AN INVESTIGATION INTO ICHTHYOSAUR ONTOGENY, SEXUAL DIMORPHISM AND BODY SIZE EVOLUTION

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Declaration of Authorship

I, Samuel Patrick Bennett, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted the work of others, this is always clearly stated

Signed:

Date:

ABSTRACT

Ichthyosaurs are an extinct group of diapsid marine reptiles that existed from the Olenekian (251Ma) to end Cenomanian (93.9Ma). Morphometric data (length measurements) and meristic data (counts of repeated elements) were collected for Lower and Middle Jurassic taxa from several museums in England and one in Germany. Additional morphometric data were collected from the published record.

Principal Components Analysis (PCA), Principal Coordinate Analysis (PCO) and Reduced Major Axis Regression (RMA) were used to analyse morphometric data relating to ontogeny. Linear Regression, also known as Ordinary Least Squares (OLS) was used to analyse meristic data relating to ontogeny as well as body size evolution. Sexual dimorphism was analysed using the Mann-Whitney test as well as Discriminant Analysis.

The analysis of ichthyosaur ontogeny showed that neonate and juvenile ichthyosaurs had significantly larger skulls and eyes compared to body length. Once maturity is reached growth becomes isometric, and no other features varied with relative age. The numbers of repeated elements in ichthyosaurs remain stable throughout life, with the exception of post-flexural caudal vertebrae, where the numbers increase with the size of the tail, and therefore, age.

Investigation of sexual dimorphism indicated that inferred males are isometrically larger than pregnant females. However, the age at which maturity is reached cannot currently be identified in individual specimens. Furthermore, the gender of an individual cannot currently be determined, with the exception of pregnant females.

The study of body size evolution was not conclusive and no statistically significant trends were identified. Due to the nature of the fossil record, only 53% of the taxa examined could be used in the analysis. More taxa, particularly from the Triassic and Cretaceous, need to be included to improve the understanding of ichthyosaur body size evolution.

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1: ICHTHYOSAUR ONTOGENY, SEXUAL DIMORPHISM AND BODY SIZE EVOLUTION: AN INTRODUCTION

1.1: INTRODUCTION TO ICHTHYOSAURS

Ichthyosaurs form a monophyletic clade of marine diapsid reptiles (Fig. 1.2) known exclusively from the Mesozoic. They first appear in the Olenekian (Lower Triassic) and become extinct at the end of the Cenomanian (Upper Cretaceous) (Fig. 1.1) (McGowan & Motani, 2003). They form a group of their own (Ichthyosauria) which most likely forms a sister group with the Lepidosauriformes (Massare & Callaway, 1990; Motani *et*. *al*., 1998; Benton, 2005).

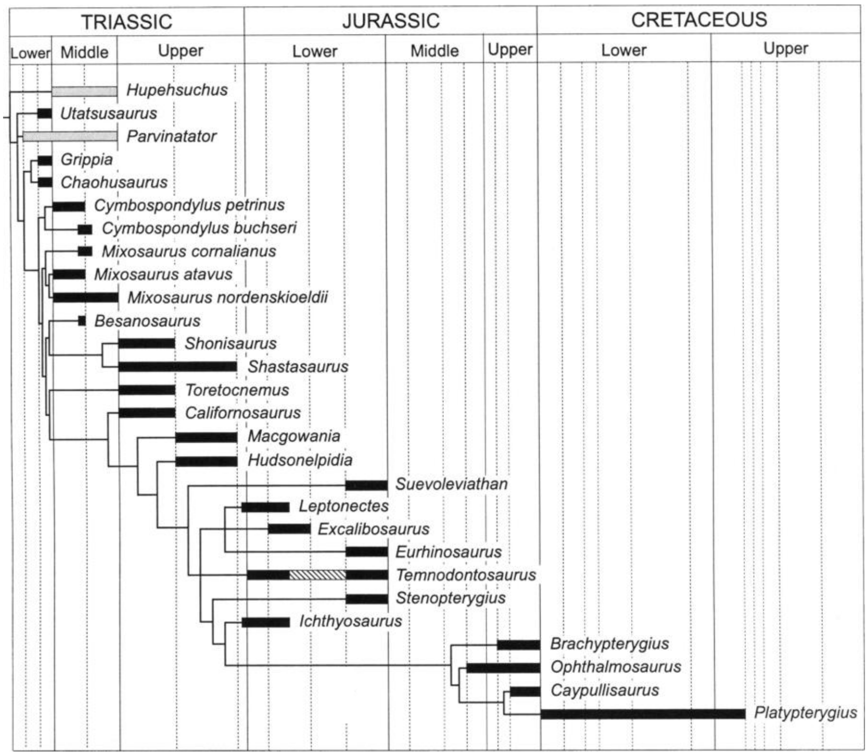


Fig. 1.1: A phylogram of ichthyosaur genera (non-exhaustive list). Black bars used when stratigraphy of a taxon is described with accuracy at stage level or finer. Grey bars used when the stratigraphy of a taxon is uncertain within two or more stages. Hatched bar lines indicate the absence from the fossil record between two data points (from Motani, 1999B). The range of *Ichthyosaurus* has since been extended into the Pliensbachian (Bennett *et al*., 2012).

Diapsids are characterised by two openings in the skull (temporal fenestra). Although some diapsids have lost one or both of these fenestrae (ichthyosaurs retain only the upper temporal fenestra), they are still classified as diapsids based on the ancestral trait. Skulls of basal ichthyosaurs such as *Grippia* have been examined and it is concluded that ichthyosaurs belong in the diapsid group (Motani, 2000).

Ichthyosaurs have been studied for 200 years, with the first description of a fossil ichthyosaur reported in 1814 (Home 1814). However, limited research has been conducted on ichthyosaur ontogeny to date. Ichthyosaur specimens range widely in size, indicating a growth series for most well represented genera, such as *Ichthyosaurus* de la Beche and Conybeare, 1821 and *Stenopterygius* Jaekel, 1904. Exceptional preservation has resulted in gravid females having been preserved as well as specimens with associated neonates (Hauff & Hauff, 1981; Deeming *et al*., 1993). The occurrence of embryos inside adult (sexually mature) individuals has been reported for at least six genera of ichthyosaurs, including *Besanosaurus* Dal Sasso & Pinna, 199) and *Mixosaurus* Baur, 1887 from the Middle Triassic, *Ichthyosaurus*, *Stenopterygius*, *Temnodontosaurus* (Lydekker, 1889) and *Leptonectes* (Lomax & Massare, 2012) from the Lower Jurassic, and an undetermined ophthalmosaurid from the Lower Cretaceous (Motani 2005). This direct evidence of gender means that studies of sexual dimorphism can also be conducted. Ichthyosaur embryos have also been preserved in the fossil record as stomach contents in the remains of a plesiosaur (O’Keefe et. al. 2009). There are two key sites of exceptional preservation containing ichthyosaur remains, one in Germany and one in England. Both of these sites are Lower Jurassic. The large number of exceptionally preserved specimens makes the Lower Jurassic an appropriate time interval for the study of ontogeny and sexual dimorphism.

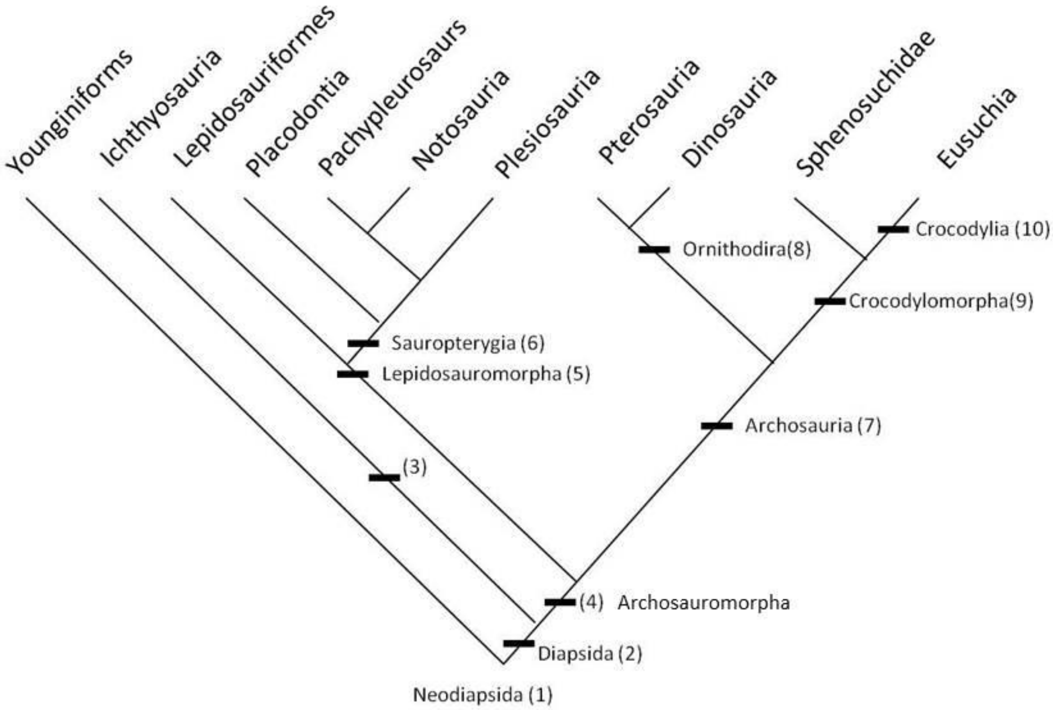


Fig. 1.2: Cladogram showing the position of the Ichthyosauria within Diapsida (modified from Benton, 2005). Synapomorphies as follows: - **1**. anterior process of the squamosal narrow, trunk ribs mostly single-headed, ends of humerus robust. **2**. upper and lower temporal fenestrae, suborbital fenestra, ossified sternum, complex tibio-astragalar joint, first metatarsal less than half the length of the fourth metatarsal. **3**. external naris close to the midline, sphenethmoid absent, presacral intercentra absent, entepicondylar foramen in humerus absent, radius as long as ulna, fifth distal tarsal absent. **4**. tabular absent, squamosal mainly restricted to the top of the skull, quadrate deeply emarginated posteriorly, stapes slender, cleithrum absent, lateral central in hand small or absent, fifth distal tarsal absent, fifth metatarsal hooked. **5**. supratemporal absent, teeth absent on transverse pterygoid flanges, dorsal intracentra absent, thyroid fenestra in pelvic girdle. **6**. premaxilla large, lacrimal absent, upper temporal fenestra larger than orbit, lower temporal fenestra open ventrally, anterior premaxillary and dentary teeth procumbent (slope forward), cervical intracentra absent, three or more sacral ribs, clavicles positioned anteroventrally to interclavicles and meet medial surface of scapula, humerus curved, humerus with reduced epicondyles, radius and ulna of equal length, fifth metatarsal long and slender, straight fifth metatarsal. **7**. anorbital fenestra in snout wall between nostril and orbit, laterally flattened teeth with serrations, ossified laterosphenoid in braincase, lateral mandibular foramen in posterior lower jaw bones. **8.** presacral centrum 8 longer then presacral centrum 18, deltopectoral crest on humerus subrectangular, fibula tapering and calcaneum reduced in size, astragalar posterior groove and calcaneal tuber rudimentary or absent. **9**. maxillae enter secondary palate, squamosal broadly overhangs quadrate laterally, postfrontal absent, primary contact of quadrate head with prootic, quadratojugal contacts postorbital, pneumatic basisphenoid and prootic, proximal carpals elongate. **10**. basisphenoid rostrum dorsoventrally expanded, basipterygoid processes reduced, lower portion of coracoid expanded, and anterior margin concave, scapula very broad dorsally (Benton, 2005).

1.2: INTRODUCTION TO ONTOGENY

Ontogeny is the development or developmental history of an individual taxon through time (Gould, 1977; McNamara, 1997; Hammer & Harper, 2006). The evolution of new features is controlled by developmental processes which can be fuelled by allometric growth. The examination of a possible growth series (typically based on size) can be used to establish ontogenetic features (Delfino & Sánchez-Villagra, 2010). Directly observing any anatomical changes along a growth series and observing in what order these changes occur, is one method that has been employed in order to study ontogeny (Johnson, 1977; McNamara, 1997).

It is important to understand the ontogeny of an individual organism for several reasons: (i) Taxonomy. Neonates and juvenile organisms can, in some cases, look very different from their mature forms. Without a full understanding of ontogeny, juvenile organisms could be mistaken for an adult form of a different genus or species. Furthermore, juveniles of different genera can look similar to each other based on qualitative observations (McGowan, 1979) as well as quantitative observations (Jones & Goswami, 2010). Quantitative observations could highlight subtle features that could help with accurate taxonomic assignment. (ii) Heterochrony. Changes in the timing and rate of development can affect the appearance of an individual at different stages of maturity, such as an adult (sexually mature) specimen appearing similar to a juvenile stage of an ancestor. The relative timings of onset and offset of growth can relate to relative age of an individual. (iii) Physical changes with age can relate to changes in habitats and feeding strategies. For example, organisms that become edentulous with age will change their feeding strategy (e.g. a change to suction feeding with tooth loss). Furthermore, some organisms, like the salamander, lead an aquatic lifestyle as juveniles and change to a more terrestrial lifestyle once they are sexually mature (McKinney & McNamara, 1991). This change in habitat is reflected in their physical appearance. Without the proper understanding of ontogeny, it would be easy to identify these two stages of one species as two different species. Growth series are not always available for study in the fossil record. It is therefore important to study growth series when they are available. Ichthyosaurs are well represented in the fossil record with specimens of varying sizes, therefore allowing the possibility of studying ontogeny in the fossil record.

1.3: INTRODUCTION TO SEXUAL DIMORPHISM

Sexual dimorphism is a naturally occurring phenomenon where males and females of the same species possess different physical features, which can result in specimens appearing very different from one another. Sexual dimorphism can be expressed in a number of ways such as simple size difference where one species is larger than another, different features such as large antlers, tusks or spines in one gender with these features absent or reduced in size in the other. Colour can also be sexually dimorphic where one gender displays different colours compared to the other. In many cases, sexual dimorphism in a species can be observed in many of these aspects and as a result, males and females can appear very different from one another (Williams & Caroll, 2009). If sexual dimorphism is not fully understood, then males and females of the same species could be misidentified as juveniles or as separate species (Fig. 1.10).

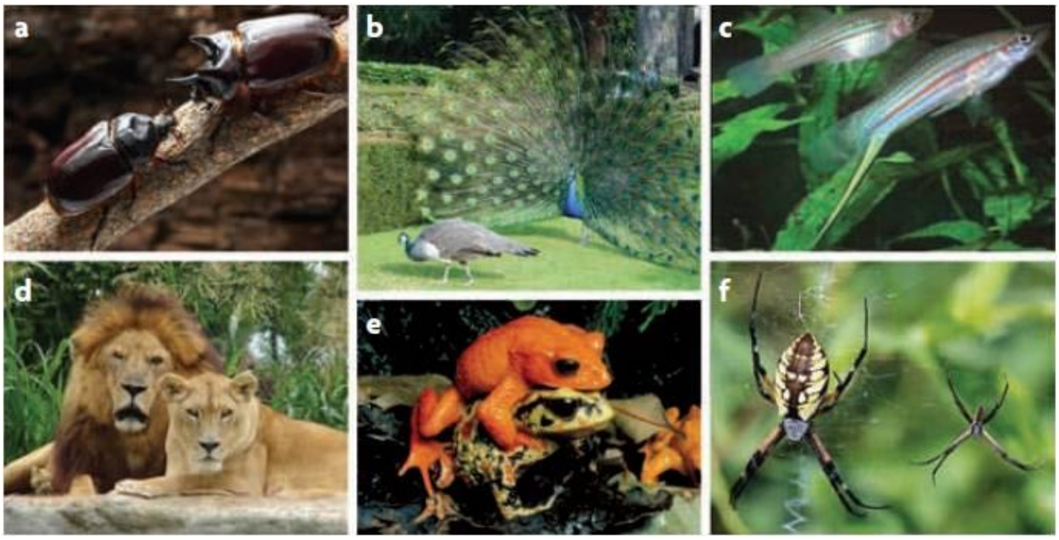


Fig. 1.3: Some examples of sexual dimorphism with elaborate male morphology (A-D) such as the horns of an (a) ox beetle (*Strategus aloeus*); (b) the peacock's tail (*Pavo cristatus*); (c) the caudal 'sword' of the swordtail fish (*Xiphophorus helleri*) and (d) the lion's mane (*Panthera leo*). The two genders can differ in colour as in (e) the golden toad (*Bufo periglenes*). A mixture of traits can be observed in some organisms such as (f) female garden spiders (*Argiope aurantia*) which are larger and more colourful than the males (from Williams & Carroll, 2009).

There are two main theories developed to explain sexual dimorphism: sexual selection and intraspecific niche divergence (Shine, 1989). Intraspecific niche divergence occurs where a physical characteristic provides an advantage for an individual such as a larger size or a type of ‘weapon’ such as tusks or antlers which could provide an advantage in competition (usually male-male) for a mate or for a defence of territory. Sexual selection is where a physical characteristic is selected for by a mate that ‘prefers’ that trait, such as a bright display in birds. For an overview of sexual dimorphism in extant and extinct reptiles, amphibians, birds and mammals, with specific examples, and the implications for the study of sexual dimorphism in ichthyosaurs, see Chapter 5.

The analysis of sexual dimorphism must be conducted on sexually mature specimens so that sexually dimorphic signals are not confused with ontogenetic features. This can cause problems in extinct organisms as it is not always possible to be sure that the specimens under study are sexually mature. However, in ichthyosaurs many pregnant specimens (typically specimens of *Stenopterygius*) are known and well documented. Pregnancy is unequivocal evidence of sexual maturity in an individual specimen, thus providing an opportunity to study sexual dimorphism in ichthyosaurs.

1.4: INTRODUCTION TO BODY SIZE EVOLUTION

Body size evolution examines the changes in overall size of an adult organism using a direct measure of body size or a proxy for size, such as body mass, length of a composite body part, length of an individual skeletal element or an estimate of body size. This measure of total body size, or a proxy, can remain constant, increase or decrease through phylogeny and/or geological time. Such size changes can relate to macroevolutionary changes in metabolism, population ecology, locomotion and reproduction (Hone *et*. *al*., 2008; Carrano, 2006) as well as changes in lifestyle such as trophic level and habitat. Cope’s rule suggests that organisms generally increase in body size throughout time (Hone & Benton, 2005). However, other studies suggest that this is not always the case and that Cope’s rule is too simple (MacFadden, 1986; Lomolino, 2005). For more details on body size evolution, as well as trends in extinct and extant reptiles, birds and mammals with specific examples, see Chapter 6.

A large number of ichthyosaur species are known from the Mesozoic and large numbers of specimens are known, which provides an opportunity to investigate body size evolution in these marine reptiles. Despite this, a study of ichthyosaur body size evolution has not previously been conducted.

1.5: AIMS AND OBJECTIVES

The purpose of this thesis is to investigate the ontogeny, sexual dimorphism and body size evolution of ichthyosaurs, all of which are currently very poorly understood. This study aims to establish a method of estimating relative age and sex of an individual ichthyosaur specimen regardless of size as well as to identify periods of body size increase or decrease.

It is the aim of this study to assess changes in physical characteristics of ichthyosaurs using morphometric techniques (a detailed description of the specific methods is provided in Chapter 2). A morphometric approach will also be used for testing whether growth is isometric or allometric for different parts of the body through ontogeny. The null hypothesis that growth across the whole ichthyosaur skeleton is isometric throughout life and no growth is allometric, will be further tested in this study (see chapter two for detailed hypotheses and the approaches used). If the null hypothesis is not supported, measurements obtained during the course of this project will provide ratios that may be related to growth. For example, negative allometric growth occurring in an area of the body (e.g., skull) during a juvenile stage of life would present a low ratio when skull length and body length are compared. If a low ratio for skull length compared to body length was observed in another specimen it could then be inferred that this specimen is also a juvenile. The same data set will be used to examine inferred adult specimens from a single genus, comparing pregnant and non-pregnant specimens in order to observe any sexually dimorphic characteristics. The null hypothesis is that there are no sexually dimorphic features of the skeleton that can be used to differentiate between males and females. If the null hypothesis is not supported, further tests will be carried out using size corrected data in order to test whether the results are species differences rather than sexually dimorphic features.

Body size evolution in ichthyosaurs will be tested using data on body length, or a proxy for body length, gathered from this study as well as from the published record. Taxa included will be based on a recent phylogeny or a composite phylogeny and taxa will be plotted at the earliest known occurrence. Regression analysis will test the strength of a relationship between size and time and will test the null hypothesis that there is no increase or decrease in body size with time. If the null hypothesis is not supported, the possible reasons behind any changes of size will be explored.

1.6: THESIS OVERVIEW

Chapter 2 explains the methods including why these techniques have been selected, how they work and their strengths and weaknesses. The categories of data collected (including measurements, skeletal elements/composite body parts used and taxa studied) are listed along with the definitions for the measurements. The overall hypotheses for the project are identified here.

Chapter 3 investigates ichthyosaur ontogeny using morphometric analyses based on length and width data of individual skeletal elements and composite body parts (forelimb and skull) from Lower Jurassic specimens. Principal Component Analysis (PCA) and Principal Coordinate analysis (PCO) are the multivariate analyses that are used in this section of the study. Reduced Major Axis regression (RMA) is used to further examine relationships that are suggested from the multivariate analyses in order to show whether growth is isometric or allometric. Pearson’s R and Bootstrap tests are used in conjunction with RMA in order to establish confidence intervals for the results.

Chapter 4 also investigates ontogeny in ichthyosaurs (same specimens as in Chapter 3) but is based on meristic (counted) data. Ordinary Least Squares regression is used to assess changes in counts compared to total body length. Numbers of vertebrae, digits and phalanges are analysed in this chapter.

Chapter 5 examines sexual dimorphism within ichthyosaurs. Mann-Whitney tests and discriminant analysis are used to compare gravid females to non-pregnant specimens to identify any morphological differences. This work is conducted using *Stenopterygius* (Toarcian, Lower Jurassic) as very few gravid specimens are known for other genera. Size corrected data is subsequently used for additional discriminant analysis in order to assess whether any positive results are caused by species differences rather than sexually dimorphic traits.

Chapter 6 examines ichthyosaur body size evolution throughout the Mesozoic. Total body size, or a proxy for body size data are derived from the literature and personal observation and based on a recent or composite phylogeny. Taxa are plotted against the time of earliest occurrence. An Ordinary Least Squares analysis is used to test the strength of any relationships observed between size and geological time.

Chapter 7 is a discussion that integrates all the results of this study. Biological and ecological ramifications are discussed and the data and methods are critiqued. The effects of potential bias in preservation and collection are evaluated. Suggestions for future study are provided and viability of these is discussed.

Chapter 8 summarises the conclusions of the study.

2: METHODOLOGY

2.1: INTRODUCTION

2.1.1: Overview

One key aim of the thesis is to determine a method of identifying relative age of individual ichthyosaur specimens, independent of size. The methods employed here have been used previously to observe physical changes through growth for a number of different organisms (O'Keefe & Miller, 2006, Hübner & Rauhut, 2010). However, for most Mesozoic marine reptiles, levels of bone fusion or closure of sutures is more commonly used to identify relative ages (Sander, 1989, Druckenmiller & Russell, 2006). Fusion does not occur in ichthyosaurs, so relative age is typically based on total body length. This does not enable distinction between a large juvenile and a small adult or recognition of opposite sexes that may be different sizes within the same species. This is covered in more detail in chapter 1. The term morphometrics refers to the measurement of the shape and size of organisms or their parts, and the analysis of such measurements (Hammer & Harper, 2006). This includes size and shape, which are the focus of the work. There are three main classes of measurement that can be defined as follows: (i) Linear measurements, such as lengths and widths; (ii) Outlines, where a large number of points can be used to define an outline in order to analyse shape where specific points are hard to define; (iii) Landmarks, where a number of homologous points are defined on a number of specimens (Hammer & Harper, 2006). The points are digitised and the changes in position of the landmarks are then used to analyse the changing shape of the organism being studied (Hammer and Harper, 2006). For this study, linear measurements were taken as well as meristic counted data. Measurements were combined in bivariate analyses, as well as multivariate analyses

This chapter aims to provide an overview of the materials studied, the measurements taken and the statistical analyses that are used.

2.2: MATERIALS

2.2.1: Institutions

Several museums were visited to examine the specimens and collect the data. These museums are; The Natural History Museum, London (NHMUK); The Grant Museum, London (LDUCZ); Dorset County Museum, Dorchester (DORCM); York Museum, York (YORM); Sedgwick Museum, Cambridge (CAMSM); Oxford University Museum, Oxford (OXFMS) and the Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS). The Hauff museum was not visited due to perceived issues relating to material housed in private collections.

These institutions were selected based on the ease of access and the amount of material available. Most of these institutions are in England which makes access easier and less costly. The Staatliches Museum für Naturkunde in Stuttgart was selected as the number of specimens available for study there is vast. This area of Germany is arguably one of the best areas in the world for exceptionally preserved ichthyosaurs in the Posidonia shales, Holzmaden, Germany. The main genus represented here is *Stenopterygius*. Some specimens in the museum also contain gravid (pregnant) female and this aspect is essential for this project.

2.2.2: Genera

A list of all specimens sampled, along with their genus, and species where known, is given in Table 2.3. The dataset consists of 136 individual specimens, in 6 genera. The genera represented are; *Ichthyosaurus* de le Beche & Conybeare, 1821; *Temnodontosaurus* Lydekker, 1889; *Leptonectes* McGowan, 1996; *Stenopterygius* Jaekel, 1904; *Suevoleviathan* Maisch, 1998 and *Aegirosaurus* Bardet & Fernández, 2000. The genera with the largest number of specimens represented in the dataset are *Ichthyosaurus* and *Stenopterygius*. These genera were selected as they are particularly well represented in the fossil record. *Ichthyosaurus* is a well-known genus from England and there are many specimens in museums. *Stenopterygius* is an extremely well represented genus as the Posidonia shale in Germany contains hundreds of specimens with more being discovered all the time. Many of these are exceptionally preserved due to anoxic ocean bottom conditions at the time of death (Rohl *et. al.*, 2001). The large number of *Stenopterygius* specimens makes it possible to conduct statistical tests on this genus alone. The other genera represented in the dataset were incorporated for two reasons; (i) to increase the number of specimens within the dataset. The higher the *n* values for the statistical tests, the more reliable and robust the results will be; (ii) to be used as a comparison. This comparison is used to try and determine if growth is the same in ichthyosaurs from the Lower Jurassic as a whole, or if growth varies between the genera.

2.2.3: Taxonomy of Lower Jurassic ichthyosaur taxa used in this study

The taxonomy of extinct vertebrates is based on diagnostic features of the skeleton that are specific to a genus or species. A large number of complete, well-preserved specimens for each species are ideally required for a detailed description. However, due to the nature of the ichthyosaur fossil record and of the organisms themselves (discussed below), these features (such as ratios of the skull, number of elements in a digit or vertebrae in a spinal column) are often subtle, difficult to identify or poorly understood. Ichthyosaur taxonomy is based typically on the arrangement of particular bones in the skull, measurements of the skull bones that are converted into ratios, and the number of digits in the forelimb as well as the number of phalangeal bones in the longest digit. However, these features can be difficult to obtain in all but the most exceptionally preserved specimens.

Due to their extreme adaptions to a marine environment, with limbs adapted into paddles, a tail adapted into a caudal fin that is used as the main form of propulsion and the presence of a dorsal fin, ichthyosaurs all tend to appear superficially similar to each another as all possess this constraining set of features. Even the most basal ichthyosaurs, such as *Grippia longirostris*, are totally adapted to life in the marine realm. This increases the difficultly in determining which features of a taxon can be used to distinguish between species as many of the potential differences can be very subtle.

Differential preservation can also add a level of uncertainty when identifying taxa. Ichthyosaurs are commonly preserved in two dimensions and those preserved in three dimensions are uncommon and known only from a few species. Furthermore, post-burial compression of the remains can alter the position of bones and lead to deformation, particularly in the skull, and can result in features being lost or incorrect (such as the ratios between skull bone measurements). In addition to this, there are comparatively few complete ichthyosaur specimens and, therefore, only a limited number of species can be fully described.

Some postcranial elements of ichthyosaurs, such as distal limb phalanges or caudal vertebrae, are typically minute, measuring 1 mm in length or less. It is very easy for these tiny bones to be lost as a result of taphonomic processes, with even the lightest of currents being able to remove bones from a carcass. Moreover, even in the most exceptionally preserved specimens, such as those of *Stenopterygius*, it is possible that these fine bones could be lost during preparation. The use of fine drills and air abrasives can easily cause very small bones to be removed from the matrix and not recovered. Furthermore, historically collected specimens could be more profoundly affected as tools were less precise. This, as well as the nature of the fossil record, means that counts of phalangeal and vertebral numbers could be inaccurate, even in well-known and well preserved specimens. Furthermore, the nature of a limb differs taxonomically, with some species having a compact manus where all elements are in contact with one another while other species show a splayed manus where the elements are separated from one another (Fig. 2.1). This affects the measurement of limb length and length of the longest digit. Bones that are well spaced could give a less accurate measurement than those that are compact. This issue could be further compounded as elements could be moved, providing an even larger error in the measurement. Despite this, the measurement of well-spaced elements is still the best representation of digit length available for study. Therefore, measurements that cross multiple bones are included in the analysis with the exception of when they have obviously been displaced (only obvious in species with ‘compact’ limb elements).

Fig.2.1: Photograph of two forefins. *Suevoleviathan disinteger* (left) with well-spaced elements and *Ichthyosaurus communis* (right) with compact elements. Scales measure 100mm. Photographs by the author.

A discussion of the validity of the genera included in this study is provided below, with comments on the validity of the species in each genus.

The main taxa used in this project (*Ichthyosaurus*, *Leptonectes*, *Stenopterygius*, *Suevoleviathan* and *Temnodontosaurus*) will be discussed in the following sections. The validity of each taxon will be discussed and comments on the ease of identification will also be mentioned. All of the taxa mentioned are from the Lower Jurassic. The taxonomic scheme followed below and all taxon diagnoses are from McGowan & Motani (2003) unless stated otherwise.

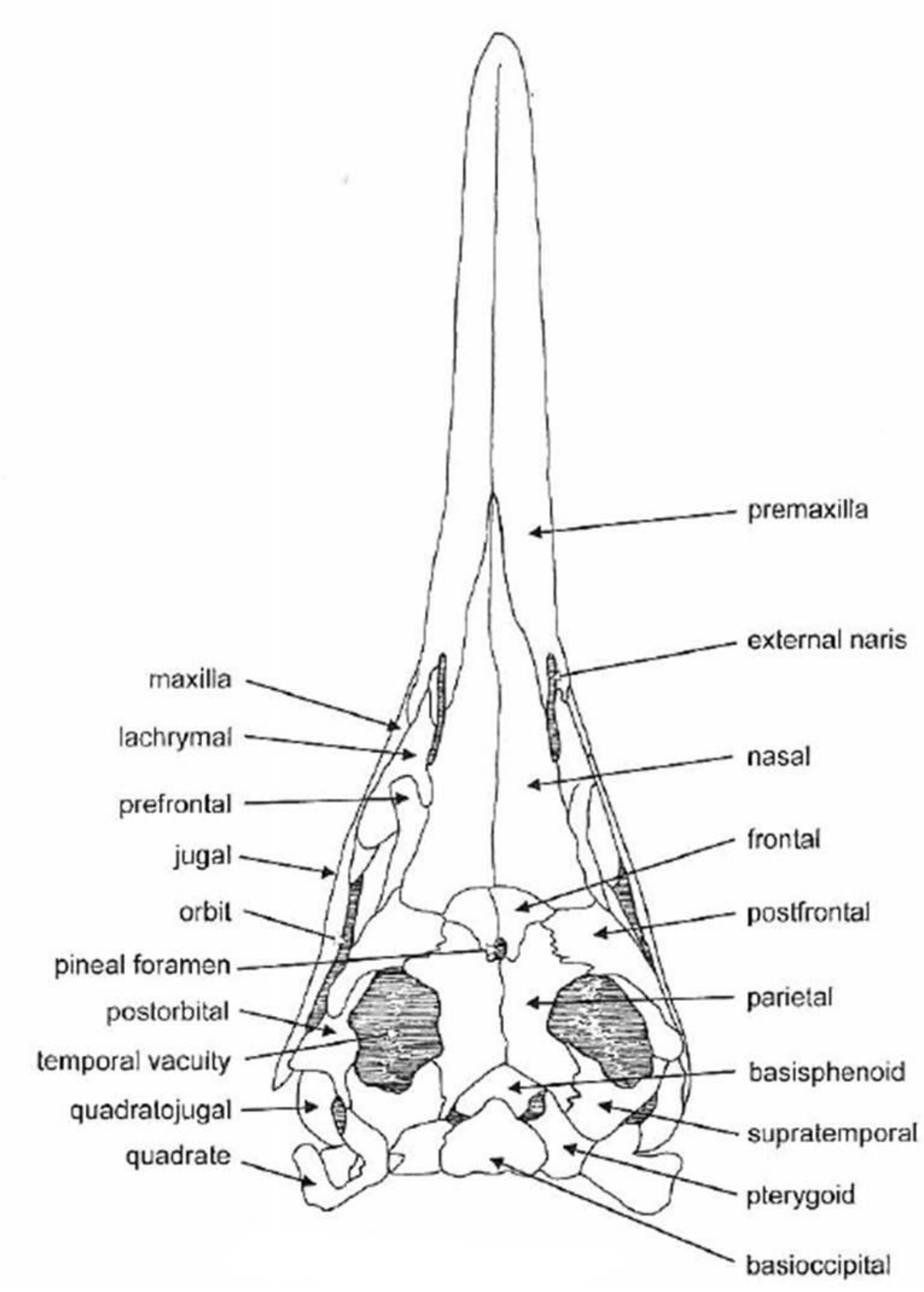


Fig. 2.2: Line diagram of an ichthyosaur skull in dorsal view with the elements labelled (from McGowan & Motani, 2003).

Temnodontosaurus Lydekker, 1889

Temnodontosaurus is represented by typically large, robust specimens known mainly from the Lower Lias of England and Germany. *Temnodontosaurus* is relatively well known but there are very few complete specimens.

The diagnostic features for *Temnodontosaurus* are: forefin probably <5 digits; ulnare smaller than intermedium; no digital bifurcation; at least some notching in anterior-most elements of leading edge, sometimes involving most elements; phalanges may be well spaced distally; distal ends of humerus markedly wider than proximal end, probably with prominent preaxial facet. Pubis and ischium separate, but may be partially fused. Preflexural vertebrae probably >80. Mandible not markedly shorter than skull. Orbit relatively small, orbital ratio ≤0.21, and often <0.18; maxilla probably long, premaxillary ratio ≤0.43 but >0.32; external naris frequently large, prenarial ratio >0.45; basioccipital with extensive extracondylar area and probably a small basioccipital peg. Teeth of modest size, largest ones at least 30 mm high and often >40 mm. Large ichthyosaurs: skull and jaw length >1 m in mature individuals, and often >1.5 m; total body length usually >6m and may reach 9m (McGowan & Motani, 2003).

McGowan & Motani (2003) consider five species valid (*T. platyodon*; *T. trigonodon*; *T. crassimanus*; *T. eurycephalus*; *T. acutirostris*). *T. platyodon* is one of the better known species with at least a few complete or nearly complete specimens known. However, there has previously been some confusion. A new species was described, based primarily on the presence of a distinct upturned rostrum, and named *T. risor*. However, subsequent investigation showed that *T. risor* was a juvenile *T. platyodon* (McGowan, 1974) and that the upturned rostrum is an ontogenetic feature rather than a taxonomic feature (Fig. 2.3).

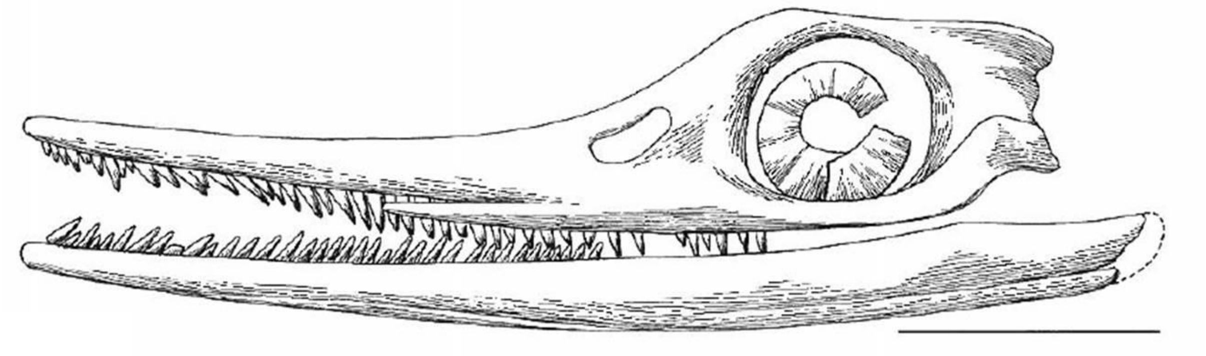


Fig. 2.3: Line drawing of the skull of a juvenile *Temnodontosaurus platyodon*, showing a distinct upturned rostrum. Scale measures 200 mm, from McGowan and Motani (2003.)

Temnodontosaurus platyodon Conybeare, 1822

T. platyodon is the type species for *Temnodontosaurus*. The holotype comprises a single tooth which is now lost. McGowan (1974) designated a large and almost complete specimen the neotype. The features that further distinguish *T. platyodon* are: forefin notching restricted to radius and next one or two elements; forefin not exceptionally long, number of elements in the longest digit probably <17; presacral vertebrae probably <48; rostrum not exceptionally long, snout ratio usually <0.65 but >0.59.

Most of the referred specimens of *T. platyodon* are incomplete and therefore the species is not well known, which reduces the confidence in the diagnosis. It is possible that the fairly wide range of variation among specimens might be due to inadvertent 'lumping' of large individuals of more than one taxon, rather than to individual variation within a single species (McGowan, 1996).

Temnodontosaurus trigonodon Theodori, 1843

The holotype of *T. trigonodon* comprises a complete skull and forefin and a partial postcranial skeleton. However, at least one complete and well preserved specimen is known. *T. trigonodon* is distinguished from *T. platyodon* by the following features: forefin notching in most elements in the leading edge; forefin long (Fig. 2.4), number of elements in the longest digit probably >17; presacral vertebrae probably >48; rostrum relatively long, snout ratio usually <0.65.

Fig. 2.4: Photograph of forefin of *Temnodontosaurus trigonodon* illustrating the elongate shape and notching in elements in the leading edge (top of picture). From McGowan & Motani (2003). Scale measures 500 mm.

T. trigonodon, although of comparable size to *T. platyodon*, can be further distinguished by the triangular cross-section of the tooth crowns (Maisch, 1998). However, Maisch (1998) stated that the triangular cross-section of the tooth crowns is an ontogenetic, rather than taxonomic, feature. This was supported by observations that smaller individuals had two rather than three carinae while some larger, isolated teeth posses four carinae. Huene (1922) had previously made the same observations and therefore this feature has no taxonomic significance. Furthermore, Maisch (1998) considered a small ventral extension of the lacrimal that overlies the premaxilla and jugal in the holotype as significantly different from other species of *Temnodontosaurus*. However, McGowan and Motani (2003) stated that the cranial sutures are difficult to observe and, therefore, that any variation in the shape of the lacrimal is not well established: they did not regard this as a taxonomically useful feature.

Temnodontosaurus crassimanus Blake, 1876

The holotype of *T. crassimanus* is a nearly complete but poorly preserved specimen. As a result of this very little is known about this species. *T. crassimanus* is distinguished from *T. platyodon* by the following features: forefin notching probably does not involve more than four elements and certainly does not involve all elements in the leading edge; presacral vertebrae probably >48.

Blake (1876) also observed that the forefin is almost twice the length of the hindfin. This differs from *T. platyodon* where the fins are of comparable length. However, McGowan and Motani (2003) noted that there are too few complete specimens of *Temnodontosaurus* to determine whether there are any consistent differences between the relative length of fore- and hindfins and therefore, Blake's feature is currently of little taxonomic use. Despite this, McGowan and Motani (2003) noted that the specimens referred to *T. crassimanus* are sufficiently distinct to warrant retention of Blake's (1876) taxon.

Temnodontosaurus eurycephalus McGowan, 1974

The holotype of *T. eurycephalus* is comprised of a single skull and no details of the postcrania are known. *T. eurycephalus* is distinguished from *T. platyodon* by the following features: short, broad rostrum (Fig. 2.5) snout ratio <0.58; orbit relatively small, orbital ratio

<0.21; maxilla relatively long, premaxillary ratio <0.36 and probably <0.30; teeth robust; skull and mandible both deep; large skull length >500mm.

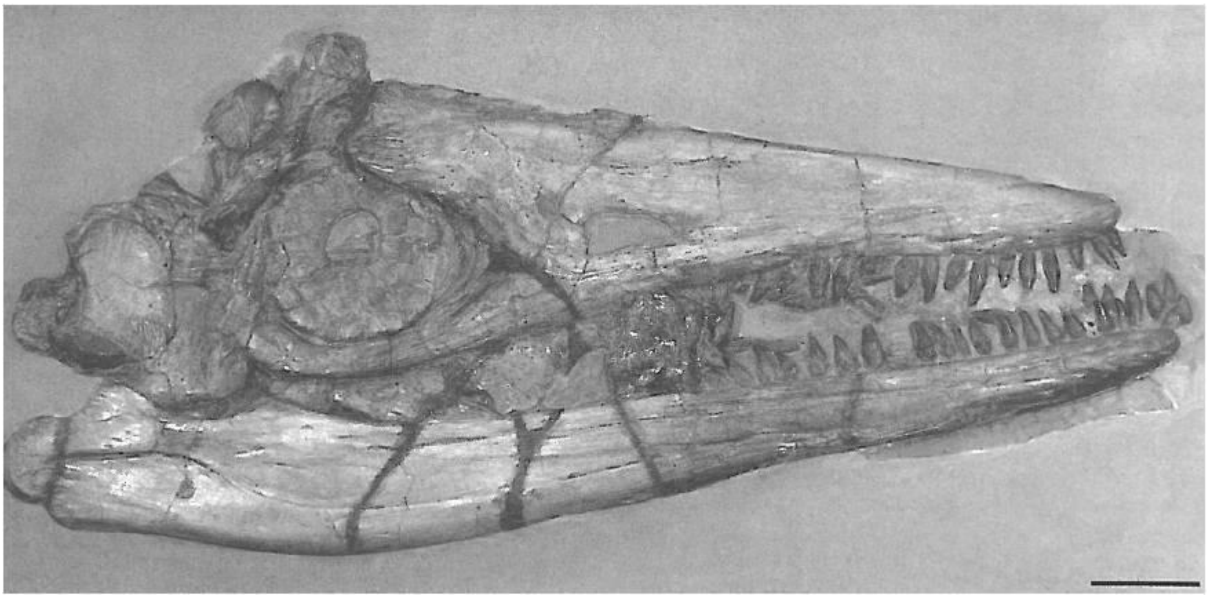


Fig. 2.5: Photograph of *Temnodontosaurus eurycephalus* skull showing a short, broad rostrum and robust skull. From McGowan & Motani (2003). Scale measures 100 mm.

McGowan & Motani (2003) stated that *T. eurycephalus* has been confused with *I. breviceps* in the past due to the short rostrum, but did not provide a reference to support this contention. The skull of *T. eurycephalus* is much larger than that of *I. breviceps* and whereas *I. breviceps* has a gracile skull that of *T. eurycephalus* is very robust. Furthermore, *I. breviceps* has a large orbit that dominates the skull while the orbit in *T. eurycephalus* is relatively small.

Temnodontosaurus acutirostris Owen, 1840

The holotype of *T. acutirostris* is comprised of a skull, one complete forefin with a few proximal elements from the other, a coracoid and other parts of the pectoral girdle, and several ribs (Lydekker, 1889). The specimen has since lost the anterior part of the snout (McGowan & Motani, 2003). *T. acutirostris* is distinguished from *T. platyodon* by the following features: teeth numerous with no tendency towards reduction in size or number; snout long, slender and probably tapering to a sharp point, snout ratio usually ≥0.64; orbit small, orbital ratio <0.24; premaxillary ratio probably ≤0.42; forefin probably elongate, number of elements in the longest digit maybe >30; notching occurs, probably restricted to a few proximal elements; moderate sized ichthyosaur, skull probably <1 m.

The reconstruction of the skull from Owen (1881) shows a distinct downturn in the snout. The snout in the holotype has been lost so it is no longer possible to compare this feature in the original specimen to the description. However, similar downturns of the snout are observed in other specimens. However, it is possible that the downturn is a preservational artefact due to dorsoventral compression of the slender rostrum. Therefore, this feature is not of taxonomic use. The most distinctive feature of the holotype is the extreme length and slenderness of the forefin, which has approximately 30 elements in the longest digit. However, Owen made no mention of this in the brief original description (1840) or his later work (1881). Due to this, the forefin is currently being investigated in order to determine its authenticity (Chapman & Doyle, in preparation). Therefore, the characteristic elongation is only provisionally included in the diagnosis.

Taxonomic validity of *Temnodontosaurus*

Temnodontosaurus is a valid genus and is readily identifiable by its typically large and robust skeletons, skulls and teeth, comparatively small orbits and the presence of only 3–4 digits in the forefin. However, there are greater levels of uncertainty in the diagnoses of the species referred to this genus. There are comparatively few complete or nearly complete, well preserved specimens of *Temnodontosaurus* available to study, which has hindered description, particularly of the postcranial skeleton. Many of the descriptions are vague and give only estimates for the numbers of elements present (such as vertebrae) instead of providing direct counts. Furthermore, many specimens are referred to this genus on the basis of large size. However, this practice does not take ontogenetic change into account: neonate and juvenile specimens of this taxon will be much smaller than any adult specimens. It is possible that smaller *Temnodontosaurus* specimens have been assigned to other genera due their comparatively small size. McGowan & Motani (2003) recognise the five species listed above. However, Maisch & Hungerbühler (1997) argue for referring *Leptopterygius nuertingensis* to this genus. The holotype of the latter taxon comprises a partial skull, eight vertebrae, some ribs and a coracoid. McGowan (1979) considered the material to be too incomplete to be determinate, but Maisch & Hungerbühler (1997) stated that the skull possesses a number of distinctive features that can be used to diagnose the species. The principal feature is the union of the jugal with the premaxilla. These authors argued that this feature only occurs in *T*. *trigonodon* and is evidence of a close relationship between it and *L*. *nuertingensis*. The large size of *L*. *nuertingensis*, together with its long and robust snout, numerous large teeth and the general shape of its skull are also used as evidence for affinities with *Temnodontosaurus*. However, none of the diagnostic features of *Temnodontosaurus* are evident in the specimen, with the exception of large size. *L*. *nuertingensis* is regarded as a nomen dubium herein.

There are enough valid characteristics for the five above-mentioned species to be considered as valid on the basis of current evidence. Despite this, further material is required to describe them in detail. The extreme length of the limb is currently included as a diagnostic feature for *T. acutirostris*, but this limb is currently under examination to conform its authenticity. As it is possible that the limb has been faked, in which case, the validity of this species could be questioned. Due to the levels of uncertainty in the diagnoses of the species, it is more appropriate to examine the material as a single genus rather than as separate species. This approach has the benefit of including specifically indeterminate *Temnodontosaurus* specimens into these analyses presented herein.

Leptonectes

Leptonectes McGowan, 1996 is a genus in the family Leptonectidae, which is defined as the clade comprising the last common ancestor of *Eurhinosaurus longirostris* and *Leptonectes tenurirostris* and all of its descendants. The diagnosic features for this family are as follows: temporal region facing posterolaterally, appearing narrow in lateral view; extremely slender snout, tooth size relative to the skull width small (<0.05); tibia and fibula separated.

The diagnostic features that further distinguish *Leptonectes* are as follows: humerus with constricted shaft with a widely expanded distally with leading edge facet that is usually prominent; forefin with less than five digits; phalanges large, probably well spaced distally. Rostrum and mandible slender, snout commonly long; large orbit occupying most of the postorbital segment of the skull; teeth often slender and may be relatively small, especially in large, adult individuals; pubis and ischium separate, but may be partially fused; presacral vertebrae probably >44 and possibly >50; preflexural vertebrae >79; moderate sized to large ichthyosaurs, but skull length probably <1 m.

Leptonectes tenurirostris Conybeare, 1822

L. tenurirostris is the type species. The neotype is a complete specimen currently on display at the Natural History Museum, London. The distinguishing characteristics of *L. tenurirostris* are: forefin with four digits; phalanges large and discoidal, probably well separated; humerus with constricted shaft, widely expanded distally but distal width is less than length, leading edge facet is usually prominent; radius notched; occlusal edges of radius and ulna usually enclosing a small foramen. Snout long and slender, snout ratio >0.70; prenarial ratio >0.56; premaxillary ratio >0.48; orbit appears to be large, occupying most of the post rostral skull, but orbital ratio <0.25 and may be <0.20 (Fig. 2.6). External naris may not be simple petaloid shape, snout may extend beyond mandible giving a small overbite. Teeth predominantly slender and may be relatively small. Tail bend may not be prominent; preflexural vertebrae ≥80; presacral vertebrae ≥40, but probably <50. Tibia notched, probably also tibiale, notches probably broad. Coracoids probably rounded with an anterior notch. Mostly medium sized, with total lengths of 2.5 m but reaching up to almost 4 m.

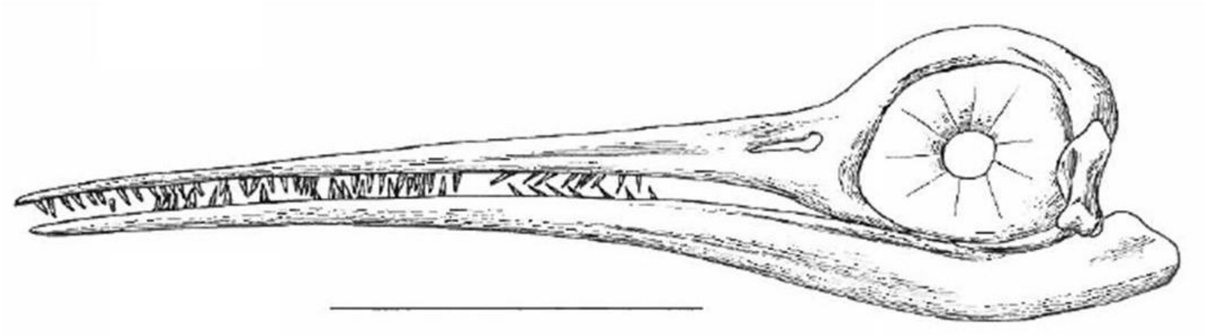


Fig. 2.6: Skull of *Leptonectes tenurirostris* showing the long and slender snout a relatively large orbit. Scale measures 200 mm, from McGowan & Motani (2003).

