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FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

Ocean and Earth Sciences

A fresh look at the genus *Ichthyosaurus*: species characteristics, morphometrics, and phylogeny

by

Jessica Danielle Lawrence Wujek

Thesis for the degree of Doctor of Philosophy

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

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A FRESH LOOK AT THE GENUS *ICHTHYOSAURUS*: SPECIES CHARACTERISTICS, MORPHOMETRICS, AND PHYLOGENY

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Ichthyosaurs are among the best known of Mesozoic marine reptiles, ranging from the Early Triassic (252-247 Ma) to the end of the Cenomanian (93.9 Ma; Fischer et al., 2016). The genus *Ichthyosaurus* was one of the first genera to be named and is arguably one of the most iconic of ichthyosaurs. Due to this abundance of specimens, and to initial inadequacies in the definition of the genus and its constituent species, *Ichthyosaurus* has become a waste-basket taxon; a poorly classified taxon with many morphologically variable specimens (Smith and Radley, 2007). Ichthyosaurus is known from an enormous number of specimens, many of which possess confusing combinations of anatomical features. Both the quantity of data and distribution of anatomical characters make it difficult to recognise distinct species within our understanding of this taxon.

To study this genus in depth, a modern problem of inaccessible specimens displayed in museums is an obstacle that needed to be overcome. A new method of parallel laser photogrammetry to bridge to gap of inaccessibility and scientific study was explored. This method has been used in other fields, but has not transitioned into palaeontology yet. The marine reptile gallery of the Natural History Museum, in London was utilised to test this method. The findings from that method were utilized in the other analyses performed. This new method allows researchers to get some scientific data from specimens that would otherwise not be utilized, but it is not a complete substitute for an up close in person examination of specimens.

To better understand the current breadth of the species *Ichthyosaurus*, multiple morphometric and phylogenetic studies were performed with a starting dataset of over 320 specimens and 66 different measurements. Each of these studies was done at the specimen level, which is a rarity. These analyses also help to determine if there is more diversity present in *Ichthyosaurus* than is currently recognized. During the course of this PhD 3 new species have been

named to this genus confirming that there is a larger amount of diversity than originally thought at the beginning of this project (Lomax and Massare, 2015 and 2016). The morphometric study focused on the measurements used in ratio characters, to determine if they were useful in separation of species. The analyses show that just measurements used in the previously defined ratios are not sufficient to separate species out by themselves. The phylogenetic study was done at the specimen level to truly see how much variation there is in the genus and species. The characters used in that study were also defined in detail as to produce replicable results. The phylogenetic results show that the species of this genus need to be more strictly defined, or that there are more species present in the genus still to be identified.

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DECLARATION OF AUTHORSHIP

I, Jessica Danielle Lawrence Wujek

declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

‘A fresh look at the genus *Ichthyosaurus*: species characteristics, morphometrics, and phylogeny ‘

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
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7. None of this work has been published before submission

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Date: 09/12/2017 ....

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Definitions and Abbreviations

- Museum acronyms
  - **AGC**, Alfred Gillett Collections, cared for by Alfred Gillett Trust (C & J Clark Ltd.), Street, U.K.
  - **BGS**, The British Geologic Survey, Keyworth, Nottingham, U.K.
  - **BIRUG**, Birmingham University Lapworth Museum, Birmingham, U.K. (non-published specimens)
  - **BU**, Birmingham University Lapworth Museum, Birmingham, U.K.
  - **BRSLI**, Bath Royal Literary and Scientific Institution, Bath, U.K.
  - **BRSMG**, Bristol City Museum and Art Gallery, Bristol, U.K.
  - **CAMSM**, Sedgewick Museum, Cambridge University, Cambridge, U.K.
  - **DONMG,** Doncaster Museum and Art Gallery, Doncaster, U.K.
  - **DORCM,** The Dorchester County Museum, Dorchester, U.K.
  - **GLAHM**, The Huntarian Museum, University of Glasglow, Glasgow, U.K.
  - **GMRC**, Glasgow Museum Resource Centre, Glasgow, U.K.
  - **GPIT**, Institute und Museum fur Geologie und Paleontologie, Univeritate Tubingen, Tubingen, Germany
  - **HCMAS**, Hampshire County Council Museum Store, Winchester, U.K.
  - **IPSMG**, Ipswich Museum, Ipswich, Suffolk, U.K.
  - **LEICT**, Leicester Arts and Museums Service, New Walk Museum and Art Gallery, New Walk, Leicester, U.K.
  - **MANCH**, Manchester Museum, Manchester, U.K.
  - **NHMUK** (formerly BMNH), The Natural History Museum, London, U.K.
  - **NMING** , National Museum of Ireland, Natural History Division, Geological Collection, Dublin, Ireland
  - **NMS**, National Museum of Scotland, Edinburgh, U.K.
  - **NOTNH**, Nottingham Natural History Museum (Wollaton Hall), Nottingham, U.K.
  - **OUMNH**, Oxford University Museum of Natural History, Oxford, U.K.
  - **PETMG** , Peterborough Museum and Art Gallery, Peterborough, U.K.
  - **PMO**, Paleontologisk Museum Oslo, Oslo, Norway
  - **RAMM**, Royal Albert Memorial Museum, Exeter, U.K.
  - **ROM**, Royal Ontario Museum, Canada
  - **RSM**, Royal Skatcashewan Museum, Canada
  - **TTNCM**, Taunton County Museum, The South West Heritage Trust (Somerset Museums Service), Taunton, U.K.
  - **UoS**, University of Southampton Collections, Southampton, U.K.
  - **WARMS,** Warwickshire Museum Service, Warwick, U.K.
  - **YORYM**, Yorkshire Museum, York, U. K.

- Other Terms
    - CI, Consistency Index
        - 'To indicate the degree of homoplasy in a given tree, either for one given character or summed for all characters.'
        - Hammer, O., and Harper, D. 2006. Paleontological Data Analysis, Blackwell Publishing, 1-351
    - CVA(or CCA), Canonical Variance Analysis
        - 'Projection of a multivariate dataset down to two or more dimensions in a way that maximizes separation between three or more given groups. CVA is the extension of discriminate analysis to more than two groups.'
        - Hammer, O., and Harper, D. 2006. Paleontological Data Analysis, Blackwell Publishing, 1-351
    - MPT, Most Parsimonious Trees
    - NMMDS, Non-metric Multidimensional Scaling
        - 'To project a multivariate dataset into two or three dimensions, in order to visualize trends and groupings. This ordination method is based on a distance matrix computed using any distance.'
        - Hammer, O., and Harper, D. 2006. Paleontological Data Analysis, Blackwell Publishing, 1-351
    - OLS, Ordinary Least Squares
        - A type of linear regression model used in statistics that tries to minimize the sum of the squares of the differences between the observed responses in the dataset and those predicted by a linear function.
    - OTU, Operational Taxonomic Units
    - PCA, Principal Components Analysis
        - 'Projection of a multivariate dataset down to a few dimensions in a way that preserves as much variance as possible, facilitating visualization of the data.'
        - Hammer, O., and Harper, D. 2006. Paleontological Data Analysis, Blackwell Publishing, 1-351
    - PCoA, Principal Coordinates Analysis
        - 'To project a multivariate dataset into two or three dimensions, in order to visualize trends and groupings. The method attempts to preserve distances between data points, as given by any distance measure.'
        - Hammer, O., and Harper, D. 2006. Paleontological Data Analysis, Blackwell Publishing, 1-351
    - RAS, Random Additional Sequences
    - RI, Retention Index
        - 'To indicate the amount of character state similarity which is interpretable as synapomorphy in a given tree, either for one given character or summed over all characters.'
        - Hammer, O., and Harper, D. 2006. Paleontological Data Analysis, Blackwell Publishing, 1-351
    - SR, Snout Ratio
        - Snout length/jaw length

    - McGowan, C. 1974. A Revision of the Latipinnate Ichthyosaurus of the Lower Jurassic of England (Reptilia: Ichthyosauria), Life Sciences Contributions, Royal Ontario Museum, 100:1-30
    - McGowan, C. 1976. The description and phonetic relationship of a new ichthyosaur genus from the Upper Jurassic of England, Canadian Journal of Earth Sciences, 13:668-683
- TBR, Tree bisection reconnection
    - An algorithm with a more complete branch-swapping scheme than others like it. 'The tree is divided into two parts, and these are reconnected through every possible pair of branches in order to find a shorter tree. This is done after each taxon is added, and for all possible divisions of the tree. '
    - Hammer, O., and Harper, D. 2006. Paleontological Data Analysis, Blackwell Publishing, 1-35

Chapter 1.

Introduction to *Ichthyosaurus*, the taxonomic and geologic history of an iconic genus

1.1 Ichthyosaurs Background

In England, almost every museum no matter how small seems to have a specimen of an ichthyosaur and often a specimen from the genus *Ichthyosaurus*. Few of these have been examined since their arrival into the museum. Most of the more recent examinations of museum specimens have been conducted either to determine generic/specific identifications or to clean and slow down the pyrite decay that plagues many specimens from the Lyme Regis area. However, with the resurgence of ichthyosaur studies, it is vital to acquire more information from these specimens, as well as to reanalyse older studies. Thus, the broad goal of this project is to re-examine ichthyosaur specimens in museum collections in order to test the reproducibility and validity of previously published data in order to add to our understanding of the specimens.

Ichthyosaurs are a clade of marine reptile that is known from the Early Triassic (252-247 Ma) to the end of the Cenomanian (93.9 Ma; Fischer *et al*., 2016). This group of reptiles are secondarily adapted to a marine lifestyle as can be seen in their anatomy, still retaining features or reduced features of their former land relatives. Some examples of these features are a non-functional elbow joint, reduced limbs, and a reduced pelvic girdle that is not attached to the vertebral column. Ichthyosaurs have also made adaptations to a fully marine lifestyle including ovoviviparity, or giving birth to live young (Pearce, 1846). Although, it was once originally thought that some marine reptiles might be able to pull or beach themselves up onto land like modern turtles to lay eggs, further study of anatomy and preservation of young both in and expelled from the womb of ichthyosaur specimens, have changed that idea (Motani, *et al*., 2014).

The general body morphology of ichthyosaurs consists of four major body plans. McGowan and Motani (2003) referred to these body plan styles as ‘basal’, ‘stem’, ‘mixosauruan’ and ‘parvipelvian’. The ‘parvipelvian’ style body plan is the most recognisable, and *Ichthyosaurus* is one of the most iconic. The more recognisable ichthyosaurs, the ‘parvipelvian’ or ‘thunniform’ forms have distinctive vertical lunate shaped tails that have a similar morphology to that of a shark. Based on this body plan and vertebral column, along with evidence of a smooth hydrodynamic skin, it is assumed that these ichthyosaurs were well adapted for high speed swimming (Lingham-Soliar, 2003; Motani, 2002; and Buchholtz, 2001). Earlier forms of ichthyosaurs with the basal, ‘stem’ and ‘mixosaurian’ body plans, did not possess the upper lobe of the lunate tail as far as is known(McGowan and Motani, 2003). As no bones are present in the upper lobe of the tail in ichthyosaurs, the presence of this lobe is only seen when there is exceptional preservation of soft tissue. It is therefore not clear when the transition occurred between the two types of tails, as soft tissue preservation is not common. The origins of this upper tail lobe will only be elucidated if more specimens with associated soft tissue preservation are found.

Along with these body plans, ichthyosaurs also had a diverse array of feeding and living styles, including deep diving, shallow living, eating fish or squid and ammonites (Lingham-Soliar, 2003; Massare, 1987 and Pollard, 1968). This is known from fossil sites where preservation of stomach contents and even in situ coprolites are present, which show bones, fish scales and squid hooklets clearly present (Massare, 1987and Pollard, 1968). Eight feeding guilds are present in marine reptiles from the Jurassic and Cretaceous, and three tooth types seem to be present in ichthyosaurs. The ichthyosaurs from the Lower Lias of Dorset, England, represent at least five of these feeding guilds (Massare, 1987), though these findings are debated (Buchy, 2010 and Valkenburgh, 1995). More recent work has discussed the similarity of tooth morphology of

Platypterygius specimens to that of extant animals, such as orcas and bottlenose dolphins (Lingham-Soliar, 2003). The deep diving or shallow nabitat preferences of certain specimens is based on anatomy, especially the teeth, and therefore what the animal was eating, along with bone histology (Fischer *et al*., 2014 and Padian and Lamm, 2013). *Ichthyosaurus* has been interpreted as a fast swimming predator that most likely spent time in deep water environments, predating upon mainly fish and squid as food sources. Böttcher (1989) provided evidence that larger ichthyosaurs could have eaten smaller ichthyosaurs, but there is no indication of this in *Ichthyosaurus*.

The most iconic locality for ichthyosaurs is Lyme Regis, in the county of Dorset, Southern England. This is where Mary Anning and her brother Joseph found the first ichthyosaur specimens around 1809-1811 (Torrens, 1995). This first specimen was represented by a skull and part of the post cranial material, and was excavated over two seasons (McGowan and Motani, 2003 and Torrens, 1995). Mary's father was a carpenter by trade, but he taught both Mary and Joseph how to look for and excavate fossils. Mary was the one to take more of an interest in fossil collecting and later made her living selling fossils and giving guided tours along the Lyme Regis coast. She was very highly regarded by the intellectuals of the day; she often sold her more complete specimens (Woodard, 1907; Clary and Wandersee, 2006). In fact many specimens found by Mary Anning can be found in the Sedgwick Museum collection in Cambridge, England, bought by Mr. Adam Sedgwick (Price, 1986). The Jurassic Coast of Dorset is still producing numerous fossils of ichthyosaurs as well as many other organisms, as can be seen in private collections and the Lyme Regis Philpot Museum (LYMPH). This location is seen as a fossil preservational lagerstätte due to the high number and quality of material coming out of the Lower Lias Group, which has yielded numerous ichthyosaur specimens that are complete or nearly complete, but often preserved in a laterally compressed condition (Seilacher, 1970). This study aims to utilize as many specimens of ichthyosaur as possible from the localities of Southern England (Figure 1) to demonstrate the morphological range, variation and diversity within the genus *Ichthyosaurus*.

A study of this nature is a uniquely important opportunity. By examining a large number of specimens at generic and specific level, the true span of individual variation is more likely to be obtained. This includes the range of variation due to ontogeny, possibly sexual dimorphism if present, and the variation within and between species. This type of study cannot be done with a small number of specimens, nor without some presence of soft tissue preservation and/or gastric contents. Therefore lagerstätten localities are ideal for a study such as this. The *Ichthyosaurus* body is of a medium size when compared to other ichthyosaurs (using humerus length as a proxy), and is therefore less likely to dissociate into smaller skeletal elements than larger genera (Cleary *et al*., 2015). While more complete specimens are ideal for this type of study, partial specimens or even certain bones can also be useful. This study examined all available specimens, including smaller ones, in hopes of adding to the knowledge of individual variation.

Figure 1. Map of England showing the discovery locations of *Ichthyosaurus* specimens utilized and examined in this study. Stratigraphic correlation between all of these locations is not necessarily well known. A list of locations can be found in Appendix A.

1.2 Historical Overview of Lower Lias Ichthyosaurs

There are at least six genera described from the Lower Jurassic of the UK: *Ichthyosaurus*, *Temnodontosaurus*, *Excalibosaurus*, *Eurhinosaurus*, *Leptonectes, Hauffiopteryx* and *Wahlisaurus* (Lomax, 2016; Caine and Benton, 2011; McGowan and Motani, 2003). Although many palaeontologists had found and discussed these creatures before, the first publication of the genus *Ichthyosaurus* appears to be that of König (1818). Home (1819) had mentioned a skeleton previously and named it *Proteosaurus*, the generic name *Ichthyosaurus* had already been used and was acknowledged by the author. De La Beche and Conybeare (1821) provided only a brief description of a specimen referrable to the genus, but no figures. Only much later did McGowan and Motani (2003) use the description by De La Beche and Conybeare (1821) to help define a neotype (NHMUK PV R1162), which is now displayed on the “Wall of marine reptiles” in the Natural History Museum in London. Many species have since been assigned to the genus *Ichthyosaurus,* and indeed many have been removed as *nomina dubia* (see list in McGowan and Motani, 2003 pg 157), *nomina nuda*, or shown to be synonyms (McGowan and Motani, 2003 pg 158). Six species of *Ichthyosaurus* are now recognized: *Ichthyosaurus communis* (Conybeare, 1822), *Ichthyosaurus breviceps* (Owen, 1881), *Ichthyosaurus conybeari* (Lydekker, 1888), *Ichthyosaurus anningae* (Lomax and Massare, 2015), *Ichthyosaurus somersetensis* (Lomax and Massare, 2016) and *Ichthyosaurus larkini* (Lomax and Massare, 2016).

1.3 *Ichthyosaurus* Taxonomic Question

One of the goals of this project is to determine if there is more species diversity present in the genus *Ichthyosaurus* than is currently recognized. Greater species diversity could indicate different life styles, different feeding mechanisms and therefore different niches occupation. However, a high diversity of species does not always equate to more disparity. Many species present in one time may all have the same type of feeding style due to a high abundance of one type of prey. Recognizing the diversity present in a genus, in addition to comparing it to other genera and organisms present at a certain time will provide a greater understanding of communities and community structure at that time. Currently, one of the ways to validate the existence of a new species or genus is through phylogenetic studies. Such a study must be started with a review of previous studies and an assessment of the morphological characters that have been employed. This will permit a greater understanding of diversity and nature of the ecosystem present.

Many authors have produced phylogenetic studies (Fischer *et al*., 2013, 2014,; Roberts *et al*., 2014; Druckenmiller and Maxwell, 2010; Fernandez, 2007; Sander, 2000; Maisch and Matzke, 2000; Motani, 1999; Callaway, 1989; McGowan, 1974). These employ various character sets, and not all character sets are the same between authors; certain authors employ characters utilized in previous works, sometimes modified slightly, and add new characters of their own. Many of these studies have used characters based on morphological ratios put forth by McGowan (1974). These ratios have also been used to constrain the morphological ranges for different species and genera (Maisch and Matzke, 2000; Sander 2000; Motani, 1999). The validity of these ratios and ranges is discussed in Chapter 3 herein.

1.4 New Photogrammetry Technique

To fully assess the taxonomy of *Ichthyosaurus*, a new technique was devised to combat the inaccessibility of specimens displayed on walls of museums like The Natural History Museum in London (U.K.), and others. To properly study these specimens it is ideal if a detailed unrestricted examination can be made of the specimens, but in the aforementioned cases the specimens are not only displayed high up on walls, but sit behind glass in Victorian wooden boxes. The boxes are fragile and thus difficult and expensive to remove from the walls in order to facilitate study of the specimens they house. Thus, if specimens cannot be removed from their display locations, the display elevations on some walls would require the erection of scaffolding (with funding implications) in order to access the specimens for study, and this may well entail parts of the displays to be sectioned off and rendered inaccessible to visitors whilst such studies are conducted. As this is not an ideal situation for either researchers or museums, alternatives to this approach have been explored.

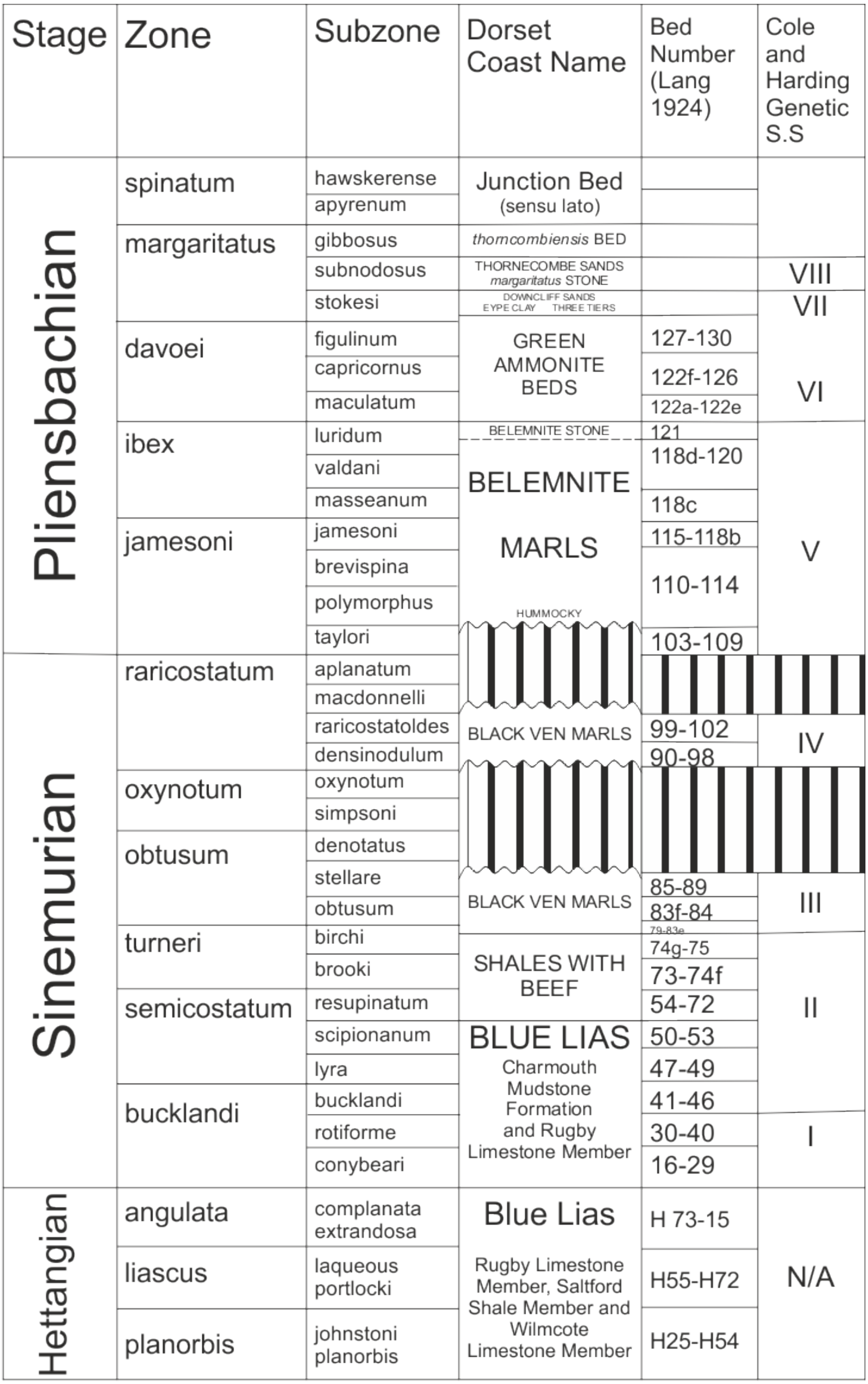
A new technique is described which provides a means to obtain a detailed, scaled image or images that will permit researchers to obtain accurate measurements of wall-mounted specimens, and thus to compare individual specimens properly. To succeed, the technique requires that the camera be level with and perpendicular to the specimen being studied. A simple method has been devised used to increase the availability of this method to all researchers. Whilst the photographs obtained by employing this new method are not a substitute for a detailed, close examination, they will provide scientists with useful information that could not be otherwise obtained.

The method is based around the use of a device called a Pixie Pole, which was invented for aerial photography purposes. This pole is sturdier than other large poles (like painter's poles) that can extend for the purposes of painting or cutting branches of tall trees. The Pixie Pole is easier to extend and made out of a light, but sturdy aluminium. As this pole was created for photography it also has attachments for attaching DSLR cameras, and also has the facility to tilt the camera, and is equipped with a level and a foam-padded plate to help protect the camera if the pole is dropped. An infrared wireless remote control allows pictures to be taken when the operator is separated from the shutter release mechanism by the length of the Pixie Pole.

The final part of the puzzle to solve was getting a known scale into these images, as without a scale, accurate measurements of elements of the specimens could not be made. The use of parallel lasers for deriving scale has been employed in biological and oceanographic disciplines (Bergeron, 2007; Rothman et al., 2008; Webster et al., 2010; Deakos, 2010; Rohner et al., 2011) but it is believed that employing such scaling mechanisms in this new method is the first time it has been used in palaeontological analyses.

1.5 Geology of the Lias

The sediments which are exposed around Lyme Regis span the Triassic, Jurassic and Cretaceous periods of geological time, but the specimens examined for this project mostly originate from the Lower Lias (See Figure 2). The geology around Lyme Regis has been studied in great detail, and the Lower Lias comprises units from the Blue Lias through the Shales with Beef, Black Venn Marls, Belemnite Marls, Belemnite Stone and the Green Ammonite Beds. The most detailed stratigraphic work is that of Lang (1924). Lang produced a detailed summary of most of the formations present around Lyme Regis, providing a detailed bed-by-bed numbering system. Many of the names and numbers of the beds described by Lang are still used today by collectors. Of the *Ichthyosaurus* specimens that have been discovered more recently, most come from Lang's Bed 32, known as the Gumption Shales, in the Blue Lias (*pers. com.*, Richard Edmonds). These specimens come mostly from two of the four paper shale layers within Bed 32. The Gumption Shales are 4 feet 2 inches (~1.25 m) in thickness and made up of bedded and conchoidal marls, including four layers of paper shales (Lang, 1924). These shales are mainly found on Broad Ledge (see figure 3). This area is covered by the sea most days of the year, aside from the extremes of Spring tides.



Stage	Zone	Subzone	Dorset Coast Name	Bed Number (Lang 1924)	Cole and Harding Genetic S.S
Pliensbachian	spinatum	hawskerense	Junction Bed (sensu lato)		
		apyrenum			
	margaritatus	gibbosus	*thorncombiensis* BED		
		subnodosus	THORNECOMBE SANDS *margaritatus* STONE		VIII
		stokesi	DOWNCLIFF SANDS EYPE CLAY THREE TIERS		VII
	davoei	figulinum	GREEN AMMONITE BEDS	127-130	VI
		capricornus		122f-126	
		maculatum		122a-122e	
	ibex	luridum	BELEMNITE STONE	121	V
		valdani	BELEMNITE MARLS	118d-120	
		masseanum		118c	
	jamesoni	jamesoni		115-118b	
		brevispina		110-114	
		polymorphus	HUMMOCKY		
		taylori		103-109	
Sinemurian	raricostatum	aplanatum			
		macdonnelli			
		raricostatoides	BLACK VEN MARLS	99-102	IV
		densinodulum		90-98	
	oxynotum	oxynotum			
		simpsoni			
	obtusum	denotatus			
		stellare	BLACK VEN MARLS	85-89	III
		obtusum		83f-84	
	turneri	birchi	SHALES WITH BEEF	79-83e 74g-75	II
		brooki		73-74f	
	semicostatum	resupinatum		54-72	
		scipionanum	BLUE LIAS Charmouth Mudstone Formation and Rugby Limestone Member	50-53	
		lyra		47-49	
	bucklandi	bucklandi		41-46	
		rotiforme		30-40	I
		conybeari		16-29	
Hettangian	angulata	complanata extrandosa	Blue Lias Rugby Limestone Member, Saltford Shale Member and Wilmcote Limestone Member	H 73-15	N/A
	liascus	laqueous portlocki		H55-H72	
	planorbis	johnstoni planorbis		H25-H54	

Figure 2. Stratigraphy of the Lower Lias of Dorset with specific stages, ammonite zones, Lang Bed numbers and Genetic Sequence Stratigraphy from Cole and Harding (1998) and Cope *et al*. (1980).

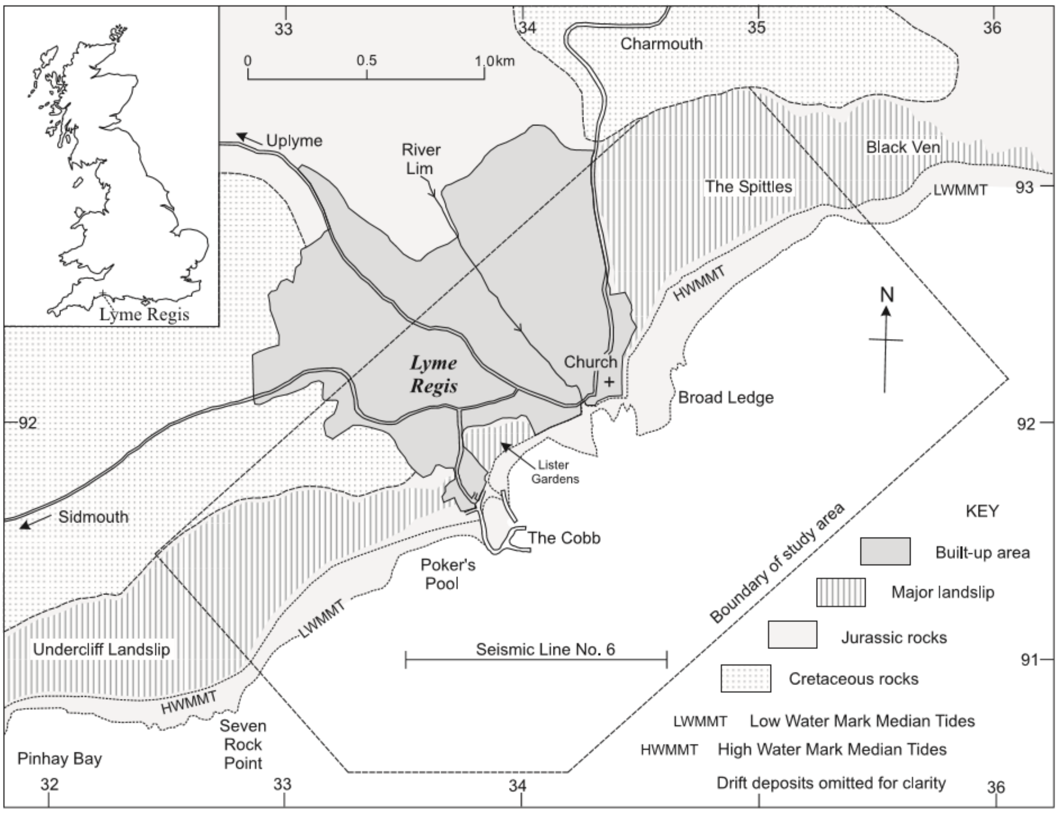


Figure 3. General view of Lyme Regis, showing the area referred to as Broad Ledge where the Gumption Shales are located and where many fossils are found. This figure is taken from Gallois and Davis (2001, Figure 1. Page 184).

The Lower Lias of the Street area of Somerset is Lower Hettangian in age (Benson et al., 2012 and McGowan, 1974). It has been argued that there are different 'types' of ichthyosaurs present at Street from those found at Lyme Regis, and as the Street localities are younger in age than the productive horizons at Lyme Regis, and new species such as *Ichthyosaurus somersetensis* (Lomax and Massare, 2016) are only known from the nominative locality, there may be some truth in this assertion.

The Lower Lias of Warwickshire comprises the Wilmcote Limestone Member and Salford Shale Member, thelatter being capped by the Rugby Limestone Member (Radley, 2003, 2005). These Members are the equivalent to the Blue Lias Formation seen at Lyme Regis. The Wilmcote Limestone Member and Saltford Shale Member are Hettangian in age (Radley, 2003), although the Wilmcote may even extend back into the latest Triassic (Ambrose, 2001). These age designations are based upon macrofossils such as ammonites. There is no mention of microfossils in the literature cited. Unfortunately, age-diagnostic macrofossils such as ammonites are rarely associated with the specimens of ichthyosaurs found in museum collections.

1.6 Palynological Analyses

Each specimen's stratigraphic location (Figure 1) was recorded when possible. In many specimens, this was a very general designation to 'The Lower Lias', which includes the Blue Lias Formation, Shales with Beef Formation, Black Ven Marls Formation, Belemnite Marls, Belemnite Stone and the Green Ammonite Beds. Such broad and stratigraphically imprecise locations pertain for many historic specimens, as the importance of accurately recording the stratigraphic location of each specimen was not appreciated at the time that they were collected. Many specimens were collected from quarries that no longer exist in the areas surrounding Street, Somerset. Personal communication with numerous collectors in the Lyme Regis area indicate that Lang's Bed 32 within the Blue Lias Formation is the most productive for ichthyosaur remains of the Lower Lias strata, and specimens mostly come from one of the 4 shale horizons in Lang's Bed 32. Samples were taken of these 4 layers in hopes of being able to distinguish between them using palynological techniques.

Samples were processed using palynological techniques (Wood *et al*., 1996; Bryant *et al*., 1988; Phipps, 1984; Van Erve, 1977). This included collecting 5 grams of matrix from each specimen and dissolving the inorganic (mineral) material with concentrated hydrofluoric (HF) and hydrochloric acids (HCl). After the use of HF, the sample was diluted and left to settle for 2 hours. After the sample had settled, the water was removed from the top of the beaker. This process is repeated until the supernatant has been neutralized. The samples were then sieved through a nylon mesh of 6 µm to remove smaller particles (typically a 15 µm mesh is used, but the palynomorphs in the Lower Lias are often smaller than this). The material was then processed in boiling HCl to remove any neo-formed fluorides. The sample was again sieved at 6 µm and the organic material placed into a small labelled plastic vial. The resulting concentrated organic material is then mounted on glass microscope coverslip as an aqueous strew, allowed to dry and cemented onto a glass microscope slide with Elvacite to be examined closely under an Olympus BH-2 transmitted light microscope.

Fifteen samples (Table 1) from various ichthyosaur specimens and some collected from field exposures were processed in the above manner, but only the first five samples processed were initially examined to determine the viability of the technique. In the five samples initially processed, *Micrhystridium sp*., and *Tasmanities sp*. (Figure 4 A and B) were found, but none were able to be identified to species level. The marine palynomorphs of most biostratigraphic utility in sediments from the Dorset Lias are two of the earliest-known dinoflagellate cysts, diagnostic of the Margaritatus Ammonite Zone of the Pliensbachian: *Nannoceratopsis gracilis* and *Luehndea spinosa* (Woollam and Riding, 1983), but neither were found in any of the residues examined. While some acritarchs, pollen and spores were found, all were stratigraphically long-ranging and thus unable to more closely constrain the age of the ichthyosaur specimens. The fifteen samples processed demonstrated that the samples from Lyme Regis produced greater abundances of organic matter per gram of sediment than those from other known localities, the Blue Lias, including Lang Bed 32, being more organic-rich than other units. Specimen UoS 16958 (the skull of an ichthyosaur) had a matrix of light grey limestone and was labelled as coming from the Black Ven Marls: a sample of the matrix produce very little organic material and almost no amorphous organic material (AOM). However, as the pilot study of the initial five samples proved inconclusive, project time constraints dictatd that this aspect of the study could not be explored in greater depth.

Table 1. List of samples processed, the museum specimens from which the matrix samples were obtained.

Specimen	Ichthyosaur Specimen	Stratigraphy Known	Analysed Yes/No
UoS 15177	UoS 15177	Unknown	Yes
UoS 15344	UoS 15344	Blue Lias	Yes
UoS 16564	UoS 16564	Unknown	Yes

UoS 16958	UoS 16958	Black Ven Marls, A. obtusum zone	Yes
UoS 2109	UoS 2109	Blue Lias	Yes
HCMAS 92009.1	HCMAS 92009.1	Unknown	No
GPIT 1796/1	GPIT 1796/1	Lower Lias, Lyme Regis	No
LB32B1	N/A	Blue Lias, Lang Bed 32, horizon 1	No
LB32B2	N/A	Blue Lias, Lang Bed 32, horizon 2	No
LB32B3	N/A	Blue Lias, Lang Bed 32, horizon 3	No
LB32B4	N/A	Blue Lias, Lang Bed 32, horizon 4	No
HCMAS NoNum	HCMAS NoNum	Unknown	No
PMO227.578	PMO227.578	Lyme Regis	No
RSM P2314.14	RSM P2314.1	Swords or Wards, England	No
UoS Sk1	UoS Skull	Unknown	No

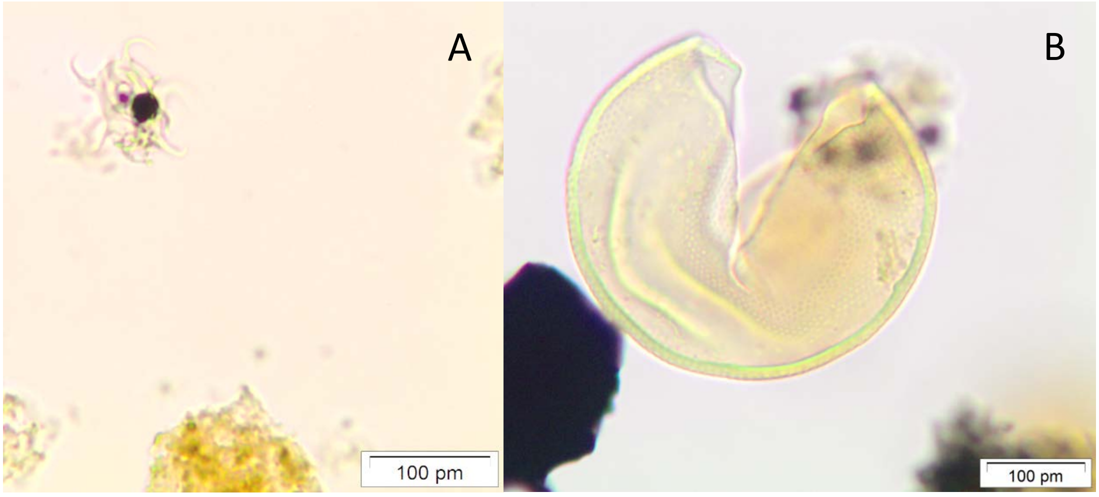


Figure 4. A. *Micrhystridium sp.* from the matrix sample from specimen UoS 2109 (top left corner of image). B. *Tasmanites sp*. from the matrix sample from specimen UoS 16564.

1.7 Conclusions

The genus *Ichthyosaurus* has had a long slightly confusing history. This genus seems to have been under almost constant revision, at least in terms of the species allocated to the genus. This thesis represents the first study to specifically focus on the morphological diversity present within the genus. As mentioned, many phylogenetic studies include this genus in their analyses, but few have conducted a study solely on *Ichthyosaurus*.

Although the initial palynological studies yielded no positive results, further work may prove beneficial on other specimens. If diagnostic palynomorphs can be found to differentiate certain stratigraphic horizons in the Lower Lias from a study of the microfossil assemblages, then identification of the stratigraphic provenance of individual *Icthyosaurus* specimens may be possible. This would allow a comparison between the stratigraphic occurrences and a specimen-level phylogenetic tree. The comparison could give insight into how environmental conditions may have impacted ichthyosaur evolution.

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Chapter 2.

Conquering the wall: measuring fossil specimens mounted on walls and behind glass using parallel lasers and aerial photography equipment

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Conquering the wall: measuring fossil specimens mounted on walls and behind glass using parallel lasers and aerial photography equipment

Keywords: Methods, photography, parallel lasers, photogrammetry, ichthyosaurs

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ABSTRACT

The modern problem of specimens being displayed in inaccessible positions in museums is a unique issue palaeontologist and curators struggle to overcome. This paper presents a new method using parallel laser photogrammetry to bridge the gap between inaccessibility and scientific study. The use of parallel lasers to provide a scale has been used in the disciplines of biology and oceanography (Bergeron, 2007; Rothman *et al*., 2008; Webster *et al*., 2010; Deakos, 2010; Rohner *et al*., 2011), but this is the first time the method has been adapted for use in paleontology. We utilized the marine reptile gallery of the Natural History Museum, in London, U.K., to test this method. A simple approach has been devised in order to increase the availability of this method to all researchers. Whilst the photographs acquired using this method are not substitutes for detailed, close examination, this method will provide scientists with useful information that could not otherwise be obtained.

2.1 INTRODUCTION

Palaeontologists who hope to study museum specimens mounted for display purposes have long faced a list of practical difficulties, many of which inhibit the researcher's ability to view and examine specimens directly: specimens may be mounted in awkward locations that are difficult to access, inhibit or prevent close examination. The focus of this paper is on those specimens that researchers may have difficulty in accessing due to display issues, and specifically on marine reptile displays produced during the Victorian Era. During this time it was popular to mount large blocks containing the specimens in wooden boxes with a glass front (Figure 1). The glass fronts were typically screwed onto the frame and therefore cannot be easily removed or opened. This style of housing is seen predominantly in the marine reptile gallery at the Natural History Museum in London (NHMUK), an impressive display of over a hundred marine reptiles, many of which are holotypes and neotypes (Figure 2). Although the resulting display is impressive and highly appealing, it has caused many problems for scientific researchers. The glass fronts are expensive to remove, and in addition to the costs and practical difficulties involved in the removal of the glass fronts, the cost associated of scaffolding and lighting in the hallway also have to be considered. To access such specimens it would also be necessary to close areas of the hallway off to the public to allow removal of the wooden boxes from the walls. Victorian display boxes of this sort are present in many other museums, some of which are mounted on walls, including the Oxford University Museum of Natural History (OUMNH), Taunton County Museum, the South West Heritage Trust (Somerset Museums Service) (TTNCM), the Royal Albert Memorial Museum (RAMM), and others, although not all possess protective glass fronts.

A key aspect of analysing palaeontological specimens is obtaining morphological and morphometric data. However, when access to the specimens is problematic, most of this information may need to be acquired from high quality photographs. Photographs can yield morphometric data if both the focal length of the camera lens and the subject's distance from the lens are known, a methodology used extensively in biological research (Jaquet, 2006 and Breuer *et al*., 2007), but not incorporated into palaeontological studies. Another method utilises stereophotographs: images are taken with a pair of carefully aligned cameras to produce images that overlap. This overlap in the images is used along with mathematical equations to determine the size of the object in the two photos, as described by Klimley and Brown (1983).

This paper describes a technique to acquire morphological and morphometric data from specimens which addresses these problems of access, and moreover one which removes the need for either the specimens to be taken from their wall mountings or the removal of glass box fronts. Furthermore this new technique requires little equipment and is therefore cost-effective.

The methodology described in this paper adapts the techniques outlined by Bergeron (2007), Rothman *et al*. (2008), Webster et al. (2010), Deakos (2010), and Rohner *et al*. (2011), and utilizes a scale produced in images by projecting parallel laser beams onto the specimen(s) being photographed. The scale is determined by the set distance between the parallel laser beams. This technique has previously been utilised by biologists aiming to better estimate the size of animals in the wild (Bergeron, 2007; Rothman et al., 2008; Webster *et al*., 2010; Deakos, 2010 and Rohner, *et al*., 2011); to the author’s knowledge this method has not previously been used in palaeontological studies. The advantage of this method is that it does not require the researcher to know focal lengths of camera lenses nor distance from the object being studied, nor is there a need for multiple cameras, as long as the lasers are properly aligned. This method of scaling images was combined with the use of equipment used for aerial photography in order to access the specimens mounted high up on walls, thus obviating the need to use expensive and cumbersome scaffolding. This technique therefore provides a fast and non-intrusive method of collecting scaled images of specimens which can then be used to obtain detailed and accurate morphometric data.

Institutional Abbreviations—**NHMUK**, (formerly BMNH), Natural History Museum, London, U.K.; **OUM(NH)**, Oxford University Museum of Natural History, Oxford, U.K.; **RAMM**, Royal Albert Memorial Museum and Art Gallery, Exeter, U.K.; **TTNCM**, Taunton County Museum, The South West Heritage Trust (Somerset Museums Service), Taunton, U.K.

2.2 MATERIALS AND METHODS

Materials for aerial photography were purchased via Nitsua Global LLC and comprised a Pixie Pole, digital single-lens reflex camera (DSLR) and 360° ball-head tilting camera mount, and foam padded resting plate. The Pixie Pole is constructed with hex-aluminium material to be more study and stable than other similar poles used for photography (Figure 3). The pole is telescopic and is 173 cm in height when collapsed, but extends to 5.50 m; it is manually controlled and extended to the desired length. The pole can be locked at the desired height with no twisting of the pole required (in contrast to other, similar poles): this is a significant advantage and makes the Pixie Pole preferable for the technique discussed here. The 360° ball-head tilting camera mount (Figure 4) is needed to attach the DSLR camera to the Pixie Pole. The camera mount is equipped with a spirit level allowing the camera system to be erected in a level position. The foam-padded resting plate is used to protect the camera if the pole is dropped, but is also used as an attachment point for the lasers in this study. A Nikon DSLR D70S camera with an 18-70mm lens was used to record images.

Inexpensive laser pointers attached to keychains were purchased and (with the keychain portion removed) mounted on the foam resting plate (Figure 5). The laser pointers were attached to the resting plate via the use of Sugaru, a putty-like substance that sets to an inflexible plastic material within 24 hours. This allowed the continual adjustment of the laser beams over a prolonged period of time, something not possible with a quicker drying mounting medium. To ensure accuracy of the attached lasers and the methodology before traveling to a museum, tests were made on specimens not mounted behind glass, so that a comparison could be made between measurements made using the laser beam assembly and those measured with callipers or tape measure. It was at this point that it was discovered that the laser beams were not projecting parallel to the long axis of the pointer housings, and despite the pointers being mounted parallel the beams were not projecting the same distance apart on the specimen at successively increased distances away from the specimen. To ensure the laser beams projected parallel to each other, lines were drawn 50 mm apart on a surface and used to align the laser beams. To ensure accuracy of alignment, the mounted laser assembly was tested by incrementally moving the assembly up to 0.5 meters away from the marked surface to ensure constant beam separation. This step may be repeated until the lasers project parallel to each other. The process was then repeated not relying on the laser pointer housing, but instead utilizing the positions where the laser spots hit the wall to ensure they were projecting parallel to each other.

As wall-mounted specimens are often out of reach, an infrared wireless remote control for the Nikon DSLR camera was used to release the camera shutter and capture the images. As the remote control sensor on the camera is on the front, it was more practical for one person to hold the camera pole steady whilst a second worked the remote control. A step ladder was employed to assist with capturing images of specimens mounted higher on walls.

Once acquired, the program RadCor Version 2 (Radical Correction) was employed with the imported image to allow for correction of lens distortion. The program requires the type of camera, model and lens to properly correct the distortion. The undistorted images were then saved. The undistorted images were then imported into ImageJ (Hammer *et al*., 2001), in order to measure the specimens. This software package converts user-chosen distances across the image into measurements based on the number of image pixels between the laser beam points used for the scale.

2.2.1 TRIAL RUN AND ISSUES ENCOUNTERED

During field testing at the NHMUK, several difficulties were experienced. The first is that one of the mounted lasers fell off the mount in transit to the museum. The Sugaru mounting medium requires 24 hours to dry to the right plastic consistency, which necessitated a ‘quick fix’, the laser pointer being reattached to the resting plate using cyanoacrylate. This meant that the lasers were not mounted precisely parallel to one other. The lasers were also slightly offset vertically. Three set distances of 1 ft., 3 ft. and 6 ft. between the specimens and camera were used and laser distances measured for each (53.08mm, 58.91 mm and 64.33 mm respectively). The distance between the lasers was measured with a digital calliper to the nearest 0.01 mm. The direct diagonal line from one point to the other was measured as there was some slight vertical offset. The number of photographs taken of each specimen and each distance from specimen to the camera was noted so that the laser distance in each photograph would be accurate.

During examining of the images to ensure the specimens were properly framed, aligned and in focus, it was noted that reflections of the laser beams had been captured on some images. This was a result of the glass box fronts on the specimens, something not observed when testing the method on specimens that lacked glass fronts. Although not all images displayed reflections of this nature, in those that did, the 'original' laser points could be distinguished as they were in the same position in each photograph, and the laser points were stronger in intensity than the reflections. Pixlr Online Photo Editor's 'spot heal' tool was used to remove the laser reflections and minimize confusion.

The technique was employed during an early morning visit to the museum before doors were open to the public, so as to not endanger visitors walking nearby. The display area is partially lit by natural light in addition to artificial lights; however, the overall lighting is of low intensity, thus necessitating the use of flash photography. Consequently, photographs taken at recorded glare from the camera flash, reflecting both from the glass and from the edges of the wooden cases. The glare was still present in images shot later in the morning when the lights were on and there more natural light was present. Although it has been suggested that taking images with the camera close to the glass surface may reduce glare and reflection (Mallison and Wings, 2014), this technique is most applicable to specimens located some distance away from the glass of the cabinets that contain them: it is not helpful where the fossils are mounted very close to the glass as was the case here. The glare from the glass was not always on same spot on the specimen as multiple images were taken of each specimen in slightly different locations. To adjust for the darker images taken without a flash, the brightness and contrast of the photos were changed in photo manipulation programs later. Alternatives for dealing with this issue are present in the discussion section of this paper.

One of the biggest obstacles was getting the infrared wireless remote control in range of the camera's sensors. Infrared operates by line of sight, which is difficult to establish when the sensor is 5 meters above your head. An alternative is the use of a shutter cable release, but this only allows for a reach of 1 meter at the time of the search. Alternative lengths are available which would work with this set-up and eliminate the issue with wireless remote control. With a different camera or set up other options may be available to other users. Given that the sensor is located in the front part of the camera; two people are required to take pictures with the set up described here. The person operating the remote control would also benefit from a step ladder to align the remote within range of the sensor. The remote control was cited as having a range of 4.88 meters, but this is a horizontal measurement away from the camera, not the vertical distance relevant to the study described here. After a day of trial and error with the remote control we were able to find those areas in which the sensor worked best. A step ladder was provided the second day, this enabling the remote control user to get closer to the sensor for the specimens on the very top row of the wall (Figure 6).

2.3 RESULTS AND WORKFLOW

A workflow model has been devised in the same style of Mallison and Wings (2014) but providing the minimum work path for this parallel laser set up (Figure 7). The work flow for parallel laser photogrammetry is the same as that involved in regular photogrammetry, in that it has two or three main actions: 1. Photography, 2. Image editing (if necessary) and 3. Specimen analysis. The first stage of photography is not significantly different from normal photography, merely involving the additional role of a Pixie Pole and remote control. The Pixie Pole is easy to operate, but the remote control used was rendered it difficult to maintain line of sight. When the laser is set up correctly the image editing phase should be straightforward as the scale will be the same in every picture. Specimen analysis will vary based on how many measurements are taken or the type of analysis done. At the end of the procedure, the results enable scientists to obtain measurements and undertake closer inspection of those inaccessible specimens than has been conventionally possible. An example of this is provided in Table 1, where measurements have been taken of the hard-to-access holotype of *Nannopterygius enthekiodon* (Figure 8), a specimen mounted high in the upper part of the Marine Reptile Gallery display at the NHMUK.

2.4 DISCUSSION

Previous researchers have assembled mounting systems that allow the application and calibration of lasers (Rohner *et al*., 2011): while the set-ups used in these cases could increase accuracy, they are less cost efficient than the technique described here. One aim of our study was to keep costs as low as possible to make this technique accessible to as many palaeontologists as possible. Other adjustments could be made to the mounting methods, such as setting lasers on either side of the camera instead of below the camera, so as to have the laser spots in a more central location in the resulting image. This would lessen the problems of the lasers becoming detached from the assembly. More efficient and expensive lasers could be used: if of higher quality, they would produce more reliable and directional beams, and setting up parallel beams would be more straightforward. This would reduce the possible error in measurements taken from the specimens.

Other photographic techniques could be combined with the technique described here such as the use of a polarizing filter to reduce reflections from surfaces like that of the glass fronts on the Victorian cases. Use of a filter would also allow for reduction in reflection and hence more clearly defined images of specimens. The cost of polarizing filters varies widely. Another option to reduce glare would be to set a long exposure, but this could cause blurriness of the image as the Pixie Pole is much sturdier than other poles, but can still wobble if user is not careful. Glare can also be combatted by taking multiple pictures at different positions relative to the specimens in order to obtain clear pictures of all parts of given specimens.

This method is presented as a low cost alternative to more expensive techniques of examining inaccessible specimens. Further work needs to be done to assess the accuracy of this method, such as discussed by Deakos (2010). Testing the degree of accuracy in the measurements requires that the dimensions of the objects being measured are known, but none of the specimens involved in our study have previously been measured accurately (images have been published with applied scales but there is no indication if those scales were estimates or measured). Overall the method proposed here will facilitate much future research that otherwise could not be achieved, or would rely upon a significant amount of funding.

2.5 CHAPTER ACKNOWLEDGMENTS

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CAPTIONS

Table 1. Measurements (in mm)of *Nannopterygius enthekiodon* (NHMUK PV OR46497) from a picture obtain using the method described in this paper. The image uses was corrected for lens distortion in RadCor and measurements taken in ImageJ.

Figure 1. A close up picture of the types of wooden Victorian style boxes without the protective glass fronts that can be seen in the Natural History Museum in London. This specimen is NHMUK PVOR36256.

Figure 2. The marine reptile hallway from the far end showing some of the ichthyosaur specimens present in wooden boxes with protective glass fronts.

Figure 3. Image if the pixie pole in use at the Natural History Museum in London. The pole is much more stable at height than a standard painter’s pole.

Figure 4. Image of the DSLR tilting mount, notice the level built in to make sure the camera was at the optimum level.

Figure 5. Image of the foam-padded plate with lasers mounted onto it with Sugaru and superglue. Notice the laser housings are not parallel, but the laser beams that come out of the housing are.

Figure 6. Image of the Pixie Pole, and parallel laser in use at the Natural History Museum, London. Pole in use by Jessica Wujek and Rebecca Bennion is on the step ladder using the remote control.

Figure 7. Workflow figure showing the method proposed by the author.

Figure 8. Image of notoriously difficult to picture specimen, *Nannopterygius enthekiodon* (NHMUK PV OR46497) taken with Pixie Pole and parallel lasers and the scale between the laser points is 64.61mm.

TABLES

Coracoid width left	122.998
Coracoid height left	85.867
Coracoid width right	123.639
Coracoid height right	77.434
Humerus length left	69.887
Humerus medial width left	67.810
Humerus distal width left	54.791
Humerus length right	71.831
Humerus medial width right	66.391
Humerus distal width right	56.798
Lower jaw length	674.516
Total length of specimen	2762.091

FIGURES

Figure 1.

Figure 2.

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

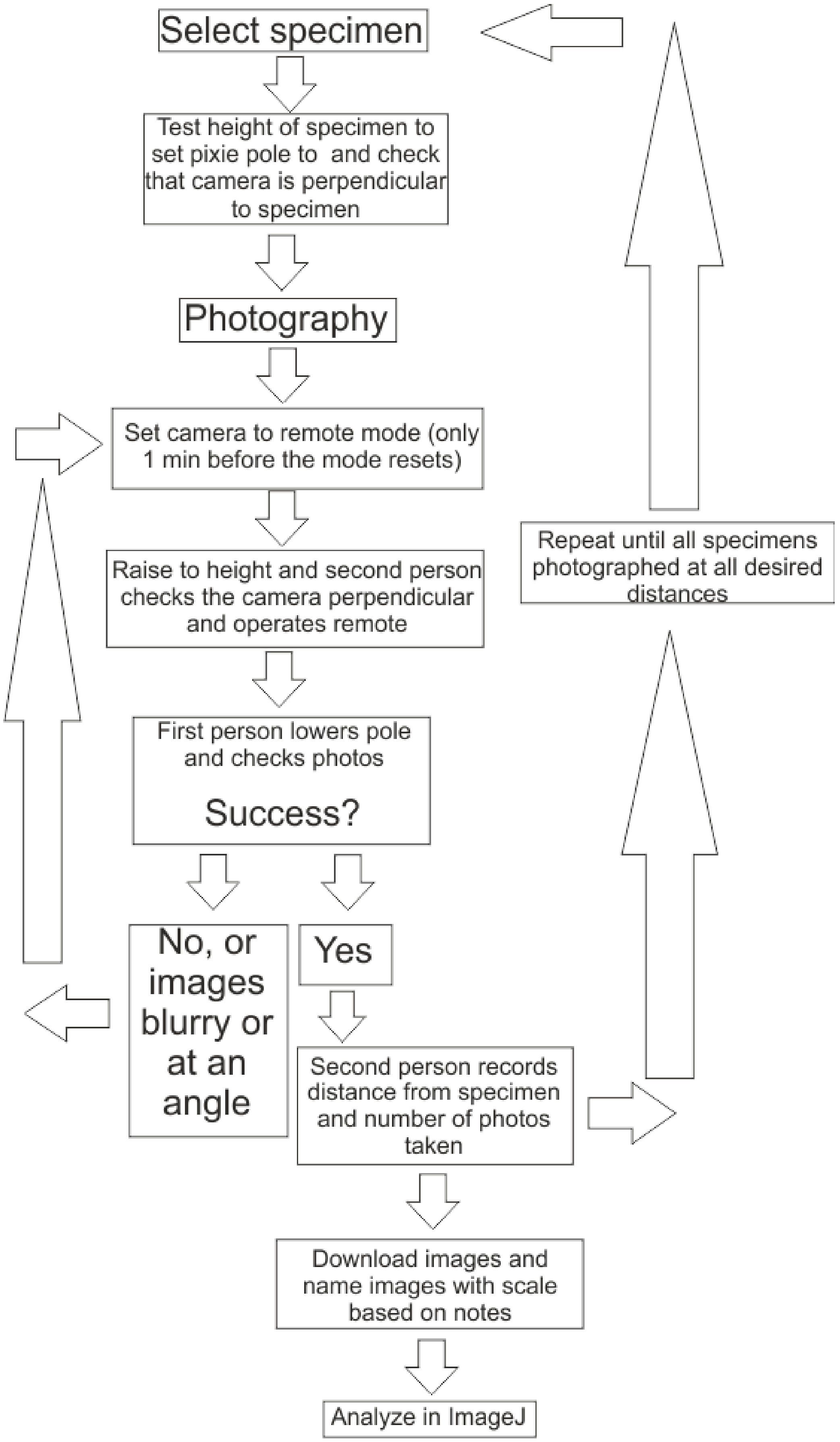
Select specimen
Test height of specimen to set pixie pole to and check that camera is perpendicular to specimen
Photography
Set camera to remote mode (only 1 min before the mode resets)
Raise to height and second person checks the camera perpendicular and operates remote
First person lowers pole and checks photos
Success?
No, or images blurry or at an angle
Yes
Second person records distance from specimen and number of photos taken
Download images and name images with scale based on notes
Analyze in ImageJ
Repeat until all specimens photographed at all desired distances

Figure 8


46497
Ichthyosaur
Nannopterygius entheciodon (Hulke)
155 - 152 million years old
Upper Jurassic
Kimmeridge Bay, Dorset
This deep-bodied kind of ichthyosaur is known only from this incomplete skeleton.
46497 Presented by J C Mansel-Pleydell in 1871
Ichthyosaur
Ichthyosaur

Chapter 3.

