 cm	76.3 cm

The longest *Ichthyosaurus* skull that we examined was OUMNH J.10330, with a skull length of 56 cm, a jaw length of 58.5 cm, but a humerus length of only 8.2 cm (Table 1). By comparison, it seems the skull and jaw estimates for YORYM 2005.2411 should be larger, considering that the humerus is 40% larger. OUMNH J.10330 has a relatively longer rostrum than most *Ichthyosaurus* specimens, and it may be a composite (pers. obs. DRL). Other specimens with humeri over 7.5 cm have jaw lengths that range from 36.6 cm to 50.2 cm (Table 1), all shorter than our estimate for YORYM 2005.2411. If each of these specimens is used individually to estimate the jaw length of YORYM 2005.2411 by calculating a simple scaling factor, the estimates range from 55.5 cm to 83.5 cm (Table 1). Most of the estimates are larger than the estimate from the regression equation probably because they assume isometric growth. Estimates based on a single individual are extremely variable and simple scaling is not the best method to estimate size (Liston and Noè, 2004; Therien and Henderson, 2007). Nonetheless, this method is often used, especially when comparative material is limited (e.g., Buchy et al., 2003; Naish et al., 2004; Carpenter, 2006).

Finally, the relationship between vertebral column length and humerus length for 25 fairly complete skeletons of *Ichthyosaurus* (Appendix 4) was examined. The model assumed isometric growth of elements of the postcranial skeleton (Figure 9). The linear regression is statistically significant ($p < 0.001$), with a goodness of fit of 90%. From the regression equation, (vertebral column length) = 19.55 (humerus length) + 8.78, the length of the vertebral column of YORYM 2005.2411 was estimated as 238 cm. Adding that to the estimated skull length above, the total length of the ichthyosaur was just under 3.0 m.

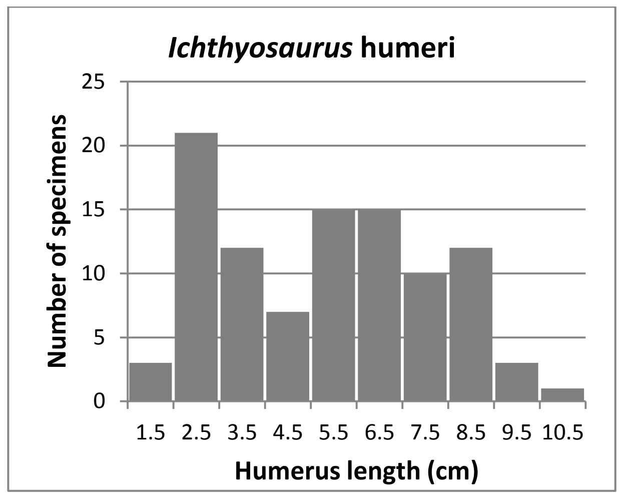

FIGURE 4. Histogram of humerus lengths for *Ichthyosaurus* specimens (n=99; Appendix 1). Where a specimen preserved both humeri, only the larger of the two measurements was used. The humerus of YORYM 2005.2411 is 11.7 cm long, larger than any specimen included here.

ICHTHYOSAURUS FROM OUTSIDE OF THE U.K.

During the 19th century, numerous ichthyosaur specimens from around the world were referred to the genus *Ichthyosaurus*, with over 50 species described before 1900 (McGowan and Motani, 2003). Subsequently, many of those species were referred to other genera, synonomized with other species, or deemed *nomina dubia* or *nomina nuda* (McGowan, 1974; McGowan and Motani, 2003). Presently, four species are considered valid: *I. communis*, *I. breviceps*, *I. conybeari*, and *I. anningae* (McGowan and Motani,

FIGURE 5: NHMUK R224 (holotype of *I. longimanus* Owen, 1884), an isolated but complete right forefin in dorsal view, from the Lias of Barrow-Upon-Soar. Anterior to the right. Scale = 10 cm.