Although a few complete or near complete specimens are known for *L. tenurirostris*, such specimens are rare, adding an element of uncertainty to this diagnosis. However, the complete specimens are well preserved and there is little doubt that the characteristics described thus far are accurate.

Leptonectes solei McGowan, 1993

The holotype of *L. solei* is an incomplete specimen that includes a poorly preserved skull and some postcranial material (Fig. 2.7). The characteristics that further distinguish *L. solei* are: large ichthyosaurs, skull length and jaw length >1 m; presacral vertebrae probably >45 and possible >50. Snout long and slender, snout ratio probably >0.64 but might not exceed 0.70; orbit small, orbital ratio might not exceed 0.18. Humerus widely expanded distally, especially preaxially, distal width may exceed length; leading edge facet on distal end of humerus, but may not be prominent, radius notched; occlusal edges of radius and ulna not enclosing a small foramen; radius and ulna probably not fused. Pelvic girdle probably tripartite, without fusion between pubis and ischium; pubis much broader than ischium, especially proximally, and is sub-rectangular; ischium widely flared distally, ilium only slightly curved.

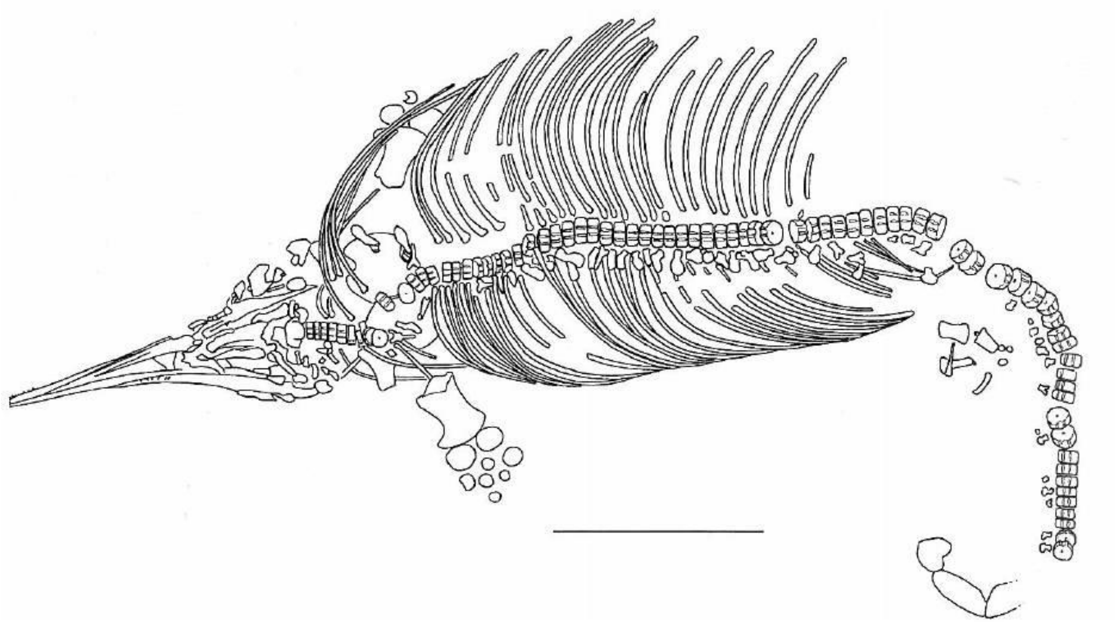


Fig. 2.7: Line drawing of the holotype of *Leptonectes solei* illustrating the incomplete nature of the specimen and the disarticulated pelvic girdle. Scale measures 1 m, from McGowan & Motani,(2003)

The holotype is the best-preserved and most complete specimen found thus far. As it is incomplete and partially disarticulated, the description is also incomplete adding uncertainty to the diagnosis of the taxon. Furthermore, a large proportion of the distinguishing characters are based on the pelvic girdle. In the holotype, the pelvic girdle is disarticulated and the individual elements are partially scattered. It is likely that these elements do belong to this specimen but there is no direct proof of this. It is possible that the other elements are introduced by taphonomic processes or as a result of scavenging. If this is the case then part of the diagnosis is incorrect.

Leptonectes moorei McGowan & Milner, 1999

The holotype of *L. moorei* is an incomplete specimen with a relatively well-preserved skull, particularly in left lateral aspect, and the forefins. Very little of the postcranial skeleton is preserved. The features that distinguish *L. moorei* are: snout and mandible slender, snout not long (Fig. 2.8), snout ratio <0.70, and probably <0.64; prenarial ratio <0.56, but probably not <0.43; premaxillary ratio <0.48 and probably <0.44; orbit large occupying most of the post-rostral skull, orbital ratio >0.20 and probably >0.25. Radius probably not notched; radius and ulna probably not enclosing small foramen.

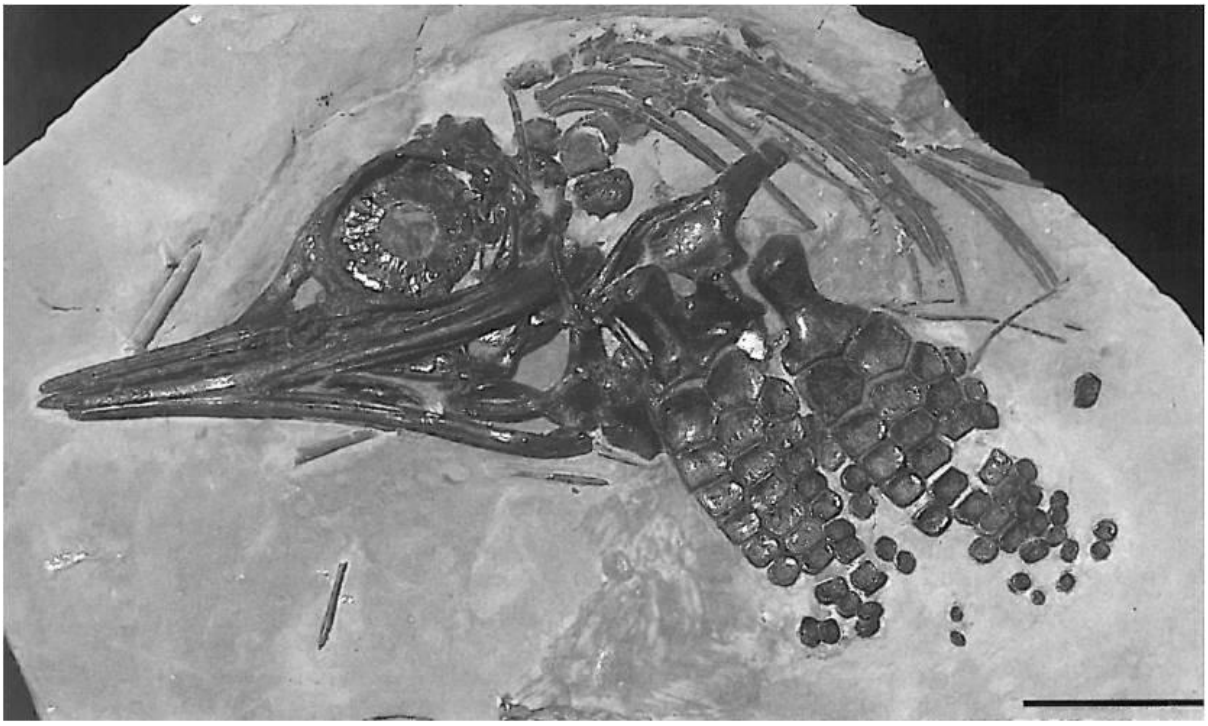


Fig. 2.8: Photograph of *Leptonectes moorei* illustrating the extremely short snout and large orbits. Scale measures 100 mm (McGowan & Milner, 1999).

This is the only known specimen of *L. moorei* and its incomplete nature means that many potentially diagnostic features are currently unknown. Despite this, the remarkably short snout, a feature not seen in other taxa, clearly distinguishes it from other species of *Leptonectes*. Additional specimens are required in order to provide a more accurate and detailed description of this taxon.

Taxonomic validity of *Leoptonectes*

Leptonectes is a readily identifiable genus comprised of medium sized, gracile species with exceptionally large orbits compared to skull size. However, the species are not well diagnosed. *L. tenurirostris* is the only species with complete, articulated specimens but these are exceedingly rare. As a result of this, ontogenetic, intraspecific or sexually dimorphic features will not have been identified. *L. moorei* and *L. solei* are represented by incomplete and partially disarticulated specimens. As a consequence many features that could be used for taxonomic assignment, such as vertebral counts and features of the pelvic girdle, are unknown. Although a scattered pelvic girdle is preserved with *L. solei*, the associations of these elements are uncertain and the descriptive characteristics of this should be used with caution. For this reason, specimens of *Leptonectes* are analysed in this thesis at genus level only.

Suevoleviathan Maisch, 1998

Suevoleviathan contains a single species and belongs to the family Suevoleviathanidae. The type species is *Suevoleviathan disinteger* Huene, 1926

Suevoleviathan disinteger

The diagnostic characteristics for this species are: large ichthyosaurs, total body length >4 m; forefin digits widely splayed distally; probably more than five digits; no notching; forefin not much longer than hindfin; notching in most elements of the leading edge of the hindfin. Pelvic girdle tripartite; pubis slender and curved; ischium subrectangular; ilium with anterior process. Preflexural vertebrae >80; postflexural segment long and seemingly flexible. Maxilla short, premaxillary ratio >0.42; orbital ratio <0.22. Teeth robust (Fig. 2.9), posterior maxillary teeth reduced in number.

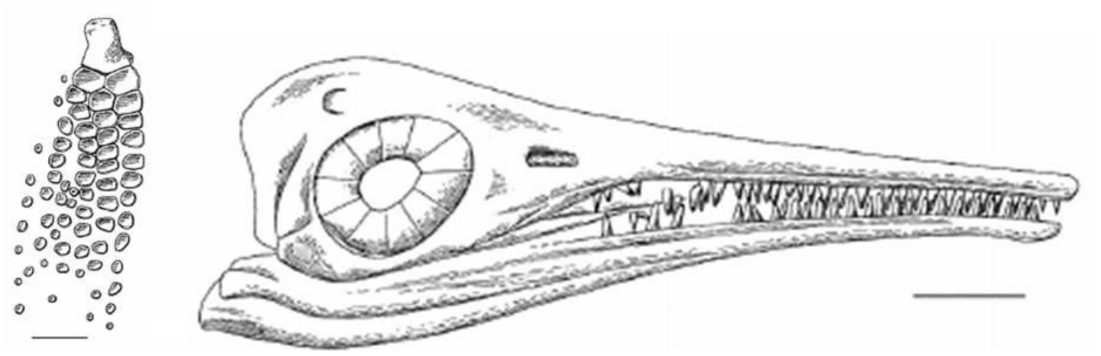


Fig. 2.9: Line drawing of skull and forefin of *Suevoleviathan* illustrating distally splayed fin elements and robust teeth in the skull. Scale bars measure 100 mm, from McGowan & Motani (2003).

Taxonomic validity of *Suevolveiathan*

S. disinteger is a rare but easily identifiable species, partially due to the size, but also due to the unique combination of the notching seen in elements of the hindfin and the absence of notching from the forefin. This is the reverse of the condition typically observed in other ichthyosaurs. Furthermore, the holotype is a complete, extremely well preserved specimen, which suggests these features are reliable However, as *S. disinteger* is so rare, ontogenetic, intraspecific and sexually dimorphic variation cannot be assessed. Despite this, the characters described are currently thought to be unique for the genus.

Ichthyosaurus De La Beche & Conybeare, 1821

The family Ichthyosauridae, which contains the genus *Ichthyosaurus*, belongs in the superfamily Ichthyosauroidea. The superfamily is defined as the last common ancestor of *Stenopterygius quadriscissus*, *Ichthyosaurus communis* and *Ophthalmosaurus icenicus* and all its descendants. The diagnostic feature for this superfamily is that the forefin is twice as long as the hindfin. The diagnostic features for the genus are as follows: forefin with no fewer than five digits; ulnare larger than intermedium; digital bifurcation occurs, anterior to the primary axis; phalanges numerous and close-packed; distal end of humerus wider than proximal end; pelvic girdle tripartite, without fusion between pubis and ischium; preflexural vertebrae <80; basioccipital with extensive extracondylar area and well developed basioccipital peg.

Ichthyosaurus communis De La Beche & Conybeare, 1821

Ichthyosaurus communis is the type species of the genus. The holotype is a partial skeleton mentioned by De La Beche and Conybeare (1821) but no illustrations were provided and the specimen can no longer be located. McGowan (1974) designated a complete specimen as the neotype. The diagnostic features for *I. communis* are as follows: preflexural vertebrae >74 but <80; presacral vertebrae >41. Snout relatively long, snout ratio >0.57; orbit not exceptionally large, orbital ratio typically <0.26. Forefins variable, with differences between Somerset and Dorset specimens. Former have fewer digits, usually six or less, with fewer elements in the longest digit (typically not more than 20); phalanges more angular than rounded; notching usual in some preaxial elements. Dorset specimens normally with at least six digits and upwards of nine (Fig. 2.10); number of elements in the longest digit >25; no notching. Medium sized reaching total body lengths of about 2.5 m.

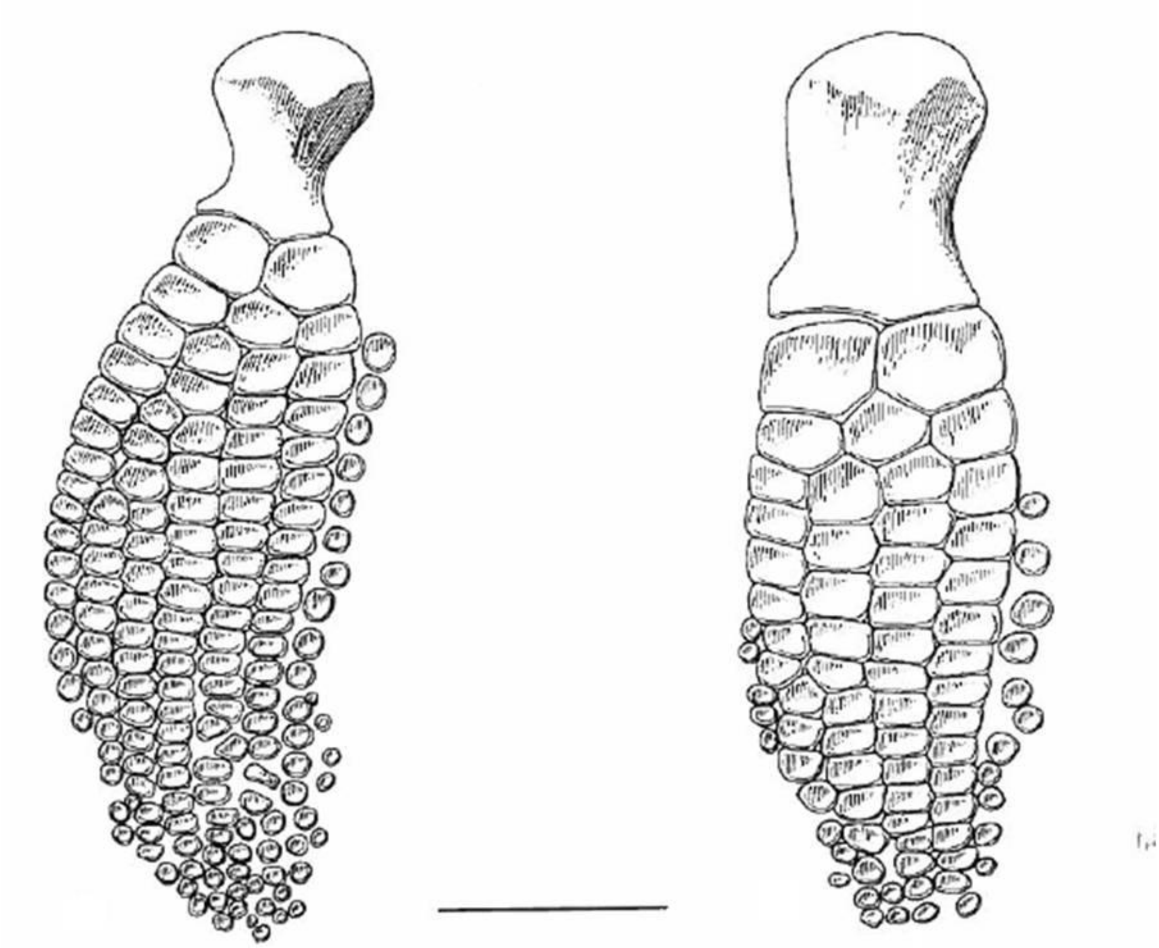


Fig. 2.10: Line drawings of the forefins of *Ichthyosaurus communis* from Dorset (left) and Somerset (right) showing the difference in numbers of digits. From McGowan & Motani (2003). Scale measures 50 mm.

Ichthyosaurus is one of the most common species found in the Lower Lias of England and is well known as a consequence. Despite this, there are some areas of contention in the taxonomy. Maisch (1997) argued for the retention of *I. intermedius* as a separate species based on features of a partial skull figured by Conybeare (1822) that distinguish it from *I. communis*. These features (also shared by another specimen: SMNS 13111) are a shortened quadratojugal and a high maxillary tooth count in excess of 20. Furthermore, SMNS 13111 has 'waisted' teeth where the crown is narrow and the root widened. This feature was figured by Conybeare (1822). However, McGowan & Motani (2003) noted that, in both specimens, the quadratojugal has been displaced such that the proximal end lies both posterior and ventral to the normal position and is no longer in articulation with the supratemporal. This could explain why it does not appear to extend far down towards the distal end of the quadrate. Furthermore, it is typically impossible to determine the true extent of the quadratojugal in flattened specimens, which reduces the usefulness of this feature. McGowan & Motani (2003) also stated that tooth numbers are highly variable, and therefore, this type of diagnostic feature is not reliable. For these reasons, *I. intermedius* is not currently considered as a valid species and specimens identified as such are regarded as *I. communis* herein.

Ichthyosaurus breviceps Owen, 1881

The holotype of *I. breviceps* is a complete specimen. The diagnostic features for this species are: preflexural vertebrae <74; presacral vertebrae probably >41 and probably <44. Snout markedly short, snout ratio <0.57 (Fig. 2.11); orbit large, orbital ratio ≥0.26. Forefin probably with at least seven digits; elements in the longest digit >20; no notching. Fairly small with total body lengths <2 m and may not exceed 1.5 m.

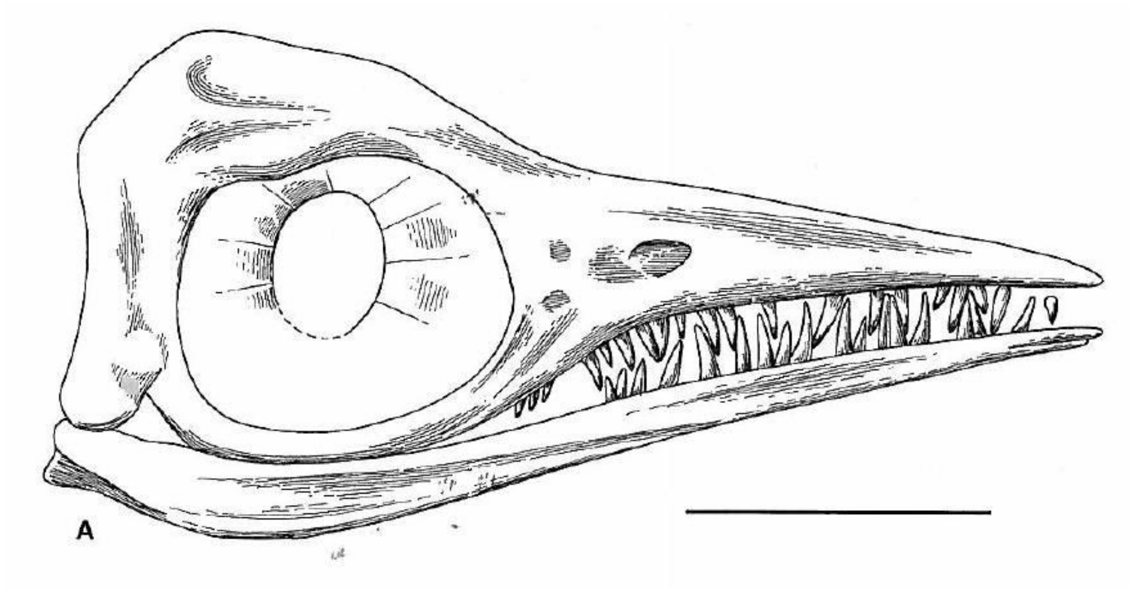


Fig. 2.11: Line drawing of the skull of *Ichthyosaurus breviceps* illustrating the very short snout and large orbit. From McGowan & Motani (2003). Scale measures 50 mm.

The specimen is well preserved and complete which means that the entire specimen can be described, which adds confidence to the accuracy of its description. However, this is a particularly rare species and few specimens are known. This reduces the reliability of the taxon as variability within the species cannot be assessed. Features that could relate to ontogeny or sexual dimorphism are currently unknown.

Ichthyosaurus conybeari Lydekker, 1888

I. conybeari is a very rare species from the Lower Lias and the holotype is an incomplete and poorly preserved specimen. The diagnostic characteristics for *I. conybeari* are: preflexural vertebrae >74; presacral vertebrae <42. Snout long and slender (Fig. 2.12); snout ratio probably >0.57; orbital ratio <0.28. Notching occurs in some preaxial elements of the forefin, six digits, elements in the longest digit <25. A small species with an estimated maximum body length of 1.5 m.

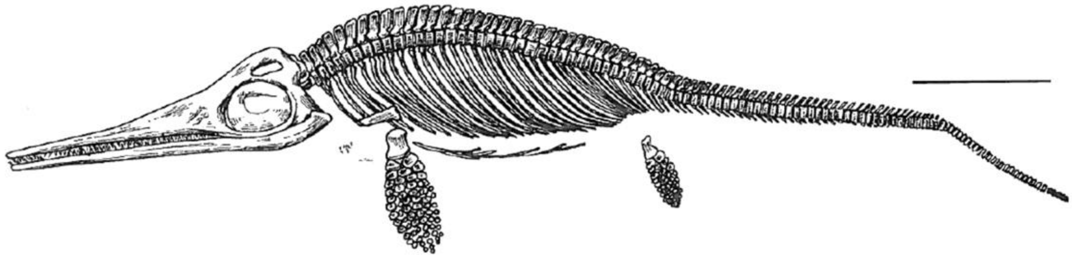


Fig. 2.12: Line drawing of complete *Ichthyosaurus conybeari* showing a slender, elongate snout. From McGowan & Motani (2003). Scale measures 100 mm.

As with *I. breviceps*, the rarity of the specimens reduces the reliability of the diagnosis as natural variability within the species is unknown as are features that could relate to ontogeny or sexual dimorphism. Furthermore, the specimen is incomplete and poorly preserved which further reduces the reliability and accuracy of measurements. However, the features listed above are sufficient to support its recognition as a distinct species.

Taxonomic validity of *Ichthyosaurus*

The validity of *Ichthyosaurus* is without doubt as specimens from this genus are relatively common. Many of the specimens recovered are complete or nearly complete, well preserved, and in some cases, articulated. Despite this, there are some areas of uncertainty with respect to the taxonomic validity of its component species.

The most common species, *I. communis*, is well represented in the fossil record and there are many descriptions from several specimens. The number of specimens found increases confidence in the reliability and accuracy of the proposed diagnostic features. However, there are still areas of uncertainty within this species as some authors argue for the retention of *I. intermedius* as a valid species while others argue that there are too few clearly defined characteristics to warrant this conclusion. Furthermore, there is a discrepancy in the anatomy of the forefin between specimens from Somerset and Dorset (section 3.4.1). Although it is possible that the differences in the numbers of digits in the forefin is a result of natural intraspecific variation, it is also possible that this represents another species, or a sub-species of *I. communis*. These unresolved variations add some uncertainty to the taxonomic validity of this species.

I. brevicpes and *I. conybeari* are both very rare species. *I. conybeari* is known from one specimen only while there are only a few specimens of *I. breviceps*. Although both of these taxa are valid, their descriptions are limited, adding uncertainty to their diagnoses. Due to uncertainty in the species-level taxonomy of *Ichthyosaurus*, it is more appropriate to examine these specimens at the generic level.

Stenopterygius Jaekel, 1904

Stenopterygius belongs in the family Stenopterygiidae Kuhn, 1934. Many specimens of *Stenopterygius* have been recovered due to exceptional preservation in the Posidonia shale near Holzmaden, Germany. The diagnostic characteristics for *Stenopterygius* are as follows: pelvic girdle bipartite, ischium and pubis fused to form a single element. Forefin with 4-6 digits; individual elements tightly packed proximally; notching in some elements of the leading edge; humerus with two distal facets. Paired fins disproportionate in length, forefin at least twice the length of the hindfin. Preflexural vertebrae <90. Small to moderate sized, skull and jaw length <1 m, total length <6 m and commonly <4 m.

Stenopterygius quadriscissus

S. quadriscissus Quenstedt, 1856 is the type species of *Stenopterygius*. The diagnostic features for this species are: teeth extremely reduced in size and number with maturity, leading to complete loss. Presacral vertebrae ≤45; preflexural vertebrae <82. Forefin usually with five digits (Fig. 2.13), rarely four or six. Snout moderate to long, snout ratio >0.60 but often >0.66; orbit not e3specially large, orbital ratio ≤0.24, and usually <0.22 or equal. Medium sized, total body length <0.35 m; skull length <650 mm.

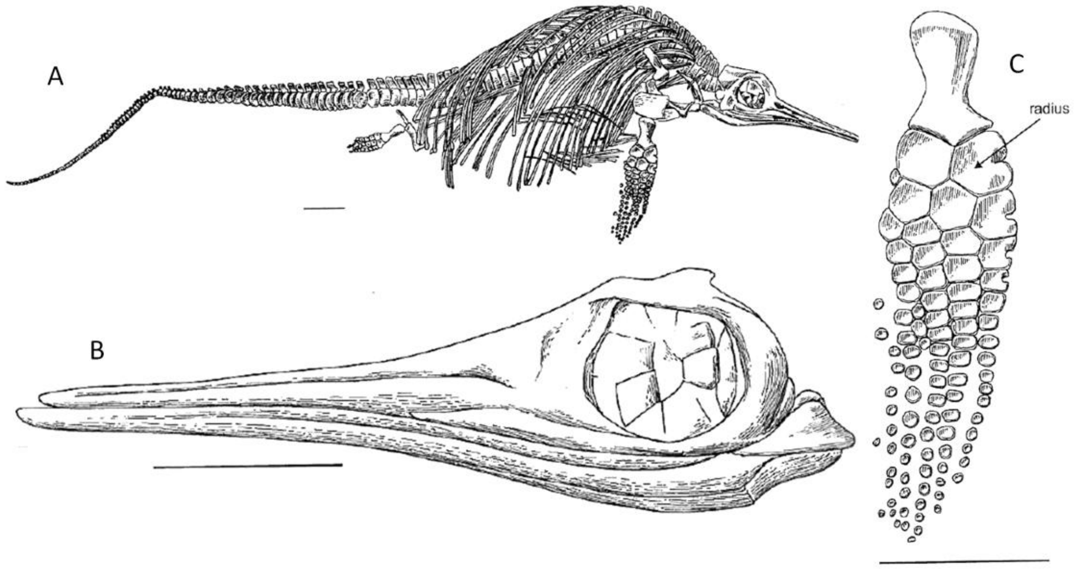


Fig. 2.13: Line drawing of complete specimen (A), skull showing a lack of teeth and a long, slender rostrum (B) and a forefin (C) with five digits. Modified from McGowan & Motani (2003). Scales measure 100 mm.

McGowan (1979) stated that the most striking feature of *S. quadriscissus* is the complete loss or extreme reduction in tooth number in large (inferred mature) individuals. Maturity appears to correspond with a mandibular length of 400 mm (McGowan, 1979). McGowan (1979) went on to state that aside from this feature, *S. quadriscissus* lacks any distinguishing features and appears a very 'ordinary' looking ichthyosaur. However, tooth loss is an unreliable feature in ichthyosaurs as teeth are typically set in a dental groove and are only held in place by soft tissues. Once this soft tissue breaks down, it would be easy for teeth to be lost as a result of taphonomic processes, even in very low energy environments. Although tooth number can be a useful feature for taxonomic assignment, it is suggested that it should only be used in conjunction with other evidence (pers. obs.). Despite this, there can be no doubt that the description and diagnostic features for this species are very reliable due to the numbers of exceptionally preserved and articulated specimens known.

Stenopterygius hauffianus Huene, 1922

S. hauffianus is found in the Upper Lias (Toarcian). The diagnostic features for this species are: snout short (Fig. 2.14), snout ratio usually ≤0.66; orbit large, orbital ratio >0.22. Teeth usually small, often sparse, but never absent. Skull appears small for body size.

Presacral vertebrae ≥45; preflexural vertebrae probably >82. Forefins short and wide, aspect ratio <2.7. Moderate sized, total length <3.5 m; skull length <600 mm.

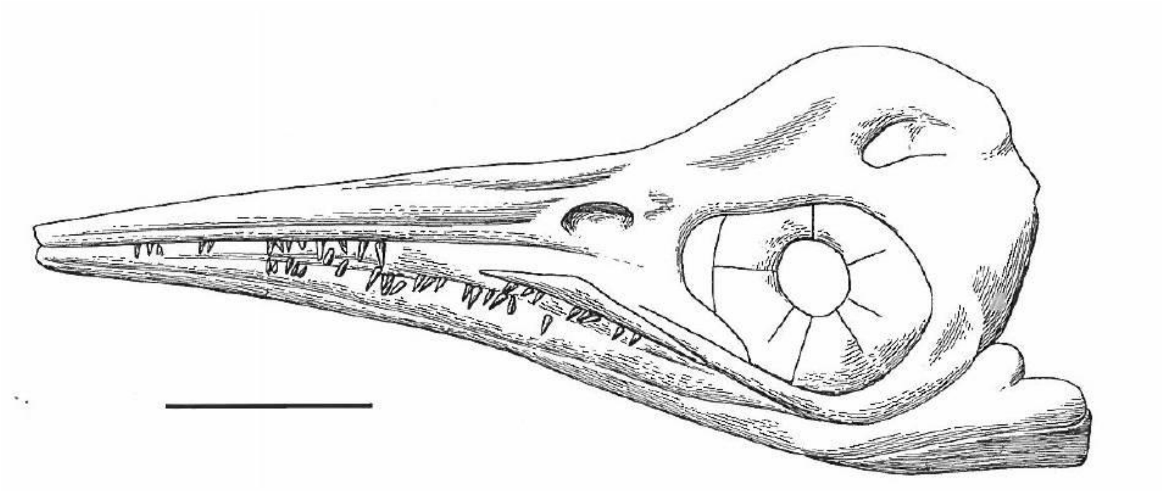


Fig. 2.14: Line drawing of the skull of *Stenopterygius hauffianus* showing a short snout and small, sparse teeth. From McGowan & Motani (2003). Scale measures 100 mm.

McGowan & Motani (2003) note that this species is most commonly confused with *S. quadriscissus* due to the reduction in tooth number. They go on to state that *S. hauffianus* always retains teeth. As with *S. quadriscissus*, tooth number is not a reliable feature and it is plausible that there are specimens of *S. hauffianus* that have lost all the teeth due to taphonomic processes. One of the characteristics mentioned is that the teeth are small, which makes it easier for them to be removed as they would be lighter than more robust teeth. It is plausible that specimens of *S. hauffianus* are misidentified due to this. However, the comparatively short snout and large orbit can be used to distinguish these species, as can the comparatively small skull in relation to body length.

Stenopterygius megacephalus Huene 1922

The diagnostic features for *S. megacephalus* are: teeth numerous with no tendency towards reduction in size or number. Presacral vertebrae ≥45; preflexural vertebrae ≥80. Skull long and slender with long snout (Fig. 2.15), snout ratio probably <0.70. Orbit not especially large, orbital ratio ≤0.22; snout ratio ≥0.64; premaxillary ratio >0.42. Head relatively large compared to body. Forefin not markedly elongate, aspect ratio <0.27. modest sized, total body length <3 m; skull length <500 mm.

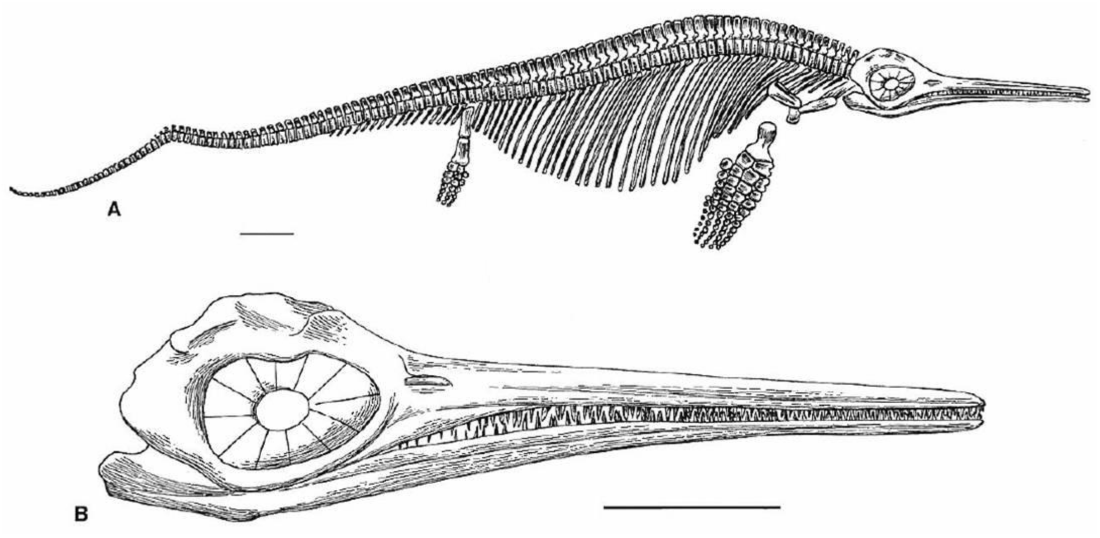


Fig. 2.15: Line drawing of a complete specimen of *Stenopterygius megacephalus* (A) and the skull (B) illustrating a long and slender snout with numerous teeth and a moderate sized orbit. From McGowan & Motani (2003). Scales measure 100 mm.

McGowan & Motani (2003) noted that this small species lacks any striking distinguishing features. However, they argued that it is can be separated from *S. quadriscissus* and *S. hauffianus* by the lack of a reduction in tooth number. It is possible that this is not a separate species and that it simply has all the teeth preserved: Maisch (1998) synonymised this species with *S. quadriscissus*. Furthermore, if the reduction in tooth number is an ontogenetic feature, than this small species could simply be an immature specimen of another species.

Stenopterygius megalorhinus Huene, 1922

The lectotype of *S. megalorhinus* is a well-preserved, complete specimen. The diagnostic features for this species are: teeth numerous with no tendency towards reduction in size or number (Fig. 2.16). Presacral vertebrae <45; preflexural vertebrae usually <80, but >75. Skull appears long and slender, with long snout; snout ratio probably <0.70, but >0.64; premaxillary ratio >0.42. Orbit not especially large, orbital ratio <0.22. Forefins elongate, distal elements probably well spaced, aspect ratio >2.7. Moderate sized, total length <3.5 m; skull length <650 mm.

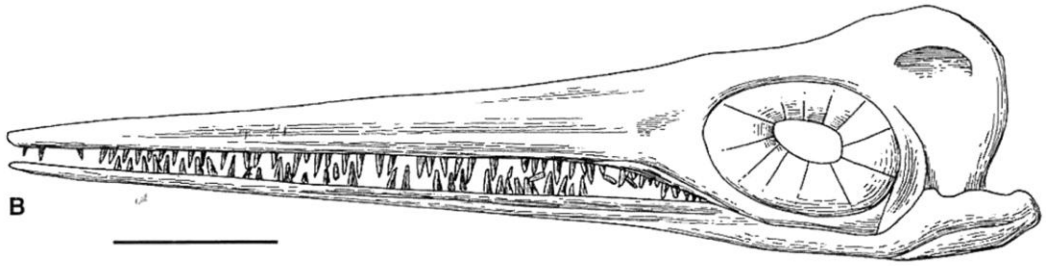


Fig. 2.16: Line drawing of the skull of *Stenopterygius megalorhinus* showing the relatively large number of teeth. From McGowan & Motani (2003). Scale measures 100 mm.

McGowan & Motani (2003) state that *S. megalorhinus* and *S. megacephalus* bear a superficial resemblance to one another due to the high tooth counts in both species. However, these two species can be differentiated based on *S. megalorhinus* having lower presacral and preflexural vertebral counts and a more elongate forefin with a higher aspect ratio.

Stenopterygius longipes Wurstemberger, 1876

The holotype of *S. longipes* is a complete but poorly preserved skeleton from which few measurements can be obtained. The diagnostic features of this species are: fins long and slender, aspect ratio of forefin >3.0. Preflexural vertebrae <75. Skull large, teeth well developed without tendency towards degeneration. Large ichthyosaurs, total length >3.5 m. Skull length >700 mm.

The most striking feature that sets *S. longipes* apart from the other species in the genus is the remarkably low preflexural vertebral count of 71. This raises the question of whether the referred specimen (SMNS 3145: McGowan, 1979), from which most of the data was gathered, was altered during preparation. Maisch (1998) suggests that this feature is an artefact. Furthermore, a forefin figured by Quenstedt (1885) is markedly long and slender with at least 30 elements in the longest of the three digits. It is also possible that this fin has been modified but this can only be verified by locating and examining the original specimen.

Stenopterygius macrophasma McGowan, 1979

The holotype of *S. macrophasma* is a complete, exceptionally preserved specimen with the soft body outline preserved as a carbonaceous film. The diagnostic characteristics of this species are: teeth numerous with no tendency towards reduction in size or number. Skull small for body size. Presacral vertebrae <45; preflexural vertebrae <80. Orbit large, orbital ratio probably >0.22; snout not markedly long, snout ratio probably <0.64; premaxillary ratio <0.42. Forefin not long, aspect ratio <2.7. moderate sized, total body length <3.5 m; skull length <650 mm and may be <500 mm.

Godefroit (1994) contends that this species should be referred to *S. quadriscissus* but McGowan & Motani (2003) refuted this suggestion based on the presence of numerous teeth in even large specimens. It is possible that this is the same species and that the teeth are simply preserved in this specimen and not in specimens referred to *S. quadriscissus*.

Stenopterygius cuneiceps

The holotype of *S. cuneiceps* McGowan, 1979 is a complete, well preserved specimen. The diagnostic characteristics for this species are: teeth numerous and of moderate size, tending towards being small. Snout abbreviated, snout ratio <0.66 (Fig. 2.17); orbit not large, orbital ratio ≤0.22. Presacral vertebrae usually ≥45; preflexural vertebrae ≤82. Forefin long and narrow, aspect ratio 0.27. tend to be large, total body length >3 m and possibly exceed 3.5 m; skull length >500 mm and often >650 mm.

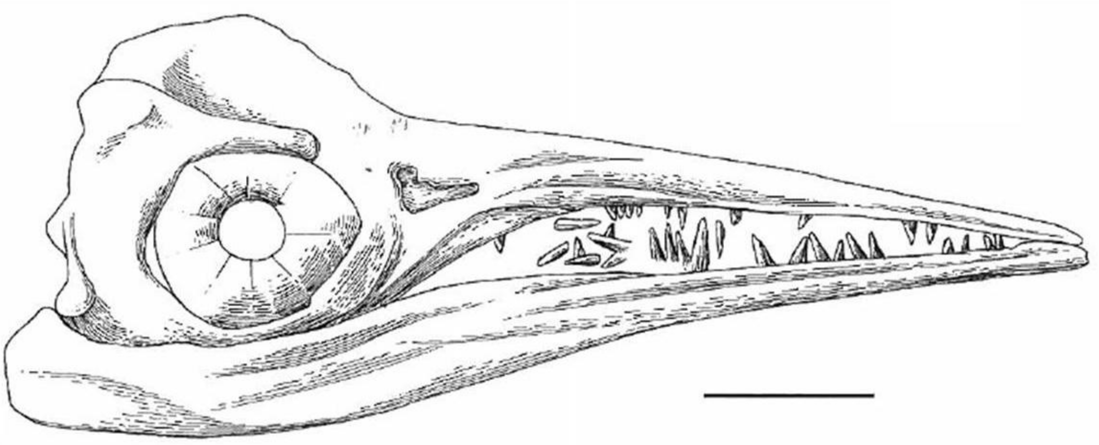


Fig. 2.17: Line drawing of the skull of *Stenopterygius cuneiceps* illustrating the extremely abbreviated snout and comparatively small teeth. From McGowan & Motani (2003). Scale measures 100 mm.

This species is similar to *S. hauffianus* in possessing a short snout and a tendency towards tooth reduction. However, it differs in having slender forefins with a high aspect ratio, often exceeding 3.0, a smaller orbit and more preflexural vertebrae. Maisch (1998) synonymised *S. cuneiceps* with *S. megalorhinus*, arguing that the skull of the holotype was compressed thus giving the illusion of having a short snout. McGowan & Motani (2003) argued that, if this were the case, the orbit and other areas of the skull would also show signs of anteroposterior compression.

Stenopterygius longifrons Owen, 1881

The holotype of *S. longifrons* is a well-preserved, three-dimensional skull, that is incomplete beyond the external naris. The diagnostic features of this species are: maxilla reaches ventral border of external naris, no contact between the frontals and postfrontals.

Owen's description of *I. longifrons* (1881) comprised a brief reference to the three-dimensional skull. The skull was also figured by Lydekker (1889) who noted similarities to *I. zetlandicus* and the two species were synonymised. Godefroit (1993) considered *S. longifrons* a separate species and gave an emended diagnosis based in part on additional materials. McGowan & Motani (2003) do not list the features provided in the emended diagnosis. McGowan & Motani (2003) stated that the new diagnostic features appear valid and the species is provisionally considered valid. The incomplete nature of the specimens referred to this species result in a lot of uncertainty in the description. No features of the postcranial skeleton are known. It is not possible to provide a more detailed description of this taxon until new material is found.

Taxonomic validity of *Stenopterygius*

The validity of *Stenopterygius* is not in doubt. There are very large numbers of exceptionally preserved specimens known from the Posidonia shales near Holzmaden, Germany. However, all of the specimens from this area are compressed and two-dimensional. Very few three-dimensional specimens are known for this genus. Despite this, the large numbers available consistently provide reliable diagnostic features.

However, there is considerable confusion in species identifications. McGowan & Motani (2003) considered eight species valid. However, the primary diagnostic features for some of these species are based on tooth numbers, which are notoriously variable. The key difference between *S. quadriscissus* and *S. hauffianus* is that *S. hauffianus* always retains teeth. It is entirely plausible that a specimen could lose the teeth as a result of malnutrition, illness, or as a result of taphonomic processes after death. In this instance, this specimen would be identified as *S. quadriscissus*. The opposite is true of *S. quadriscissus* where a specimen could be preserved with teeth leading it to be identified as *S. hauffianus*. The teeth in ichthyosaurs are typically set in a dental groove and only held in place by soft tissue. The number, or complete lack of teeth, is an unreliable feature and should not be used exclusively to distinguish between two otherwise very similar species. Maxwell (2012) re-examined *Stenopterygius* and summarised the conclusions made by several previous authors. Huene (1922, 1931, 1939, 1949), over the course of his career, considered 11 species to be valid while McGowan (1979) and McGowan & Motani (2003) considered eight species to be valid. Conversely, Godefroit (1994) only considered three species valid while Maisch (2008) considered four species valid. Maxwell (2012) concluded that only three valid species were known from the Posidonia shale (see Chapter 6, section 6.5.2 for full discussion). Due to the levels of uncertainty in taxonomic assignments at the specific level, it is recommended that *Stenopterygius* is examined at the generic level.

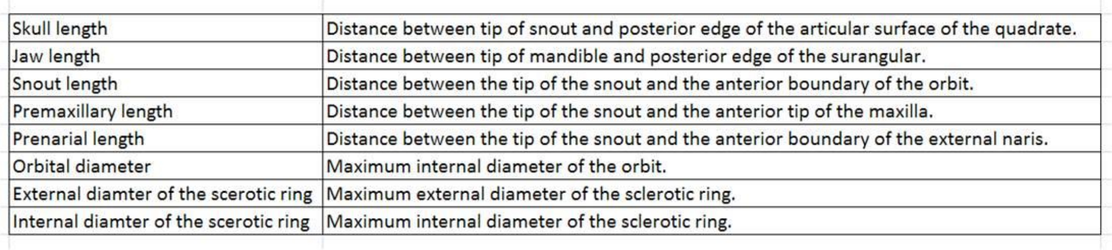
2.2.4: Key implications for the thesis

Uncertainties in the strength of the diagnoses have been noted frequently in section 2.2.3 and it has been suggested that the taxa should be considered reliable only at the generic level. Furthermore, no single species in the dataset contains enough specimens for a reliable analysis to be conducted. Therefore, the specimens will be analysed at the generic level, despite the possibility for interspecific variation to potentially influence the results. Larger numbers of a single species are required before studies into ontogeny and sexual dimorphism can be conducted. *Stenopterygius* is the most well represented genus, and analyses will be conducted on this genus alone as well as on the complete dataset.

2.3: MORPHOMETRIC DATA

Linear measurements were taken from many bones and parts of the body throughout the skeleton (Table 2.1). Images showing measurements taken are given in chapter 3. The measurements were defined with specific points in order to be easily repeatable and to limit error. Some elements could not be measured even though present on the specimen, for example if broken or obscured by overlapping bones. If two measurements were available on the same specimen (e.g., if both humeri are visible in one specimen) then both measurements are taken and the average is used in the analysis.

The PAST (Palaeontological Statistics) programme (Hammer and Harper, 2006) was used for all of the statistical tests outlined in this chapter.



Skull length	Distance between tip of snout and posterior edge of the articular surface of the quadrate.
Jaw length	Distance between tip of mandible and posterior edge of the surangular.
Snout length	Distance between the tip of the snout and the anterior boundary of the orbit.
Premaxillary length	Distance between the tip of the snout and the anterior tip of the maxilla.
Prenarial length	Distance between the tip of the snout and the anterior boundary of the external naris.
Orbital diameter	Maximum internal diameter of the orbit.
External diamter of the scerotic ring	Maximum external diameter of the sclerotic ring.
Internal diamter of the scerotic ring	Maximum internal diameter of the sclerotic ring.

Table 2.1: Skull measurements and definitions. All from McGowan & Motani (2003) except sclerotic ring measurements defined by the author

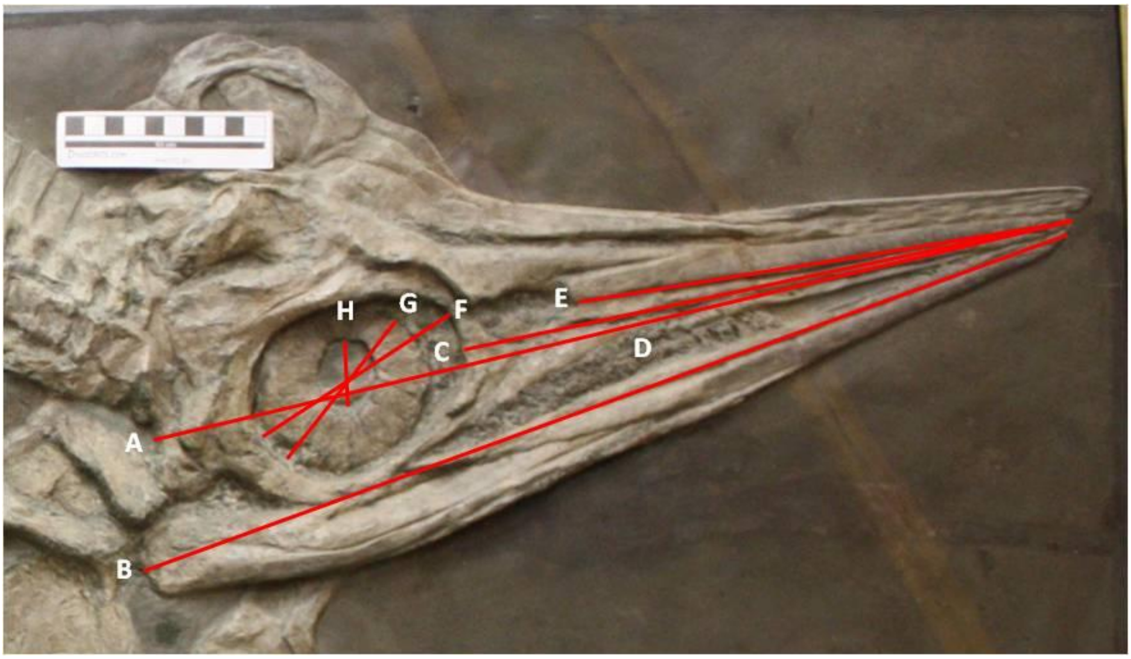
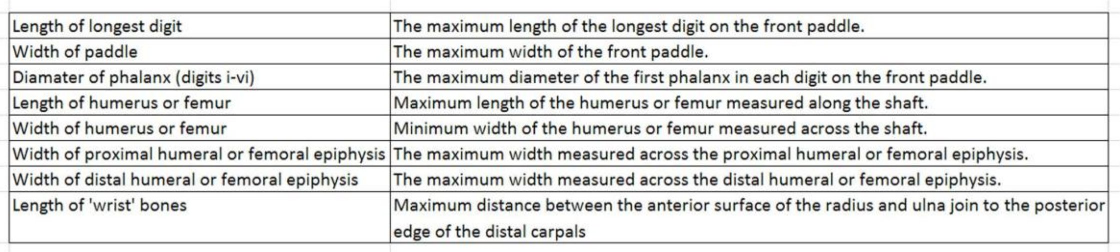


Fig. 2.18: Illustration of the skull measurements. A, Skull length; B, Jaw length; C, Snout length; D, Premaxillary length; E, Prenarial length; F, Orbital diameter; G, external diameter of the sclerotic ring; H, internal diameter of the sclerotic ring. Scale measures 10 cm.