Testing the reliability of linear ratio measurements in distinguishing species of *Ichthyosaurus* (Reptilia; Ichthyosauria): an in-depth morphometric approach

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Testing the reliability of linear ratio measurements in distinguishing species of Ichthyosaurus (Reptilia; Ichthyosauria): an in-depth morphometric approach

Keywords: Ichthyosauria, *Ichthyosaurus*, morphometrics, species delineation

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Lawrence Wujek did the data collection, fixed outlier issues, performed the analyses (PCoA, NMDS, and Cluster) and wrote the manuscript.

Kelley checked the data for outliers, performed analyses (bivariate plots, box plots and LDA) and assisted with manuscript editing and writing.

Harding assisted with manuscript editing and writing.

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ABSTRACT

Ichthyosaurus is known from an enormous number of specimens, many of which possess confusing combinations of anatomical features. Both the quantity of data and distribution of anatomical characters make it difficult to recognise distinct species with our current understanding of this taxon. One obstacle to a better understanding of the genus is that few morphological characters can be consistently identified across all fossil specimens since they often vary at both the species and specimen level; indeed some characters are not diagnostic at the generic level (e.g., those concerning ribs and vertebrae). A review of the literature has revealed that studies too often utilize characters that have not been rigorously evaluated. Indeed the use of many such characters has been pervasive in phylogenetic analyses of Ichthyosauria despite the fact that the validity of a character or its applicability to different types of datasets (e.g., generic, specific or specimen level) has not been tested. The use of measurement ratios is the most problematic. This method of analysing measurement data has been used to minimise the effects of size bias resulting from variations in individual specimens and ontogenic stage. In this study, to produce more quantitative rather than qualitative or morphology based character(s), linear measurements are utilized instead of the ratio values. Ratios and their observed and found ranges for species within the genus *Ichthyosaurus* were initially used by McGowan (1974), and although they have been used in many phylogenetic studies as autapomorphies for different *Ichthyosaurus* species since then, a robust evaluation of their validity has not yet been performed. With a dataset of 56-70 specimens and 12-56 measurements of each specimen, we use multiple morphometric analyses (PCoA, NMDS, Cluster and LDA), to test these measurements, and show that they provide no significant separation of taxa. These results demonstrate the need for a more strict evaluation of characters that utilize linear measurements from ratios and ranges of measurements in phylogenetic analyses.

3.1 INTRODUCTION

Ichthyosaurs are among the best known of Mesozoic marine reptiles and are well known from the Lower Jurassic of southern England, in particular localities of Lyme Regis and Street, the former being the site of the first ichthyosaur discovery by Joseph and Mary Anning between 1809 and 1811 (Torrens, 1995). At least nine genera have been described from the Lower Jurassic of the UK: *Ichthyosaurus*, *Protoichthyosaurus*, *Temnodontosaurus*, *Excalibosaurus*, *Eurhinosaurus*, *Leptonectes, Stenopterygius, Hauffiopteryx* and *Wahlisaurus* (Jaekel, 1904; McGowan and Motani, 2003; Maisch, 2008; Lomax 2016, Lomax *et al*., 2017). Many specimens from the English Lias are complete or near complete, but most are preserved in a laterally compressed condition. Additionally, the skeletal elements of these specimens are often slightly scattered as a result of the energetics of the depositional environment, or distorted by diagenesis and compaction. At the same time it is important to note that specimens have often been modified (typically by Victorian preparators) to appear more complete, or are composites which incorporate elements from more than one individual, or even different types of reptiles (McGowan, 1990; Massare and Lomax, 2014).

Due to this abundance of specimens, and to initial inadequacies in the definition of the genus and its constituent species, *Ichthyosaurus* has become a waste-basket taxon (Smith and Radley, 2007). One early description of the genus was ‘A marine quadruped, nearly resembling the crocodile, in the osteology of its head, and its mode of dentition. Vertebrae having both faces of their body deeply concave as in fishes. Extremities having no distinct radius and ulna, but the humerus immediately supporting a very numerous series of small polygonal bones, forming a very flexible paddle. Anterior extremities much larger than the posterior.’ (de La Beche and Conybeare, 1821). This and other vague descriptions resulted in this genus accommodating most ichthyosaurs found early on, until more specific descriptions were created. As more specimens were found, the genus and species descriptions became more circumscribed and other genera were created. Many other genera from the Jurassic of southern England were initially allocated to *Ichthyosaurus,* including some specimens now considered to reside within *Leptonectes* and

Temnodontosaurus (McGowan and Motani, 2003). Six species of *Ichthyosaurus* are currently recognized: *Ichthyosaurus communis* (de La Beche and Conybeare, 1821), *Ichthyosaurus breviceps* (Owen, 1881), *Ichthyosaurus conybeari* (Lydekker, 1888), *Ichthyosaurus anningae* (Lomax and Massare, 2015), *Ichthyosaurus larkini* and *Ichthyosaurus sommersetensis* (Lomax and Massare, 2016).

Considerable intraspecific variation is present across specimens identified as *I. communis* (Appleby, 1979), and consequently there have been several attempts to reclassify these specimens as different species or even allocate them to different genera. One genus, *Protoichthyosaurus*, (Appleby, 1979) was argued to be a junior synonym of *I. communis* by Maisch and Hungerbühler, 1997. However, this genus has recently been revived by Lomax and Massare (2017) and some specimens of that genus were included in the present analysis prior to publication of the latter paper. The description of *Ichthyosaurus intermedius* (Lydekker, 1888) was another attempt to clarify species within the genus *Ichthyosaurus*, however McGowan and Motani (2003) described a specimen that had characteristics of both *I. intermedius* and *I. communis* and thus considered the former to be a junior synonym of *I. communis* (McGowan and Motani, 2003; McGowan, 1974). *Ichthyosaurus conybeari* has recently been more rigorously defined by Massare and Lomax (2016). Whilst the latter authors have increased the number of known specimens of *I. conybeari*, it is still considered a rare species (McGowan, 1974). *Ichthyosaurus breviceps* is predominantly diagnosed on the basis of its short snout or reduced rostrum, large orbit and slightly smaller size. Fewer than ten specimens have been referred to this species, in marked contrast to the hundreds of specimens referred to the morphologically variable *I. communis*. *I. breviceps* is therefore in need of re-examination for the same reasons as *I. conybeari*. Only a small number of specimens have so far been referred to the new species *I. larkini* and *I. sommersetensis*, although it is to be expected that new specimens will be identified as these species; there are currently more *I. sommersetensis* specimens than *I. larkini*.

Historically, morphological ratios (Table 1) have been used to reduce the effect of size variations in specimens (McGowan, 1974). Whereas size can sometimes be used to determine species-level identity, the complications of ontogeny and allometric variation can render it problematic (McGowan, 1973). Whilst the use of ratios did permit separation of the species of *Ichthyosaurus* then known, their use has persisted in many more recent phylogenetic studies (Motani, 1999; Sander, 2000; McGowan and Motani, 2003; and Fischer *et al*., 2013). The work of Fischer *et al*. (2013) did not include one of the ratios used in Fischer *et al*. (2011), although the reason for this omission was not explained. Conversely, authors have noted that some of the ratios become unreliable when considered within the context of a larger dataset (Kirton, 1983; McGowan, 1997; Maxwell, 2010; Massare and Lomax, 2016). This lack of reliability became apparent during data collection for the current phylogenetic research (Table 2). While ratios have been used successfully in some phylogenetic and other analyses, their reliability in distinguishing the species within *Ichthyosaurus* has not been tested statistically since 1974 (McGowan, 1974). Linear measurements have proven useful in distinguishing species within other genera (Maxwell, 2010), but this approach has not been tested in *Ichthyosaurus*. In an effort to better resolve the species-level diversity of *Ichthyosaurus*, this study tests the validity of the use of the linear measurements used in ratios by creating linear measurement cross-plots, Principal Coordinates Analysis (PCoA) and Non-metric Multi-Dimensional Scaling (NMDS), cluster analysis and Linear Discriminate Analysis (LDA) as means of distinguishing those species.

INSTITUTIONAL ABBREVIATIONS

AGC— Alfred Gillett Collections, cared for by Alfred Gillett Trust (C & J Clark Ltd.); **BRLSI**— Bath Royal Literary and Scientific Institution, Bath, U.K.; **BRSMG**—Bristol Museum and Art Gallery, Bristol, U.K.;**BU**—Birmingham University Lapworth Museum, Birmingham, U.K.; **BRSMG**—Bristol Museum and Art Gallery, Bristol, U.K.; **CAMSM**—Cambridge Museum of Natural History, Cambridge, U.K.; **DORCM—**The Dorchester County Museum, Dorchester, U.K.;**GLAHM**—The Hunterian Museum, University of Glasgow, Glasgow, U.K.; **IPSMG**— Ipswich Museum, Ipswich, Suffolk, U.K.; **LEICT**— Leicester Arts and Museums Service, New Walk Museum and Art Gallery, New Walk, Leicester, U.K.; **NHMUK**—(formerly BMNH), Natural History Museum, London, U.K.; **NMING**—National Museum of Ireland, Natural History Division, Geological Collection, Dublin, Ireland; **MANCH**—Manchester Museum, Manchester, U.K.; **OUMNH**—Oxford University Museum of Natural History, Oxford, U.K.; **PETMG** — Peterborough Museum and Art Gallery, Peterborough, U.K.; **PMO**— Paleontologisk Museum Oslo, Oslo, Norway; **TTNCM**—Taunton County Museum, The South West Heritage Trust (Somerset Museums Service), Taunton, U.K.

3.2 MATERIALS AND METHODS

Data were collected from specimens referred to *Ichthyosaurus* housed in more than 20 international museums. A full list of the 59 morphological measurements utilized in this study can be found in Table 3 and are illustrated in Figure 1. A variety of factors (e.g., incomplete preservation, specimen orientation, etc.), meant it was not possible to take all 59 measurements from all specimens, and indeed no specimen in this study includes all measurements. A total of 320 specimens were measured, but due to the constraints of the different analyses, two subsets of these data were used (See Appendix B). In one, 70 specimens including more than 20 of 59 measurements (34%) were utilized in the PCoA, NMDS, and cluster analyses. In another subset a total of 56 specimens providing 12 measurements were utilised for LDA. The subset of measurements is listed in Table 3. The first subset (70 specimens) of the 320 specimens was performed as the analyses need overlapping information for the specimens involved. The total number of measurements taken for each specimen was recorded, and then specimens lacking less than a certain number of measurements were deleted and the analysis was tried again until it could run. With this method, the analyses were not able to be run until all specimens with less than 20 measurements taken were deleted. The second selection of specimens (56 specimens) for the second subset was made by first selecting measurements that were well represented across many specimens and/or utilized to calculate ratios previously used to separate species (e.g., orbit diameter, jaw length). From this reduced dataset, exploratory analyses were conducted to identify the maximum discrimination among species that could be achieved using LDA.

For measurements under 150 mm, digital callipers were used, data being recorded to the nearest 0.1 mm. Measurements larger than 150 mm were made with a tape measure and recorded to the nearest millimeter. All measurements of broken or distorted bones were noted as such by use of an asterisk, and complete or undistorted size was estimated when indications of the full size of the bone was present (e.g., impressions in the sediment or plaster) and only complete measurements were used in the study. In specimens where right and left sides were exposed and each equally well preserved (e.g., left and right femur), measurements of both elements were taken and then averaged. If one measurement was ambiguous (i.e., it concerned a broken or distorted bone) the measurement more likely to represent the original anatomical condition was used. Photographs were taken of specimens that could not be measured directly, using a Nikon DSLR D70S with an 18-70mm lens. Some photographic data were recorded using the parallel laser measurement method outlined in Chapter 2 of this volume, while the rest of the images were taken with a scale bar for calibration purposes. Multiple images were taken orientated perpendicular to the specimen at various points in order to correct for perspective shift in specimens which could not be photographed in their entirety, to minimise error. In addition, multiple overlapping images were taken of less accessible specimens. The photographs were then imported to ImageJ (Schneider *et al*., 2012) to derive digital measurements. The software reported the measurements to the 0.001 mm and they were recorded to 0.01 mm.

Where possible, the ontogenetic stage of each specimen was noted. However, given that the identification of a specimen as a juvenile is based largely on size or histology, juvenile status is often difficult to determine (Johnson, 1977). It has been suggested that the convexity or shape of the proximal end of the thunnosaurian humerus and the rugosity of the bone on the shaft of the humerus can be used as an indicator of juvenile status, but studies demonstrating this for *Ichthyosaurus* have yet to be published (Johnson, 1977). Fernandez *et al*. (2005) stated that the ratio of the internal sclerotic ring to orbit diameter can be used to determine juvenile status in some ichthyosaurs, but was criticised in Fischer et al. (2014). None of these approaches have been tested specifically for *Ichthyosaurus* so these criteria have not been employed. Therefore, the few specimens regarded as juveniles (Table 4) were identified as such on the basis of extremely small size, the possession of disproportionally large orbits (between 25–40% of skull size) and/or bones that do not appear to have reached the typical adult condition. These specimens were then removed from the study to not skew the results.

In most cases, museum specimen labels were utilized for initial identification of specimens to species level. Although many labels do not indicate who made the original identification of the specimens. When possible, obvious skeletal features or autapomorphies currently within the recognized parameters of the species or genus were utilized to allow the identification of a specimen as belonging to a different taxon than the one labelled, accordingly the identification was changed in these cases. Recent descriptions of *I. conybeari* have changed the original identifications of some specimens (Massare and Lomax, 2016) and these have been included in the present study. The recent publication (Lomax and Massare, 2016) of two new species (*Ichthyosaurus sommersetensis* and *Ichthyosaurus larkini*) of *Ichthyosaurus* were incorporated by examining the pictures and descriptions of each specimen to identify additional specimens of this new species. It should be noted that the rare species *I. anningae, I. breviceps,* and *I. conybeari* are underrepresented compared to other species in the dataset, as are the two newer species. Although *I. intermedius* has been synonymized with *I. communis* (McGowan and Motani, 2003), we treated it as a distinct taxon in all analyses except the cluster analysis, and plots for the purposes of comparison.

Consideration must be made of the possible biases that arise with the use of historic specimens. Many have been manipulated and/or are composite specimens (Massare and Lomax, 2014). Most such specimens have been set in painted plaster and joints between individual blocks of sediment on which the specimen falls have been covered with the same plaster and paint.

Without close examination it can be difficult to differentiate whether the skeletal elements are preserved in one block or many, and this can make it difficult to tell whether the specimen is a composite. Given that many specimens are now in sealed boxes with protective glass covers, close-up examination can be impossible. An additional problem arises due to the historical value of the display cases with their delicate Victorian-era glass, and the associated costs of dismantling such cases without damaging the specimen or the display. In such situations (e.g., the specimens on display at Natural History Museum in London), measurements were taken based on the use of parallel lasers to create a scale (see Chapter 2 of this volume). This methodology, whilst by no means preferable to the close-up examination that can be performed with display cases removed, does provide a practical solution to the issue. At the National Museum of Ireland, Natural History Division, a thick resin obscures many of the specimens' features and additional analysis beyond the scope of the present study is required to determine whether or not the specimens are composites. When possible composite specimens were identified and examined, measurements were only used from the portions confidently identified as belonging to a single individual. If thought to be from two or more separate specimens, the specimens were considered as such.

Preservational bias occurs in most specimens, and ichthyosaurs are commonly preserved in lateral view and slightly crushed or compressed due to subsequent burial and diagenesis (Cleary *et al.*, 2015). Total body length (snout tip to end of tail, Figure 1) measurements were recorded but not used in this study, as many specimens are incomplete and do not represent true total length (McGowan, 1973). Although snout tip to end of preflexural vertebrae has been used as an overall size proxy in the past, we chose to use the measurement from the atlas-axis to the pelvic girdle, as the snout tip is also often broken. The pelvic girdle was chosen, due to the fact that the tail bend is not always obvious in specimens with twisted vertebrae. Other measurements, such as skull length or jaw length, were used in some cases, but again are not always indicative of total size. These biases can translate into a loss of data that is inherent with two dimensional preservation of a three dimensional object. Undistorted skull width, posterior skull and braincase elements are often either not preserved or not exposed, and such measurements might only be obtained with the use of CT-scanning or net node formation, techniques that could be used in future studies. Preservation in lateral view can often obscure pectoral and pelvic girdle elements, unless shifted to a slightly ventral or oblique orientation. Ribs can also cover the vertebral column, along with pectoral, forefin, pelvic and hindfin elements. Distortion of specimens during diagenesis can also occur, and in the present study such features were recorded wherever observed. Bones can break prior to deposition, during burial, during excavation, or during preparation. Breakages were noted and where possible estimations were made of the unbroken length. Distal elements of the fins and the posterior portion of the tail are often missing or lost, and most likely lost due to transportation processes during deposition and bone/particle size.

3.2.1 Quantitative analysis

Historically, the characteristics used to distinguish species of *Ichthyosaurus* include: preflexural vertebrae count, snout ratio, orbit ratio, the presence of notching in phalanges, forefin digit counts, longest digit element counts (a character subject to completeness of the specimen, thus not very reliable), and total length (McGowan and Motani, 2003). The recent addition of new species to the genus – *Ichthyosaurus anningae*, *Ichthyosaurus sommersetensis*, and *Ichthyosaurus larkini* – has resulted in the use of additional characters to distinguish *Ichthyosaurus* species. For *I. anningae t*hese include the presence of a short robust humerus with a deltopectoral crest that is larger than the dorsal process and over half the length of the shaft; the anterior edge of the humeral shaft being shorter than posterior; presence of a circular depression on the articular surface of the humerus; dorsoventral constriction in the humeral head, and a femur almost as wide distally as proximally with a relatively short shaft (Lomax and Massare, 2015). New characteristics present in *I. larkini* are an elongated and narrow external naris, a broad jugal (though broad is vague) with a blunt anterior end that extends to the middle of the external naris and also separates the maxilla and the lacrimal, the jugal also makes up a portion of the posterior part of the orbit, the hindfin has three digits contacting the astragalus, and an element of digit III that almost separates astragalus from tibiale (Lomax and Massare, 2016). New characteristics present in *I. sommersetensis* are a broad and asymmetrical maxilla with long anterior process, the maxilla also has a very long posterior process in lateral view, a tritadiating lacrimal with a posterior shelf at the base of the dorsal process, a jugal with an almost straight dorsal ramus that does not have a right angle dorsal bend, the jugal anterior process extends beyond the anterior edge of the orbit, a high and narrow postorbital that makes up most of the posterior margin of the orbit and separates the jugal from the orbit, a large prefrontal which forms at least half of the anterior orbit and excluded the dorsal process of the lacrimal from the orbit margin, the presence of an irregular depression on the articular surface of the humerus, an illium that is wide relative to length and more oblong than rib-like (Lomax and Massare, 2016). Massare and Lomax (2016) also listed new characters that might help diagnose *Ichthyosaurus conybeari*, including a large external naris; a narrow separation between naris and orbit; a short, wide humerus with a distinct rim on the dorsal process at top of the shaft; humerus length ≤ 1.4 length of the femur; a femur longer than ischium; five primary digits in the hindfin; one digit extending from the astragalus, proximal and distal digital bifurcation; a narrow postorbital; a slender maxilla with a narrow, long , delicate premaxillary process that is longer than the jugal process; a humerus dorsal process offset anteriorly from the centre; a fibula much larger dorsoventrally and mediodistally than the tibia; a notched tibia, and a wide rectangular ischium that is much shorter than the pubis (Massare and Lomax, 2016). These new characteristics need to be examined in more detail, as some of them are not independent from each other, such as a large external naris and a narrow separation between naris and orbit and a short, wide humerus with a distinct rim on the dorsal process at top of the shaft and a humerus length ≤ 1.4 length of the femur. Other characteristics use terms that are very subjective such as ‘broad’ and ‘narrow’, and make phylogenetic studies more difficult to replicate. All of the foregoing characters were utilized in the present study in order to determine the validity of the current means of species-level identification stated by the museum labels. Any change in species assignment by comparison to the museum designation was noted and curators have been informed in applicable cases.

3.2.2 Bivariate analysis

Simple XY plots or bivariate plots were constructed using the linear measurements from ratios (Table 1) that have been used in previous ichthyosaur studies. Bivariate plots and box-and-whisker plot insets were constructed from raw data in the statistics program R 3.3.0 (R Core Team, 2016). Raw data were utilized to make the plots easier to interpret visually. Ordinary Least Squares (OLS) lines were added to the plots in R.3.3.0 (R Core Team, 2016) and represent the value of the ratio for each species. The ease of use of bivariate plots also allows unidentified specimens to potentially be classified or added to the plot without having to repeat the analysis as in multivariate analyses (Maxwell, 2012). Bivariate plots are more reliable method if there is good separation in the analysis of the groups being studied.

3.2.3 Multivariate analysis

The two subsets of the more complete *Ichthyosaurus* specimens described above were used for different multivariate analyses. Missing data restricts the use of every specimen. For example, there needs to be an overlap of data to compare: specimens consisting only of skulls cannot be compared with specimens preserving only postcranial material. The first subset included 70 specimens from which 20 or more measurements were present and was used for all the bivariate and multivariate analyses except for the Linear Discriminate Analysis (LDA). The second subset of 56 specimens that had at least 50% of the 12 measurements utilized was created for LDA. Both raw and log transformed data was utilized for the PCoA and log transform data was utilized for the other analyses. Both datasets are present in Appendix B and showing both the raw and log transformed data for the larger subset. These datasets were analysed using Paleontological Statistics or PAST software project (Hammer *et al*., 2001) to perform the multivariate analyses described below.

Multivariate analyses involve projecting a multidimensional dataset onto fewer axes in order to better visualize variance or another distance metric. Each technique does this in a slightly different way, making it crucial to select the best analysis for specific datasets. Principal Component Analysis (PCA) compensates for missing data by utilising an average value, that value being based on the average of the data from other specimens for which those data are known. Principal Coordinates Analysis (PCoA), on the other hand, uses pairwise deletion to deal with missing data - for a missing value that is being compared to another existing value, only that particular data pair is deleted from the analysis, not the entire set of data pairs. PCoA can be used to visualize trends and groupings within the data, whilst PCA is used to preserve as much variance as possible in a multivariate data set, and facilitates the visualization of data (Hammer and Harper, 2006). PCoA was therefore regarded as the most appropriate analytical method for this study. Both the unmodified and log transformed data were used for the PCoA for comparison. Non-metric Multi-dimensional Scaling (NMDS) has also been used to project multivariate datasets onto two axes in PAST (Hammer and Harper, 2006). PCA and PCoA project datasets onto more than three axes and compare the distances of the measurements. NMDS ranks these distances and then compares the ranked distances instead of the absolute distances (Hammer and Harper, 2006). Cluster K-means analysis is a non-hierarcical clustering that needs a specification of group numbers prior to running the analysis (Hammer and Harper, 2006). Therefore this is often used to test a hypothesis involving groups or the number of groups in a dataset. Linear Discriminant Analysis (LDA) which is the same as Canonical Variance Analysis (CVA) projects datasets onto two or more dimensions to maximize separation between groups (Hammer and Harper, 2006). Jackknifing of the LDA results, which is a leave-one-out validation technique, was used to test the reproducibility of the results (Hammer and Harper, 2006). These analyses combine to provide a representative visualization of the data.

3.3 RESULTS

3.3.1 Bivariate analysis

Bivariate plots of the measurements most commonly used in ratios and applied to the differentiation of species of *Ichthyosaurus* are plotted in figures 2-5. Multiple bivariate analyses were created, but the four most informative plots or ones that shoed the most species separation are presented here. Specimens referred to '*I. intermedius*' are plotted as a distinct species, but, as noted above, it should be noted that this species is generally considered synonymous with *I. communis* (McGowan and Motani, 2003; Massare and Lomax, 2017) and is included here only for the sake of comparison. The first three plots (figures 2-4) represent ratios that all deal with bones in the snout of the ichthyosaur.

In Figure 2, the Snout Ratio (SR) compares the snout length (anterior orbit to the tip of the snout) to the lower jaw length (posterior most part of the surangular to the anterior most tip of the dentary). The SR is not clearly separated among species within *Ichthyosaurus,* with the possible exception of *I. breviceps*. The OLS regressions have similar slopes, although the data for *I. communis* have considerable scatter. Considerable overlap can be seen on the inset in Figure 2b, which shows the values of the ratio for each species. *I. breviceps* is the only species that shows some separation in both parts of the figure. This separation is due to the species' characteristic short snout and consequently low SR values. All but one of the *I. breviceps* specimens included in this analysis fall below the 0.57 SR threshold proposed for this species by McGowan (1974). Note however, that two specimens of *I. communis* (SR = 0.45 and 0.51) and one *I. conybeari* (SR = 0.50) actually have SR values that are lower than the lowest value recorded for *I. breviceps* (0.52). Furthermore, one additional *I. conybeari* specimen and one *I. somersetensis* specimen fall below the 0.57 SR threshold. *I. communis* has the largest scatter of points, likely due to the large number of specimens assigned to the species.

The Premaxillary Ratio bivariate plot (Figure 3a) compares the length of the premaxillary bone to the lower jaw. The inset plot (Figure 3b)shows overlap of the ratio ranges of species from *Ichthyosaurus*. The OLS regression lines have more varying slopes than in Figure 2a. The slopes of the plots for *I. breviceps*, *I. anningae*, and *I. sommersetensis* are less steep than the other species. The slope of *I. breviceps* is the least steep due to the short snout possessed by the species. The OLS regression line slope is steeper for *I. conybeari* than in other species. With smaller snouts for smaller specimens and longer snouts for larger specimens, there may be evidence for positive allometry in this taxon, but more analysis would have to be done on the species to demonstrate this definitively, as allometry is not supported by all plots presented. Potential separation of some species using the Premaxillary Ratio is suggested in the whisker-and-box plot inset (Figure 3b), but extensive overlap with the highly variable values observed in *I. communis* outweighs any clear taxonomic signal in this ratio.

The Prenarial Ratio bivariate plot (Figure 4a) compares the prenarial segment of the snout (anterior of external naris to tip of the snout) to the lower jaw length. This plot shows overlap similar to Figure 2a, with slight separation of *I. breviceps* in the inset box-and-whisker plot (Figure 4b). The OLS regressions have varying slopes, similar to those seen in Figure 3a. The slopes of *I. anningae* and *I. conybeari* are the most dissimilar to other species. The slope for *I. conybeari* is also steepest in this plot, again indicating that there may be positive allometry in the snout for this species. The slope of *I. anningae* is based on only two specimens, which may well skew the results, but plots very closely with *I. communis*. As the original description of *I. anningae* focuses mainly on postcranial differences, this is to be expected. *I. communis* has the largest scatter of points, but is also the species with the most numerous specimens.

The Orbital Ratio bivariate plot (Figure 5a) compares the orbit diameter to the lower jaw length. The inset box-and-whisker plot shows (Figure 5b) the least amount of overlap of all box-and-whisker plots due to the smaller ranges of the ratios for each species, but there is still no clear separation of species, with the possible exception of *I. breviceps*. The OLS regressions have varying slopes, with *I. breviceps* showing a negative slope, but this is strongly influenced by an outlier specimen with an exceptionally large orbit.

3.3.2 Multivariate analysis

The first analysis was a PCoA in which the raw data was used and not transformed in any way (Figures 6). In the PCoA, the first axis accounts for 38.3% of the variation seen (Figure 6), and in the log PCoA (Figure 8) the first axis accounts for 45.5% of the variation seen. The first axis explains the variation of body size. The second axis only accounts for 7.1% of the variation for the non-transformed (figures 6 and 7) and 4.9% of the log- transformed analyses (figures 8 and 9).

The third axis accounts for 6.2% of the variation for the non-transformed (Figure 7) and 3.6% of the log- transformed analyses (Figure 9). Large overlaps in the morphospace of species are seen in all PCoA plots of (figures 6-9). In the PCoA and log PCoA plots most of the ranges fall within the morphospace of *I. communis*.

In the non-transformed PCoA plots (figures 6 and 7) show no clear separation of species. In Figure 6 there is a large amount of overlap of the morphospace where most ranges fall within the range of *I. communis*. In both PCA plots there are a few specimens that plot away from the other specimen and the species; these will be referred to as outliers. The outliers are labelled with their museum specimen number, especially those that fall far outside the zone of overlapping morphospace. Most specimens identified as outliers in one plot are also outliers in all plots, although specimens ACG 9 and ACG 14 are only present as outliers in Figure 6, whereas specimens CAMSM J69477, NMING F8745, NMING F8746, NMING F8747 and OUMNH J.29352 are present as outliers only in Figure 7.

The log PCoA plots (figures 5 and 6) delineate slightly different morphospaces for each species when compared to figures 6 and 7, but no clear separation of species is seen. As in the non-transformed plots, most species tend to overlap the morphospace of *I. communis* with a few outliers that extend the morphospace beyond this range, especially specimens of *I. sommersetensis* in Figure 8. Most outlier specimens are seen in each log-transformed plot, although specimens ACG 8, IPSMG 1800-1, NHMUK BGS956, and NHMUK PV OR38523 (holotype) are present as outliers in Figure 5 only, and specimens ACG 15, NHMUK PV OR120, OUMNH J2983B, and TTNCM 16/2015 are only outliers in Figure 9. These results indicate that the measurements used for these analyses do not serve to separate species within this genus.

Two figures of the NMDS analysis are presented, one using Euclidean similarity index (Figure 10), and one using the Gower similarity index (Figure 11). In both plots the axes presented are the second and third. No significant separation of the species’ morphospaces is present in these analyses. Even when examining the NMDS plot, ignoring the assigned species symbols and colours, it is hard to resolve any separation of groups for newly defined species. There are outliers present in both plots and many of them are the same in each of the NMDS plots, although specimens NHMUK BGS956, OUMNH 10301, LEICT G123.1992, and PMO 227578 are only outliers in the NMDS Euclidean plot, and specimens DORCM G.10741, NMING F8770, NMING F8751, and ACG 16 are only outliers in the NMDS Gower plot. Overlap of all species' morphospaces is seen in both plots, the only difference is slight shifts in morphospace between both plots and some outlier specimens.

The cluster analysis using K-means can be seen in Table 5. This analysis was run using 6 clusters to represent the six known species (*I. intermedius* is not considered a valid species, but labelled as such for interpretation), to determine if they group together. This analysis was run four times as there is not a single output for this method. In general, all six clusters contain a combination of multiple species in most of these runs, which is highlighted in the results for the species *I. conybeari*. In contrast there are a few promising results, which include as *I. breviceps* being grouped together in Run3, and some subsets of *I. sommersetensis* being identified together in several of the runs. There is also a group of *I. communis* (and one *I. intermedius* specimen) that group together in all four runs. This group consists of specimens AGC 9, BRSLI M3562, DORCM G.00001, IPSMG 1880-1, LEICT G125.1992, PETMG R174, TTNCM 5804 and NMING F8763, although there are also 2 specimens of *I. sommersetensis* that group with them, AGC 15 and BRSMG Cc921, and one specimen of *I.* sp, (LEICT G126.1992). There are three potential factors that could be causing this to happen. Firstly, size is over represented in these results, meaning that the size of the specimens is the main factor of separation, but is most likely due to differences in ontogenetic stage of the specimens. The measurements analysed do not fully represent the morphological differences seen in these species or there are more or less species or groups in this set of data. This result provides further evidence that the measurements used in the 'traditional' ratios do not clearly delineate species in the ways that have previously been reported.

For the LDA, all specimens of *I. intermedius* are considered synonymous with *I. communis,* but shown as *I. intermedius* for comparison purposes. The LDA confusion matrix shows that the classification percentage is 83.67% with the subset of specimens used. When these results are jackknifed the classification goes down to 53.06%. The drop in the classification percentage is due to some of the species consisting of a small number of specimens, and is thus to be expected. The scatter plot is shown in Figure 12, but no morphospace is shown for the species *I. anningae*, as only two specimens were able to be used in this analysis. This plot shows separation of *I. conybeari* and *I. breviceps* from all other species. The two newest species, *I. sommersetensis* and *I. larkini,* also show more separation than in other plots, and the overlap seen is only caused by six specimens. As *I. anningae* was only represented by two specimens, the fact that one specimen does fall in the morphospace of *I. communis*, means that there would be some overlap in this plot.

In Figure 13, Axis 1 is the overall size, and Axis 2 is relative size of the skull, the same plot as Figure 12, but with the different measurements used for the analysis imposed on the plot. This plot also allows some generalizations to be made about each species, such as *I. breviceps* having short skulls, *I. anningae* is a shorter species overall but with a larger skull, and that the specimens originally labeled *I. intermedius* tend to plot at the larger end of the body size of *I. communis* and also have a relatively small skull size. This further indicates that the synonymisation of *I. intermedius* and I. *communis* is valid.

3.4 DISCUSSION/CONCLUSIONS

Ratios of linear measurements have been used in various ichthyosaur studies since McGowan's (1974) paper, and have since been used to help normalize the size variations seen in individuals of each species. These ratios have been used to delimit various taxonomic groups at specific and generic level, and use of feeding guilds (Buchy, 2010 and Massare, 1987). Our study of 70 specimens utilising up to 56 individual measurements of single specimens has permitted us to re-evaluate the validity of the linear measurements used in these ratios on a larger scale than ever before for the genus *Ichthyosaurus*. Based on our results shown in the four bivariate plots (figures 2-5), the extensive overlap of the ranges of the ratios and the lack of clear separation of the OLS regression lines, neither these measurements nor ratios appear to produce clear, statistically valid separations of the majority of species within the genus *Ichthyosaurus*. There is also a high degree of variability seen across *I. communis* and *I. intermedius,* and due to the large amount of overlap in these data ranges there is every indication the proposed synonymisation of these taxa is valid (McGowan and Motani, 2003 and Massare and Lomax, 2017). Interestingly, of these latter specimens, most of the larger specimens have previously been assigned to *I. intermedius*, which may suggest that these two originally distinct taxa might actually represent sexual dimorphs within a single species.

The species *I. breviceps* tends to separate more distinctly or has a greater difference in slope in the bivariate and box-and-whisker plots. This lends support for this taxon being a distinct species and one of the few which can be separated by the use of ratio measurements. However, in contrast, *I. conybeari* exhibits high intraspecific variation, especially for the small number of specimens analysed in this study. *I. conybeari* also largely overlaps with the ranges of *I. communis*, suggesting that the former species is not readily separated using these types of measurements, and is better separated using other morphological characteristics. The more recently described species of *I. anningae*, *I. sommersetensis* and *I. larkini* show some separation from *I. communis*, but this is minimal for *I. anningae*. *I. sommersetensis* and *I. larkini* are known from larger specimens that show modest separation from I. communis, but their morphospaces largely overlap with each other. However, these three species are mainly distinguished by morphological characteristics of the forefin, and most of the measurements evaluated here are based on the skull, so in this context the result is not unexpected

In the four PCoA plots we can demonstrate no clear separation of the species' morphospaces, and overlap is seen in all plots. Some outliers separate some species slightly in each plot, but there are no specimens present in these large areas of offset. The extensive overlap of morphospaces and lack of clearly definition of separate species using the measurements utilised by previous authors might be taken as a clear indication that *Ichthyosaurus* as a whole might be a wastebasket taxon. However, this is contradicted by the fact that all six species possess distinct, discrete morphological differences that are not based on the measurements discussed here. In our analyses, most of the morphospace ranges of all species of *Ichthyosaurus* fall within the range of *I. communis*. This could mean that either *I. communis* exhibits a large amount of variation, perhaps due to the comparatively large number of specimens referred, or that more species are present within the genus than are currently recognized.

Both NMDS analysis and cluster analyses further confirm these overlapping morphospaces, save for one or two outliers in some species. The cluster analysis shows that the multiple runs, species as currently defined do not group together, and the same specimens do not always group together either. This indicates that there might be considerable individual variation within these species that may be causing these results or that multiple specimens are allocated to the wrong species. The LDA analyses are the only ones to clearly demonstrate a separation of species within the genus, but only for *I. conybeari* and *I. breviceps*. This is likely to be the result of the reduced dataset for these species, which eliminated several measurement characters that have been found to vary considerably in individual specimens of other species.

Another factor that could be added into these analyses is the use of time or anagenesis. Due to the use of individual specimens in these analyses, and the limited/lack of age or age range data for many of these historical specimens it would be difficult accomplish. Initial studies (see Chapter 1 of this volume) were conducted on the palynomorphs of some sediment associated with specimens. No diagnostic palynomorphs were found to distinguish beyond parts of the Lower Lias. At best, local data may be able to be determined with a more detailed study. Therefore utilising time as a way of separating out specimen and seeing how forms may have changed overtime was not considered, but could be in the future if other ways of more accurately identifying time ranges for historic specimens was discovered.

Whilst effort has been taken to minimize all possible biases in our analyses, bias cannot be entirely avoided. Data was log transformed in most of our analyses to minimise the bias induced by the variation seen in the total length of specimens. In addition, when examining the two PCoA plots produced with the two different datasets of 56 and 70 specimens, there are differences seen that may be minimizing the size bias. The other significant bias concerns the identification of specimens: a much larger number of specimens have previously been referred to *I. communis* than to the other species of *Ichthyosaurus*, potentially meaning that *I. communis* is either more common or that there are more species within the genus than are currently recognised. As mentioned previously, there has recently been an increase in the number of morphological characters which authors have used to define species within the genus *Ichthyosaurus,* and most recently also a review of the characters used to define *I. conybeari* (Massare and Lomax, 2016). More specimens of the five other species are needed to determine the true morphospace extent of these species. At this time, ratios of linear measurements that can distinguish the named *Ichthyosaurus* species in a statistically significant way have yet to be identified.

These results will be sensitive to the inclusion of an even greater number of specimens. Furthermore, if named species were better defined, or if additional species were found to be present in this genus, improved separation concerning the historical measurements of ratios might hypothetically occur. Though, in some analyses like the LDA, more specimens lowered the classification percentage. A possible solution to the use of ratio characters in phylogenetic analyses is to use continuous characters, and to utilise phylogenetic programs such as T.N.T. (Goloboff *et al*., 2008) to determine where the gaps in measurements or ratios typically used to separate species or genera, should be placed. Other ratios of linear measurements may be proven to achieve better discrimination of taxa in the future, and measurement ratios for *Ichthyosaurus* could also be compared to other closely related genera to determine if such parameters can be used constructively at the generic level (e.g., Lower Jurassic genera including *Leptonectes* and *Temnodontosaurus*).

In short, our understanding of how the linear measurements used in ratios might be applicable to the separation of ichthyosaur taxa is still at an early stage. Analyses like that of Massare and Lomax (2016) should be made of each species within *Ichthyosaurus,* and a more robust phylogenetic study of all of the species of *Ichthyosaurus* is currently being undertaken by the first author.

3.5 CHAPTER ACKNOWLEDGMENTS

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CAPTIONS

Figure 1. Diagrammatic representation of the measurements listed in Table 3. Numbers correspond to the ones in Table 3. a. is based on NHMUK PV R1162, b. is based on NHMUK PV OR39263, c. is based on NHMUK PV R224, d. is based on NHMUK PV R288, e. is based on NHMUK PV R1061, and f. is based on NHMUK PV OR85791. Scale bar in a. is 58.46 mm and all other bars are 50 mm.

Figure 2. Bivariate plot (a) of the Snout Ratio of *Ichthyosaurus* species with an inset box-and-whisker plot (b)of the range of the ratio values for each species to highlight the overlap in value. Ordinary Least Squares (OLS) lines are present and represent the maximum likelihood of each ratio value for the species.

Figure 3. Bivariate plot (a) of the Premaxillary Ratio of *Ichthyosaurus* species with an inset box-and-whisker plot (b)of the range of the ratio values for each species to highlight the overlap in value. Ordinary Least Squares (OLS) lines are present and represent the maximum likelihood of each ratio value for the species.

Figure 4. Bivariate plot (a) of the Prenarial Ratio of *Ichthyosaurus* species with an inset box-and-whisker plot (b) of the range of the ratio values for each species to highlight the overlap in value. Ordinary Least Squares (OLS) lines are present and represent the maximum likelihood of each ratio value for the species.

Figure 5. Bivariate plot (a) of the Orbit Ratio of *Ichthyosaurus* species with an inset box-and-whisker plot (b) of the range of the ratio values for each species to highlight the overlap in value. Ordinary Least Squares (OLS) lines are present and represent the maximum likelihood of each ratio value for the species.

Figure 6. Principal Cordinates Analysis (PCoA) plots of the linear measurements of specimens from the genus *Ichthyosaurus*, showing coordinates one and two. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple

asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Figure 7. Principal Cordinates Analysis (PCoA) plots of the linear measurements of specimens from the genus *Ichthyosaurus* showing coordinates 1 and 3. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Figure 8. Principal Cordinates Analysis (PCoA) plot of the log transformed measurement data of specimens from the genus *Ichthyosaurus*, showing coordinates one and two. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Figure 9. Principal Cordinates Analysis (PCoA) plot of the log transformed measurement data of specimens from the genus *Ichthyosaurus*, showing coordinates one and three. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Figure 10. Non-metric Multidimensional scaling (NMDS) analysis of specimens from the genus *Ichthyosaurus* using Euclidean similarity index. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Figure 11. Non-metric Multidimensional scaling (NMDS) analysis of specimens from the genus *Ichthyosaurus* using Gower similarity index. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Figure 12. Linear Discriminant Analysis (LDA) of specimens from the genus *Ichthyosaurus*. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Figure 13. Linear Discriminant Analysis (LDA) of specimens from the genus *Ichthyosaurus* with measurements imposed on the plot. Blue diamonds represent *I. communis*, red squares represent *I. intermedius*, green triangles represent *I. breviceps*, purple asterisks represent *I. conybeari*, yellow dots represent *I. anningae*, light salmon crosses represent *I. sommersetensis*, orange open circles represent *I. larkini*, and grey diamonds represent *Ichthyosaurus* sp.

Table 1. Measurement ratios and definitions that have been used historically for specific or generic separation purposes. The other 66 measurements can be seen in Table 3 and Figure1.

Table 2. Ratio ranges reported by other authors (McGowan, 1974; McGowan and Motani, 2003; and Massare and Lomax, 2015), and those observed in the over 300 specimens analysed for species of *Ichthyosaurus*.

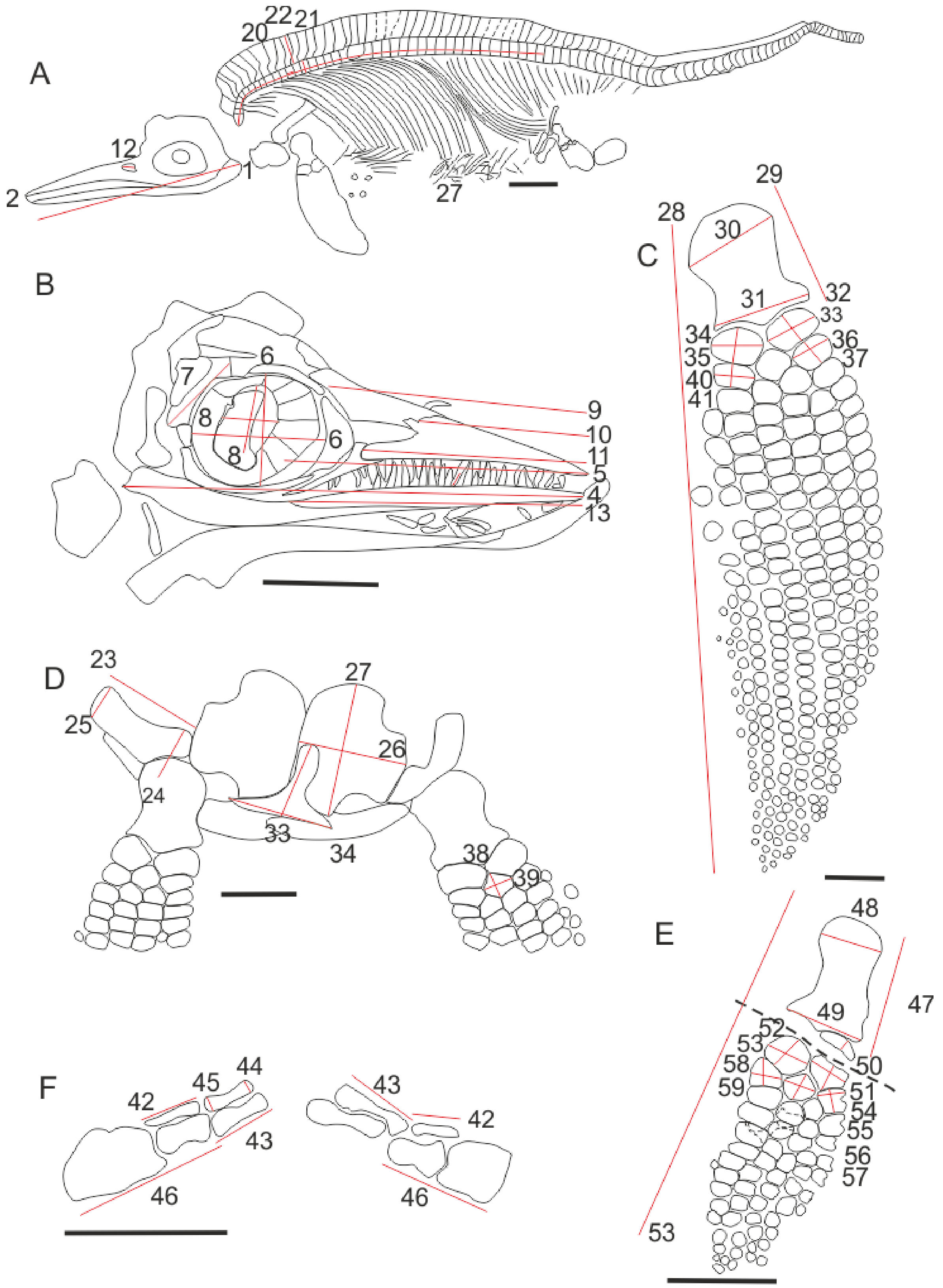
Table 3. The measurements utilised in this study. The numbers with an asterisk by it are the measurements used in the second data subset.

Table 4. Juvenile specimens identified and removed from this study, with the criteria on which the designation to juvenile was made.

Table 5. Clustering results using K-means on the larger subset of specimens. Four runs are shown here, with an input for six clusters to represent the six known species of *Ichthyosaurus*. The groups in each run is represented by color; yellow- group 1, orange- group 2, blue- group 3, group 4- light green, group 5-red, and group 6 is dark green.

FIGURES

Figure 1.



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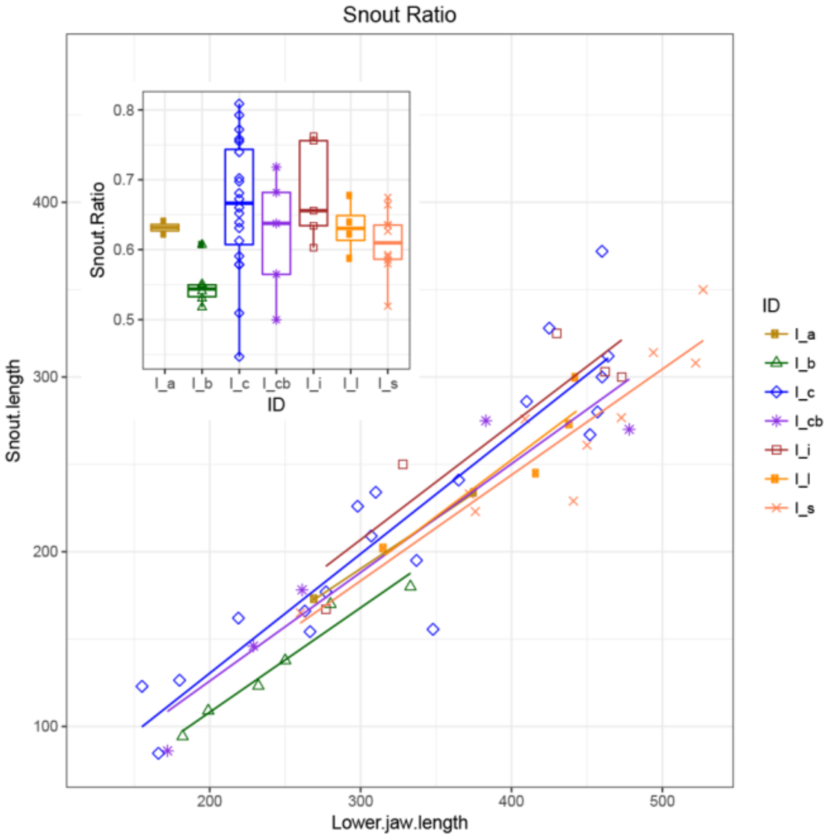

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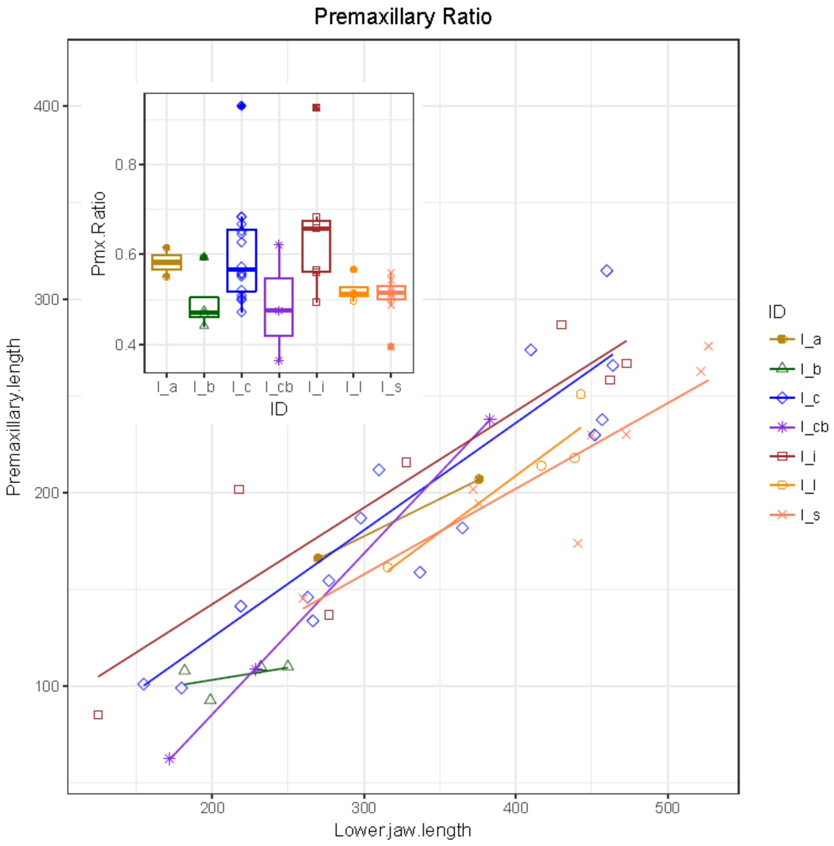

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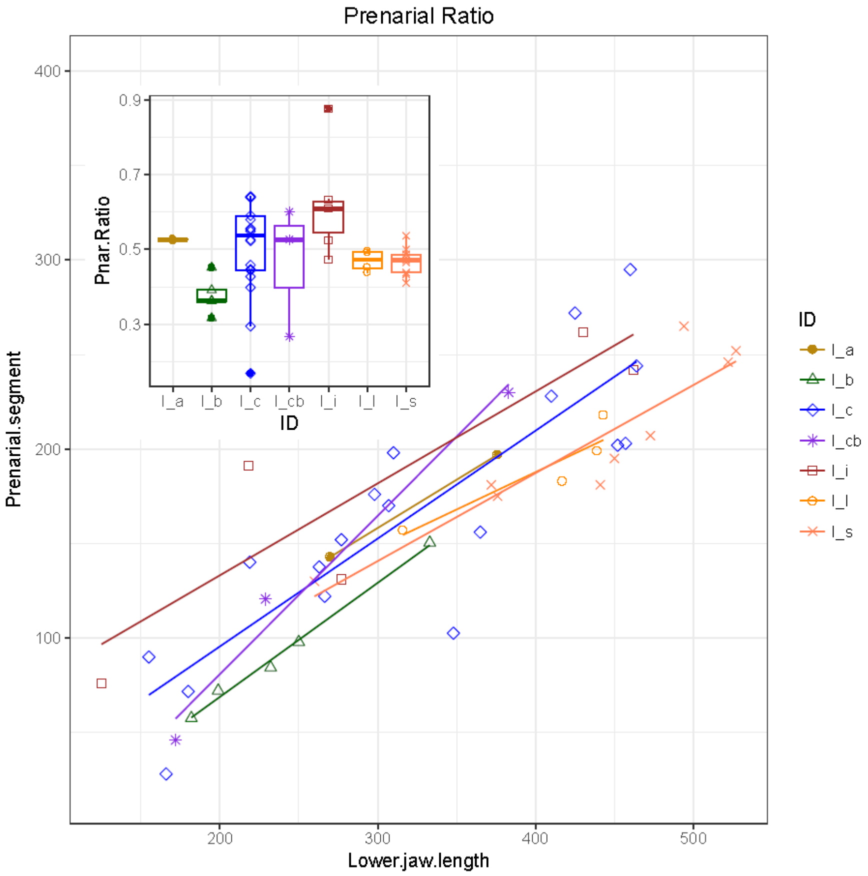

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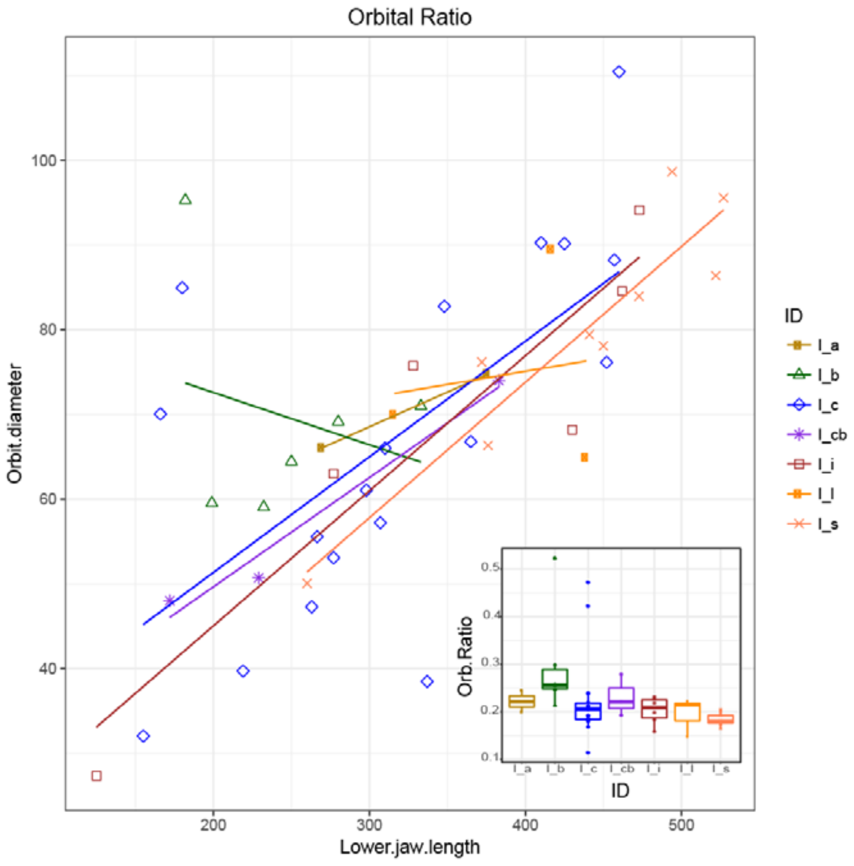