2003; Lomax and Massare, 2015), although some authors recognize a fifth species, *I. intermedius* (Maisch, 1997; Maisch and Matzke, 2000). A more recent report of the genus outside of the U.K. was *Ichthyosaurus janiceps* from the Upper Triassic of British Columbia (McGowan, 1996), but it has since been designated as the type species of *Macgowania janiceps* (Motani, 1999b).

Fragments of a large ichthyosaur skull from the Lower Sinemurian of Frick, northern Switzerland, have been attributed to *Ichthyosaurus communis* (Maisch et al., 2008). The specimen is preserved in a slab of matrix and comprises a skull represented by a portion of the right narial region, left lateral surface of the skull, a nearly complete braincase in dorsal view, a few teeth, and other fragments. Maisch et al. (2008) estimated that the specimen would have had a jaw length of 90 cm, more than 50% larger than the largest specimen from the U.K. (McGowan, 1974 and this study). We have not seen the specimen and the comments here rely on the published interpretive sketches. The specimen displays some features shared with *Ichthyosaurus*: a large lacrimal (also in *Leptonectes* and *Temnodontosaurus*), the lacrimal and premaxilla forming the ventral border of the external naris (also in *Leptonectes* and *Temnodontosaurus*), a prefrontal-parietal contact (also in *Stenopterygius*), nasals forming almost the entire dorsal border of the external naris (also in *Stenopterygius*), and large nasals (McGowan and Motani, 2003, fig. 69). The nasals of the Frick specimen do not appear as expanded posteriorly as they are in *Ichthyosaurus*, although the specimen is fragmentary. The preserved tooth crowns are similar to those of some *Ichthyosaurus* species, but two of the three teeth might be maxillary teeth, which tend to be robust and recurved in many taxa. The deep infolding of the tooth roots occurs in some *Ichthyosaurus* and *Temnodontosaurus* species. In general, tooth morphologies are not unique to specific ichthyosaurian taxa (Massare, 1987) and may not be useful in taxonomy (McGowan and Motani, 2003). At least two features of the Frick specimen, however, are different from *Ichthyosaurus*. The pineal foramen of *Ichthyosaurus* is enclosed by the frontals (Motani, 2005), whereas the pineal foramen of the Frick ichthyosaur is on the posterior edge of the frontals (Maisch, et al., 2008, fig. 6b), somewhat like that of *Temnodontosaurus*, *Leptonectes* (McGowan and Motani, 2003, fig. 69), and an undescribed taxon (Motani, 2005, fig. 3A-C). The frontals of *Ichthyosaurus* are small and roughly semicircular in outline (Motani, 2005), whereas the frontals of the Frick ichthyosaur have an elongated, narrow anterior process that separates the nasals along the midline (Maisch, et al., 2008, fig. 6b). Because of these differences, the material cannot be assigned