Length of longest digit	The maximum length of the longest digit on the front paddle.
Width of paddle	The maximum width of the front paddle.
Diamater of phalanx (digits i-vi)	The maximum diameter of the first phalanx in each digit on the front paddle.
Length of humerus or femur	Maximum length of the humerus or femur measured along the shaft.
Width of humerus or femur	Minimum width of the humerus or femur measured across the shaft.
Width of proximal humeral or femoral epiphysis	The maximum width measured across the proximal humeral or femoral epiphysis.
Width of distal humeral or femoral epiphysis	The maximum width measured across the distal humeral or femoral epiphysis.
Length of 'wrist' bones	Maximum distance between the anterior surface of the radius and ulna join to the posterior edge of the distal carpals

Table 2.2: Limb measurements and definitions. All measurements defined by the author.

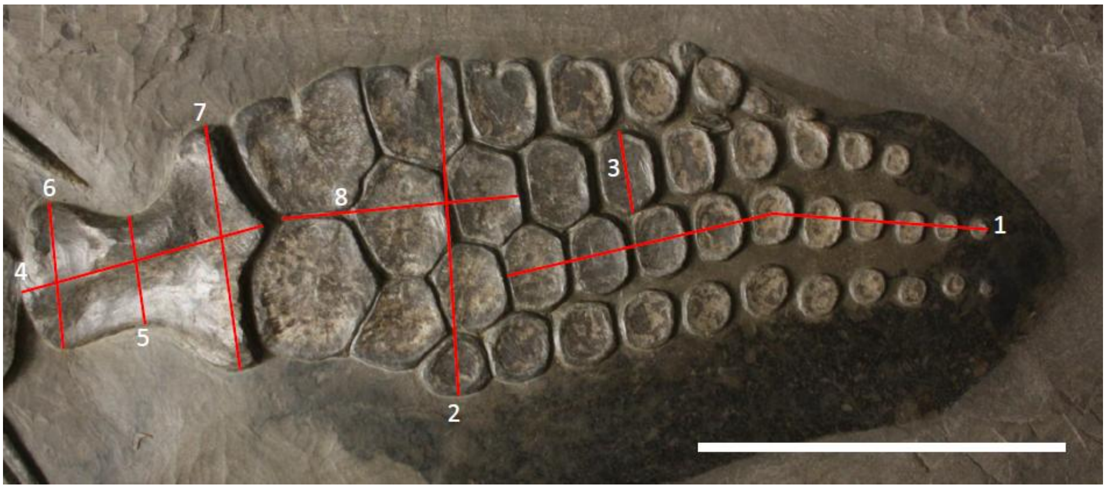


Fig. 2.19: Illustration of the limb measurements: 1, length of longest digit; 2, width of manus; 3, diameter of phalange; 4, length of humerus; 5, width of humerus; 6, width of proximal epiphysis; 7, width of distal epiphysis; 8, length of 'wrist' bones. Scale measures 10cm.

2.4: MERISTIC (COUNTED) DATA

Several repeated elements within the body are counted in order to see if these numbers increase or decrease with age, if at all. The elements counted are; (i) the total number of vertebrae; (ii) the number of presacral (those lying posterior to the posterior most part of the femur) vertebrae; (iii) the number of dorsal vertebrae; (iv) the number of preflexural vertebrae; (v) the number of postflexural vertebrae; (vi) the number of dorsal vertebrae; (vii) number of digits in the front limb; (viii) number of phalanges in the longest digit; (ix) the number of digits in the hind limb; (x) the number of phalanges in the longest digit on the hind limb.

These skeletal elements were selected as they are well represented in the fossil record. Furthermore, using meristic counts of these elements for ontogenetic research has not previously been attempted. Currently, it is not known if these skeletal elements change with ontogeny. This project will show if the elements can be used as ontogenetic markers.

2.5: MULTIVARIATE ANALYSIS

2.5.1: Principal Components Analysis (PCA)

The purpose of the Principal Component Analysis is to reduce a multivariate dataset into fewer dimensions by identifying sets of co-varying variables and using these new combination variables to define new axes of variation, thereby representing the original variation in many fewer axes. The axes of maximum variance (principal components) can then be examined and possibly interpreted biologically (Hammer & Harper, 2006). The data that is required for this is any multivariate dataset. The PCA is an exploratory technique that does not make any statistical assumptions but it will usually give more useful results for a dataset with a normal distribution (Hammer & Harper, 2006). This analysis requires linear data to be log-transformed. The data is transformed into natural logarithms to treat for the large size range within the data.

The procedure finds variables (components) that account for all of the variance in the dataset. The axis that accounts for the largest percentage of variation will become Principal Component 1 (PC1). The first principal component corresponds to a line that passes through the multidimensional mean and minimizes the sum of squares of the distances of the points from the line. PC2 will account for the axis that shows the second highest percentage of variation within the dataset and so on until all the variation is accounted for. The combination of axes that account for 95% of the variation within the data will be studied.

The first stage of PCA is to normalise the data. The dimension with the largest spread will appear to have the most variance. By normalising the data, this bias is removed. The formula for normalising the data is

$$X_i = \frac{x_i - \bar{x}}{\sigma}$$

Where X_i is the normalised data, x_i is the original data, $\bar{x}$ is the mean of the original data and σ is the standard deviation of the original data.

The next step of PCA is to calculate the variance or covariance of the normalised data. This is then captured in a matrix. For example, if you were deriving a covariance matrix comparing three variables then you would have three dimensions (x, y and z). Therefore, the covariance would work out cov[x, y], cov[x, z] and cov[y, z]. The formula for the covariance is

$$\text{Covariance} = \tfrac{1}{N-1}\sum_{i=1}^{N}(y_i - \bar{y})(x_i - \bar{x})$$

The covariance matrix would be

$$C = \begin{pmatrix} \operatorname{cov}(x,x) & \operatorname{cov}(y,x) & \operatorname{cov}(z,x) \\ \operatorname{cov}(x,y) & \operatorname{cov}(y,y) & \operatorname{cov}(z,y) \\ \operatorname{cov}(x,z) & \operatorname{cov}(y,z) & \operatorname{cov}(z,z) \end{pmatrix}$$

From the correlation matrix, the eigenvalues and eigenvectors can be established as shown below

$$\begin{pmatrix} \operatorname{cov}(x,x) & \operatorname{cov}(y,x) & \operatorname{cov}(z,x) \\ \operatorname{cov}(x,y) & \operatorname{cov}(y,y) & \operatorname{cov}(z,y) \\ \operatorname{cov}(x,z) & \operatorname{cov}(y,z) & \operatorname{cov}(z,z) \end{pmatrix}\begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} = n\begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix}$$

Where the cov values show the covariance matrix, the x values show the Eigenvectors and n represents the eigenvalue (Fig. 2.20).

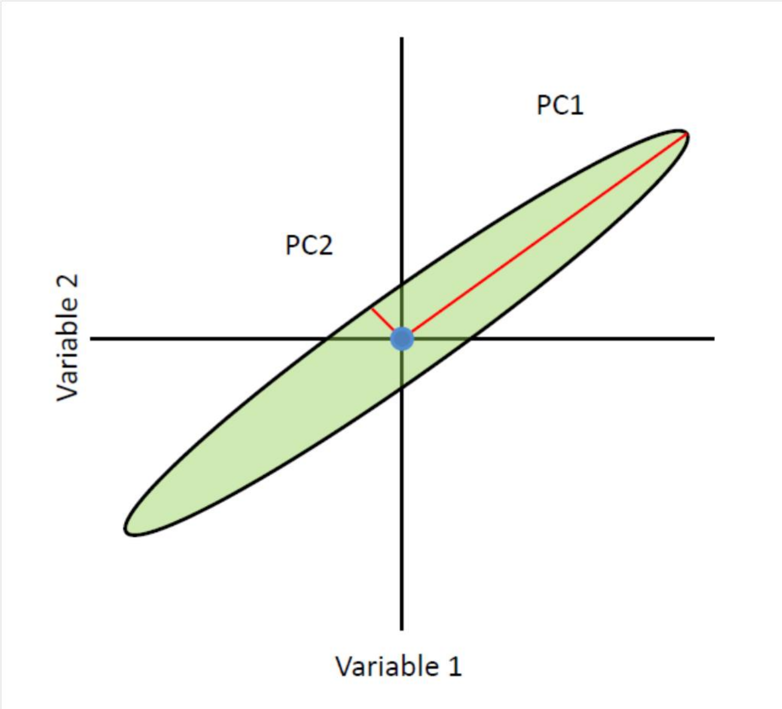


Fig. 2.20: A hypothetical PCA showing the cluster related to the original variables. The green oval represents the cluster of data points with the red lines showing the Eigenvalues. (Modified from MacLeod, pers. comm. 2013)

The eigenvalue is the length of a Principal Component from the edge of the cluster to the mean. The percentage that each variable contributes to the total variance is calculated using the Eigenvalues. Furthermore, Eigenvectors can also be calculated. Eigenvectors are gained from the angles of the Principal Components compared to the original variables. The angles will show which variable the Principal Components lie closest to thus indicating what is causing the variance within each component. From this, loadings can be created. The loadings show how much each variable contributes to the overall variance within the dataset on a single principal component. The loading value can be compared to a calculated number called the isometric scaling coefficient. This value represents isometry. This is calculated using the equation;

$$1/p^{0.5}$$

where p is the number of variables used. This calculated figure is the number that represents isometric growth. Any number that deviates from the isometric scaling coefficient indicates allometric growth, with higher numbers demonstrating positive allometry and lower numbers representing negative allometry. This only applies to PC1. PC1 typically represents size-related shape change, i.e. allometry.

The next step with PCA is to rotate the scatter so that PC1 and PC2 become the new x and y axes. This new graph can then be used to help identify correlations and groupings that would otherwise not be observed within the dataset.

PCA was used to test individual skeletal elements as well as composite body parts. The individual skeletal elements that were selected for this analysis are the humerus and femur. These skeletal elements were selected as they are well represented in the fossil record. Furthermore, the measurements of the individual elements (length, width, width of proximal epiphysis, width of distal epiphysis) can still be measured even if the elements have been moved from life position. The composite body part selected for the PCA is the skull. The skull was selected as skull ratios are typically used to differentiate between different genera and species (McGowan & Motani, 2003). This suggests that growth and shape of the skull vary between ichthyosaurs taxa and hence this aspect was investigated. All data entered into the PCA is log transformed. This creates a linear relationship of the data when plotted in Cartesian space (unlogged data would form a curved line in Cartesian space). Furthermore, the log transformed data reduces the size range commonly associated with biological data.

PCA has a number of advantages. To begin with, this is a descriptive and exploratory method. This is because the axes are changed in a PCA and therefore do not represent the data. The use of this method can give a good idea of where growth appears to be isometric and where it appears to be allometric. This information can be used to identify areas for further exploration using other statistical methods. Furthermore, it also provides an opportunity to identify what features from that data are causing the most amount of variance.

However, this method does also have some drawbacks. PCA does not explicitly test hypotheses and must be followed up using additional statistical tests. Therefore, other statistical methods must be used to provide viable results while the PCA can only be used in support of these other methods. Another negative aspect of PCA is that is that it cannot take into account absent data. All measurements in the dataset must be present in order for a specimen to be used in an analysis. Due to the nature of the fossil record, it is not always possible to obtain all the measurements. Therefore, the number of specimens used in an analysis can be greatly reduced from the number of all possible specimens available.

PCA has been used by a number of authors to analyses the ontogeny of a number of different organisms. Vincent *et*. *al*. (2004) used PCA to analyse the ontogeny of head shape in pit vipers. PCA has been used to analyse the ontogeny of foraminifera (Wei *et*. *al*., 1992) as well as for fossil reptiles such as Pachypleurosaurs (O'Keefe *et*. *al*. 1999) and in Neanderthals and modern humans (Bastir *et*. *al*., 2007).

2.5.2: Principal Coordinate Analysis (PCO)

The purpose of the Principal Coordinate Analysis (also known as metric multidimensional scaling) is to project a multivariate dataset into two or three dimensions, in order to visualise groupings. The method also preserves distances between data points as given by any distance measure. This method can use any type of multivariate data. This analysis requires the linear data to be log-transformed. The raw data is transformed to natural logarithms to treat for log-linear relationships common in biological data with large size ranges, while maintaining the differences in size and shape.

The logic for the positioning of the points on the plot is that the Euclidean distances in low-dimensional space should reflect the original distances as measured in the multi-dimensional space (Hammer & Harper, 2006). This means that specimens that are similar should plot closely together. Therefore, if smaller specimens plot separate from larger specimens, allometric growth is indicated. However, if there are no groupings, or if the groupings reflect genera, then isometric growth is indicated.

As with PCA, each principal coordinate axis has associated with it an eigenvalue which indicates the amount of variation in the data explained by that axis. Similar to PCA this is a positive aspect of this analysis. The eigenvalue indicating the amount of variation provides an insight as to what feature is causing the majority of the variation within the dataset. This then provides specific points of interest for further analysis. Furthermore, unlike PCA, PCO can account for absent data. This can increase the number of specimens that can be used in the analysis, which in turn creates more reliable results.

However, one drawback of PCO is that some distance measures can produce negative eigenvalues. These negative eigenvalues are usually connected with the least important PCO axis and can be disregarded (Hammer & Harper, 2006). In some cases, large negative eigenvalues can be created and if this occurs then the dataset should be considered suspect.

2.5.3: Reduced Major Axis Regression (RMA)

Reduced Major Axis regression is used in morphometrics to test the fit of a bivariate dataset to a straight line, or linear model (Hammer and Harper, 2006). Although this method can be used on any bivariate dataset, it does however make some assumptions about the data. It assumes that the data is independently collected, and therefore, the errors within the data are normally distributed. It also assumes that the variance of the error does not vary systematically with any of the variates (Hammer and Harper, 2006). This analysis requires the data to be log-transformed. The data is log-transformed to account for the large size range within the dataset.

In RMA, it is assumed that the data on the both the *x* and the *y* axes is collected in the same way, and therefore contains the same errors. Therefore, the data on the *x* and *y* axis are treated in a symmetrical fashion. RMA is used for the morphometric analysis (Chapter 3) as the data on both axes are length or width measurements, which were measured in the same way. This analysis will determine if growth is isometric or allometric which can be tested for statistical significance.

The Model I regression of RMA is used for the meristic data (Chapter 4) as the data on the axis are obtained in a different way. In this case, measurements are compared to counts of repeated elements (e.g. vertebrae, phalanges etc.). In this case, the counts are known exactly and the error will be contained within the measured data.

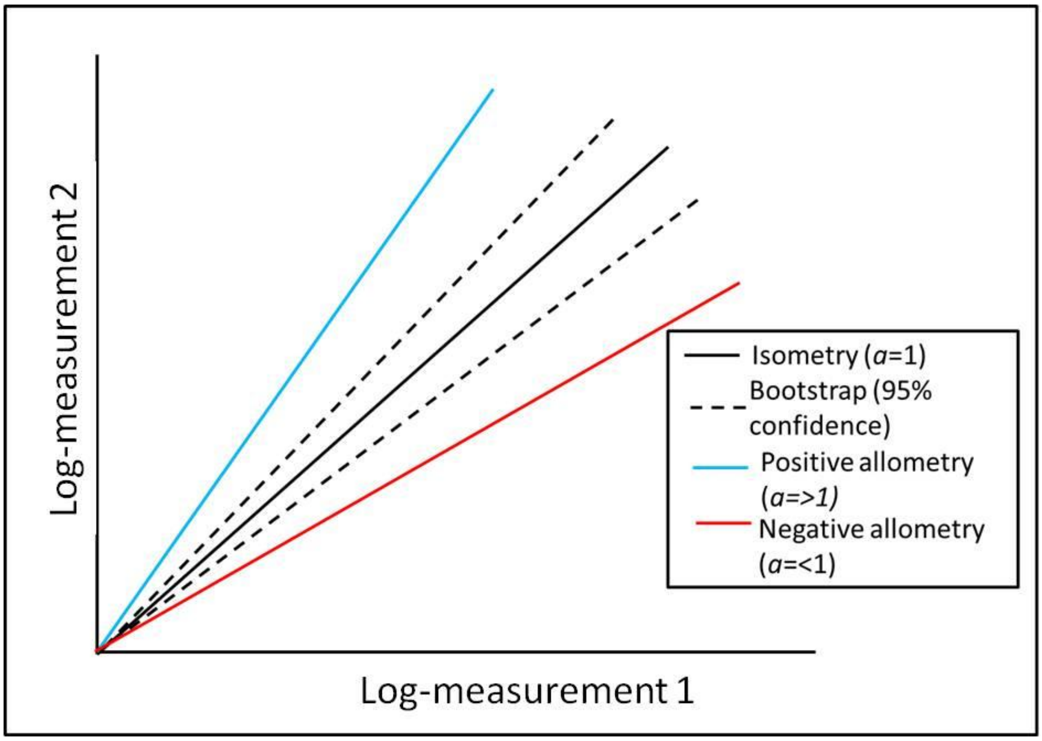


Fig. 2.21: Theoretical illustration of positive and negative allometry and isometry with the 95% confidence intervals from the Bootstrap test

The RMA is a very useful test and was selected as it is very quick and easy to get clear, statistically significant results. Any bivariate dataset can be applied in order to investigate any relationship to see if growth is allometric or isometric. Bootstrap and the Pearson's R Correlation are used in conjunction with this technique as this will increase the ability to statistically assess the results.

2.5.3.1: Bootstrap Test

The Bootstrap test is used to estimate 95% confidence interval for the mean. The mean is represented by the *a* value, which is also the value for the line (slope of the line of best fit) which is automatically created by the PAST programme (Hammer & Harper, 2006). This confidence interval shows that there is a 95% chance that *a* will lie between the two points created by this technique. This can be used to indicate isometric or allometric growth. Isometric growth is where *a* is equal to one. Therefore, if a Bootstrap test displays a result of 0.95-1.05, then isometric growth is indicated. However, if both of the Bootstrap figures are above or below one, then positive or negative allometric growth are indicated respectively

(Fig 2.21). This is a very useful method for testing the deviation from the mean, and therefore is used in this project.

2.5.3.2: Pearson's R Correlation

Pearson's R Correlation measures the correlation (linear dependence) between two variables. The results are always between -1 and 1. A value of -1 indicates a strong negative relationship while a value of 1 indicates a strong positive relationship. A value of 0 would indicate no relationship at all between the variables under study. Pearson's R Correlation therefore is used to strengthen and support the results of the RMA, as the *r* value proves or disproves a relationship between two variables, thereby showing the results for the RMA are not coincidental. For this reason it has been selected for use in this project.

2.5.3.3: Discriminant Analysis

The purpose of this analysis is to project a multivariate dataset into one dimension in a way that maximises the separation between two *a priori* determined groups. The axis of maximal separation (discriminant axis) can be examined in order to establish the main difference between the two groups (Fig. 2.22).

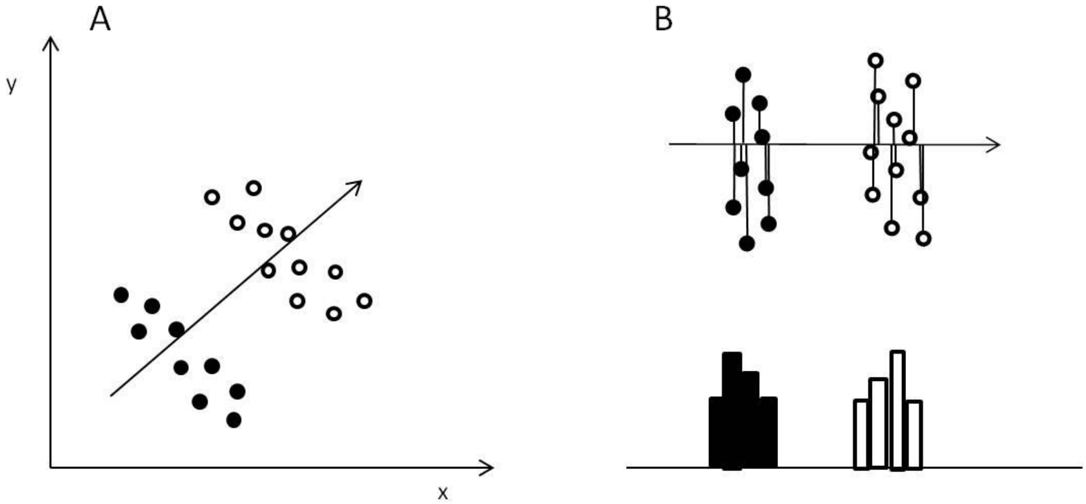


Fig. 2.22: Discriminant analysis with variables *x* and *y*. (A) The data points are plotted in the coordinate system spanned by the original variables. The discriminant axis (arrow) is the direction along which separation between the two predetermined groups is maximised. (B) The datasets are projected onto the discriminant axis, which creates the histogram (modified from Hammer & Harper, 2006).

For this project the groups are defined as pregnant specimens and non-pregnant specimens. It is possible that the discriminant analysis could highlight anatomical differences other than those relating to sexual dimorphism, such as ontogenetic or taxonomic differences. In order to reduce the chance of taxonomic features being highlighted by the analysis, a single genus (*Stenopterygius*) was selected. Furthermore, in order to be able to reasonably infer sexual maturity, any specimen smaller than the smallest pregnant specimen has been excluded from the analyses. Additional discriminant analyses were performed on all specimens of *Stenopterygius* as there is a possibility that sexually mature males are smaller than females and would otherwise have been excluded from the analysis. The formula for discriminant analysis is given below (Hammer & Harper, 2010).

If A is the matrix of observations on group A, with n_A observations in rows and variates in columns. Similarly, B is the matrix of observations on group B. Define the matrices S^A and S^B as:

$$\mathrm{S}_{jk}^{\mathrm{A}} = \sum_{i=1}^{n_\mathrm{A}} \mathrm{A}_{ij}\,\mathrm{A}_{ik} - \frac{\sum_{i=1}^{n_\mathrm{A}} \mathrm{A}_{ij} \sum_{i=1}^{n_\mathrm{A}} \mathrm{A}_{ik}}{n_\mathrm{A}}$$

$$\mathrm{S}_{jk}^{\mathrm{B}} = \sum_{i=1}^{n_{\mathrm{B}}} \mathrm{B}_{ij}\,\mathrm{B}_{ik} - \frac{\sum_{i=1}^{n_{\mathrm{B}}} \mathrm{B}_{ij} \sum_{i=1}^{n_{\mathrm{B}}} \mathrm{B}_{ik}}{n_{\mathrm{B}}}$$

Then the matrix S of pooled variance-covariance is created:

$$\mathrm{S} = \frac{\mathrm{S}^{\mathrm{A}} + \mathrm{S}^{\mathrm{B}}}{n_A + n_{\mathrm{B}} - 2}$$

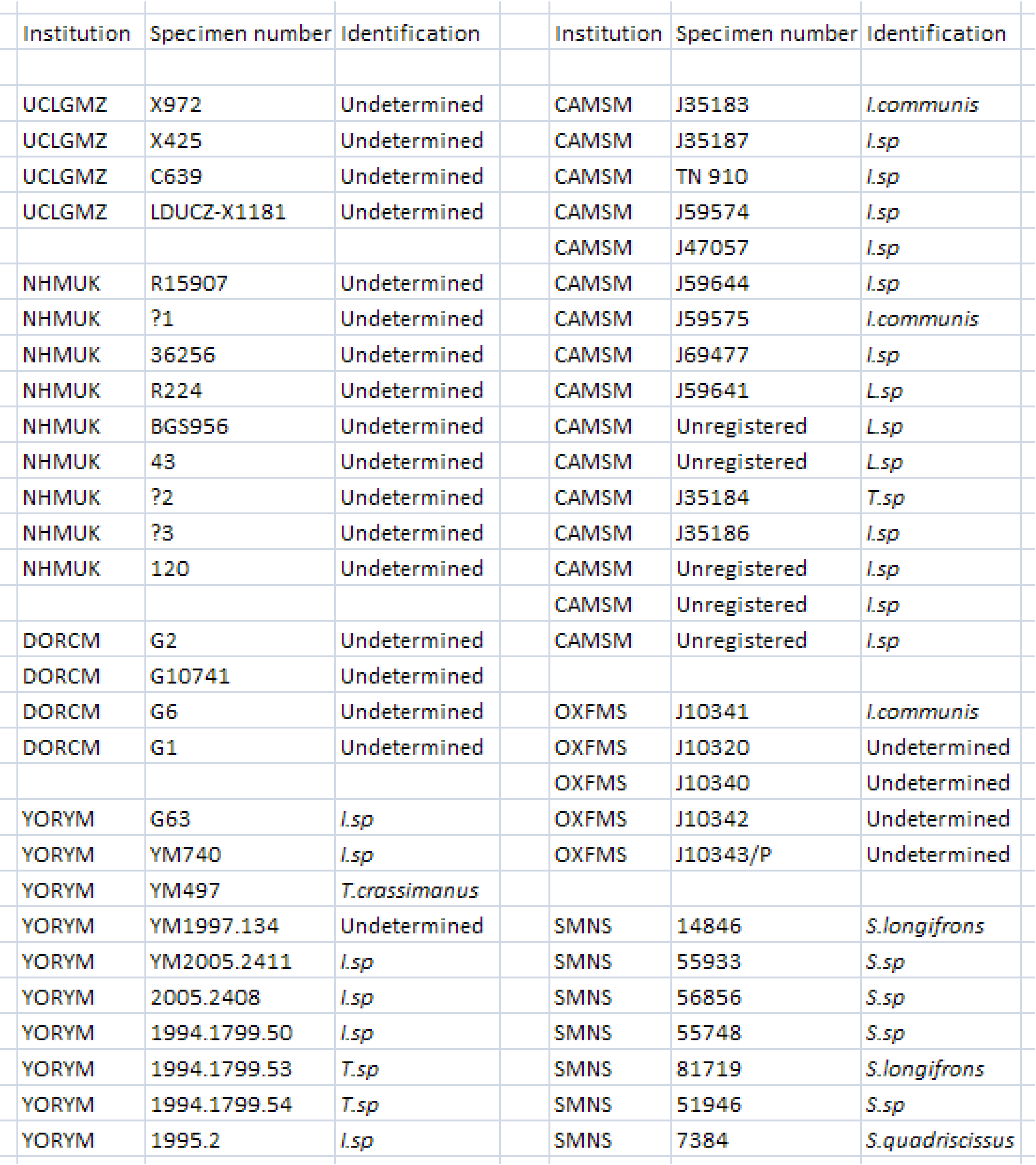
If g is the vector of differences between the means of each variate:

$$\mathrm{g}_i = \frac{\sum_i A_{\mathrm{ij}}}{n_{\mathrm{A}}} - \frac{\sum_i B_{ij}}{n_B}$$

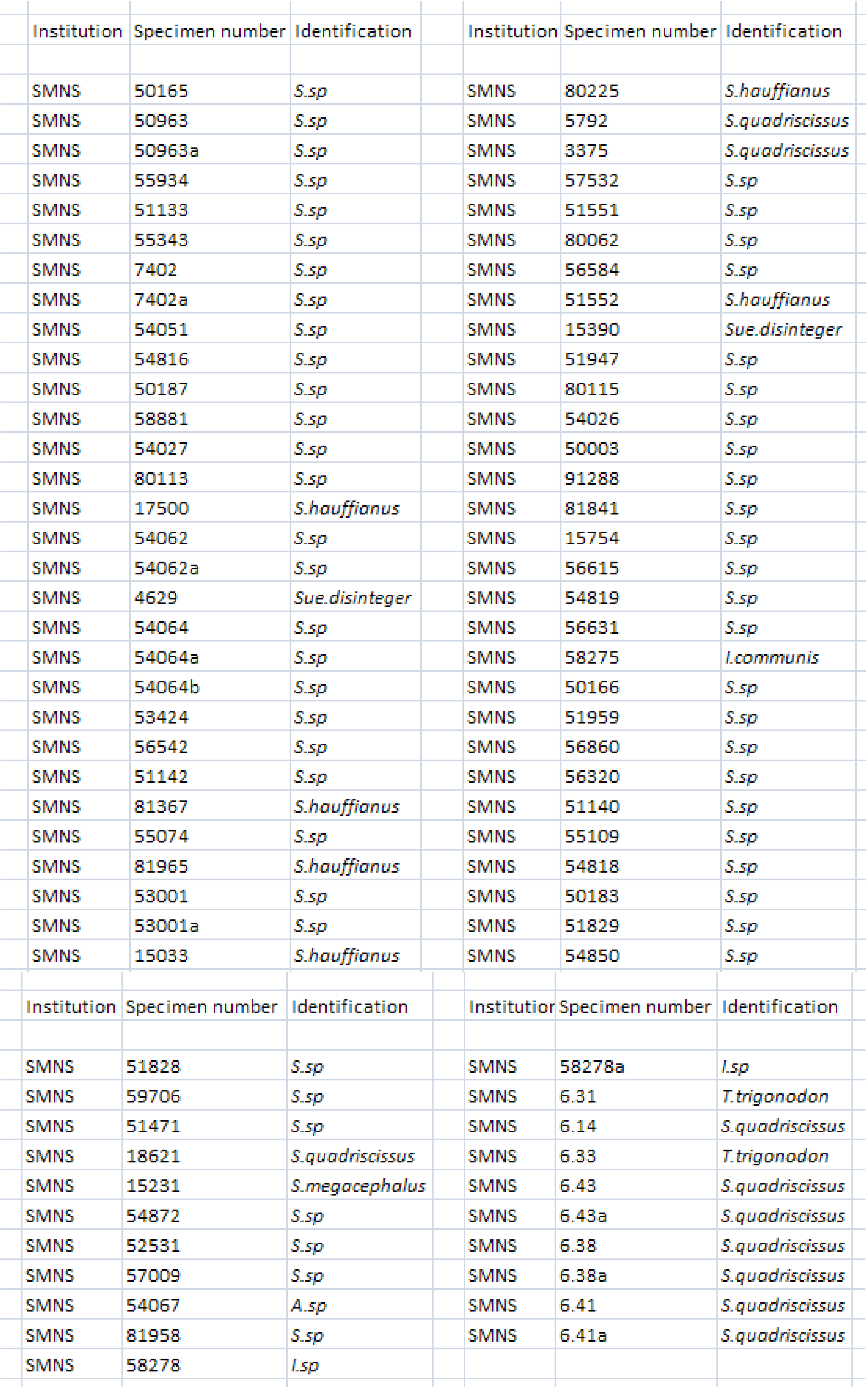
Then the coefficient of the (linear) discriminant function are now given by:

$$\mathrm{d} = \mathrm{S}^{-1}\mathrm{g}$$

Discriminant analysis is a commonly used technique and has previously been implemented in the study of sexual dimorphism by several authors (Butler *et al.*, 2007; Kaliontzopoulou *et al.*, 2007).



Institution	Specimen number	Identification	Institution	Specimen number	Identification
UCLGMZ	X972	Undetermined	CAMSM	J35183	*I.communis*
UCLGMZ	X425	Undetermined	CAMSM	J35187	*I.sp*
UCLGMZ	C639	Undetermined	CAMSM	TN 910	*I.sp*
UCLGMZ	LDUCZ-X1181	Undetermined	CAMSM	J59574	*I.sp*
			CAMSM	J47057	*I.sp*
NHMUK	R15907	Undetermined	CAMSM	J59644	*I.sp*
NHMUK	?1	Undetermined	CAMSM	J59575	*I.communis*
NHMUK	36256	Undetermined	CAMSM	J69477	*I.sp*
NHMUK	R224	Undetermined	CAMSM	J59641	*L.sp*
NHMUK	BGS956	Undetermined	CAMSM	Unregistered	*L.sp*
NHMUK	43	Undetermined	CAMSM	Unregistered	*L.sp*
NHMUK	?2	Undetermined	CAMSM	J35184	*T.sp*
NHMUK	?3	Undetermined	CAMSM	J35186	*I.sp*
NHMUK	120	Undetermined	CAMSM	Unregistered	*I.sp*
			CAMSM	Unregistered	*I.sp*
DORCM	G2	Undetermined	CAMSM	Unregistered	*I.sp*
DORCM	G10741	Undetermined			
DORCM	G6	Undetermined	OXFMS	J10341	*I.communis*
DORCM	G1	Undetermined	OXFMS	J10320	Undetermined
			OXFMS	J10340	Undetermined
YORYM	G63	*I.sp*	OXFMS	J10342	Undetermined
YORYM	YM740	*I.sp*	OXFMS	J10343/P	Undetermined
YORYM	YM497	*T.crassimanus*			
YORYM	YM1997.134	Undetermined	SMNS	14846	*S.longifrons*
YORYM	YM2005.2411	*I.sp*	SMNS	55933	*S.sp*
YORYM	2005.2408	*I.sp*	SMNS	56856	*S.sp*
YORYM	1994.1799.50	*I.sp*	SMNS	55748	*S.sp*
YORYM	1994.1799.53	*T.sp*	SMNS	81719	*S.longifrons*
YORYM	1994.1799.54	*T.sp*	SMNS	51946	*S.sp*
YORYM	1995.2	*I.sp*	SMNS	7384	*S.quadriscissus*



Institution	Specimen number	Identification	Institution	Specimen number	Identification
SMNS	50165	*S.sp*	SMNS	80225	*S.hauffianus*
SMNS	50963	*S.sp*	SMNS	5792	*S.quadriscissus*
SMNS	50963a	*S.sp*	SMNS	3375	*S.quadriscissus*
SMNS	55934	*S.sp*	SMNS	57532	*S.sp*
SMNS	51133	*S.sp*	SMNS	51551	*S.sp*
SMNS	55343	*S.sp*	SMNS	80062	*S.sp*
SMNS	7402	*S.sp*	SMNS	56584	*S.sp*
SMNS	7402a	*S.sp*	SMNS	51552	*S.hauffianus*
SMNS	54051	*S.sp*	SMNS	15390	*Sue.disinteger*
SMNS	54816	*S.sp*	SMNS	51947	*S.sp*
SMNS	50187	*S.sp*	SMNS	80115	*S.sp*
SMNS	58881	*S.sp*	SMNS	54026	*S.sp*
SMNS	54027	*S.sp*	SMNS	50003	*S.sp*
SMNS	80113	*S.sp*	SMNS	91288	*S.sp*
SMNS	17500	*S.hauffianus*	SMNS	81841	*S.sp*
SMNS	54062	*S.sp*	SMNS	15754	*S.sp*
SMNS	54062a	*S.sp*	SMNS	56615	*S.sp*
SMNS	4629	*Sue.disinteger*	SMNS	54819	*S.sp*
SMNS	54064	*S.sp*	SMNS	56631	*S.sp*
SMNS	54064a	*S.sp*	SMNS	58275	*I.communis*
SMNS	54064b	*S.sp*	SMNS	50166	*S.sp*
SMNS	53424	*S.sp*	SMNS	51959	*S.sp*
SMNS	56542	*S.sp*	SMNS	56860	*S.sp*
SMNS	51142	*S.sp*	SMNS	56320	*S.sp*
SMNS	81367	*S.hauffianus*	SMNS	51140	*S.sp*
SMNS	55074	*S.sp*	SMNS	55109	*S.sp*
SMNS	81965	*S.hauffianus*	SMNS	54818	*S.sp*
SMNS	53001	*S.sp*	SMNS	50183	*S.sp*
SMNS	53001a	*S.sp*	SMNS	51829	*S.sp*
SMNS	15033	*S.hauffianus*	SMNS	54850	*S.sp*

Institution	Specimen number	Identification	Institutior	Specimen number	Identification
SMNS	51828	*S.sp*	SMNS	58278a	*I.sp*
SMNS	59706	*S.sp*	SMNS	6.31	*T.trigonodon*
SMNS	51471	*S.sp*	SMNS	6.14	*S.quadriscissus*
SMNS	18621	*S.quadriscissus*	SMNS	6.33	*T.trigonodon*
SMNS	15231	*S.megacephalus*	SMNS	6.43	*S.quadriscissus*
SMNS	54872	*S.sp*	SMNS	6.43a	*S.quadriscissus*
SMNS	52531	*S.sp*	SMNS	6.38	*S.quadriscissus*
SMNS	57009	*S.sp*	SMNS	6.38a	*S.quadriscissus*
SMNS	54067	*A.sp*	SMNS	6.41	*S.quadriscissus*
SMNS	81958	*S.sp*	SMNS	6.41a	*S.quadriscissus*
SMNS	58278	*I.sp*			

Table 2.3: List of taxa used in the study with identification where known. A = *Aegirosaurus*; I = *Ichthyosaurus*; L = *Leptonectes*; S = *Stenopterygius*; sp = unknown species; Sue = *Suevoleviathan*; T = *Temnodontosaurus*.

3: INVESTIGATING ICHTHYOSAUR GROWTH: A MORPHOMETRIC APPROACH

3.1: OVERVIEW

In order to gain an understanding of any organisms, it is important to understand their ontogeny. Inferred neonate or juvenile ichthyosaurs can differ significantly in shape and morphology from inferred adults (McGowan, 1979). One example of this is the distinct upturned rostrum in juvenile *T. platydon* (McGowan, 1995). This change of appearance or shape is important to understand as ignoring ontogeny can lead to taxonomic mistakes where new species are created for ontogenetic variants of the same taxon (McGowan, 1995). Errors such as this can affect future studies in palaeogeography, phylogeny, diversity etc. Ichthyosaur ontogeny is not well known, with the vast majority of references to ontogeny in the literature being unsupported and anecdotal. Bone fusion, or closure of sutures has typically been used to identify relative ages in other Mesozoic marine reptiles (Irmis, 2007; Kear, 2007; Bardet *et al.*, 2008) but this is not possible for ichthyosaurs as their bones do not typically fuse during ontogeny. (See more details in Chapter 1). Therefore, this chapter approaches the issue of ichthyosaur ontogeny with a morphometric approach. Morphometrics uses statistical techniques to analyse changes in the size and shapes of organisms. This approach will be used to determine types of growth and create ratios between the sizes of various skeletal elements on composite body parts. These can then be used to establish markers for the identification of relative ages in ichthyosaur taxa.

Three main statistical methods are used herein to investigate the allometric scaling relationships between the proportions of various individual skeletal elements, composite body parts such as the limbs, and their relationships to each other. The multivariate methods used for the analysis are Principal Components Analysis (PCA) and Principal Coordinate Analysis (PCO). The bivariate methods used are Reduced Major Axis regression (RMA) with Bootstrap tests and Pearson's R Correlation. A Bootstrap test is used to create a 95% confidence interval for the line of best fit (α). This is used to test the deviation from an allometric coefficient of 1.0 (a coefficient of 1.0 showing isometric growth), while the Person's R Correlation is used to test the strength of the relationship between the two variables in the RMA test. The techniques applied are described, with references to the literature, in (Chapter 2).

3.2: DEFINITIONS: ONTOGENY, HETEROCHRONY AND ALLOMETRY

Heterochrony and allometry are important processes to consider when looking at the development of an organism. Allometry relates to changes in proportions of the body while heterochrony relates to changes in the timing of development.

Heterochrony and allometry are processes that have been studied in detail (e.g. Gould, 1977). Heterochrony can be defined as change in the timing of the onset and duration of development of a particular feature relative to that occurring in the ancestor or closest relative of the taxon of interest (Alberch *et al.,* 1979; Klingenberg, 1998; McNamara, 2012). Heterochrony takes the form of both increased and decreased degrees of development known as “peramorphosis” and “paedomorphosis” respectively. Peramorphosis and paedomorphosis are consequences of processes that change the duration of the period of an individual’s (or an individual feature’s) growth, either starting it or stopping it earlier or later or speeding up or slowing down compared to the ancestor. Human evolution was fuelled by heterochrony, with some traits, such as a large brain, being peramorphic, while other traits, such as a reduced jaw size are paedomorphic (McNamara, 2012). However, peramorphosis and paedomorphosis are not evolutionary processes themselves but are descriptive terms. They can each be produced by various heterochronic processes (Fig. 3.1).

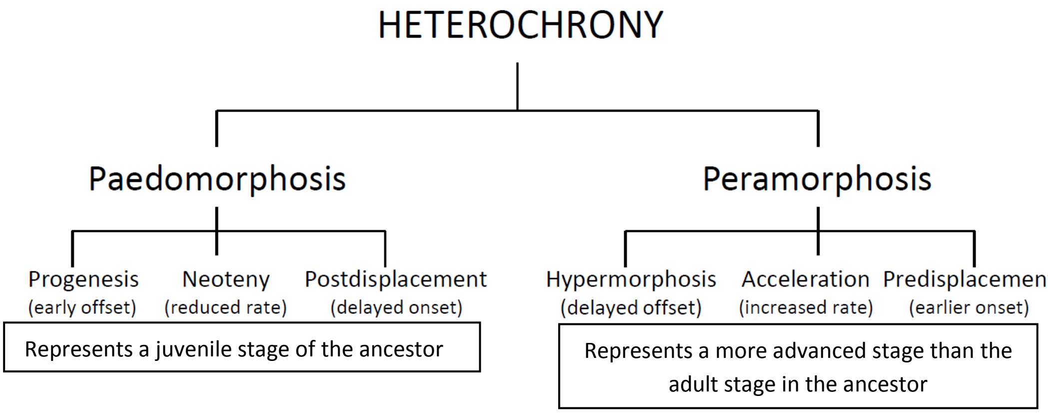


Fig. 3.1: Diagram showing heterochronic processes (based on Alberch *et al*., 1979)

The terminology of heterochrony (Fig. 3.1) can be used to describe changes in size and shape of structures as well as the size and shape of the whole organism (McNamara, 2012). Paedomorphosis occurs in three different ways; (i) Progenesis, where the period of growth in the descendant is stopped prematurely (hypomorphosis in Reilly *et al*., 1997); (ii) Neoteny, where the rate of the growth is reduced in the descendant compared with the rate in the ancestor (deceleration in Reilly *et al*., 1997); (iii) Postdisplacement, where onset of growth is delayed. All of these processes result in the morphology of an organism representing a juvenile stage of the ancestor (Fig. 3.1). A good example of paedomorphosis is the salamander (Gould, 1977; Albrech *et al*., 1979; McKinney & McNamara, 1991). The larval stage of most salamanders is aquatic and when maturity is reached they leave water and lead a terrestrial lifestyle. However, some salamanders retain this larval stage at sexual maturity and lead an entirely aquatic lifestyle (Duellman & Trueb, 1986; Whiteman, 1994).

Peramorphosis also occurs in three different ways; (i) Hypermorphosis, where the period of growth is extended in the descendant relative to its ancestor; (ii) Acceleration, where the growth rate is increased in the descendant compared to the ancestor; (iii) Predisplacement, where the onset of growth occurs earlier in the descendant compared to the ancestor (Fig. 3.1).

A change in the size and shape of an individual element, composite body part or the total size of the specimen is known as allometry. Allometry arises from differential rates of growth between different parts of the body or individual element (McNamara, 2012). If the relative size and shape of a structure remains the same throughout ontogeny, relative to an organism's body size, then growth is described as isometric. However, if the relative size of a structure increases compared to body size through ontogeny, then growth is described as positively allometric. The opposite growth, where the size of a structure decreases relative to body size through ontogeny is described as negatively allometric. Therefore, there is a close relationship between allometry and heterochrony. Positive and negative allometries are a consequence of changing growth rates (acceleration and neoteny). Organisms that undergo pronounced allometric changes during growth are more likely to generate very different descendant adult morphologies, especially if rates or durations of growth have changed with time (McNamara, 2012).

3.3: THE IMPORTANCE OF UNDERSTANDING ONTOGENY

Ontogeny is the development or developmental history of an individual organism through time (Gould, 1977; McNamara & McNamara, 1997; Hammer & Harper, 2006). The evolution of new features is controlled by developmental processes that can be fuelled by allometric growth. The examination of a possible growth series can (typically based on size) can be used to establish ontogenetic features (Delfino & Sánchez-Villagra, 2010). Directly observing any anatomical changes along a growth series and observing in what order these changes occur is one method that has been employed in order to study ontogeny (Johnson, 1977; McNamara & McNamara, 1997).

It is important to understand the ontogeny of an individual organism for several reasons: (i) Taxonomy. Neonates and juvenile organisms can, in some cases, look very different from their adult forms. Without a full understanding of ontogeny, juvenile organisms could be mistaken for an adult form of a different genus or species. Furthermore, juveniles of different genera can look similar to each other based on qualitative observations (McGowan, 1979) as well as quantitative observations (Jones & Goswami, 2010). Quantitative observations could highlight subtle features that could help with accurate taxonomic assignment. (ii) Heterochrony. Changes in the timing and rate of development can affect the appearance of an individual at different stages of maturity, such as an adult (sexually mature) specimen appearing similar to a juvenile stage of an ancestor, which could, in turn lead to errors in identification. (iii) Physical changes with age can relate to changes in habitats and feeding strategies. For example, organisms that become edentulous with age will change their feeding strategy (e.g. a change to suction feeding with tooth loss). Furthermore, some organisms, like the salamander, lead an aquatic lifestyle as juveniles and change to a more terrestrial lifestyle once they are sexually mature (McKinney & McNamara, 1991). This change in habitat is reflected in their physical appearance. Without the proper understanding of ontogeny, it would be easy to identify these two stages of one species as two different species. Growth series are not always available for study in the fossil record. It is therefore important to study growth series when they are available. Ichthyosaurs are well represented in the fossil record and therefore allow the possibility of studying ontogeny in the fossil record.

3.4: APPROACHES TO STUDYING DIAPSID ONTOGENY IN THE FOSSIL RECORD

Several physical changes are known to occur during growth in diapsids (Johnson, 1977; Sander, 1989A; Kolb *et al*., 2011; O'Keefe, 2002), which can be used to indicate the relative age of an organism, independently of size. It is important that scientists understand the ontogeny of different organisms because, in some cases, the physical differences occurring during ontogeny are very pronounced (McGowan, 1995). In cases where the ontogeny of the organism is not fully understood, new genera or species may be mistakenly erected (McGowan, 1995). This can occur as fossil species and genera are erected based on morphology. Morphologies vary between juveniles and adults of a single species, so if this is not understood the different morphologies can be interpreted as different genera or species. Incorrect identification of new taxa often adversely affects subsequent research on diversity, distribution, evolution and palaeogeography. A study of the evolution of a taxon would have to take into account the majority of the genera within the group. The same can be said of a study of diversity. If extra genera or species have been erroneously added into the taxon, the group would appear more diverse. Studies into distribution and palaeogeography can be similarly affected by the input of misidentified data. Therefore, an understanding of ontogeny is extremely important to several areas of research.

The ontogeny of various diapsids, both extinct and extant, has been studied (Larsson, 1998; Delfino & Sánchez-Villagra, 2010). It is already clear for a number of taxa that bone fusion (closure and fusion of sutures, e.g. closure of the formen magnum in humans) occurs with age (Sander, 1989; Druckenmiller & Russell, 2006). It has been suggested that the more fusion between bones in both extinct and extant specimens, the older the individual and this is the main technique that is employed to assess relative age. As a result, the ontogeny of the sauroptergian pachypleurosaurs and plesiosaurs is relatively well known. Bone histology has been used to assess rates of growth and ontogenetic stages can be identified in individual specimens of many groups of organisms such as pterosaurs, ceratopsians and sauropods, regardless of size (Bennett, 1993, Erickson & Tumanova, 2000, Klein & Sander, 2008). However, little is understood about the ontogeny of ichthyosaurs (see below for an in-depth review of the literature). Despite large growth series being preserved for several genera, including gravid females, relative age is estimated for an individual based on size. This project aims to conduct an in-depth study on the ontogeny of ichthyosaurs, establish a method of identifying the relative age of an individual independent of size and investigate possible sexual dimorphism, with a view to highlighting the physical differences, if any, between male and female specimens. The project will also examine whether or not body size changes with deep time and the reasons behind any rapid increases or decreases in size will be discussed. The hypotheses that will be tested and the approaches that will be used to achieve these aims will be described in detail in the methodology section.

3.4.1: An introduction to ichthyosaur ontogeny

In ichthyosaurs, total body length, or a proxy for body length, such as humerus length, is commonly used to provide a basic estimate of the relative age of a specimen (Kolb *et*. *al*., 2011) (Fig. 3.2). The body length of a specimen under study is compared with that of the longest known for that species. However, this technique has limitations. One being the differences between a large juvenile and small adult cannot be shown using this method alone. The point at which a juvenile reaches sexual maturity cannot currently be shown in an individual specimen with the exception of pregnant females.