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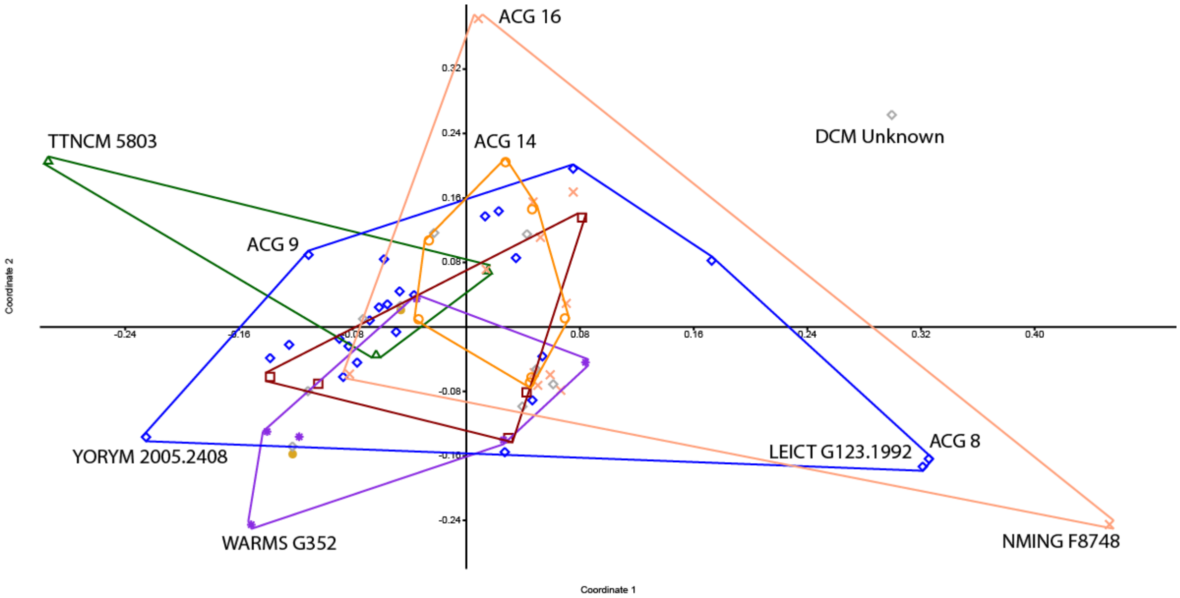

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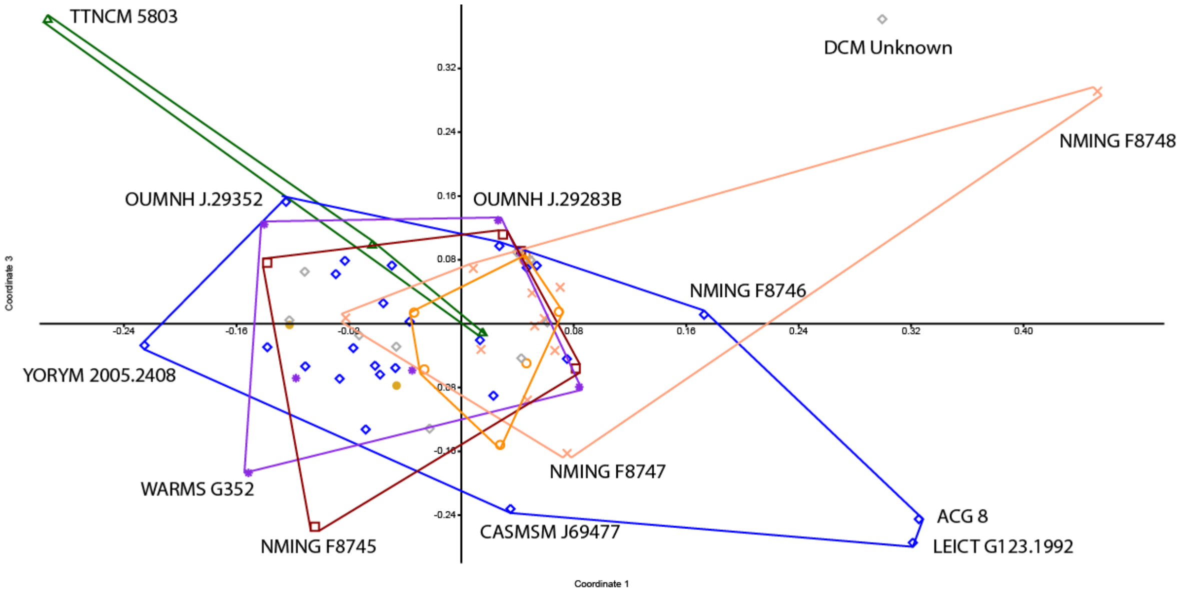

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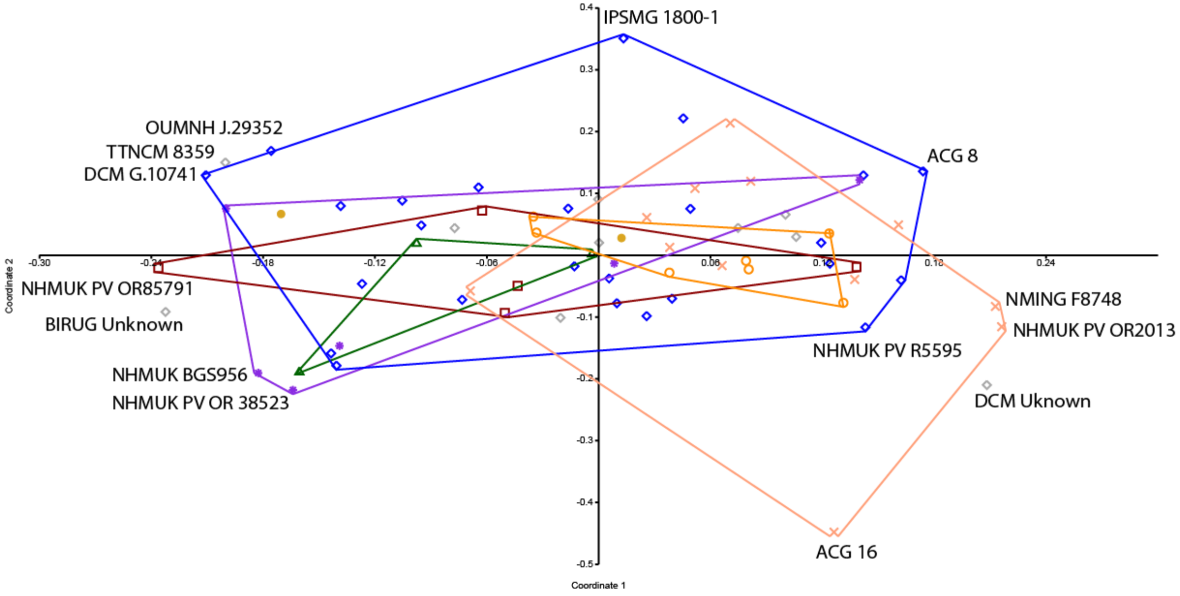

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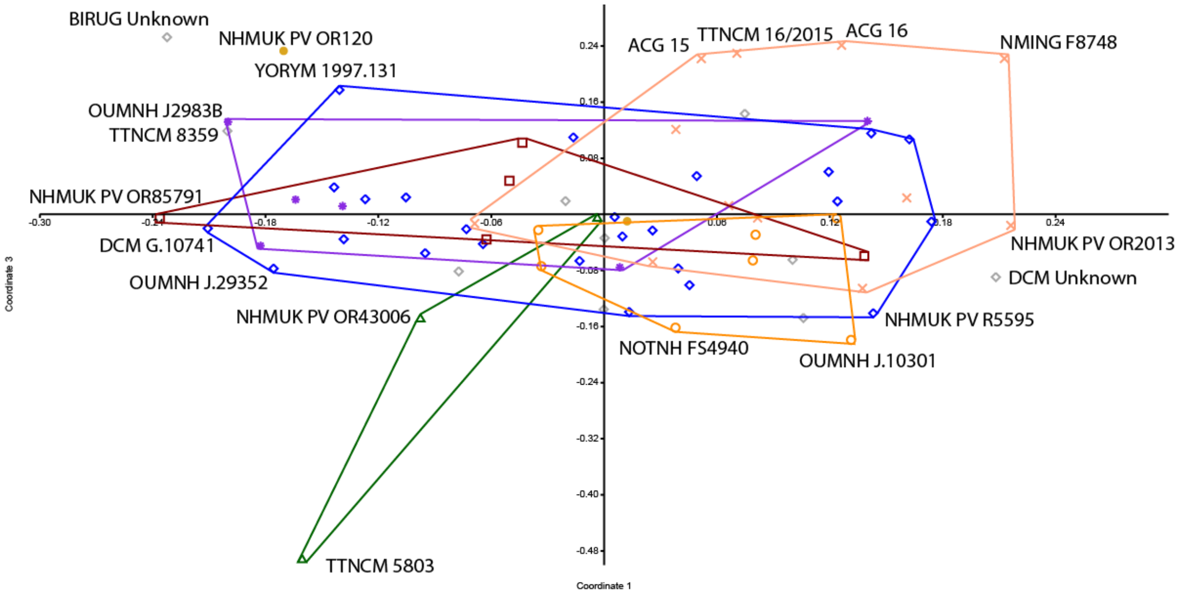

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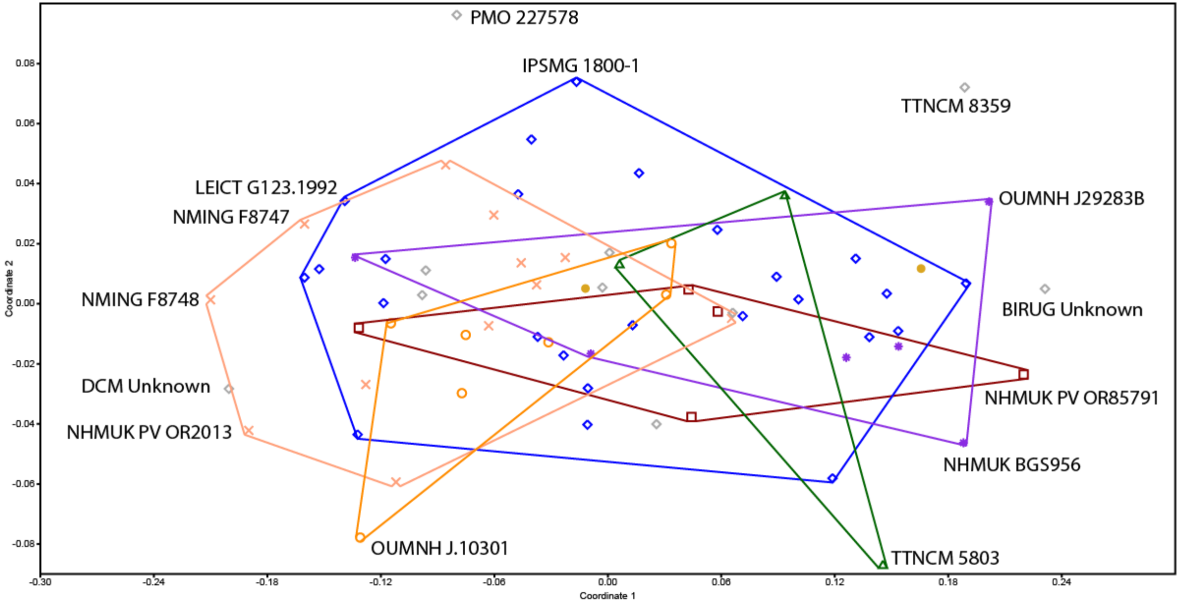
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DCM Unknown
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NHMUK PV OR2013
NHMUK BGS956
OUMNH J.10301
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0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
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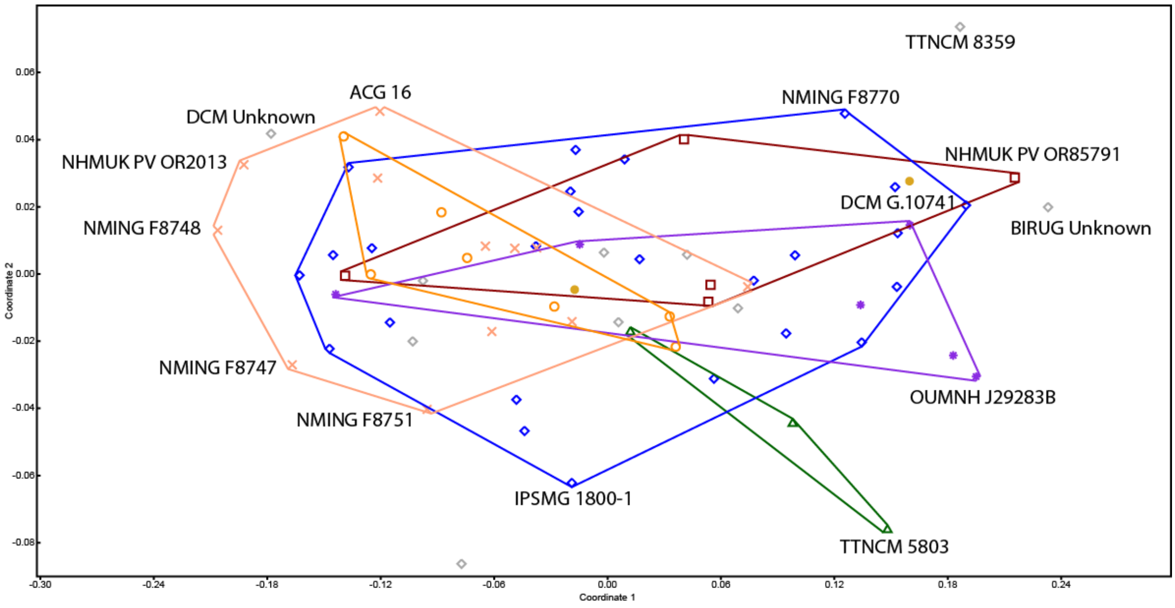
Coordinate 1

Figure 11.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OUMNH J29283B
NMING F8751
IPSMG 1800-1
TTNCM 5803
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
Coordinate 2
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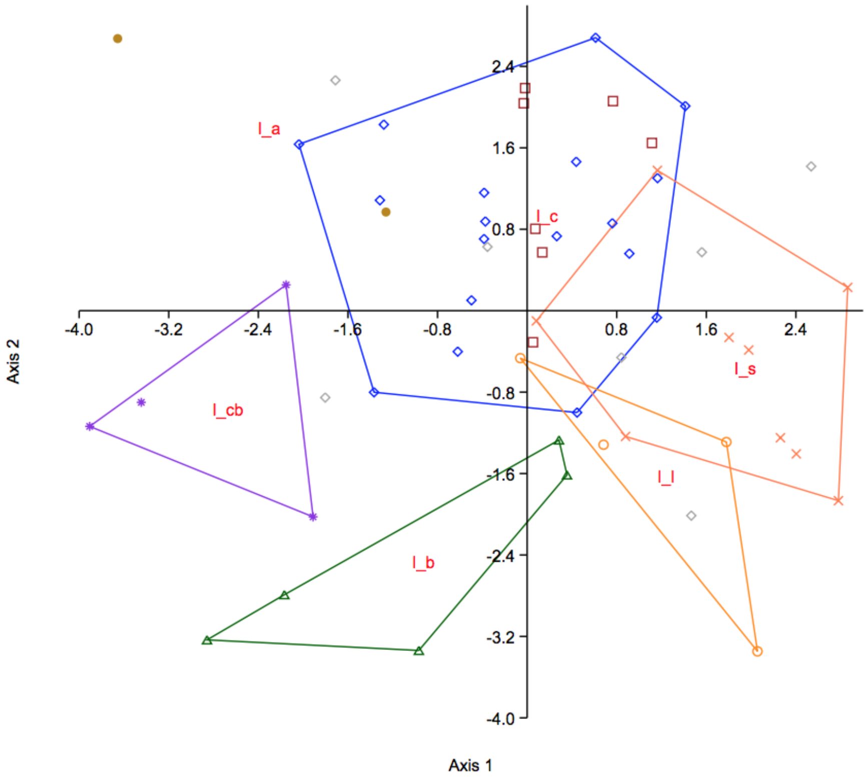
Coordinate 1


l_a
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Axis 2
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0.8
1.6
2.4
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0.8
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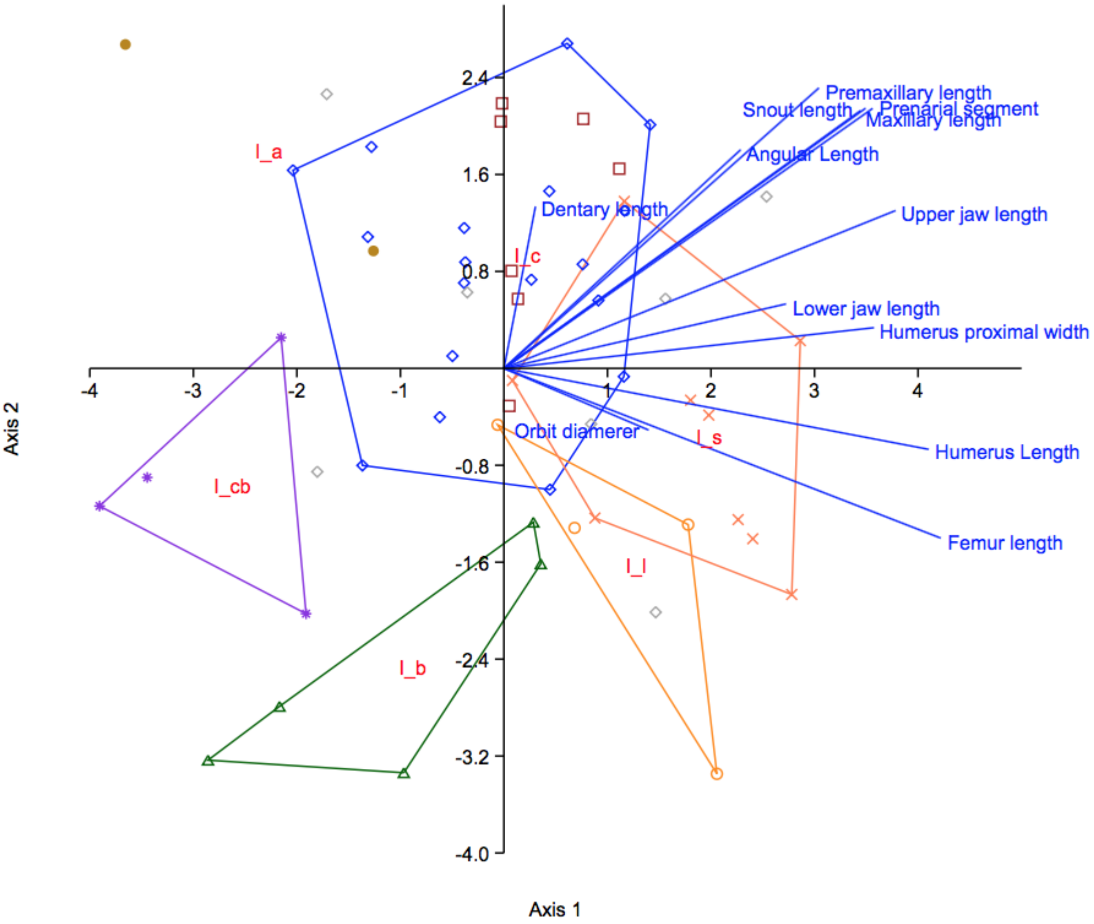
-4.0

Figure 12.

Figure 13.


l_a
l_c
l_cb
l_b
l_l
l_s
Premaxillary length
Snout length
Prenarial segment
Maxillary length
Angular Length
Dentary length
Upper jaw length
Lower jaw length
Humerus proximal width
Humerus Length
Femur length
Orbit diamerer
2.4
1.6
0.8
-0.8
-1.6
-2.4
-3.2
-4.0
-4
-3
-2
-1
1
2
3
4
Axis 1
Axis 2

TABLES

Table 1.

Ratio	**Definition**	**Originator(s)**
Snout Ratio	Snout length/jaw length	McGowan , 1974 and 1976
Premaxillary Ratio	Premaxillary length/jaw length	McGowan, 1974 and 1976
Prenarial Ratio	Prenarial length/jaw length	McGowan, 1974 and 1976
Orbital Ratio	Orbital diameter/ jaw length	McGowan, 1974 and 1976
Relative Tooth Size	Height of tooth crown/skull width	Massare, 1987
Relative Tooth Size	=10x largest crown height/ basioccipital width	McGowan and Motani, 2003; Fischer et al., 2014
Ratio Sclerotic Aperture	Internal diameter of sclerotic ring to diameter of orbit	Fernandez et al., 2005

Table 2.

Ratios	*Ichthyosaurus communis*	*Ichthyosaurus intermedius*	*Ichthyosaurus breviceps*	*Ichthyosaurus conybeari*	*Ichthyosaurus anningae*
Snout Ratio Reported	> 0.57	--	< 0.57	> 0.57	0.60- 0.65
Snout Ratio Observed	0.45-0.79	0.43-0.76	0.52-0.61	0.68	0.59-0.64
Premaxillary Ratio Observed	0.39-0.93	0.30-0.93	0.47-0.69	0.66	0.52-0.61
Orbital Ratio Reported	< 0.26	--	≥ 0.26	< 0.28	--
Orbital Ratio Observed	0.15-0.47	0.16-0.26	0.21-0.52	--	0.18-0.24
Relative Tooth Size Observed	0.04-0.11	0.03-0.15	0.11	0.06	--
Relative Tooth Size x10 Observed	1.33-3.29	1.86-5.20	1.82-2.52	--	--
Ratio ‘Orbit’ Observed	1.39-2.11	1.80-1.99	1.70-1.77	--	1.82
Skull vs Total Length Observed	0.16-0.70	0.18-0.3	0.18-0.72	0.29-0.47	0.29-0.42
Forefin vs Body Length Observed	0.03-0.41	0.07-0.24	0.05-0.16	0.12-0.32	0.15-0.21
Hindfin vs. Body Length Observed	0.04-0.17	0.06-0.08	0.06-0.07	0.07	0.05
Humerus vs. Femur length Observed	0.35-1.14	0.67-0.98	0.55-1.18	0.63-0.73	0.56-0.58
Forefin vs. Hindffin Length Observed	0.31-3.01	1.60-2.54	0.90-2.18	1.68	3.14

Table 3.

Number	Measurement description	Number	Measurement description
1	Post cranial to pelvic girldle	31	Humerus distal width
2	Skull length	32	Radius length
3	Skull width	33	Radius width
4*	Lower jaw length	34	Ulna length
5*	Upper jaw length	35	Ulna width
6*	Orbit diameter	36	Radiale length
7	Postorbital length	37	Radiale width
8	Sclerotic ring internal diameter	38	Intermedium length
9*	Snout length	39	Intermedium width
10*	Prenarial segment	40	Ulnare length
11*	Premaxillary length	41	Ulnare width
12	External naris length	42	Illium length
13*	Dentary length	43	Ischiopubis length
14*	Maxillary length	44	Pubis medial width
15	Upper temporal fenestrae width	45	Pubis distal width
16	Upper temporal fenestrae length	46	Hindfin length
17	Parietal table length	47*	Femur length
18*	Angular length	48	Femur proximal width
19	Basioccipital width	49	Femur distal width
20	Vertebral width average	50	Tibia length
21	Vertebral length average	51	Tibia width
22	Neural spine height average	52	Fibula length
23	Scapula length	53	Fibula width
24	Scapula medial width	54	Distal tarsis II length
25	Scapula distal width	55	Distal tarsis II width
26	Coracoid height	56	Astragalus length
27	Coracoid width	57	Astragalus width
28	Forefin length	58	Calcaneum length
29*	Humerus length	59	Calcaneum width
30*	Humerus proximal width		

Table 4.

Specimen	Criterion
BU 5289	Small size, large orbit, bones not fully formed (humerus)
BIRUG Unknown	Small size, large sclerotic ring in orbit
BRSLI M644	Small size
BRSLI M653	Small size
BRSMG Ce16611b	Small, large orbit, bones not fully formed (humerus), embryonic
BRSMG Ce17660	Small size, large sclerotic ring in orbit
CAMSM J35187	Small size, large orbit
CAMSM J.46928	Small size, large orbit and sclerotic ring
CAMSM TN910	Small size, large orbit, bones not fully formed (coracoids)
CAMSM Paddle Display	Bones not fully formed (humerus)
GLAHM 132312	Small size, large orbit, bones not fully formed (humerus)
NHMUK PV OR33595	Small size, large orbit
NHMUK PV OR36256	Small size, bones not fully formed (humerus, maybe coracoids)
NMING F8750	Small size, large orbit, not fully formed bones (humerus)
NMING F8755	Small size
NMING F8766	Small size, not fully formed bones (humerus)
NMS 1866.13.2	Small size
MANCH LL.8000	Small size,
MANCH L9556	Small size, large orbit
OUMNH J.13810	Small size, not fully formed bones (humerus and coracoid)
OUMNH J.13592	Small size
OUMNH J.10303	Small size, not fully formed bones (coracoids)
OUMNH J.10325	Small size
OUMNH J.10363	Small size, not fully formed bones (humerus and coracoid)
RAMM 57/2009	Small size, large orbit
TTNCM 14/2015	Small size, large orbit
TTNCM 8349	Small, large orbit, bones not fully formed (coracoids and humerus)
TTNCM 100/2001/945	Small size, large orbit
YORYM 2011.751	Small size, not fully formed bones (humerus and coracoids)

Table 5.

		K-means Cluster			
Specimen	**Sp.**	**Run 1**	**Run 2**	**Run 3**	**Run 4**
DONMG 1983.8	**I_a**	6	6	5	3

NHMUK PV OR120	I_a	4	3	1	4
GLAHM V1179	I_b	6	2	2	3
NHMUK PV OR43006	I_b	4	2	2	4
TTNCM 5803	I_b	4	1	2	5
CAMSMX.50187	I_b	4	2	2	6
ACG 8	I_c	5	6	5	1
LEICT G123.1992	I_c	5	6	5	1
NMING F8746	I_c	2	6	6	1
ACG 7	I_c	6	2	5	3
NMING F8767	I_c	6	2	5	3
ACG 9	I_c	6	6	5	3
BRSLI M3562	I_c	6	6	5	3
DCM G.00001	I_c	6	6	5	3
IM 1880-1	I_c	6	6	5	3
LEICT G125.1992	I_c	6	6	5	3
PETMG:R174	I_c	6	6	5	3
TTNCM 5804	I_c	6	6	5	3
NHMUK PV OR36256	I_c	1	3	1	4
DCM G.10741	I_c	3	3	1	4
OUM J.29352	I_c	3	3	1	4
NHMUK PV OR85791	I_c	4	3	1	4
NHMUK PV R1162	I_c	4	3	2	4
NMING F8770	I_c	4	3	2	4
TTNCM 116/1992	I_c	4	3	2	4
TTNCM 120/1996	I_c	4	3	2	4
YORYM 2005.2408	I_c	4	2	2	5
BRSLI M653	I_c	4	1	4	5
CAMSM J35183	I_c	4	2	2	6
MANCH LL11835	I_cb	5	6	5	1
NHMUK PV OR38523	I_cb	4	3	2	4
OUM J.29283 B	I_cb	3	3	1	5
NHMUK PV BGS956	I_cb	1	3	3	5
WARMS G352	I_cb	4	5	4	5
CAMSM J.35186	I_cb	6	2	5	6
NMING F8772	i_i	2	6	6	1
NMING 8757	i_i	6	2	2	3

NMING F8745	i_i	6	2	2	3
NMING F8753	i_i	6	2	5	3
NMING F8763	i_i	6	6	5	3
NMING F8750	i_i	4	2	4	5
OUM J.10301	l_l	2	6	5	1
ACG 14	l_l	2	6	6	1
CAMSM 5975	l_l	2	4	5	2
ACG 11	l_l	6	2	2	3
CAMSM 59642	l_l	6	2	2	3
NOTNH FS4940	l_l	6	6	5	3
TTNCM 8373	l_l	2	6	5	6
ACG 12	l_s	2	6	5	1
ACG 16	l_s	2	6	6	1
NMING F8751	l_s	2	6	6	1
NMING F8747	l_s	2	6	6	1
ACG 17	l_s	5	6	6	1
NMING F8748	l_s	5	6	6	1
BRSMG Cb3578	l_s	4	2	2	3
ACG 15	l_s	6	6	5	3
BRSMG Cc921	l_s	6	6	5	3
CAMSM J69477	?	2	6	5	1
CAMSM 59644	?	2	6	5	1
NMING F8774	?	2	6	6	1
PMO 227578	?	6	4	5	2
CAMSM J35189	?	4	2	2	3
IM (FNB#8)	?	6	2	5	3
LEICT G126.1992	?	6	6	5	3
RAMM 57/2009	?	4	3	1	4
TTNCM 8359	?	4	3	1	4
OUM J.13592	?	4	3	2	4
OUM J.13810	?	1	5	1	5
OUM J.10363	?	3	5	1	5
YORYM 1997.131	?	4	3	2	5

1

Chapter 4.

A specimen-level phylogenetic study of *Ichthyosaurus* with a critical consideration of phylogenetic characters

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TITLE

A specimen-level phylogenetic study of *Ichthyosaurus* with and in-depth analysis of phylogenetic characters

Authors

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Darren Naish,

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Author Contributions:

Lawrence Wujek did the data collection, analyses and paper writing

Naish assisted in wording of characters, especially helping with correct anatomical terms and character states, interpretation of results, and writing of paper

Harding assisted with the writing of the paper and interpretation of results

Names mentioned in acknowledgments gave useful advice and edits for this paper

Abstract. The well- known and morphologically variable *Ichthyosaurus*, best known from the Jurassic sediments of southern England, is studied here in four specimen-based phylogenetic analyses. With a large number of specimens from the Lower Jurassic present in England, it is possible to do a specimen based analyses more likely to encompass the true diversity of each species. 99 characters for this study have been compiled and examined to ensure the most pertinent and complete collection of characters was utilised. These analyses demonstrate that the genus encompasses a wide range of morphological variability and there is no clear morphological separation of individual species, even in light of the recent description of two new morphologically well-defined species and one newly defined genus. This may be result of individual variability or the limits of the analyses.

4.1 Introduction. Ichthyosaurs are among the best known of Mesozoic marine reptiles, ranging from the Early Triassic (252–247 Ma) to the end of the Cenomanian (Late Cretaceous; 93.9 Ma; Bardet, 1992; Fischer et al., 2016). McGowan and Motani (2003) identified four ichthyosaurian bauplans present during ichthyosaur evolution: ‘basal’, ‘stem’, ‘mixosaurian’, and ‘parvipelvian’. The parvipelvian style body plan is the most familiar and recognisable, epitomised by *Ichthyosaurus*. Early parvipelvian ichthyosaurs are well known from the Lower Jurassic of southern England, in particular Lyme Regis (Dorset) and Street (Somerset). The first of these localities was the site of the famous ichthyosaur discovery by Joseph and Mary Anning between 1809 and 1811 that led to recognition of the taxon (Torrens, 1995). At least nine genera have been described from the Lower Jurassic of the UK: *Ichthyosaurus, Protoichthyosaurus*, *Temnodontosaurus*, *Excalibosaurus*, *Eurhinosaurus*, *Leptonectes*, *Stenopterygius*, *Hauffiopteryx and Wahlisaurus* (Jaekel, 1904; McGowan and Motani, 2003; Maisch, 2008; Caine & Benton, 2011; Lomax 2016, Lomax *et al*., 2017). As both a konservat- and konzentrat-lagerstätte, the English Lias Group has produced numerous ichthyosaur specimens that are complete or nearly complete, but often preserved in a laterally compressed condition (Seilacher, 1970).

Ichthyosaurus was the first still valid genus of ichthyosaur to be named (Lomax and Massare, 2015). The name *Proteosaurus* (Home, 1819) had precedent over the name, but was rarely used and has become a forgotten name. Two centuries of study have led to *Ichthyosaurus* becoming a waste basket taxon: a poorly defined taxon with many morphologically variable specimens assigned to it (Smith and Radley, 2007; Vincent *et al*., 2014). Several taxa originally classified as *Ichthyosaurus* are now recognized as belonging to other genera, such as *Temnodontosaurus* and *Leptonectes* (McGowan and Motani, 2003). *Ichthyosaurus* is defined mainly by a forefin with no fewer than five digits; an ulnare larger than the intermedium; digital bifurcation (intermedium bifurcation); closely packed and numerous phalanges; the distal end of the humerus is wider than the proximal end; pelvic girdle is tripartite with no fusion between the pubis and ischium; a preflexural vertebral count of less than 80; and a basioccipital with an extensive extracondylar area and a well-developed basioccipital peg (McGowan and Motani, 2003). Six species of *Ichthyosaurus* are currently recognized: *Ichthyosaurus communis* Conybeare, 1822, *Ichthyosaurus breviceps* Owen, 1881, *Ichthyosaurus conybeari* Lydekker, 1888, *Ichthyosaurus anningae* Lomax and Massare, 2015, *Ichthyosaurus somersetensis* Lomax and Massare, 2016a and *Ichthyosaurus larkini* Lomax and Massare, 2016a. However the morphological boundaries and separation of these species have not been thoroughly tested by morphological and phylogenetic analysis.

Modern cladistics have seen an increase in the use of large datasets, the assumption being that application of a large dataset will generate a more accurate result (Simoes et al., 2016); the general guideline being that characters included need to be independent of each other. Although there is therefore strong impetus to discover and include additional characters, the issue with the addition of new characters is that the independence of these characters is not always critically evaluated. In ichthyosaur phylogenetics, some studies have criticised the assignment and use of ambiguous characters (e.g. Sander, 2000; Fischer et al., 2011). Arguably, some fundamental characters appear to stand the test of time, with a growing number of analyses in which authors identify the characters as justified and valuable. Naturally, which characters are used is subject to variation dependent upon the taxon. Another significant problem in modern cladistics is the miscommunication of characters and character states. One author's interpretation of a character may therefore be different from another if the definition is incomplete or ambiguous, thereby reducing replicability and critical evaluation in these studies.

This paper presents a complete, large-scale collection of ichthyosaurian phylogenetic characters. The coding of 304 specimens of *Ichthyosaurus* was completed to include the wide variation of morphology and all species in *Ichthyosauru*s. This study uses a cladistic analysis of these specimens to identify potential taxon boundaries between specimens assigned to *Ichthyosaurus*. Additionally, by rigorously defining the collected characters, this aims to ensure robustness and replicability in future phylogenetic analyses of ichthyosaurs at any taxonomic level.

4.2 Methods. A review of published literature was conducted to compile a database of descriptions or characteristics that have been utilised in morphological descriptions of *Ichthyosaurus* (e.g., the works of De la Beche and Conybeare, 1821; Conybeare, 1822; Owen, 1881; Lydekker, 1888; McGowan, 1974; Delair, 1985; Maisch and Matzke, 2000b; McGowan and Motani, 2003; Smith and Radley, 2007; Maisch et al, 2008; Massare and Lomax, 2014). Phylogenetic studies of ichthyosaurs were also consulted (Motani, 1999; Sander, 2000; Jiang et al. 2005; Motani 2005; Fernandez, 2007; Druckenmiller and Maxwell, 2010; Fischer et al., 2011; Fischer et al., 2013; Roberts et al., 2014; Massare and Lomax, 2015 and 2016a, b; Lomax and Massare, 2016) and characters were added that apply to *Ichthyosaurus*.

A total of 99 characters was compiled and analysed for usefulness. Characters found to exhibit the same state across all the specimens studied were considered uninformative and not utilised. Informative characters were considered not only for the whole character, but for each character state; if the individual state was not present in the dataset it was removed. If the character state was too vague it was modified to be more applicable to the specimens being studied. The set of characters or descriptions typically used for *Ichthyosaurus*, but excluded from this analysis can be found in Appendix C. Most characters that utilized ratios (Massare, 1987 and McGowan, 1974) were considered separately in a morphometric study (Chapter 3, this volume). The use of these simple ratios has been used to reduce the effect of variable body size upon these characters in both morphometric and phylogenetic analyses (Koch et al., 2015). The results of that analysis showed that there is complete overlap in ratios of measurements, which result in no morphological separation of species as they are currently defined. The only ratio-style character still used is a comparison of preorbital length to jaw length (Character 17) and was included to separate short-snouted specimens. Other ratios were converted continuous characters to be used in a comparison analysis (Table 1); continuous characters have been used in morphometric and phylogenetic analyses (Koch et al., 2015), but have not previously been applied to ichthyosaurs. Five continuous characters from McGowan (1974) were calculated for the 44 core group specimens (Table 1). In addition, some counts were removed (maxilla tooth count, primary digit counts in forefin and hindfin, and various vertebral counts) as they have been shown to be widely variable.

Table 1. Measurement ratios and their definitions. These ratios have been used historically to separate specimens at specific or generic level and are also used in the phylogenetic analysis in this study.

Ratio	**Definition**	**Originator(s)**
Snout Ratio	Snout length/jaw length	McGowan , 1974a and 1976
Premaxillary Ratio	Premaxillary length/jaw length	McGowan, 1974a and 1976
Prenarial Ratio	Prenarial length/jaw length	McGowan, 1974a and 1976
Orbital Ratio	Orbital diameter/ jaw length	McGowan, 1974a and 1976
Ratio 'Orbit'	Internal diameter of sclerotic ring to diameter of orbit	Fernandez et al., 2005

The basal parvipelvians *Hudsonelpidia brevirostris* and *Macgowania janiceps*, and the more basal merriamosaurian *Californosaurus perrini* were coded as outgroups. Multiple outgroups were chosen to minimise the effect of missing data as is apparent in, for example, *Californosaurus*, which lacks its skull. Therefore, the primitive states of the characters presented here are present in some or all of these taxa; the characters are described below. Additionally the neoichthyosaurian *Temnodontosaurus* was included as an Operational Taxonomic Unit (OTU) as it is both relatively well-known, from the Lower Jurassic, and proximate enough in published phylogenies to be relevant to the evolution of *Ichthyosaurus* (Fischer et al., 2011 and 2013; Roberts et al., 2014; Lomax and Massare, 2015, 2016). For *Temnodontosaurus* the species *Temnodontosaurus trigonodon* and *Temnodontosaurus platyodon* were used for coding. Specimens assigned to the newly re-established *Protoichthyosaurus* were removed from this study as these specimens and manuscript need further evaluation before inclusion into this study. The OTUs were coded from 304 specimens based on the data gathered here for 300 *Ichthyosaurus* specimens and the descriptions in published literature for the outgroups (Maisch and Matzke, 2000b; McGowan, 1991, 1995, and 1996; Merriam, 1908; Motani, 1999; see Appendix D).

Four individual phylogenetic analyses were run on subsets of specimens taken from the complete list. Of the 300 specimens analysed, a core group of 43 were utilized in these analyses. These specimens represent holotype or neotype (referred specimens for *I. somersetensis* and *I. larkini*) specimens for the six currently valid species of *Ichthyosaurus* and 24 further specimens (See Appendix E). The 43 specimens included were specimens that have been published on and referred to a species of *Ichthyosaurus* and those that have the highest percentage of coded characters. The four analyses attempted to resolve the relationships of this subset of specimens using character sets without (Analysis 1) and with (Analysis 2) continuous characters. Analysis 3 included 19 OTUs representing only holotype/neotype specimens and the most complete other specimens (>41% for holotype/neotype characters coded; >46% other specimens characters coded). Finally, Analyses 1 and 2 used 43 OTUs and, with Analysis 4, included the three outgroups described above. Analyses 3 included only *Macgowania* and *Temnodontosaurus* as outgroups as these are most completely-coded of the outgroup taxa.

All four phylogenetic analyses were optimised using maximum parsimony in TNT version 1.5 (Goloboff and Catalano, 2016). The memory available to TNT was set at 10,000 trees. All analyses used a new technology search with 1000 random addition sequences and ratcheting with the default values (Nixon, 1999). Following this a round of additional tree bisection-reconnection (TBR) was used to ensure the most parsimonious trees (MPTs) had been found. Clade support values for the strict consensuses of the resulting MPTs from each analysis were calculated in TNT using bootstrap and jackknife resampling each with 100 replicates. Consistency (CI) and retention (RI) indices for each consensus tree were calculated using the script STATS.RUN provided with TNT. Bremer support was calculated using absolute support and TBR, retaining trees suboptimal by 15 steps. FigTree version 1.4.3 was used to visualise the resultant trees.

Institution Abbreviations. **AGC**— Alfred Gillett Collections, cared for by Alfred Gillett Trust (C & J Clark Ltd.); **BGS**, The British Geological Survey, Keyworth, Nottingham, U.K.; **BRLSI**— Bath Royal Literary and Scientific Institution, Bath, U.K.; **BRSMG**— Bristol Museum and Art Gallery, Bristol, U.K.; **BIRUG/BU**—Birmingham University Lapworth Museum, Birmingham, U.K.; **CAMSM**—Cambridge Museum of Natural History, Cambridge, U.K.; **DONMG**— Doncaster Museum and Art Gallery, Doncaster, U.K.; **DORCM—**The Dorchester County Museum, Dorchester, U.K.; **GLAHM**—The Hunterian Museum, University of Glasgow, Glasgow, U.K.; **GMRC**—Glasgow Museum Resource Centre, Glasgow, U.K.; **HCMAS**—Hampshire County Council Museum Store, Winchester, U.K.; **IPSMG**— Ipswich Museum, Ipswich, Suffolk, U.K.; **LEICT**— Leicester Arts and Museums Service, New Walk Museum and Art Gallery, New Walk, Leicester, U.K.; **NHMUK**—(formerly BMNH), Natural History Museum, London, U.K.; **NMING—**National Museum of Ireland, Natural History Division, Geological Collection, Dublin, Ireland; **NMS**— National Museum of Scotland, Edinburgh, U.K.; **NOTNH**— Nottingham Natural History Museum (Wollaton Hall), Nottingham, U.K.; **MANCH**— Manchester Museum, Manchester, U.K.; **OUMNH**—Oxford University Museum of Natural History, Oxford, U.K.; **PETMG** — Peterborough Museum and Art Gallery, Peterborough, U.K.; **PMO**— Paleontologisk Museum Oslo, Oslo, Norway; **RAMM**— Royal Albert Memorial Museum, Exeter, U.K.; **TTNCM—**Taunton County Museum, The South West Heritage Trust (Somerset Museums Service), Taunton, U.K.; **UoS—** University of Southampton Collections, Southampton, U.K.; **YORYM**— Yorkshire Museum , York, U. K.

4.3.1 Results. Character List for Phylogenetic Analysis. Characters denoted in bold are newly proposed and are based on new observations or literature descriptions. The structure of each character description is as follows: a – a detailed description of character, and b - modifications executed by other authors, and for this analysis.

Cranial

1. Premaxilla: 0-supra-and sub-narial process absent; 1- well-developed supranarial process overlying approximately one third to one half of external naris, with long subnarial process; 2- supranarial process short relative to subnarial process; 3- both processes short relative to external narial length (modified by Lomax and Massare, 2016, Char 0 from Maxwell, Fernandez, and Schoch, 2012 Char 1).
    a. In Triassic genera such as *Mixosaurus atavus*, and specimens akin to TTNCM 166/1992 (State 0) the premaxilla does not split posteriorly into two processes, instead terminates at the external naris. In other ichthyosaurs the posterior end of the premaxilla can have one or two processes that split either dorsal or ventral to the external naris before terminating. This character describes the posterior portion of the premaxilla and its interaction with the external naris. In most specimens the premaxilla splits into two processes that form the anterior borders of the external naris. State 1 is present in NHMUK PV R1162 (Figure 4) where the process dorsal to the external naris overlies the external naris 33-50%. When the supranarial process is short when compared to the subnarial process the specimen is coded as state 2 and can be seen in NHMUK PV R15907(Figure 5). When both processes are present but short (not extending beyond half the length of the external naris), the specimen is coded as state 3 and is present in NHMUK PV OR43006 (Figure 6).
    b. Modified by splitting the second character state into state 2 and 3 seen above.

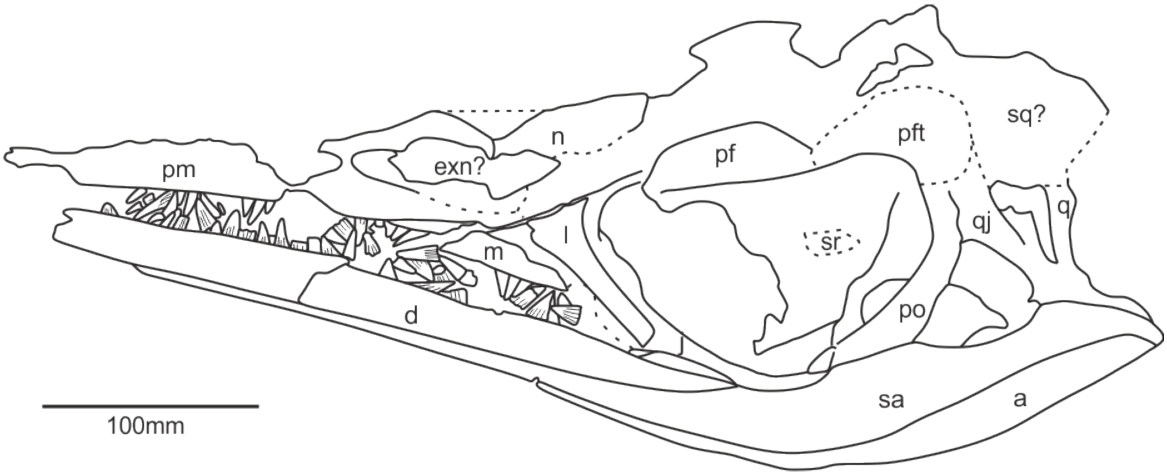
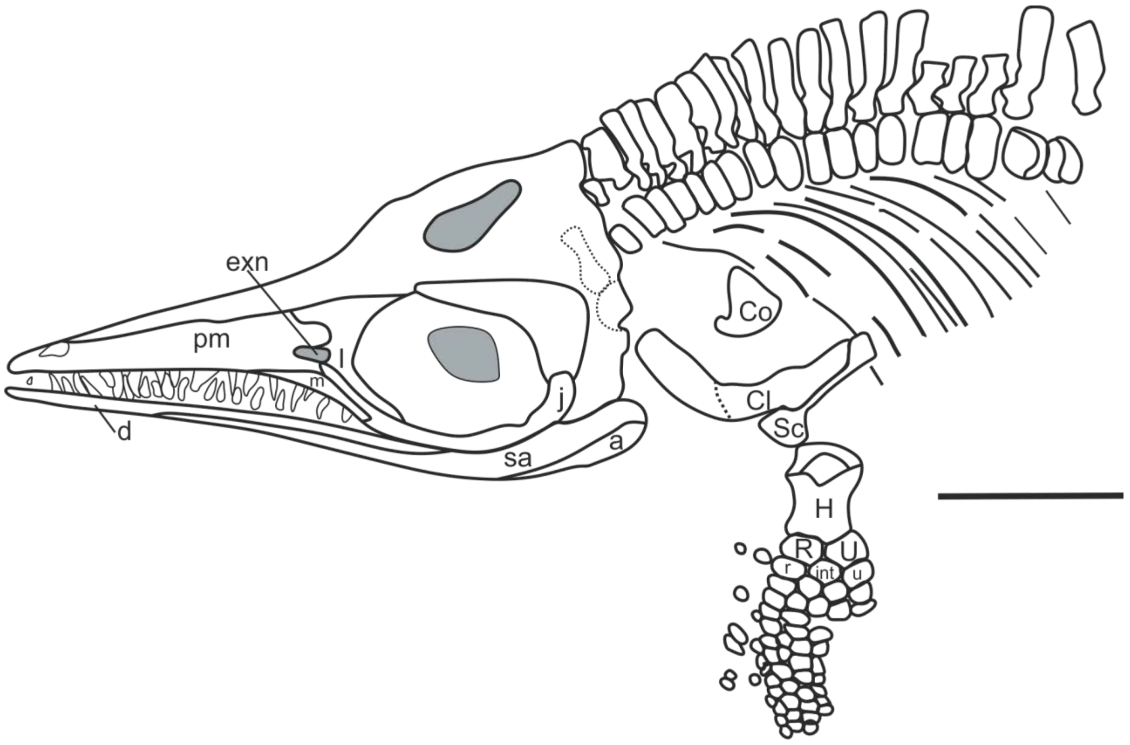


Figure 1. Skull of *Macgowania* modified from McGowan (1996, Figure 9). Dashed lines represent possible sutures between bones. **Abbreviations**: **a**, angular; **d**, dentary; **exn**, external naris; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **ptf**, postfrontal; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sq**, squamosal; **sr**, sclerotic ring.

2. Premaxilla/lacrimal contact ventral to the external nares: 0-absent; 1- narrow; 2- broad (Fernandez, 2007; Char 0).
    a. In most Triassic and some Jurassic and Cretaceous ichthyosaurs, there is no contact between the premaxilla and lacrimal as the posterior processes of the premaxilla mentioned in character 1 do not extend far enough posteriorly if present at all. This character defines if there is contact of two bones ventral to the external naris and if there is contact, if it is narrow or broader. No contact between the premaxilla and lacrimal is seen in *Macgowania* (Figure 1) and specimen AGC 16. Narrow contact is typically seen in *Leptonectes* species and some *Temnodontosaurus* species. A more broad contact is seen in specimens NHMUK PV R216 (Figure 2) and NHMUK BGS956.
    b. This character was originally used by Maisch and Matzke (1997; Character 1) and subsequently Motani (1999; Character 3). The modified version formulated by Fernandez (2007) was used in this study because that description of the character is least ambiguous. Changed ‘below’ to ‘ventral to’ to make it anatomically clear



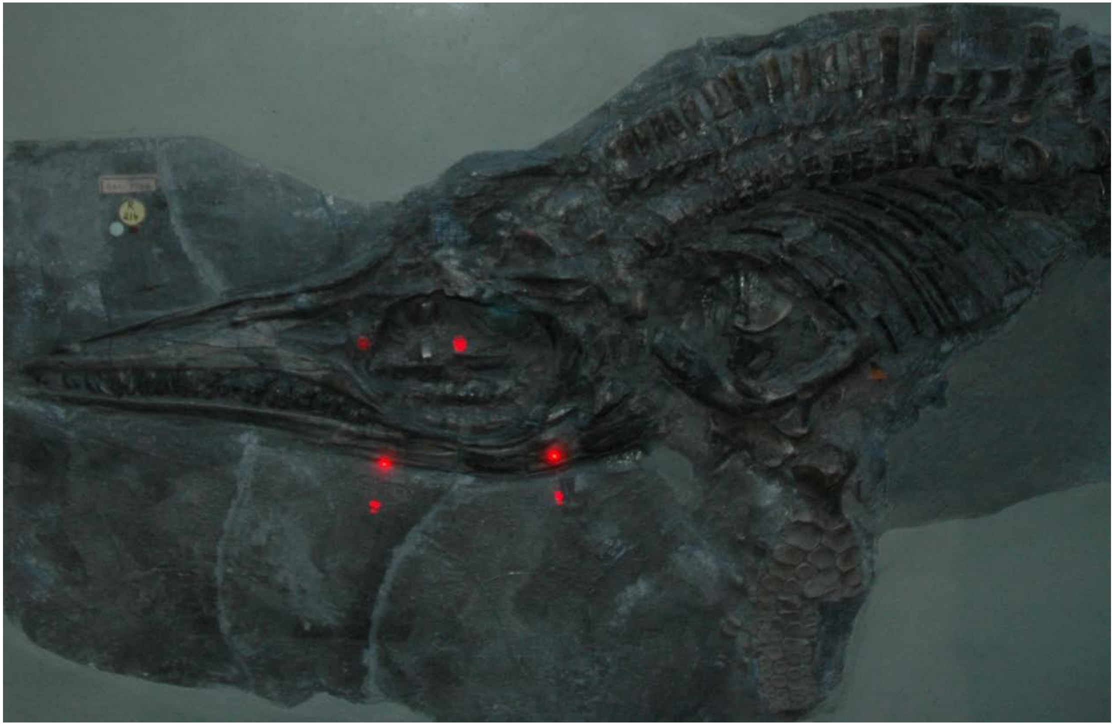


Figure 2. Interpretation line drawing (top) and image (bottom) of the anterior portion of specimen NHMUK PV R216 from species *Ichthyosaurus conybeari*. Dashed lines represent possible sutures between bones and grey areas are fenestra. Scale bar and length between two bright red dots is equal to53.52 mm. **Abbreviations**: **Cl**, clavicle; **Co**, coracoid; **d**, dentary; **exn**, external naris; **H**, humerus; **int**, intermedium; **j**, jugal; **l**, lacrimal; **m**, maxilla; **pm**, premaxilla; **R**, radius; **r**, radiale; **Sc**, scapula; **U**, ulna; **u**, ulnare.

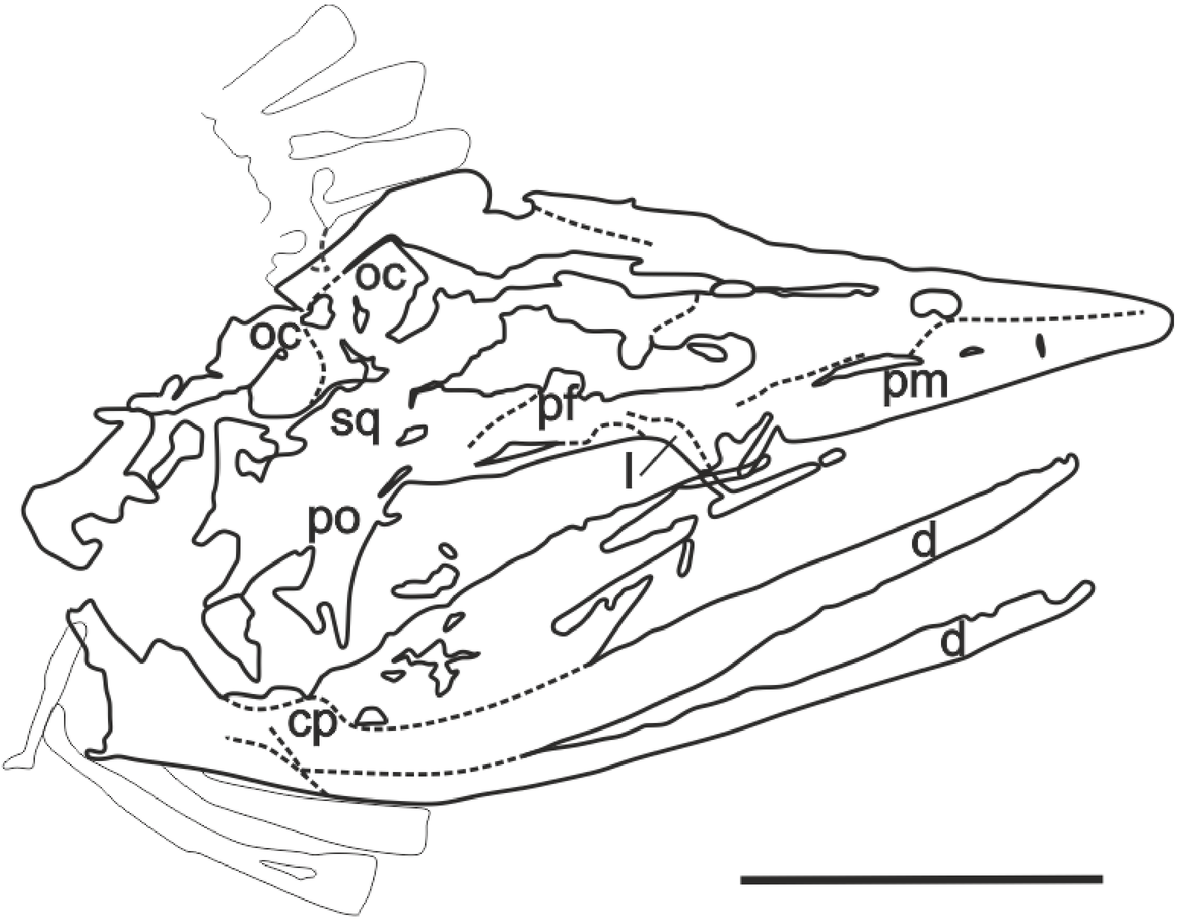


Figure 3. Skull of *Hudsonelpidia* modified from McGowan (1995, Figure 6). Dashed lines represent possible sutures between bones. **Abbreviations**: **cp**, coronoid process; **d**, dentary; **l**, lacrimal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **sq**, squamosal.