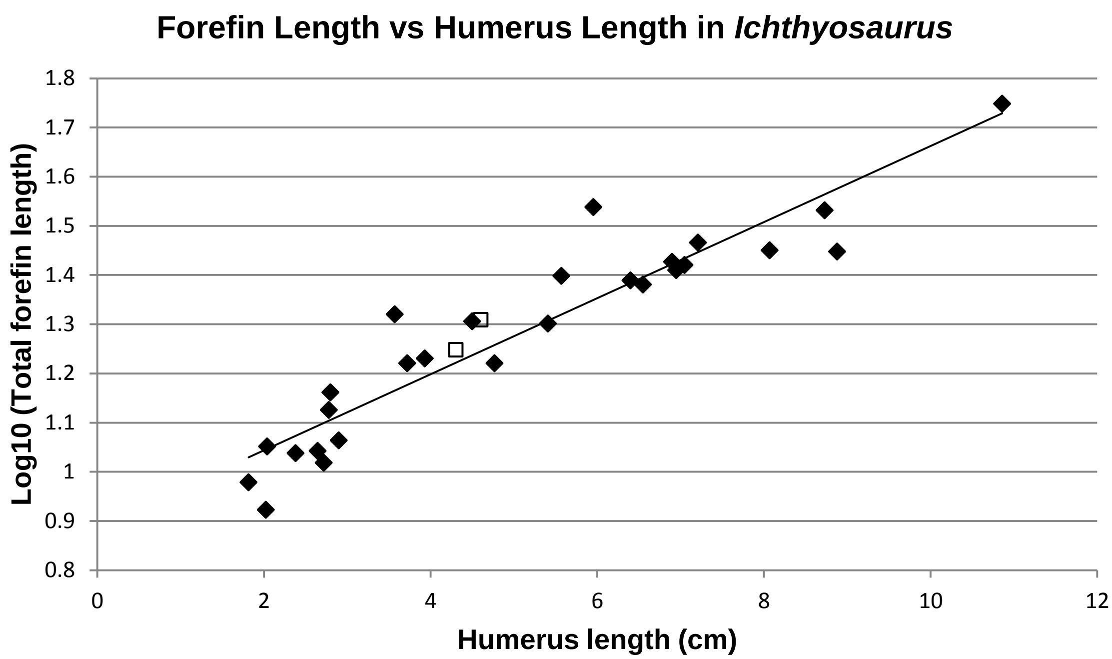

FIGURE 6. Graph of the common logarithm of forefin length vs humerus length for *Ichthyosaurus* specimens (n=27, Appendix 2). The regression assumes exponential growth of the forefin relative to the humerus. The two open squares are estimates from illustrations (McGowan and Motani, 2003) for the holotype of *I. breviceps* (NHMUK 43006) and the neotype of *I. communis* (NHMUK R1162). These two specimens were not included in the regression. The regression equation is: $\log_{10}$(forefin length) = 0.0773 (humerus length) + 0.8887. R^2 = .878