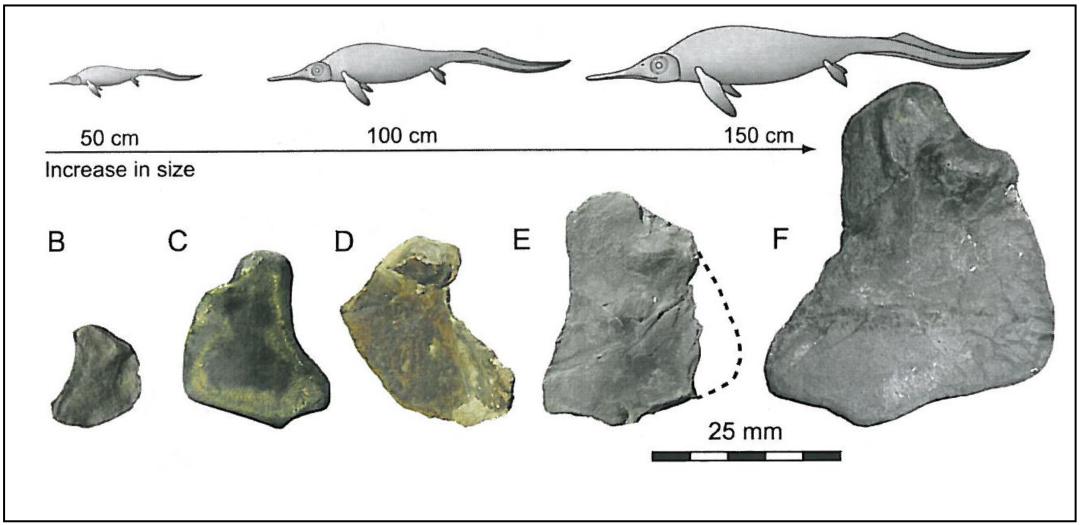


Fig. 3.2: Growth series based on size showing the change in size of the humerus in *Mixosaurus* ichthyosaurs (Kolb, *et al*., 2011)

Other drawbacks of this technique are that the natural size variation across similarly-aged individuals within a species are not taken into account, nor are differences between males and females. Natural abnormalities that can occur within a single species, such as dwarfism and gigantism, are not taken into account either. If any of these factors, other than age, cause the observed differences in size, it will result in inaccurate results for a study into ontogeny. Comments in the literature on the relative age of a specimen tend to be brief with little or no supporting evidence, typically based on qualitative observation on the relative size of the skull and eyes (Motani, 1999; Nicholls & Manabe, 2004; Delfino & Sanchez-Villagra 2009). In more comprehensive reviews of ichthyosaurs, ontogeny has not been considered in any depth (McGowan & Motani 2003, Motani 2005). A few observations have been made on ichthyosaur growth and ontogeny using different techniques, which are outlined below.

3.4.2: Size independent criteria

Only two published studies have conducted an in-depth investigation into ichthyosaur ontogeny (Johnson, 1977; Deeming *et al*., 1993). Johnson (1977) focused solely on *Stenopterygius* from the Posidonia shale Formation (Upper Lias) near Holzmaden in Germany, and made direct observations on the pectoral girdle and forelimbs of 26 complete or virtually complete specimens. Gravid females were included in the study. The specimens were arranged from smallest to largest based on the basis of increasing humeral length to establish a growth series. Humerus length was used as a measurement of comparative size against which to examine other characteristics. The changes in features not related to size were then identified and compared throughout the growth series.

Johnson (1977) suggested that characters of the pectoral girdle are inadequate for distinguishing between immature and sexually mature specimens. However, consistent differences in four characters of the front limbs were observed between larger and smaller specimens. (i) The shape of the proximal articular surface of the humerus appears flat in immature specimens and convex in mature specimens. (ii) The surface texture of the shaft of the humerus is sandpaper-like in immature individuals and smooth in sexually mature specimens (sexual maturity is only known for certain in pregnant female specimens). (iii) The sutures between the proximal fin elements are open in immature specimens, but closed in mature specimens. (iv) In certain species, notching is a characteristic feature in phalangeal elements in adult forelimbs but appears rudimentary or non-existent in immature specimens (Fig. 3.5 Notching clear in the leading edge of specimens H and I). However, Johnson (1977) did not specify in which order these characters appear and only commented on the differences between juvenile and mature specimens.

Deeming *et al*. (1993) analysed ontogeny in inferred ichthyosaurian embryos. Data was collected on skull length, length of orbit (orbital diameter) and length of vertebral column for 40 *Ichthyosaurus* specimens and 70 *Stenopterygius* specimens. All of the specimens included in the analysis were small specimens preserved in the body cavity of a much larger specimen, or free living specimens in close association with a much larger individual (Fig. 3.3). It is noted that the skull and orbits are very large compared to the length of the vertebral column. The features are compared to those of *Alligator mississippiensis* and it is concluded that the small individuals are embryos. It is concluded that small individuals of *Stenopterygius*, with skull lengths up to 29 cm, are likely to be embryos (Deeming *et al*., 1993). Although these results are very pertinent to the identification of embryos of ichthyosaurs, the results presented here do not identify trends in ontogeny after birth.

Fig. 3.3: An embryo of *Ichthyosaurus* (SMNS: 58278) showing a very large skull and orbit compared to the length of the vertebral column. Scale measures 10cm. Photo by Sam Bennett

3.4.3: Bone Histology

A number of reports have focused on the bone histology of ichthyosaurs. This technique involves examining a thin section of bone under a microscope, allowing visualisation of different types of bone tissue (Buffrénil & Mazin, 1990 & 1993; Kolb *et al*., 2011). These different bone tissue types can represent distinct stages and rates of growth of the organism. Bone histology has been employed in order to study growth and development for many organisms (Bennett, 1993; Erickson & Tumanova, 2000; Chinsamy-Turan, 2005; Klein & Sander, 2008). With regard to ichthyosaurs, Triassic and Jurassic specimens have been studied (Buffrénil & Mazin, 1993; Kolb *et al. ,* 2011; Nakajima *et al*., 2014; Maxwell *et al*., 2014). Where the physiology of a group of organisms is well understood, bone histology can be a very useful method of showing growth rates, and stages of growth. Despite this, growth can be affected by diet. If an individual goes through episodes of relative starvation, this may affect the growth of the individual, making the bone appear older than the true age of the animal. If the specimen went through periods of starvation during life then a cyclic pattern may be visible in a histological section as lines of arrested growth (LAGs). Therefore, bone histology is a technique that is ideally used in a large sample size or growth series so that comparisons can be made between several organisms of an apparent similar age. Using bone histology on a single organism would only be sufficient to estimate relative age if a growth series is available as a frame of reference.

Buffrénil & Mazin (1993) compared the bone histology of three genera, specifically, *Omphalosaurus* Wiman, 1910 from the Middle Triassic, *Stenopterygius* from the Lower Jurassic, and *Ophthalmosaurus* Seeley, 1874 from the Kimmeridgian. Total body length was used to estimate whether a specimen was juvenile or adult, with juveniles defined as measuring less than 200 cm in length (based on previous work by McGowan, 1973, 1979). For analysis, transverse sections were obtained from the middle of the shaft of ten long bones from the front and hind limbs. Buffrénil & Mazin (1993) showed that the structures of bone in *Stenopterygius* and *Ophthalmosaurus* are similar to that in *Omphalosaurus*, with four notable differences. (i) The bones of post-Triassic ichthyosaurs do not show a free medullary cavity. The mid region is occupied by loose spongy bone representing continuation of cortical bone. This could be an evolutionary change, rather than an ontogenetic characteristic. (ii) The cortex is extensively cancellous. However, in larger specimens, the outermost region of the diaphysis constitutes a layer of compact bone, whereas in smaller specimens, the cortical bone is entirely cancellous. This feature may be used to estimate relative age; although it is not known precisely at what ontogenetic stage this change occurs. Despite this, it is judged that an individual displaying a layer of compact bone is more likely to be older than an individual that does not show this feature. (iii) The alternating layers of spongy and compact bone in the cortex are not observed in post-Triassic specimens. (iv) The medullary and deep cortical regions are more significantly remodelled in *Omphalosaurus*. The remodelled layers display repeated cycles of resorption and redisposition (Buffrénil & Mazin, 1993). This suggests rapid deposition of periosteal tissue, resulting in fast bone diameter growth for all the specimens under examination. Amongst extant tetrapods, the bone structure of the ichthyosaur studied is similar to that of dolphins and leatherback turtles (Buffrénil & Mazin, 1993). In combination with earlier results (McGowan, 1973), the rapid growth of bone and increase in bone diameter suggest fast overall growth of the body with ontogeny. Cortical bone growth was continuous in post-Triassic ichthyosaurs and as a result there are no growth bands or other cyclical features that can be used to infer age. The Triassic ichthyosaur (*Omphalosaurus*) showed that a relative decrease in the rate of periosteal apposition (creation of new bone) occurred periodically (Buffrénil & Mazin, 1993). In the study, it is not made clear whether this feature can be used to estimate relative age and consequently this feature is not used to infer age.

A study on the palaeohistology of an ontogenetic series of *Mixosaurus*, a basal ichthyosaur from the Middle Triassic (Kolb *et al.*, 2011), employed similar techniques to those of Buffrénil & Mazin (1990 & 1993). The series included postnatal to large adult specimens, with relative ages inferred based on size. Kolb *et al.* (2011) showed that inferred juvenile bone (from smaller specimens) mainly consists of well-vascularised spongy tissue (Fig. 3.4). Compact primary bone deposits appear in older (larger) specimens, as well as remodelling of bone to more cancellous tissue. These features are comparable to those reported by Buffrénil & Mazin (1993). The presence of compact primary bone and remodelling can be used in future studies to indicate the relatively older specimens. Kolb *et al.* (2011) also reported high growth rates throughout ontogeny, consistent with the conclusion of Buffrénil & Mazin (1993). The features noted above have as yet not been linked to a specific growth stage.

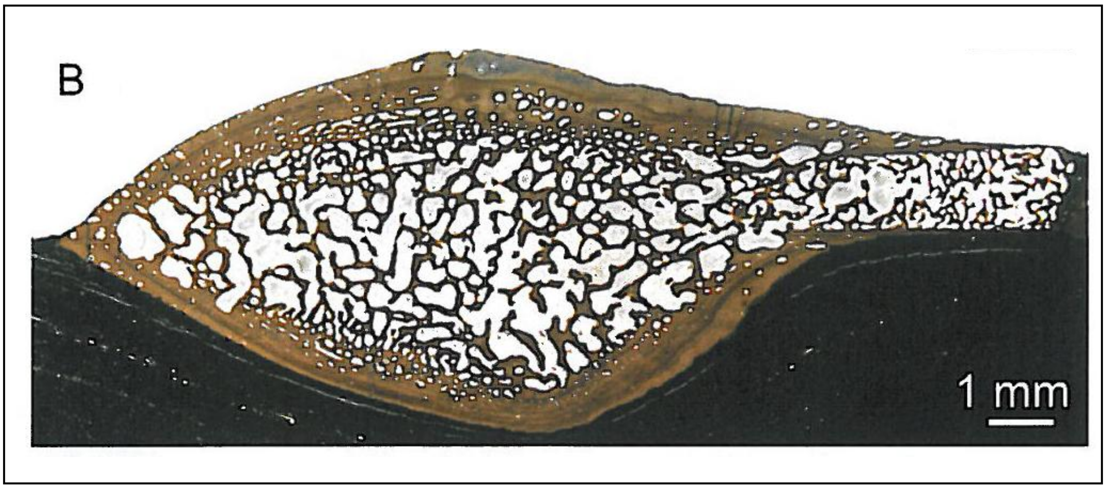


Fig. 3.4: Cross-section through a small, three dimensional humeral shaft of *Mixosaurus* showing well vascularised, spongy tissue (Kolb, *et al.* 2011) in an inferred juvenile.

Recently, Gren (2010) based an undergraduate thesis on the osteo-histology of Mesozoic marine tetrapods comparing the bone histology of sea turtles, ichthyosaurs and plesiosaurs. Gren showed that ichthyosaur bone is very cancellous and vascularized by numerous narrow canals with the outermost layer being denser than the interior of bone, similar to the findings of Buffrénil and Mazin (1993) and Kolb *et.al.* (2011). Moreover, in ichthyosaurs, the cortical bone is comprised of woven fibres and lacks the distinct cylindrical pattern indicative of a slow growth rate. This suggests a rapid growth rate, in accordance with the above reports. The research also drew comparisons with extant tetrapods, such as leatherback turtles, whales and dolphins. The same comparisons were drawn by Buffrénil & Mazin (1993). The main difference shown was that the cortex in the plesiosaur bone is significantly more compact than that in the sea turtle and ichthyosaur. However, limited conclusions could be drawn, as the author did not know the relative age of the comparative specimens. Based on the relative amount of remodelling in the thin sections, Gren deduced that the ichthyosaur and plesiosaur specimens included in the study were juveniles, while the sea turtle was more likely to be adult.

In summary, the presence of compact primary bone deposits in older (larger) specimens, as well as remodelling of bone to more cancellous tissue in ichthyosaurs can be a useful feature for estimating relative age. The compact primary bone deposits and remodelling of bones show that growth has slowed down, but has not stopped altogether. However, ichthyosaur bone histology is typically very vascular and cancellous and does not have features that can be used to estimate relative age.

3.4.4: Tooth Loss

Total tooth loss or a reduction in the number of teeth with increasing inferred age has been observed in ichthyosaurs (Nicholls & Manabe 2004). Nicholls and Manabe (2004) showed that teeth in *Shonisaurus* are set in sockets, but this has only been recorded in a few small individuals. In most ichthyosaur genera, teeth are set in a dental groove, rather than in sockets and only held in place by soft tissues. It is possible that teeth are removed by taphonomic processes. However, no teeth are found in large (inferred adult) specimens of *Shonisaurus*. This finding implies that teeth were present only in juveniles with adults being edentulous. Loss or reduction of teeth in adults has been documented in a few Jurassic taxa. Earlier, Huene (1922) and McGowan (1989) reported loss of teeth in larger and possibly more mature individuals of *Stenopterygius quadriscissus* Quenstedt, 1856. Reduction or loss of teeth has also been reported for *Leptopterygius* (McGowan 1989), *Ophthalmosaurus* (Maisch and Matzke 2000), *Temnodontosaurus azerguenguensis* (Martin *et al.*, 2012) and *Chacaicosaurus* (Fernández, 1994). As yet it is not clear if the presence or absence of teeth is related to ontogenetic stage or if the reduction in numbers or loss of teeth begins and ends at certain sizes and ages. Furthermore, it is also not clear whether this apparent change in dentition is a taxonomic difference.

The lack of evidence for teeth in large specimens of *Shonisaurus* suggests a change in feeding strategy as the individual ages. The large ceratobrachials of *Shonisaurus* are indicative of powerfully developed gular muscles that control the tongue and floor of the mouth (Nicholls & Manabe 2004), further suggesting that the larger specimens employed a suction feeding technique. The features that suggest a suction feeding technique may also apply to other taxa that exhibit tooth reduction. This feeding technique has been suggested for *Shastasaurus* (Merriam, 1895) (Sander *et al.*, 2011). Conversely, Motani *et al*. (2013) examined four features of jawed vertebrates that are closely linked to the mechanism of suction feeding, namely, hyoid corpus ossification/calcification, hyobranchial apparatus robustness, mandibular bluntness and mandibular pressure concentration. A total of eighteen species of Triassic and Early Jurassic ichthyosaurs, including presumed suction feeders were compared. Motani *et al*. (2012) concludes that hyobranchial bones are significantly more slender in ichthyosaurs and an ossified hyoid carpus (to which the hyoid retractor muscle attaches) is absent in all but one specimen included in the analysis. This indicates that ichthyosaurs unable to suction feed. Therefore, the loss of teeth could suggest a change with age related to a change in feeding technique or diet. However, as most ichthyosaur teeth are set in dental grooves they are easily removed after death. Soft tissues that hold the teeth in place would break down quickly after death and it is likely that only slight currents would be required to remove the teeth. Ichthyosaur specimens have been discovered where the teeth have been completely removed from the dental groove yet still remain nearby in the sediment associated with the specimen (Bennett *et*. *al*., 2012). It has been determined that it is likely very low energy currents would be sufficient to move teeth and other small elements away from the rest of the specimen (Bennett *et al.*, 2012; Reisdorf *et al.*, 2012). Research into ichthyosaur taphonomy is still being conducted to provide a clearer understanding of diagenetic processes (Schwermann *et al.*, 2012). Therefore, the reduction in numbers of teeth or complete loss of teeth may be an ontogenetic feature for some genera, but this should be used with caution and supported by other evidence.

3.4.5: Ossification patterns

Ossification patterns refer to the order in which elements in the skeleton ossify throughout ontogeny. One study examined limb bone ossification patterns in ichthyosaurs (Caldwell, 1997). The results, using *Stenopterygius,* showed that limb ossification follows a continuous proximal to distal sequence from the propodial elements through to the terminal elements of 1st to 4th digit in the manus and the 1st to 3rd digit in the pes (Fig. 3.5). The 5th manual and 4th pedal digit begin ossification later than more preaxial digits and also show evidence of proximal addition of elements near the distal mesopodial row in a manner consistent with delayed ossification of the 5th distal mesopodial in other diapsids (Caldwell, 1997).

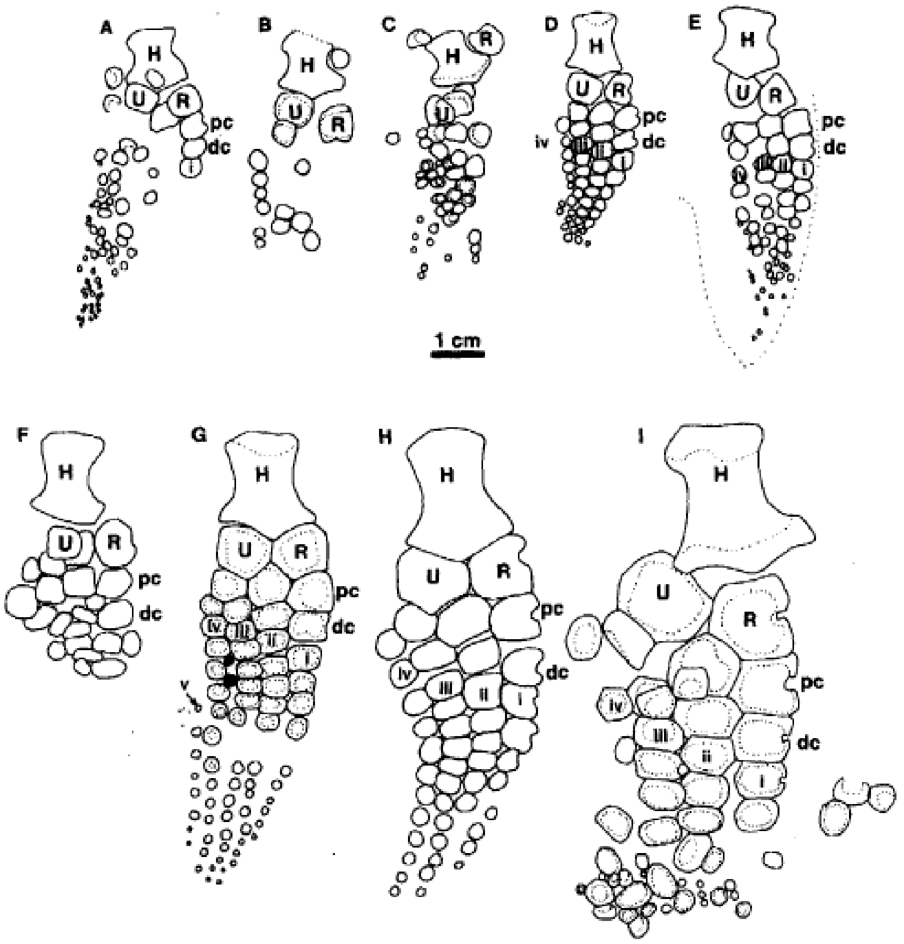


Fig. 3.5: Forelimb (manus) ontogeny of *Stenopterygius* from embryonic (A) to juvenile (I) showingproximal to distal ossification, where distal ossification is barely started in A-C, at an intermediate stage in D-G and complete or virtually complete and H-I. Abbreviations: dc, distal carpal row; h, humerus; pc, proximal carpal row; r, radius; u, ulna; (from Caldwell, 1997).

These features can be used to help estimate relative age between embryonic stage and juvenile stage. However, this does not help estimate relative ages between juveniles and adults. However, the sequence used by Caldwell (1997) may not display a proximal to distal ossification pattern (Fig. 3.5). Many of the elements have been moved, or have parts missing and it is likely that taphonomic processes have caused this. Therefore, it is possible that the smaller and lighter elements in embryonic and juvenile specimens have been removed by currents while larger elements remain. Furthermore, it also appears that smaller, distal-most elements are preserved, even in the smallest specimens (Fig. 3.5 A). Further analysis is required on ossification patterns as it is currently not possible to use this to help estimate relative ages in ichthyosaurs.

3.4.6: Other ontogenetic differences

Ichthyosaur specimens have been misidentified in the past as a result of a limited understanding of ontogeny. Physical differences may be pronounced between large and small specimens (McGowan, 1973). Occasionally, this can result in a new species being erected, when the specimen represents a juvenile stage of a pre-existing species. McGowan (1995) illustrated this problem, showing that *Temnodontosaurus risor* McGowan, 1974 is, a juvenile of *T. platyodon* Conybeare, 1822. McGowan reached this conclusion using information from Johnson (1977) analysis of ichthyosaur ontogeny (see above for the list of physical characteristics based on limb and manus bones observed in smaller and larger specimens). Material named *T. risor* has a distinct upturned rostrum and is smaller than other *Temnodontosaurus* specimens. These characteristic features resulted in a new species being erected (McGowan, 1974). However, McGowan (1995) demonstrated that the upturn of the rostrum is more likely to be a feature of ontogeny. It was shown that *T. risor* has a slightly larger orbit, smaller maxilla and an upwards curving rostrum, compared with *T. platyodon*. Additionally, McGowan (1995) noted that the skull of *T. risor* is relatively large in comparison with the rest of the body. Delfino & Sanchez-Villagra (2009) made similar observations of a large skull and a large orbit, using these features to infer a juvenile age for a specimen of *Aegirosaurus*. Reassessment of *T. risor* characters in the context of the data in Johnson (1977) revealed that three of the four above (section 1.2.3) criteria for a juvenile were met, with the only possible exception being the closure of sutures on the proximal fin elements. It could not be confirmed whether sutures were open or closed. This information strongly supports the conclusion that *T. risor* actually represents a juvenile stage of *T. platyodon.*

3.4.7: Discussion of ichthyosaur ontogeny

Three papers discussed in this section have been based on bone histology (Buffrénil & Mazin, 1993; Gren, 2010; Kolb *et al.*, 2011). Specific bone histology data can be used to estimate relative age and provide indications of whether a specimen is juvenile or adult. The bone tissue type is an indicator of relative age (reworked/remodelled bone indicates a more mature specimen, while well-vascularised, spongy tissue is suggestive of younger specimens). This information cannot be used alone, since relative age is based on size. The studies did not show whether reworking begins while the specimen is still a juvenile and whether diet affects the rate of bone growth or reworking. Reduced food intake could result in slow growth and earlier reworking, compared to a well-fed specimen (Horner *et al.*, 2000). In this case, bone tissue indicative of an adult could be present in a juvenile. Further studies with specimens where the relative age is independently known would allow confirmation of bone histology data. In cases where age can be estimated using features other than bone histology, typical characteristics of bone tissue observed for inferred juveniles and adults can be compared. However, analysing bone histology is a destructive technique that cannot be performed on all specimens. Type specimens, or those used for displays in museums, would need to be preserved with no alterations. In these situations, a non-invasive method of studying bone histology, such as CT scanning, would be more appropriate. Not all bone histology findings are useful for estimating relative age. Gren's thesis (2010) was based on longevity, growth strategies and growth rates, but ontogeny was not a focus of that study.

Interpretation of ontogeny based on teeth is only possible in cases where teeth are completely lost with age. This occurs in *Shonisaurus*, but the hypothesis that a specimen gradually becomes edentulous with age has not been conclusively proven due to the fragmentary nature of the fossil record. Natural variations occur within a species and the number of teeth is variable (McGowan and Motani, 2003). A reduction in the number of teeth can therefore only be used to support other evidence of relative age, if at all. However, it is possible that variation in tooth numbers is (at least partly) linked to ontogenetic stage.

Johnson (1977) provided the only data on size-independent physical differences. Four physical differences between certain bones of smaller and larger specimens (shape, texture, suture closure and neoteny) possibly relate to ontogeny (Johnson, 1997). However, this study was based purely on qualitative observations. Specimens were set in a size-ranked order based on the length of the humerus and no quantitative methods were employed. The study has further limitations. Specifically, all findings were based on features of the front manus and limb bones and specimens did not always have a complete preserved skeleton. The method used by Johnson cannot be applied to a specimen without preserved limbs. Furthermore, other, subtler features of ontogeny may have been overlooked due to the lack of a quantitative approach. For the above reasons, data from Johnson's (1977) paper alone are inadequate for the identification of relative age.

3.4.8: Summary of current knowledge of ichthyosaur ontogeny

- Relative age in most published studies is inferred using body length. This is not a reliable means of estimating relative age, as there is no established method of showing the differences between adults and juveniles. Analyses and comments have previously been made whereby the presence or relatively large skulls and orbits are indicative of embryos and juvenile but no supporting statistical evidence has been determined for juveniles. There are no criteria to determine the sizes at which a juvenile becomes a sexually mature adult or for distinguishing between a large juvenile and a small adult. A more quantitative procedure is required to demonstrate the physical differences between juvenile and sexually mature (adult) specimens.

- Reductions in numbers of teeth and tooth loss have been linked to ontogeny. However, there is natural variation within a species in terms of tooth number, and teeth can be easily lost during fossilisation. Tooth loss from a dental groove may occur via relatively low-energy post-mortem processes, such as water currents. Tooth loss, or reduction in numbers of teeth with age is currently not a reliable source of information to help with the estimation of relative age.

- Due to a large amount of the bone being reworked in ichthyosaurs, the use of bone histology for the estimation of relative ages is limited. However, it has been shown that a compact layer of outer bone may indicate an older (inferred adult) specimen.

- It has been argued that ossification patterns show a clear proximal to distal sequence in the limbs of ichthyosaurs. However, it appears that distal elements are preserved in even the smallest specimen included in the analysis. It is possible that smaller elements in some of the inferred juvenile specimens are removed by taphonomic processes rather than not being preserved as they are not yet ossified. Therefore, no clear pattern is observed. Further analysis is required on ossification patterns and this feature cannot currently be used to help estimate relative ages in individuals. Furthermore, the problem with this approach is that it could only be used to show the differences between inferred embryos and inferred juveniles. The features cannot be used to distinguish between juveniles and adults. Furthermore, this approach cannot be used to estimate the relative ages of an individual that does not have the limbs preserved.

3.5: ONTOGENY OF OTHER DIAPSIDS: SAUROPTERYGIANS

3.5.1: Plesiosaurs

The ontogeny of extinct marine diapsids such as plesiosaurs, pachypleurosaurs and crocodyliforms, as well as extant organisms like crocodilians is relatively well known compared to the ontogeny of ichthyosaurs. The ontogeny and methods are outlined here in order see if these techniques and inferences are applicable to ichthyosaurs.

The Plesiosauria (Diapsida: Sauropterygia) represents a group of marine tetrapods that were common in the Mesozoic, which were distantly related to ichthyosaurs (see Chapter 1) (O'Keefe, 2002). The sauropterygians form the largest and most diverse group of marine reptiles that lived throughout most of the Mesozoic (Cheng *et al.*, 2004). In much of the literature, fusion or lack of fusion between various bones has been used in ontogenetic studies to estimate relative age of plesiosaurs (Andrews, 1911; Druckenmiller & Russell, 2006; Kear, 2007; Bardet *et al.*, 2008). Druckenmiller and Russell (2006) reported several features of the pectoral girdle that they suggested were indicative of inferred fully mature adult status, where age was initially estimated based on size. They showed that, in inferred adults, the coracoids displayed considerable fusion with adjacent elements. Specifically, the left and right coracoids are fused with one another along much of the midline. The left coracoid and left scapula are additionally fused at the glenoid fossa. Other features of coracoids considered to be indicative of ontogenetic state included the development of a prominent ventrally projecting midline process and the presence of perforations along the posterior midline of the coracoids (Druckenmiller & Russell, 2006). However, the timing of these developments is unknown and the stages at which the features listed here developed are not discussed.

Kear (2007) inferred the ontogenetic stage (juvenile) of another, smaller plesiosaur specimen based on a number of characteristics. Among the cranial elements, the basioccipital lacked fusion with the basisphenoid. However, advanced ossification was observed on the articular surfaces of the basitubera and occipital condyle. Furthermore, the exoccipital-opisthotic and interparietal sutures were well ossified (Kear, 2007). These features may be extremely useful for understanding plesiosaur ontogeny as the fusion of bones, or lack of fusion, can be used to help infer relative age regardless of size. However, this approach is based on bone fusion and therefore cannot be applied to ichthyosaurs as the bones do not fuse.

The postcranial skeleton of the specimen studied by Kear (2007) displayed relatively limited ossification throughout most of its axial region (unfused neural arches, cervical ribs and centra). Limited ossification also occurred in the appendicular skeleton, including weakly developed articular surfaces on the pectoral girdle and limb bones. The mixture of fusion and lack of fusion was thought to be suggestive of a juvenile older than a neonate (Kear, 2007). Lack of ossification and lack of fusion of skeletal elements has also been described for other inferred juvenile plesiosaurs, where the authors observed a poor degree of ossification with lack of fusion between the neural arches, ribs and centra (Bardet *et al.*, 2008). Moreover, the vertebral articular surfaces were almost flat and the propodials had poorly defined extremities. These features are important as they are determined to be ontogenetically variable as the degree of ossification increases with size (and hence inferred age). Based on the evidence of both fusion, and lack of fusion, it was concluded that the individual specimen under study was that of a juvenile, but not neonate (Bardet *et al.*, 2008).

Although size was used initially to help study bone fusion, this evidence can also be used as an indication of relative ontogenetic age in plesiosaurs. This information is reliable as it can be accurately used to identify the relative ages of individual Plesiosaur specimens independent of size. This is because bones fuse at certain ages rather than at certain sizes. Bone fusion does not occur in ichthyosaurs, except in the atlas/axis complex.

Furthermore, there are histological differences related to age observed in plesiosaurs. Wiffen *et al*. (1995) examined a total of 10 homologous bones (vertebrae, humeri, ribs and phalanges) from conspecific juvenile and adult specimens from the Upper Cretaceous of New Zealand. The dataset set included both elasmosaurs and pliosaurs. The histological analysis showed that the bones of the juveniles displayed a thicker pachyosteosclerotic structure while adults displayed a lighter osteoporotic-like structure. These features could be used to provide a relative age of an individual specimen in plesiosaurs, although this is a destructive technique. This ontogenetic feature is not observed in ichthyosaur bone histology and therefore cannot be used in the same way to identify relative age in ichthyosaurs (see section 2.2.4 for details).

3.5.2: Pachypleurosaurs

Pachypleurosaurs are sauropterygians, and are distantly related to plesiosaurs, both being reasonably closely related to ichthyosaurs (see Chapter 1) (Cheng *et al.*, 2004). Several research groups have focused on the ontogeny of pachypleurosaurs (Sander, 1989; Hugi & Scheyer, 2012). A well-preserved large growth series has allowed the use of morphological and morphometric approaches.

3.5.2.1: Inferred Embryos

Sander (1989) highlighted several characteristics that facilitated the identification of a specimen as an embryo. Specifically, the skull was large (76% of the trunk length), had very large orbits, and many of the bones were poorly ossified (Fig. 3.6a). The prefrontals, jugal, postorbital and postfrontals appeared slender with very thin processes. Furthermore, the squamosal was relatively large and comprised most of the skull, the posterior ridge of the skull was not developed, and the parietals were too poorly ossified to be well defined. Few teeth were present and there was incomplete ossification of the lower jaw.

The postcranial skeleton also showed characteristics indicative of an embryonic state. In total, 26 ossified caudal vertebrae were present, which is less than two-thirds of those in an adult, based on relative size (Sander, 1989). The interclavicle was not ossified, and the clavicle and scapula were a distinct shape, compared to adult. The scapula blade was relatively large, and the ventral portion shorter (Sander, 1989). The humerus and femur appeared as simple rods with slightly expanded and poorly ossified terminations. The manus was also unossified (Sander, 1989) (Fig. 3.6a).

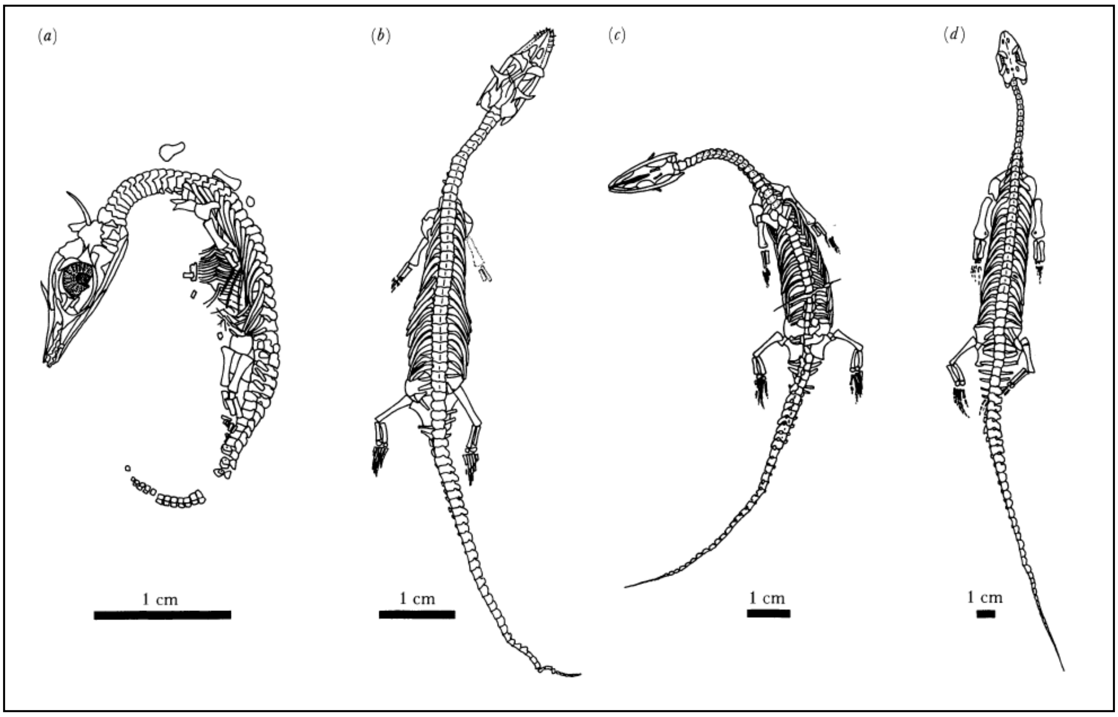


Fig. 3.6: Growth series (a, embryo; b neonate/young juvenile; c older juvenile; d, adult) of the pachypleurosaur *Neusticosaurus peyeri* showing overall changes during ontogeny (from Sander, 1989)

3.5.2.2: Inferred Juveniles

Sander (1989) listed the features signifying a juvenile stage, based on relative size. The skull displays relatively large orbits compared to larger, more mature specimens (Fig. 3.6b and c) and skull bones show small sutural connections. However, the teeth are relatively larger, compared to those of an embryonic specimen, and ossification of the jaw is incomplete. This incomplete ossification is particularly evident at the midline and in the frontals. The long bones (humerus and femur) show concave, unfinished ends and the bones themselves display a rough surface containing pits and grooves (Sander, 1989).

Specific characteristics of the postcranial skeleton also allowed inference of juvenile age. The vertebrae are developed, but appear wider and shorter than in adult specimens. The same is evident in the neural arches that appear rectangular in outline. The scapula is relatively smaller when compared to the vertebral column, while the coracoids and pubis appear less waisted than in adult specimens. One of the most important ontogenetic features is that of the suture in the clavicles, which is easily seen in juveniles. The clavicles are unfused in the inferred embryonic stage, while the suture is not visible in the inferred adult stage (Sander, 1989).

3.5.2.3: Inferred Adults

Growth continues after sexual maturity (Sander, 1989), and therefore, size cannot be used to indicate relative age of a specimen. Specific morphological features signify an inferred adult stage of life (Fig. 3.6d). The frontal bones are completely fused along the midline (Rieppel, 1989; Sander, 1989). Fusion also occurs between the frontals and nasals. The appearance of a plate-like interclavicle in inferred adults (sexually mature) is also noted. The pterygoids are in contact over the entire length along the midline and the palate is closed in inferred adults. The size of teeth is distinct in adults and is usually a maximum of 1.5 mm high. The 'unfinished' ends of the neural spines extend over the posterior half of the spines in anterior vertebrae and cover the entire spine in the posterior vertebrae. Moreover, terminal phalanges 2 and 5 in the manus do not ossify consistently until inferred adulthood. Pachyostosis (thickening of the bones) is observed in smaller specimens. Pachyostosis varies during ontogeny, but no consistent pattern has been determined to date. Additionally, the humerus shows positive allometric growth when compared to body length. Therefore, high ratios of the humerus length compared to the body length would indicate an adult specimen (Sander, 1989). The skull displays negative allometric growth, while the femur typically exhibits isometric growth when compared to body length (Sander, 1989). These features can be used to create ratios, which, in turn can be used to indicate relative age. The approach of using positive and negative allometric growth to estimate relative ages can be applied to ichthyosaurs. This study aims to identify individual skeletal elements and composite body parts that display allometric growth, which in turn will relate to ratios that could be used to help identify relative ages for ichthyosaurs.

3.5.2.4: Bone Histology

Bone histology has been examined in an ontogenetic sequence of pachypleurosaurs (Hugi & Scheyer, 2012). 244 specimens, representing 4 taxa are included in the study. The results of the analysis show that ontogenesis of pachypleurosaur limbs can be divided into two steps; (1) developmental sequences of ossification during embryology and/or in early neonates; (2a) additional primary compaction processes and (2b) additional primary and secondary endosteal compaction processes during neonate ontogeny (Hugi & Scheyer, 2012). Therefore, the differences in bone histology are useful for identifying changes in ontogeny between embryos and neonates. However, this does not help identify any ontogenetic differences between juveniles and adults.

3.5.2.5: Sexual dimorphism in pachypleurosaurs

When the same relative age is demonstrated in specimens based on the degree of fusion of sutures (as outlined above), differences in the morphology of the humerus remain. These are interpreted as features of sexual dimorphism (Rieppel, 2000). However, there is no direct evidence, such as a gravid female, preserved in the fossil record. Sex *y* shows a humerus with a distinct deltopectoral crest, which results in an angulated preaxial margin and more distinctly differential epicondyles (Rieppel, 2000). Sex *x* remains smaller and shows a lesser degree of humeral differentiation, resembling the juvenile stage of sex *y* (Rieppel, 2000). If this feature of inferred sexual dimorphism is apparent in specimens, it is deduced that sexual maturity is reached and the specimen is an adult. The feature of sexual dimorphism is important, as it shows the minimum size at which adulthood (sexual maturity) is reached. This is a very useful tool for ontogenetic analysis. Currently, this cannot be applied to ichthyosaurs as studies into sexual dimorphism have not been conducted. This study aims to investigate sexual dimorphism in ichthyosaurs.

3.5.2.6: Pachypleurosaur summary

Due to good preservation of a large growth series (Fig, 1.8), considerable information is available on the growth and ontogeny of pachypleurosaurs. A number of morphological features demonstrate the relative age of a single specimen. The variety of morphological features mean that the relative age can be estimated, independent of size, even from a partial skeleton. The presence of sexual dimorphism provides an absolute indication of the adult stage of life, supporting the other features used to distinguish the juvenile and adult stages of life.

Some of the changes observed in pachypleurosaurs could be applied in the study of ichthyosaur ontogeny. Differences in the relative size of the skull have been used in ichthyosaurs previously (McGowan, 1995). Changes in relative size and shape of the humerus and femur can also be applied to ichthyosaurs. Data will be collected on all these features in this study. However, some of the characteristics observed in pachypleurosaurs will not be useful for the study of ichthyosaur ontogeny. The fusion along the midline between the frontal bones in the skull in the juvenile and adult stages of pachypleurosaur ontogeny will not be of use as the cranial bones do not fuse in ichthyosaurs.

Furthermore, some features in inferred adults have been attributed to sexual dimorphism. Distinct features of the humerus are seen in some specimens of inferred adults specimens, but not all. It has been concluded that these features are differences between males and females. It is currently unclear if this will be applicable to ichthyosaurs.

3.6: ONTOGENY OF OTHER DIAPSIDS: CROCODYLIA

Crocodilians (Archosauria: Crocodylia) are a group of reptiles that first appeared in the Triassic. This group contains extinct species as well as the extant crocodiles and alligators. They are distantly related to ichthyosaurs but are used here as a comparison as many forms lived in marine environments during the Mesozoic.

3.6.1: Bone fusion

Several studies highlight morphological features indicative of an inferred adult stage of life (Brochu, 1996; Brochu *et al*., 2002; Buchy *et al*., 2006). As with pachypleurosaurs and plesiosaurs, emphasis is placed on bone fusion, which can indicate an adult stage of life; with adults having a high degree of fusion compared to that of juveniles. Brochu *et al*. (2002) observed that the neural arches are fused to the vertebral centrum in inferred adult specimens. Fusion also occurs between bones in the skull. The frontal bones are fused to the parietals as well as the nasal bones in an inferred adult stage of life (Buchy, *et al*., 2006). Brochu (1996) analysed 91 specimens of extant crocodilians in order to study ontogeny. The fusion of neurocentral sutures are compared to relative age (based on a measure of the geometric mean). The results show that the closure of neurocentral sutures in the crocodilian vertebral column follows a direct caudal to cranial sequence during ontogeny. The sutures in the majority of the caudal section are closed at hatching but the remaining sutures close later in ontogeny. The closure of the cervical sutures is a consistent indicator of morphological maturity and the final transformation is the closure of the axial neurocentral suture. These features can be used as an indicator of age regardless of size. However, it is not certain whether the closure of the final suture indicates the stoppage of growth (Brochu, 1996). Irmis (2007) used the same criteria to analyse ontogenetic trends in phytosaurs and established that they display the same ontogenetic trends as those shown by Brochu (1996) for crocodilians (Irmis, 2007).

The same features are observed in extant crocodilians. As with most other organisms discussed here, fusion is used as the main feature for estimating the relative age in skeletal remains of crocodilians, where exact age is unknown. Brochu (1996) assessed the closure of neurocentral sutures in the vertebral column during crocodilian ontogeny and showed that the closure follows a distinct caudal to cranial sequence. The sutures in most caudal vertebrae are fully closed by hatching stage while closure of the remaining sutures occurs later in ontogeny. Additionally, closure of the cervical neurocentral sutures is a consistent indicator of relative age in *Alligator mississippiensis* Daudin, 1802, *Osteolaemus tetraspis* Cope, 1851 and *Crocodylus acutus* Cuvier, 1807 (Brochu, 1996). The final transformation is the closure of the axial neurocentral suture, which occurs after closure of the axis-odontoid suture. These changes occur towards the end of ontogeny, regardless of the size of the individual.

3.6.2: Other ontogenetic features

However, features other than bone fusion are also used to estimate relative ages in crocodyliforms (Brochu *et al*., 2002). Brochu *et* al. (2002) examined a specimen of a Dryosaurid crocodyliform, tentatively referred to *Rhabdognathus*. The quadrate ramus in hatchlings projects ventrally and rotates to a posterior projection in inferred adult specimens. Moreover, a single eustachian opening is externally visible in inferred adults (Brochu *et al*., 2002). Buchy *et al*. (2006) additionally noted that juveniles are characterised by a sub-circular supratemporal fenestra that becomes oval in inferred adults. The same study showed that the ascending process of the palatines is not fused to the descending process of the prefrontals in the specimen studied. In view of the observation that these elements are unfused, the authors concluded that the individual (a new Thalattosuchian species of *Geosaurus*) is not fully-grown. Therefore, a specimen showing fusion of these elements could be considered as a mature adult. These features of ontogeny are unsuitable for application ichthyosaurs as there is no fusion between the bones in ichthyosaurs.

3.7: ONTOGENY OF OTHER DIAPSIDS: DINOSAURS

3.7.1: *Triceratops*

Dinosaurs are an extensively studied group of Mesozoic archosaurs. Growth series are known for several genera and the ontogeny has been studied. *Triceratops* is famous for its cranial structures of three horns and large parietal-squamosal frills. Horner and Goodwin (2006) examined the major changes in the cranial structures of *Triceratops* with ontogeny, with age inferred from size. A growth series of 10 skulls, ranging from a 38 cm long inferred juvenile to a 200 cm long inferred adult (Horner & Goodwin, 2006) was studied. They concluded that four growth stages correspond to a suite of ontogenetic characteristics expressed in the postorbital horns, frill, nasal, epinasal horn and epoccipitals. Postorbital horns are straight stubs in early ontogeny, curve posteriorly in juveniles, straighten in sub-adults and recurve anteriorly in adults. The posterior margin of the baby frill is deeply scalloped. In early juveniles, the frill margin becomes ornamented by 17-19 delta-shaped epoccipitals. The epoccipitals are dorsoventrally compressed in sub-adults, strongly compressed and elongated in adults and ultimately merge onto the posterior frill margin in older adults (Fig. 3.7). Ontogenetic trends within and between growth stages include: posterior frill margins change from scalloped to wavy and smooth; progressive exclusions of the supraoccipital from the foramen magnum; internal hollowing at the base of the postorbital horns; closure of the midline nasal suture; fusion of the epinasal onto the nasal; and epinasal expansion into a morphologically variable nasal horn (Horner & Goodwin, 2006).

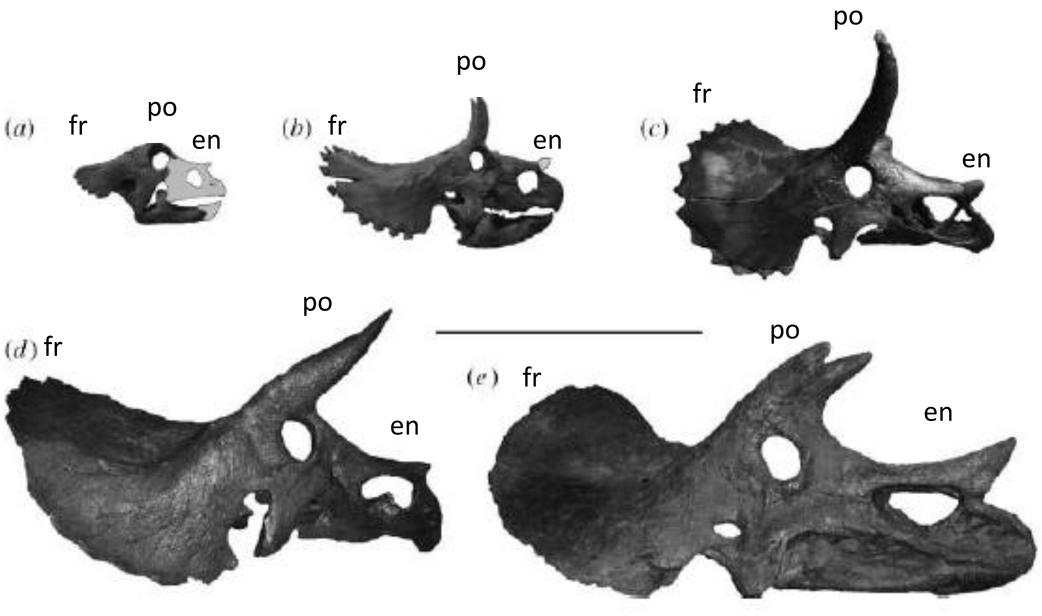


Fig. 3.7: Examples of *Triceratops* crania showing ontogenetic change where: (a) inferred baby; (b) small inferred juvenile; (c) large inferred juvenile; (d) inferred sub-adult; and (e) inferred adult. Scale bar measures 1m. Abbreviations: en, epinasal horn; fr, frill; po, post orbital horn (from Horner & Goodwin, 2006).

This study used changes in the cranial structures as well as closure of sutures giving a variety of features for estimating relative age of an individual. However, all these observations are based on qualitative observations and no quantitative data was used. The features that have been used here for relative age estimation cannot be used for estimating relative ages in ichthyosaurs as they lack cranial horns or frills.

3.8: SUMMARY OF EVIDENCE FOR ONTOGENY

- Bone fusion is the main feature used to identify relative ages in the other extinct organisms mentioned above. The degree of fusion clearly increases with age in an individual.
- The size and shape of features can change with age and these are used to help estimate relative ages. Inferred embryonic and juvenile pachypleurosaurs tend to display larger skulls and larger eyes compared to the length of the body. Ratios

created from skull length and body length can then be used to infer relative ages. However, this feature is not useful once maturity is reached.

- Bone histology is also used in some cases to help estimate relative age. However, this is not seen in all of the cases as this method is destructive and is not always possible. The bones in younger organisms tend to be more cancellous with larger spongy areas and become more compact with age.
- Some organisms display decorative structures that change with age, such as the decorative frills and horns of *Triceratops*. This well documented change is used to help identify relative ages. Furthermore, features such as this can be used for competition with other members of the same species and as a result, only grow as the organism reaches sexual maturity.

3.9: IMPLICATIONS FOR ICHTHYOSAUR ONTOGENY

A variety of features that relate to ontogeny are expressed in the organisms discussed above. However, the majority of the ontogenetic features expressed in plesiosaurs, pachypleurosaurs and crocodilians are based on bone fusion. This cannot be examined in ichthyosaurs as the majority of the bones do not typically fuse. Other features of ontogeny relate to ornamentation, such as observed in the frill and horns of *Triceratops*. Ichthyosaurs do not possess similar ornamentation, and therefore this type of investigation is not suitable. However, large skulls, compared to body length, is expressed in plesiosaurs and pachypleurosaurs and this can be examined in ichthyosaurs. Ontogenetic features expressed in bone histology have previously been studied for ichthyosaurs and therefore, will be not examined in this study.

3.10: MATERIALS AND METHODS

Twenty-eight measurements were taken from the skull, femur, humerus, manus and ribs, as well as total body length (data in Appendix 1, sheet 1). The measurements were chosen as those that best represent the size of the organism, individual element or composite body part. These are primarily length and width measurements. The skull measurements were previously defined as were the humeral and femoral lengths and widths

(McGowan and Motani, 2003). Further information on the measurements is in the Methodology chapter (Chapter 2). The points from which measurements were taken have been identified so that they are easily repeatable. If a point was not visible on a specific specimen, the measurement was omitted. Where more than one measurement for a paired was possible on a single specimen (e.g. if both humeri were visible) then both measurements were taken and the average of the two was used in the morphometric tests. Measurements were used from the whole data set, including all taxa (Appendix 1, sheet 1). In order to test whether a taxonomic signal was highlighted, the same analyses were conducted on the dataset for *Stenopterygius* (Appendix 1, sheet 2).

The hypotheses that will be tested in this chapter are: (i) growth of individual skeletal elements are isometric (ii) growth of the skull is isometric compared to the jaw (iii) the skull is relatively larger in inferred younger specimens compared to total body length.