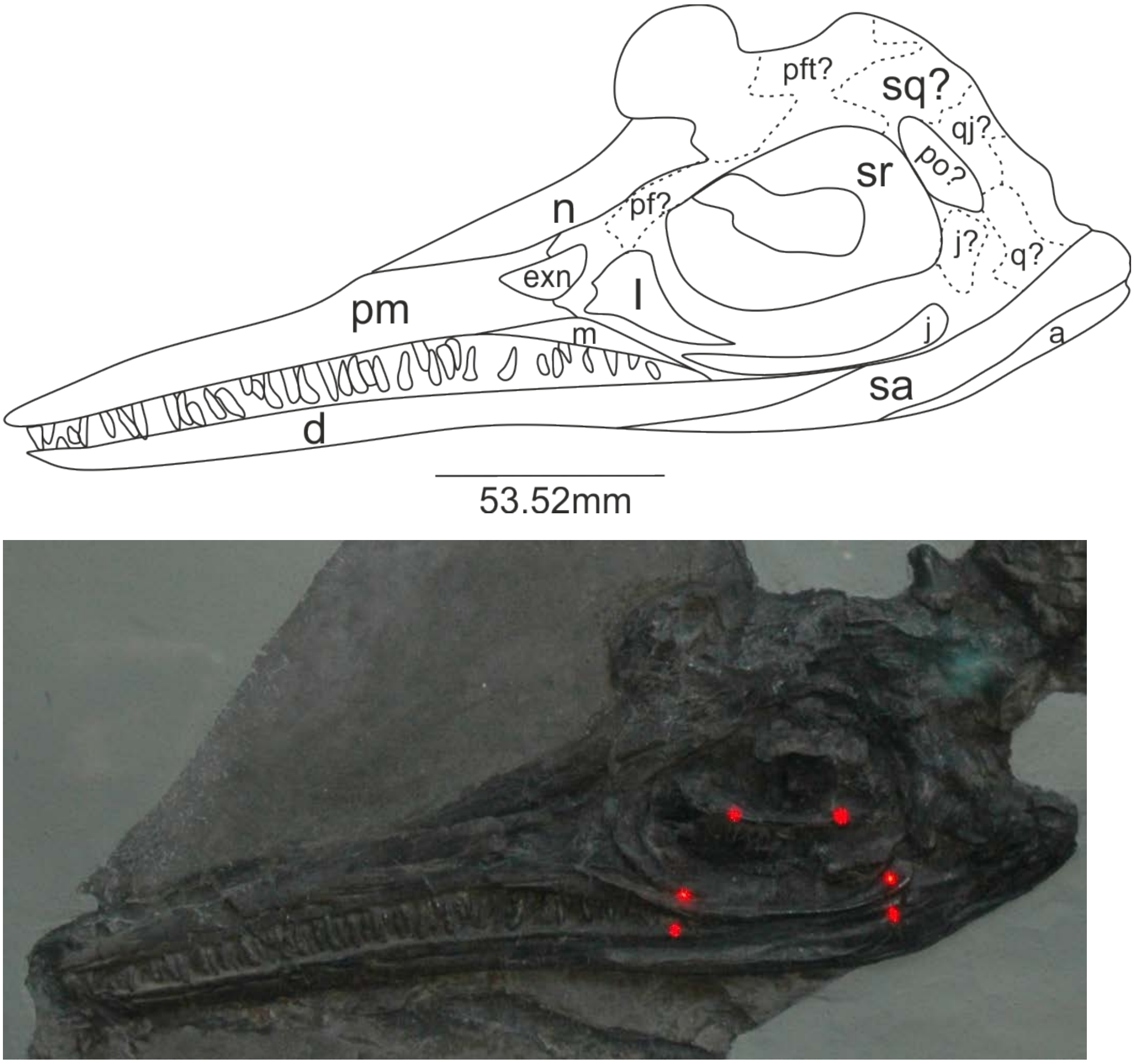


Figure 4. Skull of *Ichthyosaurus communis* (NHMUK PV R1162) modified from McGowan (1996, Figure 9) (top). Image of specimen housed behind glass at the NHMUK, London(bottom). The length between the middle set of red dots is 53.52mm. Dashed lines represent possible sutures between bones. **Abbreviations**: **a**, angular; **d**, dentary; **exn**, external naris; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **ptf**, postfrontal; **q**, quadrate; **qj**, quadratojugal; **sa**, surangular; **sq**, squamosal; **sr**, sclerotic ring.

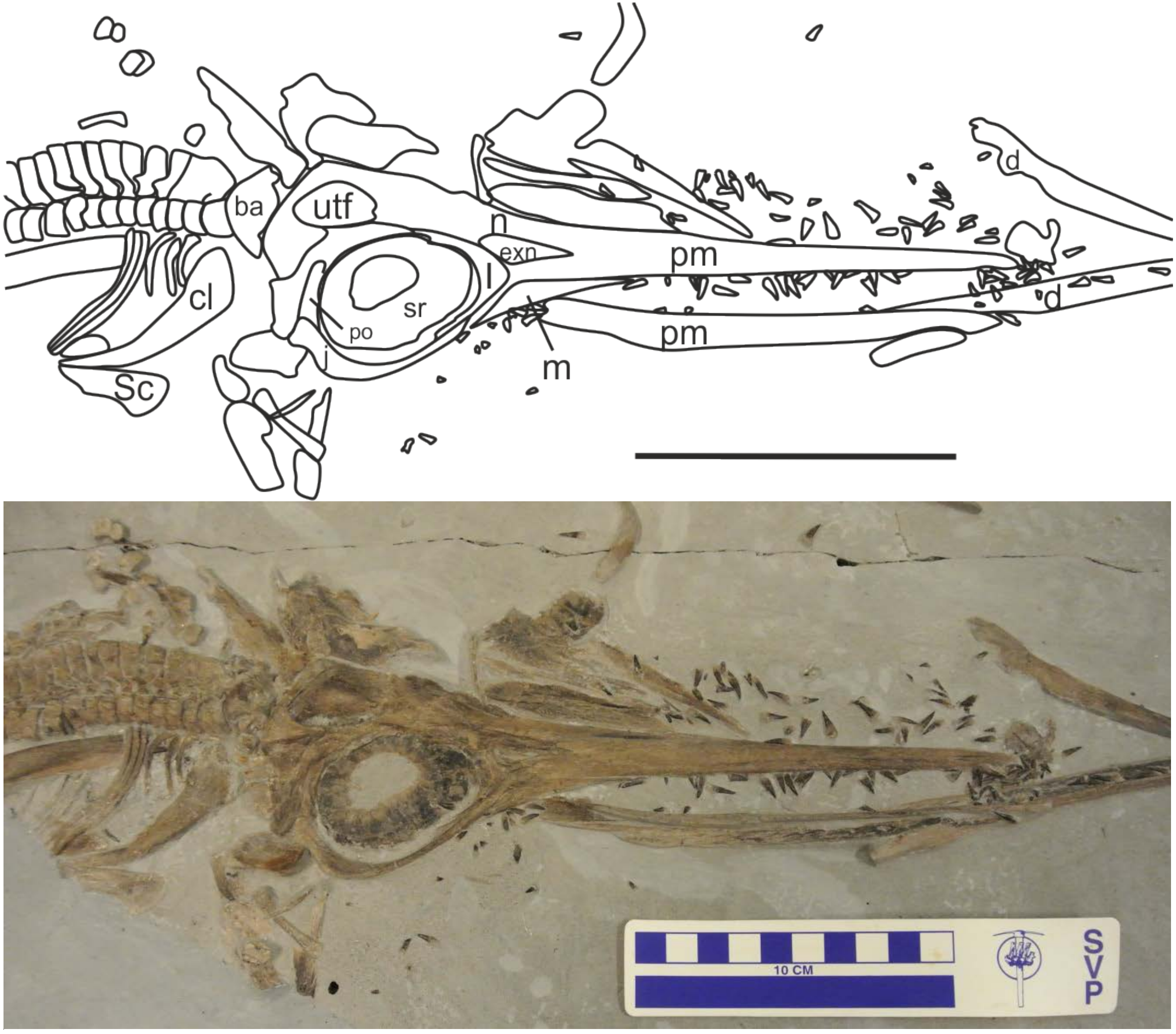
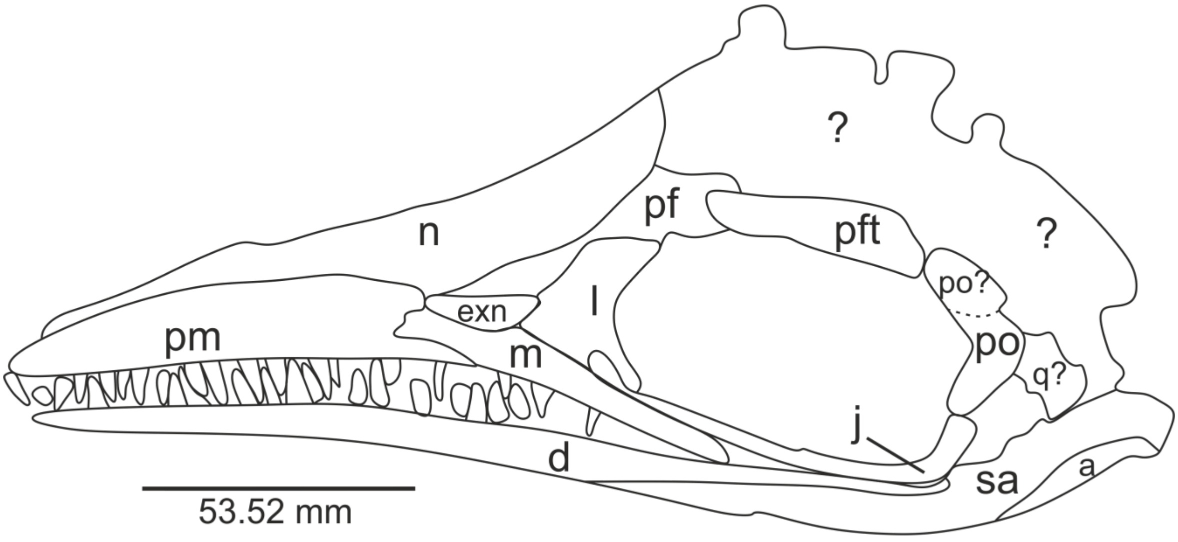


Figure 5. Interpretation line drawing (top) and image (bottom) of skull and pectoral area of specimen NHMUK PV R15907. Scale bar equals 100 mm. **Abbreviations**: **ba**, basioccipital; **d**, dentary; **exn**, external naris; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pm**, premaxilla; **po**, postorbital; **sc**, scapula; **sr**, sclerotic ring; **utf**, upper temporal fenestra.



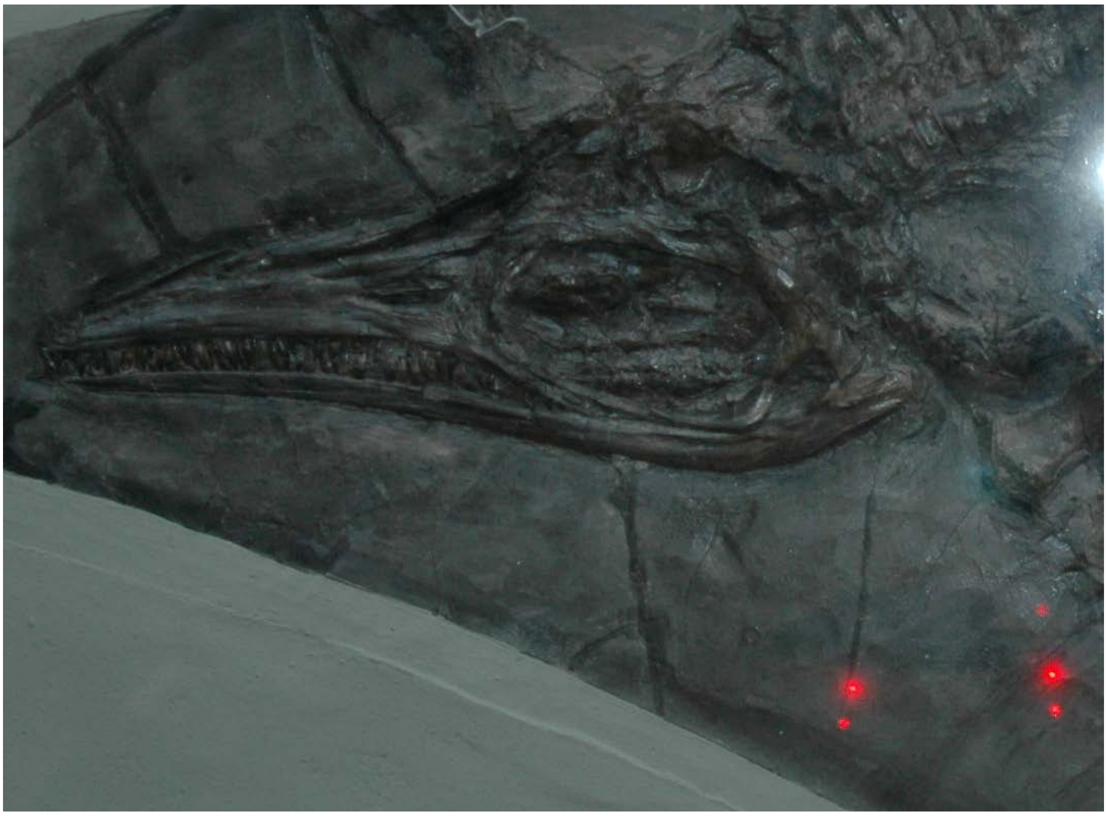


Figure 6. Interpretation line drawing (top) and image (bottom) of the skull of *Ichthyosaurus breviceps* (NHMUK PV OR43006). Dashed lines represent possible sutures between bones. Scale for image between the bright red dots is equal to 53.52mm. **Abbreviations**: **a**, angular; **d**, dentary; **exn**, external naris; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **ptf**, postfrontal; **sa**, surangular; **sq**, squamosal.

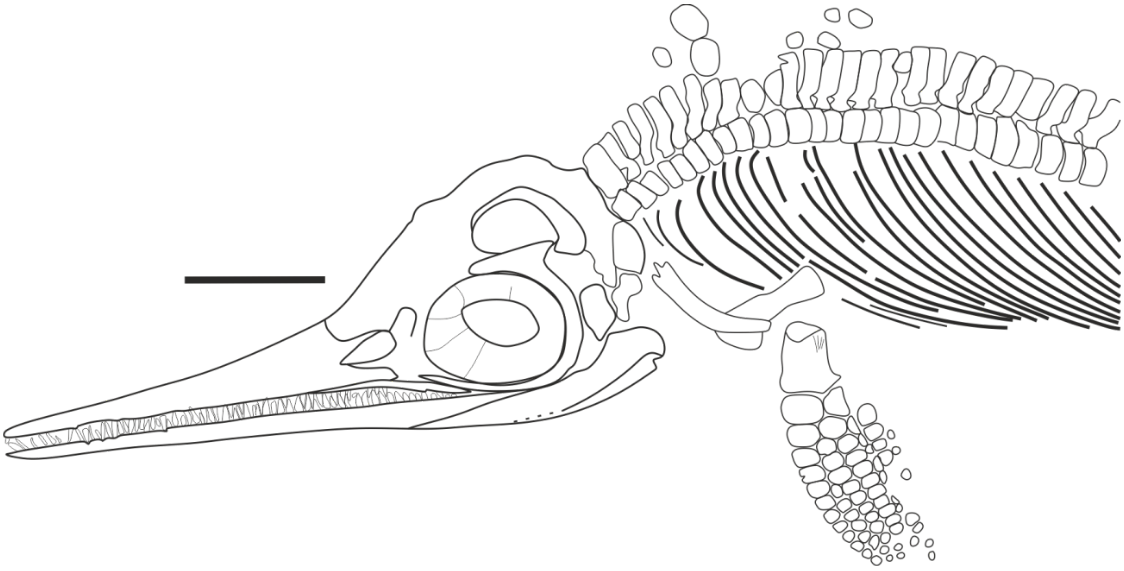


Figure 7. Interpretation line drawing (top) and image (bottom) of the skull and anterior portion of *Ichthyosaurus conybeari* (NHMUK BGS956). Dashed lines represent possible sutures between bones. Scale bar equals 50 mm.

3. **Premaxilla: 0- straight; 1- downturned towards tip.**
    a. Mentioned in Massare and Lomax (2014), as something unique pertaining to *I. breviceps*, though not seen in all of specimens of this taxon (NHMUK PV R1062, OUMNH J.13810 (Figure 8), and YORYM 1995.2). However, character state 1 is also seen in outgroup taxa *Hudsonelpidia* (Figure 3) and *Macgowania* (Figure 1) so it may not be an autapomorphy for *I. breviceps* as mentioned in Massare and Lomax (2014). More investigation along with this study will need to occur to confirm or deny this.

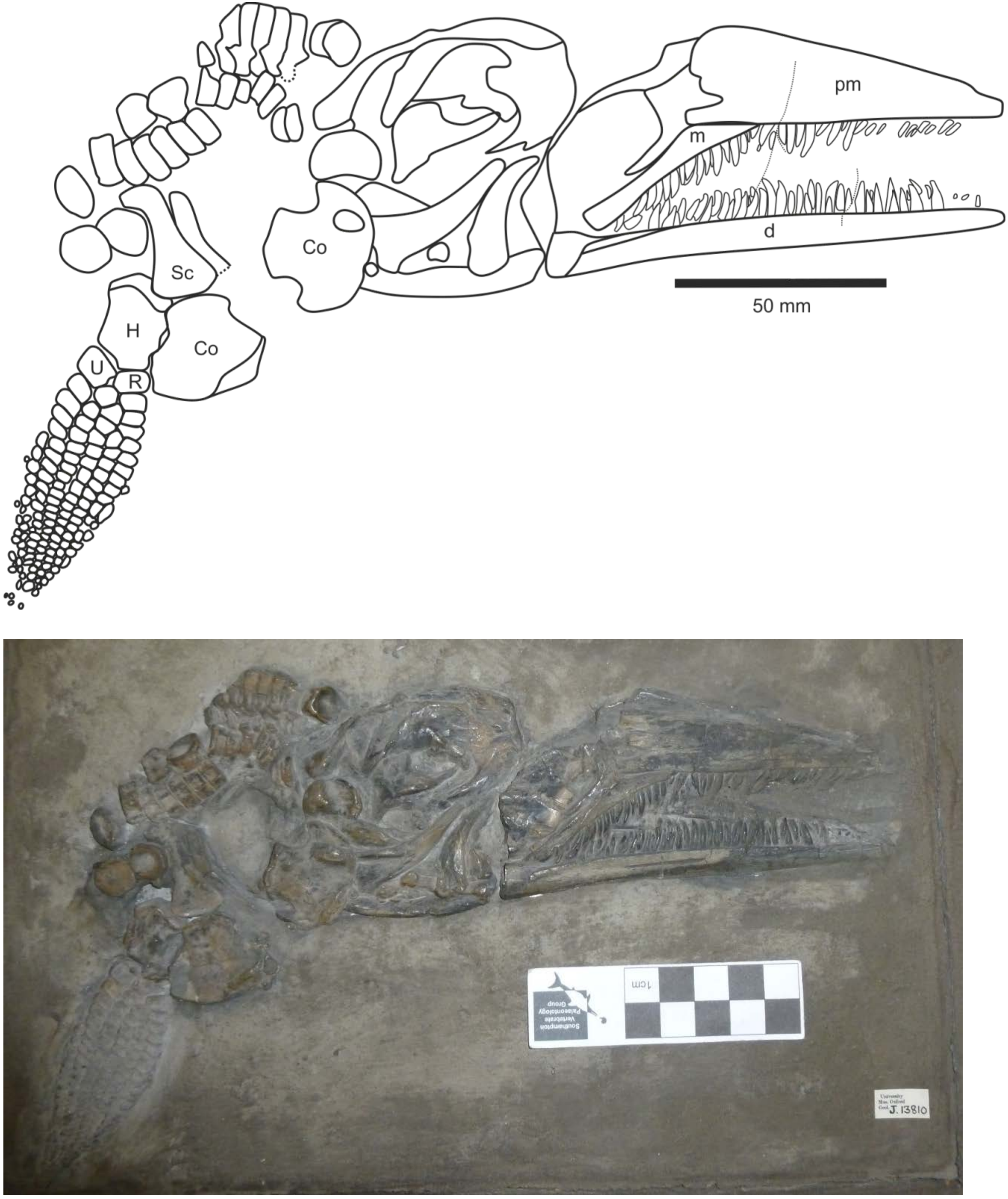


Figure 8. Interpretation line drawing (top) and image (bottom) (photo credit Rebecca Bennion) of the skull and anterior portion of *Ichthyosaurus conybeari* (OUMNH J.13810). **Abbreviations**: **Co**, coracoid; **d**, dentary; **H**, humerus; **m**, maxilla; **pm**, premaxilla; **R**, radius; **Sc**, scapula; **U**, ulna.

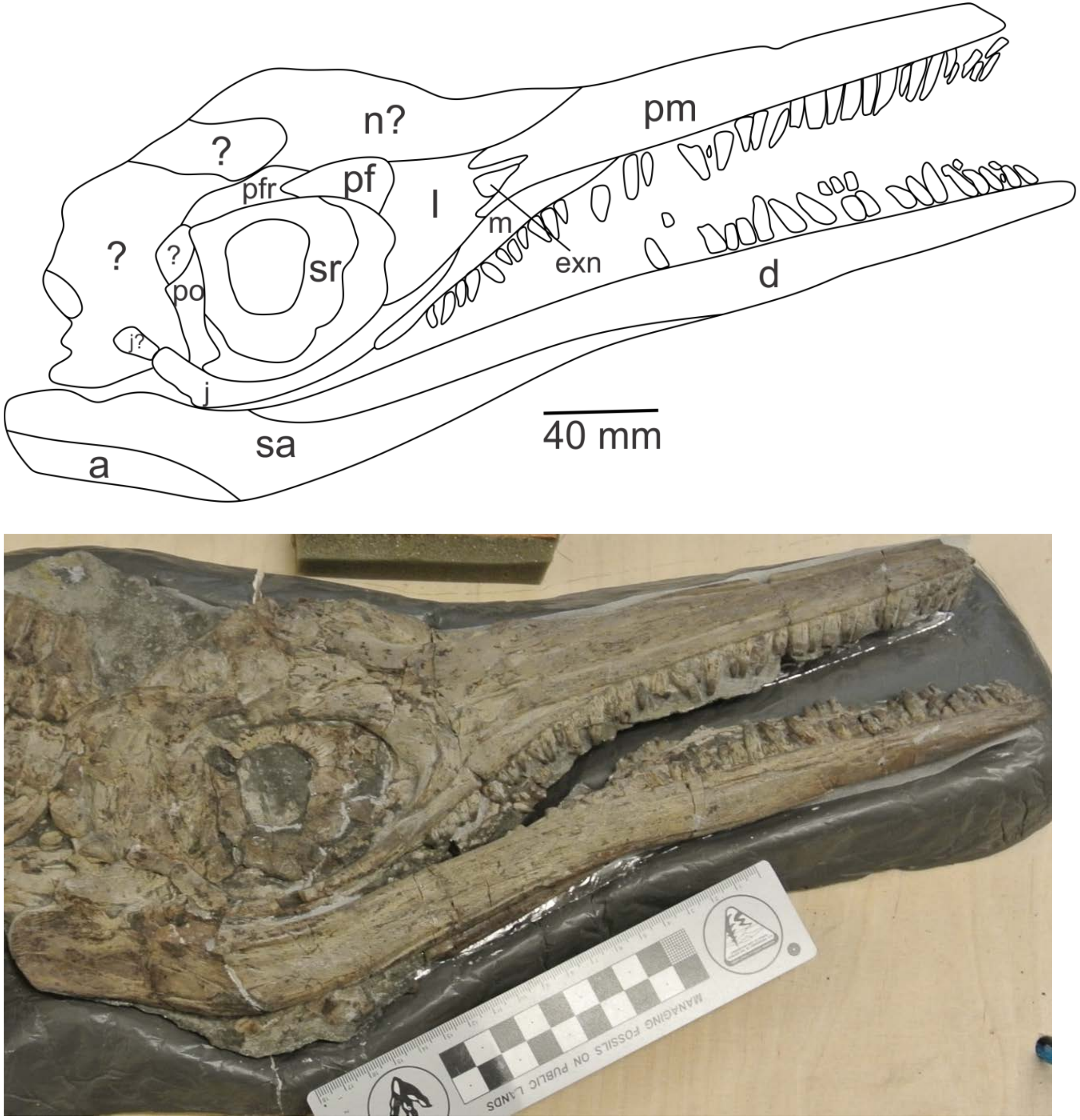


Figure 9. Interpretation line drawing (top) and image (bottom) of the skull of *Ichthyosaurus somersetensis* (BRSMG Cc921). **Abbreviations**: **a**, angular; **d**, dentary; **exn**, external naris; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **pf**, prefrontal; **pm**, premaxilla; **po**, postorbital; **ptf**, postfrontal; **sa**, surangular; **sq**, squamosal; **sr**, sclerotic ring.

4. **Lower jaw/mandibular-0- angled anteriorly due to large orbit; 1- straight**
    a. State 0 of this character is present in *Hudsonelpidia* (Figure 3) and *Macgowania* (Figure 1), but character state 1 is present in most *Ichthyosaurus* specimens including the four of the now six holotypes (NHMUK PV R1162 (Figure 4), NHMUK PV OR38523 (Figure 10), NHMUK PV OR43006 (Figure 6), and DONMG 1983.98(Figure 11)).

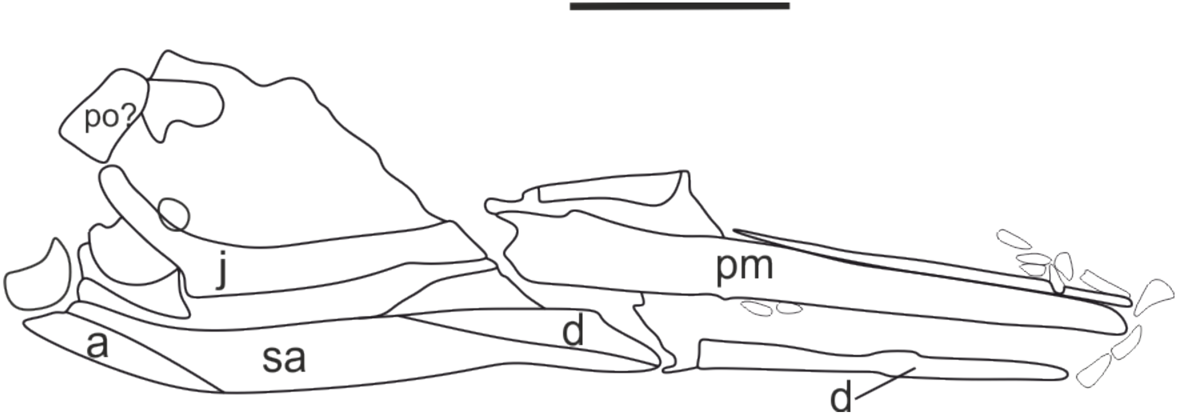


Figure 10. Interpretation line drawing of the skull of NHMUK PV OR38523 the holotype for *Ichthyosaurus conybeari*. Scale bar is equal to 53.52 mm. **Abbreviations**: **a**, angular; **d**, dentary; **exn**, external naris; **j**, jugal; **pm**, premaxilla; **sa**, surangular; **po**, postorbital.

Figure 11. Interpretation line drawing DONMG 1983.98 the holotype for *Ichthyosaurus anningae*. Scale bar is equal to 100 mm.

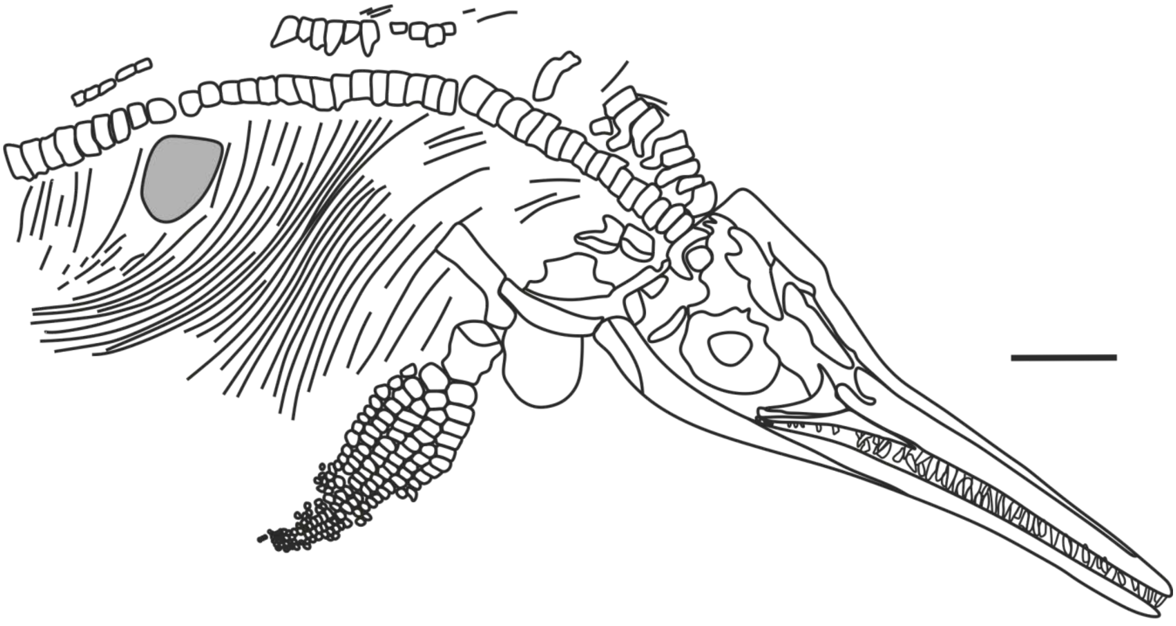


Figure 12. Interpretation line drawing (top) and image (bottom) line drawing of anterior portion of NHMUK PV OR120 a specimen of the species *Ichthyosaurus anningae*. Scale bar is equal to 50 mm, and grey mass in rib cage is most likely stomach contents.

5. **Coronoid process (process on the anterior of the surangular towards the posterior margin); 0- posterior to posterior margin of orbit; 1- even with the posterior margin of orbit; 2- process absent (mentioned in McGowan, 1974).**
    a. Small process on the surangular towards the posterior of the orbit. The position and presence of this process varies from the middle of the orbit to posterior of the orbit. Significant distortion was taken in to account when present and coded as unknown. In *Hudsonelpidia* (Figure 3) and NHMUK OR43006 (Figure 6) the coronoid process is posterior to the posterior of the orbit, in *Macgowania* and NHMUK PV R1162 (Figure 4) the coronoid process is even with the posterior margin of the orbit and it is absent in NHMUK OR38523 (Figure 10).
6. 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 anterior (within half of naris length) to anterior edge of external naris; 2- anterior end of maxilla extends well beyond anterior edge of the external naris (modified by Lomax and Massare, 2016 Char 7 from Maxwell, et al., 2012 Char 2 modified from Fernandez, 2007 Char 1).
    a. In most Triassic ichthyosaurs the maxilla extends well beyond the edge of the external naris and can also been seen in Jurassic ichthyosaurs such as *Temnodontosaurus* and some specimens of *Ichthyosaurus* (DONMG 1938.8 (Figure 11), NHMUK PV OR120 (Figure 12), and NHMUK PV R15907 (Figure 5)). In *Macgowania* the maxilla does not extend beyond the external naris. In specimens NHMUK PV OR43006 and NHMUK PV R1162 shows character state 1. This character quantifies the position at which the anterior part of the maxilla is positioned in reference to other bones.

   b. Modified by Massare and Lomax (2016) by clarifying the character with where the maxilla starts. This now also clarifies how long the maxilla is with respect to other bones.

7. Posterior end of maxilla: 0- ends at the leading edge of the orbit; 1- ends at the leading edge of the sclerotic ring; 2- ends posterior to leading edge of sclerotic ring (modified from Maxwell, et al., 2012 Char 3).
   a. This character discusses where the posterior part of the maxilla (located ventral to orbit and slightly anterior) ends in relation to the orbit and sclerotic ring positions. This character will only work for specimens that have a sclerotic ring present and are not clearly distorted in this area and bones are very close to 'life position' or the centre of the orbit. State 0 is seen in *Macgowania* (Figure 1), *Temnodontosaurus* and DONMG 1983.98 (Figure 11), state 1 is present in NHMUK PV R1162, and state 2 is present in NHMUK PV OR43006.
   b. Similar to character 3 from Maxwell, et al. (2012) but altered to describe where the posterior portion of the maxilla terminates as opposed to classifying it as long or short.
8. Highest point (dorsoventrally) of maxilla: 0- posterior to external nares; 1- anterior to external nares; 2- even with the middle of the external nares (modified by Lomax and Massare, 2016 Char 3 from Druckenmiller and Maxwell, 2010 Char 4).
   a. This refers to the highest point (or place where maxilla becomes most dorsal) of the maxilla and quantifying where that occurs. The specimens in which the highest point is found towards the very posterior of the external naris or posterior to the external naris are coded as possessing state 0 and are *Temnodontosaurus* and NHMUK PV OR43006. The specimens where the highest point is anterior to the external naris are NHMUK PV R1162 and DONMG 1983.98 (Figure 11). In *Macgowania* (Figure 1) and AGC11 the highest point is even with the middle of the external naris.
   b. Modified by Massare and Lomax (2016) by adding character state 2.
9. **Maxilla: 0- straight or with an angle of 0-15°; 1-slightly curved along the tooth row or with an angle of 15-45°; 2-significantly curved along tooth row or having and angle greater than 45° (mentioned in Massare and Lomax, 2014).**
   a. This character refers to the angle of downturn or curvature present in the maxilla, a character that may have a relationship with the relative size of the orbit, an observation based on the presence of greater maxillary curvature in taxa with larger orbits(pers. obs.). Specimens with an angle of 0-15° between the anterior process and jugal process were coded as possessing state 0, and this is present in *Macgowania* (Figure 1), *Temnodontosaurus*, and DONMG 1983.98. Those between 15-45° were coded as possessing state 1 and are present in AGC11 and BRSMG Cc921(Figure 9). Those greater than 45° were coded as possessing state 2 and is present in NHMUK PV R1162 (Figure 4) and NHMUK OR43006 (Figure 6).
10. Processus narialis of the maxilla in lateral view: 0- present; 1- absent (Fischer et al., 2013 Char 9, and Fischer et al., 2011 Char 9 inverted coding).

  a. This character refers to a process on the dorsal part of the maxilla that ascends towards the naris and separates the external naris from the orbit. State 0 of this character is only present in outgroup taxa such as *Macgowania* (Figure 1). This process is absent (state 1) in taxa or specimens akin to *Temnodontosaurus*, NHMUK PV R1162
  b. Unmodified.

11. Jugal, dorsal ramus angle: 0- well-developed and strongly curved dorsally (almost 90° bend); 1- poorly developed, jugal essentially straight (modified by Lomax and Massare, 2016 Char 8 from Maxwell, Fernandez, and Schoch, 2012 Char 7).
    a. Discussing the degree to which the jugal is bending or curving. State 0 can be seen on *Leptonectes tenuirostris* and *Ophthalmosaurus icenicus* and is often found in *Ichthyosaurus* specimens such as, NHMUK PV R1162, NHMUK PV OR43006, and DONMG 1983.98(Figure 11). State 1 can be found in *Shastasaurus pacificus*, *Temnodontosaurus platyodon* and *Macgowania* (Figure 1) (McGowan and Motani, 2003).
    b. Modified by Massare and Lomax, by adding in the almost 90 degree bend.
12. Anterior margin of the jugal: 0- not tapering bluntly ends with contact of lacrimal and/or maxilla; 1- tapering, running between lacrimal and maxilla (modified from Druckenmiller and Maxwell, 2010 Char 6).
    a. Jugal is the bone beneath the orbit, and this character typically deals with the portion closest to the snout. Tapering refers to the narrowing of the bone into a (typically) rounded point. In the primitive state the jugal does not narrow, but stays about the same width and can end with little to no rounding at termination; this is present in *Macgowania* (Figure 1) and NHMUK PV OR43006. Where the jugal tapers between the lacrimal and maxilla it is coded as state 1 and is present in *Temnodontosaurus*, NHMUK PV R1162, and DONMG 1983.98.
    b. The primitive state of this character has been added to reflect the observations made for this study. States 1 and 2 have not been modified from Druckenmiller and Maxwell, 2010.
13. **Jaw line /snout: 0- straight; 1- ventrally convex anterior to orbit; 2- ventrally convex anterior to external naris.**
    a. New character used to reflect the variation in the bending of the jaw line or snout seen in some ichthyosaurs. This character needs to be evaluated carefully to make sure the curvature is not due to deformation of the specimen. The straight state is present in *Macgowania* (Figure 1), *Hudsonelpidia* (Figure 3), *Temnodontosaurus*, NHMUK PV R1162 (Figure 4 and 10), and NHMUK PV OR38523 (Figure 10). A jaw line that is ventrally convex anterior to orbit is present in NHMUK PV OR14567 and NHMUK PV OR39263. A jaw line that is ventrally convex anterior to external naris is present in NHMUK PV OR43006 (Figure 6) and NMUK PV R216.
14. Size of lacrimal relative to external naris: 0- small triangular lacrimal with long narrow anterior process; 1- small triangular lacrimal with broad anterior process; 2- large triangular lacrimal with long narrow anterior process; 3- large triangular

lacrimal with short anterior process (Modified from Lomax and Massare, 2016 Char 15).

   a. The lacrimal is the bone directly anterior of the orbit and posterior to the external naris and maxilla. This character is referring to the shape and processes that make up this bone. State 0 is present in *Macgowania* (Figure 1) and NHMUK PV R1162(Figure 4); state 1 is present in NHMUK PV BGS956 and DONMG 1983.3 (Figure 11); state 2 is present in *Temnodontosaurus* (maybe state 1 and 2) and specimens NHMUK OR2013 and NHMUK PV R216 (Figure 2); and state 3 is present in *Suevoleviathan* and specimen BRSMG Cc921(Figure 9).
   b. Modified to clarify the terms large and small and by changing state one from large too small.

15. Descending process of the nasal on the posterior dorsal border of the nares: 0- absent, 1-present (Fernandez, 2007 Char 2).
    a. This is a process on the nasal that extends ventrally and interacts with the dorsal boarder of the external nares. This process can eventually divide the external naris into two openings instead of one. The only specimen where this process is present is NMING F78746 (this specimen is a composite and this state is seen in main part of specimen, not the hindfin which is thought to have been an addition from another specimen [Massare and Lomax, 2016a]).
    b. Unmodified.
16. Nasals, lateral view: 0- extend as far forward as the anterior process of the maxilla; 1- do not extend as far forward as the anterior process of maxilla (Lomax and Massare, 2016 Char 12).
    a. This character is trying to quantify the extent and size of the external nares in relation to other bones adjacent to it. State 0 is present in *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 4), NHMUK PV OR43006 (Figure 6), and DONMG 1983.98 (Figure 11). State 1 is present in *Macgowania* (Figure 1) and specimen NHMUK BGS956.
    b. Unmodified.
17. Rostrum relative length (snout ratio=preorbital length/jaw length [McGowan, 1974]): 0- short rostrum, snout ratio <0.6; 1- fairly long rostrum, snout ratio 0.6-0.7; 2- extremely long rostrum, snout ratio >0.7 (Lomax and Massare, 2016 Char 10).
    a. This is the only ratio character used in this analysis as initial TNT runs did not separate out short snouted specimens. A ratio used to distinguish short snouted species, such as *I. breviceps* from other species. The ratio was introduced by McGowan, 1974 to help compensate the variation of strict measurements due to ontogeny and individual specimen variation. A short rostrum is present in *Macgowania* (Figure 1), *Hudsonelpidia* , and *Temnodontosaurus eurycephalus* and in specimen NHMUK PV OR43006 (Figure 6). A relatively long rostrum is present in NHMUK PV OR38523 (Figure 10) and DONMG 1983.98. An extremely long snout is present in AGC9.
    b. Unmodified.

18. The anterior processes of the right and left parietals: 0- contacting each other anteriorly, eliminating frontal from pineal foramen; 1- narrowly separated anteriorly, forming parietal fork; 2- widely open, resulting in the absence of a clear fork (Mazin, 1982 Char 2).
    a. The parietal bone is present on the anterior part of the skull near the pineal foramen. This character describes the interaction of the bones around the pineal foramen. State 0 is present in OUMNH J.10301 and the frontal has no contact with the pineal foramen on the dorsal surface. The parietal fork is present in *Temnodontosaurus* and specimen LEICT G151.1991. The left and right parietal opening widely is seen in NHMUK PV R216 and NHMUK PV OR2013 (Figure 13).
    b. Modified from Fernandez, 2007, but ambiguous as state 0 was not used in the coding. Motani, 1999 provides figures that display each of the states which clarify the matter.

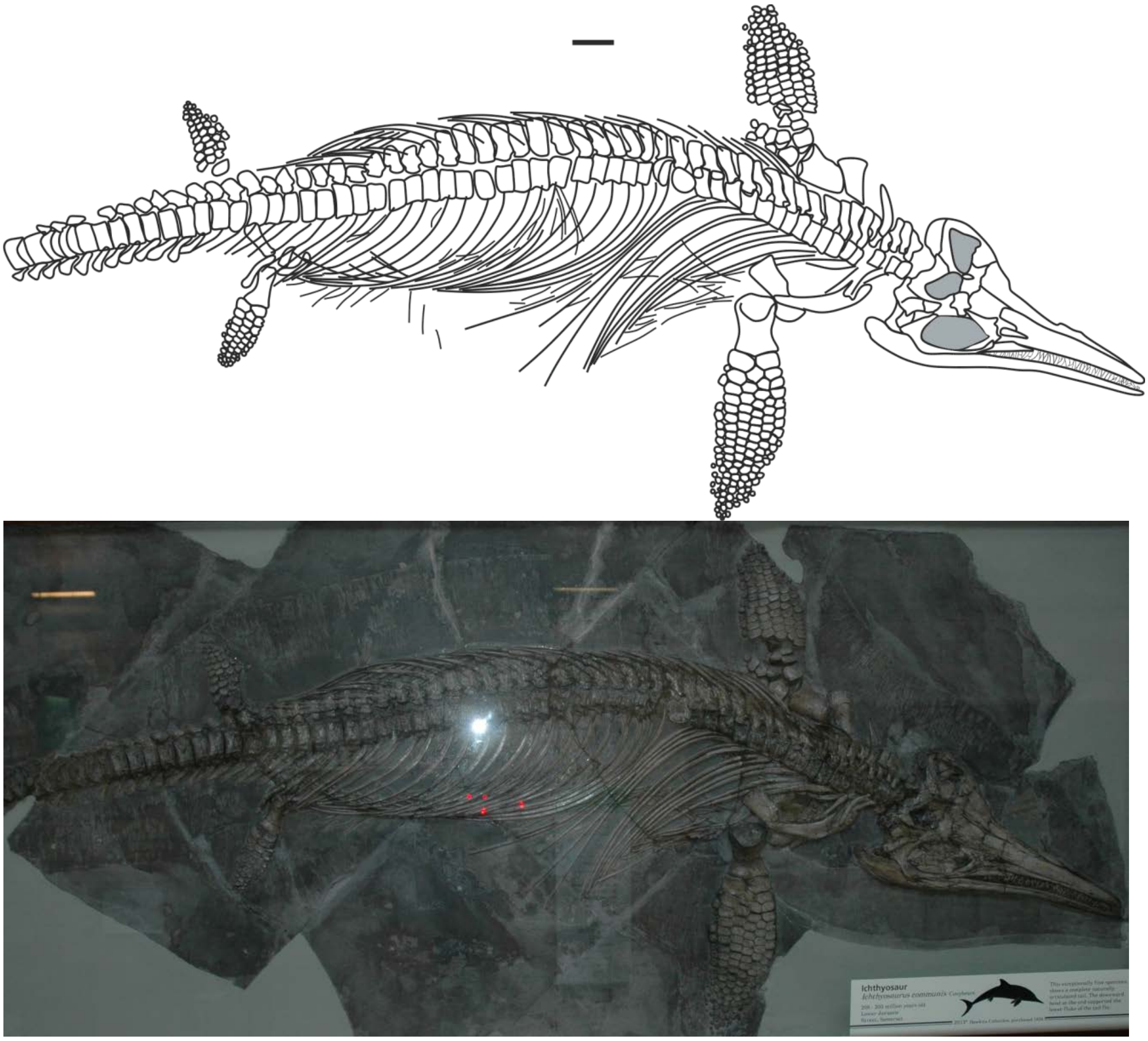


Figure 13. Interpretation line drawing (top) and image (bottom) of specimen NHMUK PV OR2013 a member of the species *Ichthyosaurus somersetensis*. Scale bar and distance between the 2 brighter red dots is equal to 64.61 mm and grey areas indicate fenestra.

19. Supratemporal-postorbital contact: 0-present; 1-absent (Sander, 2000 Char 27).

   a. The supratemporal bone is present posterior to the upper temporal fenestra and is sometimes in contact with the postorbital posterior to the orbit. The presence or absence of this contact cannot always be seen in lateral view and is therefore often not very informative in specimens that are preserved in lateral view. Contact between the two bones is present in *Temnodontosaurus* and specimens NHMUK BGS956 and NHMUK PV R216. Absence of this contact is present in *Macgowania* and specimens DONMG 1983.98 (Figure 11) and BRSMG Cc921.
   b. Inverted coding seen in Fischer et al., 2011, but as it is not clear in the outgroup what the states are; I have kept it as the original coding.

20. Width of upper temporal fenestrae in dorsal aspect: 0- posterior half conspicuously narrower than anterior half; 1-anterior and posterior halves approximately equal in width (Druckenmiller and Maxwell, 2010 Char 11).
    a. Referring to the difference in width of the anterior and posterior parts of the upper temporal fenestra. A narrow posterior half of the upper temporal fenestrae is present in NHMUK PV OR2013 (Figure 13) and OUMNH J10301. Equal anterior and posterior halves of the upper temporal fenestrae are present in AGC14, and LEICT G151.1991.
    b. Unmodified.
21. Broad contact or overlapping postfrontal-postorbital contact: 0- present; 1- absent (modified from Roberts et al., 2014 Char 16).
    b. This refers to the contact on the exterior of the skull as well as interior, so this may be difficult to see on the inside of non- 3D specimens. The broad or overlapping postfrontal-postorbital is present in *Macgowania* (Figure 1), *Temnodontosaurus* and NHMUK OR43006 (Figure 6). Absence of broad or overlapping contact is present in DONMG 1983.98 (Figure 11) and BRSMG Cc921 (Figure 9).
    c. This was modified from Roberts et al., 2014 for clarification as in a personal communication with A.J. Roberts, it was established that the term broad mainly referred to the overlap of the bones.
22. Postorbital: 0- narrow; 1- broad (Modified from Fernandez, 2007 Char 7).
    a. This deals with the anterior-posterior thickness or broadness of the bone directly anterior to the orbit. Narrow and broad tend to be quite subjective terms, but the specimens concerned have broader postorbitals than the outgroup taxa in this study. Fernandez (2007) hypothesised that this was a result of the orbit becoming larger, and so the postorbital would shrink to accommodate larger eye. A narrow postorbital is present in *Macgowania* (Figure 1), *Hudsonelpidia* (Figure 3) and specimens NHMUK PV R1162 (Figure 4), NHMUK PV OR43006 (Figure 6), and DONMG 1983.98 (Figure 11). A broad postorbital is present in *Temnodontosaurus* and specimens NHMUK PV OR2013 (Figure 13) and OUMNH J.10330.
    b. Reversed coding for states.
23. Squamosal shape: 0- triangular; 1- squared; 2- squamosal absent (Fischer et al., 2011 Char 16).
    a. The squamosal is present posterior to the postorbital, dorsal to the quadrate and ventral to the supratemporal. Maisch and Matzke (2000a) identified that

some specimens of *Ichthyosaurus* retained a squamosal. A triangular shaped squamosal is present in *Macgowania* (Figure 1) and specimens BRSMG Cc921 (Figure 9) and NHMUK PV R216. A squared squamosal is present in *Hudsonelpidia* (Figure 3), *Temnodontosaurus* and NHMUK R1162 (Figure 4). The squamosal appears to be absent in NHMUK BGS956.

   b. Unmodified.

24. Lateral exposure of angular in posterior portion of mandibular ramus: 0- much smaller than surangular exposure; 1- approximately equal to surangular; 2- larger than surangular (modified from Motani, 1999 Char 32 and Fernandez, 2007 Char 9).
    a. This character refers to how much of the angular is seen in lateral view compared to that of the surangular. Both the angular and surangular are present towards the posterior of the skull in the lower jaw. This comparison was made towards the posterior margin of the jaw. An exposure of the angular that is much smaller than the surangular is most the most common state seen in this analysis and is seen in *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 4), NHMUK PV OR43006 (Figure 6), and DONMG 1983.98 (Figure 11). State 1 is present in *Macgowania* (Figure 1) and AGC11. A larger angular than surangular is least common, and is present in CAMSM 5975.
    b. Modified by adding a third character state (2) as in Druckenmiller and Maxwell, 2010 and states reordered by the author for this analysis.
25. Basioccipital peg: 0- present; 1- absent or reduced (Motani 1999, Char 29).
    a. The posteriorly projecting peg is located on the anterior side of the basioccipital (opposite side of the basioccipital condyle). This can only be seen in skulls where the basioccipital is visible in anterior view, and is therefore not applicable for many of the specimens in this study (predominantly those preserved in lateral orientation). This character is uninformative for this study, yet may be informative where specimens are preserved three dimensionally. State 0 is present in *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 4) and DONMG 1983.98. No specimens reflect state 1 in this study.
    b. Unmodified.
26. Extracondylar area of basioccipital: 0- wide area extending to each side of the condyle; 1- reduced but still present ventrally and laterally; 2- extremely reduced, being nonexistent at least ventrally (modified from Fernandez, 2007 Char 10).
    a. This is the area present in the middle of the skull in posterior view. A wide area on both sides of the condyle is present in AGC9 and an area reduced but still present in AGC17 and OUMNH J.13810. No specimens in this study show the extracondylar area as extremely reduced (see Figure 14).
    b. State 0 is modified in this character to better explain the assignation of the term ‘wide’. The other two states are not modified.

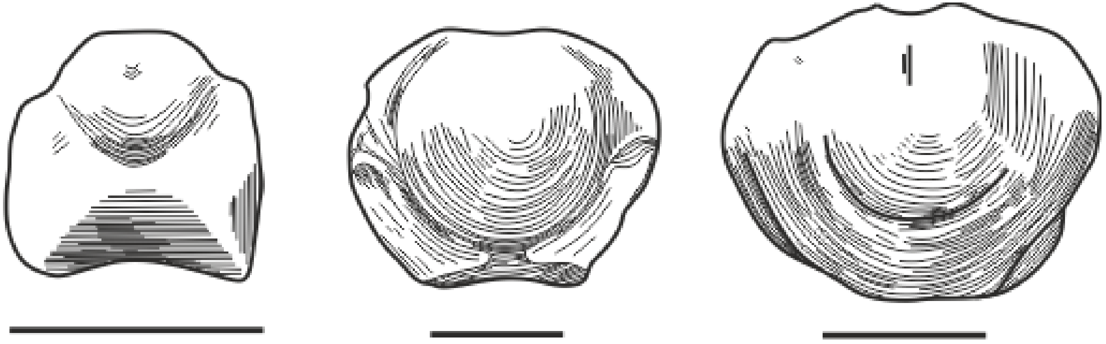


Figure 14. Three basioccipitals in posterior view showing the different states of Character 34. The far left is based on a specimen of *Ichthyosaurus* (OUMNH J29172 and J2242a) and represents state 0 of Character 34. The middle is based on a specimen of *Opthalmosaurus* (YORYM? 100’1949/48) and shows state 1 of Character 34. The far right is based on a specimen of *Brachypterygius* (CAMSM J68515) and shows state 2 of Character 34. All scale bars are equal to 40 mm (modified from Mcgowan and Motani, 2003).

27. Ventral notch on the extracondylar area of the basioccipital: 0-present; 1- absent (Fischer et al., 2012 Char 19).
    a. Small notch or embayment on the ventral side of the basioccipital. A notch is seen in *Temnodontosaurus* and absent in specimens AGC17 and OUMNH J.13810. This character is often obscured by other bones or because the specimen is preserved in lateral view.
    b. Unmodified.
28. Basipterygoid processes: 0- short, giving basisphenoid a square outline in dorsal view; 1- markedly expanded laterally, giving basisphenoid wing-like shape (Fischer et al., 2011 Char 18).
    a. The basisphenoid is present at the posterior portion on the skull ventral to the basioccipital. The basisphenoid is only visible in posterior or ventral view of skull, and so is dependent upon preservation. A square basisphenoid is present in AGC16, NHMUK BGS956, and OUMNH J.10301. A wing-like basisphenoid is present in AGC7, AGC8 and CAMSM TN910.
    b. Unmodified.
29. Overbite: 0- absent; 1-slight; 2- present, and clear (Modified from Motani, 1999 Char 33).
    a. Overbite is absent in *Macgowania* (Figure 1), slight in NHMUK PV OR38523 (Figure 10) and NHMUK PV R1162 (Figure 4). The overbite is seen as present and clear in NHMUK BGS956, NHMUK PV OR120 (Figure 12) and OUMNH J.13810 (Figure 8).
    b. This was modified to separate the absent and slight categories from the original coding. For studies that include *Excalibosaurus* or *Eurhinosaurus* another state could be identified as large or extreme.
30. Mid to anterior rostrum tooth shape: 0- teeth robust; 1- teeth moderately slender; 2- teeth very slender (Massare and Lomax, 2016 Char 21).
    a. General morphology of teeth in the mid to anterior portion of the jaw. This section is identified for clarity, considering the change in tooth morphology

from anterior to posterior. Robust teeth are seen in *Temnodontosaurus* and specimens BRSMG Cc921 (Figure 9), CAMSM 5975. Moderately slender teeth are seen in NHMUK PV R1162 (Figure 4), NHMUK PV OR43006 Figure 6), and DONMG 1983.98 (Figure 11). Very slender teeth are present in NHMUK BGS956 (Figure 7), NHMUK PV OR120 (Figure 12), and OUMNH J.13810 (Figure 8).
    b. Unmodified.

31. Crown striations: 0- Crown enamel finely or subtly ridged; **1- Crown enamel robustly ridged;** 2- Crown smooth (Modified from Druckenmiller and Maxwell, 2010 Char 25).
    a. This character separates the types of ridges are present on the crown of the teeth. This often varies from the root of the tooth (see Char 44). State 0 is present in *Macgowania* (Figure 1), *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 4), NHMUK PV OR43006 (Figure 6), and DONMG1983.3. State 1 is present in BRSMG Cc921 (Figure 9).State 2 is present in OUMNH J.13810.
    b. Modified by Fischer et al. (2013) by removing the basal state (presence of deep longitudinal ridges) for this analysis as it was not seen in any specimens. The second state was split into two character states to distinguish tooth variation. Character state 1 was also added.
32. Base of enamel layer: 0- well defined, precise; 1- poorly defined, invisible (Fischer et al., 2011, Char 2).
    a. This character can only be seen in teeth that are completely exposed with enamel preserved. Well defined base of enamel is present in *Macgowania* (Figure 1), *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 4), NHMUK PV OR4006 (Figure 6), and DONMG1983.3. Poorly define enamel layers are present in NHMUK PV OR38523 (Figure 16), NHMUK PV OR2013 (Figure 13) and OUMNH J.13810.
    b. Unmodified.
33. Tooth root diameter on most mid- to anterior rostrum teeth: 0- root abruptly expanded compared to base of crown; 1- crown and root continuous, gradual expansion of root. It can be noted that posterior maxillary teeth frequently have abruptly expanded roots and short, wide crowns. State 0 is referred to by Maisch (1997) as a ‘waisted’ tooth. (Lomax and Massare, 2016 Char 20).
    a. Significant expansion of roots in teeth compared to that of crown, giving the teeth a ‘waisted’ appearance is another way of explaining state 0 and is present in AGC11, and TTNCM 120/1996. A continuous root was more common in this study and is present in *Macgowania* (Figure 1) and specimens NHMUK PV R1162 (Figure 4), NHMUK PV OR38523 (Figure 16), and NHMUK PV OR43006 (Figure 6).
    b. Unmodified
34. Striations on tooth root: 0- absent; 1- present and small; 2-present and robust (Modified Fischer et al., 2012 Char 4).
    a. On the roots of teeth there may be ridges present. State 0 is present in specimens NHMUK PV BGS956, NHMUK PV R1162 (Figure 4), and

NHMUK PV OR43006 (Figure 6). State 1 is only present in *Hudsonelpidia* and state 2 is present in *Macgowania* (Figure 1) and *Temnodontosaurus*.

b. Reverse coding as Fischer et al., 2014. Change from absent or subtle to just absent. Present has been separated, due to observations of both small and robust ridges on specimens.

Axial Skeleton

35. **Atlas-axis fusion: 0-present, completely fused; 1- functionally separate, never fused**
    a. The atlas–axis complex refers to the first two vertebrae present posterior to the skull. The fusion of this complex and potential other vertebrae varies extensively (VanBuren and Evans, 2016). The fusion of this complex within other organisms has been studied (Buchholtz, 2001a, 2001b, 2004), but has not been studied or included in any ichthyosaur phylogenetic studies to date. The function and significance of this fusion could potentially be better understood if included in future phylogenetic work. The atlas-axis complex is seldom mentioned nor figured in the literature and the fusion or lack thereof rarely commented upon (pers. obs.). A fused atlas-axis is present in *Temnodontosaurus* and specimen AGC11 (Figure 18). A functionally separate atlas-axis is present in NHMUK PV OR43006 (See Figure 15).