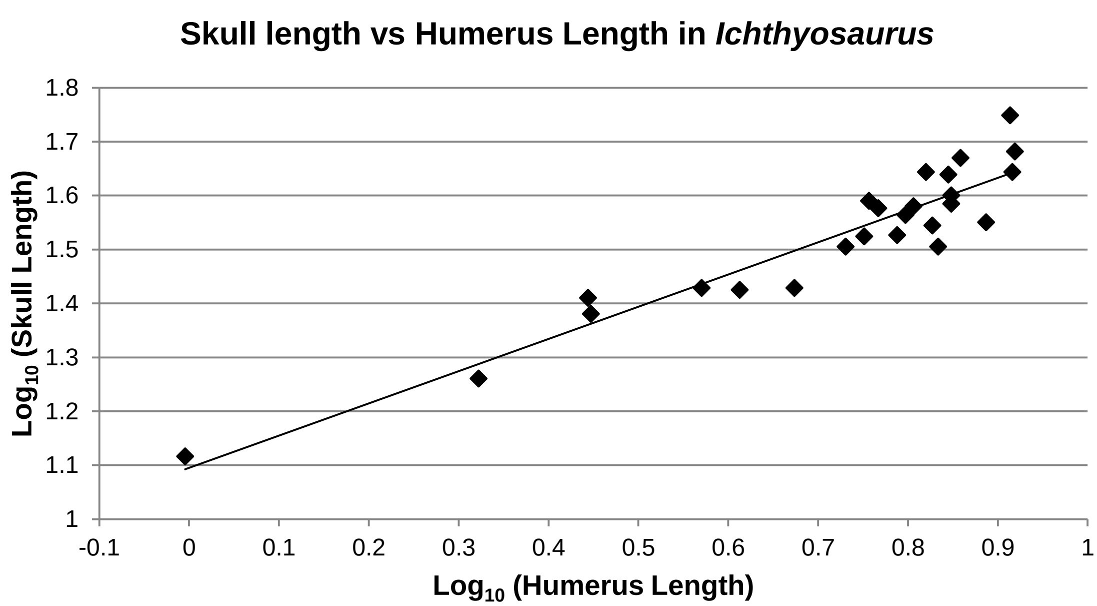

FIGURE 7. Skull length vs humerus length for partial to nearly complete skeletons of *Ichthyosaurus* (n= 25). The regression assumes allometric growth. Humerus and skull lengths measured in cm (Appendix 3). *I. breviceps* was excluded from the analysis because it has a much shorter rostrum than other species of *Ichthyosaurus*. The regression equation is: $\log_{10}$(skull length) = 0.5974 $\log_{10}$ (humerus length) + 1.095. R^2 = 0.885.

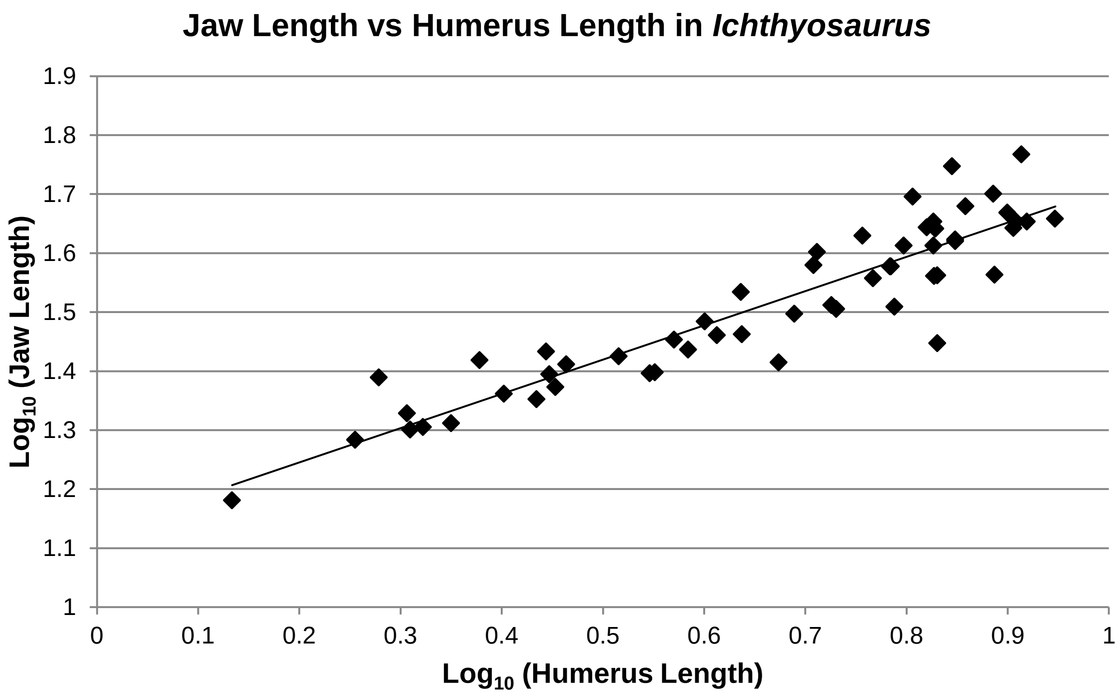

FIGURE 8. Jaw length vs humerus length for partial to nearly complete skeletons of *Ichthyosaurus* (n=55), assuming allometric growth. The regression assumes allometric growth. Humerus and skull lengths measured in cm (Appendix 3). *I. breviceps* was excluded from the analysis because it has a much shorter rostrum than other species of *Ichthyosaurus*. The regression equation is: $\log_{10}$(jaw length) = 0.5809 $\log_{10}$ (humerus length) + 1.1292. $R^2 = 0.848$.