3.11: RESULTS AND INTERPRETATION

3.11.1: Multivariate Analysis: PCA

PCA was conducted first as this is an exploratory technique which identifies any variance within the dataset, which could suggest shape change relating to size in organisms, and therefore ontogeny. These areas that display variance can then be further examined to test whether it relates to ontogeny. PCA was used to compare different measurements taken from the same element against each other in order to display the distribution of taxa in morphospace, and indicate whether growth was isometric or allometric. The results of the PCA were then used to provide a basis for further study to identify skeletal elements or composite body parts that show the greatest change with age. The body parts that were selected for these multivariate analyses were the humerus, femur and skull. The humerus and femur were selected as these elements are readily preserved and well represented within the dataset. Another advantage of using the humerus and femur is that measurements can be obtained when the skeletal elements have been moved from life position. The skull was selected as measurements of the skull and ratios between skull portions (such as snout length and skull length) are used to aid genus and species identification (McGowan & Motani, 2003). It has also been observed in many other organisms that the skull is relatively larger compared to body length in inferred younger specimens than in adult specimens. (e.g., Maiorana, 1976; Vitt & Colli, 1994; Herrel *et al.*, 2008).

3.11.1.1: PCA Analysis: Humerus

The four measurements from the humerus included in the PCA analysis were (A) maximum humerus length; (B) humerus width (minimum width as measured on the shaft of the bone); (C) maximum width of proximal epiphysis; and (D) maximum width of distal epiphysis. These measurements were selected as they best represent the size and shape of the humerus. All measurements were log-transformed before analysis (Fig 3.1). The isometric scaling coefficient used to compare the values in the loadings is calculated using the equation $1/p^{0.5}$ where p is the number of variables (see Chapter 2).

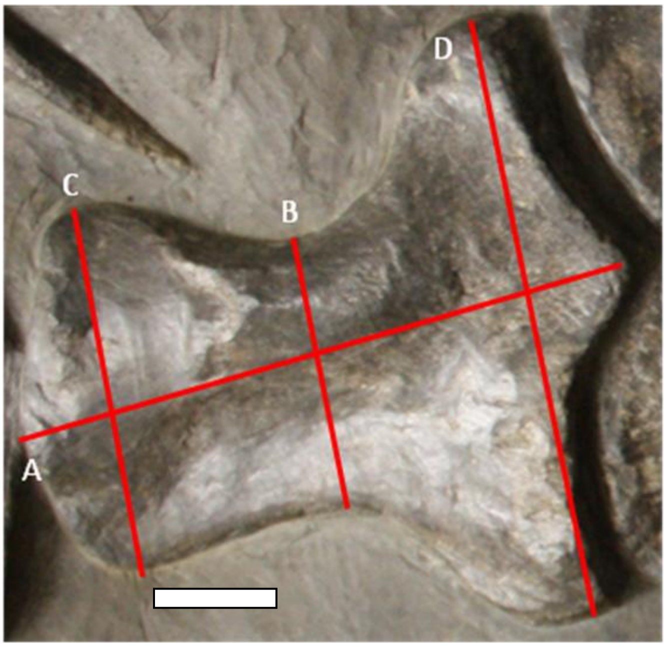


Fig. 3.8: A humerus illustrating the measurements taken; A – Humerus length; B – Humerus width; C – Width of proximal humeral epiphysis; D – Width of distal humeral epiphysis. Scale measures 2cm.

The value of the isometric scaling coefficient for the humerus is 0.5. The loadings (see Chapter 2) show that growth is isometric or very close to isometric for each of the measurements taken (Fig. 3.9A). The loading for log-humerus length is 0.54. Although this is slightly positive allometric growth, it is not markedly different from isometric growth. The loading value for the log-humerus width is 0.46 (Fig 3.2A). Although this is slightly negative allometric growth, it is also not markedly different from the value for isometry. The loading values for the log-proximal and log-distal epiphyses are both 0.5. This shows clear isometric growth. As PC1 accounts for 97.4% for the variance, it can be inferred that this represents size. The specimen indicated by an arrow in the lower left-hand side of the plot (Fig. 3.9B) is an embryo of *Stenopterygius* (SMNS 54064a) and the specimen indicated by the arrow at the right-hand side of PC1 is a large specimen of *Temnodontosaurus* (YORYM 497; Fig. 3.9B). It is therefore likely that PC1 represents relative size differences within the dataset.

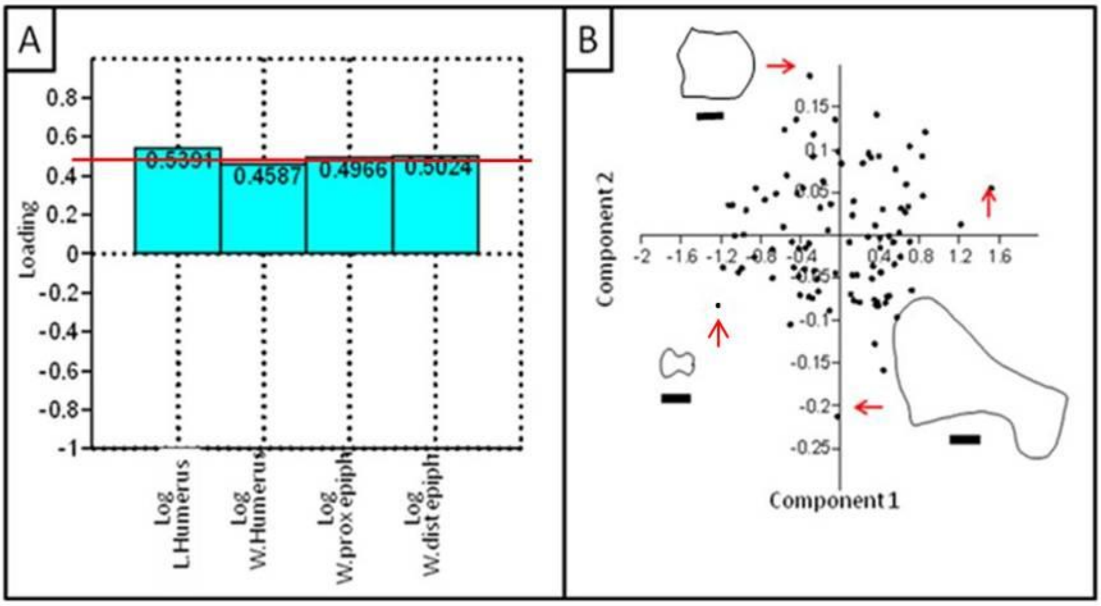


Fig. 3.9: PCA for Humerus (PC1) using the whole dataset showing growth close to isometry (red line on A) with arrows indicating points referred to in the text with A showing the loadings and B showing the scatter plot (n = 100, PC1 = 97.4%, PC2 = 1.55%) Scales measure 1cm in B.

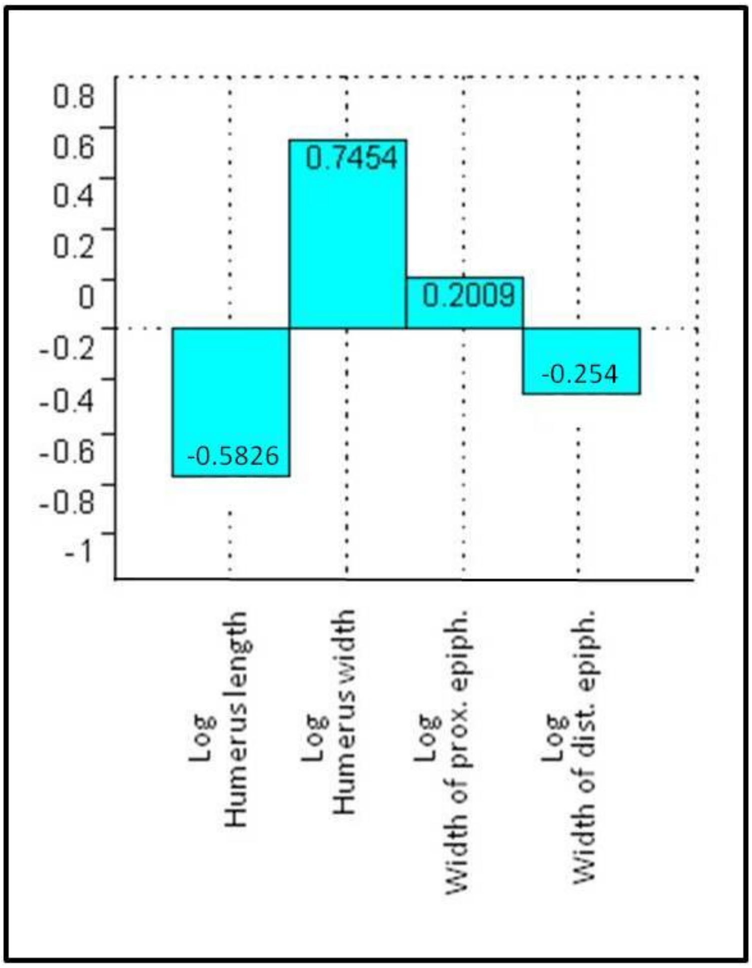


Fig. 3.10: PCA loadings for the humerus (PC2) using the whole dataset showing that humerus length and width are the main contributors to variance on PC2.

This specimen of *Stenopterygius* displays a humeral length of 68.8mm and width of 17.1mm. The difference between the length and width of the humerus is much more pronounced in SMNS 51133 compared to that of NHMUK OR120. Furthermore, the widths of the distal epiphyses also differ with NHMUK OR120 having a width of 25.4mm and SMNS 51133 has a width of 44mm. The loadings on PC2 (Fig. 3.10) show that the main variables contributing to the variance of PC2 are the log-length and log-width of the humerus. This shows that the humerus gets relatively wider with age. However, as this widening is so slight, it cannot be used as an indicator of relative age.

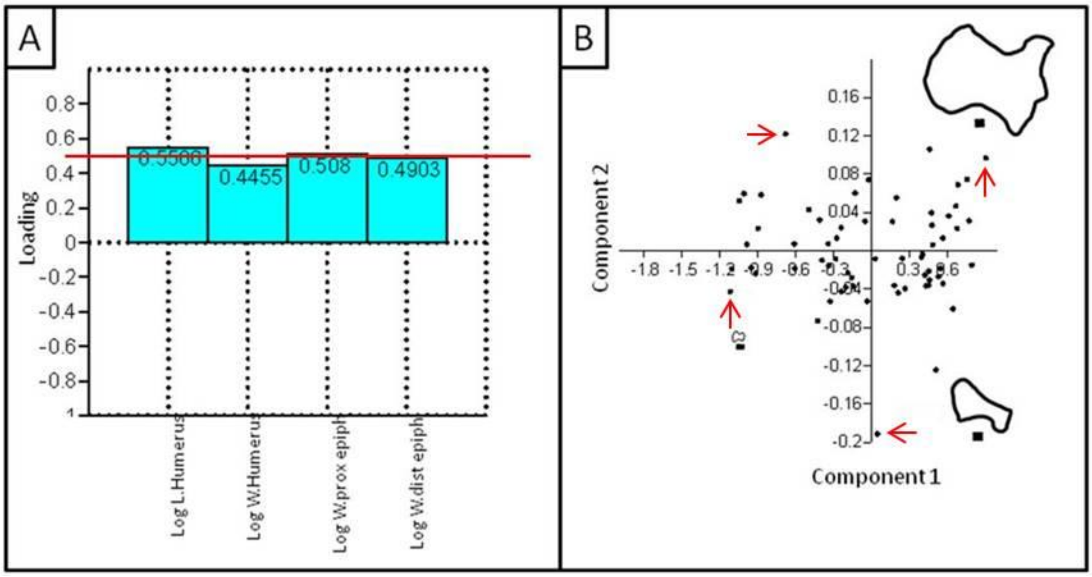


Fig. 3.11: PCA for humerus (PC1) using *Stenopterygius* displaying growth close to isometry (red line in A) with arrows used to indicate outliers covered in the text. A shows the loadings and B shows the scatter plot (n = 64, PC1 = 98.3%, PC2 = 0.82%). Scale bars measure 1cm in B.

The value for the isometric scaling coefficient for the humerus of *Stenopterygius* is 0.5 (Fig. 3.11A). This is used as a comparison to the whole dataset to determine if growth specific to this single genus differs from that of ichthyosaurs as a whole, as represented by the whole dataset. The loading value for the log-humerus length is 0.55 (Fig. 3.11A). This is very close to the value for isometry (0.5) and not sufficiently different to be considered allometric. This is the same as humerus length for the dataset as a whole. The log-width of the humerus for *Stenopterygius* shows slightly negative allometric growth. This is the same as the log-humerus width for the whole dataset and, as with the whole dataset, the value of 0.45 is not considered to differ greatly from isometry. The loading values for the log-width of the proximal and distal epiphyses are 0.51 and 0.5 respectively. This shows the same isometric growth for *Stenopterygius* as for the dataset as a whole. PC1 represents 98.3% of the variance within the dataset. The extreme specimens on PC1 are represented by SMNS 54064a, an embryo of a specimen of *Stenopterygius* sp. and SMNS 17500, a specimen of *Stenopterygius hauffianus*, a large species of *Stenopterygius* (both indicated by arrows). It is therefore likely that PC1 captures the size differences within the dataset. The lowest specimen in the plot on PC2 (Fig. 3.11B) is a specifically indeterminate individual of *Stenopterygius* (SMNS 51133) that displays a relatively large humerus (in all measurements), while the top-most specimen on the PC2 plot (SMNS 51140) is another unidentified species of *Stenopterygius* that displays a relatively small humerus (in all measurements). The loadings for PC2 (Fig. 3.12) show that the log-humerus length and the log-humerus width are the main variables contributing to the variance on PC2. As with humerus for the whole dataset, the humerus for *Stenopterygius* becomes wider with relative age compared to the length.

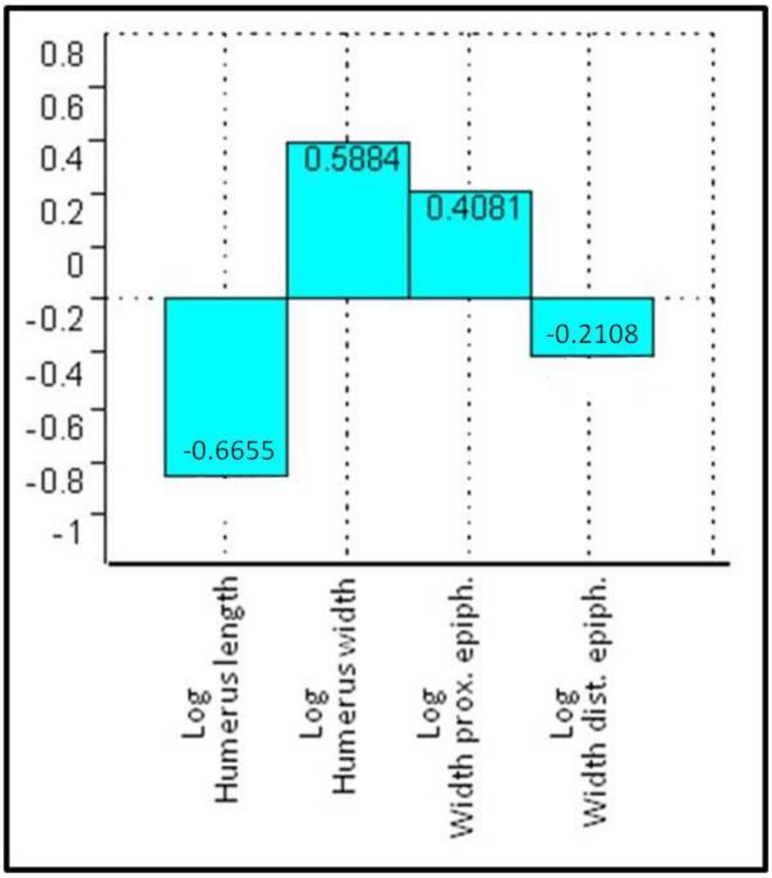


Fig. 3.12: PCA for humerus (PC2) using *Stenopterygius* showing that log-humerus length and log-humerus width are the variables that contribute most to the variance on PC2

In summary, the data shows that growth is largely isometric for the humerus, with the aspect ratio remaining the same at all sizes (and relative ages). Principal Component 1 (PC1) accounts for 97.4% of the variation for the dataset as a whole and 98.3% for *Stenopterygius*. It is most likely that PC1 represents specimen size and accounts for the majority of the variation within the whole dataset as well as for that of *Stenopterygius*. As a result of this, no changes in humerus shape can be used to estimate relative ages in ichthyosaurs.

3.11.1.2: PCA Analysis: Femur

The four measurements from the femur used for the PCA analysis were: (A) maximum femoral length; (B) femoral width (the minimum width of the femur at any point along the shaft); (C) maximum width of the proximal epiphysis; and (D) maximum width of the distal epiphysis (Fig. 3.13). These measurements were log-transformed before being inputted into the analysis. The value for isometry is calculated using the same formula outlined in 3.3.1.1 and the value for isometry on the loadings is 0.5.

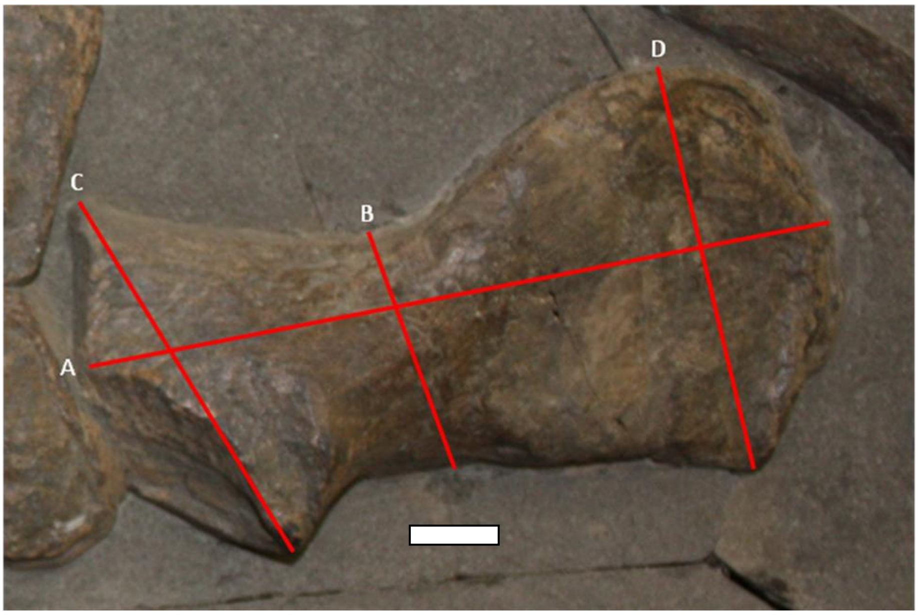


Fig. 3.13: A Femur illustrating the measurements taken; A – Femoral length; B – Femoral width; C – Width of proximal femoral epiphysis; D – Width of distal femoral epiphysis. Scale measures 1cm.

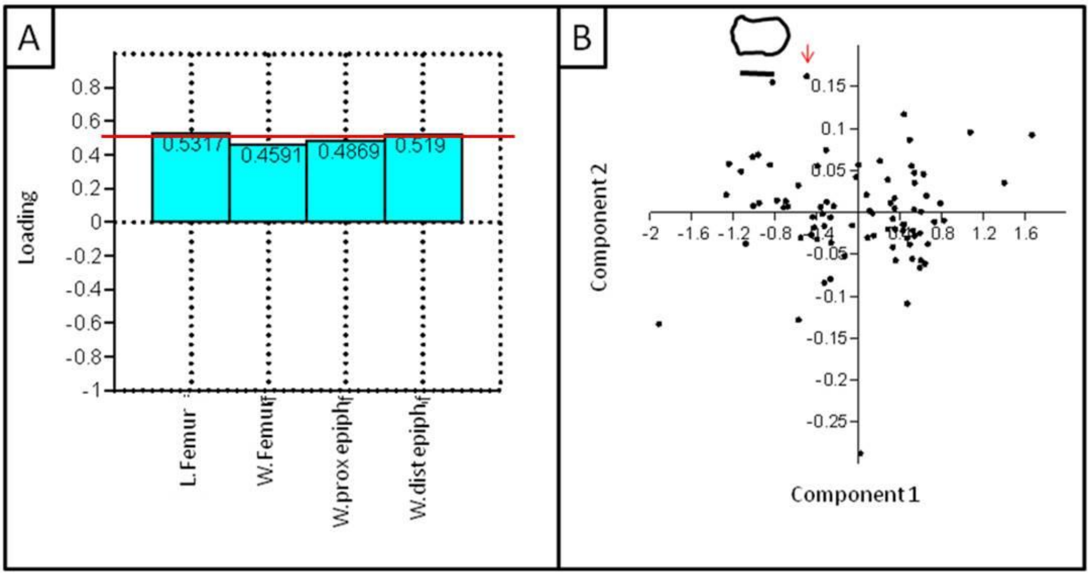


Fig. 3.14: PCA for femur (PC1) using the whole dataset displaying growth close to isometry (indicated by the red line), with A showing the loadings and B showing the scatter plot (n = 84, PC1 = 98.1%, PC2 = 0.89%). Scale measures 1cm in B.

The PCA for the femur of the whole dataset (Fig. 3.14) shows that growth appears to be isometric. The loading value for log-femoral length is 0.53 (Fig. 3.14). This is very close to the value for isometry and is not significantly different to be considered allometric growth. The loading value for the log-width of the femur is 0.46. This value shows slightly negative allometry however it is not considered significantly different from the value for isometric growth. The values for the log-width of the proximal and distal epiphyses are 0.49 and 0.52 respectively. Although these both show allometric growth, again they are not considered to be significantly different from isometry. Consequently, the femur is not a good indicator of relative age in ichthyosaurs.

PC1 accounts for 98.1% of the variance for the dataset. The specimens at either end of PC1 are SMNS 50963a (left-hand side), which is an embryo of an unknown species of *Stenopterygius*, and YORYM 497 (right-hand side), a large specimen of *Temnodontosaurus crassimanus* (Fig. 3.14B). This indicates that size is the main cause of the variance within PC1. PC2 accounts for only 0.89% of the variance. The low outlier on PC2 is represented by an unidentified species of *Stenopterygius* (SMNS 51947) that shows a large femur, with a thin femoral width. The specimen at the top of PC2 is an unidentified specimen that displays a small femur (NHMUK OR120, Fig. 3.14B). As with the humerus, this indicates that PC2 shows that size is the cause of the variance within the dataset.

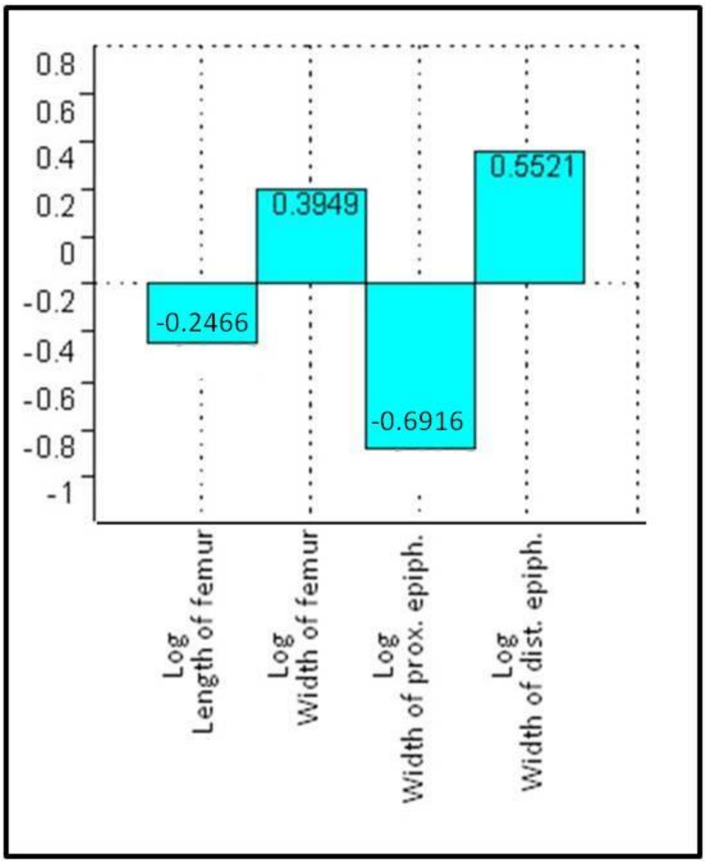


Fig. 3.15: PCA for femur (PC2) using the whole dataset showing the log-width of the epiphyses are the main cause of variance within in PC2.

The loadings for PC2 (Fig. 3.15) show that the main causes of the variance is log-width of the proximal and distal femoral epiphysis. The loadings indicate that the proximal femoral epiphysis gets relatively thinner with age while the distal epiphysis becomes relatively wider.

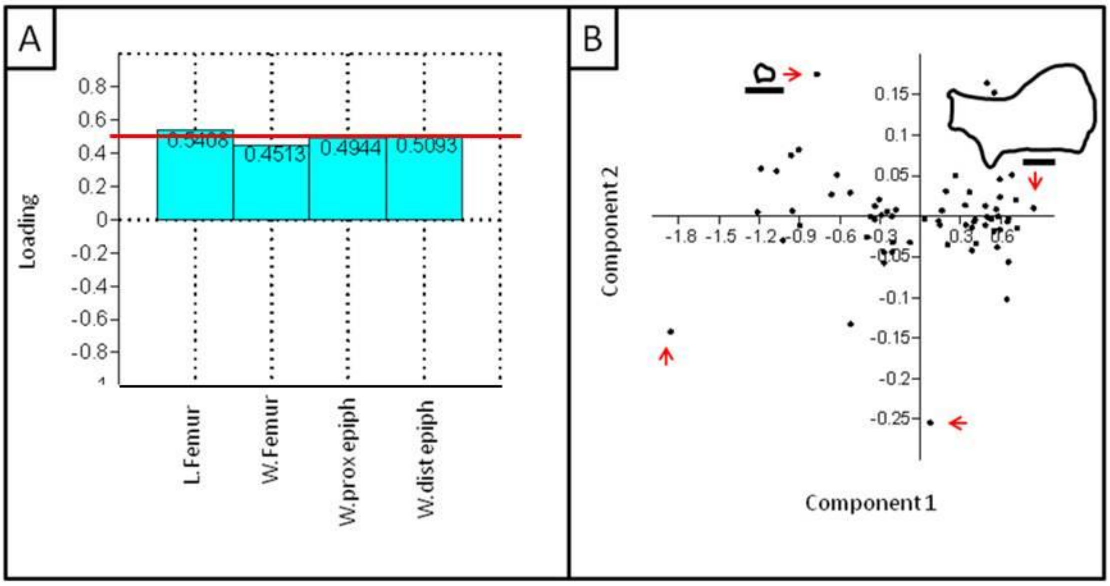


Fig. 3.16: PCA for femur (PC1) using *Stenopterygius* showing growth close to isometry (indicated by the red line), with A showing the loadings and the B showing the scatter plot (n = 65, PC1 = 97.9%, PC2 = 1.0%). Scale measured 2cm in B.

The loadings for the femur of *Stenopterygius* show mostly isometric growth, as for the dataset as a whole. The loading for the log-length of the femur is 0.54 (Fig. 3.16). This shows slight positive allometric growth, but it does not diverge significantly from the value for isometric growth (0.5). The value of the loading for the log-width of the femur is 0.45 (Fig. 3.16). This value shows slight negative allometry but as with log-femoral length, it is not considered a substantial difference from 0.5 which is the value for isometric growth. The loading values for the log-width of the proximal and distal epiphyses are both 0.5. These values show that the growth for the epiphyses is isometric. All of these values show that overall, the femur shows isometric growth and therefore cannot be used as an indicator of relative age. These results are the same as those for the dataset as a whole.

PC1 accounts for 97.9% of the variation in the dataset for *Stenopterygius* femora. The specimens that are positioned as extreme points on PC1 are SMNS 50963a, an embryo of an unidentified species of *Stenopterygius* and SMNS 17500, a large specimen of *S.hauffianus* (Fig. 3.16B). As with the PCA for the whole dataset, the variation on PC1 is most likely caused by the under-developed or poorly preserved proximal femoral epiphysis of SMNS 50963a, an embryo of *Stenopterygius* sp. The cause of the variance between the embryo and a large specimen is most likely to be size. PC2 accounts for only 1.0% of the variation within the dataset. The outlier at the base of PC2 is SMNS 51947. This is an unidentified species of *Stenopterygius* that displays a large femur with a small femoral width. The uppermost specimen of PC2 is SMNS 7402a (Fig. 3.16B). This specimen is an embryo of an unidentified species of *Stenopterygius* and is small. As a result of this, it can be interpreted that the variance in PC2 is caused by the variety of sizes of the specimens.

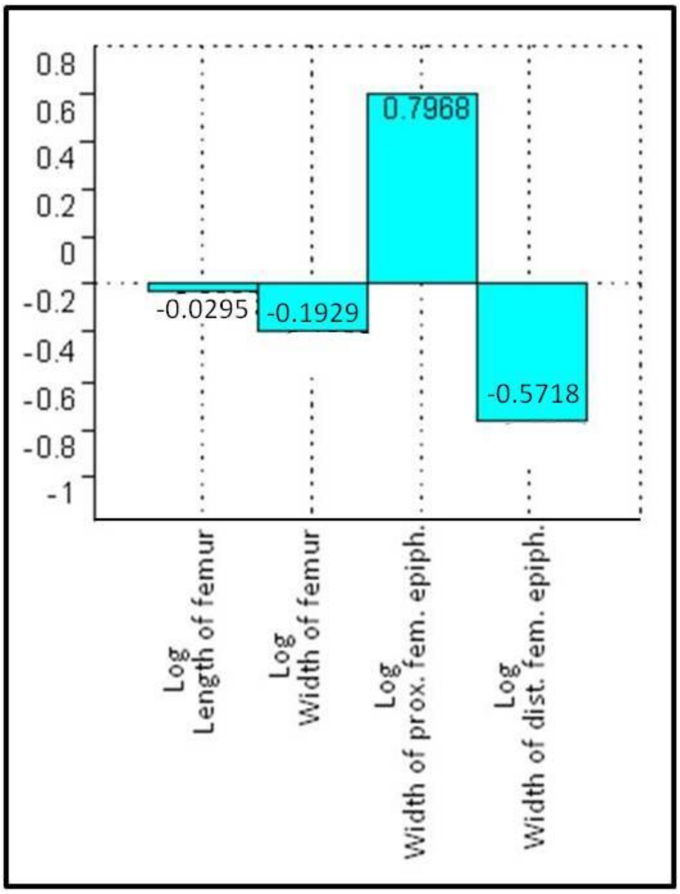


Fig. 3.17: PCA for femur (PC2) using *Stenopterygius* showing that the epiphyses are the main cause of variance for PC2

The loadings for the femur of *Stenopterygius* (PC2) show that the log-width of the proximal and distal epiphyses of the femur are the main cause for the variance within PC2 (Fig. 3.17). This is consistent with PC2 of the femur for the whole dataset. However, for *Stenopterygius* alone, the proximal femoral epiphysis becomes relatively wider with age while the distal epiphysis becomes relatively thinner. The opposite is observed for the dataset as a whole. This may feature may be unique to *Stenopterygius* which suggests that PC2 captures a taxonomic difference within the dataset.

In summary, the result of the PCA analysis for the femur shows that growth was isometric for the whole dataset as well as for *Stenopterygius*. As a result of this, the femur cannot be used to estimate relative age. For the dataset as a whole, PC1 represents size and accounts for the vast majority of the variance. PC2 represents differences in the width of the epiphyses, which could represent an ontogenetic stage, development of the bone or an aspect of preservation. However, as the difference is so slight, this difference cannot be used to estimate relative ages.

3.11.1.3: PCA Analysis: Skull

The eight measurements from the skull that are used for the PCA Analysis are: (A) skull length (distance between the tip of the snout (most distal point of the premaxilla) and the posterior edge of the articular surface of the quadrate); (B) jaw length (distance between the tip of the mandible and the posterior edge of the surangular); (C) snout length (distance between the tip of the snout and the anterior boundary of the orbit); (D) premaxillary length (distance between the tip of the snout and the anterior tip of the maxilla); (E) prenarial length (distance between tip of the snout and the anterior boundary of the external naris); (F) maximum internal diameter of the orbit; (G) maximum external diameter of the sclerotic ring; and (H) maximum internal diameter of the sclerotic ring. The measurements were log-transformed before being analysed (Fig. 3.18).

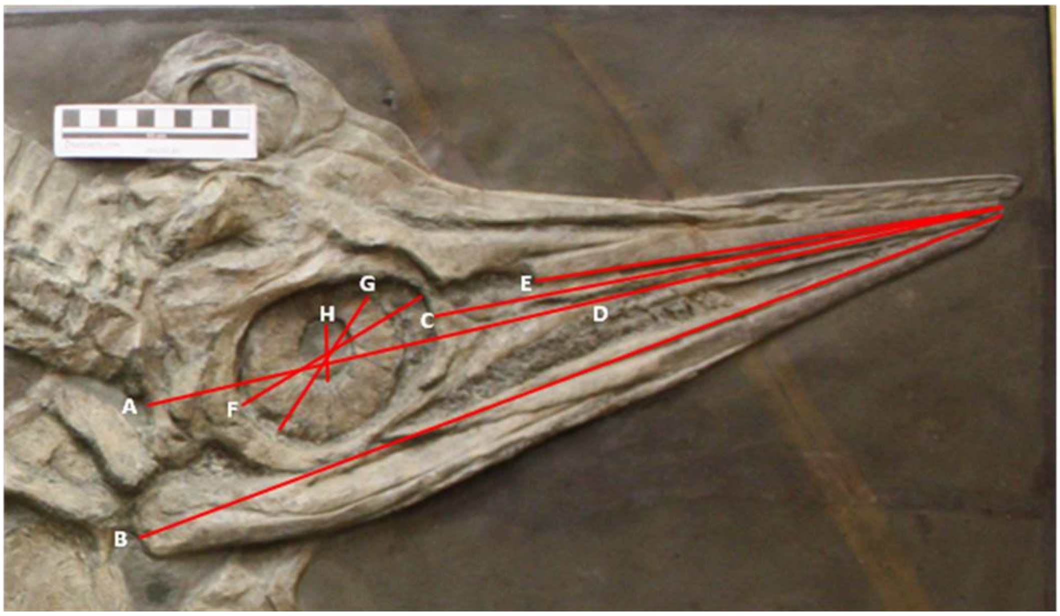


Fig. 3.18: Skull of *Stenopterygius* sp. illustrating the measurements taken.

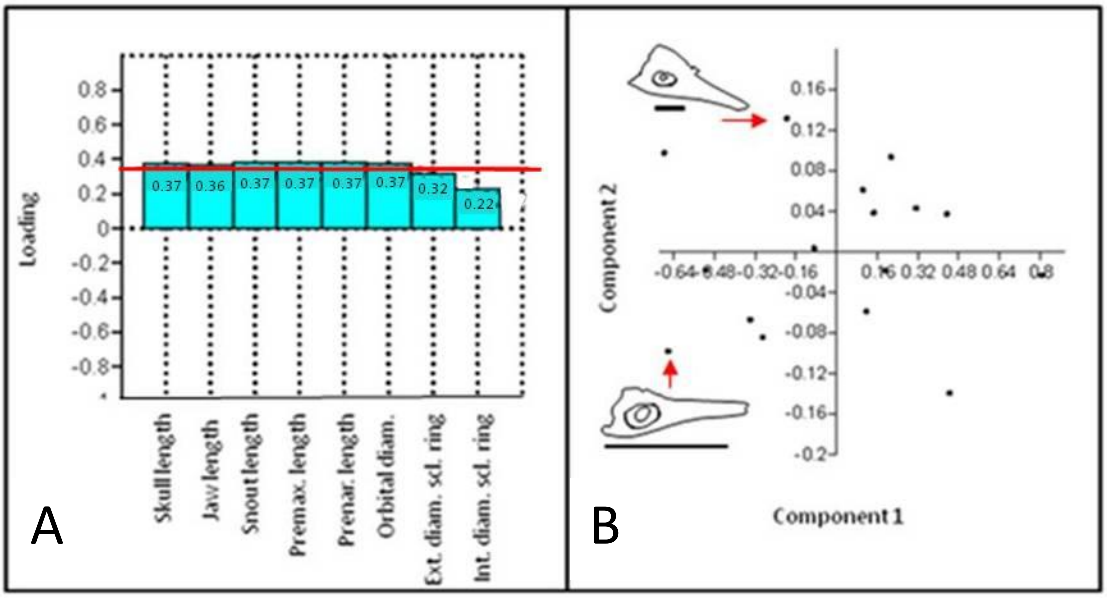


Fig. 3.19: PCA for the skull using the whole dataset showing allometric growth in the sclerotic ring with A showing the loadings (the red line indicates the value of isometry) and B showing the scatter plot (n = 16, PC1 = 94.4%, PC2 = 3.30%). Scale measures 20cm in B.

The value for isometry for the loadings of the skull is 0.35. The log-skull length, log-jaw length, log-snout length, log-premaxillary length, log-prenarial length and log-orbital diameter show loading values between 0.36 and 0.38 (Fig. 3.19A). All of these values indicate slight positive allometric growth but, with the femur and the humerus, they are not very different from the value for isometric growth. The loadings show that the growth patterns exhibited by these elements are all very similar. However, the loading values (Fig. 3.19) drop significantly for the log-diameters of the internal and external edges of the sclerotic ring and are 0.23 and 0.31, respectively, thereby showing significant negative allometry. Consequently, the sclerotic ring becomes relatively smaller as the length of the skull increases. This indicates that it may be possible to use a ratio of the sclerotic ring to skull length/or jaw length to estimate relative age in ichthyosaurs.

PC1 accounts for 94.4% of the variance within the data matrix. The specimen representing the lowest value on PC1 is CAMSM 47057. This is a specimen of *Ichthyosaurus* while the specimen representing the highest value on PC1 is *Suevolethiathan disinteger* (SMNS 15390). It is therefore likely that the variance displayed in PC1 is the result of size differences within the dataset as *Suevolethiathan* is one of the largest genera represented. PC2 accounts for 3.30% of the variance.

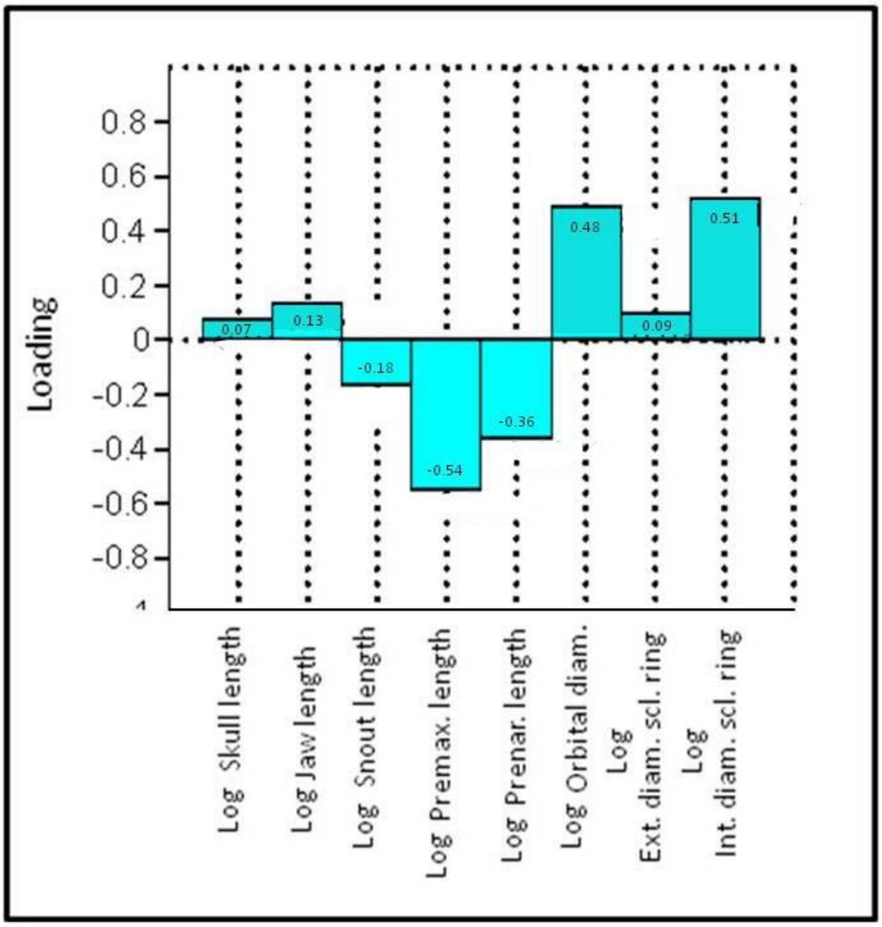


Fig. 3.20: PCA for skull using whole dataset (PC2) showing that prenarial length and the internal diameter of the sclerotic ring are the main contributors to the variance in PC2.

The lowest point on the PC2 axis is SMNS 14846 (Fig. 3.19B). This specimen is *Stenopterygius longifrons* which is a relatively large specimen. The highest point on the PC2 plot is SMNS 7384, a specimen of *Stenopterygius quadriscissus* that displays a much smaller skull. Despite negative allometry being shown, it is still likely that PC2 is accounting for overall size variation. The loadings for PC2 (Fig. 3.20) shows that the premaxillary length, the orbital diameter and the internal diameter of the sclerotic ring are the main contributors to the variance for PC2.

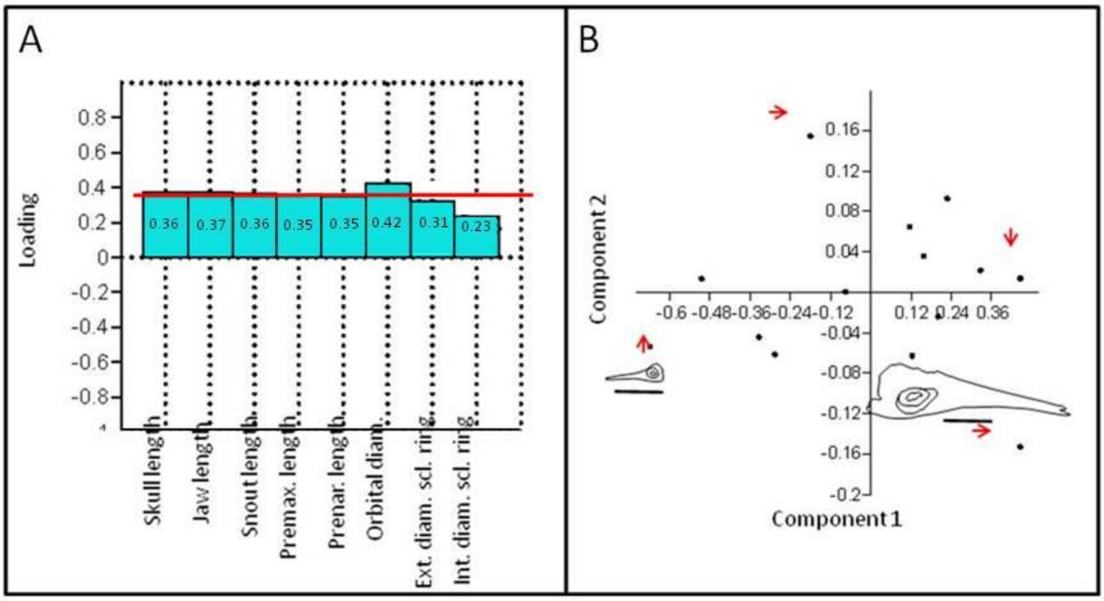


Fig. 3.21: PCA for the skull using *Stenopterygius* showing allometric growth in the sclerotic ring, with A showing the loadings (red line indicates the value of isometry) and B showing the scatter plot (n = 14, PC1 = 92.8%, PC2 = 4.45%). Scale bars measure 20cm in B.

The value for isometry for Fig 3.14A is 0.35. As with the PCA analysis of the skull for the whole dataset, the values for log-skull length, log-jaw length, log-snout length, log-premaxillary length and log-prenarial length for *Stenopterygius* show slight positive allometric growth with loading values ranging between 0.35 and 0.37 (Fig. 3.21A). Again these values are not considered to differ sufficiently from isometry. The loading value for the log-orbital diameter is 0.43 showing positive allometric growth, while the loading values for the log-external and log-internal diameter of the sclerotic ring are 0.32 and 0.23 respectively showing negative allometric growth. These features show that the size of the sclerotic ring becomes smaller as the skull grows, and the orbital diameter expands slightly. Bardet & Fernández (2000) noted that in very small and inferred young individuals, the external edge of the sclerotic ring touches the internal edge of the orbit while in larger and inferred older specimens, the external edge of the sclerotic ring is not in contact with the orbit. The values shown by the PCA analysis in this study fully support this observation both for *Stenopterygius* and for the whole dataset.

PC1 accounts for 92.8% of the variance within the *Stenopterygius* dataset (Fig. 3.21B). The specimen occupying the lowest position on the PC1 axis is SMNS 55109 (3.14B), a specifically indeterminate specimen of *Stenopterygius*. The specimen with the highest value on the PC1 axis is SMNS 51552, which is *Stenopterygius hauffianus* (Fig. 3.21B). The variation on PC1 could be a result of taxonomic differences between the specimens. However, specimen SMNS 55109 possesses a gap between the external edge of the sclerotic ring and the internal edge of the orbit, whereas there is no gap in specimen SMNS 51552, in which the sclerotic ring fills the orbit. It is also possible, therefore, that it is this ontogenetic feature that is causing at least some of the variance captured by PC1.

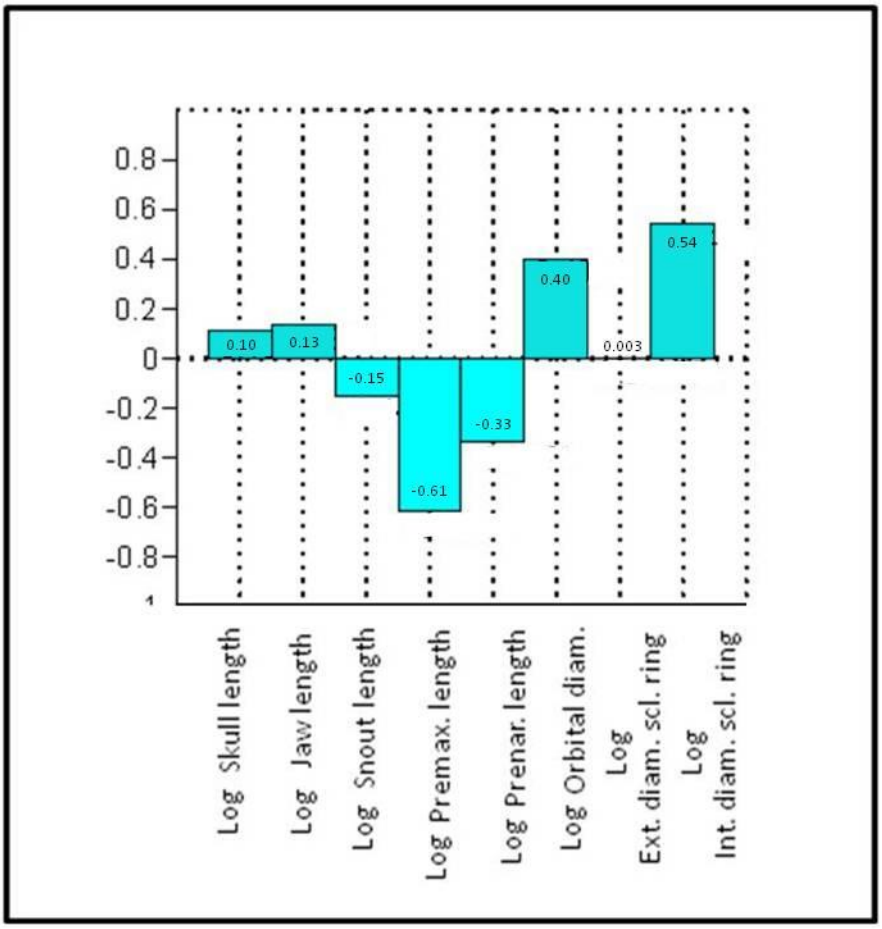


Fig. 3.22: PCA loadings for *Stenopterygius* (PC2) showing that premaxillary length and the internal diameter of the sclerotic ring are the main cause of variance in PC2.

PC2 accounts for 4.45% of the variance within the dataset. The specimen with the lowest value on the PC2 axis is specimen SMNS 14846 (Fig. 3.21B) which is referable to *Stenopterygius zetlandicus*, a taxon with a relatively large skull. The specimen with the highest value on the PC2 axis is specimen SMNS 7384 which is an individual of *Stenopterygius quadriscissus* that displays a relatively small skull. The percentage of variation accounted for by PC2 in the analysis of skull measurements is less than those for the PCA analyses of the humerus and femur. The loadings for PC2 (Fig. 3.22) indicate premaxillary length and the internal diameter of the sclerotic ring account for the majority of the variation within PC2.

3.11.1.4: PCA analysis of all measurements

The measurements used for the PCA are: (i) skull length; (ii) jaw length; (iii) snout length; (iv) premaxillary length; (v) prenarial length; (vi) maximum orbital diameter; (vii) maximum external diameter of the sclerotic ring; (viii) maximum internal diameter of the sclerotic ring; (ix) length of longest digit (average of both if visible, or just one if only left or right is visible; (x) maximum width of manus (average of both if visible, or just one if only left or right is visible); (xi) maximum length of humerus; (xii) minimum width of humerus; (xiii) maximum width of proximal humeral epiphysis; (xiv) maximum width of distal humeral epiphysis; (xv) maximum length of femur; (xvi) minimum width of femur; (xvii) maximum width of proximal femoral epiphysis; (xviii) body length (measured from the tip of the snout to the tip of the tail along the spinal column); and (xvx) body length excluding post-flexural vertebrae to the tail bend (measured from the tip of the snout to the middle of the tail bend). The measurements are all log-transformed.