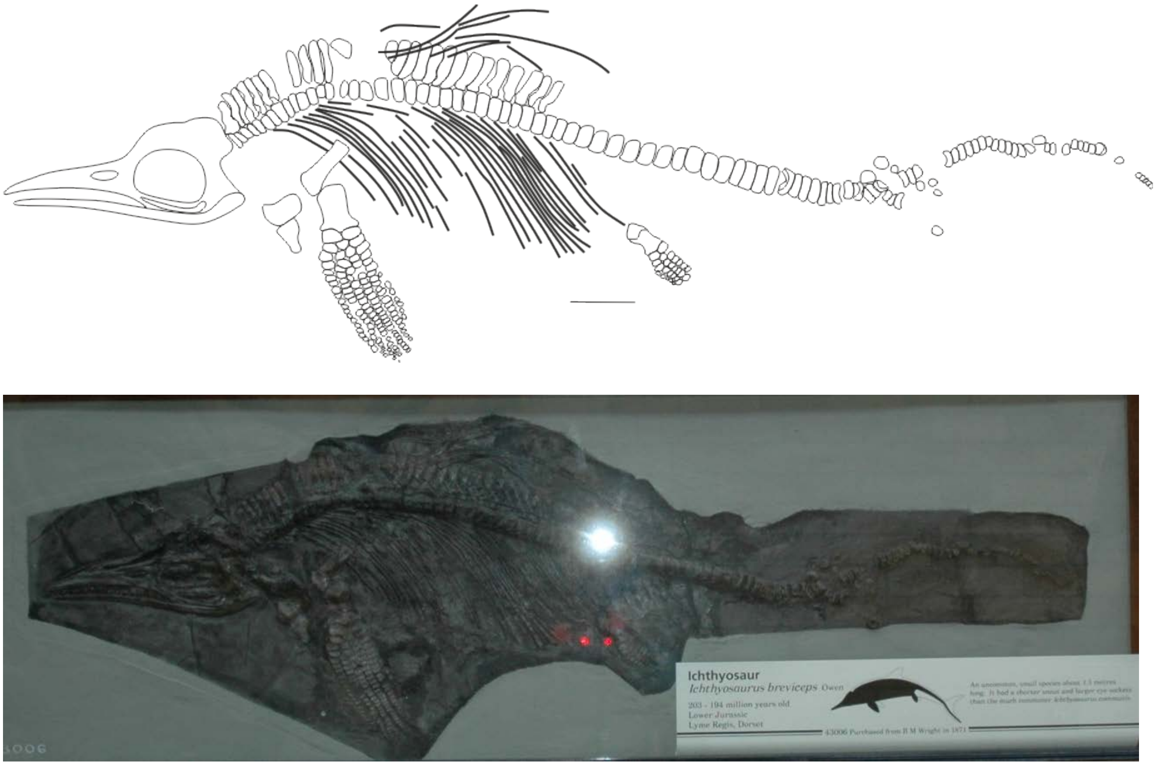


Figure 15. Interpretation line drawing (top) and image (bottom) of NHMUK PV OR43006 the holotype for *Ichthyosaurus breviceps*. Scale bar is equal to 64.61 mm.

36. Neural arches of atlas and axis: 0- completely overlapping may be fused; 1- functionally separate, never fused (Druckenmiller and Maxwell, 2011 Char 26).
    a. Referring to the neural arches on the atlas-axis complex. This fusion, seen on the atlas-axis is rarely discussed (pers. obs.). Fused neural spines are

present in *Temnodontosaurus* and specimens NHMUK PV OR2013 (Figure 13), and NHMUK BGS956. Separate neural spines are present in NHMUK PV R1162 (See Figure 17), NHMUK PV OR38523 (Figure 16) and AGC11 (Figure 18).

  b. Unmodified.

37. Anterior to middle dorsal neural arches: 0- narrow, relatively short and straight; 1- narrow, straight, height, increasing in height to mid-dorsal; 2- narrow straight high, of constant height to mid-dorsal (modified by Lomax and Massare, 2016 Char 64 from Calloway, 1989 Char 16). Note that this can be difficult to score as displaced ribs, centra, or matrix often obscures the neural spines.
    d. Referring to the shape and height of the neural arches and how this changes from cervical/the atlas-axis complex to sacral region of the specimen. Narrow short and straight neural spines are present in *Californosaurus*, *Temnodontosaurus* and specimen AGC11 (Figure 18). Narrow, straight and increasing in height neural spines are present in *Hudsonelpidia* and specimens NHMUK PVOR43006 and NHMUK PV OR32103. Narrow straight and of constant height neural spines are present in specimens NHMUK PV R1162 (Figure 17), and TTNCM 120/1996.
    e. Modified by Massare and Lomax (2016) to be more descriptive than quantitative.

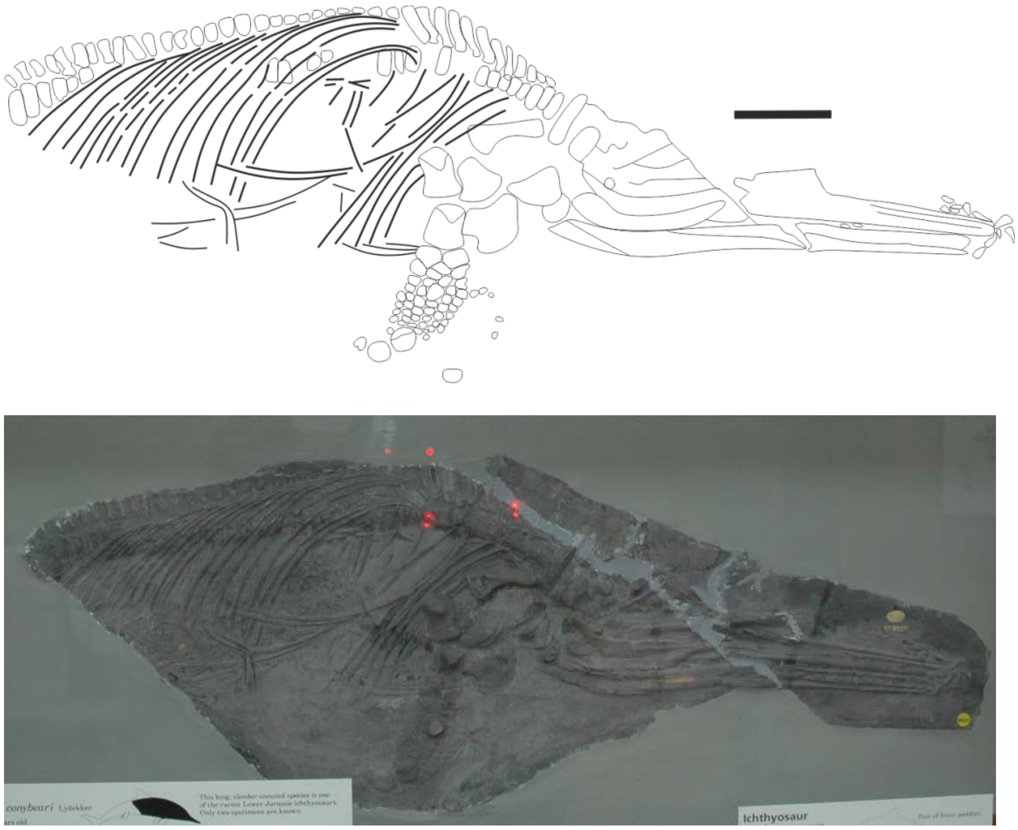


Figure 16. Interpretation line drawing (top) and image (bottom) of NHMUK PV OR38523 the holotype for *Ichthyosaurus conybeari*. Scale bar is equal to 53.52 mm.

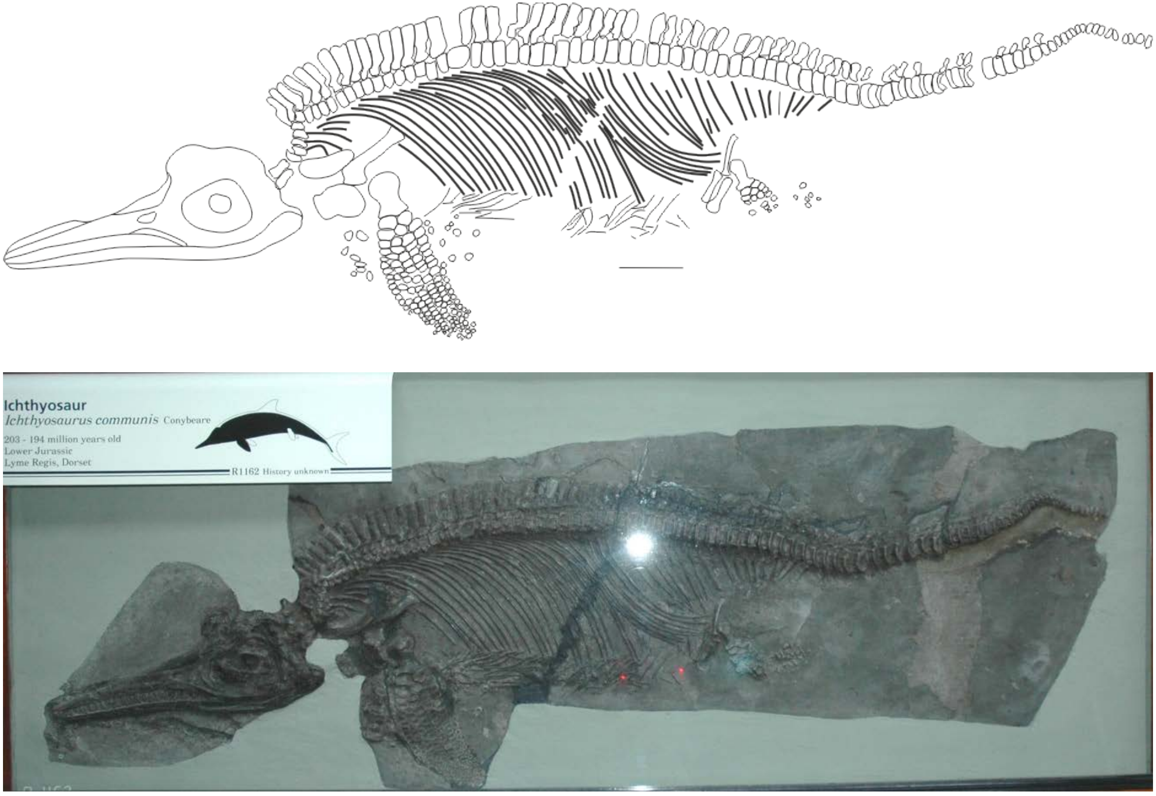


Figure 17. Interpretation line drawing (top) and image (bottom) of NHMUK PV R1162 the neotype for *Ichthyosaurus communis*. Scale bar is equal to 64.61 mm.

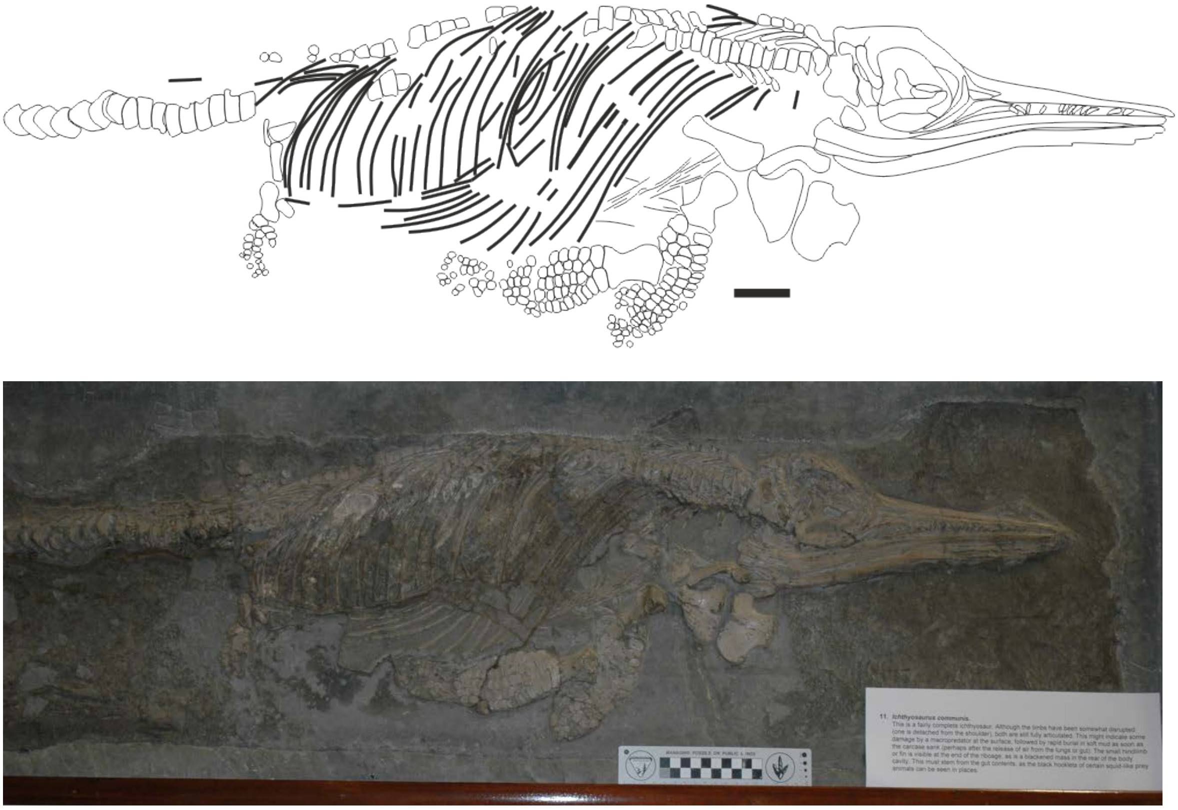


Figure 18. Interpretation line drawing (top) and image (bottom) of specimen number AGC 11. The distal part of the tail is not present in this interpretation and image, but is present in the specimen. Scale bar is equal to 50 mm.

38. ‘Cervical’ centra (diapophysis-neural arch facet contact): 0- extend up to middle dorsal region; 1- anterior dorsal region (Fischer et al., 2011 modified from Sander, 2000: character 66).
    a. Referring to the region at which the rib facet loses contact with the neural arch facet, starting at the atlas axis. This may only be useful in separating out other genera from *Ichthyosaurus*. Contact extending up to the middle dorsal is present in *Californosaurus* and specimens NHMUK BGS956 and NHMUK PV OR120 (Figure 12). Contact extending to anterior dorsal region is present in NHMUK PV OR43006 (Figure 15), and NHMUK PV OR2013 (Figure 13).
    b. Modified by Fischer et al. (2011) by providing more details to the character and changing the states.
39. Rib articulation in dorsal region: 0- predominantly unicapitate; 1- exclusively bicapitate (Maisch and Matzke 2000b, Char 53).
    a. This character refers to the shape of the dorsal end of the thoracic rib where it articulates with the vertebral column. If one process is present on more than 50% of the ribs then it is coded for state 0: this is present in *Californosaurus* and specimens NHMUK BGS956 and NHMUK PV OR43006 (Figure 15). If two processes are present on the rib articulation point then state 1 is given: this is present in *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 17) and AGC11 (Figure 18).
    b. Unmodified.
40. Rib cross-section at mid-shaft: 0- rounded or oval; 1-‘8’ shaped (modified by Fischer et. al. 2013 from Sander, 2000 Char 73).
    a. This refers to the general shape of the rib in cross-section in the middle area of the rib, as the shape changes if to dorsal or ventral. A rounded or oval cross-section is present in *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 and DONMG 1983.98. A figure-of-eight shaped cross-section is present in specimen OUMNH J.10301.
    b. Modified by removing the third character state 3 (wide-oval) that was used by Sander, 2000 for *Eurhinosaurus*.
41. Chevrons: 0- present; 1- lost (Sander, 2000 Char 72).
    a. The presence or absence of chevrons in specimen. This may only help to distinguish between outgroups, other genera and *Ichthyosaurus*. Little data is available as goes the presence of chevrons in post-Triassic ichthyosaurs. Chevrons are present in *Temnodontosaurus* and specimens NHMUK BGS956 and NHMUK PV OR2013 (Figure 13). Chevrons are absent in *Californosaurus* and specimens NHMUK PV R1162 (Figure 17) and NHMUK PV OR43006 (Figure 15).
    b. Unmodified.

Appendicular Skeleton (pectoral girdle)

42. Interclavicle robustness: 0- robust; 1- slender

   a. This character is designed to determine the robustness aspect of the interclavicle. The robustness is determined when comparing the interclavicle to the jugal. If the interclavicle anterior to posterior thickness is smaller than or equal to the jugal dorso-ventral length than the interclavicle is considered slender. A robust interclavicle is present in NHMUK PV OR38523 (Figure 16), and OUMNH J.10301. A slender clavicle is present in MANCH L.9908 (Figure 19), NHMUK PV OR38803, and NHMUK PV OR41849.

Figure 19. Image of specimen MANCH L.9908 where the two clavicles and 2 clavicles meet.

43. Scapula: 0- with prominent acromion process; 1- large acromion process absent but anterior expansion of ventral part of scapula present; 2- ventral expansion absent, scapula strap-shaped (modified from Maxwell, Fernandez, and Schoch, 2012 Char 31).
    a. Plesiomorphically in Baracromians and some Leptonectids, the anterior border of the scapula forms a simple concave curve. This is the present in *Hauffiopteryx*, *Stenopterygius*, *Ophthalmosaurus icenicus*, and *Platypterygius australis* (Maxwell, Fernandez, and Schoch, 2012). However, in several taxa, *Californosaurus*, *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR38523 (Figure 16), NHMUK PV OR43006 (Figure 15) and DONMG 1983.98 (Figure 11)

are coded as possessing state 1. CAMSM TN910 is coded as possessing state 2. The acromion process is located on the antero-dorsal portion of the scapula.

    b. Changed proximal to ventral part of and ventral.

44. Scapula dorsoventral length: 0- about as long as humerus (within 10%); 1- no more than 1.5 times as long as the humerus; 2- more than 1.5 times as long as the humerus (Modified from Lomax and Massare, 2016 Char 49).
    a. Comparison of scapula dorsoventral length to humerus dorsoventral length. The scapula and humerus are of approximately equal length in *Californosaurus* and specimen AGC17. In other taxa, NHMUK PV OR43006 (Figure 15), DONMG 1983.98 and AGC11 (Figure 18), the scapula is not more than 1.5 times as long as the humerus.
    b. Changed proximodistal length to dorsoventral length. And removed state 3 (scapula noticeably shorter than humerus) as no specimens have this state present.
45. Scapula shape: 0- no shaft; 1- long shaft, more than twice the proximal dimensions; 2- short shaft, no more than twice the proximal dimension (modified from Lomax and Massare, 2016 Char 50).
    a. Comparison of the dorsoventral length of the scapula to the dorsal width of scapula. *Californosaurus* has a scapula with no shaft present, meaning there is not dorsal-ventral elongation to provide a ‘strap-like’ morphology described in (McGowan and Motani, 2003). While other taxa, *Temnodontosuarus* and specimens NHMUK PV R1162 (Figure 17) and NHMUK PV OR38523 (Figure 16). In taxa NHMUK PV OR43006 (Figure 15) and DONMG 1983.98 (Figure 11) possess a short shafted scapula.
    b. Modified to add state 0 for out group.
46. Glenoid contribution of the scapula: 0- extensive, at least as large as the coracoid facet; 1-reduced, markedly smaller than the coracoid facet (Fischer et al., 2012 Char 27).
    a. Glenoid contribution is on the ventral side of the scapula and the area between that process and the coracoid is the glenoid. The glenoid contribution has been interpreted as the area or thickness of the facet (see page 38 McGowan and Motani, 2003) that contributes to the area mentioned above. The taxa that show an extensive glenoid contribution are NHMUK PV OR43006 (Figure 15), NHMUK PV R15907 (Figure 5) and CASMX50187. A smaller glenoid contribution is present in *Californosaurus*, *Temnodontosaurus* and specimen NHMUK PV OR2013 (Figure 13).
    b. Unmodified.
47. Coracoid shape: 0- mediolaterally wider than anteroposteriorly long; 1- approximately equidimensional, lengths within 10% of each other; 2- anteroposteriorly longer than mediolaterally wide (Maxwell, Fernandez, and Schoch, 2012 Char 32).
    a. The taxa AGC15 and CAMSM J35189 have a coracoid that is wider mediolaterally than anteroiorposteriorly long. A coracoid that is approximately equal in length is present in *Californosaurus*, *Macgowania*,

Temnodontosaurus and specimen NHMUK PV OR38523 (Figure 16). A coracoid that is longer anteroposteriorly is seen in DONMG 1983.98 (Figure 11) and AGC11 (Figure 18).
   b. Unmodified.

48. Anteromedial process of coracoid: 0- absent; 1- present (modified from Fischer et al., 2013 Char 37 who have modified from Fischer et al. 2011 Char29).
    a. Process present anteromedially and extending anteriorly. This process is not present in *Temnodontosaurus* but is present in *Californosaurus* and specimens NHMUK PV OR38523 (Figure 16) and DONMG 1983.98 (Figure 11).
    b. Modified from Fischer et al. 2013 to exclude the state about the anterior notch as it is addressed in next character.

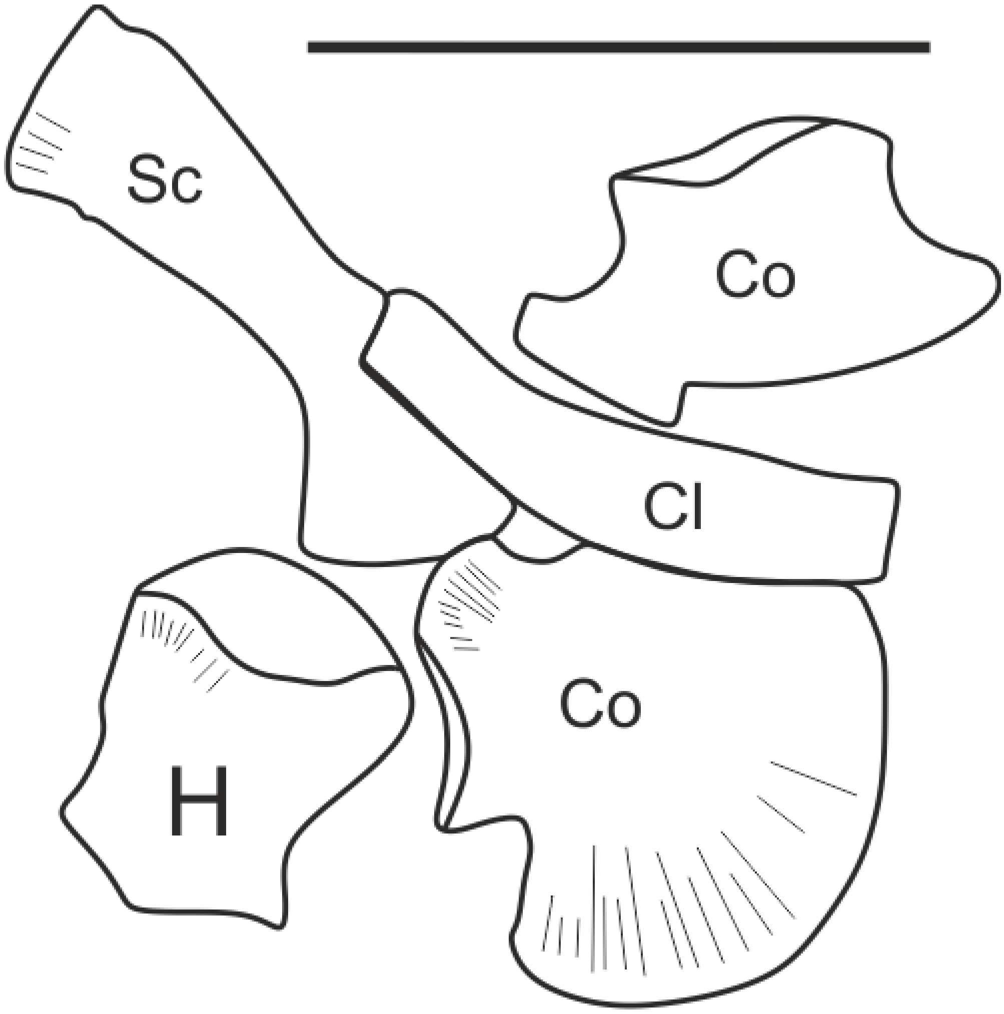


Figure 31. Interpretation of the pectoral girdle of specimen NHMUK PV OR120. Scale bar equals 50 mm. **Abbreviations: Cl**, clavicle; **Co**, corocoid; **H**, humerus; and **Sc**, scapula.

49. Coracoid anterior notch: 0- absent; 1- present but small and tightly curved; 2- present and broadly curved (Lomax and Massare, 2016 Char 53).
    a. Ancestrally the anterior notch on the coracoid is absent and this condition is present in *Cymbospondylus* and *Toretocnemus* (Mcgowan and Motani, 2003) which were not used in this study. A small and tightly curved anterior notch is present in *Californosaurus, Temnodontosaurus* and specimen

NHMUK PV OR38523 (Figure 16). A more broadly curved anterior notch is present in DONMG 1983.98 (Figure 11) and AGC11 (Figure 18).

  b. Unmodified.

50. Coracoid posterior notch: 0- absent; 1-present but small and tightly curved; 2-present and broadly curved (Lomax and Massare, 2016 Char 54).
    a. A notch similar to that of Character 61 but is independent to the shape of the anterior notch. There is no posterior notch present in basal taxa of this study, *Californosaurus* and *Temnodontosaurus*. A notch that is small and tightly curved is present in NHMUK PV OR120 (Figure 31) and OUMNH J.13810 (Figure 8). A broadly curving notch is present in DONMG 1983.98 (Figure 11) and AGC11 (Figure 18).
    b. Unmodified.

Appendicular Skeleton (forefin)

51. Humerus with anterior flange: 0- absent or largely reduced; 1- present and complete; 2- present but reduced proximally (modified by Motani, 1999 Char 53 from Callaway 1989 Char 28).
    a. A process on the anterior side of the humerus, state 1 is present in the mid anterior section of the humerus. This state is seen in taxa BU5289. In state 2, the flange is restricted to the anteridistal edge of the humerus shaft. This state is present in *Californosaurus, Temnodontosaurus, Macgowania,* and *Hudsonelpidia*. Absence or substantial reduction of the flange is present in specimens DONMG 1983.98 (Figure 11) and LEICT G125.1992.
    b. Author modified state 0 to include ‘largely reduced’. Modified by Motani (1999 Char 53). Callaway= Humerus length/maximum anteroposterior width: (0) long (l/w>3), rounded cross-section (1) short (l/w>1-2), laterally compressed (2) very short (l/w =0.7-1), laterally compressed.
52. Humerus distal and proximal ends, exclusive of anterior flange: 0- nearly equal; 1-distal end wider than proximal end (Motani, 1999 Char 55).
    a. The anterior flange is described in character 63 above. When measuring the relative widths of the humerus, the anterior flange is to be disregarded. Approximately equal ends of the humerus are present in *Californosaurus, Macgowania*, *Hudsonelpidia* and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 (Figure 15) and DONMG1983.3. A humerus with a distal end wider than the proximal end is present in *Temnodontosaurus* and specimen AGC11 (Figure 18).
    b. Unmodified.
53. **Humerus shape; 0- short and squat; 1- elongate/ slender**
    a. This character describes the elongation, or lack thereof, of the humeral shaft. A humerus that is short, squat and having little in the means of a shaft is present in *Californosaurus*, and NHMUK PV OR38523 (Figure 16). A more elongate humerus with an obvious shaft is present in *Temnodontosaurus*, *Macgowania*, *Hudsonelpidia* and specimens AGC11 (Figure 18), NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 (Figure 15), and DONMG 1983.98 (Figure 11).

54. **Humerus with constricted shaft: 0- absent; 1- present.**
    1. The middle section of the humerus is narrower than the distal and proximal ends of humerus. If the middle section is equal or nearly equal in width to either distal or proximal end, there is not a constricted shaft. No constriction is present in *Californosaurus*, *Hudsonelpidia*, and *Temnodontosaurus*. This is seen in early ichthyosaurs and others such as *Suevoleviathan*.
55. Deltopectoral crest of humerus: 0- present and large; 1- present and small (modified by Lomax and Massare, 2016 Char 23 from Maxwell, 2010 Char 20).
    1. A crest on the ventral side of the humerus and is considered large if the crest protrudes distally around 50% of the total proximal-distal length of the humerus. This state is present in DONMG 1983.98 (Figure 11), OUMNH J.10301 and BIRUG 8823. If the crest is present and less than 50% of the proximodistal length it is considered small. Small deltopectoral crests are present in NHMUK PV OR3852 (Figure 16), NHMUK BGS956 and AGC11 (Figure 18).
    2. Modified by the addition of character state 1. Character state 2 was not used in the article by Massare and Lomax (2016), nor for this study, and was therefore removed.
56. Humerus shape: 0- up to 1.5 times as long as distally wide; 1- more than 1.5 times as long as distally wide; 2- almost as distally wide as it is long (modified by Lomax and Massare, 2016 Char 24 from Callaway, 1989 Char 28).
    1. Comparing the proximal width of the humerus to the distal width and quantifying how much larger or smaller they are from each other. A humerus length of up to 1.5 times distal width is present in *Macgowania*, *Hudsonelpidia* and specimens NHMUK PV OR38523 (Figure 16), NHMUK PV OR43006 (Figure 21) and DONMG 1983.98 (Figure 11). A humerus with more than 1.5 times as long as distal width is present in NHMUK PV R11626 (Figure 17) and OUMNH J.10330. A humerus almost as distally wide as it is long is present in *Californosaurus* and specimen NHMUK PV R12.
    2. Modified by Massare and Lomax (2016) to specify distal width, as opposed to the maximum anteroposterior width. Callaway (1989) included the cross-section of the humerus, creating some ambiguity of the character.
57. Humerus shaft: 0- wide relative to distal end; 1- narrow relative to distal end (Lomax and Massare, 2016 Char 25).
    1. A comparison of the widths of shaft and distal end of humerus, assuming that the dorsal view is accessible. A shaft that is wide relative to the distal end is present in *Californosaurus*, *Macgowania*, and specimen NHMUK PV OR38523 (Figure 16). A shaft that is narrow relative to the distal end is present in *Hudsonelpidia*, *Temnodontosaurus* and NHMUK PV R1162 (Figure 17).
    2. Unmodified.

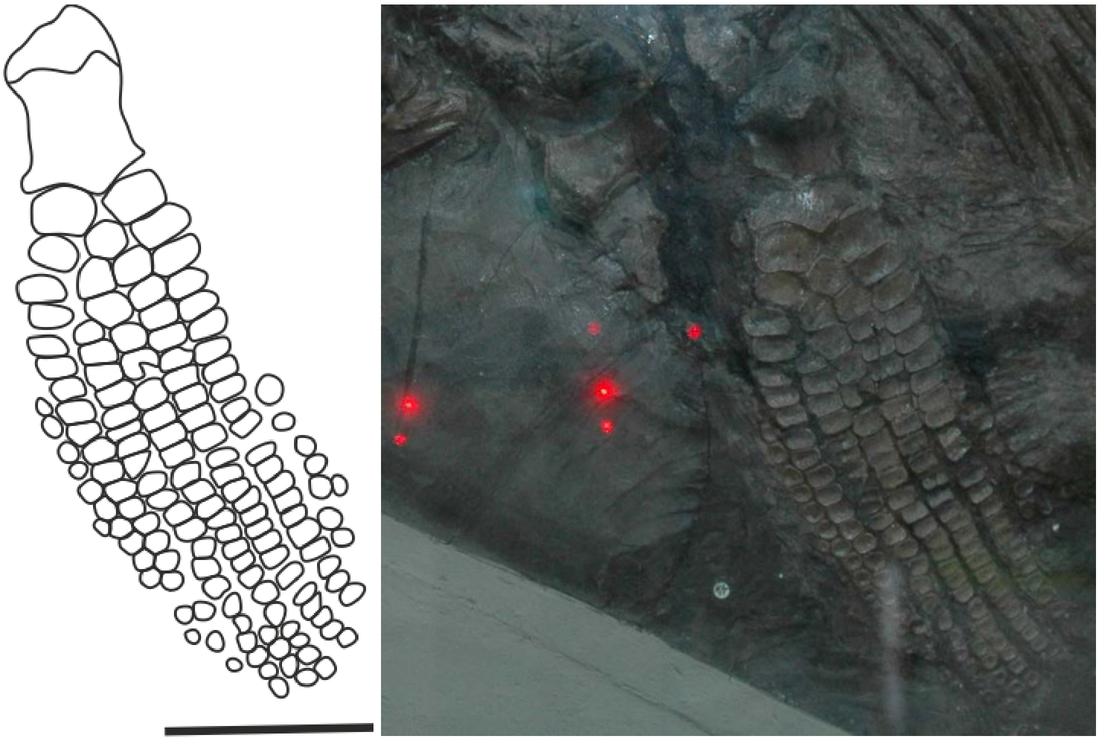


Figure 21. Forefin of *Ichthyosaurus breviceps* NHMUK PV OR43006 showing details of phlanages and accessory digits. Outline interpretation is on the left and picture of actual specimen in on the right. The scale bar and points between the bright red dots are 53.52 mm

58. Humerus, circular depression on articular surface anterior to dorsal process: 0- absent; 1- small concavity on irregular bone surface; 2- distinct oval depression on smooth bone surface (Lomax and Massare, 2016 Char 26).
    a. This character describes the two different types of depressions seen on the proximal surface of the humerus. This character is currently only relevant for distinguishing between species of *Ichthyosaurus,* as *I. communis* has the irregular concavity and *I. anningae* the smooth oval depression present (Lomax and Massare, 2016). The depression is absent in all outgroups, *Temnodontosaurus* and NHMUK PV OR38523 (Figure 16). The small irregular concavity is present in NHMUK PV R1162 (Figure 17), and OUMNH J.13592. A smooth oval depression is present in DOMG 1983.3, BRSMG Cc921, and DORCM G.13824.
    b. Unmodified.
59. Humerus dorsal process: 0- large, central; 1-small, central; 2- large, offset anteriorly from centre, formed by circular depression on head; 3- small, offset anteriorly from centre, sometimes with distinct ‘lip’ (Lomax and Massare, 2016 Char 27).
    a. Referring to process starting near proximal end of humerus on the dorsal side. This distinguishes the position of this process and how small or large it is relatively. A large central dorsal process is present on NHMUK PV R1162 (Figure 17) and NHMUK PV OR43006 (Figure 21). A small, central dorsal process is present in *Californosaurus*, *Temnodontosaurus* and specimens AGC11 (Figure 18) and NHMUK PV OR120 (Figure 22). A

large, but an anteriorly offset dorsal process is present in DONMG 1983.98 (Figure 11) and RAMM FOS1912. A small, but anteriorly offset dorsal process is present in NHMUK BGS956.

b. Unmodified.

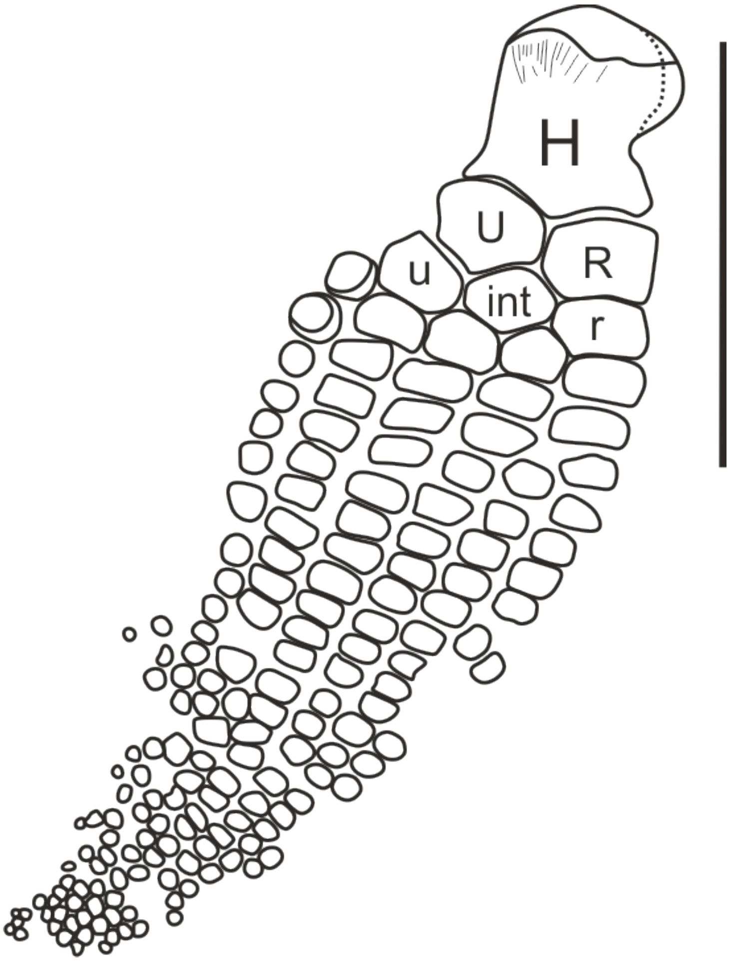


Figure 22. Interpretation of the forefin of specimen NHMUK PV OR120. Scale bar equals 50 mm. **Abbreviations**: **H**, humerus; **i**, intermedium; **R**, radius; **r**, radiale; **U**, ulna; **u**, ulnare.

60. Humerus with anterior facing radial facet: 0- absent; 1- present.

a. A new character to classify the projection angle of the radial facet. The humerus needs to be oriented with midline distal edge perpendicular to the length of the humerus. The deflection is then assessed based on that imaginary perpendicular line and the edge created by the radial facet (Figure 23). An anteriorly facing facet is considered at 25° or more from the perpendicular line. This is absent in *Californosaurus*, *Hudsonelpidia*, *Temnodontosaurus*, and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR38523 (Figure 16) and DONMG 1983.98 (Figure 11). An anterior facing radial facet is present in *Macgowania* and specimens NHMUK PV OR120 (Figure 22 and 15) NHMUK PV OR43006 (Figure 21).

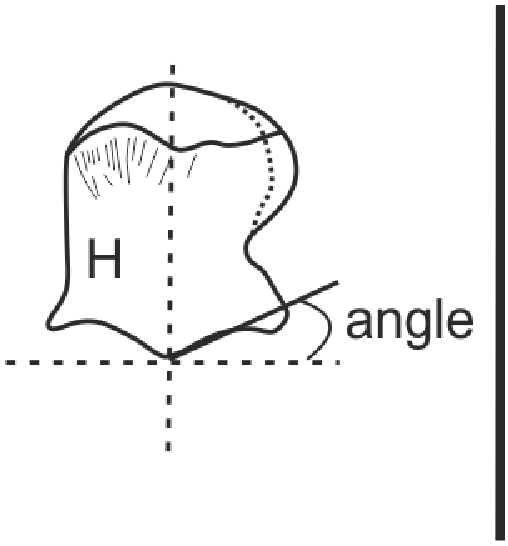


Figure 23. Figure showing how to determine the projection angle of the radial facet for Character 60. Humerus from specimen NHMUK PV OR120, showing an angle of at least 25°. Scale bar equals 50 mm. **Abbreviations**: **H**, humerus.

61. Radius and ulna are: 0- longer than wide; 1- wider than long; 2- about equal length and width (Massare and Lomax, 2014).
    a. Comparison of the dimensions of the radius and ulna, with length defined as medial-distal and width as anterior-posterior. State 0 is present in *Californosaurus*. State 1 is present in *Hudsonelpidia*, *Temnodontosaurus*, and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR38523 (Figure 16), NHMUK PV OR43006 (Figure 21) and DONMG 1983.98 (Figure 11). State 2 is present in *Macgowania* and MANCH L.9663.
    b. Unmodified.
62. Radio-ulnar foramen: 0- present; 1- absent (modified by Fischer et al., 2013 Char 46 modified from Maisch and Matzke, 2000b Char 84 modified from Dal Sasso and Pinna 1996).
    a. A notch or opening present in between the radius and ulna. Mainly used to distinguish from other genera where this is present (*Leptonectes*). The foramen is present in *Californosaurus, Hudsonelpidia* and *Macgowania*. The foramen is absent in *Macgowania* and all the holotypes/neotypes (Figure 24).
    b. Modified by Fisher et al. (2013) by slight rewording most likely for clarification, but it is not discussed by Fischer et al. (2013).
63. Intermedium: 0- in contact with one digit; 1- in contact with two digits (Modified by Lomax and Massare, 2016 Char 30 from Druckenmiller and Maxwell, 2010 char 40).
    a. This character determines if the intermedium bifurcate into two digits, used mainly in this study to distinguish between other genera. The intermediums is in contact with one digit in *Californosaurus*, and *Temnodontosaurus*. The intermedium is in contact with two digits in most other OTUs including *Macgowania* and all the holotypes/neotypes of *Ichthyosaurus*.
    b. Modified by Massare and Lomax (2016) by slight rewording and inverted coding.

64. Radiale, intermedium relative width: 0- radiale wider than intermedium; 1- intermedium wider than radiale; 2- approximately equal (Lomax and Massare, 2016 Char 32).
    a. Relative widths (anterior-posterior measurement) of the radiale (element directly distal to radius) and intermedium (element touching both radius and ulna). State 0 is present in NHMUK PV R116, DONMG 1983.98 (Figure 11), and AGC11 (Figure 18). An intermedium wider than radius is present in *Temnodontosaurus*, NHMUK PV OR38523 (Figure 16), and BRSLI M362. Approximately equal radius and intermedium is present in *Californosaurus*, *Macgowania*, and NHMUK PV OR43006 (Figure 21).
    b. Unmodified.
65. Manual pisiform: 0- present; 1- absent (Motani, 1999 Char 67).
    a. The pisiform is present distally to the ulna with the ulnae, so it is only present when the ulna bifurcates into two digits in basal forms. In derived forms the pisiform is present posteriorly to the ulna in the same line or slightly more proximal than the ulnae, and is present as its own digit. The pisiform is present in *Macgowania* and NHMUK PVR1162 (Figure 17). The pisiform is absent in *Californosaurus*, *Temnodontosaurus*, and specimens NHMUK PV OR38523 (Figure 16), NHMUK PV OR43006 (Figure 21), and DONMG 1983.98 (Figure 11).
    b. Fischer et al., 2011 inverted coding, but this is kept the same as Motani (1999) to properly reflect the outgroup used in this study.
66. Ulnare, intermedium relative width: 0- ulnare wider than intermedium; 1- intermedium wider that ulnare; 2- approximately equal (Modified by Lomax and Massare, 2016 Char 31 from Motani, 1999b Char 66).
    a. A comparison of the relative sizes of the ulnare and intermedium. The ulnare is directly distal to the ulna and the intermedium is in contact with the ulna and radius and can be slightly distal to them. Massare and Lomax (2016) define approximately equal as measurements within 10% of each other, which is a great guideline for characters similar to this. An ulnare that is wider than intermedium is present in NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 (Figure 21), DONMG1983.3. An intermedium wider than the ulnare is present in *Californosaurus*, *Hudsonelpidia*, *Macgowania* (Figure 24) and NHMUK PV OR38523 (Figure 16). Approximately equal ulnare and intermedium is present in NHMUK PV R216 (Figure 2) and OUMNH J.10330.
    b. Modified from Motani (1999b) by changing larger to wider and changing state 2 from intermedium lost to approximately equal.
67. Primary digits in forefin: 0- three; 1- four; 2- five or more (Lomax and Massare, 2016 Char 28).
    a. This character is also discussed in McGowan (1974). Primary digits refer to digits that extend the full length of the fin and extend from the radius or ulna. Postaxial or preaxial only extend for part of the length of the fin and start posterior or anterior to the ulna or radius. Three primary digits are present in *Californosaurus* and *Temnodontosaurus*. Four primary digits are present in *Macgowania* (Figure 24), and DONMG 1983.98 (Figure 11).

Five or more primary digits are present in NHMUK PV R1162 (Figure 17), NHMUK PV OR38523 (Figure 16), NHMUK PV OR43006 (Figure 21), and AGC11 (Figure 18).

b. Unmodified.

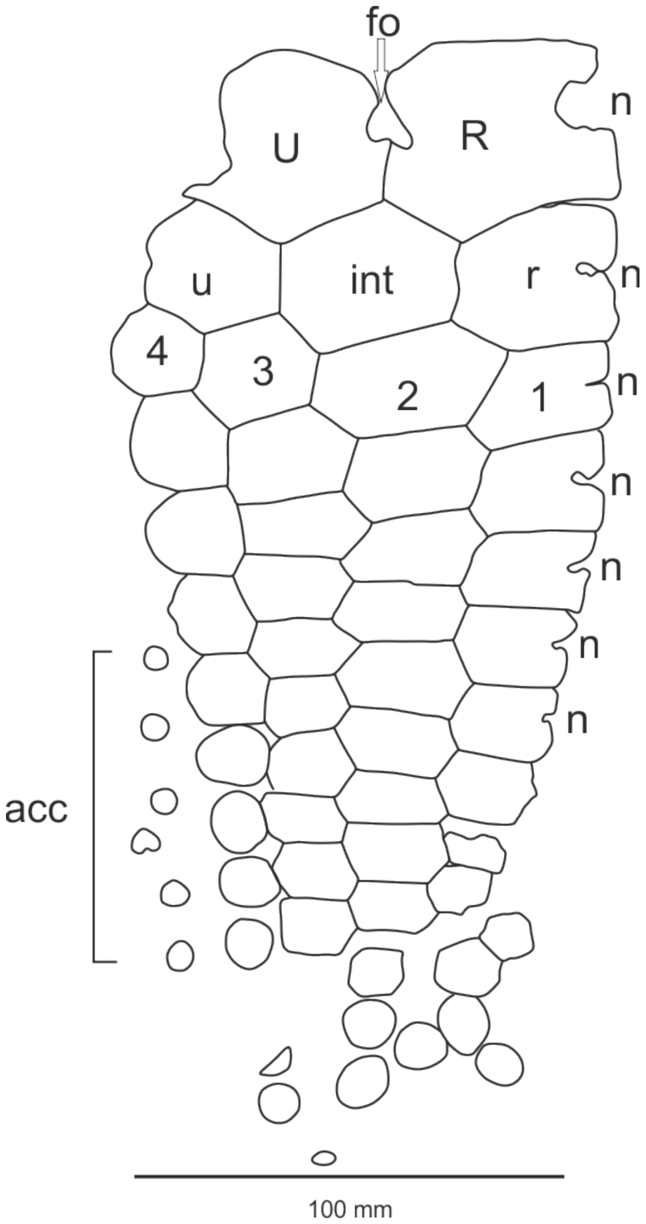


Figure 24. Forefin of *Macgowania janiceps* modified from McGowan (1996, Figure 5). **Abbreviations**: **acc**, part of small accessory digit; **fo**, foramen; **int**, intermedium; **n**, notching; **R**, radius; **r**, radiale; **U**, ulna; **u**, ulnare; **1-4**, distal carpals.

68. Separation of phalangeal elements: 0- spaced out/closely packed; 1- closely packed to point of interlocking (modified from Motani, 1999 Char 78).
    a. Motani, (1999) utilised only one character for interdigital separation. This, combined with the fact that *Ichthyosaurus* has many digits, requires that the character is only relevant as goes variation within this one taxon. Spaced out, closely packed but non- interlocking phalanges are present in *Californosaurus*. Phalanges that are closely packed to the point of interlocking are present in *Macgowania* (Figure 24), *Temnodontosaurus*, and all the holotypes/neotypes of *Ichthyosaurus*.

   b. Modified by author to add an extra state/ descriptor to the closely packed was added for the purposes of this study. State 1 is to define the close fitting nature of *Ichthyosaurus* fins.

69. Phalangeal elements 0- shaft-like; 1- angular; 2- rounded (modified from Maisch and Matzke, 2000b Char 102).
    a. Shaft-like elements refer to those elements that are elongate and have a ‘waist’. *Californosaurus* has both shaft-like elements and angular elements. Angular elements are present in *Macgowania* (Figure 24), *Temnodontosaurus*, and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR38523 (Figure 16), NHMUK PV OR43006 (Figure 21) and DONMG 1983.98 (Figure 11). More rounded phalangeal elements are present in MANCH L.9663 and TTNCM 8349.
    b. This character has been modified to separate out angular and rounded states, which are combined in Maisch and Matzke (2000b).
70. Digital bifurcation row: 0- no bifurcation; 1- occurs in metacarpal row; 2- occurs in p1 or p2 row; 3- occurs in more distal row (Lomax and Massare, 2016 Char 34).
    a. Where bifurcation, or where one element splits into two elements occurs in the forefin. This may not be identical, even in the same specimen (e.g. right and left fins may be different).Though this is also a good indication that the specimen may be a composite and the specimen needs to be examined carefully (Massare and Lomax, 2016a). The metacarpal row, p1 and p2 rows locations are shown in Figure 25. No bifurcation is present in *Californosaurus* and *Temnodontosaurus*. Bifurcation in the metacarpal row is present in *Macgowania* (Figure 24), NHMUK PV OR38523 (Figure 16), and NHMUK PV OR43006 (Figure 21). Bifurcation occurring in rows p1or p2 is present in NHMUK PV R1162 (Figure 17), and AGC11 (Figure 18). Bifurcation occurring in a more distal row than p2 is present in BRSMG Cc921 and CAMSM 5975.
    b. Unmodified.

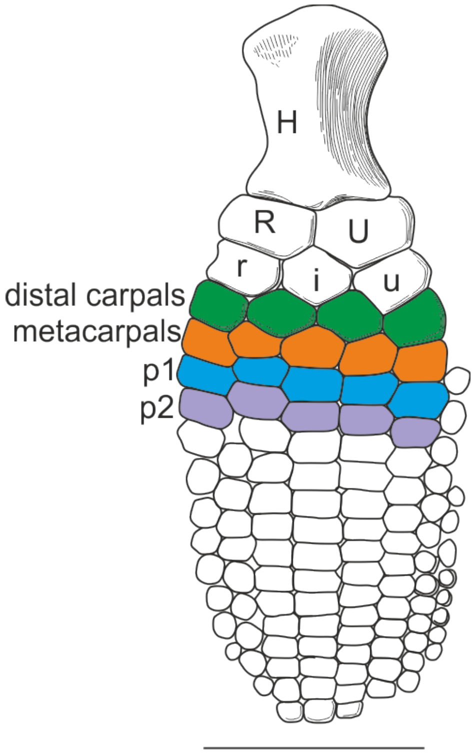


Figure 25. Forefin of *Ichthyosaurus communis* (ROM 337) in dorsal view (Modified from McGowan and Motani, 2003). Labels and colour included for the rows of digit terminology used in characters. Scale is equal to 50 mm. **Abbreviations**: **i**, intermedium; **R**, radius; **r**, radiale; **U**, ulna; **u**, ulnare; **green**, distal carpals; **orange**, metacarpals; **blue**, p1; **purple**, p2.

71. Notching in forefin elements on anterior edge of fin: 0- absent; 1- present (Modified from Motani, 1999 Char 59 and 65).
    a. Notching present on the leading or anterior edge of the forefin (Figure 24), this is different from notching seen between the radius and ulna which is not present in *Ichthyosaurus*. Absence of notching on the leading edge of the forefin is present in *Hudsonelpidia* and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 (Figure 21) and DONMG 1983.98 (Figure 11). Notching on the leading edge of the forefin is present in *Californosaurus*, *Macgowania* (Figure 24), *Temnodontosaurus* and NHMUK PV OR38523 (Figure 16).
    b. Modified to indicate the leading edge of the fin.
72. Extent of notching: 0- absent; 1-radius and other elements notched; 2- radius not notched, but other elements are; 3- radius only notched (Lomax and Massare, 2016 Char 35).
    a. Determining location of notching in the forefin. Notches or small crescent-shaped indentations on the edge of different elements. Most often seen on anterior side of elements. No notching present is present in NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 (Figure 21), and DONMG1983.3. The radius along with other elements notched, is present in *Californosaurus*, *Macgowania* (Figure 24), and *Temnodontosaurus*. The radius is not notched but other elements are is present in NHMUK PV

OR38523 (Figure 16), BRSMG Ce16611, and NHMUK PV R15907. Only the radius being notched is present in DCM G.10741 (Figure 26).

b. Unmodified.

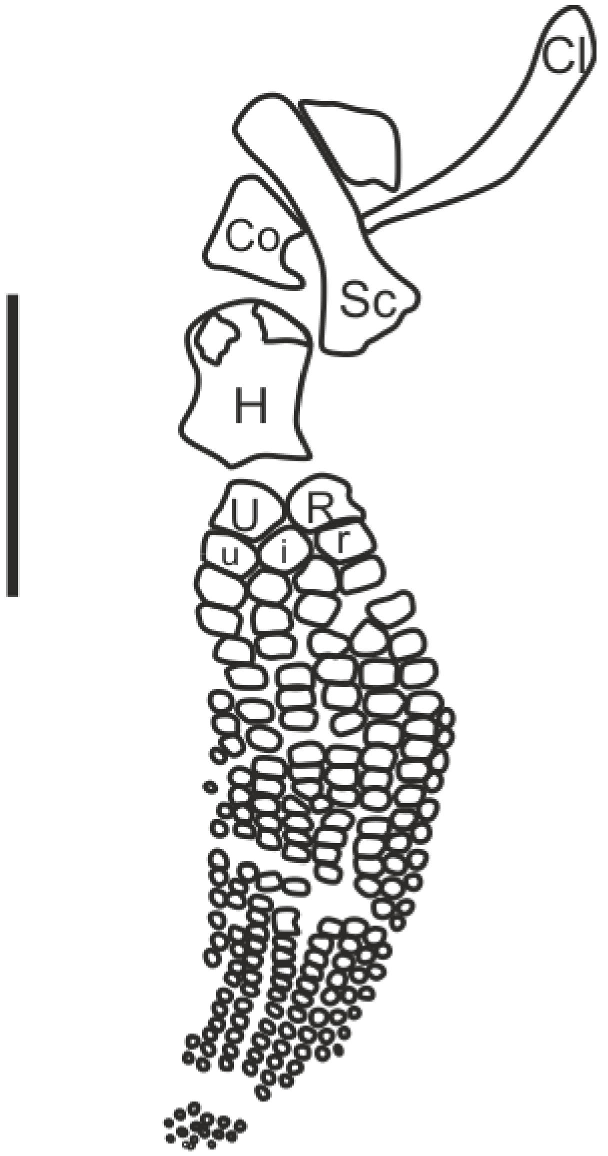


Figure 26. Interpretation of forefin and pectoral section of specimen DCM G.10741. This is only specimen of this dataset with a notched radius present. Scale bar equals 50 mm. **Abbreviations**: **Co**, coracoid; **H**, humerus; **i**, intermedium; **R**, radius; **r**, radiale; **Sc**, scapula; **U**, ulna; **u**, ulnare.

73. Anterior accessory digit: 0- absent; 1-present (Lomax and Massare, 2016 Char 36).
    a. A preaxial accessory digit can be defined as a digit that is anterior to the radius and first digit and typically does not extend the full length of the fin, meaning this digit may start distal to the radius, radiale, carpals or even further. This digit is absent in *Californosaurus*, *Macgowania* (Figure 24), *Temnodontosaurus* and NHMUK PV R1162 (Figure 17). An accessory digit is present in NHMUK PV OR38523 (Figure 16), NHMUK PV OR43006 (Figure 21), and NHMUK PV R216 (Figure 2).
    b. Unmodified.

74. Posterior accessory digit: 0- absent; 1- present (Lomax and Massare, 2016 Char 37).
    a. In *Ichthyosaurus*, a posterior accessory digit is located on the posterior edge of the fin and typically does not extend the full length of the fin, meaning the digit may start distal to the ulna, ulnare, carpals or even further. A posterior accessory digit is absent in *Californosaurus*, AGC11 (Figure 18), and AGC17. The digit is present in *Macgowania* (Figure 24), *Temnodontosaurus* and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR38523 (Figure 16), and NHMUK PV OR43006 (Figure 15).
    b. Unmodified.
75. Humerus/femur ratio (humerus length divided by femur length): 0- humerus ≤ 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 (Lomax and Massare, 2016 Char 38).
    a. This character refers to the quantifiable length (medial-distal) of the humerus and femur, presented as a ratio. This is a potentially important character as goes separating species within the genus. A humerus less than 1.4 times the length of the femur is present in *Hudsonelpidia*, *Temnodontosaurus* and NHMUK PV R11626. A humerus between 1.4 and 1.7 times the length of the femur is present in NHMUK PV OR43006, NHMUK PV OR2013 (Figure 13), and OUMNH J.10330. A humerus more than 1.7 times larger than the femur is present in DONMG 1983.98 (Figure 11), IPSMG 1880-1, and NHMUK PV OR33277.
    b. Unmodified.

Appendicular Skeleton (pelvic girdle)

76. Ilium: 0- with expanded dorsal region; 1- narrow medially and ventrally, rib-like; 2 -with expanded ventral region (modified from Lomax and Massare, 2016 Char 55 from a modified Maxwell, Fernandez, and Schoch, 2012 Char 47 modified from Sander, 2000 Char 106).
    a. This character refers to the general morphology of the ilium. No specimens in this analysis show an ilium with an expanded dorsal region. An ilium that is narrow and rib-like is present in *Temnodontosaurus*, NHMUK PV R1162 (Figure 17), and DONMG 1983.98 (Figure 11). An expanded ventral region is present in *Californosaurus* and *Hudsonelpidia*.
    b. Modified the medial region to dorsal to be more anatomically correct and be clear on how this character was interpreted. Modified state 1 and 2 to say ventral instead of distal to be more anatomically correct.
77. Iliac anteromedial prominence: 0- present (Figure 15 B, H-J); 1- absent (Figure 15 A, C-G, K-L) (Motani, 1999 Char 81)
    a. Merriam (1902 and 1908) did not have ilium orientated correctly/ consistently so provided anatomically incorrect diagnoses when describing the character states present in relevant taxa (Motani, 2003). This character mostly helps in distinguishing outgroup from ingroup taxa. An anteromedial prominence is present in *Californosaurus* and *Hudsonelpidia*. The

prominence is present in *Temnodontosaurus*, NHMUK PV R1162 (Figure 17), and DONMG1983.3.

b. Unmodified.