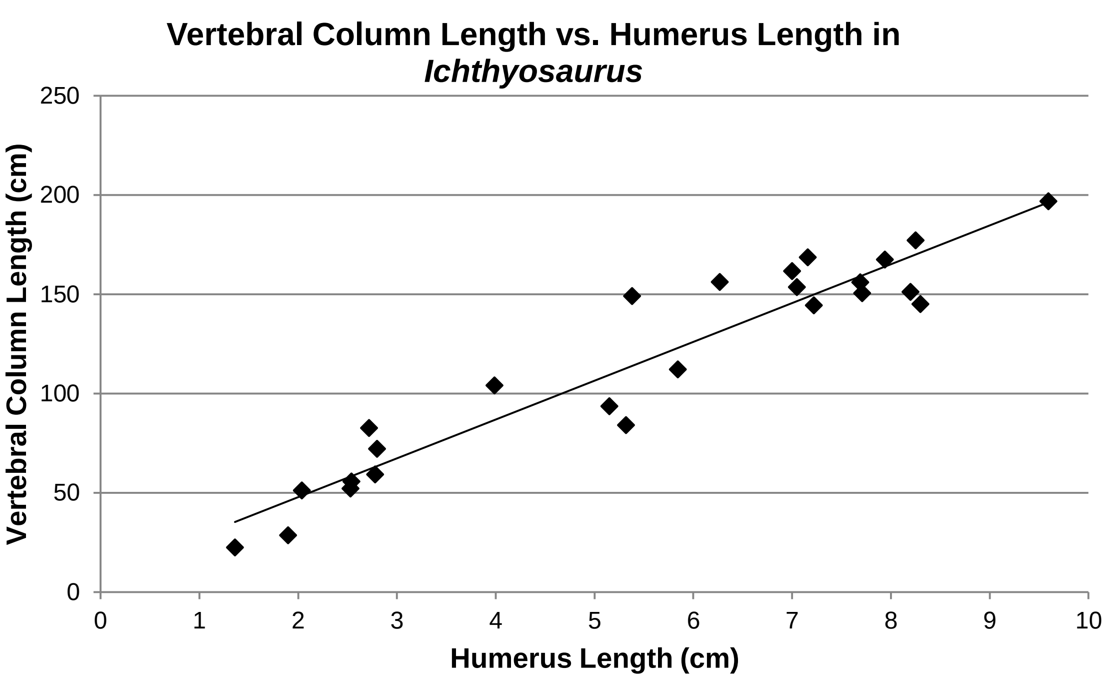

FIGURE 9. Vertebral column length vs humerus length for nearly complete skeletons of *Ichthyosaurus* (n=25, Appendix 4), assuming isometric growth. The regression equation is: (vertebral column length) = 19.55 (humerus length) + 8.78. $R^2 = 0.902$.

unequivocally to *Ichthyosaurus*. We agree with Maisch et al. (2008), however, that the material is too incomplete to assign to a new taxon.

Maisch et al. (2008) noted that an even larger specimen described by Godefroit (1996), an incomplete skull from the Upper Sinemurian of Bonnert, Belgium, is the same species as the Frick specimen. We have not examined the specimen and base our comments on the published drawings (Godefroit, 1996). The Bonnert specimen appears to have dentary teeth with large, infolded roots, which occur in species of *Ichthyosaurus* and *Temnodontosaurus*, among others, and is similar to the teeth of the Frick specimen. The frontals also have a broad contact with the postfrontals, apparently more extensive than on the Frick specimen, and a characteristic of *Ichthyosaurus*. The Bonnert specimen is similar to the Frick specimen in that it has a narrow anterior process on the frontals that separate the nasals posteriorly; the pineal foramen is at the posterior edge of the frontals; and the nasals are not as broad posteriorly as those of *Ichthyosaurus*. Because both specimens are fragmentary and display characters found in more than one genus, we suggest an identification as cf. *Ichthyosaurus*, pending additional material that might provide more morphological information.