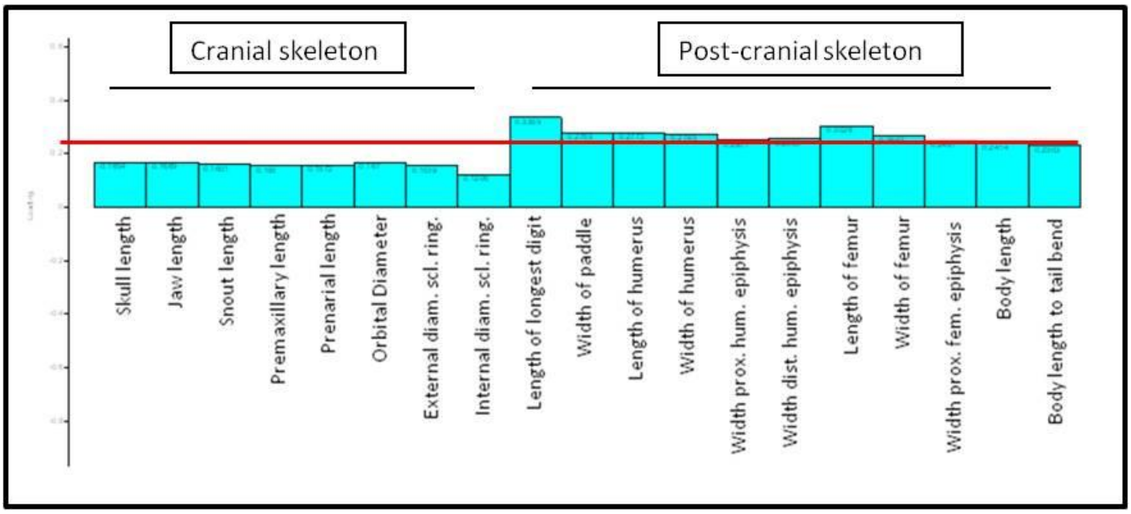


Fig. 3.23: Loadings from the PCA analysis for all measurements (n = 7. Value for isometry = 0.229, shown by the red line.

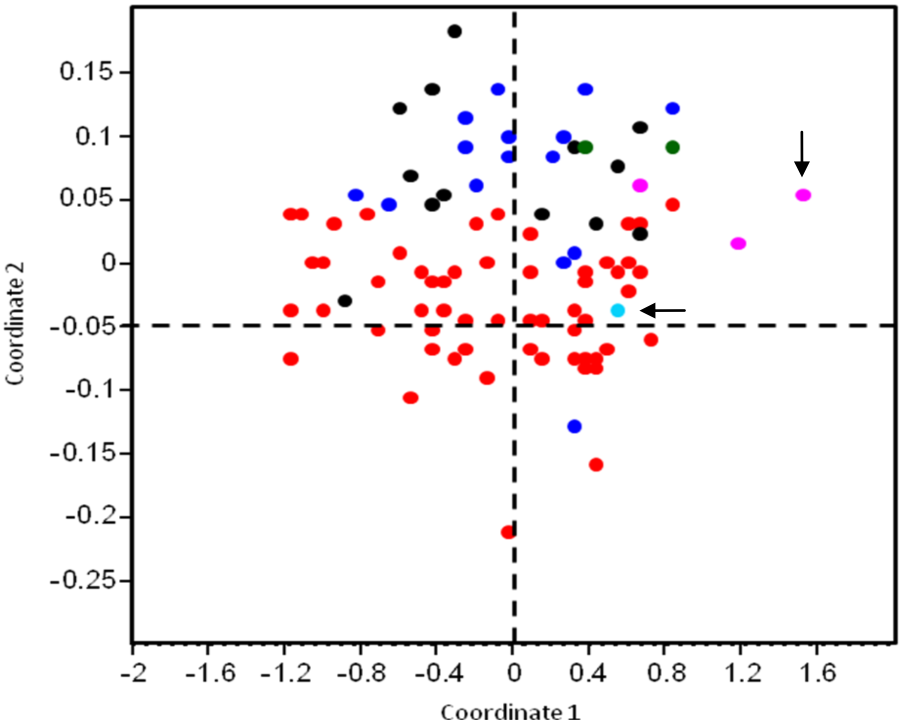
The analysis indicates that the cranial skeleton is generally negatively allometric while the postcranial skeleton is positively allometric (Fig. 3.23). This shows that the skull becomes smaller relative to the postcranial skeleton with age. Total body length and the body length anterior to the tail bend show growth that is very close to isometry. However, only seven specimens could be included in this analysis, as specimens lacking any relevant variables cannot be used. As n is so small, these results should be considered with caution.

3.11.2: Multivariate Analysis: PCO

PCO is a multivariate technique that uses the morphometric data collected to create Euclidean distances between data points. PCO is used to help highlight areas of possible allometric growth that. The results for PCO can show clusters of similar groups. Therefore, if smaller specimens cluster in one area and larger specimens cluster in other areas, allometric growth is indicated. If there are no groupings, then isometric growth is indicated. . For more details on PCO, see Chapter 2. The measurements and the data used are the same as those employed for the PCA analyses of the femur, humerus and skull (section 3.3.1). As with the PCA analysis, the measurements were all log-transformed before being entered into the analysis.

3.11.2.1: PCO analysis: Humerus

The PCO analysis of the humerus for the whole dataset shows some groupings (Fig 3.7). *Stenopterygius* occupies most of the central area of morphospace, while a cluster above this represents *Ichthyosaurus*. The majority of the taxonomically indeterminate specimens (black) also appear in the area occupied by *Ichthyosaurus* suggesting that these could be referable to this taxon. Similarly, one unidentified specimen plots within the area occupied by *Stenopterygius* suggesting that it belongs in this genus. A single specimen identified as *Ichthyosaurus* plots in the area covered by *Stenopterygius*, suggesting that this specimen has been wrongly identified. Large specimens of *Temnodontosaurus* appear in the top right-hand corner of the plot (Fig. 3.24). *Suevoleviathan*, another large genus, plots close to *Temnodontosaurus*. This suggests that this cluster potentially represents larger genera. The single specimen of *Leptonectes* plots close to *Stenopterygius*. This is expected as the specimen is similar in size to many of the *Stenopterygius* specimens. More specimens of *Leptonectes* would need to be included in the analysis in order to see if they form a coherent group. This genus is not well represented in the museums visited which have resulted in this genus being poorly represented in the dataset. Specimens of the same taxa tend to group together, which suggests that the humerus have a taxonomic signal rather than capturing ontogenetic variation.

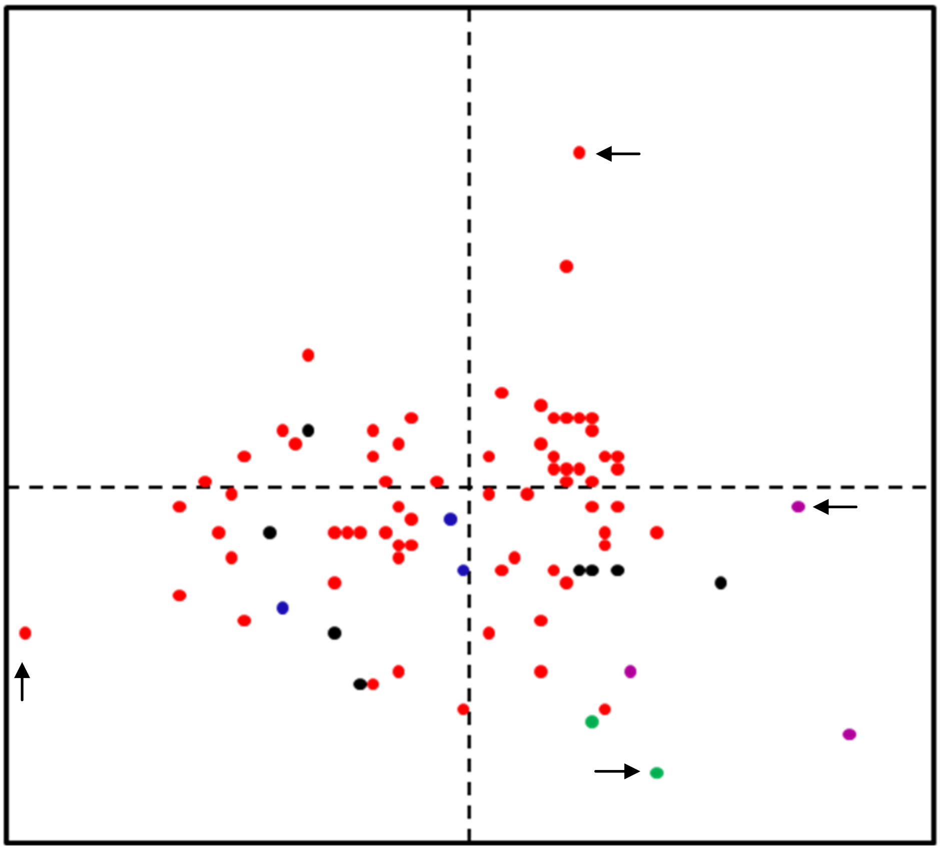


Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unidentified Pink = *Temnodontosaurus*; Green = *Suevoleviathan*; Light Blue = *Leptonectes*

Fig. 3.24: PCO for humerus using the whole dataset, illustrating groupings according to taxa with outliers referred to in the text indicated by arrows. n = 64

3.11.2.2: PCO Analysis: Femur

PCO analysis of the femoral measurements shows no clustering within the dataset (Fig 3.18). The PCO analysis shows that *Ichthyosaurus* specimens are mixed within the area occupied by *Stenopterygius*. The taxonomically indeterminate specimens also plot among *Stenopterygius* specimens. Genera that contain larger individuals, ,*Temnodontosaurus* and *Suevoleviathan*, plot in the lower right side of the plot (Fig. 3.25). However, this does still overlap the areas occupied by other taxa in the morphospace. As a result, PCO of the femoral measurements cannot be used to distinguish either ontogenetic or taxonomic characteristics. However, there are some outliers in this dataset that require further examination.

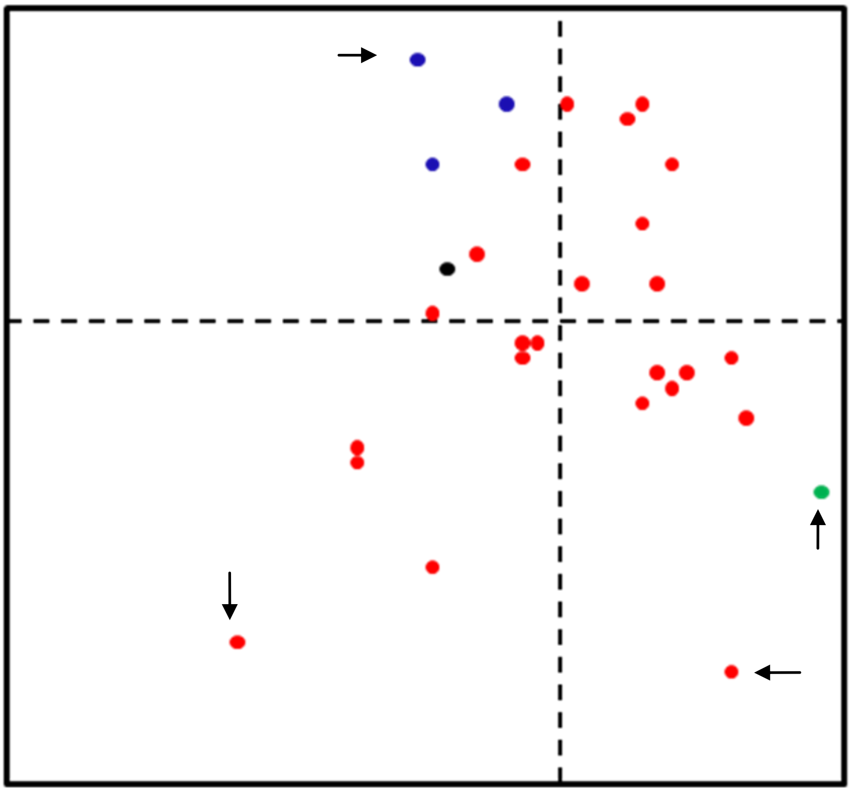


Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unknown Pink = *Temnodontosaurus*; Green = *Suevoleviathan*

Fig. 3.25: PCO for femoral measurements using the whole dataset. No obvious groupings are recovered. Outliers mentioned in the text are marked by arrows. n = 84

The extreme point at the top in the middle of the dataset (Fig. 3.25) represents specimen SMNS 55784, a specifically indeterminate individual of *Stenopterygius*. The femur of this specimen displays a narrow femoral width compared to its proximal distal epiphysis. This may be the reason for it plotting at the edge of the morphospace. The specimen at the bottom of the plot is SMNS 15390, an example of *Suevoleviathan*. The outlier positioned on the far left-hand side of the plot is represented by specimen SMNS 50963a, an embryo associated with a specifically indeterminate individual of *Stenopterygius*. The femur of the embryo is miniscule causing it to be positioned as an outlier. The outlier on the middle right-hand side of the plot (Fig. 3.25) is YORYM 497, a very large specimen of *Temnodontosaurus crassimanus* with a very large femur and is likely the main reason for it plots as an outlier. The incorporation of three additional specimens that include missing data for one measurement into this analysis does not affect these results.

3.11.2.3: PCO Analysis: Skull



Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unknown; Green = *Suevoleviathan*

Fig. 3.26: PCO for the skull measurements using the whole dataset, including specimens with absent data for one measurement, showing one grouping (n = 28).

The PCO analysis for the skull measurements does not show obvious, clear groupings (Fig. 3.26). However, it does show one small group forming at the top, representing *Ichthyosaurus*. The majority of the specimens included in the dataset belong to *Stenopterygius*. *Ichthyosaurus* plots at the top centre of the morphospace. The *n* value is relatively low so the results of this analysis are inconclusive. The extreme points on PC1 are SMNS 50963a (bottom left), an embryo of a specifically indeterminate individual of *Stenopterygius*. The extreme right-hand (green) point is SMNS 15390, a specimen of *Sue. disinteger*, a very large ichthyosaur, with a total body length of 4330 mm. The small size of the embryo skull (SMNS 50963a) and the large size of the *Suevoleviathan* cause these specimens to plot as extreme points. The highest extreme point at the top left of the PCO plot is an unidentified species of *Ichthyosaurus* from the Sedgwick Museum, Cambridge, which does not have a collection number, while the lowest point (bottom right) is SMNS 14846, a specimen of *S. longifrons*. This indicates that taxonomical differences might result in the specimens plotting as extreme points in the morphospace.

3.11.3: Bivariate Analysis: RMA

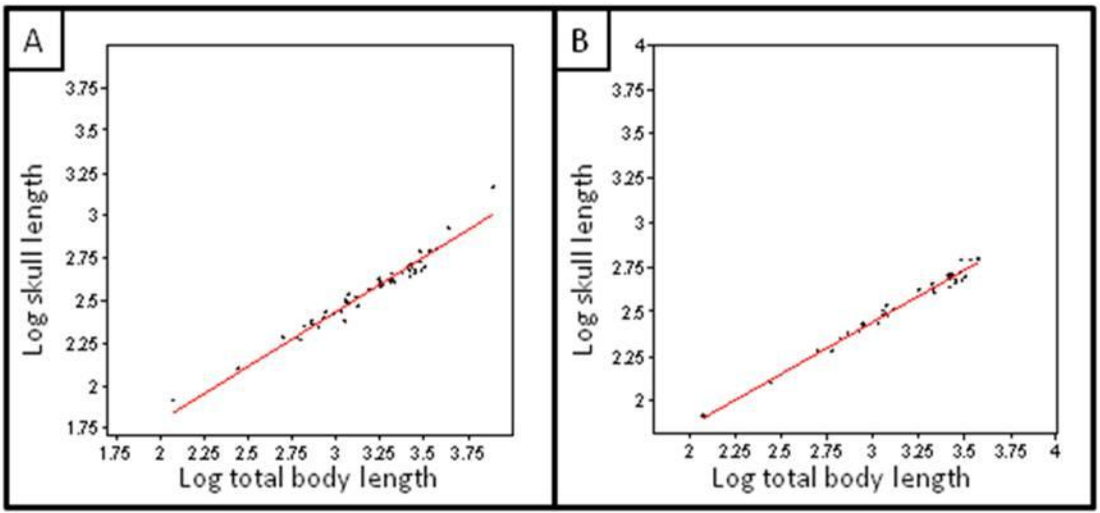
Reduced Major Axis (RMA) bivariate analysis was used to show whether growth was isometric or allometric as allometric growth can relate to ontogeny. Bivariate analyses are primarily used on areas of possible ontogenetic growth as indicated by the PCA and PCO analyses. Type II regression is employed, as the data on both the *x* and *y* axis were collected in the same way (both measured as either lengths or widths). Type II regression reduces error on both axes (Hammer and Harper, 2006). Bootstrap tests and Pearson's 'R' Correlation were also used in conjunction with the RMA analysis. The Pearson's R was used to test the strength of the relationship between the two variables. The closer to 1 this is, the stronger the relationship. A bootstrap test was used to determine the 95% confidence interval for the allometric coefficient α (the line of best fit for the data). This was used to determine if growth of any individual element deviates significantly from isometry. The Bootstrap provides two figures that are the lower and upper intervals that α has a 95% chance of passing through. For example, if the confidence intervals are 0.95-1.05 then values outside the range 0.95-1.05 would indicate either negative (<0.95) or positive (>1.05) allometry. The measurements that best represent the size and shape of the individual elements and composite body parts have been selected. These are typically length and width. In addition to these, growth that is indicated to be strongly allometric in the PCA is further tested using RMA. The skeletal elements and composite body parts being studied in this section are: the humerus and femur as individual skeletal elements; skull length vs. jaw length, length of longest digit vs. width of manus and skull length vs. total body length for composite body parts. These are then used to test the hypotheses that: (i) the growth of individual skeletal elements will be isometric; (ii) the growth of the skull will be isometric; (iii) the skull will be relatively larger in younger specimens and will therefore display allometric growth when compared to body length. Lastly, skull length vs. the external diameter of the sclerotic ring is being tested further as the PCA analysis indicated allometric growth for this relationship.

3.11.3.1: All measurements vs. total body length

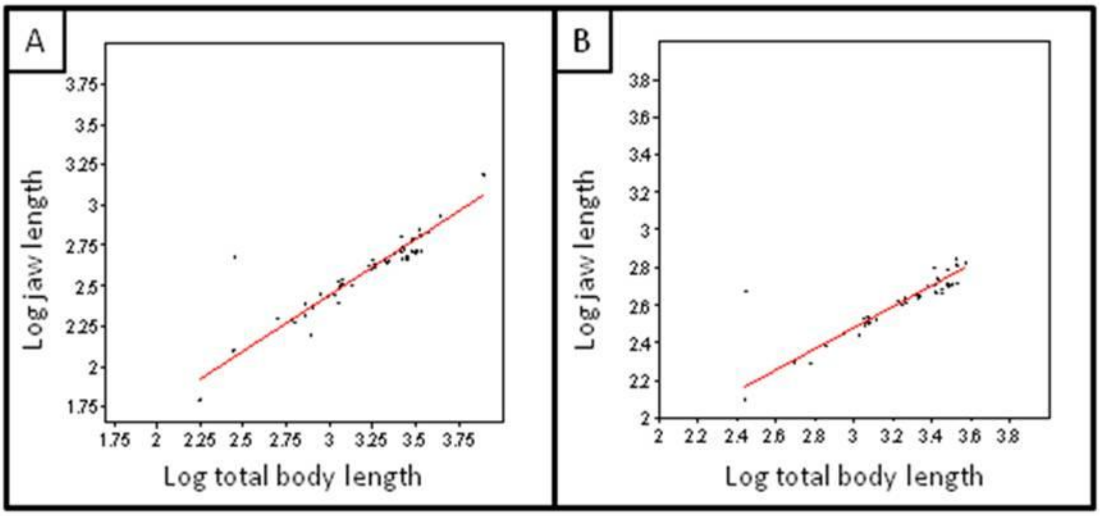
To test if there are any other areas of the body that could be used to estimate relative ages, each length and width measurement was compared to total body length. Total body length is used to represent size, and therefore the age of a specimen. If growth of a different skeletal element is allometric compared to body length, then that could be used to represent size and age.

The results show that the measurements of the cranial skeleton (skull length, jaw length, snout length, premaxillary length, prenarial length, orbital diameter and the diameters of the internal and external edges of the sclerotic ring) all show negative allometric growth when compared to the body length (Figs 3.20, 3.21, 3.22I & II). This shows that the skull grows relatively slower and therefore becomes proportionally shorter as ichthyosaurs grow larger.

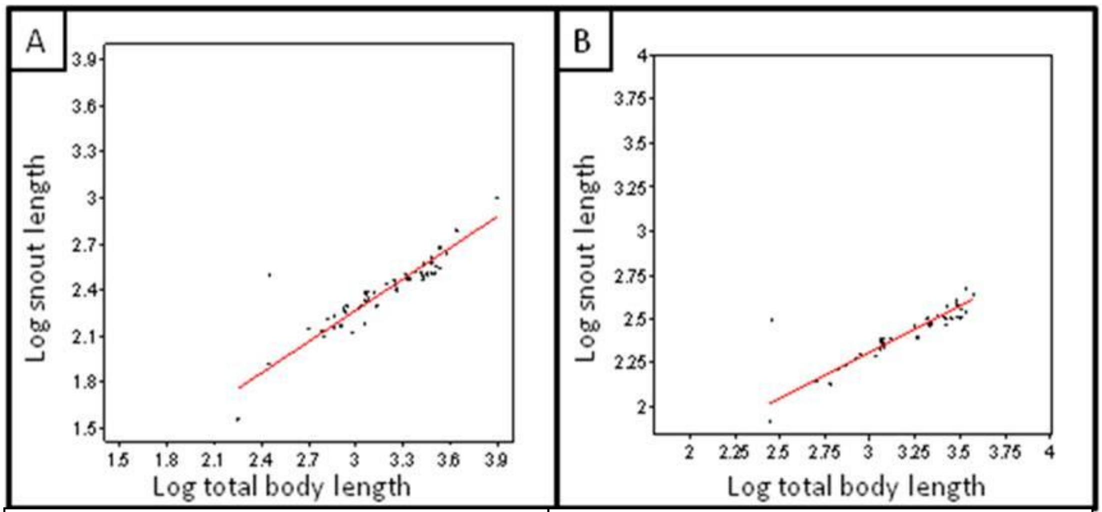
However, the results for the postcranial skeleton show isometric growth for all measurements when compared to body length (Figs 3.22III, 3.23, 3.24, 3.25, 3.26), indicating that these ichthyosaurs grow at the same rate and the aspect ratio remains the same at all ontogenetic stages. The only exception to this is the humerus length which displays slight positive allometric growth compared to body length (Fig 3.23II). Bootstrap values for the humerus length compared to body length are 1.10–1.26 for the whole dataset and 1.18–1.32 for *Stenopterygius* alone. Results for humerus length compared to body length for the whole dataset and for *Stenopterygius* alone both are very close to isometry. Consequently it is doubtful that this feature could be used to help identify ontogenetic stages for ichthyosaurs.



n = 50 *a* = 0.64 *r* = 0.98 Boot = 0.57–0.70	n = 35 *a* = 0.58 *r* = 0.99 Boot = 0.55–0.61

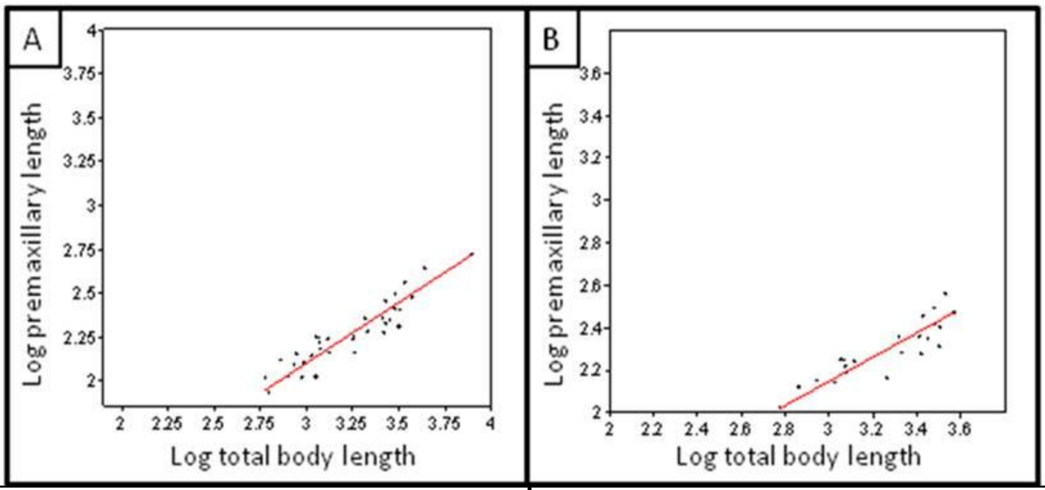


n = 53 *a* = 0.69 *r* = 0.90 Boot = 0.61–0.80	n = 39 *a* = 0.56 *r* = 0.86 Boot = 0.48–0.69



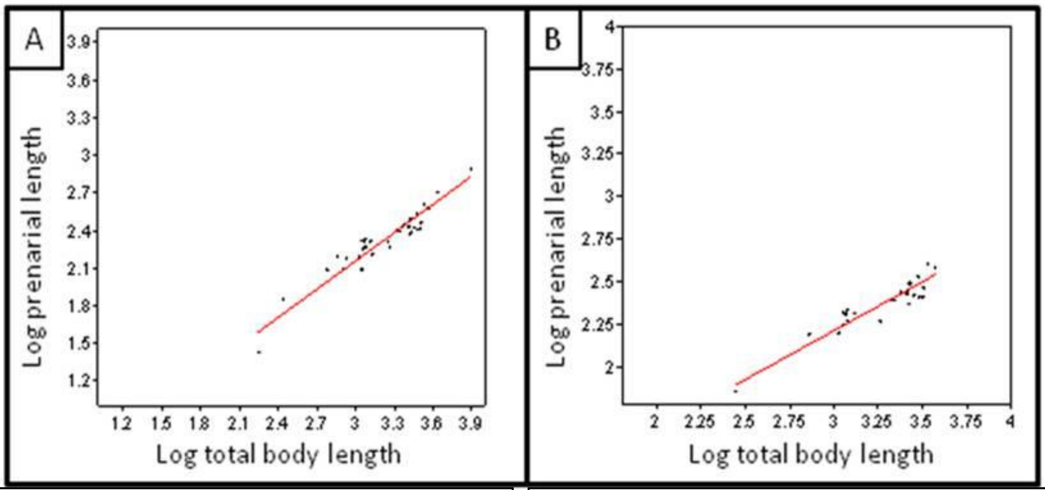
n = 53 *a* = 0.68 *r* = 0.89 Boot = 0.59–0.80	n = 37 *a* = 0.52 *r* = 0.85 Boot = 0.44–0.64

Fig. 3.27: RMA for skull length, jaw length and snout length for the whole dataset (A) and *Stenopterygius* (B), showing negative allometric growth when compared to body length.



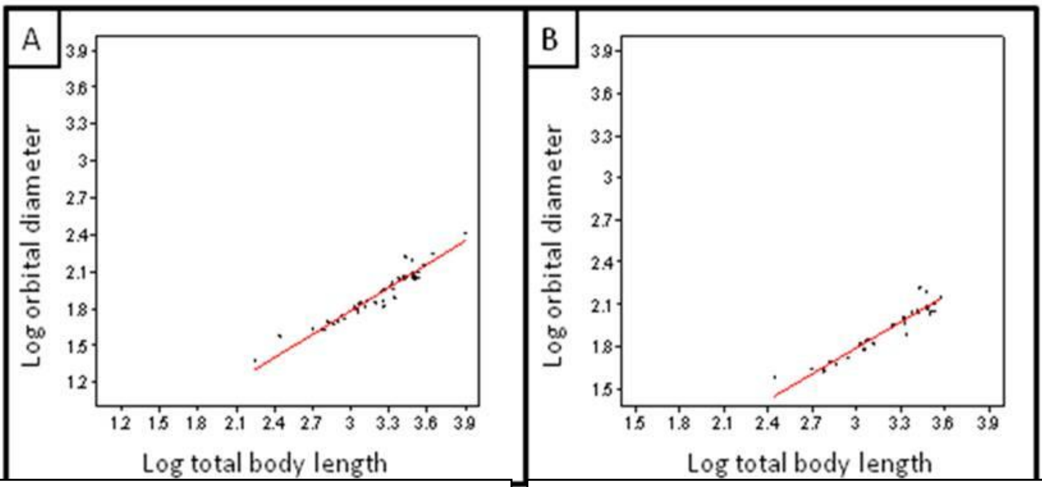
n = 35 *a* = 0.69 *r* = 0.92 Boot = 0.60–0.78

n = 22 *a* = 0.57 *r* = 0.88 Boot = 0.46–0.68



n = 35 *a* = 0.75 *r* = 0.95 Boot = 0.66–0.89

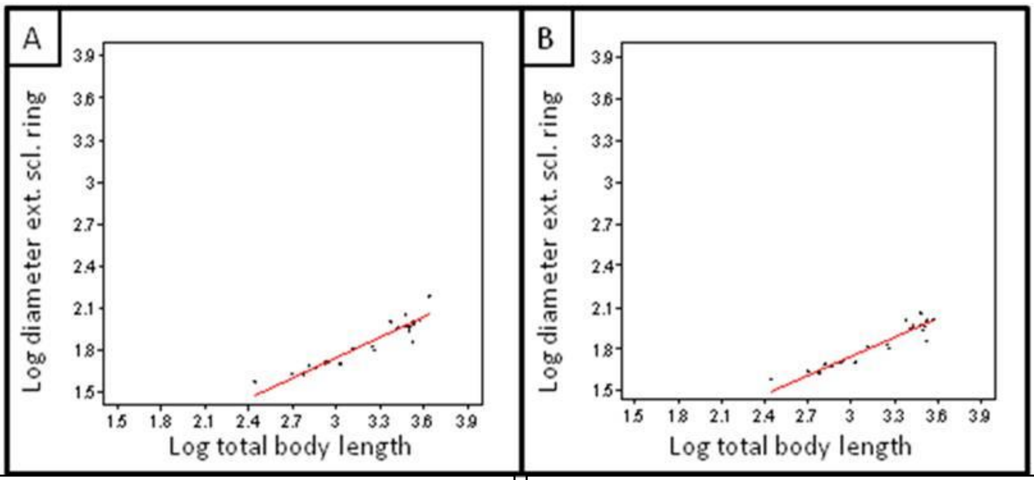
n = 25 *a* = 0.58 *r* = 0.94 Boot = 0.52–0.67



n = 45 *a* = 0.63 *r* = 0.96 Boot = 0.56–0.69

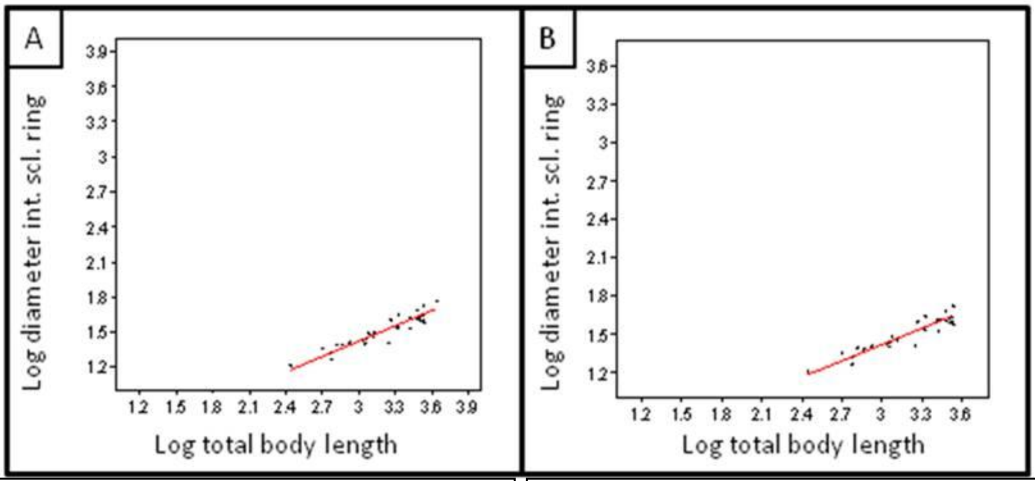
n = 32 *a* = 0.61 *r* = 0.95 Boot = 0.51–0.69

Fig. 3.28: RMA for premaxillary and prenarial length and orbital diameter for the whole dataset (A) and *Stenopterygius* (B), showing negative allometric growth compared to body length.



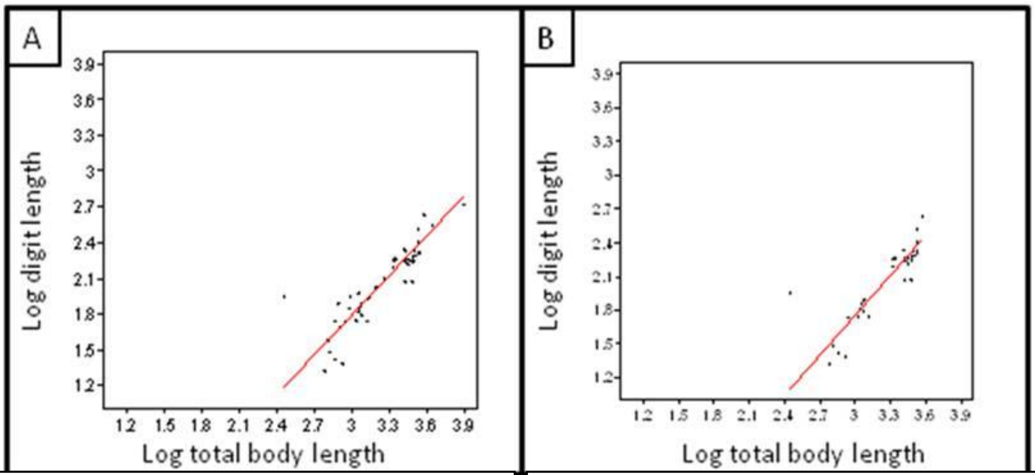
n = 26 $a = 0.48$ $r = 0.94$ Boot = 0.39–0.55

n = 23 $a = 0.45$ $r = 0.95$ Boot = 0.39–0.51



n = 31 $a = 0.44$ $r = 0.93$ Boot = 0.37–0.49

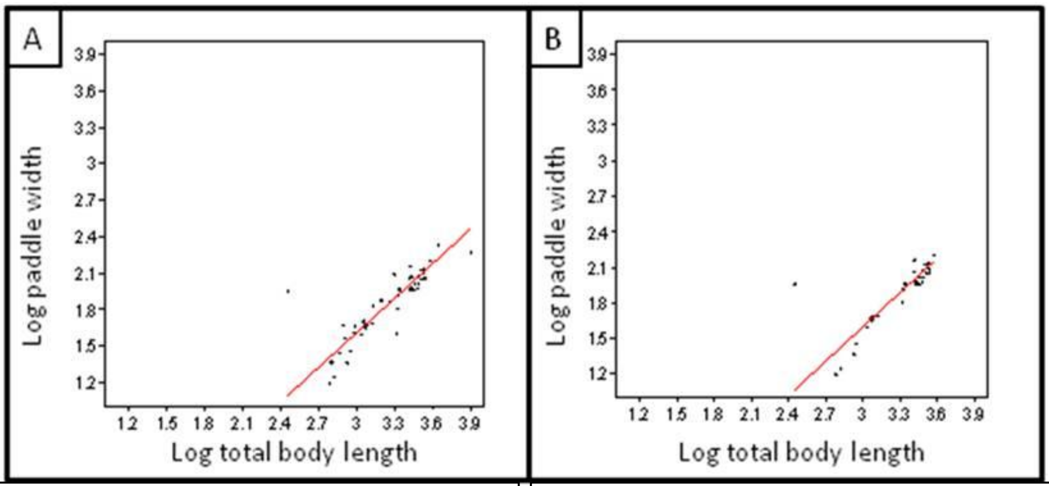
n = 27 $a = 0.42$ $r = 0.93$ Boot = 0.34–0.48



n = 47 $a = 1.11$ $r = 0.89$ Boot = 0.90–1.32

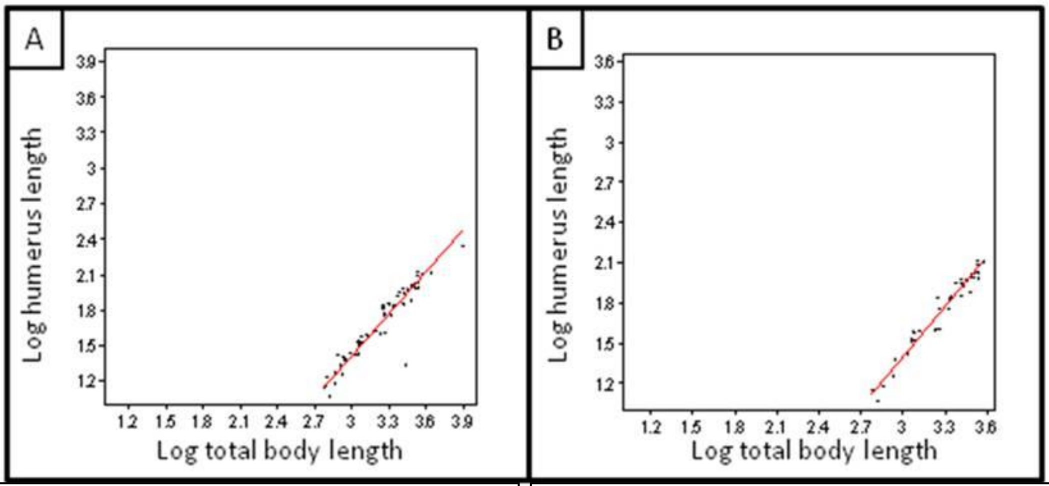
n = 33 $a = 1.18$ $r = 0.85$ Boot = 0.89–1.5

Fig. 3.29: RMA for the internal and external diameter of the sclerotic ring and the length of the longest digit for the whole dataset (A) and *Stenopterygius* (B), showing negative allometric growth for the cranial elements and isometric growth for the postcranial elements.



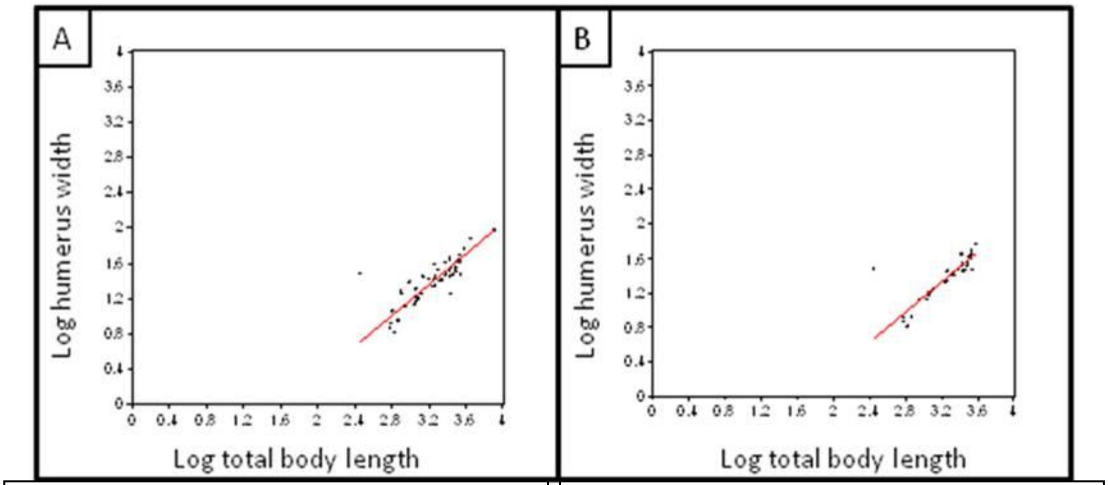
n = 49 *a* = 0.95 *r* = 0.83 Boot = 0.76–1.13

n = 33 *a* = 0.97 *r* = 0.79 Boot = 0.73–1.25



n = 55 *a* = 1.19 *r* = 0.95 Boot = 1.10–1.26

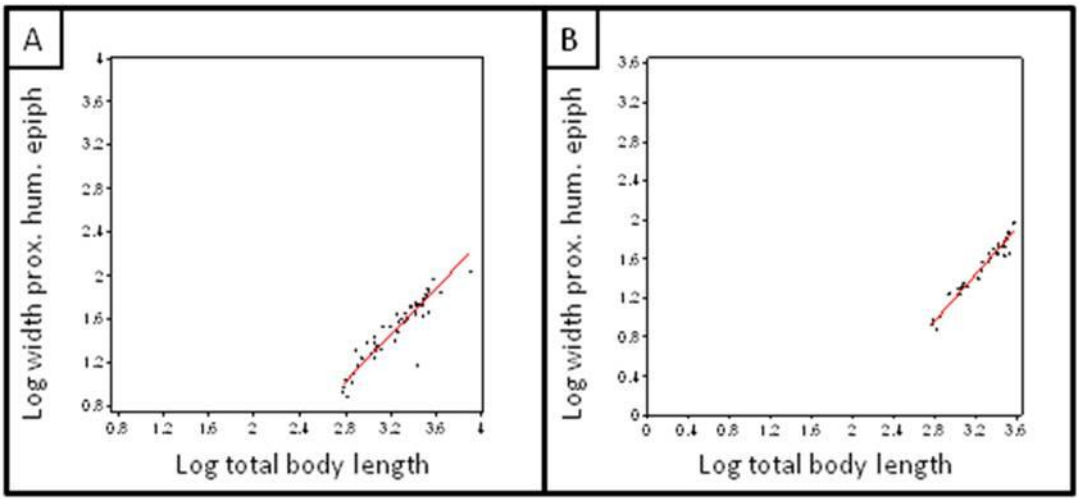
n = 38 *a* = 1.25 *r* = 0.98 Boot = 1.18–1.32



n = 55 *a* = 0.88 *r* = 0.81 Boot = 0.73–1.03

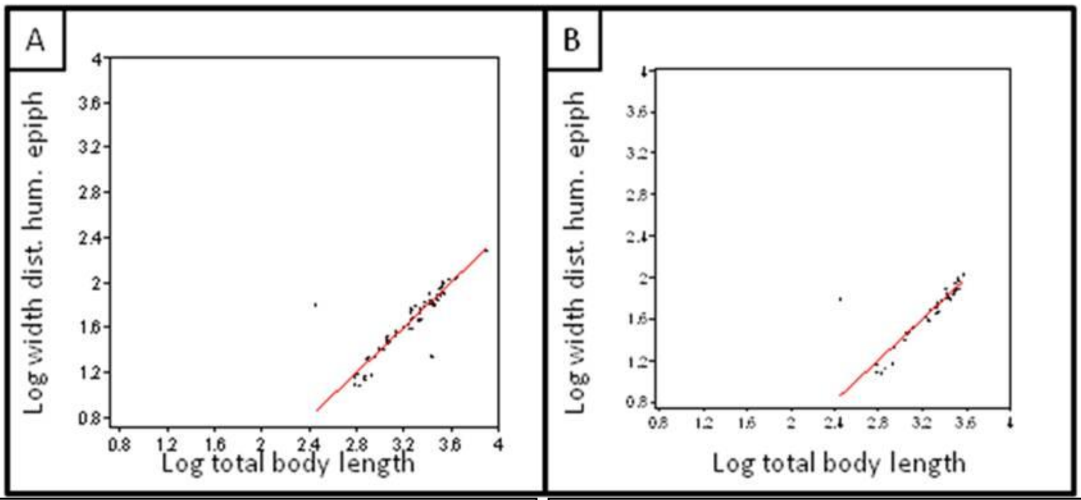
n = 39 *a* = 0.88 *r* = 0.80 Boot = 0.69–1.11

Fig. 3.30: RMA for manus width, humerus length and width for the whole dataset (A) and *Stenopterygius* (B), showing isometric growth when compared to body length, with the exception of humerus length that shows positive allometric growth when compared to body length



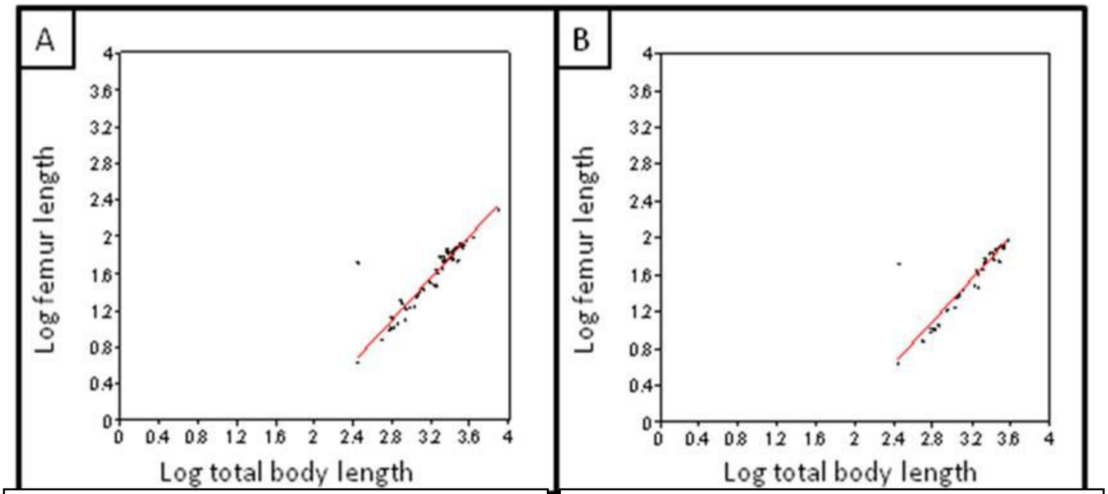
n = 52 a = 1.08 r = 0.92 Boot = 0.98–1.19

n = 36 a = 1.19 r = 0.98 Boot = 1.12–1.28



n = 56 a = 1.00 r = 0.85 Boot = 0.88–1.16

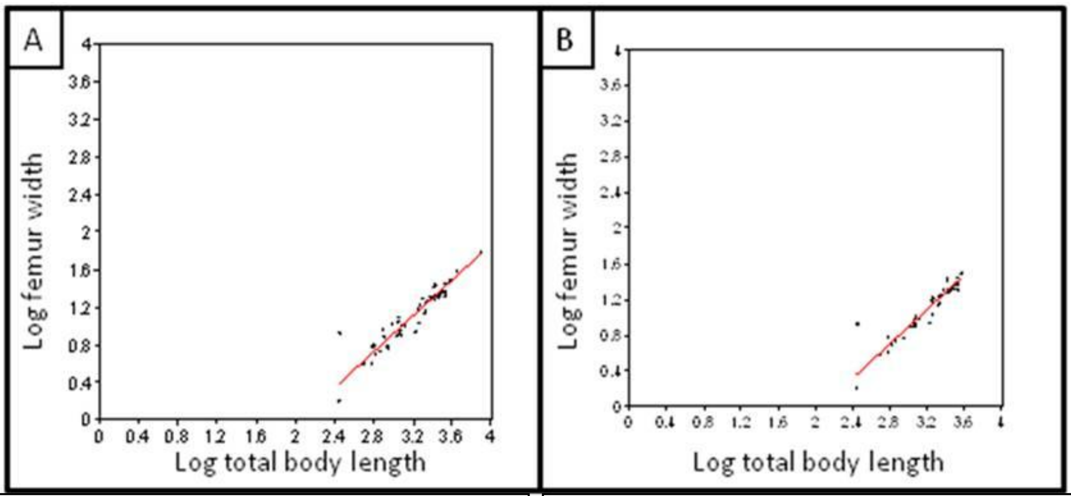
n = 40 a = 0.99 r = 0.82 Boot = 0.80–1.22



n = 55 a = 1.15 r = 0.90 Boot = 1.03–1.29

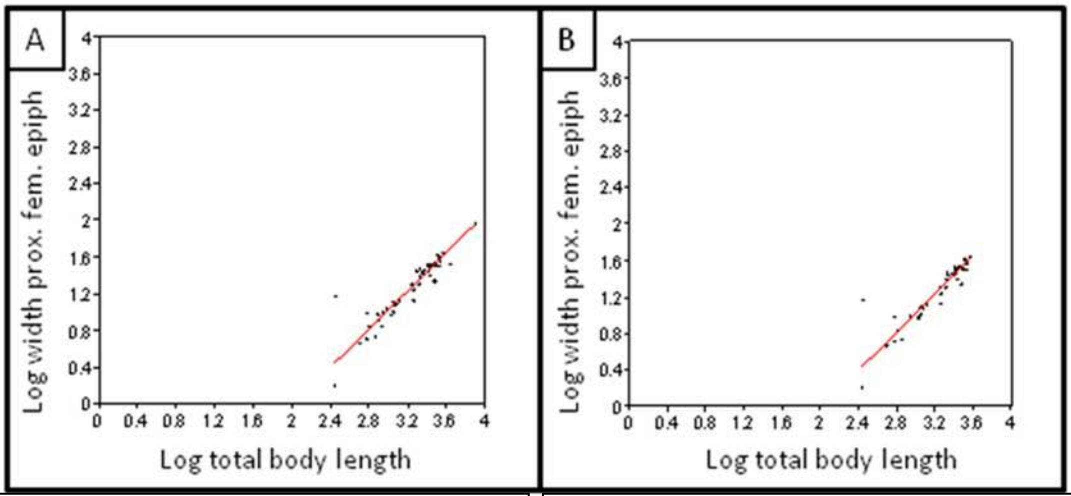
n = 41 a = 1.14 r = 0.87 Boot = 1.0–1.36

Fig. 3.31: RMA for the width of the proximal and distal humeral epiphyses and femur length for the whole dataset (A) and *Stenopterygius* (B), showing isometric growth when compared to body length.