78. Ilium, pubis relative length: 0- nearly equal; 1- ilium length longer than pubis; 2- pubis longer than ilium (Lomax and Massare, 2016 Char 58).
    a. Lengths of the ilium and pubis are nearly equal in *Californosaurus* and TTNCM 120/1996. A longer ilium longer than the pubis is present in *Hudsonelpidia*, *Temnodontosaurus*, and NHMUK PV R1162 (Figure 17). A pubis longer than ilium is present in AGC17 and CAMSM J35187.
    b. Unmodified.
79. Ilium, ischium relative length: 0- nearly equal; 1- ilium longer than ischium; 2- ischium longer than ilium (Lomax and Massare, 2016 Char 59).
    a. Lengths of the ilium and ischium are nearly equal in *Hudsonelpidia*, NHMUK PV R1162 (Figure 17), and NHMUK PV OR2013. A longer ilium than ischium is present in CASMX50187, CAMSM J35183 and CAMSM TN910. A longer ischium than ilium is present in *Californosaurus, Temnodontosaurus,* and LEICT G126.1992.
    b. Unmodified.
80. Ilium, femur relative length: 0- nearly equal; 1- ilium longer than femur; 2- femur longer than ilium (Lomax and Massare, 2016 Char 61).
    a. Lengths of the ilium and femur being nearly equal are present in TTNCM 120/1996. A longer ilium than femur is present in *Californosaurus*, *Hudsonelpidia*, and specimens NHMUK PV R1162 (Figure 17) and DONMG1983.3. A longer femur than ilium is present in AGC17 and NHMUK PV OR2013 (Figure 13).
    b. Unmodified.
81. Ischium shape: 0- plate-like (Figure 14 F-K); 1- styloid (Figure 14 L-N) (Motani, 1999 Char 87).
    a. This character refers to the general shape of the ischium which is it broad and plate-like or more styloid or rod-like. This enables the distinction between ingroup from outgroup specimens. A plate-like ischium is present in *Californosaurus*, *Hudsonelpidia* and *Temnodontosaurus*. A styloid ischium is present in NHMUK PV R1162 (Figure 17), AGC11 (Figure 18) and AGC17.
    b. Unmodified.
82. Ischium, femur relative length: 0- nearly equal; 1- ischium longer than femur; 2- femur longer than ischium (Lomax and Massare, 2016 Char 63).
    a. An ischium and femur that are nearly equal in length is present in AGC17 and BU 5289 (Figure 27). A longer ischium than femur is present in NHMUK PV R1162 (Figure 17) and AGC11 (Figure 18). A longer femur than ischium is present in *Californosaurus, Hudsonelpidia*, and *Temnodontosaurus*.
    b. Unmodified.

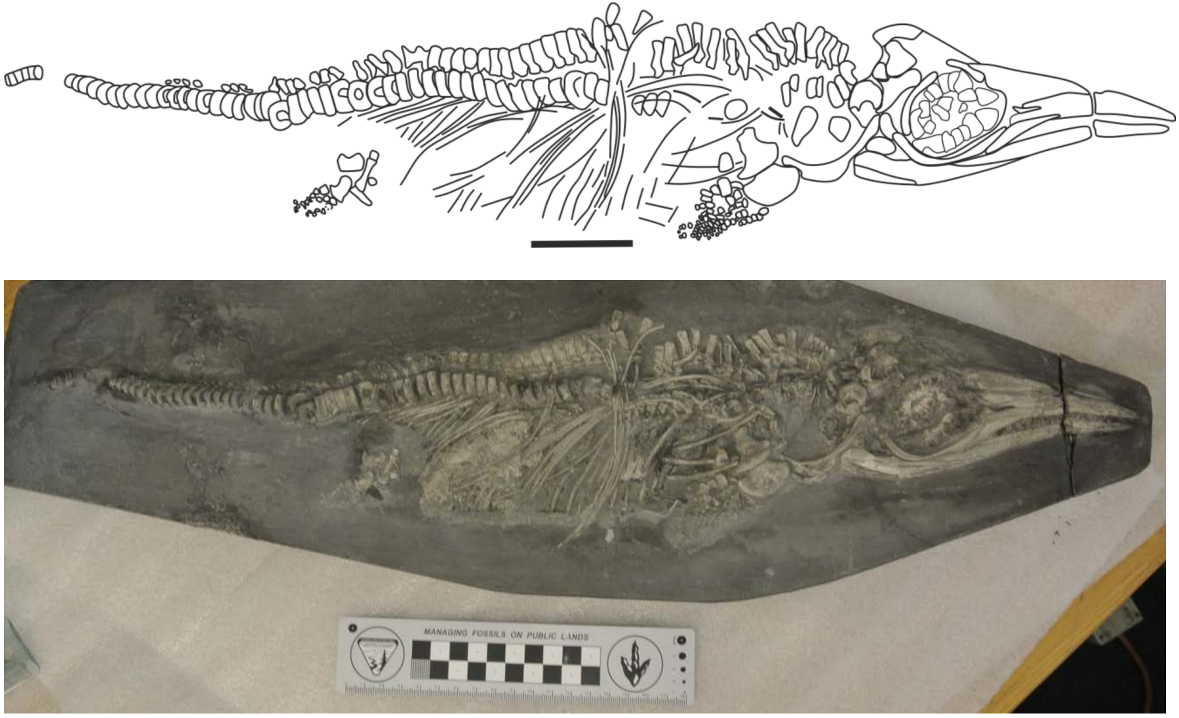


Figure 27. Interpretation line drawing (top) and image (bottom) of specimen BU 5289 from species *Ichthyosaurus conybeari*. Teeth are present in the specimen but were left out of interpretation. Scale bar is equal to 50 mm.

83. Pubis shape: 0- long and rod-like, not expanded ventrally; 1- long shaft with moderate expansion ventrally, 'spatulate' shape; 2- long shaft with wide expansion ventrally 'fan' shaped, can be asymmetric (modified from Lomax and Massare, 2016 Char 56).
    a. This character describes the state of the pubis. A long, rod-like pubis is present in NHMUK PV R1162 (Figure 17) and LEICT G126.1992. A long shafted pubis with a spatulate or expanded ventral end is present in *Hudsonelpidia*, *Temnodontosaurus* and NHMUK PV R15907. A long shafted pubis with an even more expanded ventral end to make a more fan-like shape is present in *Californosaurus*, and specimens AGC17 and TTNCM 120/1996.
    b. Modified to change distal terms to ventral to be more anatomically correct.
84. Pubis, ischium relative length: 0- nearly equal; 1- pubis longer than ischium; 2- ischium longer than pubis (Modified by Lomax and Massare, 2016 Char 60 from Motani, 1999b Char 86).
    a. A nearly equal pubis and ischium is present in *Californosaurus*, *Hudsonelpidia*, and specimens NHMUK PV R1162 (Figure 17), and NHMUK PV OR2013. A pubis longer than ischium is present in CASMX50187 and BU 5289 (Figure 27). A longer ischium than pubis is present in *Temnodontosaurus* and specimens AGC17 and CAMSM J35183.
    b. Unmodified.
85. Pubis, femur relative length: 0- nearly equal; 1- pubis longer than femur; 2- femur longer than pubis (Lomax and Massare, 2016 Char 62).
    a. A nearly equal pubis and femur is present in *Temnodontosaurus*, and specimens AGC17 and TTNCM 120/1996. A pubis that is longer than

femur is present in NHMUK PV R1162 (Figure 17), NHMUK R15907 and AGC16. A femur that is longer than pubis is present in *Californosaurus*, *Hudsonelpidia*, and NHMUK PV OR2013 (Figure 13).
   b. Unmodified.

Appendicular Skeleton (hindfin)

86. **Raised ridge present on anterior margin of femur: 0-absent; 1-present**
    a. This character refers to the presence or absence of a small process called a raised ridge on the anterior margin of the femur. This small process is absent in *Californosaurus*, *Hudsonelpidia*, *Temnodontosaurus* and specimens NHMUK PV R1162, and NHMUK PV OR43006. McGowan and Motani (2003) state this is found on *I. communis* specimens, but as stated previously, is not found on the neotype. This small process is present in AGC11, NHMUK PV OR2013, and TTNCM 120/1996.
87. **Constricted shaft of femur: 0-present; 1-absent**
    a. This character reflects character 66, using the same classification of a constricted shaft. A constricted shaft is present in *Californosaurus*, *Temnodontosaurus*, and specimens NHMUK PV OR430006, and DONMG 1983.98 (Figure 11). A constricted shaft is absent in NHMUK PV R1162 and CASMX50187.
88. Number of articular facets on the distal end of the femur: 0-two, 1-three. (Maxwell 2010: character 32)
    a. The number of facets observed on the distal end of the femur may be two (tibial articular facet and fibular articular facet), or three (to include an articular facet for the astragalus). Two facets present is a state seen in most specimens in this study including all out group taxa, *Temnodontosaurus* and holotypes/neotypes. Three facets present on the distal end of the femur are present in OUMNH J.10301 and CAMSM 59642.
    b. Unmodified.
89. Distal, proximal end of femur: 0- nearly equal in width; 1- distal end wider than proximal end (Lomax and Massare, 2016 Char 39).
    a. This character refers to the anterior- posterior width of the proximal and distal ends of the femur, where the femur can be observed in dorsal view. Nearly equal distal and proximal ends are present in AGC17, NHMUK PV R15907, and NHMUK PV OR120. A wider distal end is present in *Californosaurus*, *Hudsonelpidia*, *Temnodontosaurus*, and specimens NHMUK R1162, NHMUK OR43006 and DONMG1983.3.
    b. Unmodified. In future studies, another state might need to be added to distinguish *Leptonectes* from other specimens and genera. *Leptonectes* has a very slender proximal femur that flares out distally.
90. **Vertical facet is present on the distal anterior edge of femora: 0-absent; 1-present (mentioned in Massare and Lomax, 2014 in section 3.c.)**
    a. From observation, this feature can be interpreted as a facet that runs parallel to medial-distal length of the femur and is present on the anterior edge of the distal part of the femur. This facet is absent in *Hudsonelpidia*,

Temnodontosaurus and AGC11. This vertical facet is present in *Californosaurus*, and specimens NHMUK PV R1162 (Figure 17) and NHMUK OR43006.

91. Femur shape: 0- length approximately equal to distal width; 1- length no more than 1.5 times distal width; 2- length more than 1.5 times distal width (Lomax and Massare, 2016 Char 40).
    a. This compares the relative medial-distal length to the distal anterior-posterior width. A femur length that is nearly equal to the distal width is present in *Californosaurus*. A length that is not more than 1.5 times the width of the distal part of femur is present in *Temnodontosaurus*, and specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR43006, and DONMG 1983.98 (Figure 11). A femur length more than 1.5 times the distal width is present in AGC11 (Figure 18), and TTNCM 120/1996.
    b. Unmodified.
92. Primary digits in hindfin: 0- three; 1- four; 2- five (Modified from Lomax and Massare, 2016 Char 41).
    a. Primary digits refer to digits that extend the full length of the fin and extend from the tibia or fibula. Postaxial or preaxial digits only extend for part of the length of the fin and start posterior or anterior to the tibia or fibula. Three primary digits in the hindfin are present in Hudsonelpidia, and *Temnodontosaurus*. Four primary digits in the hindfin are present in NHMUK PV OR43006 (Figure 15), NHMUK PV OR120, and AGC11 (Figure 18). Five primary digits in the hindfin are present in NHMUK PV R1162 (Figure 17), and NHMUK BGS956.
    b. No specimens in this study had six primary digits present in the hindfin and this state was therefore removed from this character.
93. Tibia, fibula relative sizes: 0- tibia larger than fibula; 1- approximately equal; 2- fibula anteroposteriorly and proximodistally larger than tibia; 3- fibula proximodistally larger than tibia but anteroposteriorly approximately equal; 4- fibula anteroposteriorly larger but proximodistally approximately equal (modified by Lomax and Massare, 2016 Char 42 from Maxwell, Fernandez, and Schoch, 2012 Char 56).
    a. Differences in dimensions of tibia and fibula compared to each other, including anterior-posterior and proximodistal measurements. A tibia that is larger than the fibula is not present in this study. Approximately equal tibia and fibula dimensions are present in *Temnodontosaurus*, and specimens NHMUK PV OR2013 (Figure 13) and TTNCM 5803. A larger fibula to tibia is present in NHMUK PV OR43006 (Figure 15), NHMUK BGS956, and AGC11 (Figure 18). A fibula that is proximodistally larger than tibia, but anteroposteriorly equal is present in specimens NHMUK PV R1162 (Figure 17), NHMUK PV OR120 and GLAHM V1165. A fibula that is anteroposteriorly larger than tibia, but proximodistally equal is present in *Californosaurus* and specimens AGC16 and DCM .10741.
    b. Modified by Massare and Lomax (2016) by adding more character states to describe the difference in morphology of tibia and fibula in a more detailed manner.

94. Spatium interosseum between tibia and fibula: 0- present; 1- absent (modified by Fischer et al. 2013 from Maisch and Matzke 2000b char 114).
    a. The presence or absence of the spatium interosseum is utilised predominantly to distinguish outgroup and ingroup taxa. This foramen is present in *Californosaurus*, *Temnodontosaurus* and NHMUK PV R44. This foramen is absent or unknown in the rest of the specimens in this study.
    b. In Maisch and Matzke (2000b) this character was defining the presence or absence of a big spatium interosseum, the ‘big’ has been taken away by Fischer et al. (2003).
95. Number of digits in contact with the astragalus: 0- one; 1- two (Lomax and Massare, 2016 Char 43).
    a. The astragalus is typically in contact with the tibia and fibula, and is positioned slightly distally to these bones. This refers to the number of digits that come off the astragalus and in some specimens this digit bifurcates. Sometimes the astragalus is in contact with digit three, digits two and three, digits three and four or digits two, three and four. One digit in contact with the astragalus is present in *Temnodontosaurus* and NHMUK BGS956 (Figure 28). Two digits in contact with the astragalus are present in NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 (Figure 15), NHMUK PV OR120, and TTNCM 120/1996.
    b. Unmodified.
96. Digital bifurcation: 0- absent; 1- in metatarsal row; 2- in metatarsal row and second more distal bifurcation (Lomax and Massare, 2016 Char 44).
    a. This character identifies the location at which digit row bifurcation occurs (if at all) (Figure 28). This may not be identical, even in the same specimen (e.g. right and left fins may be different).Though this is also a good indication that the specimen may be a composite and the specimen needs to be examined carefully (Massare and Lomax, 2016a). No bifurcation is seen in *Temnodontosaurus* or in TTNCM 120/1996. Bifurcation in the metatarsal row is present in NHMUK PV R1162 (Figure 17), NHMUK PV OR43006 (Figure 15), and NHMUK PV OR120. Bifurcation that occurs in the metatarsal row as well as a more distal row is present in NHMUK BGS956 (Figure 28), NHMUK PV OR36256a, NHMUK PV OR85791, and BIRUG 4176.
    b. Unmodified.
97. Anterior accessory digit: 0- absent; 1- present (Lomax and Massare, 2016 Char 45).
    a. A preaxial accessory digit can be defined as a digit that is anterior to the tibia and first digit and typically does not extend the full length of the fin, meaning this digit may start distal to the tibia, tibiale, tarsals or even further. No anterior accessory digits are present in *Temnodontosaurus*, NHMUK PV R1162 (Figure 17), and NHMUK PV OR43006 (Figure 15). An anterior accessory digit(s) is present in CASMX50187.
    b. Unmodified
98. Posterior accessory digit: 0- absent; 1- present (Lomax and Massare, 2016 Char 46).

a. In *Ichthyosaurus*, a posterior accessory digit is located on the posterior edge of the fin and typically does not extend the full length of the fin, meaning the digit may start distal to the fibia, fibulare, tarsals or even further. No posterior accessory digit is present in *Temnodontosaurus*, and specimens NHMUK PV OR43006 (Figure 15), and NHMUK PV R1162 (Figure 17). A posterior accessory digit(s) is present in NHMUK R1162, NHMUK OR2013, CASMX50187 and BRSMG Ce16611.
b. Unmodified.

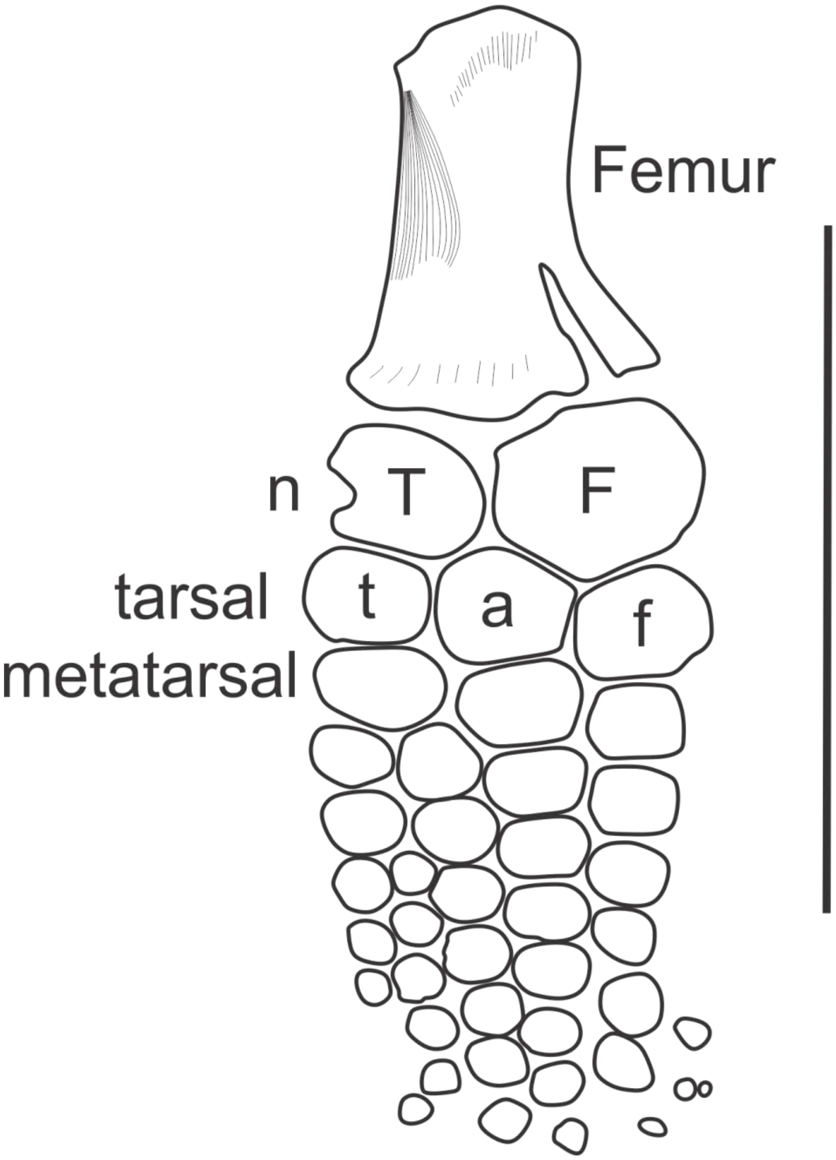


Figure 28. Hindfin of *Ichthyosaurus conybeari* (NHMUK BGS956) in dorsal view. Labels included for the rows of digit terminology used in characters. Scale is equal to 30 mm. **Abbreviations**: **a**, astragalus (some call intermedium); **F**, fibula; **f**, fibulare; **n**, notching; **T**, tibia; **t**, tibiale.

99. Extent of notching: 0- absent; 1- tibia and other elements notched; 2- tibia not notched, but other elements are; 3- only tibia notched (Lomax and Massare, 2016 Char 47).

a. This character specifies the location of notching on the hindfin. Absence of notching is present in NHMUK PV OR43006 (Figure 15), NHMUK PV R1162 (Figure 17), and AGC11 (Figure 18). A notched tibia and other elements in the anterior edge of the hind fin are present in *Californosaurus* and *Temnodontosaurus*. A tibia that is not notched, but other elements on the anterior edge are notched is present in NHMUK PV OR2013 (Figure 13), and BRSMG Ce16611. A tibia that is the only notched element on the hindfin is present in NHMUK BGS956 (Figure 28), MANCH L.9663, and YORYM 2005.2388C.
b. Unmodified.

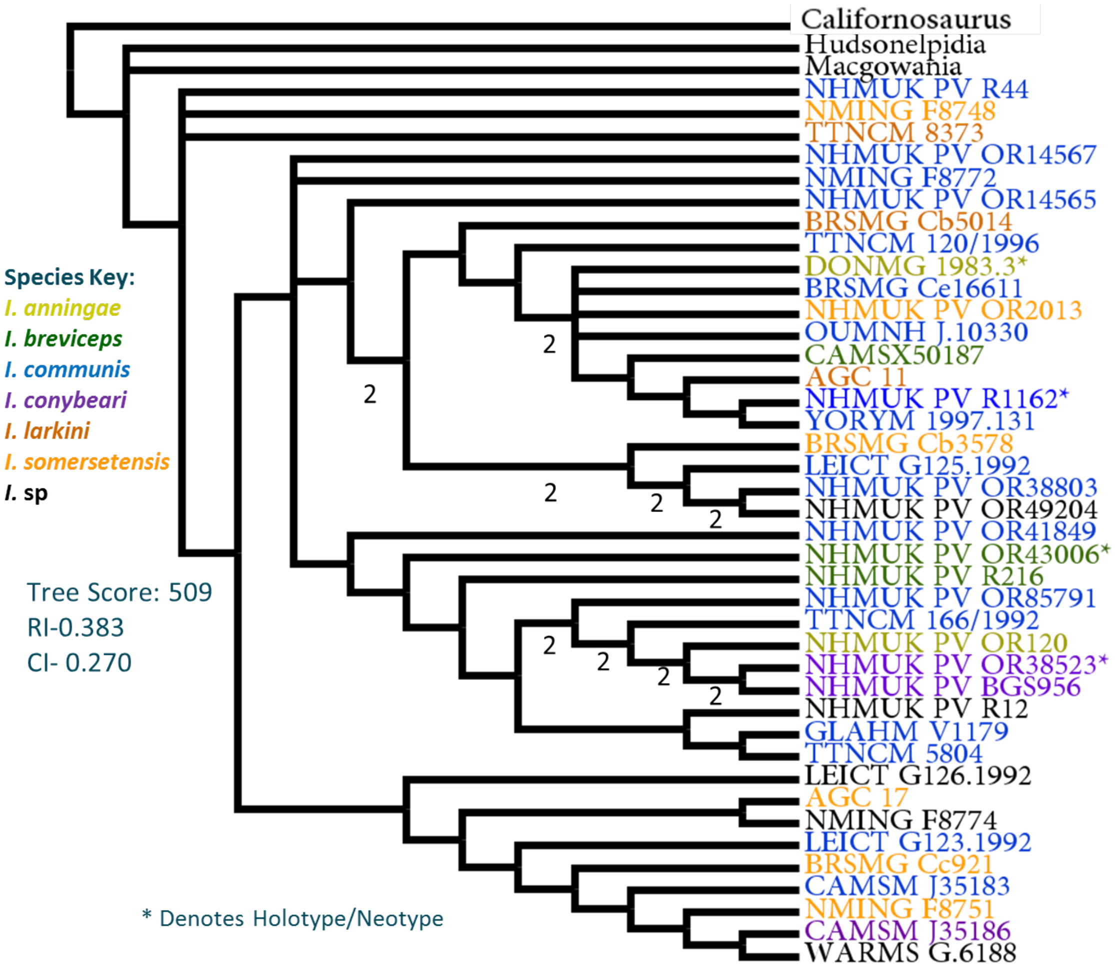


Figure 29. Analysis 1 phylogenetic tree for core group of specimens, 43 OTUs without continuous characters. New Technology search with ratchet with 1000 RAS resulting in 191 most parsimonious trees. TBR was performed on the resulting trees and resulted in 24 trees and the strict consensus of those trees is presented here. Bootstrap and jackknife values are all below 13%. Bremer support values greater than one are shown below the branch.

4.3.2 Phylogenetic Results and Discussion. All analyses consist of 99 characters and run in TNT. In Analysis 1, 43 OTUs were analyzed without the use of continuous characters. The support values are all below 13 for the bootstrap, jackknife, and low values for the consistency index and retention index. The six known species of *Ichthyosaurus* notably do not group together (Figure 29) though in some cases two or more of the same species will group together, in fact, *I. breviceps* and *I. conybeari* fall as sister groups to each other in this tree (Figure 29). Some specimens do group together with the neotypes and holotypes included in the present study, though all holotypes seem to plot closely with at least on other specimen from the species aside from *I. anningae*. The specimens of *I. somersetensis* (6 specimens)and *I. larkini* (3 specimens) do not group together as species and mostly fall separate from each other in the tree aside from the small polytomy with specimens NHMUK PV R44, NMING F8748 and TTNCM 8373. Most *I. communis* specimens are scattered throughout the tree.

When comparing this more inclusive study to the only other specimen based study that includes all current species of *Ichthyosaurus*, you can see the addition of more specimens adds chaos and creates lower support values to the tree. Other species level analyses have been done on ichthyosaurs in general, but only Mazin (1982) has multiple species from *Ichthyosaurus* and the genus presents as a polytomy in the presented tree. A similar tree is presented in Massare and Lomax (2016a), but did not include *I. somersetensis* and *I. larkini* as those species had not been created yet. The study shown in Figure 30, also only uses 17 characters opposed to the 99 utilized for Figure 29. These trees bring up an important point, showing that maybe these trees are showing the limits of TNT analyses; a large specimen based study may be beyond the limits of this type of analysis, at least for this genus. In Figure 30, *I. conybeari* and *I. breviceps* fall as sister groups on the tree, which is seen in most other trees of this study. As only one specimen, the neotype for *I. communis*, is used in Figure 30, no many comparisons can be made for *I. communis*.

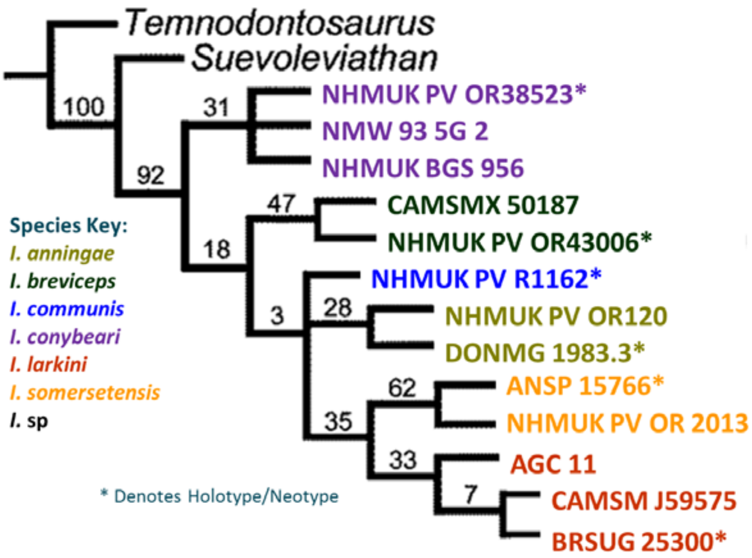


Figure 30. Phylogenetic tree modified from Lomax and Massare (2016; Figure 8, pg 17). Analysis was completed in TNT using implicit enumeration, one tree with a best score of 95, CI= 0.653 and RI= 0.686. Bootstrap values with 1000 replicates are shown to the left of each node.

In Analysis 2 (Figure 31) 43 OTUs were analyzed with the use of 99 characters and well as 5 continuous characters. The resulting tree is similar in its support to Analysis 1(Figure 29), but the addition of the continuous characters has changed the shape of the tree and position of specimens on the tree. The support values are all below 18% for the bootstrap, jacknife, and low values for the consistency index and retention index. With the addition of continuous characters the only holotype to be recovered as the immediate sister taxon to another specimen of the same species is *I. conybeari* (specimens NHMUK PV OR38523 and NHMUK PV BGS956). The holotype of *I. breviceps* falls close to one (NHMUK PV R216) of the two other specimens from the species, but this clade also contains specimens referred to *I. somerestensis* and *I. communis*. Several clades have the same taxonomic components as in Analysis 1 (Figure 29) for example AGC 17 and NMING F8774; LEICT G123.1992, BRSMG Cc921, CAMSM J35183, NMING F8751, CAMSM J35186, and WARMS G. 6188; LEICT G125.1992, NHMUK PV OR38803, and NHMUK PV OR49204; and BRSMG Cb5014, TTNCM 120/1996, CASMX50187, DONMG 1983.3, OUMNH J.10330, and BRSMG Ce16611. Inclusion of continuous characters has resolved the polytomies present in Analysis 1, but only minorly increased the support values which indicates that homoplasy is high and the tree might not represent the true phylogenetic signal.

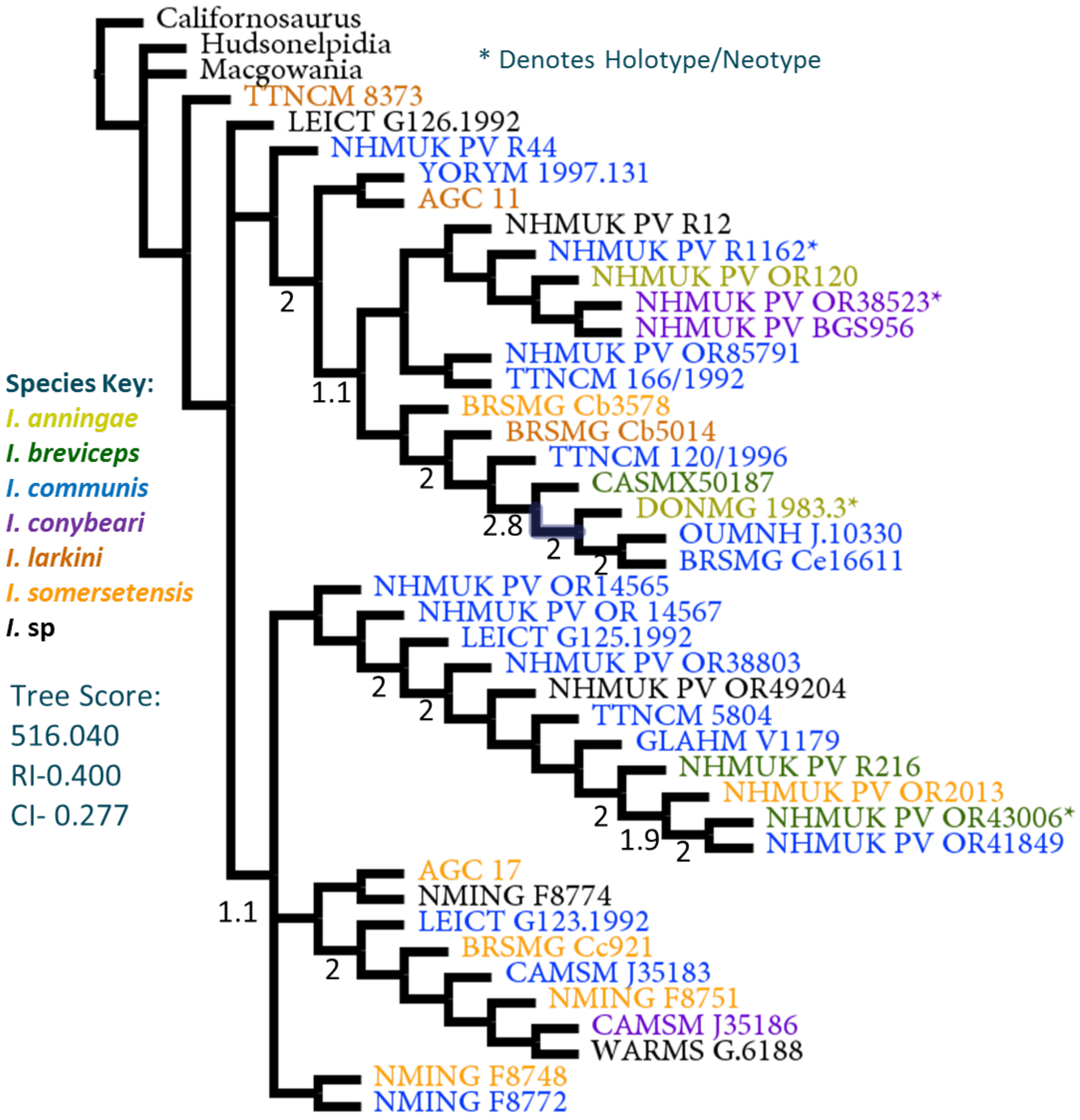


Figure 31. Analysis 2 phylogenetic tree for core group of specimens with 43 OTUs and the use of continuous characters. New Technology search Ratchet with 1000 RAS resulting in 191 trees. TBR was performed on the resulting trees and resulted in 6 trees. The strict consensus of these two trees is presented here. Bootstrap and jackknife values are all below 18. Bremer support values greater than one are shown below the branch.

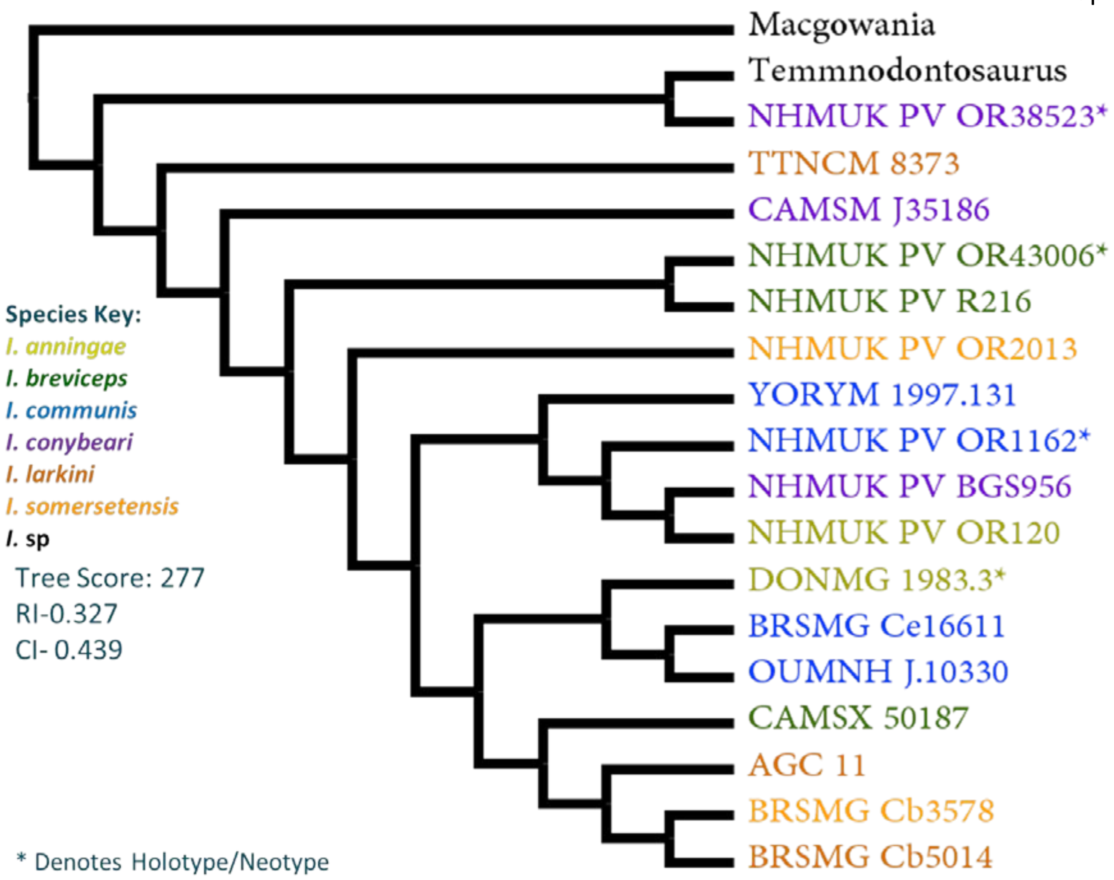


Figure 32. Analysis 3 phylogenetic tree for a subset of core group of specimens, 19 OTUs. New Technology search Ratchet with 1000 RAS resulting in 44 trees. TBR was performed on the resulting trees and resulted in 4 trees. The strict consensus of these four trees is presented here. Bootstrap and jackknife values are all below 18%. Bremer support values are all less than 1.

In Analysis 3 (Figure 32) 19 OTUs were utilised and with the use of 99 characters. This analysis also uses two outgroups instead of three and a new addition of *Temnodontosaurus*. Analysis 3 (Figure 32) is fully resolved with several distinct clades formed. The holotype of *I. conybeari* is unexpectedly recovered as the sister taxon to the intended outgroup taxon, *Temnodontosaurus*. Each holotype/neotype specimen appears to support its own small clade, but the specimen components of each of the do not correspond to the taxon referrals. One of these clades comprises a specimen of *I. conybeari* (NHMUK BGS956) with the holotype of *I. communis*, a referred specimen of *I. communis* (YORYM 1997.131) and a referred specimen of I. *anningae* (NHMUK PV OR120). This clade shows the variability the individual specimens of this genus, with four of the six species of *Ichthyosaurus* represented. This also compares well with Figure 30, showing the close relationship between *I. communis* and *I. anningae*. Another clade is present without an associated holotype or neotype specimen but includes two specimens of *I. larkini* (AGC 11 and BRSMG Cb5014), one specimen of *I. breviceps* (CAMSX 50187) and one specimen of *I. somersetensis* (BRSMG Cb3578). This grouping shows that these two species can be quite similar but is contradicted but the large separation from the other specimens of the two species as well. As with the first two analyses, there does appear to be some superficial separation with multiple groupings of two specimens from the same referred species, but no significant separation of the currently recognized species. Support values are low throughout, it is hard to say if these associations are due to high amounts of homoplasy, or represents a real phylogenetic signal.

The last analysis (Figure 33) shows three polytomies present in the tree. The presence of polytomies indicates that there is a lack of certain phylogenetic signal in the character coding which indicates a lower amount of individual variation present in this dataset. This analysis also shows support values that are greater than previous trees, but with slightly higher Bremer support values indicating larger sets of consistent characters on a few branches of the tree. The specimens that are most similar to the neotype of *I. communis* are present in one of the three polytomies and include YORYM 1997.131, BRSMG Ce16611 and OUMNH J.10330. The specimen YORYM 1997.131 has also grouped closely with the neotype for *I. communis* in Analysis 3 (Figure 32) and Analysis 1 (Figure 29). Another grouping of specimens BRSMG Ce16611 and OUMNH J.10330 are present in this tree along with the trees from Analysis 2(Figure 31) and Analysis 3 (Figure 32). No other groupings are present in multiple trees.

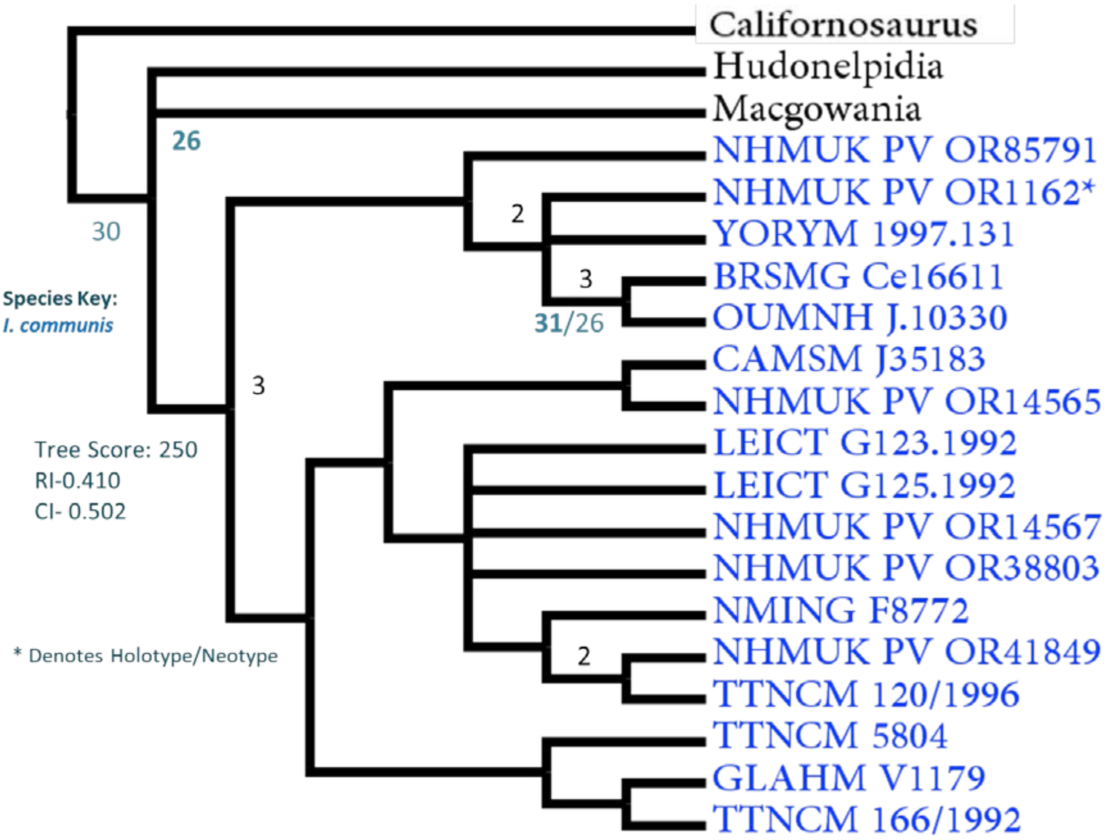


Figure 33. Analysis 4 phylogenetic tree for *Ichthyosaurus communis* most complete specimens, 20 OTUs. New Technology search Ratchet with 1000 RAS resulting in 63 trees. TBR was performed on the resulting trees and resulted in 12 trees. Presented here is the strict consensus of those 12 trees. Bootstrap and jackknife values above 25 are presented with bootstrap values in bold lettering below the branch. Bremer support values greater than one are shown above the branch.

4.4 Conclusions. Further work is needed to clarify the taxonomy of *Ichthyosaurus* at the specific level. This may be due to there being under-utilised aspects of ichthyosaur anatomy such as the pelvic girdle and hindfin. More characters for these and other areas may be helpful. The low support values for the trees may be due to limitations of phylogenetic analyses at the specimen level. Phylogenetic analysis are not often performed at the specimen level, other than to see to which species a new specimen belongs or to which it is closely related (Tschopp et al, 2015). It is documented that *Ichthyosaurus* shows extensive intraspecific variation (Chapter 3; Lomax and Massare, 2015 & 2016; McGowan and Motani, 2003). The cause of this variation is currently unclear but has resulted in the wastebasket nature of *Ichthyosaurus,* so that there may be more species and genera present than are currently recognised. Alternatively, it may be that the sheer number of specimens produced by the Lias Group lagerstätten is providing an extraordinary sample set that could exhibit broad intra- and interspecific variation that has clouded attempts to rigidly define taxa (Cleary et al., 2015; Lomax and Massare, 2015 & 2016). Similarly, the taxonomy of *Stenopterygius* has been repeatedly redefined and has been represented by an even larger number of exceptionally-preserved specimens (Maxwell, 2012). The other issue which is problematic to address is that there are also likely to be some composite specimens in museum collections that are difficult to identify, but may significantly confuse results (Massare and Lomax, 2016a, b)

The species *I. communis* shows the potential for sub species or other species to be present, but further work needs to be done on the morphological variation exhibited to determine this. The close relationship of *I. conybeari* and *I. breviceps* should also be explored further as this grouping appears in several of the trees in this study and in previous studies (Massare and Lomax, 2016a). It is possible that some of the rare species, could be considered subspecies, but this is beyond the scope of this project. This would be improved by the addition of more complete specimens of each of the species, especially *I. conybeari*, *I. breviceps*, and *I. anningae*. These species should also be analyzed alongside the newly re-described genus *Protoichthyosaurus* (Appleby, 1979) and new species (*P. prostaxalis* and *P. applebyi*) within the genus (Lomax et al., 2017).

The main results of this study show (1) that specimens do not always cluster to match the assigned species (also seen in Chapter 3 of this volume); (2) the specimens do not always cluster as a monophyletic genus; (3) support values, CI & RI for all clades in all trees are low, suggesting homoplasy is abundant in the trees presented which makes their true form extremely uncertain; (4) I. communis exhibits large variations between specimens (also seen in Chapter 3 of this volume) and thus the generic description probably needs revision; (5) only a small amount of obvious clustering is present, suggesting that the characters being current being used in do not adequately delimit taxa.

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Chapter 5.

Conclusions

5.1 Chapter 2. Conquering the wall: measuring fossil specimens mounted on walls and behind glass using parallel lasers and aerial photography equipment

- Review
    - Presenting a new method using parallel laser photogrammetry to bridge the gap between inaccessibility and scientific study. This study was conceived to work with specimens like those at the NHMUK, London that are mounted as to be inaccessible to researchers.
- Conclusions
    - One aim of the new technique study was to keep costs as low as possible to make this technique more accessible to other palaeontologists. Other adjustments could be made to mounting, such as setting lasers on either side of the camera instead of below the camera to have the lasers in a more central location in the image. More efficient and expensive lasers could be used: if of higher quality, they are less likely to not be parallel to each other. This would reduce the possible error in measurements taken from the specimens.
    - Other photographic techniques could be combined with the technique described here such as the use of a polarising filter to reduce reflections of surfaces like that of the glass fronts to the Victorian cases. The cost of polarizing filters varies widely. While glares were present in pictures, multiple pictures were taken at different positions to get clear pictures of all parts of given specimens.
    - Future work needs to be done the accuracy of this method, and on ways to improve the accuracy beyond what is discussed in this paper. Deakos (2010) discussed methods used in testing the accuracy of their methods. Testing accuracy requires known lengths of the objects tested and none of the specimens involved in our study here have reported measurements taken from behind glass (images have been published with scales but there is no indication if those scales are estimates or real).

5.2 Chapter 3. Testing the reliability of linear ratio measurements in distinguishing species of Ichthyosaurus (Reptilia; Ichthyosauria): an in-depth morphometric approach

- Review
    - The genus Ichthyosaurus was analysed for separation of species. With a dataset of 56-70 specimens and 12-56 measurements of each specimen, we use multiple morphometric analyses (PCoA, NMDS, Cluster and LDA), to test these measurements, and show that they provide no significant separation of taxa. These results demonstrate the need for a more strict evaluation of characters that utilise linear measurements from ratios and ranges of measurements in phylogenetic analyses.
- Conclusions
    - Ratios of linear measurements have been used in various ichthyosaur studies since McGowan's (1974) paper and have since been used to help normalize the size variations seen in individuals of each species. Based on the results of 70 specimens and 56 measurements, presented, these measurements do not appear to represent a valid means for the separation of species within *Ichthyosaurus*.

- Based on our results shown in the four bivariate plots (figures 2-5), the extensive overlap of the ranges of the ratios and the lack of clear separation of the OLS regression lines, neither these measurements nor ratios appear to produce clear, statistically valid separations of the majority of species within the genus *Ichthyosaurus*.
- There is also a high degree of variability seen across *I. communis* and *I. intermedius*, and due to the large amount of overlap in these data ranges there is every indication the proposed synonymisation of these taxa is valid (McGowan and Motani, 2003 and Massare and Lomax, 2017). Interestingly, of these latter specimens, most of the larger specimens have previously been assigned to *I. intermedius*, which may suggest that these two originally distinct taxa might actually represent sexual dimorphs within a single species.
- In the four PCoA plots presented, no clear demonstration of separation of species is found. The extensive overlap of morphospaces and lack of clearly definition of separate species using the measurements utilised by previous authors might be taken as a clear indication that *Ichthyosaurus* as a whole might be a wastebasket taxon. This is also contradicted by the fact that all species possess distinct and discrete morphological differences. As these differences are not based on the measurements studied in these results, it is likely that the species are valid, but that the measurements presented here are not enough to separate the species by themselves.
- The NMDS and cluster analyses further confirm the overlap of morphospaces of species.
- The LDA analyses are the only ones to clearly demonstrate a separation of species within the genus, but only for *I. conybeari* and *I. breviceps*. This is likely to be the result of the reduced dataset for these species, which eliminated several measurement characters that have been found to vary considerably in individual specimens of other species.
- Anagenesis was not considered in this study as there was not enough specific data to conduct a study on the specimen level.
- The significant bias concerns the identification of specimens: a much larger number of specimens have been referred to *I. communis* and *I. intermedius* than to the other named *Ichthyosaurus* species, potentially meaning that the species were either more common or that there are more species within the genus.
- There has been an increase in the number of morphological characters used to define species within the genus *Ichthyosaurus,* and also a review of the characters used to define *I. conybeari* (Massare and Lomax, 2016). Along with the identification of 2 new species*, I. somersetensis* and *I. larkni*, with newly referred specimens presented in this analysis. More specimens of *I. conybeari*, *I. breviceps* and *I. anningae* are needed to determine the true extent of the morphospace of these species. At this time, linear measurements from ratios that reliably distinguish the named *Ichthyosaurus* species in a statistically significant way have yet to be identified.

  - It is conceivable that these results could be sensitive to the inclusion of an even greater number of specimens. Furthermore, if named species were better defined, or if additional species were found to be present in this genus, improved separation concerning the historical measurements of ratios might hypothetically occur. *Ichthyosaurus* could be compared to other closely related genera in more depth to see if the measurements can be used at the genus level.

5.3 Chapter 4.

- Review
  - 99 characters were utilized for this study have been compiled and examined to ensure the most pertinent and complete collection of characters. These four analyses demonstrate that the genus encompasses a wide range of morphological variability and there is no clear morphological separation of individual species, even in light of the recent description of two new morphologically well-defined species and one newly defined genus.
- Conclusions
  - Further work is needed to clarify the taxonomy of *Ichthyosaurus* at the specific level.
  - More characters for under-utilised areas such as the pelvic girdle and hindfin may be helpful.
  - The low support values for the trees may be due to limitations of phylogenetic analyses at the specimen level. Phylogenetic analysis are not often performed at the specimen level, other than to see to which species a new specimen belongs or to which it is closely related(Tschopp et al, 2015).
  - The main results of this study show
    - (1) that specimens do not always cluster to match the assigned species (also seen in Chapter 3 of this volume);
    - (2) the specimens do not always cluster as a monophyletic genus;
    - (3) support values, CI & RI for all clades in all trees are low, suggesting homoplasy is abundant in the trees presented which makes their true form extremely uncertain;
    - (4*) I. communis* exhibits large variations between specimens (also seen in Chapter 3 of this volume) and thus the generic description probably needs revision;
    - (5) only a small amount of obvious clustering is present, suggesting that the characters being current being used in do not adequately delimit taxa.
  - The close relationship of *I. communis* and *I. breviceps* should also be explored further as that grouping appears in several of the trees in this study and in previous studies (Massare and Lomax, 2016a).

5.4 General Conclusions

Chapter 2 outlines a great method to access specimens that are displayed in inaccessible areas. This method has been utilised in other fields and updated in this chapter for use in vertebrate palaeontology. There are improvements that can be made on the method as what is presented here is a cost efficient way of doing the method. These improvements would provide more accessibility to researchers. This method could also be used to do more traditional photogrammetry of the specimens in question, given more time and access to the specimens themselves. As there were 70+ specimens present on the wall of the NHMUK, London alone, figuring a way to get useful data from them was vital to the study of the genus.

While many small studies have been done recently on the genus *Ichthyosaurus* (Lomax and Massare, 2015 and 2016; Massare and Lomax, 2016a, 2016b, and 2014), I feel that the work done in Chapters 3 and 4 are the first attempt to look at the genus as a whole to assess the current state of it. *Ichthyosaurus* is especially interesting to study as there are so many specimens available for study. Many museums around the world have specimens that have not undergone any analysis since being accessioned into collections. While I was not able to utilise all the specimens observed in these studies there will be some used in projects to come. The biggest project would be looking at the ontogeny of different species, as there are a range of juveniles present which were not able to be utilised in Chapter 3 or 4 as the differences in appearance may skew the results.

I also think more work could be done on the sediments associated with specimens to find either the locality origin or improve the time range for specimens, especially historic ones that have spotty records. Whilst the palynomorphs studies conducted in the early stages of this project were not as fruitful as we had hoped, there are still things like coccolithophores and diatoms that can be studied. This would be a very interesting project that would cross over a few different fields of study. The biggest conclusion drawn from these studies is that the genus *Ichthyosaurus* is in no way completely understood. Many advances forward have been made including the finding presented in this study, but there is still more to come. It is highly possible there are subspecies present within this genus or potentially even more species.

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Appendix A.

List of Locations of *Ichthyosaurus* Specimens

1. Locations of Specimens
    a. Lyme Regis/Charmouth
    b. Other localities
        i. Street
            1. Walton, Street, Somerset
            2. Watchet, North Devon
            3. Blue Anchor, Old Cleeve
            4. Staple Fitzpane, Taunton
            5. Lilstock, Somerset
            6. Foreshore near Klive, Somerset
            7. Charlton Mackrell, Mendip
            8. Shepton Mallet Area, Mendip
        ii. Near Bristol
            1. Binton, near Stratford-upon-Avon
            2. Stoke Gifford, Bristol
            3. Fretherne, Glouchestershire
            4. Bishopsworth
            5. Keynsham Bypass
        iii. Near Bath
            1. Timsbury, Somerset
                a. Hodder’s Quarry
                b. Lower Lias, Spirifer Bank
            2. Avon, Bath
        iv. Nottingham
            1. Cropwell Bishop
            2. Cropwell Butler, Rushcliffe
        v. Yorkshire
            1. Robin Hood’s Bay
            2. Whitby
        vi. Leicester
            1. Barrow-on-Soar
            2. Barnstone
        vii. Warwickshire
            1. Wilmcote
                a. ‘Grizzle Bed’
            2. Temple Grafton
            3. Napton on the Hill

Appendix B.

TWO LISTS OF SPECIMENS AND MESUREMENTS ASSOCIATED WITH THEM FOR USE IN MORPHOMETRIC ANALYSES

1. **Measurements and counts for first set of specimens, all measurements listed in mm:**

Specimen Number   Species ID   Postcranial to pelvic   Skull length   Skull width
Lower jaw length   Upper jaw length   Orbit diamerer   Postorbital length
Sclerotic ring internal diameter   Snout length   Prenarial segment   Premaxillary length
External naris length   Dentary length   Maxillary length   Upper temporal fenestrae width
Upper temporal fenestrae length   Parietal table length   Angular length
Basioccipital width   Vertebra width (avg)   Vertebra length (avg)
Neural spine height   (avg)   Scapula length   Scapula Proximal   Scapula Distal
Coracoid Width   Coracoid Height   Forefin length   Humerus Length
Humerus proximal width   Humerus distal width   Radius length   Radius width
Ulna length   Ulna width   Radiale length   Radiale width   Intermedium length
Intermedium width   Ulnare length   Ulnare width   Illium length   Ischiopubis length
Pubis proximal width   Pubis distal width   Hindfin length   Femur length
Femur prioximal width   Femur distal width   Tibia length   Tibia width
Fibula length   Fibula width   Distal tarsis II length   Distal tarsis II width
Astragalus length   Astragalus width   Calcaneum length   Calcaneum width

AGC 7   *Ichthyosaurus communis*   573   326   ?   325   ?   ?   ?   ?
?   ?   ?   ?   240   ?   ?   ?   ?   ?   35.77
10.32   21.06   24.26   65.25   35.12   22.69   72.45   55.79   127.24   53.92   38.96
37.49   ?   ?   17.43   25.59   ?   ?   11.16   14.34   10.95   15.85
40.6   39.1   6.54   18.52   79.26   36.83   19.85   ?   ?   ?   ?   ?
?   ?   ?   ?   ?   ?

AGC 8   *Ichthyosaurus communis*   1463   455   146.61   442   ?   ?   ?   ?
?   ?   ?   ?   ?   ?   ?   ?   ?   ?   46.81
19.43   38.59   43.55   109.48   ?   37.43   102.4   102.5   274   85.48   58.56
60.03   27.01   38.51   28.08   38.51   17.61   27.32   25.61   25.73   16.88   27.41   ?
?   ?   ?   ?   ?   ?   ?   ?   ?   ?   ?   ?
?   ?   ?   ?   ?

AGC 9   *Ichthyosaurus communis*   475   357   ?   298   262   61.06   ?   ?
226   176   187   24.22   ?   80.24   ?   ?   ?   ?   ?
15.71   25.41   29.42   71.23   37.55   17.12   76.56   56.72   ?   58.81   44.45

39.84 ? ? ? ? ? ? ? ? ? ?
43.81 ? ? ? ? 42.42 22.89 24.16 ? ? ? ?
? ? ? ? ? ?

BRSLI M3562 *Ichthyosaurus communis* 449 374 183 ? 267 58.33
46.9 24.04 249 206 236.5 39.63 ? 103.52 26.37 48.63 ? ?
? 9.12 21.99 29.39 ? ? ? ? ? 181.33 34.92
24.47 ? 17.26 24.52 20.83 27.7 10.26 18.53 12.87 17.74 12.42
20.9 45.19 ? ? ? 112.93 38.29 12.84 17.74 ? ?
11.41 15.59 11.35 14.66 ? ? ? ?

BRSMG Ce16611 *Ichthyosaurus communis* ? ? ? ? ? ?
66.7 ? ? ? ? ? 344.25 107.06 ? ? ? ?
? ? ? ? 99.02 48.95 27.67 118.84 98.84 192.31 75.2
46.69 61.58 25.8 33.05 25.95 36.95 15 26.1 22.15 24.64 18.38
26.51 ? 65.08 34.12 11.07 133.05 60.65 26.82 ? 37.28 19.44
15.65 23.52 12.69 14.15 14.15 15.49 14.72 17.62

CAMSM J35183 *Ichthyosaurus communis* 425 278 ? 277 194
53.09 43.43 ? 177 152 154.68 13.58 208 68.21 ? ? ?
75.19 29.34 7.67 17.04 22.45 54.14 ? ? 63.34 44.65 142.45
42.63 28.28 28.25 13.1 20.94 14.96 20.45 8.29 15.37 11.43 12.68
9.61 13.48 28.07 34.28 ? 16.56 ? 29.1 15.61 17.57 ? ?
? ? ? ? ? ? ? ?