CONCLUSION

An incomplete forefin (YORYM 2005.2411) from the Lias of Yorkshire, has the largest humerus known for the genus *Ichthyosaurus*, 11.7 cm. The specimen can be used to estimate the maximum size of *Ichthyosaurus* from the U.K. The individual represented by YORYM 2005.2411 had estimated a jaw length of 56 cm, and an estimated body length, from the tip of the snout to the tail bend, of just under 3 m, based on the regression analyses described herein. McGowan and Motani (2003) gave the maximum length of the largest *Ichthyosaurus* species, *I. communis*, as 2.5 m. The YORYM 2005.2411 individual was thus about 20% larger, and represents the largest specimen of the genus thus far reported from the U.K. Fragmentary skull material from two specimens that may be *Ichthyosaurus* have been reported from Belgium and Switzerland (Godefroit, 1996; Maisch et al., 2008). Although these specimens are larger than the individual represented by YORYM 2005.2411, the lack of forefin material makes a direct comparison impossible.

ACKNOWLEDGEMENTS

We are grateful to R. Clark for access to the Alfred Gillett Collection, Street. We also thank the collections managers and curators at the institutions we visited: C. Berry, J. Saunders, J. Mather, and A. Southern, AGT; E. Gilmore and E. Daeschler, ANSP; L. Neep, P. Shepherd and M. Howe, BGS; R. Vaughan, BRSMG; C. Hildebrandt, BRSUG; M. Riley and S. Finney, CAMSM; P. Robinson, DONMG; M. Evans, LEICT; P. Howe and C, Andrew, LYMPH; D. Gelsthorpe, MAN; D. Parsons, MOS; S. Chapman and P. Barrett, NHMUK; S. Walsh and Y. Candela, NMS; C. Howells, NMW; E. Howlett, OUMNH; K. Seymour, ROM; and S. King and I. Gladstone, YORYM; for access to and assistance with specimens in their collections. We thank N. Larkin for providing images of the described specimen after his conservation work on it. Thanks also to V. Fischer and L. Noè for their helpful reviews and suggestions. JAM travel was partially funded by a faculty research grant from SUNY College at Brockport. DRL travel was partially funded by a Karl Hirsch Memorial Grant awarded from the Western Interior Paleontological Society (WIPS).

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APPENDIX 1

Measurements of proximal-distal length of the humerus on isolated forefins and partial to complete skeletons of *Ichthyosaurus* specimens (n=99), used to construct Figure 4. When both humeri were preserved, only the larger measurement is included here.

Specimen	Humerus length (cm)
AGC No 7	5.5
AGC No 8	8.9
AGC No 9	5.9
AGC No 11	5.4
AGC No 12	6.3
AGC No 14	8.3
AGC No 15	6.9
AGC No 17	8.9
ANSP 15766	8.9
ANSP 17429	6.7
BGS 37-26636	1.4
BGS 484343	4.9
BGS 85780	2.8
BGS 85793	3.3
BGS 955	2.7
BGS 956	2.6
BGS No number	7.2
BGS 118514	5.6
BGS 26634	9.8
BRSMG Cb3578	4.8
BRSMG Cc921	6.1
BRSMG Ce16611*	7.4
BRSUG 25300	7.7
CAMSM J35183	3.8
CAMSM J35187	4.0
CAMSM 68412	4.3
CAMSM J35186	5.1
CAMSM J59575	8.0

Specimen	Humerus length (cm)
CAMSM J59584	7.9
CAMSM J69477	8.1
CAMSM X50187	5.0
DONMG 1983.98	5.2
LEICT G123.1992	7.2
LEICT G125.1992	6.8
LYMPH 2006/72	5.0
MAN L4325	2.6
MAN LL11835	7.4
MAN LL8000	1.9
MAN P939	4.0
MOS 12/1988	8.4
MOS 12/1988 b	8.5
MOS 12/1988 d	5.8
MOS 166/1992	2.8
MOS 5803	3.8
MOS 5804	5.6
MOS 5810	6.0
MOS 8351	3.9
MOS 8373	7.1
MOS TV52	6.1
NHMUK 10019	8.7
NHMUK 120	2.8
NHMUK 224	10.8
NHMUK 35566	2.9
NHMUK 36256	2.0
NHMUK 44808	6.0
NHMUK 85791	2.0
NHMUK unnum.	2.5