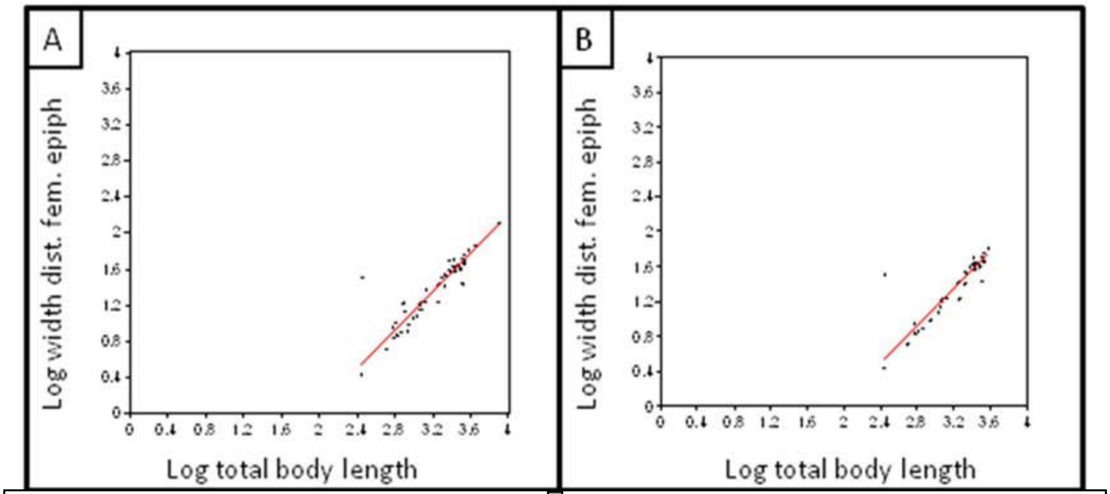
n = 53 *a* = 0.95 *r* = 0.94 Boot = 0.85–1.09

n = 41 *a* = 0.96 *r* = 0.93 Boot = 0.82–1.15



n = 51 *a* = 1.04 *r* = 0.92 Boot = 0.90–1.21

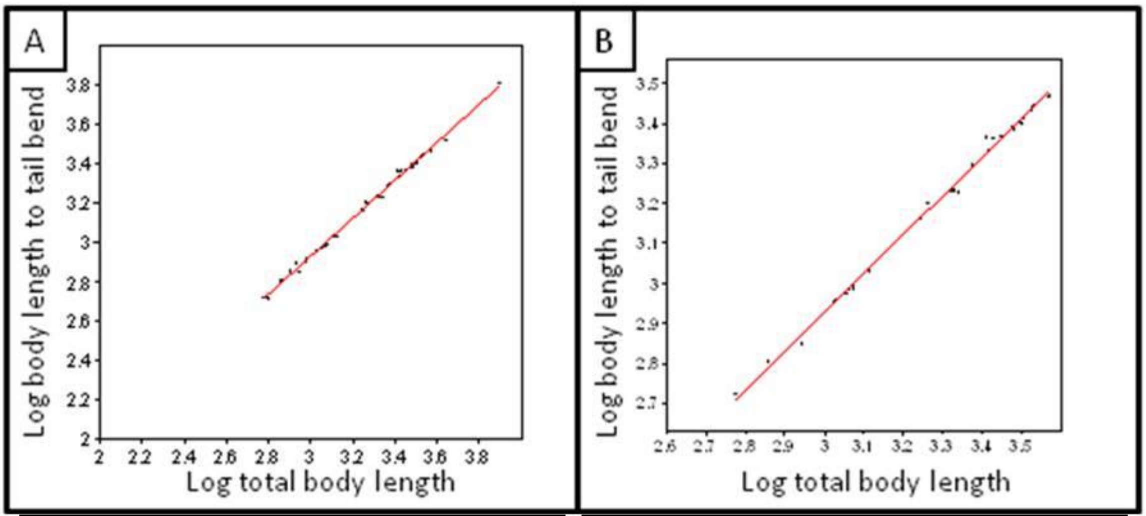
n = 40 *a* = 1.05 *r* = 0.90 Boot = 0.88–1.29



n = 51 *a* = 1.08 *r* = 0.89 Boot = 0.96–1.23

n = 39 *a* = 1.07 *r* = 0.86 Boot = 0.92–1.28

Fig. 3.32: RMA for femoral width and width of the proximal and distal femoral epiphyses for the whole dataset (A) and *Stenopterygius* (B), showing isometric growth when compared to body length.



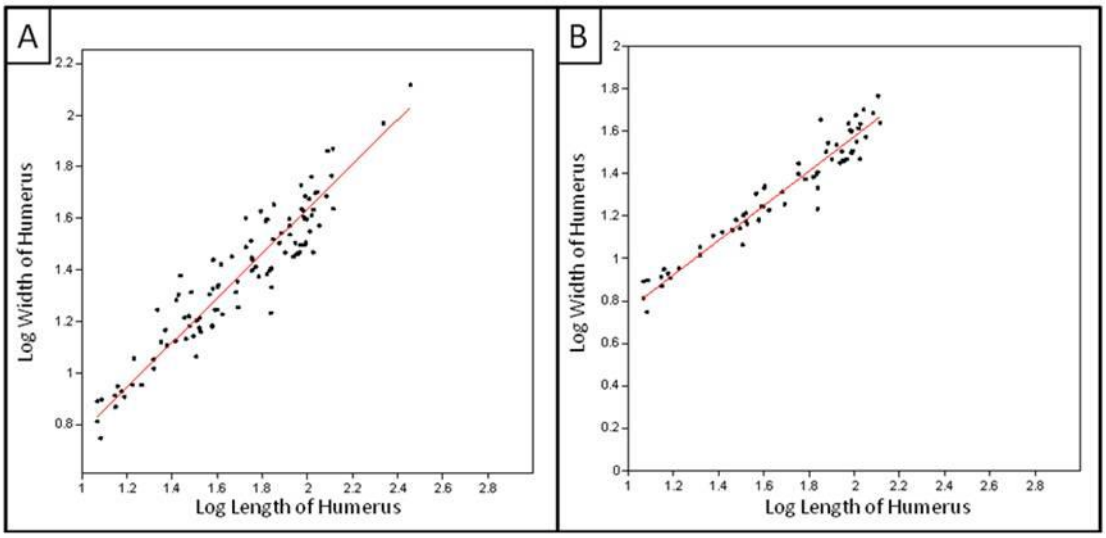
n = 43 *a* = 0.96 *r* = 0.99 Boot = 0.95–0.98

n = 32 *a* = 0.97 *r* = 0.99 Boot = 0.95–0.99

Fig. 3.33: RMA for body length to tail bend for the whole dataset (A) and *Stenopterygius* (B), showing very slight negative allometric growth when compared to total body length.

3.11.3.2: Humerus length vs. humerus width

The bivariate analysis for humerus length and width shows that growth of the humerus width is slightly negatively allometric compared to length of the humerus. The whole dataset shows the value of α to be 0.86 (Bootstrap 0.82–0.92) showing slightly negative allometric growth for humerus width (Fig 3.27). The relationship is strong as the *r* value is 0.94. The results for *Stenopterygius* are very similar. The value for α is 0.81 (Bootstrap 0.76–0.86) showing slight negative allometric growth for the width of the humerus compared to the length of the humerus. The relationship is very strong with an *r* value of 0.97 (Fig 3.27). However, the results for the whole dataset show slight negative allometry but are very close to isometry. Therefore, it is unlikely that the humeral growth can be used to estimate relative ages in ichthyosaurs. However, when considering *Stenopterygius* alone, the allometry is more pronounced suggesting that humeral growth may be useful and an age estimator for this genus. The dataset as a whole confirms the results shown in the PCA analysis.



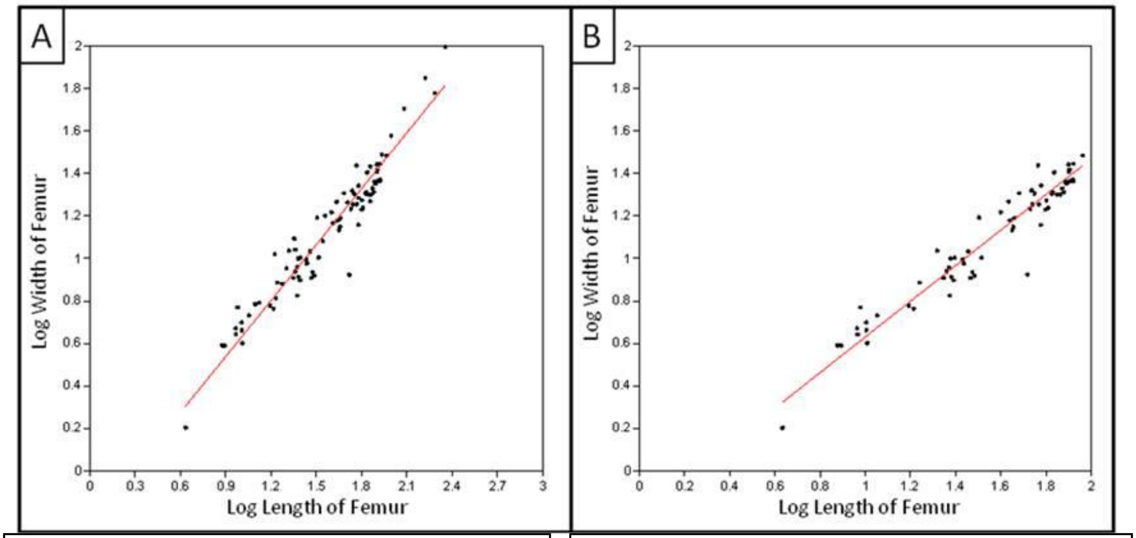
n = 105; *a* = 0.86; *r* = 0.94; Boot = 0.82–0.92

n = 66; *a* = 0.81; *r* = 0.97; Boot = 0.76–0.86

Fig. 3.34: RMA for log-humerus length vs. log-humerus width the whole dataset (A) and *Stenopterygius* showing slight negative allometry (B).

3.11.3.3: Femur length vs. femur width

As with the humerus, the results for the width of the femur show slightly negatively allometric growth compared to length of the femur (Fig. 3.35). The dataset as a whole shows very similar results to the data for *Stenopterygius* alone. The α value for the whole dataset is 0.86 and is 0.81 for *Stenopterygius*. Both of these values show negatively allometric growth for the femoral width compared to the femoral length. This is further confirmed by the values for the 95% confidence Bootstrap values which are 0.83–0.94 (whole dataset) and 0.78–0.88 (*Stenopterygius*). The relationship between the length and width of the femur is clearly strong for both *Stenopterygius* and the dataset as a whole as the *r* value is 0.96 for both analyses. These results confirm what is observed in the PCA analysis for the femur. However, as the values showing negative allometric growth for the width of the femur compared to the length of the femur (the upper value of the Bootstrap test) are close to the values for isometry. Although this allometry may be marginally significant, it is unlikely that the proportions of the femur can be used to determine relative age in ichthyosaur growth.



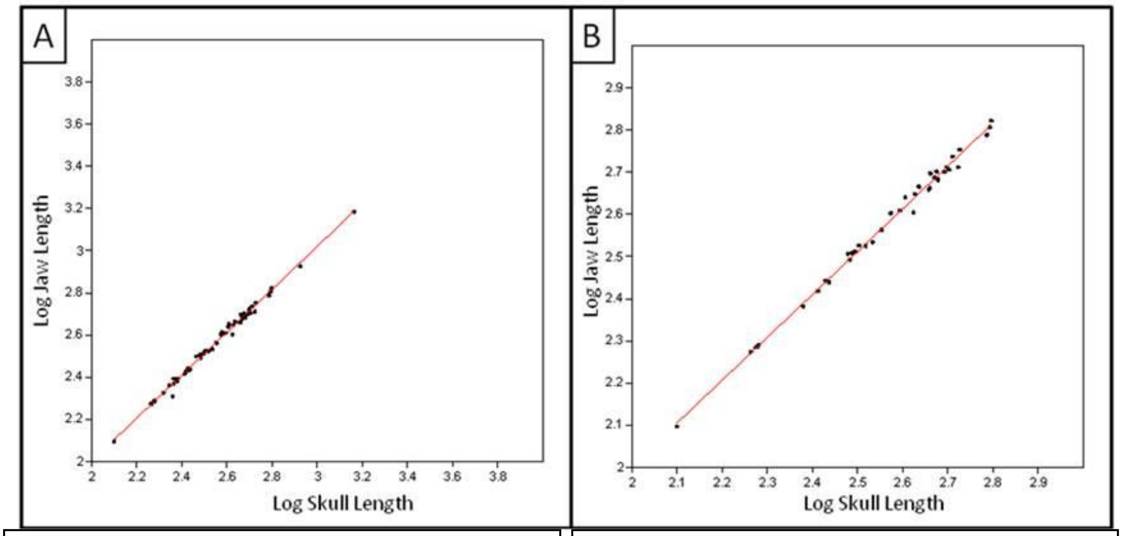
n = 89; *a* = 0.88; *r* = 0.96; Boot = 0.83–0.94

n = 67; *a* = 0.84; *r* = 0.96; Boot = 0.78–0.88

Fig. 3.35: RMA for femoral length vs. femoral width for the whole dataset (A) and *Stenopterygius* (B) showing slight negative allometric growth for the width of the femur compared to the length.

3.11.3.4: Skull length vs. jaw length

The measurements in this section are defined as: (i) skull length, measured from the tip of the snout to the posterior edge of the articular surface of the quadrate; and (ii) jaw length, measured from the tip of the mandible to the posterior edge of the surangular. The results of the RMA analysis show that growth is isometric for both the whole dataset and for *Stenopterygius* alone with an α value of 1.02. This value clearly demonstrates isometric growth for jaw length when compared to skull length which is confirmed by the Bootstrap values of 0.99–1.04 for the whole dataset and 0.99–1.03 for *Stenopterygius* alone. The relationship is very strong displaying *r* values of 0.998 for both the whole dataset as well as for that of *Stenopterygius*. This result shows that these features cannot be used for the estimation of relative ages of ichthyosaurs.



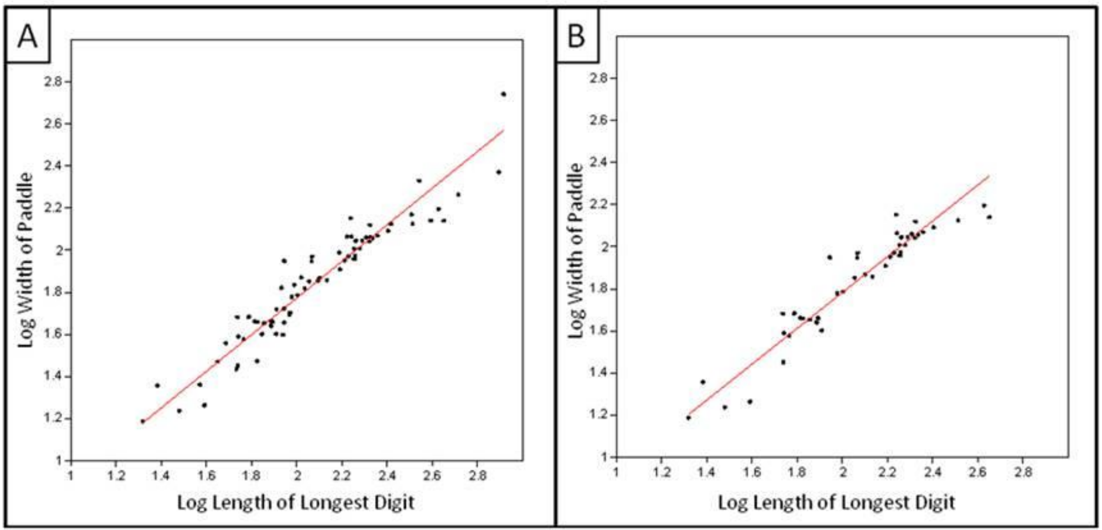
n = 57; *a* = 1.02; *r* = 0.99; Boot = 0.99–1.04

n = 39; *a* = 1.02; *r* = 0.99; Boot = 0.99–1.03

Fig. 3.36: RMA for Skull length vs. jaw length showing the whole dataset (A) and *Stenopterygius* (B) displaying isometric growth for the jaw length when compared to the skull length.

3.11.3.5: Length of longest digit vs. width of forefin

The result of the RMA analysis (Fig. 3.37) shows that growth is slightly negatively allometric for the width of the forefin compared to the length of the longest digit, showing that the forefin becomes longer and thinner with age. The α value for the whole dataset is 0.86 and 0.85 for *Stenopterygius* alone. These results indicate that growth of the forefin is slightly negatively allometric. These results are confirmed by the Bootstrap values which are 0.78–0.95 for the dataset as a whole and 0.75–0.95 for *Stenopterygius*. The relationship is a strong one with *r* values of 0.96 for the whole dataset and 0.95 for *Stenopterygius*.



n = 72; *a* = 0.86; *r* = 0.96; Boot = 0.78–0.95

n = 44; *a* = 0.85; *r* = 0.95; Boot = 0.75–0.95

Fig. 3.37: RMA for digit length vs. forefin width showing the whole dataset (A) and *Stenopterygius* (B) and displaying slight negative allometry.

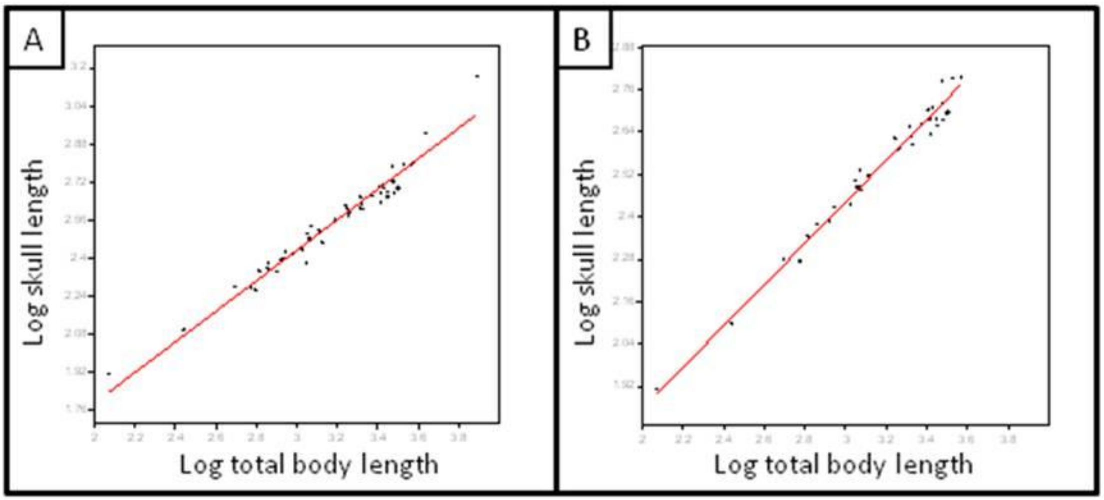
However, the upper limit for the α value, as indicated by the upper figure of the Bootstrap, shows a value that is very close to that of isometric growth. As the upper values of this 95% confidence interval is close to that of isometry. Slight negative allometry is shown for the width of the forefin compared to the length of the longest digit, and it could be marginally significant. Furthermore, the measurements in this analysis include interbone boundaries which could increase or decrease the actual measurement if the elements have been moved. This adds uncertainty into the result and therefore, it is unlikely that the forefin shape can be used to estimate relative ages of ichthyosaurs.

3.11.3.6: Total body length vs. skull length

The total body length of an ichthyosaur is measured from the tip of the rostrum to the tip of the tail and is measured along the spine. This analysis will show if the skull grows relatively faster or slower than the body. If growth is positively allometric, the skull would be comparatively larger at an early age.

The RMA analysis clearly displays negative allometric growth for the skull when compared to the body length (Fig. 3.38). The dataset as a whole has an α value of 0.64. This is significantly lower than the value for isometric growth. Furthermore, the negative allometric growth is confirmed by the results of the Bootstrap test, which, at a 95% confidence interval, gives values of 0.57–0.70. The relationship is also very strong with an *r* value of 0.98. This is clear negative allometric growth showing that the length of the skull becomes relatively shorter compared to body length with age.

The results for *Stenopterygius* also show negative allometric growth for skull length when compared to body length, with an α value of 0.58 which shows that the allometric growth is even more pronounced in *Stenopterygius* compared to the dataset as a whole. The Bootstrap results again confirm the negative allometric growth with values of 0.56–0.761 which is a very significant difference from the value for isometry. It is possible that these measurements can be used to estimate stages of growth for ichthyosaurs with assumed younger specimens displaying a relatively larger skull compared to total body length.



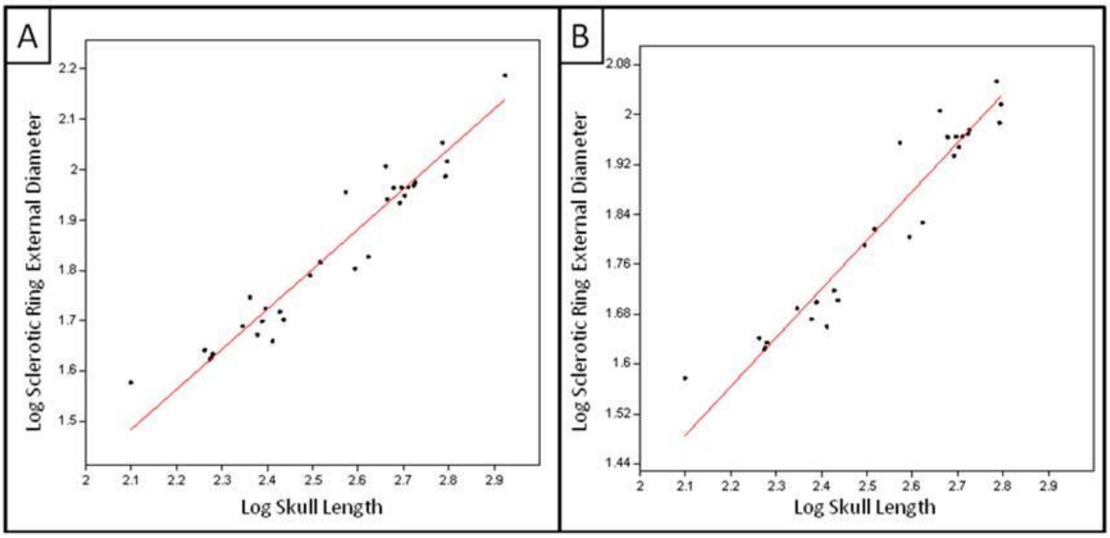
n = 50; α = 0.64; *r* = 0.98; Boot = 0.57–0.70

n = 35; α = 0.58; *r* = 0.99; Boot = 0.56–0.61

Fig. 3.38: RMA for skull length vs. total body length showing the whole dataset (A) and *Stenopterygius* (B) displaying significant positive allometry.

3.11.3.7: Skull length vs. external diameter of the sclerotic ring

The RMA analysis shows negative allometric growth for the external diameter of the sclerotic ring when compared to the skull length, which shows that the external diameter of the sclerotic ring gets relatively smaller as the skull gets larger. The value of α for the dataset as a whole is 0.80 which shows negative allometric growth. The Bootstrap values confirm this with values of 0.71–0.87. The *r* value is 0.96 that shows there is a strong relationship between the two variables. The results for *Stenopterygius* alone are similar to those of the whole dataset but this is expected as there are only four specimens that are not *Stenopterygius* in this analysis. The value for α in the *Stenopterygius* analysis is 0.78 while the Bootstrap values are 0.68–0.86. This is consistent with the negative allometry observed in the analysis of the whole dataset. The relationship is also strong with *r* values being calculated at 0.96. The feature of a relatively large sclerotic ring compared to the size of the skull could be used as a method of estimating relative ages of ichthyosaurs.



n = 31; *a* = 0.80; *r* = 0.96; Boot = 0.71–0.87

n = 27; *a* = 0.78; *r* = 0.96; Boot = 0.68–0.86

Fig. 3.39: RMA for skull length vs. external diameter of the sclerotic ring showing the whole dataset (A) and *Stenopterygius* (B) displaying significant negative allometry.

3.12: DISCUSSION

3.12.1: Limitations of the Data

The sample size varies drastically between the approaches used. The nature of the fossil record is such that the measurements are not always available. The PCA analysis does not account for absent data. Any specimen included in the PCA multivariate analysis must have all the required measurements in order to be used. This is not an issue when the number of variables is low and the relevant elements (e.g. humerus) or composite body parts are well represented in the fossil record. However, if the skeletal element or composite body part is less well represented or easily broken up, the *n* number is greatly reduced. The prime example of reduced *n* values is the skull, where the *n* value for the PCA for *Stenopterygius* is fourteen. Furthermore, the *n* value for the PCA of all of the measurements is seven. As the number of specimens included in the analysis for all the measurements is low, these results should be regarded as tentative and should only be used in support of other more conclusive results. This problem is partly overcome by using more than one statistical test to investigate ontogeny.

As well as the problem of dataset size, there are other potential problems with the data. For example, it is likely that there is a bias in the data collection. This is due to the exceptional preservation of the Posidonia shale material. Due to the large collection of well preserved *Stenopterygius* specimens in the Staatliches Museum für Naturkunde Stuttgart, Germany, the majority of the specimens used belong to this genus. This may skew the results to capture aspects of *Stenopterygius* growth rather than representing Lower Jurassic ichthyosaur growth as a whole. However, the majority of the data collected is *Stenopterygius* is also an advantage as this allows comparisons to be made between growth for a single genus and for the whole dataset.

The use of composite body parts may result in error. Any measurement that crosses a boundary between elements could be incorrect. If the individual elements have been moved by taphonomic processes then the measurement could be larger or smaller than the true measurement. Taxonomic variation may also be a factor. Some taxa have very close and compact elements in the limbs while others have distally well-spaced elements. The latter would result in a longer measurement.

3.12.2: Significance of Results

Some of the results showed in this chapter support several analyses that were mentioned previously in the literature. The results show negative allometric growth of the sclerotic ring compared to the length of the skull (Fig 3.14); an observation previously in the literature by Bardet & Fernández (2000). However, their original observation was only a comment and they provided no quantitative support. The results presented in this chapter support their observation. Furthermore, Bardet & Fernández (2000) made this observation with reference to a single genus, *Aegirosaurus*. My results now demonstrate that the relative reduction in sclerotic ring size in comparison with skull size is under ontogenetic control and can apply to other ichthyosaur taxa, not just *Aegirosaurus*.

As noted in Chapter 1, there is only one study that examines ichthyosaur ontogeny (Johnson, 1977). This work investigated size independent criteria for estimating relative age of ichthyosaurs and dealt only with *Stenopterygius*. The focus of the paper was on the pectoral girdle and forelimbs of 26 complete specimens and humeral length was used as a proxy for size. One of the characteristics that Johnson (1977) considered important was the shape of the proximal articular surface of the humerus. In inferred immature specimens, this surface is flat while in inferred sexually mature specimens it is convex. This may relate to the width of the epiphysis. By contrast, the results in this chapter show that the growth of the humerus alone is very close to isometric (Fig 3.1), and the width of the humeral epiphyses as well as the width of the humerus all grow isometrically when compared with body length (Figs 3.29 & 3.30). This suggests that the epiphysis did not widen with age. However, the exact change in shape as discussed by Johnson (1977) cannot be captured by these measurements, though none of the results presented here support the conclusion that the humerus changes shape with relative age. However, Johnson's (1977) results should not be dismissed on the basis of the analysis conducted herein.

The skull, when compared to total body length displays negative allometric growth (Fig. 3.20) that shows that the skull is relatively large in inferred younger specimens. This feature has also been mentioned previously (McGowan, 1973, 1976) for ichthyosaurs. The results in this chapter confirm this.

3.12.3: Comparisons with other organisms

Morphometric analysis has been conducted on many organisms with the purpose of understanding the ontogeny, in both an evolutionary context as well as examining growth of an individual. Some of these studies are mentioned here. However, morphometrics is not typically used to study ontogeny for extinct marine reptiles (see Chapter 1 for details). Some of the papers are compared below.

PCA was used to examine pachypleurosaur ontogeny (O'Keefe *et al.*, 1999) on a growth series from Switzerland. The results show that pachypleurosaurs display negative skull allometry,a feature also observed for ichthyosaurs. The forelimb displays marked positive allometric growth. This feature is not observed in ichthyosaurs. This is likely a result of the limbs being used as a means of propulsion in pachypleurosaurs, where as the tail is the driving force behind locomotion for ichthyosaurs and it is likely that the limbs are not used to the same degree. Furthermore, the growth of the hind limb is negatively allometric for *Serpianosaurus* but isometric for *Neusticosaurus* and the femur shifts from isometric growth to negatively allometric growth between *Serapianosaurus* and *Neusticosaurus*. Isometric growth is observed for the femur of ichthyosaurs. Although this paper looks at ontogeny in an evolutionary view (examining a clade) the authors still identify types of growth in individual skeletal elements and composite body parts (O'Keefe, *et al.*, 1999). These features could be used to help identify relative ages for pachypleurosaurs.

Morphometric analysis has been performed on plesiosaurs and pliosaurs (O'Keefe, 2001). As with ichthyosaurs, plesiosaurs and pliosaurs are secondary adapted Mesozoic marine reptiles. Again, this is using morphometrics to study ontogeny in an evolutionary context in order to establish trends in the taxonomy. However, there are still conclusions that can be established from this paper that are relevant to the ontogeny of an individual. After using PCA, O'Keefe, 2001concludes that specimens with a larger head usually also have a shorter neck on plesiosaurs. This is likely that supporting a larger head with a long neck is not advantageous to the organism. Furthermore, the PCA indicates that long-necked, small-headed plesiosaurs tend to have longer scapulae, longer humeri, and shorter ischia than short-necked, large-headed taxa (O'Keefe, 2001). These results suggest that growth of individual plesiosaurs was allometric. The author goes on to mention that two obvious juveniles obscure patterns on the graphs as the growth of the juveniles is allometric. The author does not mention which parts of the body display allometric growth, nor does he explain why the specimens are obviously juvenile. The ontogeny of plesiosaurs tends to be based on fusion of bones and closure of sutures rather than morphometrics (see Chapter 1).

Further research into plesiosaur ontogeny using morphometrics has been conducted (O'Keefe, 2006). The length of the vertebrae were analysed using PCA. The results show that there is marked allometry among all the vertebrae. The adult centra are relatively longer than those of juveniles by 20% or more. Furthermore, the positive allometry in mid-cervical centra is larger than at either end of the neck. Consequently, adults show a bow-shaped curve in this region where juveniles are flatter (O'Keefe, 2006). These features can easily be used to help estimate relative ages within plesiosaurs. Plesiosaurs typically have long necks whereas ichthyosaurs have very short necks. As a result of this it is unlikely that the cervical vertebrae of ichthyosaurs will display similar trends to those of plesiosaurs. However, it is unknown whether the vertebrae of ichthyosaurs show similar features in the cervical region of the spinal column, or any other region. As ichthyosaur vertebrae are generally flatter, in contrast to those of plesiosaurs that are elongate, it was thought to be unlikely that they would yield useful growth information and hence they were not included in the analyses.

3.13: Conclusions

Generally, individual elements and composite body parts grow isometrically, or very slightly allometrically. Therefore, very little visual change would occur in the individual elements and composite body parts with age (humerus, femur, forefin and skull). The exception to this is the size of the eyes (maximum orbital diameter, maximum diameter of the internal and external boundary of the sclerotic ring). Compared to the skull, the orbit and the sclerotic ring display negative allometry. This suggests that the size of the orbit and sclerotic ring, compared to the length of the skull, can be used as an indicator of relative age in ichthyosaurs.

However, when compared to total body length, all of the skull measurements show negative allometric growth. This shows that the size of the skull became relatively smaller compared to total body length as ichthyosaurs grew. This feature can also be used to help estimate relative ages of ichthyosaurs. Furthermore, when compared to the body length, all of the postcranial measurements display isometric growth, with the exception of the humerus length. The humerus length displays slightly positive allometric growth showing that the humerus increases in length relative to total body length. This could be used to help estimate relative ages in ichthyosaurs. However, the positive allometry is slight, so this feature may not be of as much use as the features of the skull and orbit.

The hypothesis that the individual skeletal elements show isometric growth is demonstrated to be partially incorrect. The RMA analysis shows that the length of the humerus and the length of the femur show slight negative allometric growth, compared to the width. However, there would be significant overlap of ratios which makes it difficult to estimate relative age using these features. Furthermore, the length of the longest digit also displayed slight negative allometric growth compared to the maximum forelimb width. As with the humerus and femur, the allometric growth is slight and the issue of overlapping ratios make it unlikely that this feature can be used to estimate relative ages of specimens.

The hypothesis that growth of the skull will be isometric is proved to be true. The comparison of skull length compared to the jaw length shows very clear isometric growth. This means that this feature cannot be used to infer relative ages. However, the PCA for the skull indicated that the sclerotic ring grows allometrically. The RMA comparing the external diameter of the sclerotic ring shows strong positive allometric growth showing that the sclerotic ring is larger in inferred younger specimens. In some specimens, the sclerotic ring fills the entire orbit while in others there is a gap between the external edge of the sclerotic ring and the internal edge of the orbit. This feature can be used to help estimate relative ages of ichthyosaurs. However, there is negative allometric growth for the skull when compared to the body length and this feature can be used to estimate relative ages for ichthyosaurs.

The hypothesis that the skull will be relatively larger in inferred younger specimens and will therefore display allometric growth when compared to body length is also proven to be true. The RMA analysis for skull length compared to body length displays clear negative allometry. This feature can also be used to help estimate the relative age of ichthyosaurs.

4: INVESTIGATING ICHTHYOSAUR GROWTH: A MERISTIC APPROACH

4.1: OVERVIEW

Lengths and widths of individual skeletal elements or composite body parts are not the only features that can vary with ontogeny. The number of repeated skeletal elements or structures within the skeleton of an individual can also change with age. Some counts of repeated skeletal structures are used as generic identification in ichthyosaurs such as the numbers of ossified digits in the forelimb (McGowan & Motani, 2003). If these structures vary with ontogeny, then the validity of some of the taxonomic identifications could be called into question. Furthermore, a proximal to distal ossification sequence in ichthyosaur limbs has been observed for *Stenopterygius* (Caldwell, 1997) but this focuses on embryos and neonates. A reduction in numbers of teeth has previously been suggested for ichthyosaurs (see Chapter 3). However, as teeth in ichthyosaurs are typically set in a dental groove as opposed to a socket, and held in by soft tissue, small teeth are easily lost by taphonomic processes. Therefore, this is not a reliable indicator of relative age and, as such, is not analysed in this study. It is not known if the numbers of other ossified skeletal elements (such as the number of phalanges or the numbers of ossified caudal vertebrae) vary with age between juveniles and adults. An overview of ontogeny in ichthyosaurs and in other diapsids is provided in Chapter 3. This chapter aims to analyse repeated ossified elements to see if numbers increase or decrease with relative age.

4.2: MATERIALS & METHODS

The materials used in this chapter are the same as those used in Chapter 3. See section 3.2 for full details. The data studied comprises the numbers of vertebrae within different sections of the vertebral column, the numbers of digits in the front limb and the number of phalanges in the longest digit of the front limb.

The statistical method employed to analyse changes in meristic characteristics is Linear Regression, also known as Ordinary Least Squares Regression (OLS). The purpose of this method is to fit a bivariate dataset to a straight line, assuming one independent and one dependant variable. The method makes the assumptions that: (i) the data is independently collected; (ii) the residual errors are normally distributed and independent; (iii) the variance of the error does not vary systematically with any of the variates (Hammer & Harper, 2006).

The straight line equation is $y = ax + b$, where α is the slope and b is the intercept, which are constant. However, due to errors gained while taking measurements, a given set of any (x, y) pairs will not fit perfectly on a straight line, assuming there are no errors on the x axis (the independent variable). Therefore, the model contains a linear component without error and a random error component (residual) e. Therefore;

$$y_i = ax_i + b + e_i$$

The process of finding a and b in a way that minimises e_i with a given set of (x_i, y_i) values is linear regression. Least squares regression is used to minimise the error in the dependant variable, the minimisation of the sum of squares of e_i. From this, standard errors can be calculated. Non-linear relationships between the x and y variables can be 'linearised' by log-transforming the data.

The Bonferroni correction was used to lower the cut-off for the p-value. This method is used to correct for errors where more than one hypothesis is tested using the same dataset. This reduces the likelihood of false positives in the results. The Bonferroni correction divides the p-value cut off point, in this case 0.05 (95% confidence), by the number of hypotheses tested by one dataset. For example, if one dataset was used to test two different hypotheses, then the p-value cut off would be 0.025 (0.05/2 = 0.025) and this value is used as a comparison to establish if the results are statistically significant.

Linear regression was used for this study rather than PCA because the numerical data consists of integers and does not contain measurement errors. Conversely, the length measurement, in this case body length or limb length, is subject to error. PCA is used where both variables contain potential error. As this is not the case here, linear regression is more appropriate.

4.3: MERISTICS RESULTS: VERTEBRAE

4.3.1: Presacral Vertebrae

The presacral vertebrae were defined as those lying anterior to the anterior margin of the femur. The numbers of presacral vertebrae were counted on specimens where the spinal column was complete in this area. Data were not collected from specimens where the vertebrae or the femur were absent or disarticulated. The same techniques have been applied to the dataset as a whole, as well as *Stenopterygius* alone, to see if any change that does occur is genus-specific or applicable to ichthyosaurs as a whole. The Bonferroni correction for the presacral vertebrates (0.05/4) is 0.0125, as four hypotheses were tested using this dataset.

Ichthyosaurs are unusual amongst vertebrates in that the numbers of presacral vertebrae vary within genera and species, as shown by the diagnoses of taxa by McGowan and Motani (2003) which contain ranges of presacral numbers and that are used taxonomically. The numbers of presacral vertebrae are typically set in the embryo and do not vary to the same extent with size in any other vertebrates (Upchurch, 1995; Galis, 1999; O'Keefe, 2002; O'Keefe, 2004; Kardong, 2006). Although it is unlikely that vertebral numbers are affected by growth, it is important to observe whether there is a correlation between vertebral numbers and body length to test if numbers are size related or potentially taxonomically useful. Ossification patterns are potentially useful indicators of relative age. If there is a proximal to distal ossification sequence of vertebrae, then changing numbers of distal (caudal) vertebrae could be affected. This would not affect numbers of presacrals as any unossified vertebrae would likely be represented by gaps in the spinal column.

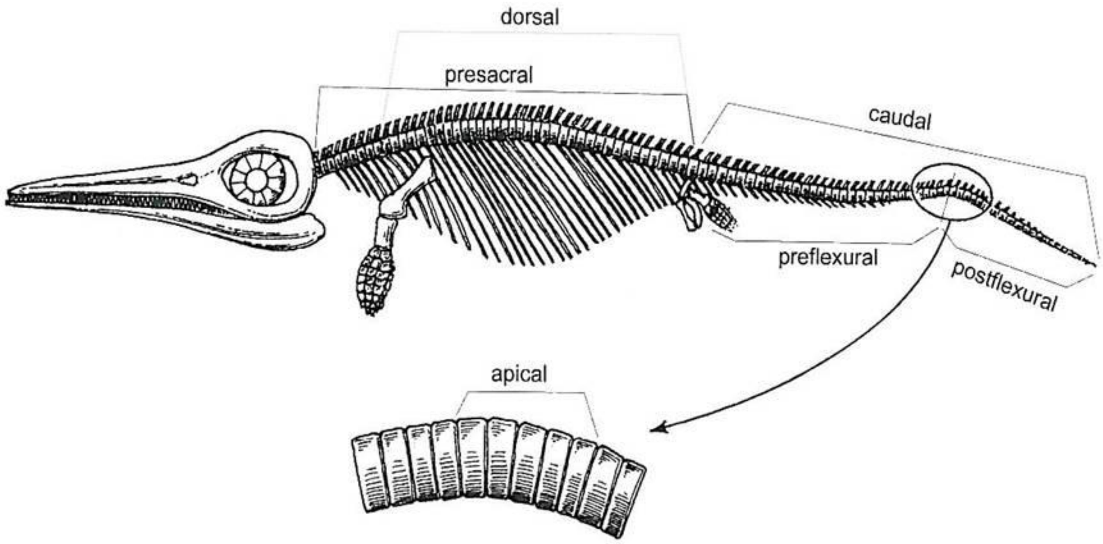
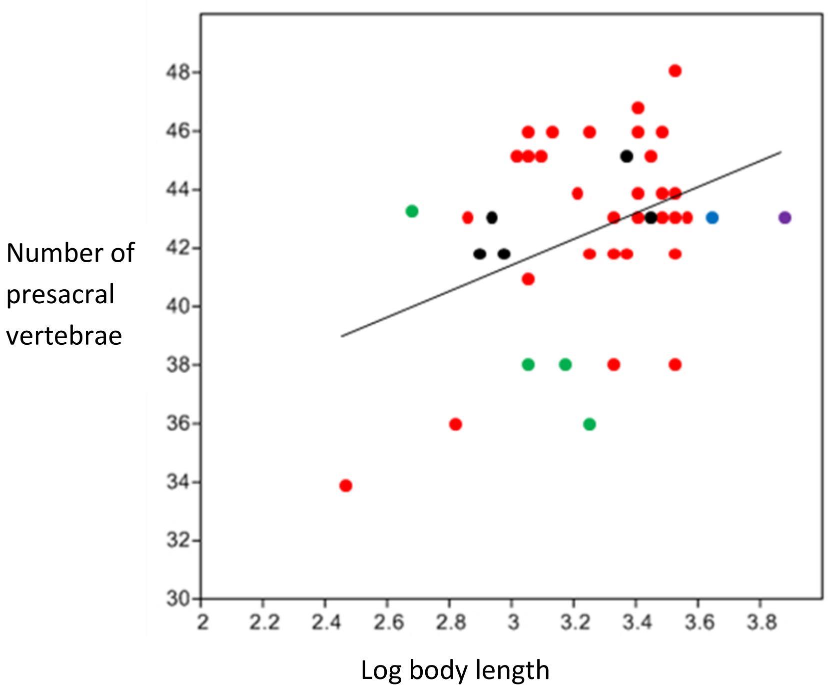


Fig. 4.1: Definitions of vertebrae from McGowan & Motani, 2003

4.3.1.1: Results for the whole dataset

The results for the whole dataset do not support a strong relationship between the numbers of presacral vertebrae and total body length. The value for the slope (*a*) is 4.47 and not very high indicating a weak relationship. Furthermore, the r value shows that the correlation is weak (0.38) and the r^2 value shows that only 15% of the variance in the number of presacral vertebrate is explained by total body length. The bootstrap values are also very far apart (-11.17 – 8.85) again indicating a large margin of error for the *a* value (Fig. 4.2).



a=4.47 r=0.38 r^2=0.151 p(uncor)=0.011 p(a=1)=0.045 B=-1.168-8.852 n=42

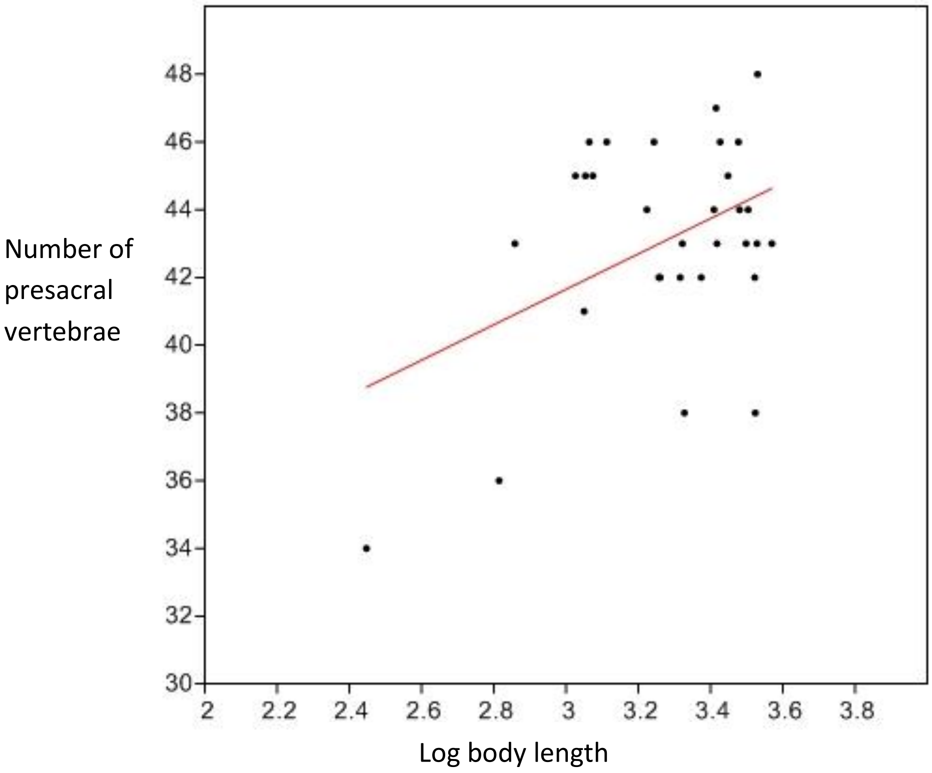
Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unidentified Pink = *Temnodontosaurus*; Green = *Suevoleviathan*; Light Blue = *Leptonectes*

Fig. 4.2: OLS of the whole dataset showing a weak relationship between total body length and the number of presacral vertebrae.

However, the p(uncor) value is 0.011 which lies slightly below the value provided by the Bonferroni correction (0.0125). This shows that the results are statistically significant. However, the significant results only account for 15% of the variation within the dataset (Fig. 4.2). Despite the results being significant it is unlikely that the numbers of presacral vertebrae change with size in ichthyosaurs. This result is similar to that observed in plesiosaurs, where the numbers of presacral vertebrae (mainly cervical vertebrae) do not vary with size. The number of presacral vertebrae is more stable in plesiosaurs than in ichthyosaurs and are also used for taxonomic assignments (O'Keefe, 2002, 2004). Furthermore, the weak correlation indicates that size is not the only feature related to variability in presacral vertebral counts.

4.3.1.2: Results for *Stenopterygius*

The results for the restricted *Stenopterygius* dataset are similar to those of the complete dataset. The value for the slope is 5.23 and the bootstrap values are widely separated (-1.4–13.19) which suggests a weak relationship. The r value shows a correlation of 0.43 while the r^2 values show that only 19% of the variation in the number of presacral vertebrae is explained by total body length. The p value is 0.016, which shows the results are not statistically significant. Furthermore, the probability that *a* is equal to 1 is 0.047 (roughly 5%) (Fig. 4.3).



a=5.23 r=0.431 r^2=0.186 p(uncor)=0.016 p(a=1)=0.047 B=-1.404-13.19 n=31

Fig. 4.3: OLS for *Stenopterygius* showing a weak relationship between number of presacral vertebrae and total body length.

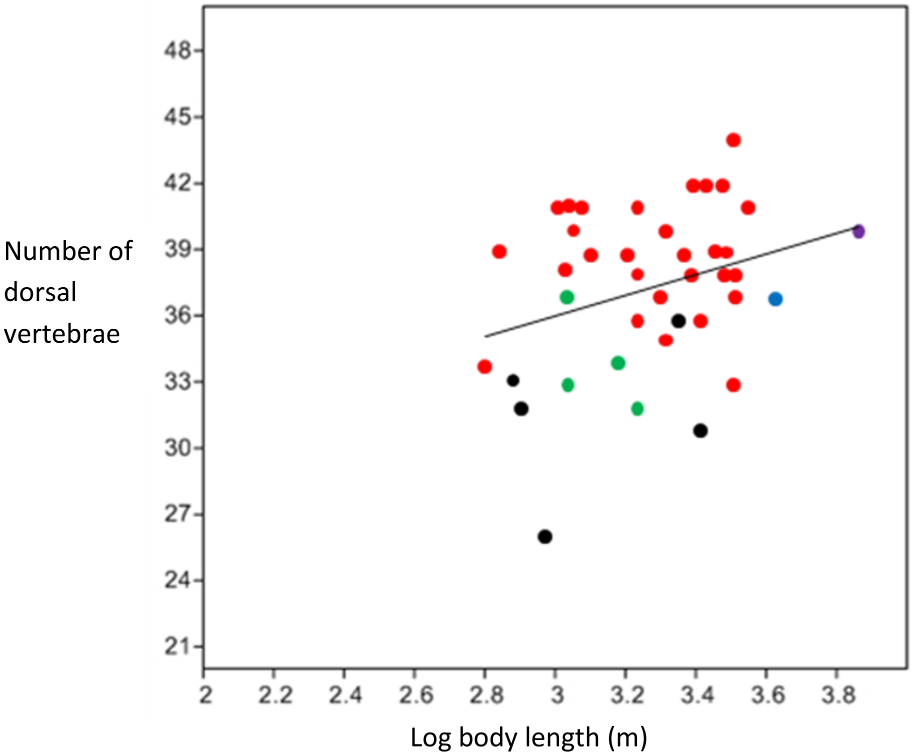
The Bonferroni correction gives a p value of 0.0125. This is a lower value than the p(uncor) value of 0.016 showing that there is no significant correlation between total body length and the number of presacral vertebrae (Fig. 4.3). This supports the results from the whole dataset showing that the numbers of presacral vertebrae do not vary with size in ichthyosaurs. The slight variation in numbers of presacral vertebrae is more likely to be related to taxonomy as several species are represented in the analysis.

4.3.2: Dorsal vertebrae

The dorsal vertebral series consists of the presacral section of the thorax, excluding the cervical vertebrae. As the cervical/dorsal boundary is difficult to identify morphologically, the dorsal vertebrae are defined here as those that are positioned between the pectoral girdle (Fig. 4.1) and a point directly above the position of the femur. This dataset for the dorsal vertebrae is part of the presacral dataset so the Bonferroni correction is the same (0.0125).

4.3.2.1: Dorsal vertebrae for the whole dataset

The results of the Least Squares analysis for the dorsal vertebrae does not show a strong relationship between number of dorsal vertebrae and body length, similar to the results obtained for the presacral vertebrae. The α value is very low at 4.79 and the bootstrap values are not well constrained (-0.01 – 9.74). The correlation between these variables is weak, with an r value of 0.315. The r^2 value of 0.099 shows that only 10% of the variance in the number of dorsal vertebrae is related to total body length. The p(uncor) value is 0.045 which is higher than the value of 0.0125, calculated from the Bonferroni correction. This shows that the results are not statistically significant (Fig. 4.4). These results indicate that the numbers of dorsal vertebrae do not vary with size of ichthyosaurs and are therefore not of potential use in taxonomic assignments. It is likely that the slight correlation is a result of differences between taxa rather than any ontogenetic feature and the correlation is meaningless.