CAMSM J69477 *Ichthyosaurus communis* 769 434 140 452 282
76.15 ? 42.45 267 202 230 55.48 338 108.18 30.5 55.6
63.82 ? ? 11.88 24.39 49.09 98.63 ? ? ? ? 193
83.14 45.81 51.22 23.84 33.63 28.22 36.9 17.36 24.15 24.97 23.82
20.72 28.34 ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ?

DCM G.00001 *Ichthyosaurus communis* 786.48 395.51 167.09 ? ? ? ?
? ? ? ? ? 290.18 ? ? ? ? 276.11
40.74 17.08 35.69 ? ? ? ? 112.11 71.01 169.24 52.73
50.05 52.4 16.7 26.13 14.54 27.39 11.41 21.31 15.85 20.24 9.04
22.4 ? 37.85 ? ? 83.71 30.78 27.64 24.12 ? ? ?
? ? ? 5.62 10.05 5.48 10.53

DCM G.10741 *Ichthyosaurus communis* 336.22 ? ? ? ? 46.57
29.55 21.23 ? ? ? 11.94 ? 48.4 ? ? ? ?
? 7.13 15.7 16.21 45.43 ? ? ? 32.05 141.26 29.83
20.76 23.64 9.01 12.72 9.2 11.84 6.22 9.29 8.41 9.14 5.99
9.58 26.97 ? ? ? 60.42 17.56 10.93 8.29 5.09 6.61
4.87 7.71 4.94 5.94 5 5.42 4.22 6

GLAHM V1179 *Ichthyosaurus communis* 490 300 ? 337 205 38.5 ?
? 195 ? 159 17.56 226 77.91 ? ? ? ? ?
? ? ? ? ? ? 48.12 51.17 218 39.54 26.91
31.56 13.61 22.47 13.53 19.72 10.69 17.75 11.25 16.07 9.88 12.94
41.46 ? ? ? 86.97 29.8 16.08 18.84 5.8 10.73 5.59
12.7 4.89 8.58 6.79 8.4 ? 8.34

IPSMG 1880-1 *Ichthyosaurus communis* 900 410 205 460 ? ?
? ? 300 ? ? ? ? ? 29.3 40.33 ? ?
42.86 ? ? ? 93.22 ? ? ? ? 320 58.47
42.83 33.41 17.11 27.17 17.13 27.48 13.15 17.44 14.73 18.31 12.14
17.18 32.02 ? ? ? 144.68 30.49 16.41 15.58 8.19 8.53
7.73 8.95 4.18 6.13 7.46 8.04 5.06 8.17

LEICT G123.1992 *Ichthyosaurus communis* 1558 468 275 464 325 ?
? 30.84 312 244 266 41.77 351 129.67 63.23 64.13 75.24 ?
? 15.14 32.33 45.14 93.78 ? ? 106.7 95.22 253 75.27
51.48 56.77 22.1 35.1 28.51 39.56 15.68 24.49 20.47 25.26 17.9
29.43 ? ? ? ? 83.92 ? ? ? ? ? ?
? ? ? ? ? ? ?

LEICT G125.1992 *Ichthyosaurus communis* 521 381 123 ? ? ?
? ? 212 162 ? 28.96 ? ? 31.68 43.27 49.15 ?
32.45 11.38 23.04 32.81 87 ? ? ? ? 175 41.39
34.59 40.06 19.65 25.11 21.27 30.3 12.84 18.36 16.31 19.11 13.41
22.46 ? ? ? ? 99.07 47.15 17.18 29.04 13.9 16.8
14.25 18.97 ? ? ? ? ? ?

NHMUK PV R1162** *Ichthyosaurus communis* 470.08 273.15 ? 266.47 161.36
55.58 30.45 20.85 154.21 122.07 133.89 21.76 195.53 56.81 ? ? ?
? 25.11 8.03 15.17 27.92 68.82 23.04 16.16 ? ? 172.72
40.78 25.9 29.573 11.28 18.41 10.56 17.93 10.36 14.35 10.93 12.73
7.62 15.61 37.34 37.64 7.81 7.11 71.88 28.3 12.21 17.19 7
10.47 6.97 9.25 5.08 8.18 7.42 8.24 4.89 8.5

NHMUK PV R5595 *Ichthyosaurus communis* 712.12 368.19 125.76 ? ? ?
? ? ? 201.93 ? ? ? 55.23 22.25 54.22 69.69 ?
42.33 ? ? ? 94.69 48.05 28.29 ? ? 304.09 82.76
49.48 62.1 28.03 28.14 28.74 39.32 16.64 28.31 21.38 26.12 18.18
26.89 60.362 ? ? ? 178.21 63.41 28.39 33.6 14.9 19.87
17.21 22.98 11.77 13.6 13.99 16.89 10.93 14.88

NMING F8746 *Ichthyosaurus communis* 1301 ? ? 425 348 90.17
42.55 36.2 328 272 ? 44.1 ? 75.22 33.84 48.13 55.32 ?
? 11.72 19.13 55.45 97.95 45.43 28.01 107.56 83.89 191.08 74.91
45.64 49.93 25.33 32.72 21.42 31.15 13.44 21.87 16.6 22.6 17.53

28.95 54.13 56.5 10.7 28.6 ? 53.2 20.97 34.44 15.3 20.44
22.47 22.96 ? ? ? ? ? ?

NMING F8767 *Ichthyosaurus communis* 469 366 ? 365 255 66.79 ?
? 241 156 182 38.88 ? 92.04 ? ? 38.33 ? ?
11.49 23.51 35.3 ? ? ? 59.48 40.78 206.79 62.25 ?
40.57 14.41 23.47 17.46 21.48 11.09 17.85 11.25 12.55 10.66 17.95 ?
? ? ? ? 21.99 20.22 11.3 ? ? ? ? ?
? ? ? ? ?

NMING F8770 *Ichthyosaurus communis* 416 266 102.48 ? ? ? ?
27.09 164 129.15 147.32 23.58 ? ? 23.53 47.88 53.33 ?
32.1 20.56 20.23 28.24 46.35 ? 11.52 ? ? 104.36 31.9
22.77 25.62 11.43 15.39 9.26 15.26 5.45 10.47 8.77 10.92 7.1
11.16 ? ? ? ? 76.06 23.99 11.74 13.8 ? ? ?
? ? ? ? ? ? ?

OUMNH J.29352 *Ichthyosaurus communis* 236.06 ? 110.4 ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? 36.09 22.21 ? 48.87 34.74 93.7 30.67
25.03 23.82 10.72 15.55 9.73 14.54 6.8 12.65 10.09 12.91 7.67
11.82 28.95 30.06 11.26 6.95 65.81 22.68 8.65 12.66 5.98 7
6.38 8.81 4.61 6.72 5.42 7.46 4.98 6.57

PETMG:R174 *Ichthyosaurus communis* 520 330 71.88 310 253 66.03 ?
? 234 198 212 22.68 250 80.62 ? ? ? 152.27 ?
9.51 19.21 21.73 ? ? ? ? 60.92 210 45.25 23.59
44.97 16.98 27.53 18.25 25.92 12.34 21.02 15.58 16.87 13.48 19.04 ?
? ? ? 124.24 39.06 19.46 26.42 9.93 12.02 12.38 16.06
7.87 10.46 8.87 11.14 13.92 9.68

TTNCM 120/1996 *Ichthyosaurus communis* 301 289 ? 307 230
57.22 31.53 24.92 209 170 286 25.24 233 ? ? ? ?
? ? 6.55 14.74 20.94 50.1 ? ? ? ? 124.04
40.73 22.8 26.49 12.55 17.44 15.44 19.19 7.34 13.25 10.22 12.25
9.64 13 30.92 28.35 7.7 5.45 65.88 29.46 12.01 13.97 6.87
8.71 7.53 9.39 5.38 6.38 6.77 7.77 6.19 7.14

TTNCM 116/1992 *Ichthyosaurus communis* 320 240 126.14 ? ? ?
19.72 ? ? ? ? ? 167.01 ? ? ? ? ?
23.18 5.53 10.2 ? ? ? ? ? ? 128.99 30.75
25.92 30.77 9.36 17.41 14.15 15.91 8.04 15.85 9.09 13.13 8.33
11.19 23.98 28.05 6.44 8.45 87.73 23.68 12.46 14.61 ? ? ?
? ? ? ? ? ? ?

TTNCM 5804 *Ichthyosaurus communis* ? ? ? 348 215 82.77 ?
28.41 155.55 102.5 ? 26.33 ? 161 29.04 72.49 60.31 175
34.31 13.27 25.08 48.28 ? ? ? ? ? 162 55.45
44.9 49.28 19.49 27.47 17.73 31.82 13.81 21.87 14.64 19.42 12.94
22.4 ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ?

YORYM 1997.131 *Ichthyosaurus communis* ? 255 64.32 263 177
47.3 26.33 20.66 166 137.59 146.1 25.01 187 66.26 20.86 28.6
34.55 119.68 ? ? ? ? 45.84 14.47 20.07 45.75 35.44
119.17 28.75 19.56 ? 9.73 15.38 10.36 13.83 6.6 12.07 8.42
9.99 6.72 11.72 ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ?

YORYM 2005.2408 *Ichthyosaurus communis* 345 249 ? 219 168
39.73 ? ? 162 140.11 141.44 11.78 152 48.97 ? ? ?
? 27.48 6.89 14.65 21.83 ? ? ? ? ? 129.92
29.73 23.78 24.91 ? ? ? ? ? ? ? ? ?
? ? ? ? ? 56.68 21.73 ? ? ? ? ?
? ? ? ? ? ? ?

NHMUK PV OR85791 *Ichthyosaurus intermedius* 277 246 118.3 246 ? ?
? ? ? ? ? ? ? ? ? ? ? ?
? 6.98 ? ? 43.1 ? ? ? ? 122.93 22.9
19.69 20.64 7.29 11.11 8.08 12.12 4.79 8.68 6.94 7.88 5.99
8.17 ? 24.31 6.83 ? 51.28 16.92 8.7 ? 4.33 5.72 4.5
7.36 7.99 16.8 ? ? ? ?

NMING 8757 *Ichthyosaurus intermedius* ? 264 ? 277 193 63.02
47.14 30.94 167 131 137 18.57 197 ? ? ? 32.53 ?
? ? 17.07 34.34 62.99 25.82 16.49 ? ? 177 41.32
26.84 37.2 14.93 20.6 15.6 24.35 ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ?

NMING F8744 *Ichthyosaurus intermedius* ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? 58.4 57.62 102.92 44.73 22.18
33.34 12.04 20.41 14.28 23.54 8.56 16.24 14.83 13.02 11.18 15.6 ?
? ? ? 64.26 ? ? ? ? ? 9.48 14.99 7.9
7.87 7.57 9.52 6.49 8.64

NMING F8745 *Ichthyosaurus intermedius* 494 333 91.53 ? ? 81.92
29.05 25.79 211 178 197 27.69 ? ? 21.07 31.1 36.59 ?
28.3 11.32 19.71 34.78 ? ? ? ? ? 90.38 34.02 ?
36.53 11.24 23.07 ? ? 12.09 15.64 11.58 15.02 10.09 15.52 ?

? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ?

NMING F8772 *Ichthyosaurus intermedius* 930 455 ? 473 321 94.11
42.07 ? 300 ? 267 52.95 341 109.43 34.27 61.81 64.85 ?
32.95 15.87 29.95 55.54 109.69 54.26 26 85.62 83.04 305 76.32
36.38 54.91 23.83 31.95 28.44 34.21 17.5 23.7 23.85 22.29 23.3
27.06 60.53 ? ? ? 167 60.11 28.15 35.34 13.46 16.44
13.27 20.42 11.24 13.39 12.06 14.43 11.04 13.52

CAMSMX.50187 *Ichthyosaurus breviceps* 787 296 85.48 333 180 71
? ? 179.98 150.43 ? 18.19 232 72.1 ? ? ? 194
? 12.61 24.6 40.92 79.99 ? ? 55.34 48.36 180 50.12
29.21 34.43 15.42 21 15.32 23.14 11.59 15.97 13.79 16.77 10.95
17.45 54.55 52.56 13.86 15.7 109.67 35.73 17.35 22.28 9.78 12.73
9.16 13.6 ? ? ? ? ? ?

NHMUK PV OR43006** *Ichthyosaurus breviceps* 445.23 220.55 ? 232.23
148.24 59.07 33.14 ? 123.13 84.3 110.16 25.04 184.79 51.32 ? ?
? 49.43 ? 7.62 15.26 41.31 59.29 25.86 15.62 ? ?
188.65 48.81 26.69 30.03 13.56 17.55 10.47 17.66 9.32 13.63 11.16
11.11 7.67 14.51 ? ? ? ? 86.71 26.61 13.6 17.48
5.88 10.23 8.24 11.09 5.61 8.49 6.85 7.95 6.16 6.9

TTNCM 5803 *Ichthyosaurus breviceps* 350 205 ? 154.09 103.74 ? ?
? ? ? ? ? ? ? ? ? ? ?
28.25 8.86 19.4 19.92 ? ? ? ? ? ? 23.02 ?
? ? ? ? ? ? ? ? ? ? ?
29.66 25.53 7.01 7.57 41.03 27.18 16.76 17.41 7.53 9.99 7.43
8.75 ? ? ? ? ? ?

CAMSM J.35186 *Ichthyosaurus conybeari* 498 402 120 383 274
73.98 28.81 ? 275 230 238 25.13 ? 48.77 56.73 41.14
34.87 ? 26.25 9.22 17.81 32.61 67.97 ? ? ? ? 193
42.58 32.61 38.83 16.25 26.8 16.72 25.73 12.28 20.98 13.97 18.57
12.77 20.47 34.7 ? ? ? 108.35 39.71 18.06 24.07 10.59
13.57 11.18 14.95 ? ? ? ? ? ?

MANCH LL11835 *Ichthyosaurus conybeari* ? 478 265 478 ? ?
? ? 270 ? ? ? 358 130.75 ? ? ? ?
? ? ? 47.03 96.05 54.34 37.46 108.37 91.09 185 75.75
52.34 58.89 25.28 34.77 28.11 44.21 15.12 26.42 19.51 24.49 18.73
26.65 ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ?

NHMUK BGS956			*Ichthyosaurus conybeari*				244	241	?	229	116	
	50.72	?	26.49	146	120.61	108.73	17.64	171	67.26	?	26.17	?
	24.54	?	5.12	10.15	13.27	?	?	?	?	?	95.06	
	25.97	16.83	21.49	10.2	14.32	11.39	?	8.1	11.77	?	?	
	7.48	11.39	?	?	?	?	56.64	19.05	8.14	?	5.91	
	7.36	7.81	9.21	8.89	18.57	?	?	?	?			
NHMUK PV OR38523**				*Ichthyosaurus conybeari*				368.05	271.71	?	261.19	?
	?	?	?	178.12	?	?	?	180.45	?	?	?	?
	51.14	23.04	7.22	15.41	18.96	46.51	21.65	11.51	40.94	36.28	97.01	
	29.46	20.73	25.89	10.71	15.32	11.44	12.23	6.56	11.52	7.76	10.77	
	5.91	11.4	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?	?				
OUMNH J.29283 B			*Ichthyosaurus conybeari*				?	195	88.02	?	145.26	
	45.66	?	?	126.58	110.58	116.79	9.63	?	44.34	?	?	?
	?	?	?	?	?	?	?	?	42.47	31.34	131.26	
	24.5	12.05	14.67	11.8	15.74	10.94	13.94	8.58	12.47	9.62	12.61	
	7.83	10.19	?	28.72	6.77	3.91	?	15.49	7.59	11.79	?	?
	?	?	?	?	?	?	?	?				
WARMS G352		*Ichthyosaurus conybeari*				260	?	73.43	?	?	48.01	
	21.87	20.61	?	?	?	23.93	?	57.51	18.66	27.07	27.21	?
	22.85	8.73	16.32	20.6	?	?	?	46.8	34.73	106.14	36.1	
	21.83	27.71	11.27	17.21	?	18.43	7.61	12.96	9.03	11.53	7.59	
	11.97	?	?	?	?	?	?	?	?	?	?	?
	?	?	?	?	?	?	?					
DONMG 1983.8**			*Ichthyosaurus anningae*				476	394	?	376	222	
	74.77	56.63	?	234	197	207	25.25	276	71.12	?	?	?
	190	?	13.3	27.6	24.12	85.88	37.57	20.27	85.95	58.64	194	
	50.9	38.59	40.58	15.09	24.52	16.93	23.36	11.96	17.68	15.57	16	
	10.93	18.55	39.54	?	?	?	?	29.66	19.48	20.15	?	?
	?	?	?	?	?	?	?	?				
NHMUK PV OR120			*Ichthyosaurus anningae*				240	262	?	270	170	
	66.09	21.59	18.97	173	142.87	166	12.07	184	66.83	?	?	
	29.29	?	?	5.8	13.13	25.16	35.98	?	?	?	?	
	136.51	28.67	23.14	22.51	10.7	13.88	11.05	15.42	7.41	11.15	9.25	
	11.22	7.91	10.76	?		?	?	43.49	15.95	10.71	?	?
	?	3.83	6.26	?	?	?	?	?	?			
AGC 12		*Ichthyosaurus sommersetensis*					695	?	135.03	441	230	
	79.43	54.27	30.71	229	181	174	31.86	265	93.11	?	?	?
	210	?	10.61	21.63	40.34	84.9	34.38	19.31	84.65	74.39	202	
	58.77	34.68	50.52	23.8	28.67	21.45	29.36	12.08	21.54	18.61	21.3	

14.21 22.51 ? ? ? ? 131.47 49.88 ? 29.08 11.22
15.97 13.11 18.63 8.58 13.33 9.7 14.33 10.2 11.61

AGC 15 *Ichthyosaurus sommersetensis* ? 369 ? 372 262
76.19 40.86 ? 233 181 202 19.94 261 99.56 ? ? ?
315 ? ? ? 38.75 56.49 26 ? 89.73 65.34 234
67.6 46.86 49.12 16.93 26.48 19.06 30.28 12.14 20.72 15.28 19.83
12.73 21.54 ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ?

AGC 16 *Ichthyosaurus sommersetensis* 780 440 ? 450 312
78.09 ? ? 261 195 230 27.49 ? 118.45 ? ? ?
? ? 13.2 31.86 24.93 ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
63.23 54.8 14.22 20.83 189 66.62 30.49 41.32 16.92 20.26 15.85
24.74 15.45 13.73 13.18 16.71 13.37 26.7

AGC 17 *Ichthyosaurus sommersetensis* 870 ? ? ? 254 ?
? ? 256 199 215 33.89 ? 73.67 42.59 42.19 39.3 ?
49.67 18.06 36.18 42.8 87.26 45.75 35.36 103.22 104.78 261 82.57
55.73 58.04 23.22 32.13 23.38 33.72 24.64 22.17 20.56 23.84 19.31
25.38 49.52 65.67 15.96 31.08 122.71 62.71 34.83 32.94 11.6 16.45
13.06 16.11 11.38 12.86 12.39 14.46 11.38 15.54

BRSMG Cb3578 *Ichthyosaurus sommersetensis* 383 270 ? 260 175
50.08 ? ? 165 130 145.5 22.63 175 69.85 ? ?
24.57 ? ? 8.82 19.43 24.15 59.02 30.77 15.26 65.99 51.42 125
47.47 34.74 36.46 13.58 20.81 15.18 23.04 6.68 14.49 11.7 12.82
9.15 14.49 35.1 40.53 6.32 15.51 ? 32.82 12.61 15.14 ? ?
? ? ? ? ? ? ? ?

BRSMG Cc921 *Ichthyosaurus sommersetensis* ? 350 ? 376 255
66.36 43.86 29.38 223 175 194.5 30.55 174 104.92 ? ? ?
? ? 11.38 20.1 42.85 ? ? ? ? ? 194
62.53 43.01 47.12 17.53 25.58 18.89 29.93 11.49 19.71 14.83 18.49
12.55 22.23 ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ?

BRSMG Cc924 *Ichthyosaurus sommersetensis* ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? 53.96 ? 39.05 82.98 61.26 190 58.8
40.8 45.57 15.81 24.06 17.04 26.26 8.44 19.07 13.71 18.46 11.2
18.39 ? ? ? ? ? 45.46 21.35 24.57 ? ? ?
? ? ? ? ? ? ?

NHMUK PV OR2013 *Ichthyosaurus sommersetensis* ? ? ? 472.77 ?
83.96 ? ? 276.69 207.08 230.32 ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? 388.1
105.98 96.87 70.36 29.06 40.51 29.79 42.77 17.44 28.48 28.54 29.83
21.39 34.725 69.87 ? ? ? 171.02 75.46 34.07 43.45 18.25
23.32 16.59 25.63 14.76 14.39 16.43 18.17 14.06 17.49

NMING F8747 *Ichthyosaurus sommersetensis* 890 480 ? 527 376 95.58
55.9 28.17 350 252 276 43.68 374 139.38 54 73.22 24 187
? 13.36 27.05 63.15 ? ? ? ? ? 286 89.73
48.08 66.44 28.47 35.6 25.94 29.46 17.2 30.22 25.51 31.8 19.58
31.32 42.29 72.94 17.27 22.15 ? 70.36 26.94 31.18 ? ? ?
? ? ? ? ? ? ?

NMING F8748 *Ichthyosaurus sommersetensis* 2140 523 251 522 334
86.38 47.18 ? 308 246 263 40.53 345 104.07 43.39 64.38
49.28 ? 59.94 19.27 35.89 40.86 122.11 75.98 45.11 80.57 100.1 367
99.11 72.81 73.5 29.46 40.77 35.48 37.87 17.42 30.38 29.26 34.04
22.86 34.63 71.13 ? ? ? 193 73.88 30.88 ? 41.6
18.89 21.4 20.33 19.98 15.6 14.17 16.49 16.79 19.31

NMING F8751 *Ichthyosaurus sommersetensis* 785 470 ? 494 373
98.65 43.24 31.92 314 265 ? 35.98 375 147.39 ? ? ?
? ? 20.02 31.61 45.45 93.63 35.53 ? ? ? 267
64.05 23.62 45.39 18.58 30.84 19.89 29.46 12 ? 16.77 21.39
16.79 22.17 38.55 ? ? ? 121.85 46.38 18.91 27.84 ? ?
10.19 16.99 8.3 4.49 11.14 13.98 11.57 15.31

TTNCM 16/2015 *Ichthyosaurus sommersetensis* ? ? 174 409 ?
? ? ? 276 ? ? ? ? 187 ? ? ?
227 ? ? ? ? 86.29 ? ? ? ? 178
61.25 39.38 52.09 17.35 28.11 18.15 29.57 13.59 19.45 16.81 19.53
11.03 23.89 ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ?

ACG 11 *Ichthyosaurus larkini* 510 317 128.57 316 230 70.01 43.43 ?
202 157 161.34 31.03 ? 78.8 ? ? ? 103.83 38.83
8.05 17.01 20.29 74.07 38.24 21.09 70.06 52.58 187 53.57 36.96
35.9 12.33 21.18 13.93 20.87 8.89 16.2 12.2 14.24 13.51 14.26
33.55 ? ? ? 87.89 40.42 16.33 19.96 7.92 10.04 8.83
11.48 5.32 7.81 7.45 8.13 ? ?

AGC 14 *Ichthyosaurus larkini* 756 462 146 443 297 ? 61.91 ?
300 218 251 ? ? ? 30.44 61.86 61 ? ?
14.93 29.36 48.51 107.62 ? 28.5 ? ? 332.22 82.22 41.33
61.67 22.37 35.03 ? ? 13.44 27.11 16.07 23.85 ? ?

59.54 64.68 11.55 32.47 ? 54.1 26.06 29.02 ? ? ? ?
? ? ? ? ? ?

CAMSM 59642 *Ichthyosaurus larkini* ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
9.39 23.15 42.56 65.57 ? ? 72.76 37.72 147.67 49.87 ?
27.44 14.04 20 14.27 24.24 9.4 14.56 14.34 14.42 9.04 16.38 ?
45.59 13.11 11.4 93.57 34.63 15.88 18.32 ? ? ? ? ?
? ? ? ? ?

CAMSM 5975 *Ichthyosaurus larkini* 548 422 ? 439 250 64.93 37.81 ?
273 199 218 ? 297 71.64 ? ? ? 123 ? ?
? ? 94.77 ? ? 94.75 94.96 246 77.67 25.33 45.61
24.89 30.75 23.1 31.98 12.6 22.64 19.42 18.91 16.73 24.45 57.17
57.68 10.36 22.58 112.07 59.15 16.69 20.9 12.51 15.7 14.34 19.59 ?
? ? ? ? ?

NOTNH FS4940 *Ichthyosaurus larkini* ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
15.03 28.35 28.72 69.49 ? ? ? ? 133.78 55.6 36.64
37.73 18.27 23.95 21.7 26.32 ? ? ? ? ? ?
41.17 44.59 7.99 17.95 126.6 46.43 16.61 28.81 9.84 14.39 11.88
16.53 8.58 10.05 10.51 12.72 8.51 10.68

OUMNH J.10301 *Ichthyosaurus larkini* ? 464 194 497 ? ? ?
? ? ? ? ? 392 ? 27.26 50.61 30.19 83.33
35.69 15.56 37.65 11.53 116.07 ? ? ? ? 297 85.13
55.4 60.78 26.38 35.57 24.18 31.67 17.04 25.58 24.52 22.48 16.83
22.82 ? ? ? ? 116.98 57.15 27.43 30.73 16.92 18.68
15.75 22.32 ? ? ? ? ? ?

TTNCM 8373 *Ichthyosaurus larkini* 863 412 ? 417 276 89.49 ? ?
245 183 214 38.09 245 93.57 ? ? ? 90.28 34.17 ?
? ? 91.42 ? ? ? ? 222.5 72.38 49.05 45.73
20.12 26.99 21.21 29.5 14.32 20.85 17.61 20.79 13.74 21.75 51.44
52.83 14.86 9.71 127 53.07 22.6 27.38 10.8 13.26 13.98 16.06 ?
? ? ? ? ?

BIRUG Unknown *Ichthyosaurus* sp. 292 185 ? 211 145 49.96
27.87 15.39 128.05 98.88 115.93 19.82 176 54.83 ? ? ?
114.67 ? 5.4 11.66 13.79 32.66 ? ? 36.14 38.6 118.17
25.35 19.16 20.01 7.85 11.68 7.2 11.58 4.68 8.83 7.06 9.12
5.59 8.69 ? 22.58 3.27 5.42 ? 10.97 ? 10.96 ? ?
? ? ? ? ? ? ? ?

CAMSM 35189 *Ichthyosaurus* sp. 485 ? ? 285 ? ? ? ?
155 ? ? ? ? ? ? ? ? ? ?
9.37 18.66 ? 64.127 28.549 15.415 69.53 49.11 106 39.56 29.12
34.36 13.61 21.38 13.37 20.68 8.61 15.58 9.36 15.42 8.99 15.85
32.49 ? ? ? 73.86 28.1 ? ? 6.91 10.55 7.15
11.92 ? ? ? ? ? ?

CAMSM 59644 *Ichthyosaurus* sp. 635 375 150 362 ? ? ? ?
? ? ? ? ? ? ? ? ? ? 31.98
10.94 25.76 47.03 91.17 ? ? 75.13 64.84 270 72.86 49.26
53.74 22.3 28.62 27.69 35.22 15.64 23.91 19.01 24.68 16.58 25.85
43.6 ? ? ? ? 67.93 28.76 19.43 ? ? ? ?
? ? ? ? ? ?

DCM Uknown *Ichthyosaurus* sp. 1445 460 300 458 ? ? ? ?
? ? ? ? 215 ? ? ? ? ? ?
12.76 27.55 ? 108.46 57.13 22.9 108.34 89.21 ? 85.16 50.59
67.96 42.33 44.98 41.31 40.63 ? ? ? ? ? ? ?
56.44 13.64 ? 180 71.93 31.03 44.72 27.63 17.85 21.62 20.12
15.83 13.67 ? ? 19.16 20.17

IPSMG Unknown *Ichthyosaurus* sp. ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? 216 52.08 41.58
34.72 13.4 20.6 16.72 24.23 10.15 15.12 14.61 17.63 10.16 17.3
50.96 49.78 13.74 18.98 101.98 39.51 15.52 21.55 9.12 14.47 9.11
11.62 7.31 9.9 8.99 9.54 7.11 10.2

LEICT G126.1992 *Ichthyosaurus* sp. 495 340 ? 365 234 79.27
38.55 ? 227 159 188 42.84 194 97.87 24.57 54.76 ? ?
? 9.22 18.99 33.66 70.32 ? ? ? ? 198.54 50.16
34.65 39.75 16.51 25.46 16.3 22.53 10.54 17.77 14.39 15.93 13.13
19.62 ? 36.56 ? ? 56.09 40.5 14.21 25.25 9.38 13.84
9.74 15.13 ? ? ? ? ? ?

NMING F8774 *Ichthyosaurus* sp. 802 458 150 ? 327 89.78 56.04 ?
308 248 275 50.15 ? 117.13 54.05 73.65 69.21 ? ?
20.11 31 52.48 83.74 38.37 28.02 ? ? 206 64.44 41.08
50.26 20.21 28.82 21.41 32.67 12.54 23.87 18.93 22.1 14.89 24.32
54.68 ? ? ? 114.16 54.95 16.67 28.73 11.78 18.69 12.74
17.23 9.75 12.24 12.31 13.13 12.81 14.65

OUMNH J.13800 *Ichthyosaurus* sp. ? 272 ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ?
32.74 ? ? ? 69.62 ? ? 60.83 54.07 133 46.17
35.65 36.81 15.52 18.02 14.5 20.54 8.83 11.81 12.81 14.35 8.98

15.98 ? ? ? ? ? 48.49 35.04 32 ? ? ?
? ? ? ? ? ? ?

PMO 227578 *Ichthyosaurus* sp. ? ? ? 411.7 ? ? ? ?
? ? ? ? 309.09 ? ? ? ? 280.37 38.46 ?
? ? 96.41 41.26 31.88 ? ? 139.26 67.97 33.9 50.29
29.4 18.39 29.3 19.94 19.74 10.55 21.59 21.34 21.32 13.75 ? ?
? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ?

TTNCM 8359 *Ichthyosaurus* sp. 286 263 170 274 182 51.44 38.55 ?
191 ? ? ? ? ? ? ? ? ? 46.98
6.15 11.89 22.31 110.82 ? ? ? ? 110.82 31.63 ?
20.04 8.9 11.22 8.49 12.44 5.48 8.78 7.57 9.32 5.79 7.81 ?
? ? ? 41.41 17.39 7.24 12.79 4.48 6.05 5.51 7.29 3
5 11 ? ? ?

2. Measurements and counts for second set of specimens, all measurements listed in mm:

Specimen Number Species ID Lower jaw length Snout length Humerus Length
Humerus proximal width Prenarial segment Upper jaw length
Orbit diamerer Maxillary lengthPremaxillary length Femur length Dentary length
Angular Length

NHMUK PV OR120 *Ichthyosaurus anningae* 2.431363764 2.238046103
1.457427693 1.364363355 2.154941045 2.230448921 1.820135752
1.824971461 2.220108088 1.202760687 2.264817823 ?

DONMG 1983.8** *Ichthyosaurus anningae* 2.575187845 2.369215857
1.706717782 1.586474779 2.294466226 2.346352974 1.873727381
1.851991748 2.315970345 1.472171147 2.440909082 2.278753601

NHMUK PV R1062 *Ichthyosaurus breviceps* 2.260071388 1.9741431
1.556061159 1.31386722 1.760271661 2.025633511 1.979047327
1.650598898 2.033705151 ? ? 2.011528154

NHMUK PV OR39263 *Ichthyosaurus breviceps* 2.298853076 2.036948112 ? ?
1.857995496 2.095483186 1.774881766 1.650501795 1.967828679 ?
2.126456113 ?

CAMSMX.50187 *Ichthyosaurus breviceps* 2.522444234 2.255224247
1.700011062 1.465531557 2.177334456 2.255272505 1.851258349
1.857935265 ? 1.553033016 2.365487985 2.28780173

OUMNH J.10312 *Ichthyosaurus breviceps* 2.397940009 2.1389024 ? ?
1.990516444 ? 1.809155532 1.888740961 2.042339205 ?
2.053116875 1.978864984

NHMUK PV OR43006** *Ichthyosaurus breviceps* 2.365918322 2.090363879
1.688508808 1.426348574 1.925827575 2.170965406 1.771366971
1.710286648 2.042023927 1.425044875 2.266678465 1.69399061

NMING F8767 *Ichthyosaurus communis* 2.562292864 2.382017043 1.794139356 ?
2.193124598 2.40654018 1.824711443 1.96397661 2.260071388
1.342225229 ? ?

PETMG R174 *Ichthyosaurus communis* 2.491361694 2.369215857 1.655618584
1.372727941 2.29666519 2.403120521 1.819741297 1.906442794
2.326335861 1.591732239 2.397940009 2.182614348

CAMSM J35183 *Ichthyosaurus communis* 2.442479769 2.247973266
1.629715333 1.451479405 2.181843588 2.28780173 1.725012725 1.83384805
2.189434163 1.463892989 2.318063335 1.876160085

NMING F16625 *Ichthyosaurus communis* 2.255272505 2.101712714 ? ?
1.855276804 2.159747611 1.929214504 2.057133367 1.996292719 ? ?
2.166400509

NMING F16604 *Ichthyosaurus communis* 2.220108088 1.927113612 ? ?
1.447313109 1.948852906 1.845470133 2.039770927 ? ?
2.124536828 2.09649289

NHMUK PV R1162** *Ichthyosaurus communis* 2.425648322 2.188112537
1.610447221 1.413299764 2.086608945 2.207795885 1.744918542
1.754424789 2.126748142 1.451786436 2.2912134 ?

NMING F8746 *Ichthyosaurus communis* 2.62838893 2.515873844 1.874539797
1.659345636 2.434568904 2.541579244 1.95506207 1.876333329 ?
1.725911632 ? ?

YORYM 2005.2408 *Ichthyosaurus communis* 2.340444115 2.209515015
1.473194909 1.37621185 2.146469133 2.225309282 1.599118565
1.689930104 2.150572248 1.337059726 2.181843588 ?

LEICT G123.1992 *Ichthyosaurus communis* 2.666517981 2.494154594
1.876621916 1.711638538 2.387389826 2.511883361 ? 2.112839511
2.424881637 ? 2.545307116 ?

BRSLI M3562 *Ichthyosaurus communis* ? 2.396199347 1.543074235
1.388633969 2.31386722 2.426511261 1.765891976 2.015024263
2.373831145 1.583085366 ? ?

YORYM 1997.131 *Ichthyosaurus communis* 2.419955748 2.220108088
1.458637849 1.29136885 2.138586871 2.247973266 1.674861141
1.821251432 2.164650216 ? 2.271841607 2.078021581

NOTNH FS3323	*Ichthyosaurus communis*	2.6599162	2.447158031	?	?	2.307496038	2.45484486	1.945616279	1.964966375	2.376576957	?	2.555094449	2.0757294
CAMSM J69477	*Ichthyosaurus communis*	2.655138435	2.426511261	1.91981002	1.660960292	2.305351369	2.450249108	1.881669908	2.034146977	2.361727836	?	2.5289167	?
TTNCM 120/1996	*Ichthyosaurus communis*	2.487138375	2.320146286	1.60991441	1.357934847	2.230448921	2.361727836	1.757547853	?	2.456366033	1.469232743	2.367355921	?
GLAHM V1179	*Ichthyosaurus communis*	2.527629901	2.290034611	1.597036665	1.429913698	?	2.311753861	1.58546073	1.891593204	2.201397124	1.474216264	2.354108439	?
TTNCM 5804	*Ichthyosaurus communis*	2.541579244	2.191870015	1.74390155	1.652246341	2.010723865	2.33243846	1.917872955	2.206825876	?	?	?	2.243038049
TTNCM 5805	*Ichthyosaurus communis*	2.612783857	2.456366033	1.753659647	1.563243701	2.357934847	2.514547753	1.955495329	?	2.437750563	?	2.361727836	?
AGC 9	*Ichthyosaurus communis*	2.474216264	2.354108439	1.769451179	1.647871765	2.245512668	2.418301291	1.7857568	1.90439092	2.271841607	1.627570664	?	?
CAMSM J.35186	*Ichthyosaurus conybeari*	2.583198774	2.439332694	1.629205657	1.513350799	2.361727836	2.437750563	1.869114327	1.688152756	2.376576957	1.598899887	?	?
WARMS G352	*Ichthyosaurus conybeari*	2.235528447	1.934346927	1.557507202	1.339053736	1.662190991	1.941014244	1.681331706	1.759743368	1.796643704	?	?	?
NHMUK BGS956	*Ichthyosaurus conybeari*	2.359835482	2.164352856	1.41447195	1.226084116	2.081383317	2.064457989	1.705179245	1.827756863	2.036349388	1.27989498	2.23299611	1.389874558
OUMNH J.29283 B	*Ichthyosaurus conybeari*	?	2.102365091	1.389166084	1.080987047	2.043676586	2.16214604	1.659535907	1.646795689	2.067405658	1.190051418	?	?
NMING F8772	*Ichthyosaurus intermedius*	2.674861141	2.477121255	1.882638362	1.560862695	?	2.506505032	1.973635773	2.039136399	2.426511261	1.778946728	2.532754379	?

NMING F8752	*Ichthyosaurus intermedius*	2.097118424	?	?	1.43806745	1.881897974	1.720490068	1.437116093	?	1.93135615	?	1.916559219	?
NMING F8763	*Ichthyosaurus intermedius*	?	2.447158031	1.789580712	1.601190533	2.350248018	2.481442629	1.763577724	?	2.387389826	?	?	?
NMING F8760	*Ichthyosaurus intermedius*	2.515873844	2.397940009	?	?	2.318063335	2.414973348	1.879382637	1.904715545	2.334453751	?	2.465382851	?
NMING F8773	*Ichthyosaurus intermedius*	2.633468456	2.511883361	?	?	2.418301291	2.517195898	1.83372069	2.029992175	2.457881897	?	?	?
NMING 8757	*Ichthyosaurus intermedius*	2.442479769	2.222716471	1.616160313	1.428782511	2.117271296	2.285557309	1.799478399	?	2.136720567	?	2.294466226	?
WARMS G347	*Ichthyosaurus intermedius*	2.664641976	2.481442629	?	?	2.383815366	2.496929648	1.927216331	2.025756315	2.412460547	?	2.536558443	2.290034611
CAMSM 5975	*Ichthyosaurus larkini*	2.64246452	2.436162647	1.890253305	1.40363519	2.298853076	2.397940009	1.812445403	1.855155577	2.338456494	1.771954749	2.472756449	2.089905111
TTNCM 8373	*Ichthyosaurus larkini*	2.620136055	2.389166084	1.859618579	1.690639012	2.26245109	2.440909082	1.951774508	1.971136629	2.330413773	1.724849088	2.389166084	1.95559155
ACG 11	*Ichthyosaurus larkini*	2.499687083	2.305351369	1.728921646	1.567731963	2.195899652	2.361727836	1.845160078	1.896526217	2.207742053	1.606596309	?	2.016322854
AGC 14	*Ichthyosaurus larkini*	2.646403726	2.477121255	1.914977472	1.616265405	2.338456494	2.472756449	?	?	2.399673721	1.733197265	?	?
NMING F8751	*Ichthyosaurus sommersetensis*	2.693726949	2.496929648	1.806519134	1.373279893	2.423245874	2.571708832	1.99409709	2.168468019	?	1.666330744	2.574031268	?
AGC 15	*Ichthyosaurus sommersetensis*	2.57054294	2.367355921	1.829946696	1.670802284	2.257678575	2.418301291	1.881897974	1.998084888	2.305351369	?	2.416640507	2.498310554

NMING F8748 *Ichthyosaurus sommersetensis* 2.717670503 2.488550717 1.996117476
1.862191031 2.390935107 2.523746467 1.9364132 2.017325555
2.419955748 1.868526887 2.537819095 ?

AGC 12 *Ichthyosaurus sommersetensis* 2.644438589 2.359835482 1.769155691
1.540079089 2.257678575 2.361727836 1.899984563 1.968996327
2.240549248 1.697926445 2.423245874 2.322219295

AGC 17 *Ichthyosaurus sommersetensis* ? 2.408239965 1.916822285
1.746089043 2.298853076 2.404833717 ? 1.86729067 2.33243846
1.797336801 ? ?

AGC 16 *Ichthyosaurus sommersetensis* 2.653212514 2.416640507 ? ?
2.290034611 2.494154594 1.892595423 2.073535065 2.361727836
1.823604628 ? ?

NMING F8747 *Ichthyosaurus sommersetensis* 2.721810615 2.544068044 1.952937668
1.681964459 2.401400541 2.575187845 1.980367026 2.14420046
2.440909082 1.847325831 2.572871602 2.271841607

BRSMG Cb3578 *Ichthyosaurus sommersetensis* 2.414973348 2.217483944
1.676419232 1.540829814 2.113943352 2.243038049 1.69966432 1.84416641
2.162862993 1.516138577 2.243038049 ?

BRSMG Cc921 *Ichthyosaurus sommersetensis* 2.575187845 2.348304863 1.796088429
1.633569443 2.243038049 2.40654018 1.821906377 2.020858282
2.288919606 ? 1.240549248 ?

OUMNH J.7729 *Ichthyosaurus* sp. 2.271841607 2.118562313 ? ?
2.040285799 2.192260719 1.742725131 1.791971201 2.051113917 ?
2.113876533 ?

YORYM 1994.1799.51 *Ichthyosaurus* sp. 2.444044796 2.255272505 ? ?
2.150787131 2.311753861 1.743744879 1.90118578 2.206825876 ?
2.318063335 2.028042295

NMS 1898.180.30 *Ichthyosaurus* sp. 2.451786436 2.318063335 ? ?
2.255272505 2.367355921 1.753812784 1.91481898 2.255272505 ?
2.334453751 2.247973266

LEICT G126.1992 *Ichthyosaurus* sp. 2.562292864 2.356025857 1.700357528
1.539703239 2.201397124 2.369215857 1.899108858 1.990649588
2.274157849 1.607455023 2.28780173 ?

WARMS G10805 *Ichthyosaurus* sp. 2.703291378 2.51851394 ? ?
2.389166084 2.542825427 2.037705313 1.914290256 2.440121603 ?
2.580924976 2.447158031

NMING F8774	*Ichthyosaurus* sp.	?	2.488550717	1.809155532	1.613630435	2.394451681	2.514547753	1.953179601	2.068668143	2.439332694	1.739967697	?	?
OUMNH J.29221	*Ichthyosaurus* sp.	2.409933123	2.218062618	1.494711025	1.31993844	2.117834519	2.192706807	1.746556361	1.685204134	2.148108858	?	?	?

Appendix C.

Characters Not Used in Analysis and Why

Crainial

1. Bones in skull are connected by overlapping sutures (From De la Beche and Conybeare, 1821).
    a. This is a character that applies to all ichthyosaurs and was mentioned in this article as a difference between ichthyosaurs and crocodiles (De la Beche and Conybeare, 1821).
2. Number of teeth on either side of jaw ≥ 30 (From De la Beche and Conybeare, 1821).
    a. This character does not use anatomical terms, so it is unclear if they are referring to the premaxilla or the dentary of ichthyosaurs. It is unlikely that it is of the maxilla, as it is not big enough to hold close to 30 teeth. Tooth count is also an unreliable character to count as ichthyosaurs continuously replaced teeth (Edmund 1960, 1969; Motani 1997a, b). In addition, the specimens are often preserved in such a way that it can be difficult to tell which side of the jaw the teeth belong to (e.g. left or right side of jaw).
3. Tooth root cross-section in adults: 0- rounded; 1- quadrangular (Fischer et al., 2011b: character 3 modified)
    a. This characteristic was not used in this study as all ingroup specimens in this study have rounded cross-section.
4. Teeth recurved: 0-gently recurved; 1-straight; 2-significantly recurved.
    a. This character refers to the extent to which the teeth of a specimen curve towards the posterior of the skull. This was not used as it is subjective to preservation angle or having a 3D preserved and prepared.
5. Absence of brachial framework (no gills) (Owen, 1881).
    a. This characteristic is true of all ichthyosaurs, so will not be used in this study.
6. Absence of foramen behind the termination of the dental bone (From De la Beche and Conybeare, 1821).
    a. This characteristic is true of all ichthyosaurs, and was therefore removed from analysis. This feature may be present in two specimens that authors are aware of (De la Beche and Conybeare, 1821). No specific specimen was named other than it was in De la Beche collection. This character was mentioned as the difference between ichthyosaurs and crocodiles.
7. Surangular, lateral view: 0- anterior most portion of surangular seen to extend as far forward as maxilla; 1- anterior most portion does not extend as far forward as the maxilla, but extends beyond the orbit; 2- does not extend beyond the orbit (Lomax and Massare, 2016 Char 16).

   a. The surangular is the bone that makes up part of the posterior portion of the lower jaw and is directly posterior to the dentary. This character was not used as it is not independent from maxilla length.

8. External pterygoid process resting against the inside of the termination of the maxillary, and extending in a long process to the hinder extremity of the head (From De la Beche and Conybeare, 1821).
   a. This characteristic was not used as it was not clear what the author was referring to and was unlikely to be seen in many specimens due to common lateral preservation.
9. Head and jaws are about a quarter of the length of the whole animal (From De la Beche and Conybeare, 1821).
   a. This is a ratio characteristic that has not been statistically tested and therefore deemed unreliable in a phylogenetic analysis.
10. Anterior process of maxilla in lateral aspect: 0- short and narrow; 1- long and narrow (modified Fernandez 2007 Char 1).
    a. This character describes the form of the process making up the anterior portion of the maxilla, and was not used in this analysis as it is too similar and not independent from the current character 6.
11. Anterior process of maxilla: 0- extending as far as or further than nasal; 1- reduced (not extending as far as nasal) (Fischer et al. 2011, Char 7).
    a. This character was not used in this analysis as it is too similar and not independent from the current character 6.
12. Posterior and anterior extent of maxilla relative to maximum height (dorsoventral dimension); 0- jugal process of the maxilla long relative to anterior process; 1- jugal process of the maxilla approximately equal to anterior process; 2- jugal process short relative to anterior process (modified from Lomax and Massare, 2016 Char 5).
    a. This character was not used as it is not independent from current characters 6 and 7.
13. Maxilla, external naris contact: 0- absent; 1- present (Motani, 1999 Char 3).
    a. This character was not used as it is not independent from character 8 in the analysis.
14. Anterior process of maxilla in lateral aspect: 0- short and narrow; 1- long and narrow (modified Fernandez 2007 Char 1).
    a. This character was not used as a modified version of this character was used instead.
15. Nostrils distinct (Owen, 1881).
    a. This characteristic is ambiguous and dependent upon the meaning of the author, could be considered as a feature present in all ichthyosaurs.
16. Nostrils in antorbital position (Owen, 1881).
    a. This characteristic was not used as it is the state for all nostrils in ichthyosaurs in this study.
17. Lacrimal: 0- excluded from contact with external nares by dorsal process of maxilla; 1- participates in external narial opening (Sander, 2000 Char 10).
    a. This character was removed as it is the same as character 10 in this analysis.
18. Processus narialis of prefrontal: 0- absent; 1- present (Fischer et al. 2011b Char 11)
    a. Character state 1 does not show up in any species within this study, only in much more derived species and could therefore not be useful in this analysis.
19. Processus temporalis of the frontal: 0- absent; 1- present (Fischer et al. 2011b Char 14)

    a. Character state 1 does not show up in any species within this study, only in much more derived species and could therefore not be useful in this analysis.
20. Separation of external naris from orbit: 0- narrow; 1- broad (Lomax and Massare, 2016 Char 14).
    a. This character was removed as the states ‘narrow’ and ‘broad’ are subjective. This character is also not independent from eye size as a large eye would force state 0.
21. Pterygoid abuts the posterior end of the palatine absent (Druckenmiller and Maxwell, 2010 Char 18).
    a. This character will only be seen in specimens with exceptional or 3D preservation quality, which is not common in most Lower Lias material.
22. Jugal with rounded cross section (Maisch, et al., 2008).
    a. A very small quantity of jugals could be observed in cross-section, and so this would not be an informative character for the purposes of this study.
23. Quadratojugal exposure: 0- extensive; 1- small, largely covered by squamosal and postorbital (modified by Fischer et al., 2013 Char 17 and Fisher et al., 2011b from Maish and Matzke 2000 Char 20).
    a. This character was not used as most skulls are laterally compressed and so overlap would be difficult to distinguish from any preservational features. The main difference in this analysis would be seen in outgroup versus ingroup taxa.
24. Shape of the paraoccipital process of the opisthotic: 0- short and robust; 1- elongated and slender (Fischer et al., 2012 Char 20).
    a. This character was not used as it is intended for the opthalmosaurid morphology.
25. Sagittal eminence: 0-absent; 1 present (Fernández, 2007 Char 5)
    a. This character was not used, as all specimens in study reflect character state 1, rendering it uninformative.

Axial skeleton

26. ‘The centra have distinct posterior and anterior rims that stand out markedly from the sides of the centrum.’ (Massare and Lomax, 2014 pp 26)
    a. This characteristic is seen in other specimens, as well as those utilised in this study. It is not entirely clear what is meant by this statement, so for clarity it was removed.
27. Fluke centra: 0- strongly laterally compressed; 1- as wide as high (Maxwell, 2010 Char 16)
    a. This character was not used as all specimens in study reflect character state 0.
28. Dimensions of posterior dorsal and anterior caudal centra: 0- four times or more as high as long, 1-3.5 times or less as high as long (Druckenmiller and Maxwell, 2010 Char 28).
    a. This character was not used as all specimens in study reflect character state 1.
29. Ossified haemapophyses: 0- present; 1- absent (Maisch and Matzke, 2000 Char 63).
    a. ‘In all Triassic ichthyosaurs in which the caudal vertebral column is known, there are ossified haemapophyses present. In no post-Triassic ichthyosaur are there ossified haemapophyses (Maisch and Matzke, 2000 Char 63 pp 48). There are, however, cartilaginous haemapophyses present in *Eurhinosaurus longirostris* (von Huene 1928, 1931) and haemapophyseal facets are also known from *Leptonectes* (Owen, 1881), Ichthyosaurus (Hawkins 1840; Owen, 1881), at least some caudal vertebrae of *Ophthalmosaurus* (Andrews, 1910) and *Temnodontosaurus* (Von Huene, 1922), so at

   least cartilaginous haemapophyses must also have been present in these taxa (Maisch and Matzke, 2000). Haemapophesis is the second element in each half of a hemal arch, corresponding to the sternal part of a rib.

30. Preflexural vertebral count: 0- less than 80; 1-greater than 80 (Lomax and Massare, 2016 Char 65).
    a. This character was removed from the analysis as there is no evidence to support this separation of preflexural vertebral count.
31. Precaudal vertebral count: 0- <40; 1- 40-46; 2>46 (Lomax and Massare, 2016, Char 66).
    a. This character was removed from the analysis as there is no evidence to support this separation of precaudal vertebral count. .

Appendicular Skeleton (Forefin)

32. Protruding triangular deltopectoral crest on humerus: 0- absent; 1- present; 2- present and very large, matching in height the trochanter dorsalis, and bordered by concave areas (Fischer, 2011 Char 31).
    a. This character was removed as it is not independent from character 55 of the analysis.
33. Humerus intermedium contact: 0- absent; 1- present (Fernandez, 2007 Char 15)
    a. This character determines if there are two or more facets present on the humerus and was not used because this feature was absent in specimens in this study. This character is a requirement when other genera are present with this characteristic.
34. Humerus anterodistal facet for accessory zeugopodial element anterior to radius absent
    a. None of the specimens in this genus have this facet anterior to the radius, and not many of the specimens in closely related genera have it either. This could be necessary in order to distinguish from other genera.
35. Humerus with distally facing radial facet: 0-present; 1-absent (modified from Fischer, 2011 Char 34).
    a. This character is of a feature of opthalmosaurine ichthyosaurs which are not present in this study and so was not used.
36. Radius peripheral 'shaft': 0- complete or nearly complete; 1- notch or largely reduced; 2- absent (Motani, 1999 Char 59).
    a. This character was not used in this analysis, as all the specimens in this study reflect either state 1 or 2. Other characters are used in this analysis to differentiate this and the characters go into more detail.
37. Shape of the posterior surface of the ulna: 0-rounded or straight and nearly as thick as the rest of the element; 1- concave and edgy (Fischer et al. 2012 Char 36).
    a. This character would only be useful in distinguishing between more derived taxa than present in this study. It was also not clear to the author what 'edgy' refers to so was left out as to not confuse the character more.
38. Zeugo- to autopodial elements: 0- flattened and plate-like; 1- strongly thickened (Maisch and Matzke 2000 char 94).
    a. This character was not used as the state 1 is only present in *Ophthalmosaurus*, *Platypterygius*, *Brachypterygius* and *Caypullisaurus*; genera not observed for the purposes of this study.

Appendicular Skeleton (Pelvic girdle)

39. Ischium-pubis fusion in adults: 0- absent; 1- present only proximally (modified from Fischer, 2011 Char 45).
    a. This character describes how fused the ischium and pubis are in adult specimens and was not used in this study as it is not an informative character for this study.
40. Ischium shape: 0- long and slender, especially in centre; 1- long, fairly wide, oblong; 2- short compared to width, robust (Lomax and Massare, 2016 Char 57).
    a. This character was not used as Massare and Lomax (2016) provided no state 0 examples and none were listed in Motani, 1999 Char 87; from which the character was modified. Therefore Motani's 1999 Char 87 is now used in Character 96.

Appendicular Skeleton (hindfin)

41. Dorsal and ventral processes of the femur: 0- plate-like; 1- more rounded, shaft columnar (Druckenmiller and Maxwell, 2010 Char 49).
    a. This character was not used as all specimens used in this study reflect character state 1.
42. Prominent, ridge-like dorsal and ventral processes demarcated from the head of the femur and extending up to mid-shaft:0- absent; 1- present (Fischer et al. 2011b Char 46).
    a. This character was not used as it only distinguishes outgroup taxa from ingroup taxa. There were enough characters that rooted the outgroup that could be considered as more reliable than this character.
43. Wide distal femur blade: 0- present; 1- absent, the proximal and distal extremity of the femur being sub-equal in dorsal view (Fischer et al., 2013 Char 61).
    a. This character was not used as it only distinguishes outgroup taxa from ingroup taxa. There were enough characters that rooted the outgroup that could be considered as more reliable than this character.
44. Femur anterodistal facet for accessor zeugopodial element anterior to tibia: 0- absent; 1- present (Fischer et al. 2011b Char 48).
    a. Used Character 88 to addresses the presence or absence of the anterior accessory digit.
45. Astragalus/femoral contact: 0-absent; 1- present (Maxwell, 2010 Char 33).
    a. Character not used, as all specimens in this study reflect character state 0.
46. Notching in hindfin elements: 0- absent; 1- present.
    a. Not used as notching is covered by character 99.
47. Tibia peripheral 'shaft': 0- complete or nearly complete; 1- notch or largely reduced; 2- absent (Motani, 1999 Char 92).
    a. Character not used in this analysis, as all the specimens observed reflect either state 1 or 2.

Appendix D.

Character matrix for all specimens.

Character- taxon matrix with all specimens analyzed in this study. Unknown states are represented with a ‘?’, characters yet to be coded are represented with a ‘-‘, and numbers within ‘[]’ are polymorphic.

Institution Abbreviations

AGC— Alfred Gillett Collections, cared for by Alfred Gillett Trust (C & J Clark Ltd.); **BGS**, The British Geological Survey, Keyworth, Nottingham, U.K.; **BRLSI**— Bath Royal Literary and Scientific Institution, Bath, U.K.; **BRSMG**—Bristol Museum and Art Gallery, Bristol, U.K.; **BIRUG/BU**—Birmingham University Lapworth Museum, Birmingham, U.K.; **CAMSM**—Cambridge Museum of Natural History, Cambridge, U.K.; **DONMG**— Doncaster Museum and Art Gallery, Doncaster, U.K.; **DORCM—**The Dorchester County Museum, Dorchester, U.K.; **GLAHM**—The Hunterian Museum, University of Glasgow, Glasgow, U.K.; **GMRC**—Glasgow Museum Resource Centre, Glasgow, U.K.; **HCMAS**—Hampshire County Council Museum Store, Winchester, U.K.; **IPSMG**— Ipswich Museum, Ipswich, Suffolk, U.K.; **LEICT**— Leicester Arts and Museums Service, New Walk Museum and Art Gallery, New Walk, Leicester, U.K.; **NHMUK**—(formerly BMNH), Natural History Museum, London, U.K.; **NMING**—National Museum of Ireland, Natural History Division, Geological Collection, Dublin, Ireland; **NMS**—National Museum of Scotland, Edinburgh, U.K.; **NOTNH**— Nottingham Natural History Museum (Wollaton Hall), Nottingham, U.K.; **MANCH**—Manchester Museum, Manchester, U.K.; **OUMNH**—Oxford University Museum of Natural History, Oxford, U.K.; **PETMG** — Peterborough Museum and Art Gallery, Peterborough, U.K.; **PMO**— Paleontologisk Museum Oslo, Oslo, Norway; **RAMM**—Royal Albert Memorial Museum, Exeter, U.K.; **TTNCM**—Taunton County Museum, The South West Heritage Trust (Somerset Museums Service), Taunton, U.K.; **UoS**— University of Southampton Collections, Southampton, U.K.; **YORYM**— Yorkshire Museum , York, U. K.