Specimen	Humerus length (cm)
NHMUK R10028	2.2
NHMUK R1067	7.5
NHMUK R11801	2.2
NHMUK R8437	2.4
NMS 1864.12.2	3.7
NMS 1866.13.2	5.0
NMS 1898.180.29	4.5
NMS 1972.1.49	3.7
NMW 2009.35G.1	6.8
NMW 91.29G.1	7.2
NMW 93.5G2 - cast	2.5
NMW M3550	5.9
NMW M3551	8.3
NMW M3553	6.5
NMW M3554	6.4
NMW M3559	6.1
NMW M3563	9.7
NMW M3569	5.7
NMW M3571	6.1
NMW M3572	9.9
NMW unnumbered	5.8

Specimen	Humerus length (cm)
NMW G1597	4.2
NMW Old Cardiff coll	3.7
OUMNH J13587	2.2
OUMNH "K"	2.2
OUMNH J10310	4.3
OUMNH J10330	8.2
OUMNH J10340	6.2
OUMNH J10341/c	3.5
OUMNH J13799	7.1
OUMNH J29221	2.9
OUMNH J29352	2.9
ROM 12725	6.7
ROM 12802	2.6
ROM 12805	3.9
ROM 26029	5.6
ROM 52098	2.4
YORYM 1994.1799.50	8.3
YORYM 2005.2408	2.9
YORYM 2006.3803	3.6
YORYM 2006.853	2.0
YORYM YM740	6.0

APPENDIX 2

Measurements of nearly complete forefins of *Ichthyosaurus* specimens, including both isolated forefins and partial to nearly complete skeletons. These data were used in the regression analysis shown in Figure 6.

Specimen	Humerus length (cm)	Forefin length (cm)
AGC No 11	5.4	20.0
AGC No 15	6.6	24.0
AGC No 17	8.9	28.0
ANSP 15766	8.1	28.2
BGS 955	2.7	10.4
BRSMG Cb3578	4.8	16.6
BRSMG Ce16611 *	7.0	25.7
MAN L4325	2.6	11.0
NHMUK 120	2.8	13.4
NHMUK 10019	8.7	34.0
NHMUK 35566	2.9	11.6
NHMUK 36256	2.0	11.3
NHMUK 85791	1.8	9.5
NHMUK R224	10.9	56.0
NHMUK R8437	2.4	10.9
NMS 1898.180.29	4.5	20.2
NMS 1972.1.49	3.7	16.6
NMW 91.29G.1	7.2	29.2
NMW M3554	6.4	24.5
OUMNH J13799	6.9	26.7
ROM 12805	3.9	17.0
ROM 26029	5.6	25.0
MOS 166/1992	2.8	14.5
MOS 8373	7.1	26.3
YORYM 2006.853	2.0	8.4
YORYM 2006.3803	3.6	20.9
YORYM YM740	6.0	34.5
NHMUK 43006 **	4.6	20.4
NHMUK R1162 **	4.3	17.7

* measured on a cast of the specimen at LEICT

** estimated from illustrations in McGowan and Motani (2003)

APPENDIX 3

Measurements of humerus length, jaw length, and skull length on partial to nearly complete skeletons of *Ichthyosaurus*. These data were used in the regression analysis shown in Figures 7 and 8.

Specimen #	Humerus Length (cm)	Jaw Length (cm)	Skull length (cm)
AGT No 11	5.4	32.0	32.0
AGT No 12	6.3	41.0	36.6
AGT No 14	8.3		44.0
AGT No 15	6.7	36.4	35.0
AGT No 7	5.3	32.5	
AGT No 8	8.9	45.5	
ANSP 15766	7.7	50.2	
ANSP 17426	7.1	42.0	39.8
ANSP 17429	6.7	41.0	
BGS 37-2666	1.4	15.2	
BGS 484343	4.9	31.4	
BGS 85780	2.8	23.6	
BGS 85793	3.3	26.6	
BGS 955	2.7	22.5	
BGS 956	2.5	23.0	
BRUSG 25300	7.7	36.6	35.5
BRUSG Cb 3578	4.7	26.0	26.8
BRUSG Cc 921	6.1	37.8	
CAMSM J35183	3.8	27.3	
CAMSM J35186	5.1	38.0	
CAMSM J35187	4.0	30.5	
CAMSM J59574	7.9	46.6	
CAMSM J59575	8.1	43.9	
CAMSM J59644	6.8	28.0	
CAMSM J68412	4.3	29.0	
CAMSM J69477	8.1	45.0	
CAMSM TN910	1.8	19.2	
CAMSM unnum. cast	3.6	25.0	
LEICT G123.1992	7.2	47.8	46.7
LEICT G125.1992	6.8		32.0
LEICT G126.1992	5.2	40.0	
MOS 12.1996	4.1	28.9	26.6

Specimen #	Humerus Length (cm)	Jaw Length (cm)	Skull length (cm)
MOS 166/1996	2.8	24.8	24.0
MOS 5805	6.6	44.0	44.0
MOS 8373	7.1	41.7	38.4
MOS TV51	6.1	37.8	
NHMUK 85791	1.9	24.5	
NHMUK 120	2.8	27.1	25.7
NHMUK 36256	2.0	20.0	
NHMUK 41160	1.0		13.1
NMW 2009.35G.1	6.8	36.5	
NMW M3550	5.9	36.1	37.7
NMW M3551	8.3	45.0	48.0
NMW M3553	6.4	49.6	
NMW M3554	6.4		38.0
NMW M3559	5.6		33.4
NMW M3569	5.7	42.6	38.9
NMW M3571	6.1	32.3	33.6
NMW unnumbered	3.7	28.4	26.8
OUMNH J103330	8.2	58.5	56.0
OUMNH J13587	2.1	20.2	18.2
OUMNH J13799	7.0	55.9	43.5
OUMNH J10310	4.3	34.2	
OUMNH J10340	6.7	45.0	
OUMNH J10341	3.5	24.9	
OUMNH J29221	2.9	25.8	
OUMNH 'K'	2.2	20.5	
ROM 12725	6.7	43.8	
ROM 12802	2.4	26.2	
YORYM 2006.853	2.0	21.3	

APPENDIX 4

Data used in the regression analysis shown in Figure 9. The vertebral column length was measured along the column from the anterior-most exposed cervical to the tailbend, on nearly complete skeletons of specimens of *Ichthyosaurus*.

Specimen	Humerus Length (cm)	Vertebral column length (cm)
AGC No 7	5.3	84.0
AGC No 11	5.4	149.0
AGC No 12	6.3	156.0
AGC No 14	8.3	177.0
ANSP 15766	7.7	155.9
BGS 37-2666	1.4	22.3
BGS 955	2.7	82.5
BGS 956	2.5	52.0
BRSMG Cb16611*	7.2	168.5
BRUSG 25300	7.7	150.5
CAMSM J35187	4.0	104.0
CAMSM J59574	7.9	167.4
LEICT G123.1992	7.2	144.3
LEICT G126.1992	5.2	93.5
MOS 166/1996	2.8	72.0
MOS 8373	7.1	153.5
NHMUK 120	2.8	59.1
NHMUK 36256	2.0	51.0
NHMUK 85791	1.9	28.5
NMW 93.5G.2	2.5	55.6
NMW M3550	5.8	112.0
NMW M3551	8.3	145.0
NMW M3572	9.6	196.7
OUMNH J.103330	8.2	151.1
OUMNH J.13799	7.0	161.6

* measured on a cast of the specimen at LEICT