Californosaurus

????????????????????????????????????000?1?100111102000?2001000021100[02]01100?20021020202000110?0????1

Hudsonelpidia

??100???????0?0?0????01?????[01]??????11?????????????2010?010?010????????0???0201010201020101020??????

Macgowania

10101002001000010?1?0001????0[01]0012????????????1???2011?000?120120111111101??????????????0??????????

Temnodontosaurus

110[01][01]20001110[12]00[12]10[01]01100?0?[12]000[01]20?0?100?1?1110102110?2101011011101101101011112?0201200001010000001

AGC11

1101020211?10?001??????1????010002100?1???111?21222011101110111010211200000?????110???1001021?1?000

AGC12

210102[01]0010103000?0?11?0?????000021?2????1101?21212110?00031111210111200010???????????0001?20100000

AGC14

???10???????????12?1????????000002??2?1?0?111?????11?0?001301??0??11100001111220110201000102???????

AGC15

1?0??1[12]01?0?0???1?????00????010012?00?1???????01222010?0001011111011110001?????????????????????????

AGC16

1001?10010??01??0??????????0010012????100???????????1??????????????????????1100112010100010201010?2

AGC17

??????????????????2?[01]?????11??10011????10??101?21212010?00110111210111200000112221002200000020101000

AGC4

??????1?1???????????????0????100011??

AGC6

???0?????????????????????????00002??

AGC7

??0??????????????????????0???1?22010?001100?1021212220?110001?1?1??21110???01110011202000000?2???????

AGC8

????????????????????????????1?00012?0??1???????????21?1111??011101111120011?????????????????????????

AGC9

1101?20011??0???2????????00?120012????100?10212122??11???10???????????????011??2???????001?2???????

AGCB1No3
1111?11?11??22002??????1????000012????????1??12????????????????????????????????
????????????????????

AGCB1No4
??201110110111100021110011?????
????????????????????

AGCB2No6?
???11121?11100011???????
??????????????????

AGCB5 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--01?20101002

BIRUG 19855 ???--???????????-?????????????????-???????1?11??????-
?????????????????????????????????--???????????

BIRUG 19856 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--0102???????

BIRUG 19857 ???--???????????-?????????????????-???????1?20??????-
?????????????????????????????????--???????????

BIRUG 19858 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--0001???????

BIRUG 27683a-b ???--2[12]21?01?0??-10111?0?????0?1?2-?????????????????-
?????????????????????????????????--???????????

BIRUG 417/BU 5289 101--12021012300-????0?0?10?12?0??-02?1?0??????1221?-
??????????????11????10?????100111--00?10100100

BIRUG 4176 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--011[12]0102010

BIRUG 8823 ???--???????????-?????????????????-???????????????21-
1001110??????????????????????????--???????????

BIRUG Unknown 120--10201000000-?0?10?1????010011-?1?1000112???2120-
1?0001011111111110011?11?????????--???????????

BRLSI GP0650 ?20--2??21??0???-????????????01011-?????????????????-
?????????????????????????????????--???????????

BRLSI GP07 44A-B ???--???????????-?????????????????-???100??????????1-
1?11?????????????????011?12120???--???????????

BRLSI M3562 11?--2?21100?300-0?10????????00111-011??????????????-
????01???011011130001?11??1??????--01?20??1102

BRLSI M643 ???--???????????-?????????????????-???????????????21-
110100011101011120001????????????--???????????

BRLSI M644 ???--???????????-?????????????????-?????????????????-
??????011121021110001????????????--???????????

BRSMG AcNo 3/1996 ???--?????0?????-?????????????????-?????????????????-
??????????????????????11??1??????--1102???????

BRSMG Cast Unknown ???--???????????-?????????????????-???????????????20-
1101??111121211120000????????????--???????????

BRSMG Cb3578 310--20001010000-?0?1000????110000-00?10101110212220-
1100??111101021120001111221110201--01?2???????

BRSMG Cb4014 ???--???????????-?????????????????-???10??1?1?21?2??-
?????????????????????????????????--???????????

BRSMG Cb4398 ???--???????????-?????????????????-???????????????21-
1?01??0111110211200?1????????????--???????????

BRSMG Cb4997 110--110110101??-?0?11?0????000012-???1???1??1212120-
1??000011110221111201?11111120200--000?0101??2

BRSMG Cb5014 ?20--20211000000-?0?10?0????01011?-???10?0112??1??20-
1?0000111?0??111?000011111110201--01?2???????

BRSMG Cb8930 ???--???????????-?????????????????-???????????????21-
1?01??0??????????????????????????--???????????

BRSMG Cc921
12010210110003000?1?1000????001010?2??????????????2011?0021011101011130001??
??????????????????????-

BRSMG Cc924 ???--???????????-?????????????????-????0??1??1212220-
1001??0111012111200010???????????--01?2???????

BRSMG Ce16611
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12010?????112010001120201012-

BRSMG Ce16611b ??0--1002?000???-????0?0????00?0??-?????????????????-
?????????????????????????????????--???????????

BRSMG Ce17660 ??0--?[01?]001010???-????0?0????120012-????????21?????20-
1?01?00??????????????????????????--???????????

BRSMG Ce17661 ??0--2?2[01?]???0???-????????????1101?-?????????????????-
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BRSMG Ce17664 1?0--1?00???01??-????????????01012-?????????????????-
?????????????????????????????????--???????????

BRSMG Ce17665 ??0--1??0???0???-???????????000012-?????????????????-
?????????????????????????????????--???????????

BRSMG Ce17667 ??0--???0???????-???????????101112-?????????????????-
?????????????????????????????????--???????????

BRSMG Ce17668 11?--210010??100-2???????1???00?00-?????????????????-
?????????????????????????????????--???????????

BRSMG Ce17687 11?--10001???10?-????????????101?1-?????????????????-
?????????????????????????????????--???????????

BRSMG Ce17756 ???--???????????-?????????????????-???????1?21??????-
?????????????????????????????????--???????????

BRSMG Ce17757 ???--???????????-????????????00012-???????????????20-
1001?30111??0111?00?1????????????--???????????

BRSMG Ce17758 ???--???????????-?????????????????-???????1211????20-
100001111111011110001????????????--???????????

BRSMG Ce17761 ???--???????????-?????????????????-???????????2122??-
?????????????????????????????????--???????????

BRSMG Ce17764 ???--???????????-?????????????????-???????????????2?-
1??0??1??????????????????????????--???????????

BRSMG Ce17984 ???--???????????-?????????????????-???????????????21-
110101???????????????????????????--???????????

BRSMG Ce18000 ???--???????????-?????????????????-???????????????20-
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BSRLI M653 ???--???0?00????-1?101?0?????[12]0110-?2?0???111?????21-
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CAMSM 59642 ???--???????????-?????????????????-????0???????????2?-
??1???1111210211100011?????110??1--11021???010

CAMSM 5975
1?0101[01]001??0?????0?1012????00001??2?????1????11?22111111??011101011130001
0??????????0????????????-

CAMSM 5975 femur ???--???????????-?????????????????-?????????????????-
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CAMSM J35183 ?00--1?0??0?0???-?1??000????01?011-???1001111?211220-
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CAMSM J35189 ???--???????????-????????????0??1[12]-????001121001212[01]-
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CAMSM J59644 ???--???????????-????????????0?112-???10??112?21??20-
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CAMSM J69477 121--21011112100-???00??????000010-?0??01?112?????21-
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CAMSM TN910 ??0--2[12]2[01]10000??-?0?1001???101?01?-10???1?211?212121-
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CASMX50187
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DCM G.00001 ???--?????0?????-??????0?????0????-???10011?2?2112??-
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DCM G.10741 ???--?122?01????-??110?0??????2010-?1?????111?????20-
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DCM G.149 ???--???????????-????????????22002-?????????????????-
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DCM G11896 ???--???????????-?????????????????-????0??????2121??-
11???????????????????????????????--???????????

DCM G13 ???--???????????-????????????00002-?????????????????-
?????????????????????????????????--???????????

DCM G13824 ???--???????????-?????????????????-???????????212220-
1?0021011121011120001????????????--???????????

DCM G1443 ???--???????????-????????????00112-????0??1?11??2???-
?????????????????????????????????--???????????

DCM G88 ???--?2001?1?2??-2???????????[01]?110-?????????????????-
?????????????????????????????????--???????????

DCM G9 ???--???????????-?????????????????-???????????2???2?-
1???1??011101021110001???????????--???????????

DCM Unknown 11?--1121101?000-?0?00?0?????1001?-????00?????????2?-
1????????????211?0011011?101?????--01111101110

DOMG 2013.8.554 ???--???????????-?????????????????-???????????????2?-
1?????0111010111?00??????????????--???????????

DONMG 1971.305.2 ???--???????????-????????????00002-?????????????????-
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DONMG 2013.8.552 ???--???????????-?????????????????-???????????????2?-
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DONMG 2013.8.553 ???--???????????-?????????????????-???????????????2?-
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DONMG1983.3*
?1011201010101001?1?10?00????100[01]??2???0??112?21220011000220111010111?00?
?211??1?????0001?1???????-

GLAHM 13212 110--11011010000-???10?0?10?010011-???????????????21-
1?010111101011120001?????????????--???????????

GLAHM V1031 110--10201??0100-?????10????00001?-????0??????21?220-
1??0??0111???111?00??????????????--???????????

GLAHM V1091 ???--???????????-?????????????????-???10??????212121-
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GLAHM V1157(1463) ???--???????????-?????????????????-?????????????????-
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GLAHM V1165 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--01011101000

GLAHM V1178 ??0--???????0???-????????????00010-?????????????????-
?????????????????????????????????--???????????

GLAHM V1179 120--1[01]011100???-??????0????020?10-?1?1?0?121?211221-
1101010111212211100110???????????--0[01]1[12]2111010

GLAHM V1195 1?0--1?????0????-????????????10010-?????????????????-
?????????????????????????????????--???????????

GLAHM V1197 ???--???????????-?????????????????-????????????????-
??????011101211120011????????????--???????????

GLAHM V1308 ???--???????????-????????????01012-????????????????-
?????????????????????????????????--???????????

GLAHM V1583 ???--???????????-????????????00012-????????????????-
?????????????????????????????????--???????????

IPSMG 1880-1 ???--???????????-?????????????????-????00?121????20-
1?10[12]?010111211111201211??????????--00021111102

IPSMG 1931-233 1?0--11011??0300-????????????00012-????????????????-
?????????????????????????????????--???????????

IPSMG FNB#8 ???--???????????-?????????????????-?????0????????20-
1?000011111122111[01][02]010110?1??01?1--01?21101100

IPSMG Napton ???--???1???????-????????????0[01]012-????????????????-
?????????????????????????????????--???????????

LECIT 106.1991.1-2 ???--???????????-?????????????????-??????????[12]122??-
?????????????????????????????????--???????????

LEICT G108.1991 120--10201??0?00-???????????000012-????????????????-
?????????????????????????????????--???????????

LEICT G123.1992 ?11--21011?122??-??????0?1??00101?-12??00????212220-
1100??011121011120001????????????--????1?1??1?

LEICT G1239.1884.0.0 1?1--2??20??0???-????????????00012-????????????????-
?????????????????????????????????--???????????

LEICT G125.1992 ???--???????????-2?0?????????0??1?-?????1?111?[12]1??01-
0?200111110011121201?11222110011--01121101012

LEICT G126.1992 11?--2001100?001-?0??1???????00110-?1???1?111????20-
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LEICT G142.1991.0.0 10?--112010[01]?200-1?101?0?????00012-????????????????-
?????????????????????????????????--???????????

LEICT G151.1991 ???--????????00?-10111????????????-02?10??1?1?2??2??-
?????????????????????????????????--???????????

LEICT G3339.1898.0 ?20--201010?0???-201???0????[01]?????-????????????????-
?????????????????????????????????--???????????

LEICT G406.1889 ???--???????????-?????????????????-????0?????????20-
1?10??111220221120000????????????--???????????

LEICT Paddle display ???--???????????-?????????????????-?????????????????-???????1?1???11111[12]01????????????--???????????

MANCH L.548 ???--???????????-?????????????????-???10??121021?220-1000??011121221110011????????????--???????????

MANCH L.7543 120--21001010??0-????1??????000012-?????????????????-?????????????????????????????????--???????????

MANCH L.8001 ???--???????0???-??????0?10??10012-???100?????212221-1101??0??????????????111??1110???--?1?2???????

MANCH L.9381 ???--???????????-?????????????????-?????????????????-?????????????????????????????????--0102???????

MANCH L.9556 ???--10001???1??-201?1?0?????12110-?????????????????-?????????????????????????????????--???????????

MANCH L.9663 ???--???????????-?????????????????-???0???????212221-0?01??120001110211300011202120222--0102??????3

MANCH L.9664 ???--???????????-?????????????????-???1?????????????-?????????????11120001??????110201--01?11101010

MANCH L.9905 ???--???????????-?????????????????-???????????????21-1101??111121211100000????????????--???????????

MANCH L.9906 ???--???????????-?????????????????-???????????????2?-1?????011121011130000????????????--???????????

MANCH L.9908 ???--?????0?????-??????0??????????-??????1121021212?-1?01?????????????????????????????--???????????

MANCH LL.8000 ???--?????0?0???-??????1?????10111-01?1???121?????21-1?0101011101?11110000????????????--???????????

MANCH LL11835 ???--?????0?????-??????0?????00002-??????11120212121-1100??011101011120001????????????--???????????

MANCH P.393 ???--???????????-?????????????????-???????????????20-0100??01112?1????00??????????????--???????????

MANCH P.393 dist ???--???????????-?????????????????-?????????????????-?????????1?1?11110001????????????--???????????

MANCH REP022X2 ???--???????????-???????????010012-?????????????????-?????????????????????????????????--???????????

MANCH REP154X5 ???--???01?1????-????????????00012-?????????????????-?????????????????????????????????--???????????

MANCH REP177 ???--???????????-?????????????????-???????1?1???????-
?????????????????????????????????--???????????

NHMUK PV OR14565 310--10011??010?-?010???????010012-?1?100?111?????20-
1?01010111010111000011???????????--01121101002

NHMUK PV OR14567 ??1--???????1???-??????0?1??01??1?-???100?????21222[01]-
1000??111121011120001[01]11?02120???--01121101002

NHMUK PV OR2013
310101100101020012000110????0001100211100?1121????2011?01000111210211100011
11102?2?021001020111012-

NHMUK PV OR30877 110--21021000000-??10110????11?112-???10??111?211?21-
1?200301?10??????????????????????--???????????

NHMUK PV OR33277 221--?????002?0?-??????1????02?11?-???10??????212220-
1?10011???????????????211?01110???--???????????

NHMUK PV OR3359 110--11011000100-???00?001??020012-?????????????????-
?????????????????????????????????--???????????

NHMUK PV OR38803 ???--?????0?????-??????0???0??????-?????11????212121-
1100??111121211120001111021110111--00?20?0?000

NHMUK PV OR39263 201--01020011000-?0101?0????000012-?????????????????-
?????????????????????????????????--???????????

NHMUK PV OR39844 ??0--???????0???-?????10?10???????-?1??0011211211221-
11000?011121221110001011??1??????--0111???????

NHMUK PV OR41849 321--10221??23??-????0?0????01??1?-?21?001????212221-
1111??1111210211100110?????110211--01?211100??

NHMUK PV OR49204 ??0--?????0?0???-??????0????00?11?-???100?1??1????21-
1100??1111012211100011?????100211--00121101000

NHMUK PV OR8165 ???--???????????-?????????????????-??1100?????????20-
1?01011111110111200012???????????--01001111012

NHMUK PV R1061 ???--???????????-?????????????????-?????????????????-
??????????????????????11??1??????--01021111012

NHMUK PV R1062 ??0--1100?0?000?-??????0????0?????-?0?10??1110????21-
1?01??0??????????????????????????--???????????

NHMUK PV R1071 110--10001100???-????11?????01?11?-???????121?212220-
1?0101011101021110001????????????--???????????

NHMUK R12 120--21021000001-?0111?0?????[12]?11?-111100?1211????21-
1?20011111012211100010111011110221--01011?10010

NHMUK R216
121111002100220002??020????00??10??1?100?1111????2011?010101112122111001??1
1?????????????????????-

NHMUK R44 ??0--20011??0000-??????001??00?01?-?0?100?1020212121-
1100??010101011100001011002120202--00020000002

NHMUKPVBGS956
12011221110101011?0?1020???00200100010000?1221????2001100030111010211212010
11??11????0001012202003-

NHMUKPVOR120
??01121121?02??01????0??0???0200101210?0???1??2121200110001111011211200010?
?????????0000011311??0-

NHMUKPVOR36256a ??0--121?10?0???-????0?00???1[12]0011-?21100?1220211220-
1100011111???211??2112???11110???--01011112110

NHMUKPVOR38523*
??012???????0???1???????????1?011??1?????1121?111?200110003011111121111211???
?????????????????????-

NHMUKPVOR43006*
3?1101202?002??00???00?0????010011?011001?1120????2011?01?01111210211100111?
?????????0001111201000-

NHMUKPVOR85791 ???--???0?010???-??????0????11001?-??????11210211120-
1?00??101121221110011011001110101--00012112100

NHMUKPVR1162*
1101111121010000[12]????0100???11001?102?101?121?????20112111001110002112000
1011101110010101112311010-

NHMUKPVR15907
210??220010103?0??1?10??0???1200100?2???0?1??0????????????????????????????????
??111010000??2???000-

NMING F16604 ???--???????????-?????????????????-???????????????20-
1000??1111202111110001????????????--???????????

NMING F16625 11?--11221?1?000-????????????000[01]2-?????????????????-
??????????????????????????????????--???????????

NMING F16627 110--2?001?10200-?????????????????-?????????????????-
??????????????????????????????????--???????????

NMING F16694 ?11--????1??2???-???????????10001?-?????????????????-?????????????????????????????????--???????????

NMING F16699 ???--???????????-?????????????????-?????????????????-??????????????????????????????2?2--?1?1???????

NMING F8744 ???--???????????-?????????????????-???????????1???21-1101??010011011120001????????????--????0?0???[12]

NMING F8745 ???--???????????-??1??????????????-???????????????2?-1?????1112?2111??????????????????--???????????

NMING F8746 (hindfin) ???--???????????-?????????????????-?????????????????-??????????????????????110?2?0????--01?2???????

NMING F8746 (main) ???--?100100?01?-????0?0??????????-02?????1111211221-1?0101???????????????????????????--???????????

NMING F8747 ??1--22201012?0?-?0?10?0????00????-01?1??1????????21-1?01???1?121211110001?11222100?20--01?2???????

NMING F8748 111--100010?2100-1?100?0????01??1?-1111?0?1021????20-1?0101011110211110001011??0??????--01020101012

NMING F8750 ?1?--11011?1?1??-????????????10010-????00?????211121-1-?1?01111010111100110?????1?????--????1??????

NMING F8751 1?0--1020?000100-???10??????0?????-02???0?????????21-0?01?10111??2111?0001011??2??????--01?20101010

NMING F8752 ???--????????200-101?0???1????????-???????1?1???????-?????????????111?????????????????--???????????

NMING F8753 ??0--???????????-100??????????????-?2???0???????????-??????0111012111?0001????????????--???????????

NMING F8755 ???--???????????-?????????????????-?2?0?0???????????-????????????????????????????10211--???????????

NMING F8757 300--202010?020?-?0?10??????01??1?-?2?????121??????1-1101??111???11110001?????????????--???????????

NMING F8760 300--10211??0?00-????????10?000?1?-?????0?????212???-11???1???????????????????????????--???????????

NMING F8763 ???--???????????-??1?????????1??1?-???????????????21-1?010111111011100000?????????????--???????????

NMING F8765 100--1?0010???00-10111?0????0?????-?????????????????-?????????????????????????????????--???????????

NMING F8766	12?--210000???0?-????1?1?????2[02]012-?????01????????20-1000??011121?211100110?????110211--?1?????????
NMING F8767	??0--???110?21??-???10?????00?????-???????????2????2?-1?10??0111010111000012???????????--???????????
NMING F8770	1??--???????????-1?1????01???1001?-?2?????11??????20-1?01001111212211100010???????????--01021110110
NMING F8772	311--102111?2100-00?10?0????020012-????00?11111???2[01]-110000110121011110001011??0??????--01021101000
NMING F8773	200--10200000000-??1???0?10??0????-???1?0?1?21??????-?????????????????????????????????--???????????
NMING F8774	111--210210??100-??1?0????????????-?????0?????????2?-1?0?010111211111200000111???1?0???--0102010?000
NMS 1864.12.2	???--???????????-?????????????????-?1?10??121?211220-10010011?1???11?00???????????????--???????????
NMS 1866.13.2	???--???????????-????????????1001?-???????1111212220-100001011121211110000????????????--???????????
NMS 1882.65.455	???--???????????-?????????????????-???1?????????????-??????11120221110011?????????????--???????????
NMS 1972.1.49	???--???????????-?????????????????-???????????????21-1001??011111221110010????????????--???????????
NMS 1972.1.50	?1?--212?1????0?-??1???0????11-012-?????????????????-?????????????????????????????????--???????????
NMS 1974.17.7	???--???????????-?????????????????-???????1?11??????-?????????????????????????????????--???????????
NMS 1974.19	1?0--120110?0000-1?1?0?0?1???100[01]0-?????????????????-?????????????????????????????????--???????????
NMS1898.18.30	110--22101110?00-???01?0????[01]10000-?????????????????-?????????????????????????????????--???????????
NOTNH FS03449	???--???????????-???????01?0??????-01110????????????-?????????????????????????????????--???????????
NOTNH FS03450	???--???????????-?????????????????-?????????????????-?????????????????????????????????--00121111002
NOTNH FS03451	110--11211010300-????????????10112-?????????????????-?????????????????????????????????--???????????

NOTNH FS03456 ???--???????????-?????????????????-???????????????20-
111103???????????????????????????--???????????

NOTNH FS03456b ???--???????????-?????????????????-???????????????20-
0010000??????????????????????????--???????????

NOTNH FS04826 ???--???????????-?????????????????-???????????????20-
1101011??????????????????????????--???????????

NOTNH FS08195 ???--???????????-?????????????????-???100???????????-
?????????????????????????????01?0--00?2?11????

NOTNH FS08196 ???--???????????-?????????????????-???????????????21-
1101011??????????????????????????--???????????

NOTNH FS08197 ???--???????????-?????????????????-???????????2112??-
?????????????????????????????????--???????????

NOTNH FS08208 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--???????????

NOTNH FS3323 110--120010?0200-???????????110010-?????????????????-
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NOTNH FS3453 ???--???????????-?????????????????-???????????????20-
1101??011121021110010????????????--???????????

OUMNH FNB#9 ???--???????????-?????????????????-???????????????20-
1?0101111121221110011????????????--???????????

OUMNH J.103011
????????????????0?0???0???0?1?????????1?0111?????2111001001111010111200011????
????????1102??????1-

OUMNH J.10302 ??0--1?001??????-????1?????0??????-??110??1??121112?-
1100?1011????????????????????????--???????????

OUMNH J.10303 100--1[12]201??0200-????????????[12]?11?-?????0?????2122??-
?????????????????????????????????--01?1???????

OUMNH J.10311 ???--???1???0???-??????0????110010-?????????????????-
?????????????????????????????????--???????????

OUMNH J.10312 210--10201010?00-??????0????020010-?????????????????-
?????????????????????????????????--???????????

OUMNH J.10313 ???--?1?0100???1-????0?1?????001[01]2-?????????????????-
?????????????????????????????????--???????????

OUMNH J.10325	???--?????0?????-??????0?????0????-?2????11211????21-1?010[13]111101011110011011??1??????--01121110010
OUMNH J.10330	1?0112020101000?1?1?11?0????000000?20?1000111?????2011?10010111112111112011??????????000102??????0-
OUMNH J.10363	1?0--110010?000?-???00???????10?12-?2?????121?????21-1?000101110?0111?????????????????--???????????
OUMNH J.12141	???--???????????-?????????????????-???????????????21-1?0101011121011100011????????????--???????????
OUMNH J.13592	??0--???????0???-??????0????02??1?-?2??0??????212121-11011?1111011211100010?????110101--??1?1?1?1??
OUMNH J.13800	??0--???010?0???-??????0????00011?-???????1111212121-1001??011111221110000????????????--00?10??????
OUMNH J.13810	120??2?0210100010????????11?022110?02?????12112121??1????0[23]111120021111211????????????????????????-
OUMNH J.28596	???--???????????-?????????????????-???????????????2?-0??0??01111??[12]110????????????????--???????????
OUMNH J.29219	110--21011010000-???01?0?????001[01]2-?????????????????-????????????????????????????????--???????????
OUMNH J.29221	110--20201??0[13]0?-??????????0010012-01?10??121?212220-1?01010??????????????????????????--???????????
OUMNH J.29283A	110--1002100020?-1?1????????0[12]0012-?2??????????2121??-????????????????????????????????--???????????
OUMNH J.29351	???--???????????-?????????????????-?????????????????-?????????????????????11111110121--000211[01]0110
OUMNH J.29352	???--???????????-??????0??????????-????00?1121212220-1101??0111212111200010??????11???--01021111000
OUMNH J.77729	?10--21211??00??-?011?10?10??20110-02?10??1?11212???-????????????????????????????????--???????????
OUMNH J.77730	???--?1?0?00?00?-???11?0?10???????-?????????????????-????????????????????????????????--???????????
PETMG R174	120--?0201?10???-????0??????110002-?????0??????????2?-??2???0111010211100010???????????--01011111010

PETMG R243 ???--???????????-?????????????????-???10??1111112220-
1?10??0??????????????????????????--???????????

PETMG R244 ???--???????????-?????????????????-?2?10??121?2122??-
1??1?????????????????????????????--???????????

PMO227578 ???--?????00????-??????00010?10002-????0?01210????21-
1?0103011111111100000????????????--???????????

RAMM 124/2009 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--01?21110011

RAMM 125/1973 ???--???????????-?????????????????-???????????????20-
1101??011121211110011????????????--???????????

RAMM 129/1973 ???--???????????-?????????????????-???????????????20-
1001??011121211110001????????????--???????????

RAMM 539/2005 1?0--?0201??0?0?-????01????0?00?1?-?1?10??1?2???????-
?????????????????????????????????--???????????

RAMM 57/2009 110--20011000000-?0?00100??010??1?-011100?1111????20-
1100030111212111100011???????????--01121101110

RAMM Uknown ???--???????????-?????????????????-01100??121?212221-
1100??011121121110001????????????--???????????

RAMM FOS1701 ???--???????????-?????????????????-????01?????????20-
1?10??01111??????????1???????????--01120100110

RAMM FOS1705 ???--???????????-????????????1011?-?????????????????-
?????????????????????????????????--???????????

RAMM FOS1910 2?0--21211010100-1?1??10????10?11?-?0??0????????????-
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RAMM FOS1912 ???--???????????-?????????????????-???????1??1????21-
1?0112011101211110001????????????--???????????

TTNCM 100/2001/912 ??0--?121100030?-1?????0?????11010-?????????????????-
?????????????????????????????????--???????????

TTNCM 100/2001/945 211--20011?02001-????????????0[01]012-?????????????????-
?????????????????????????????????--???????????

TTNCM 12/1988 ???--???????????-??????0?????02?10-???00??????211221-
1001??11??????11?????????????????--???????????

TTNCM 12/1998b ???--???????????-?????????????????-???????1121????20-
0?1000?1?12121110001?????????????--???????????

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TTNCM 12/1998d          ???--?????0?????-??????0???0??????-???000?????212?20-
100[01]010111212111[12]0000?11?????????--???????????

TTNCM 120/1996
        1??102[01]20100??011?0?1010????0000001221??0?112???????11?01??111101011110011
0110?0??1?01000121110002-

TTNCM 13/2015           111--20201002200-????1?0?????00010-?????????????????-
?????????????????????????????????--???????????

TTNCM 14/2015           11?--20211010000-?0111?0?????10110-11?10?011??21122?-
11?1?????????????????????????????--???????????

TTNCM 16/2015           ??0--???010?0???-????0?0?????10?12-???????1211212?21-
0?01??01102101112001?????????????--???????????

TTNCM 166/1992          0?0--?10??01????-1???????1??010010-???1?????????????-
??????11110112111001101111111?101--???22?11010

TTNCM 5803              ???--?011?0?????-??????0??01?0?010-?20100???????????-
1?????????????11?????011111120102--1002?1????2

TTNCM 5804              120--2?01100?100-20?0010?????00002-010?0??1???211?21-
1?01?1011121021110001????????????--???????????

TTNCM 5805              ?10--?1?11??02??-???????01??00?112-???????????2121??-
?????????????????????????????????--???????????

TTNCM 8314              ?10--?021101020?-?0?11???????00002-?????????????????-
?????????????????????????????????--???????????

TTNCM 8332              1?1--10201001?0?-??????0?????1????-?????????????????-
?????????????????????????????????--???????????

TTNCM 8349              ??0--?????000???-???10??????002001-??????010112121??-
?????????????10200001??????120202--001211?2000

TTNCM 8359              ???--?????0?????-?0??0????????????-???1?0???????????-
??????0111111111100011???????????--01110101010

TTNCM 8373              111--10000001000-1???0?0???1100011-11110001110211220-
1?1011011121011110001011112120202--01020100102

WARMS Display 1         110--20211??0100-???????????00?012-?????????????????-
?????????????????????????????????--???????????

WARMS Display 8         ???--???????????-?????????????????-?????????????????-
1?????011[01]21211100000????????????--???????????
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WARMS G.10805 110--21201000000-10111?0?????01?12-?????????????????-
?????????????????????????????????--???????????

WARMS G.14432 ??0--2?2????????-????????????00112-?????????????????-
?????????????????????????????????--???????????

WARMS G.2813 ?10--1?211??0?0?-????????????[12]011?-?????????????????-
?????????????????????????????????--???????????

WARMS G.347 ?11--10211?121??-20110?0????000002-?????????????????-
?????????????????????????????????--???????????

WARMS G.349 ??0--???1???2???-????????????0001[02]-?????????????????-
?????????????????????????????????--???????????

WARMS G.350 ???--???????????-????????????01012-?????????????????-
?????????????????????????????????--???????????

WARMS G.3551 ?1--2??0???????-????????????00002-?????????????????-
?????????????????????????????????--???????????

WARMS G.365 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--0112???????

WARMS G.366 ???--???????????-?????????????????-???????1?11??????-
?????????????????????????????????--???????????

WARMS G.367 ???--???????????-?????????????????-???????????????2?-
11??00???????????????????????????--???????????

WARMS G.4569 ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--01010100002

WARMS G.4570 ???--???????????-?????????????????-?????????????????-
???????11101221110011????????????--???????????

WARMS G.4571 310--2??010?030?-??????0????022111-?????????????????-
?????????????????????????????????--???????????

WARMS G.4636 ???--???????????-?????????????????-???????????????2?-
1??0??0111?1211100000????????????--???????????

WARMS G.4646 ???--???????????-?????????????????-???????????????21-
110001011101211101200????????????--???????????

WARMS G.4681 ???--???????????-?????????????????-???????????2121??-
?????????????????????????????????--???????????

WARMS G.6188 ???--?????0?????-??????0??????????-???10011111212221-
1?0001011101211130010011111100201--01120100112

WARMS G.695 ???--?????0?????-2?110?0??????????-???????1???2121??-
?????????????????????????????????--???????????

WARMS G.7422 ???--???????????-?????????????????-???????1?21??????-
?????????????????????????????????--???????????

WARMS G.8345 ???--???????????-?????????????????-???????1120????21-
1?0001011?2???11?0000????????????--???????????

WARMS G352 11?--2?21101?10?-101?0?????0?10012-?1?1?0?????212120-
0?0100011101211100011????????????--???????????

WARMS Pyrite on Display ???--???????????-?????????????????-???1???1??02112??-
?????????????????????????????????--???????????

YORYM 1994.1799.50 ???--???????????-?????????????????-???????????????21-
1?0101011111211120001????????????--???????????

YORYM 1994.1799.51 110--11011010300-???00?001??120012-?????????????????-
?????????????????????????????????--???????????

YORYM 1995.2 ??0--?????0?0???-???????????0?????-????00???????????-
?????????????????????????????????--???????????

YORYM 1997.131 110--21211010000-0??0110????010112-??????1121?21222?-
1??0??011100021110000????????????--???????????

YORYM 1997.158 ???--???????????-?????????????????-???10??12??2??221-
1?01??0??????????????????????????--???????????

YORYM 2001.12968 ???--???????????-?????????????????-?????????????????-
?????????????????????????????01??--???????????

YORYM 2005.2363 ???--???????????-?????????????????-???????????????21-
1101??01111??1112110?????????????--???????????

YORYM 2005.2370 ???--???????????-?????????????????-?????????????????-
?????????????????????????????01??--???????????

YORYM 2005.2386 ?20--2[01]011010000-?0?00???????20012-?????????????????-
?????????????????????????????????--???????????

YORYM 2005.2388A ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--0???[01]100?01

YORYM 2005.2388B ???--???????????-?????????????????-???????????????20-
10010011110121111001?????????????--???????????

YORYM 2005.2388C ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--01110101013

YORYM 2005.2388D ???--???????????-?????????????????-???????????????20-
1101011??????????????????????????--???????????

YORYM 2005.2388E ???--???????????-?????????????????-?????????????????-
?????????????????????????????????--0102???????

YORYM 2005.2388F ???--???????????-?????????????????-???????????2112??-
?????????????????????????????????--???????????

YORYM 2005.2406 ???--???????????-??????0??????????-???100???????????-
?????????????????????????????????--0102???????

YORYM 2005.2407 1?0--?????010?0?-1?101????????????-???000?????????21-
1?01010??????????????0???????????--01001??????

YORYM 2005.2408 300--2100?010201-??????0????010111-????0??????2??221-
1?01000??????511?????0???????????--0??????????

YORYM 2006.10 ???--?????0?????-??1?0?0??????????-?[12]?10??1111212?21-
1111011??????????????????????????--???????????

YORYM 2006.17 30?--?020100?30?-0??01???????00112-?????????????????-
?????????????????????????????????--???????????

YORYM 2006.3803 ???--???????????-?????????????????-????0??????????21-
1?0101?1112102111???1????????????--???????????

YORYM 2011.751 ???--???????????-?????????????????-???????????21?221-
110100111121111[12]11200????????????--???????????

YORYM YM740 ???--???????????-?????????????????-???????????????20-
1101??0111???21110011????????????--???????????

Appendix E.

Character matrices for four separate analyses.

Character- taxon matrix with all specimens analyzed in this study. Unknown states are represented with a '?', characters yet to be coded are represented with a '-', and numbers within '[]' are polymorphic. Specimens with an '*' are the holotype/neotype of a species.

Institution Abbreviations

AGC— Alfred Gillett Collections, cared for by Alfred Gillett Trust (C & J Clark Ltd.); **BGS**, The British Geological Survey, Keyworth, Nottingham, U.K.; **BRLSI**— Bath Royal Literary and Scientific Institution, Bath, U.K.; **BRSMG**—Bristol Museum and Art Gallery, Bristol, U.K.; **BIRUG/BU**—Birmingham University Lapworth Museum, Birmingham, U.K.; **CAMSM**—Cambridge Museum of Natural History, Cambridge, U.K.; **DONMG**— Doncaster Museum and Art Gallery, Doncaster, U.K.; **DORCM—**The Dorchester County Museum, Dorchester, U.K.; **GLAHM**—The Hunterian Museum, University of Glasgow, Glasgow, U.K.; **GMRC**—Glasgow Museum Resource Centre, Glasgow, U.K.; **HCMAS**—Hampshire County Council Museum Store, Winchester, U.K.; **IPSMG**— Ipswich Museum, Ipswich, Suffolk, U.K.; **LEICT**— Leicester Arts and Museums Service, New Walk Museum and Art Gallery, New Walk, Leicester, U.K.; **NHMUK**—(formerly BMNH), Natural History Museum, London, U.K.; **NMING**—National Museum of Ireland, Natural History Division, Geological Collection, Dublin, Ireland; **NMS**—National Museum of Scotland, Edinburgh, U.K.; **NOTNH**— Nottingham Natural History Museum (Wollaton Hall), Nottingham, U.K.; **MANCH**—Manchester Museum, Manchester, U.K.; **OUMNH**—Oxford University Museum of Natural History, Oxford, U.K.; **PETMG** — Peterborough Museum and Art Gallery, Peterborough, U.K.; **PMO**— Paleontologisk Museum Oslo, Oslo, Norway; **RAMM**—Royal Albert Memorial Museum, Exeter, U.K.; **TTNCM**—Taunton County Museum, The South West Heritage Trust (Somerset Museums Service), Taunton, U.K.; **UoS**— University of Southampton Collections, Southampton, U.K.; **YORYM**— Yorkshire Museum , York, U. K.

Analysis 1. Character Matrix for Core Group of Specimens

Californosaurus

????????????????????????????????????000?1?100111102000?2001000021100[02]01100?20021020202000110?0????1

Hudsonelpidia

??100???????0?0?0????01?????[01]??????11?????????????2010?010?010????????0???0201010201020101020??????

Macgowania

10101002001000010?1?0001????0[01]0012????????????1???2011?000?120120111111101??????????????0??????????

Temnodontosaurus

110[01][01]20001110[12]00[12]10[01]01100?0?[12]000[01]20?0?100?1?1110102110?2101 01101110110110101112?0201200001010000001

NHMUKPVR1162*

1101111121010000[12]????0100???11001?102?101?121?????20112111001110002112000 1011101110010101112311010?

NHMUKPVOR38523*

??012???????0???1???????????1?011??1?????1121?111?2001100030111111211111211??? ??????????????????????

NHMUKPVOR43006*

3?1101202?002??00???00?0????010011?011001?1120????2011?01?01111210211100111? ?????????0001111201000?

DONMG1983.3*

?1011201010101001?1?10?00????100[01]??2???0??112?21220011000220111010111?00? ?211??1?????0001?1????????

AGC11

1101020211?10?001??????1????010002100?1???111?21222011101110111010211200000? ????110???1001021?1?000

AGC17

?????????????????2?[01]?????11??10011????10??101?21212010?00110111210111200000 112221002200000020101000

BRSMGCb3578

310??20001010000??0?1000????110000?00?10101110212220?1100??1111010211200011 11221110201??01?2???????

BRSMGCb5014

?20??20211000000??0?10?0????01011?????10?0112??1??20?1?0000111?0??111?000011 1111110201??01?2???????

BRSMGCc921

12010210110003000?1?1000????001010?2???????????????2011?0021011101011130001?? ???????????????????????

BRSMGCe16611

??01??????1?????0????1?0?????0?00??2??100012[12]121212[01]11000000111010211[12] 12010?????112010001120201012?

CAMSM5975

1?0101[01]001??0?????0?1012????00001??2?????1????11?22111111??011101011130001 0??????????0?????????????

CAMSMJ35183
?00??1?0??0?0?????1??000????01?011????1001111?211220?1100??01110121112000111
1110100120??1102???????

CAMSMJ35186
???????21??0?1???2?1?????????01??????1?00?111?????21?1?0100010101011120011011
??2????????11020103112

CASMX50187
?10102??111003?101???0?0????110000?[02]???0??1110????2011110??011101021110010
1111111111110101?21101110?

CAMSMJ69477
121??21011112100????00??????000010??0??01?112?????21?1110??111120021110001??
???????????????????????

DCMG.10741
??????122?01???????110?0??????2010??1?????111?????20?1?20?101112122211113111??
???????????0???0101110

DCMUnknown
11???1121101?000??0?00?0?????1001??????00?????????2??1????????????211?0011011?
101???????01111101110

GLAHMV1179
120??1[01]011100??????????0????020?10??1?1?0?121?211221?110101011121221110011
0?????????????0[01]1[12]2111010

LEICTG123.1992
?11??21011?122?????????0?1??00101??12??00?????212220?1100??011121011120001???
???????????????1?1??1?

LEICTG125.1992
?????????????????2?0?????????0??1???????1?111?[12]1??01?0?2001111110011121201?
11222110011??01121101012

LEICTG126.1992
11???2001100?001??0??1???????00110??1???1?111?????20?1?000101112101112000101
1222120022??010201?????

NHMUKPVOR14565
310??10011??010???010???????010012??1?100?111?????20?1?01010111010111000011?
????????????01121101002

NHMUKPVOR14567
??1?????????1??????????0?1??01??1?????100?????21222[01]?1000??111121011120001[0
1]11?02120?????01121101002

NHMUKPVOR2013

310101100101020012000110????0001100211100?1121????2011?010001112102111000111102?2?021001020111012?

NHMUKPVOR38803

??????????0????????????0???0????????????11????212121?1100??11112121112000111102111011 1??00?20?0?000

NHMUKPVOR39844

??0?????????0?????????10?10?????????1??0011211211221?11000?01112122111000101 1??1????????0111???????

NHMUKPVOR41849

321??10221??23???????0?0????01??1???21?001????212221?1111??1111210211100110?????110211??01?211100??

NHMUKPVOR49204

??0???????0?0??????????0????00?11?????100?1??1????21?1100??11110122111000 11?????100211??00121101000

NHMUK PV R12

120??21021000001??0111?0?????[12]?11??111100?1211????21?1?200111101221110001011101110221??01011?10010

NHMUK PV R216

121111002100220002 0??020????00??10??1?100?1111????2011?010101112122111001??11??????????????????????

NHMUK PV R44

??0??20011??0000???????001??00?01???0?100?1020212121?1100??0101010111000010110021202 02??00020000002

NHMUKPVBGS956

12011221110101011?0?1020???0020010001000 0?1221????200110003011101021121201011??11????0001012202003?

NHMUKPVOR120

??01121121?02??01????0??0???0200101210?0???1??2121200110001111101121120001 0??????????0000011311??0?

NHMUKPVOR85791

????????0?010??????????0????11001????????11210211120?1?00??101121221110011011001110101??00012112100

NMINGF8747

??1??22201012?0???0?10?0????00?????01?1??1????????21?1?01???1?12121110001?11222100?20??01?2???????

NMINGF8748

111??100010?2100?1?100?0????01??1??1111?0?1021????20?1?01010111021111000101 1??0????????01020101012

NMINGF8751

1?0??1020?000100????10??????0??????02???0?????????21?0?01?10111??2111?0001011 ??2????????01?20101010

NMINGF8772

311??102111?2100?00?10?0????020012?????00?11111???2[01]?11000011012101111000 1011??0????????01021101000

NMINGF8774

111??210210??100???1?0??????????????????0?????????2??1?0?01011121111120000111 ???1?0?????0102010?000

OUMNHJ.10330

1?0112020101000?1?1?11?0????000000?20?1000111?????2011?1001011111211111 2011? ?????????000102??????0?

TTNCM120/1996

1??102[01]20100??011?0?1010????0000001221??0?112???????11?01??111101011110011 0110?0??1?01000121110002?

TTNCM166/1992

0?0???10??01?????1???????1??010010????1???????????????????1111011211100110111 1111?101?????22?11010

TTNCM5804

120??2?01100?100?20?0010?????00002?010?0??1???211?21?1?01?1011121021110001?? ??????????????????????

TTNCM8373

111??10000001000?1???0?0???1100011?11110001110211220?1?10110111210111100010 11112120202??01020100102

WARMSG.6188

??????????0????????????0??????????????10011111212221?1?0001011101211130010011 111100201??01120100112

WARMSG352

11???2?21101?10??101?0?????0?10012??1?1?0?????212120?0?0100011101211100011?? ??????????????????????

YORYM1997.131

110??21211010000?0??0110????010112???????1121?21222??1??0??011100021110000?? ??????????????????????

Analysis 2. Character Matrix for Core Group of Specimens with Continuous Characters included

Continuous Characters

Californosaurus	? ? ? ? ?
Hudsonelpidia	0.500 ? 0.241 0.366 ?
Macgowania	0.560 0.430 0.350 0.280 ?
NHMUKPVR1162	0.579 0.502 0.458 0.248 0.352
NHMUKPVOR38523	0.682 ? ? ? ?
NHMUKPVOR43006	0.530 0.474 0.363 0.307 ?
DONMG1983.3	0.622 0.551 0.524 0.199 ?
AGC11	0.639 0.511 0.497 0.222 ?
AGC17	? ? ? ? ?
BRSMGCb3578	0.635 0.560 0.500 0.193 ?
BRSMGCb5014	0.638 0.579 0.508 0.198 0.433
BRSMGCc921	0.593 0.517 0.465 0.176 0.443
BRSMGCe16611	? ? ? ? ?
CAMSM5975	0.622 0.497 0.453 0.148 ?
CAMSMJ35183	0.639 ? 0.549 0.192 ?
CAMSMJ35186	0.718 0.621 0.813 0.261 ?
CASMX50187	0.540 ? 0.452 0.213 ?
CAMSMJ69477	0.591 0.509 0.447 0.168 0.557
DCMG.10741	? ? ? ? 0.456
DCMUnknown	? ? ? ? ?
GLAHMV1179	0.579 0.472 ? 0.114 ?
LEICTG123.1992	0.672 0.573 0.526 ? ?
LEICTG125.1992	? ? ? ? ?
LEICTG126.1992	0.622 0.515 0.436 0.217 ?
NHMUKPVOR14565	0.602 ? 0.447 0.210 0.422

NHMUKPVOR14567	? ? 0.433 ? ?
NHMUKPVOR2013	0.585 0.487 0.438 0.178 ?
NHMUKPVOR38803	? ? ? ? ?
NHMUKPVOR39844	? ? ? ? ?
NHMUKPVOR41849	? ? ? ? 0.453
NHMUKPVOR49204	? 0.514 ? ? ?
NHMUKPVR12	0.614 0.568 0.502 0.237 0.376
NHMUKPVR216	0.543 0.482 0.408 0.252 0.891
NHMUKPVR44	0.638 0.582 0.519 0.213 ?
NHMUKPVBGS956	? 0.655 0.727 ? ?
NHMUKPVOR120	0.641 0.615 0.529 0.245 0.287
NHMUKPVOR85791	? ? ? ? ?
NMINGF8747	0.664 0.524 0.478 0.181 0.295
NMINGF8748	0.590 0.504 0.471 0.165 ?
NMINGF8751	0.636 ? 0.536 0.200 0.324
NMINGF8772	0.634 0.564 ? 0.199 ?
NMINGF8774	? ? ? ? ?
OUMNHJ.10330	? ? ? ? ?
TTNCM120_1996	0.681 0.932 0.554 0.186 0.436
TTNCM166_1992	0.574 0.510 0.453 ? ?
TTNCM5804	0.447 ? 0.295 0.238 0.343
TTNCM8373	0.588 0.513 0.439 0.215 ?
WARMSG.6188	? ? ? ? ?
WARMSG352	0.500 0.364 0.267 0.279 0.429
YORYM1997.131	0.631 0.556 0.523 0.180 0.437

Numeric Characters

Californosaurus

?????????????????????????????????????000?1?100111102000?2001000021100[02]01100?
20021020202000110?0????1

Hudsonelpidia

??100???????0?0?0????01?????[01]??????11?????????????2010?010?010????????0???02
01010201020101020??????

Macgowania

10101002001000010?1?0001????0[01]0012?????????????1???2011?000?120120111111101
??????????????0??????????

NHMUKPVR1162*

1101111121010000[12]????0100???11001?102?101?121?????20112111001110002112000
1011101110010101112311010?

NHMUKPVOR38523*

??012???????0???1???????????1?011??1?????1121?111?20011000301111121111211???
??????????????????????

NHMUKPVOR43006*

3?1101202?002??00???00?0????010011?011001?1120????2011?01?01111210211100111?
?????????0001111201000?

DONMG1983.3*

?1011201010101001?1?10?00????100[01]??2???0??112?21220011000220111010111?00?
?211??1?????0001?1????????

AGC11

1101020211?10?001??????1????010002100?1???111?21222011101110111010211200000?
????110???1001021?1?000

AGC17

??????????????????2?[01]?????11??10011????10??101?21212010?00110111210111200000
1122210022000000020101000

BRSMGCb3578

310??20001010000??0?1000????110000?00?10101110212220?1100??1111010211200011
11221110201??01?2???????

BRSMGCb5014

?20??20211000000??0?10?0????01011?????10?0112??1??20?1?0000111?0??111?000011
1111110201??01?2???????

BRSMGCc921

12010210110003000?1?1000????001010?2???????????????2011?0021011101011130001??
??????????????????????

BRSMGCe16611
??01??????1?????0????1?0?????0?00??2??100012[12]121212[01]1100000011101021 1[12]12010?????112010001120201012?

CAMSM5975
1?0101[01]001??0?????0?1012????00001??2?????1????11?22111111??0111010111300010??????????0?????????????

CAMSMJ35183
?00??1?0??0?0?????1??000????01?011????1001111?211220?1100??01110121112000111 1110100120??1102???????

CAMSMJ35186
???????21??0?1???2?1?????????01??????1?00?111?????21?1?01000101010111200110 11??2????????11020103112

CASMX50187
?10102??111003?101???0?0????110000?[02]???0??1110????2011110??011101021110010 11111111110101?21101110?

CAMSMJ69477
121??21011112100????00??????000010??0??01?112?????21?1110??111120021110001?? ???????????????????????

DCMG.10741
??????122?01???????110?0??????2010??1?????111?????20?1?20?10111212211113111?? ???????????0???0101110

DCMUnknown
11???1121101?000??0?00?0?????1001??????00?????????2??1????????????211?0011011? 101???????01111101110

GLAHMV1179
120??1[01]011100??????????0????020?10??1?1?0?121?211221?1101010111212211100110?????????????0[01]1[12]2111010

LEICTG123.1992
?11??21011?122?????????0?1??00101??12??00?????212220?1100??0111210111200 01????????????????????1?1??1?

LEICTG125.1992
?????????????????2?0?????????0??1???????1?111?[12]1??01?0?2001111100111212 01?11222110011??01121101012

LEICTG126.1992
11???2001100?001??0??1???????00110??1???1?111?????20?1?00010111210111200010 11222120022??010201?????

NHMUKPVOR14565

310??10011??010???010???????010012??1?100?111?????20?1?01010111010111000011?????????????01121101002

NHMUKPVOR14567

??1?????????1??????????0?1??01??1?????100?????21222[01]?1000??111121011120001[01]11?02120?????01121101002

NHMUKPVOR2013

310101100101020012000110????0001100211100?1121????2011?0100011121021110001111102?2?021001020111012?

NHMUKPVOR38803

??????????0?????????????0???0?????????????11????212121?1100??111121211120001111021110111??00?20?0?000

NHMUKPVOR39844

??0?????????0?????????10?10?????????1??0011211211221?11000?01112122111000101 1??1????????0111???????

NHMUKPVOR41849

321??10221??23???????0?0????01??1???21?001????212221?1111??1111210211100110?????110211??01?211100??

NHMUKPVOR49204

??0???????0?0??????????0????00?11?????100?1??1????21?1100??11110122111000 11?????100211??00121101000

NHMUK PV R12

120??21021000001??0111?0?????[12]?11??111100?1211????21?1?2001111101221110001011101110221??01011?10010

NHMUK PV R216

121111002100220002 0??020????00??10??1?100?1111????2011?010101112122111001??11??????????????????????

NHMUK PV R44

??0??20011??0000???????001??00?01???0?100?1020212121?1100??0101010111000 01011002120202??00020000002

NHMUKPVBGS956

12011221110101011?0?1020???00200100010000?1221????20011000301110102112120 1011??11????0001012202003?

NHMUKPVOR120

??01121121?02??01????0??0???0200101210?0???1??21212001100011111011211200010?????????0000011311??0?

NHMUKPVOR85791

????????0?010??????????0????11001????????11210211120?1?00??101121221110011011001110101??00012112100

NMINGF8747

??1??22201012?0???0?10?0????00?????01?1??1????????21?1?01???1?121211110001?11222100?20??01?2???????

NMINGF8748

111??100010?2100?1?100?0????01??1??1111?0?1021????20?1?0101011110211110001011??0????????01020101012

NMINGF8751

1?0??1020?000100????10??????0??????02???0?????????21?0?01?10111??2111?0001011??2????????01?20101010

NMINGF8772

311??102111?2100?00?10?0????020012?????00?11111???2[01]?110000110121011110001011??0????????01021101000

NMINGF8774

111??210210??100???1?0???????????????????0??????????2??1?0?01011121111120000111???1?0?????0102010?000

OUMNHJ.10330

1?0112020101000?1?1?11?0????000000?20?1000111?????2011?10010111112111112011??????????000102??????0?

TTNCM120/1996

1??102[01]20100??011?0?1010????0000001221??0?112???????11?01??1111010111100110110?0??1?01000121110002?

TTNCM166/1992

0?0???10??01?????1???????1??010010????1????????????????????11110112111001101111111?101?????22?11010

TTNCM5804

120??2?01100?100?20?0010?????00002?010?0??1???211?21?1?01?1011121021110001????????????????????????

TTNCM8373

111??10000001000?1???0?0???1100011?11110001110211220?1?1011011121011110001011112120202??01020100102

WARMSG.6188

??????????0????????????0??????????????10011111212221?1?0001011101211130010011111100201??01120100112

WARMSG352

11???2?21101?10??101?0?????0?10012??1?1?0?????212120?0?010001110121110001 1???????????????????????????

YORYM1997.131

110??21211010000?0??0110????010112???????1121?21222??1??0??011100021110000????????????????????????

Analysis 3. Character Matrix for Subset of Analysis 1 Character Matrix.

Macgowania

10101002001000010?1?0001????0[01]0012????????????1???2011?000?120120111111101?????????????0??????????

Temnodontosaurus

110[01][01]20001110[12]00[12]10[01]01100?0?[12]000[01]20?0?100?1?1110102110?21010110111011011010111 2?020120000101000 0001

NHMUKPVR1162*

1101111121010000[12]????0100???11001?102?101?121?????20112111001110002112000101110111001010111 2311010?

NHMUKPVOR38523*

??012???????0???1???????????1?011??1?????1121?111?2001100030111111211112 11?????????????????????????

NHMUKPVOR43006*

3?1101202?002??00???00?0????010011?011001?1120????2011?01?01111210211100111??????????0001111201000?

DONMG1983.3*

?10112010101010 01?1?10?00????100[01]??2???0??112?21220011000220111010111?00??211??1?????0001?1????????

AGC11

1101020211?10?001??????1????010002100?1???111?21222011101110111010211200000?????110???1001021?1?000

BRSMGCb3578

310??20001010000??0?1000????110000?00?101011102122 20?1100??111101021120001111221110201??01?2???????

BRSMGCb5014

?20??20211000000??0?10?0????01011?????10?0112??1??20?1?0000111?0??111?0000111111110201??01?2???????

BRSMGCe16611

??01??????1?????0????1?0?????0?00??2??100012[12]121212[01]11000000111010211[12]
12010?????112010001120201012?

CAMSMJ35186

???????21??0?1???2?1?????????01??????1?00?111?????21?1?0100010101011120011011
??2????????11020103112

CASMX50187

?10102??111003?101???0?0????110000?[02]???0??1110????2011110??011101021110010
1111111111110101?21101110?

NHMUKPVOR2013

3101011001010200120001 10????0001100211100?1121????2011?0100011121021110001 1
11102?2?021001020111012?

NHMUK PV R216

1211110021002200020??020????00??10??1?100?1111????2011?010101112122111001??1
1??????????????????????

NHMUKPVBGS956

1201122111010101 1?0?1020???00200100010000?1221????2001100030111010211212010
11??11????0001012202003?

NHMUKPVOR120

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OUMNHJ.10330

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TTNCM8373

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11112120202??01020100102

YORYM1997.131

110??21211010000?0??0110????010112???????1121?21222??1??0??011100021110000??
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Analysis 4. *Ichthyosaurus communis* Only Analysis

Californosaurus

????????????????????????????????????000?1?100111102000?2001000021100[02]01100?
20021020202000110?0????1

Hudsonelpidia

??100???????0?0?0????01?????[01]??????11?????????????2010?010?010????????0???0201010201020101020??????

Macgowania

10101002001000010?1?0001????0[01]0012????????????1???2011?000?120120111111101??????????????0??????????

NHMUKPVR1162*

1101111121010000[12]????0100???11001?102?101?121?????2011211001110002112000101110111001010111 2311010?

BRSMGCe16611

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CAMSMJ35183

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GLAHMV1179

120??1[01]011100??????????0????020?10??1?1?0?121?211221?11010101112122111001 10?????????????0[01]1[12]2111010

LEICTG123.1992

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LEICTG125.1992

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NHMUKPVOR14565

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NMINGF8772

311??102111?2100?00?10?0????020012?????00?11111???2[01]?11000011012101111000 1011??0????????01021101000

OUMNHJ.10330

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TTNCM120/1996

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TTNCM5804

120??2?01100?100?20?0010?????00002?010?0??1???211?21?1?01?1011121021110001?? ???????????????????????

YORYM1997.131

110??21211010000?0??0110????010112???????1121?21222??1??0??011100021110000?? ???????????????????????