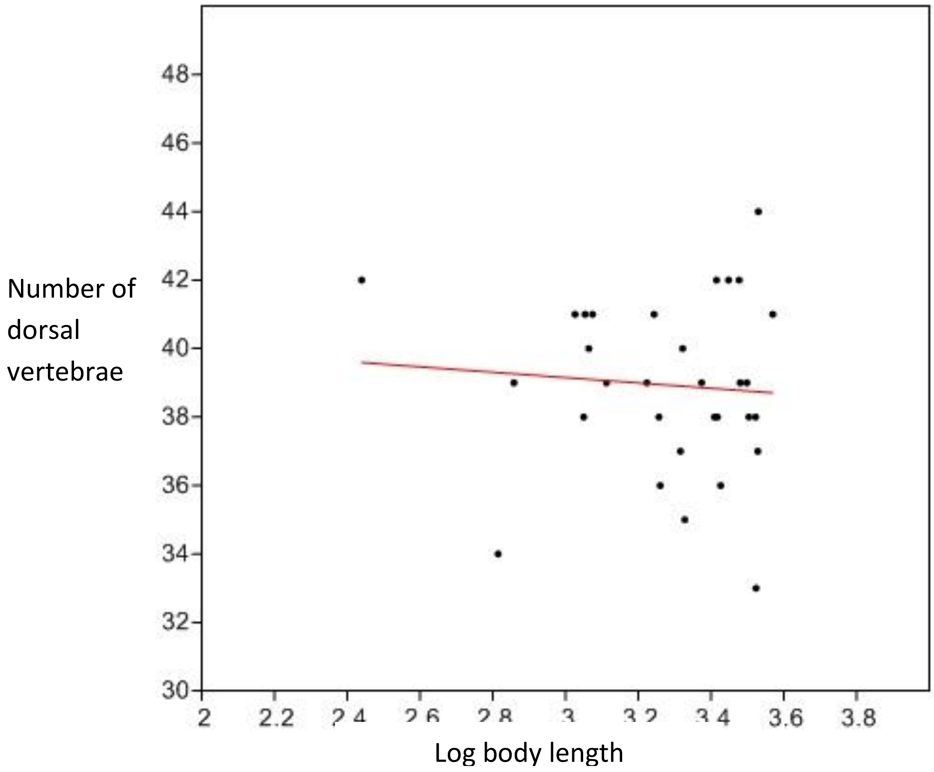


a=4.79 r=0.315 r^2=0.099 p(uncor)=0.045 p(a=1)=0.109 B=-0.012-9.736 n=41

Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unidentified Pink = *Temnodontosaurus*; Green = *Suevoleviathan*; Light Blue = *Leptonectes*

Fig. 4.4: OLS for dorsal vertebrae for the whole dataset showing a weak correlation

4.3.2.2: Dorsal vertebrae for *Stenopterygius*



a=-0.782 r=-0.080 r^2=0.006 p(uncor)=0.669 p(a=1)=0.332 B=-5.898-2.732 n=31

Fig. 4.5: OLS for *Stenopterygius* showing no relationship between dorsal vertebrae and total body length

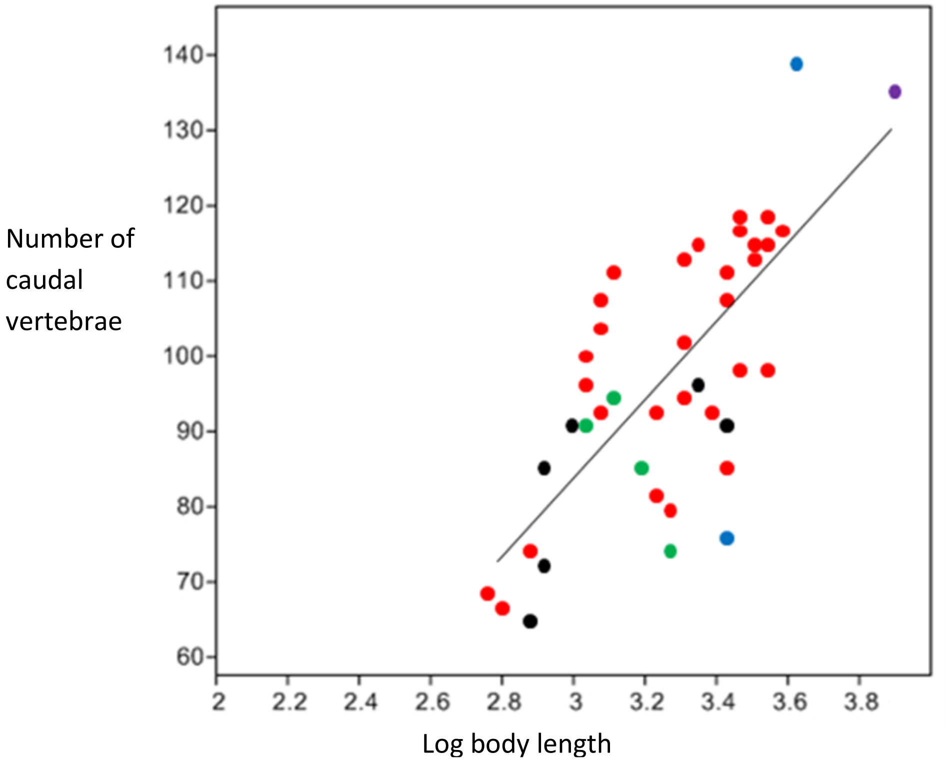
The result for the dorsal vertebrae of the reduced dataset, containing only *Stenopterygius*, does not show any clear relationship between these variables. The α value is exceptionally low at 0.782 and the bootstrap values are relatively well constrained at -5.898–2.732. The correlation is weak with an r value of 0.08. The r^2 value shows that only 0.6% of the variation in numbers of dorsal vertebrae is related to total body length (Fig. 4.5). Furthermore, the p(uncor) value is higher than the value calculated by the Bonferroni correction (0.0125). This result shows that the correlation is not statistically significant. As with the results for the whole dataset, the numbers of dorsal vertebrae do not change with size in ichthyosaurs. The slight variation in numbers of dorsal vertebrae could be of taxonomic interest in defining species within S*tenopterygius*.

4.3.3: Caudal vertebrae

For this study, the caudal vertebrae are defined by the author as those comprising the ‘tail’ region of the body and are defined as those extending from directly above the femur to the tip of the tail (Fig. 4.1). Within this dataset, the caudal vertebrae can be divided into two sections, preflexural vertebrae and postflexural vertebrae. Preflexural vertebrae are the caudal vertebrae anterior to the tail bend, while postflexural vertebrae are those posterior to it. The vertebrae in the tail bend (apical, Fig. 4.1) are identified by a wedge shape when viewed laterally. These are counted and divided evenly into preflexural and postflexural vertebrae. If the number of apical vertebrae cannot be divided equally then the larger number was included in the preflexural count. Each of these sections will be analysed using the whole dataset as well as using *Stenopterygius* alone for comparison. Therefore, six hypotheses will be tested using this dataset. The Bonferroni correction value (0.05/6) is 8.33^{-3}. Although the numbers of vertebrae will have been determined in the embryo, ossification of distal vertebrae may have varied with ontogeny. The following analyses will show if the numbers of ossified vertebrae change with size as well as showing if any change is of taxonomic or ontogenetic significance.

4.3.3.1: Caudal vertebrae results for the whole dataset

The results for the total numbers of ossified caudal vertebrae indicate that they do change with total body length (which can be regarded as a proxy for relative age). The α value is high (51.94) and the r^2 value shows that 55% of the variance within the dataset is explained by total body length. Furthermore, the Bootstrap values are relatively well constrained (59.69–78.79). The p(uncor) value is 5.94^{-9} which is far lower than the calculated p-value from the Bonferroni correction (8.33^{-3}) (Fig. 4.6). Therefore, the result is statistically significant. These results show that the number of ossified vertebrae increases in the caudal region of ichthyosaurs as size increases.

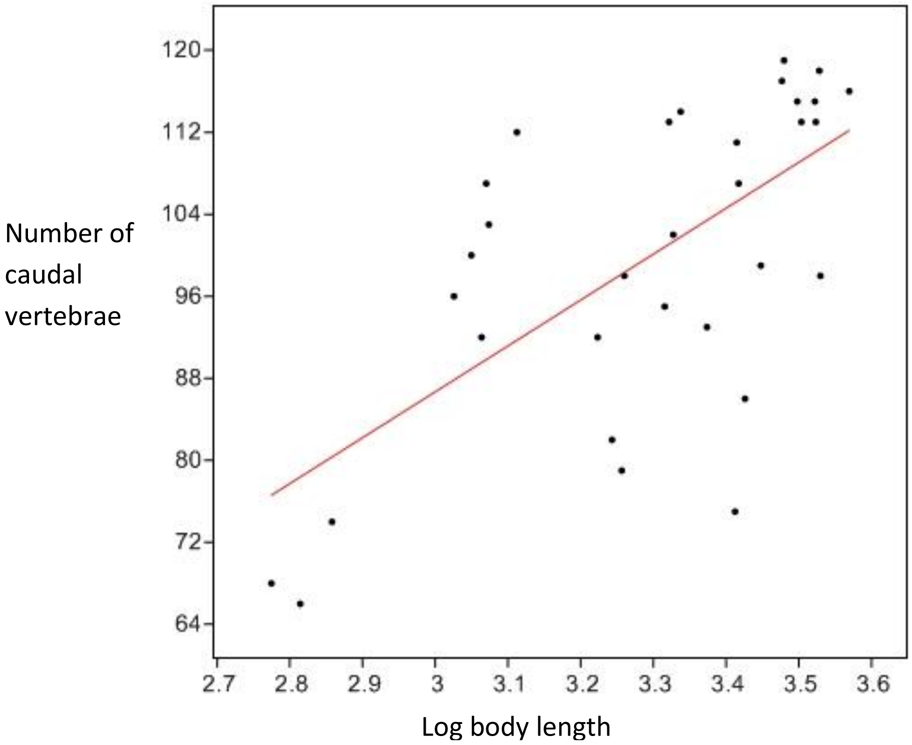


a=51.94 r=0.742 r^2=0.550 p(uncor)=5.644E-09 p(a=1)=8.975E-09 B=59.69-78.79 n=45

Fig. 4.6: OLS for the whole dataset showing a relatively strong correlation between total body length and the number of caudal vertebrae.

4.3.3.2: Results for caudal vertebrae: *Stenopterygius*.

The results for the restricted *Stenopterygius*-only dataset are similar to those for the whole dataset and show a relatively strong relationship between the numbers of total caudal vertebrae compared to total body length. The slope is steep with an α value of 44.76. The correlation is relatively strong with a r value of 0.648 while the r^2 value (0.419) show that 42% for the variation in numbers of caudal vertebrae is related to total body length. Furthermore, the p(uncor) value is lower than the calculated value of the Bonferroni correction. This shows that the correlation is statistically significant. However, these correlations are not as strong as for the whole dataset. Despite this, the results show that the numbers of caudal vertebrae do change with body length and this feature could be used to help estimate relative ages of ichthyosaurs (Fig. 4.7).



a=44.76 r=0.648 r^2=0.419 p(uncor)=6.08E-05 p(a=1)=8.156E-05 B=31.15-66.96 n=32

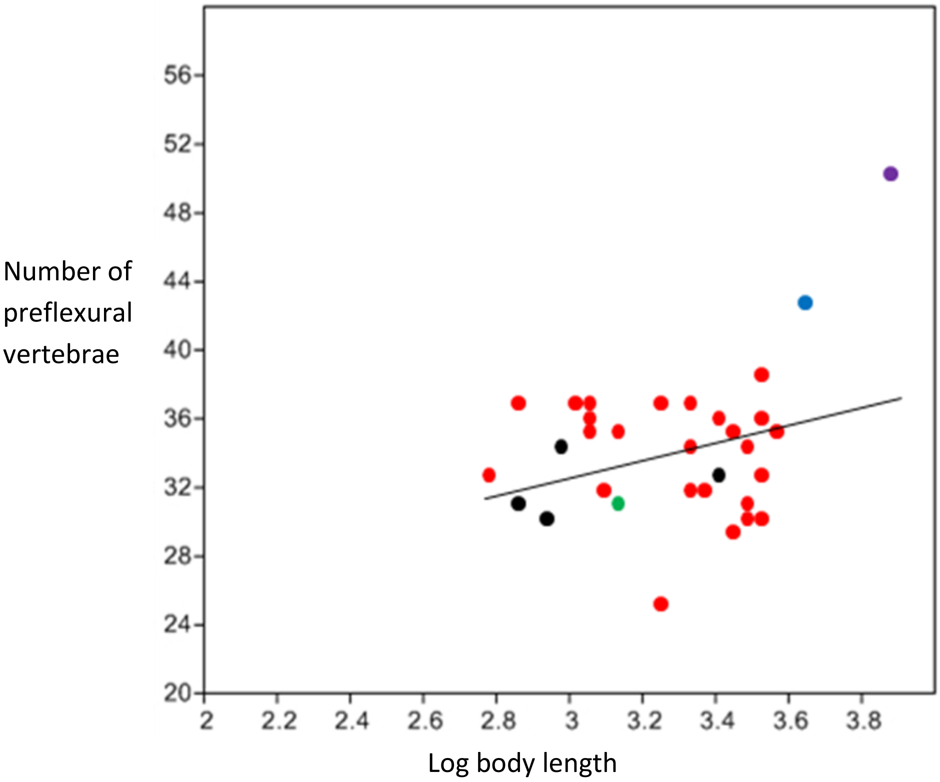
Fig. 4.7: OLS for *Stenopterygius* showing a strong relationship between the number of caudal vertebrae and total body length.

4.3.4: Preflexural vertebrae

The preflexural vertebrae are those located within the caudal region, but lie posterior to the tail bend. The data used for this analysis is part of the dataset used for the caudal vertebrae.

4.3.4.1: Results of the preflexural vertebrae for the whole dataset

The results for the numbers of preflexural vertebrae for the whole dataset do not show a strong correlation with body length. The α is low at only 4.839, a very low gradient slope. The r value is also low at 0.270 showing a weak correlation, while the r^2 value (0.073) shows that only 7% of the variance within the numbers of preflexural vertebrae is related to total body length and therefore relative age (Fig. 4.8). Furthermore, the p(uncor) value of 0.128 is higher than the number calculated by the Bonferroni correction. This shows that there is no statistical significance within the results and, therefore, the relative ages of ichthyosaurs cannot be estimated using numbers of preflexural vertebrae. The results show variation in numbers of preflexural vertebrae but this is not correlated with size and the changing in numbers of preflexural vertebrae are more likely to be taxonomically significant. Numbers of preflexural vertebrae are used in taxonomic assignments (McGowan & Motani, 2003).



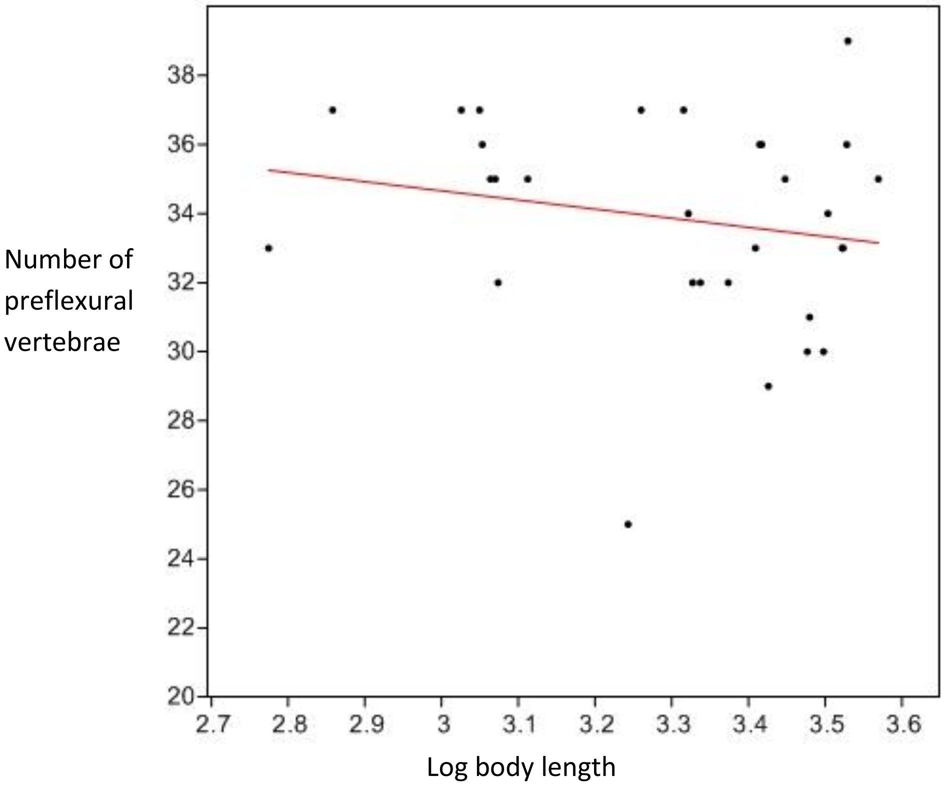
a=4.839 r=0.270 r^2=0.073 p(uncor)=0.128 p(a=1)=0.2244 B=-3.747-14.01 n=33

Fig. 4.8: OLS for the whole dataset showing a weak correlation between the number of preflexural vertebrae and total body length.

4.3.4.2: Results of the preflexural vertebrae for *Stenopterygius*

The results of the OLS for the restricted *Stenopterygius*-only dataset do not show a strong relationship, similar to the results for the whole dataset. The α value is low and slightly negative at -2.684 and the Bootstrap values are not well constrained (-6.88 – 1.696). The r value for the correlation is low at 0.194, while the r^2 value (0.0374) shows that only 4% of the variance in numbers of preflexural vertebrae is related to total body length. Again, as with the whole dataset, the p(uncor) value (0.305) is higher than the value calculated by the Bonferroni correction which shows that the results are not statistically significant (Fig. 4.9).

As with the whole dataset, it is possible to conclude the numbers of preflexural vertebrae do not vary in ichthyosaurs with age. It is therefore more likely that the slight variation shown in the results are related to taxonomic differences between the species.



$a=-2.648$ $r=0.194$ $r^2=0.0374$ p(uncor)=0.305 p(a=1)=0.161 B=-6.88-1.696 n=30

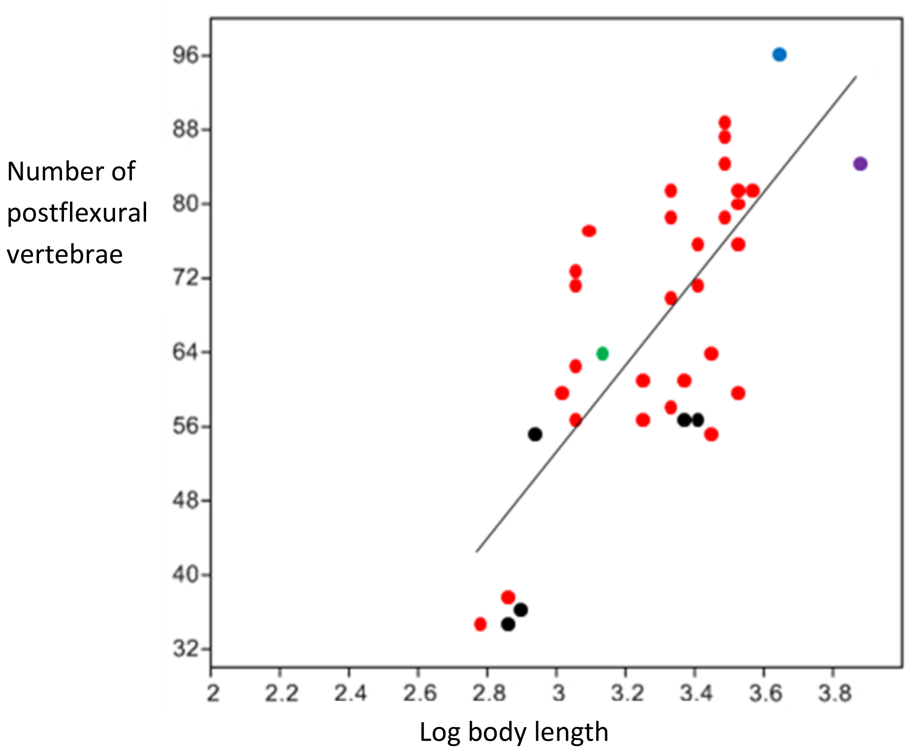
Fig. 4.9: OLS of *Stenopterygius* showing a weak relationship between the number of preflexural vertebrae and total body length

4.3.5: Postflexural vertebrae

The postflexural vertebrae are part of the caudal vertebrae. Postflexural vertebrae are those that lie posterior to the tail bend. The data used for this analysis are part of the dataset used for the caudal vertebrae.

4.3.5.1: Results of the postflexural vertebrae for the whole dataset

The results show a strong relationship between the numbers of postflexural vertebrae and total body length. The α value is high at 45.81. The r value is high as well at 0.745 which shows a relatively strong correlation while the r^2 value (0.555) shows that 55% of the variance in the numbers of postflexural vertebrae is related to body length. This result shows that it may be possible to use numbers of postflexural vertebrae in ichthyosaurs to help estimate relative ages. Furthermore, the p(uncor) value of 1.84^{-7} is lower than that calculated by the Bonferroni correction, showing that the results are statistically significant (Fig. 4.10).



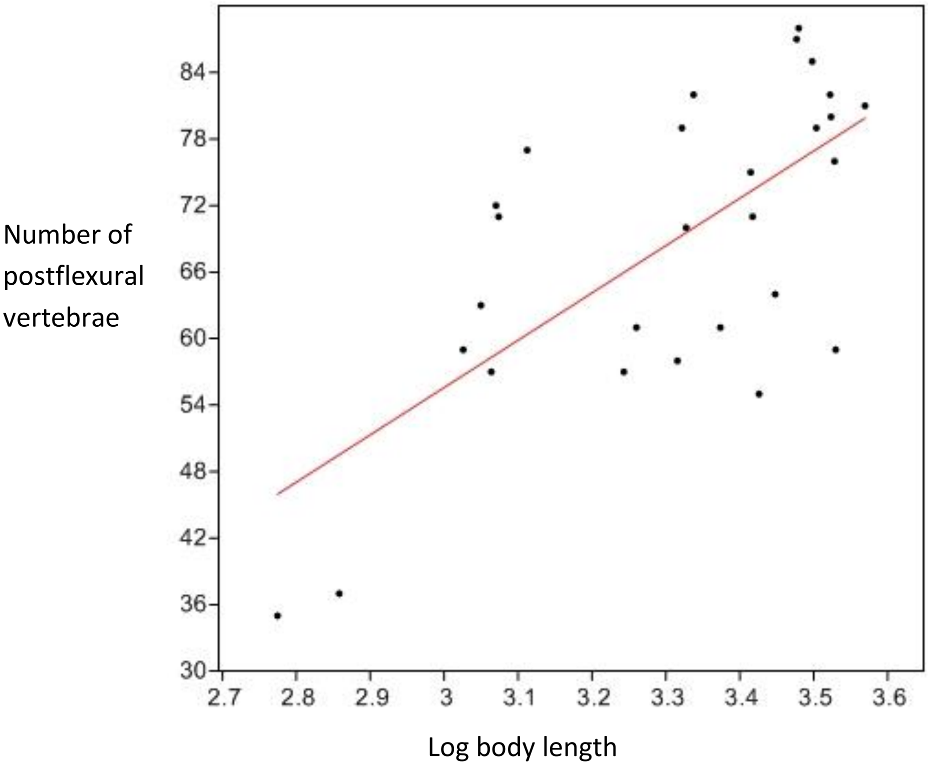
a=45.81 r=0.745 r^2=0.555 p(uncor)=1.845E-07 p(a=1)=2.811E-07 B=-33.21-60.33 n=36

Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unidentified Pink = *Temnodontosaurus*; Green = *Suevoleviathan*; Light Blue = *Leptonectes*

Fig. 4.10: OLS for the whole dataset showing a relatively strong relationship between the numbers of postflexural vertebrae and total body length

4.3.5.2: Results of the postflexural vertebrae for *Stenopterygius*

The result for the *Stenopterygius*-only dataset also shows a relatively strong correlation, although not as strong for the whole dataset. The α value is still high at 42.67 and the r value of 0.683 shows a relatively strong correlation. The r^2 value is 0.467, which shows that 47% of the variance in numbers of postflexural vertebrae is related to total body length and therefore to relative age. Furthermore, the p(uncor) value is 6.163^{-5} which is lower than the number calculated from the Bonferroni correction (Fig. 4.11). This shows that the results for the postflexural vertebrae are statistically significant and it might be possible to use the numbers of postflexural vertebrae to help estimate relative ages of *Stenopterygius*.



a=42.67 r=0.683 r^2=0.467 p(uncor)=6.163E-05 p(a=1)=8.280E-05 B=-28.58-65.91 n=28

Fig. 4.11: OLS for *Stenopterygius* showing a relatively strong correlation between the numbers of postflexural vertebrae and total body length

It is likely that the increase in numbers of caudal vertebrae seen in the whole dataset and *Stenopterygius* alone is based entirely on the signals for increasing numbers of ossified post-flexural vertebrae. The numbers of pre-flexural vertebrae remain stable with size while additional vertebrae ossify in the post-flexural region.

4.4: MERISITC RESULTS: LIMBS

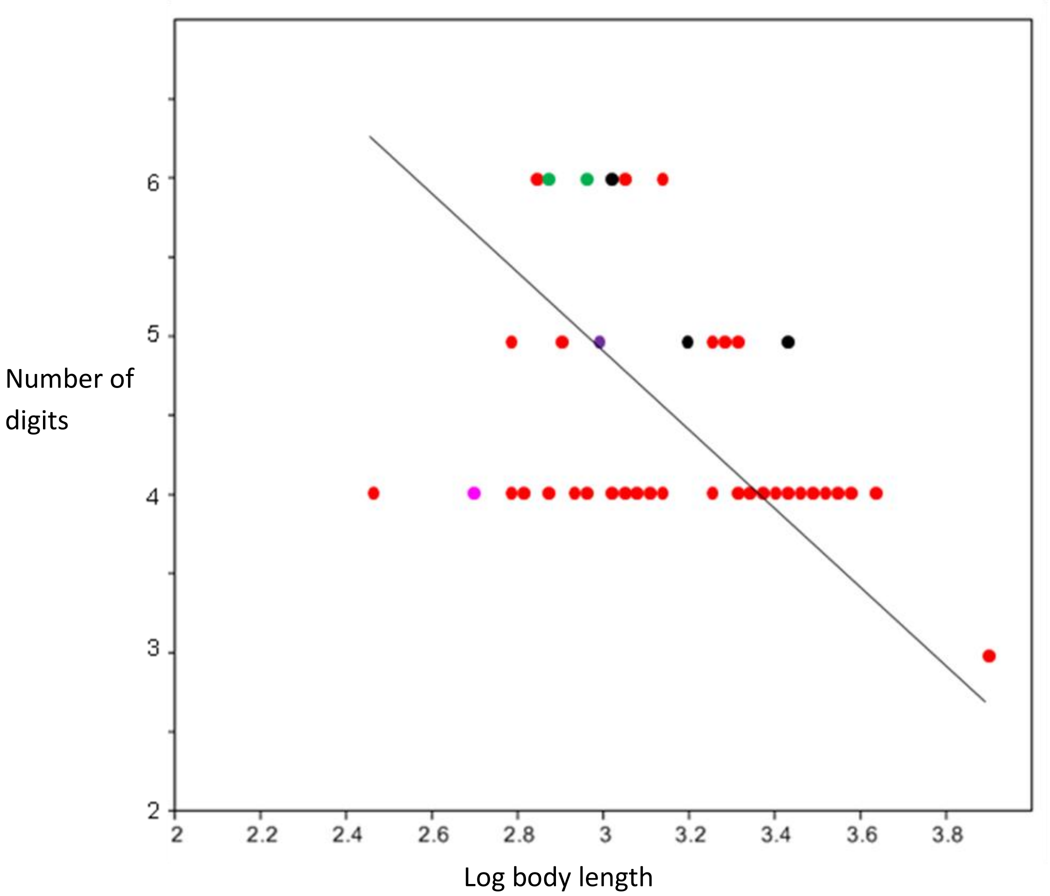
The limbs were also studied as they contain many repeated elements (phalanges) and structures (digits). These were analysed in order to see if numbers of ossified digits or phalanges within the digits changes with body size, and therefore relative age. If these features do change it may be possible to use them to help estimate relative age. Numbers of digits, and numbers of elements in digits are determined in the embryo. The purpose of these analyses is to see if digits or individual phalanges ossify after birth with age.

4.4.1: Digits

4.4.1.1: Results for the whole dataset

The results of the OLS comparing numbers of digits to log total body length does not show a strong relationship. The α value is low and slightly negative at -0.929, which explains the negative slope. However, the Bootstrap values are not well constrained and range between -1.1541–0.123. The results of the Bootstrap test show that the slope could potentially be positive. Therefore, the α value should not be taken as absolute. The correlation (r) value is 0.377, indicating that the correlation is not strong, while the r^2 value shows that only 14% of variance in the numbers of digits is related to total body length and therefore relative age. However, the p(uncor) value 0.0049 is lower than the value calculated from the Bonferroni correction (0.025). This shows that the results, although weak, are statistically significant (Fig. 4.12). From these results, it is unlikely that the numbers of ossified digits in the front limb can be used to help estimate relative ages of ichthyosaurs.

However, the numbers of digits are used for taxonomic assignment in ichthyosaurs and are not known to change with age (McGowan & Motani, 2003). Investigations into ossification sequences in ichthyosaurs have only hypothesised a proximal to distal sequence . Therefore, the variation relates only to taxonomy and the results are meaningless.



a=-0.929 r=-0.377 r^2=0.1421 p(uncor)=0.0049 p(a=1)=1.381E-07 B=-1.541—0.123 n=54

Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unidentified Pink = *Temnodontosaurus*; Green = *Suevoleviathan*; Light Blue = *Leptonectes*

Fig. 4.12: OLS for the whole dataset showing a weak relationship between the numbers of digits in the forelimb compared to total body length

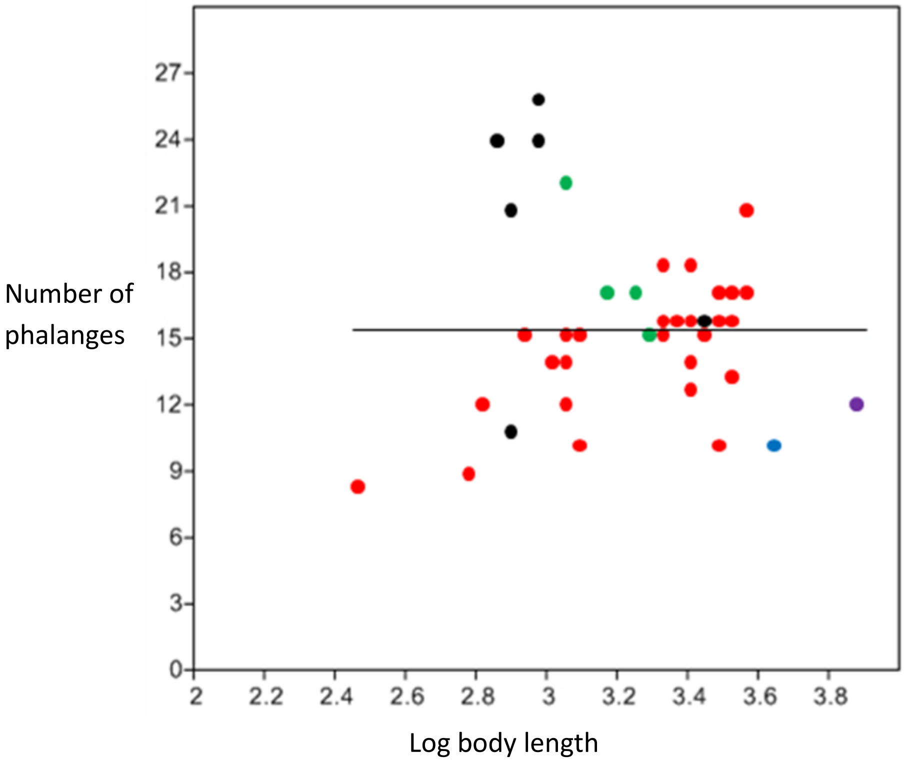
As all specimens of *Stenopterygius* possess four digits in the forelimb (McGowan & Motani, 2003), this analysis was confined to the whole dataset.

4.4.2: Phalanges

The number of phalanges in the longest digit of the forelimb was recorded in order to see if phalanges ossify after birth, and therefore relate to relative age. Caldwell (1997) identified a proximal to distal ossification sequence in the limbs of *Stenopterygius*, but this investigation was mostly based on embryos and neonates. There are two hypotheses tested using the same dataset. Therefore, the Bonferroni correction number is (0.05/2) or 0.025 for comparing the p values. This will determine if any results are statistically significant.

4.4.2.1: Results for the whole dataset

The results for the numbers of phalanges in the longest digit of the front limb versus body length show no correlation. The α value is 0.0097 indicating an extremely weak relationship. The r value is also very small at 0.0007, while the r^2 value of 5.022^{-7} shows that a fraction of a percent of the variance within numbers of phalanges relates to total body length and therefore relative age. Furthermore, the p(uncor) value of 0.9965 is much higher than the value of 0.025 calculated by the Bonferroni correction (Fig. 4.13). This result shows that there is not a significance relationship between number of phalanges and body length. It is therefore possible to conclude that the numbers of phalanges in the longest digit on the front limb do not relate to body length and cannot be used to help estimate relative age in ichthyosaurs.



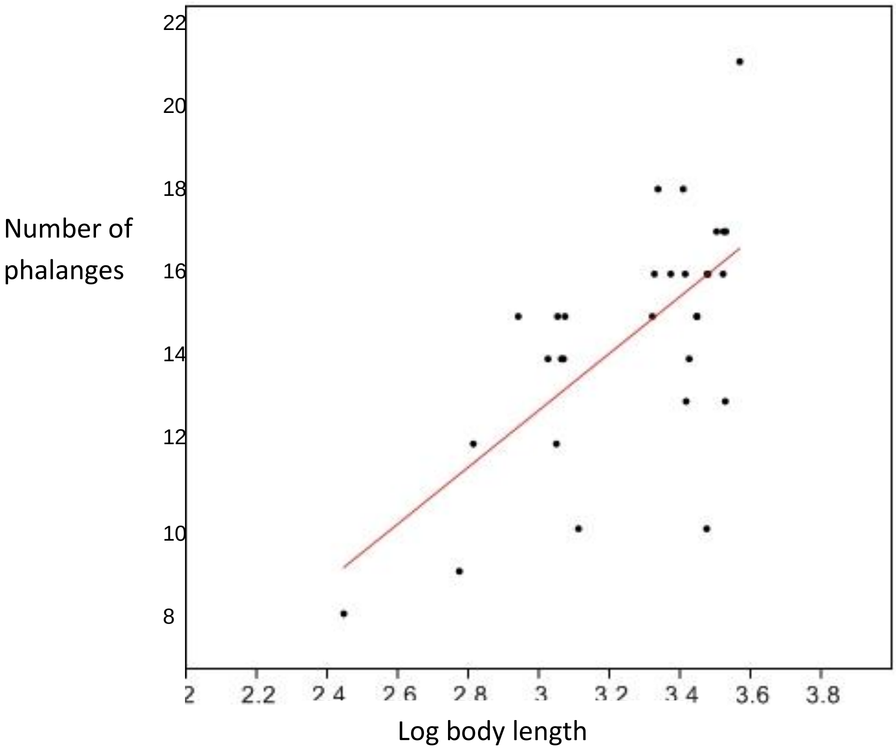
a=-0.0097 r=-0.0007 r^2=5.0218E-07 p(uncor)=0.9965 p(a=1)=0.6450 B=-4.865- - 6.399 n=42

Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unidentified Pink = *Temnodontosaurus*; Green = *Suevoleviathan*; Light Blue = *Leptonectes*

Fig. 4.13: OLS for the whole dataset, showing no relationship between the numbers of phalanges in the longest digit of the forelimb and total body length

4.4.2.2: Results for *Stenopterygius*

The results for the restricted *Stenopterygius*-only dataset show a relatively strong correlation between the numbers of phalanges in the longest digit in the forelimb compared to total body length. The α value is still relatively low at 6.695 and the Bootstrap values are well constrained (4.28 – 10.08). The r value suggests a relatively strong correlation with a value of 0.659. The r^2 value of 0.435 shows that 44% of the variance within numbers of phalanges in the longest digit is related to total body length. Furthermore, the p(uncor) value of 7.39^{-5} is lower than the number calculated by the Bonferroni correction. This shows that the results here are statistically significant (Fig. 4.14). Therefore, it is possible to conclude that the numbers of phalanges in the longest digit could be used to help estimate relative ages in *Stenopterygius*.



a=6.695 r=-0.659 r^2=0.435 p(uncor)=7.391E-5 p(a=1)=0.0005 B=4.283-10.08 n=30

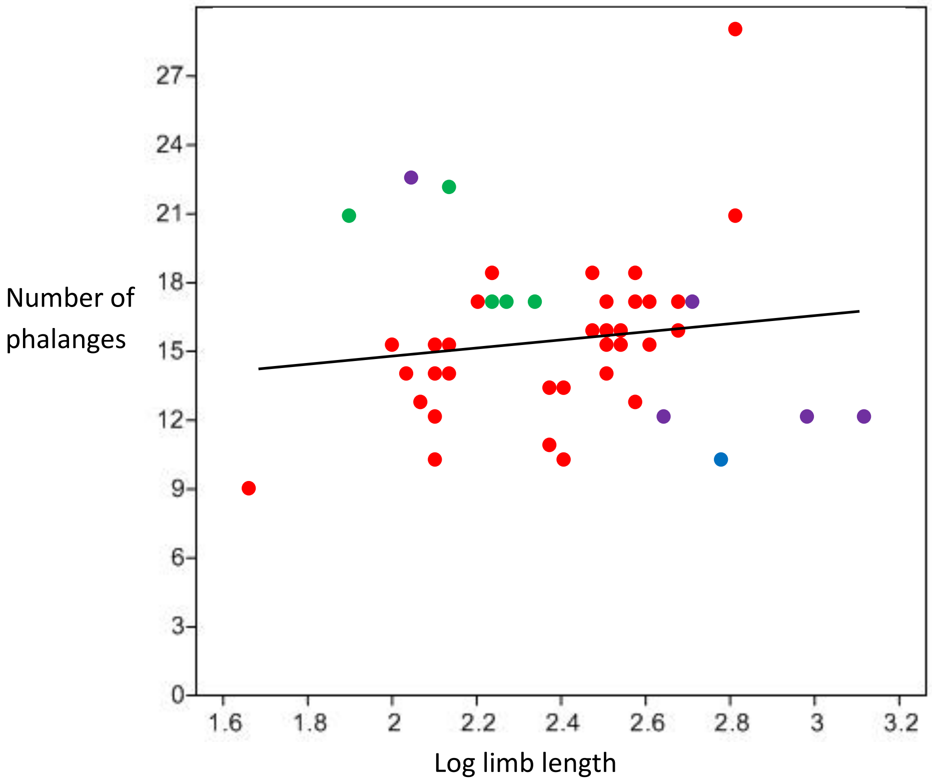
Fig. 4.14: OLS for *Stenopterygius* showing a relatively strong relationship between the numbers of phalanges compared to total body length

4.4.3: Results for the number of phalanges compared to limb length

The numbers of phalanges in the longest digit in the forelimb were compared to log limb length to establish if the number of phalanges correlates with limb length rather than total body length. This approach uses length of limb as a proxy for body size. Limb length is defined as the distance between the proximal edge of the humerus and the distal edge of the last phalanx in the longest digit. There are two hypotheses that are being tested using the same dataset. Therefore, the Bonferroni correction is 0.05/2 = 0.025.

4.4.3.1: OLS results for the whole dataset

The result for the whole dataset comparing forelimb length with number of phalanges in the longest digit does not show a strong relationship. The α value is low at 1.836, while the Bootstrap values range from -3.256–6.455 which is not well constrained.



a=1.836 r =-0.152 r^2=0.023 p(uncor)=0.320 p(a=1)=0.649 B=-3.056-6.455 n=45

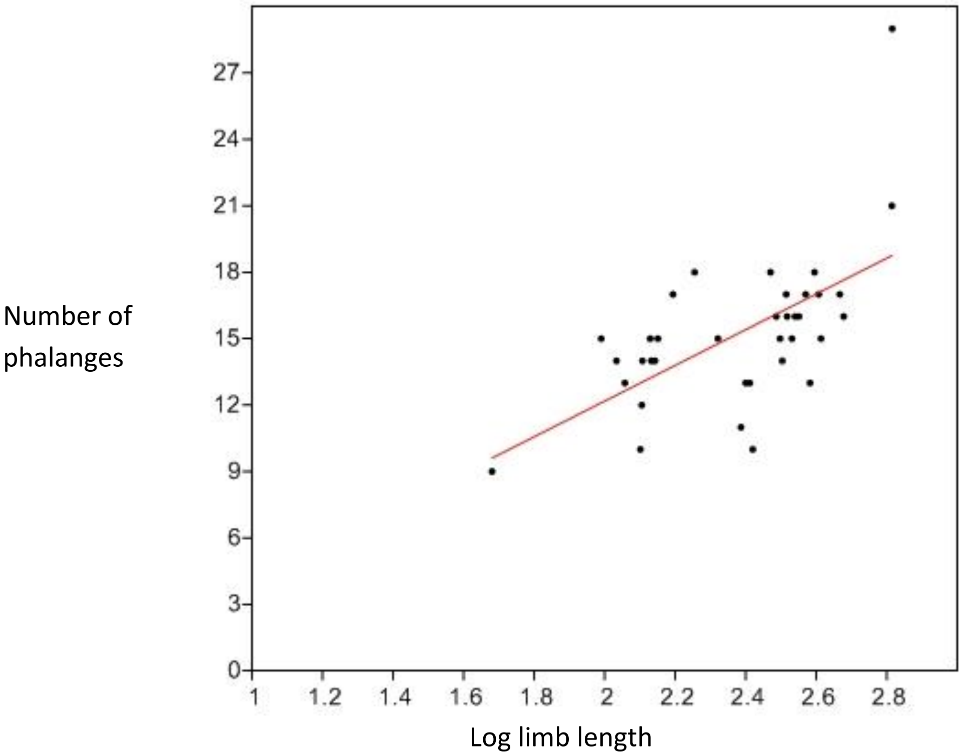
Key: Red = *Stenopterygius*; Dark Blue = *Ichthyosaurus*; Black = Unidentified Pink = *Temnodontosaurus*; Green = *Suevoleviathan*; Light Blue = *Leptonectes*

Fig. 4.15: OLS for the whole dataset showing a very weak relationship between log limb length and numbers of phalanges in the longest digit

The r value for the correlation is also low at 0.152, and the r^2 value of 0.023 shows that only 2% of the variance in the number of phalanges is related to log limb length. Furthermore, the p(uncor) value is 0.320. This value is higher than the Bonferroni corrected p-value of 0.025. This shows that the results are not statistically significant (Fig. 4.15). It is concluded that the numbers of phalanges for the whole dataset cannot be used to determine relative ages of ichthyosaurs.

4.4.3.2: OLS results for *Stenopterygius*

The results for forelimb length compared to numbers of phalanges in the longest digit shows a stronger relationship than found for the dataset as a whole. The α value is higher than the whole ichthyosaur dataset at 8.0675, but the Bootstrap values are not well constrained (-0.6043–12.52). The r value is relatively high at 0.6043, while the r^2 value of 0.365 shows that 37% of the variance within numbers of phalanges is related to log limb length.



a=8.0675 r =-0.6043 r^2=0.365 p(uncor)=9.491E-05 p(a=1)=0.0005E-05 B=-3.334-12.52 n=36

Fig. 4.16: OLS results for *Stenopterygius* showing a weak relationship for *Stenopterygius* between numbers of phalanges in the longest digit and limb length

The p(uncor) value is lower than the Bonferroni corrected p-value. This shows that the results are statistically significant (Fig. 4.16). However, the results show that only 37% of the variance is related to limb length. Despite the results, it is still unlikely that the relative ages of *Stenopterygius* can be established reliably using numbers of phalanges in the longest digit of the forelimb (elements distal to the radius and ulna) and forelimb length.

4.5: DISCUSSION

4.5.1: Limitations of the data

The sample size for many of the analyses is relatively small, with the lowest being 28. This will reduce the accuracy of the results of the analyses. The nature of the fossil record is such that measurements and counts are not available on every specimen. Distal bones in ichthyosaurs, such as phalanges or vertebrae are typically very small and light, even in species that tend to be large and robust. A consequence of the small, light bones, it would be very easy for these bones to be removed via taphonomic processes. This would affect counts of postflexural caudal vertebrae as well as the numbers of phalanges in the longest digit of the front limb. Therefore, a small margin of error could be introduced in the analyses that deal with these regions. However, if the limb or the distal tip of the tail was obviously disrupted, then the specimen was not included in the sample. Furthermore, many of the specimens, primarily *Stenopterygius*, were collected from the Posidonia shales from Holzmaden. These specimens are exceptionally preserved, sometimes with body outlines preserved around the feature of interest. In these circumstances, it is possible to be reasonably sure that none of the ossified elements have been lost due to taphonomic processes if the body outline is genuine. However, it is still possible that small distal elements could have been lost during preparation of the specimen. Drills and air abrasives could easily remove a small element and the loss might not be noticed by the preparatory.

As well as issues with sample size, there are further issues with ichthyosaur anatomy. Many other groups of reptiles have strongly regionalised axial skeletons in which the different sections are easy to distinguish on the basis of vertebral or rib morphology. The distinction between the cervical and dorsal vertebrae is very hard to define in ichthyosaurs. It has previously been defined in *Ophthalmosaurus* as the point where the most dorsal rib facet (diapophysis) loses contact with the facet for the neural arch (Appleby, 1956). However, the point where this occurs, which is variable, is positioned posterior to the position of the pectoral girdle. Furthermore, the morphology of the cervical vertebrae merges with the dorsal vertebrae without a clear transition point, particularly in laterally preserved specimens (McGowan & Motani, 2003). The distinction between the presacral and caudal vertebrae is potentially clearer and based on the position of the pelvic girdles. However, the pelves of Jurassic ichthyosaurs are not attached to the vertebral column as the hind limbs are much reduced in size. As a result of this, it is difficult to identify the boundaries between axial regions (McGowan & Motani, 2003). Therefore, there is likely to be some small margin of error in the numbers of vertebrae assigned to each vertebral region. The boundary between preflexural and postflexural vertebrae is defined as the centre of the apical vertebrae, which are those vertebrae that form the tail bend. The apical vertebrae are distinct as they typically are wider dorsally and more narrow ventrally, resulting in a wedge shape when viewed laterally, and are thus easily defined (McGowan & Motani, 2003).

4.5.2: Implications of the results

4.5.2.1: Results for Vertebrae

There is considerable variation in the numbers of vertebrae within species of ichthyosaurs. Taxonomic descriptions typically give a range of presacral vertebral numbers, or an indication of a ‘more than’ or ‘less than’ value (McGowan & Motani, 2003), which is unusual for amniotes. The numbers of presacral vertebrae in *Ichthyosaurus communis* ranges from 74 to 80 while the given numbers of presacral vertebrae for *Temnodontosaurus platyodon* is ‘probably >48’. Although variability in numbers of vertebrae, particularly presacral vertebrae is observed in ichthyosaurs, the results shown in this chapter show that they are of more use taxonomically than ontogenetically. In plesiosaurs, the pectoral vertebrae are easy to define in inferred juveniles since the neural arch and centra are not fused. Once they are fused in adult specimens they are less well defined. As a result, numbers of cervical, pectoral and dorsal vertebrae must be estimated based on a comparison to the juvenile form. Furthermore, the position of the transition is difficult to identify in ichthyosaurs (McGowan & Motani, 2003). The numbers of presacral vertebrae in plesiosaurs are more stable than those in ichthyosaurs and are used for taxonomic assignment. Some diapsids such as snakes do have variation in numbers of vertebrae where this feature is sexually dimorphic (Shine, 2000).

The only result that shows a significant relationship in ichthyosaurs is between the number of ossified postflexural vertebrae and total body length. This shows that 55% of the variance in numbers of postflexural vertebrae is related to total body length and, therefore, can potentially be used as an indicator of relative age when the information in the complete ichthyosaur dataset is considered. This result is further confirmed by comparing it to those obtained for the restricted *Stenopterygius*-only dataset, which shows that slightly less than 50% of the variance in the numbers of postflexural vertebrae relates to total body length. It seems likely that the other 50% of the change in total body length relates to the lengthening of the individual vertebrae rather than an increase in their numbers. However, the width measurements of vertebrae were not collected as part of this study and further research would be required in order to see if this is the case. The changing numbers of ossified postflexural vertebrae could therefore be used to help estimate relative ages of ichthyosaurs. The results shown here make biological sense as the postflexural vertebrae form the lower half of the semi-lunate tail. The length of the vertebral column formed by the postflexural vertebrae is therefore representative of tail size. As the tail is the main form of propulsion for ichthyosaurs, it is logical that the total surface area of the tail would increase significantly, as well as gain in strength in order to withstand greater stresses, as the body size of the organism increases with age. It is possible that the size increase required to maintain efficient propulsion could not be achieved purely by lengthening of the vertebrae (see discussion below). Numbers of vertebrae and the relationship to swim performance have been studied in fish (Brainerd & Patek, 1998). Brianerd and Patek (1998) analysed escape swimming in 19 specimens of fish, representing 6 different species. They concluded that a greater number of vertebrae results in a more efficient swim style and a faster swim speed due to an increase in the angle of flexibility in the vertebral column. However, the increase in ichthyosaur vertebrae occurs in the distal tip of the tail and would not affect the angle of flex in the remainder of the vertebral column.

4.5.2.2: Results for forelimbs

The majority of the results presented regarding the number of digits and phalanges in the forelimb show a weak relationship between the numbers of elements present and either body length or limb length. The results for the numbers of digits in the forelimb compared to total body length show a weak, but statistically significant, relationship. As this result is based on the whole ichthyosaur dataset, it is possible that these results are misleading, as variability in digit numbers may be a result of taxonomic differences rather than ontogenetic change. The numbers of digits in the limbs of ichthyosaurs are used frequently in taxonomic diagnoses (e.g., McGowan & Motani, 2003). The relative age of an individual ichthyosaur cannot be assessed using numbers of digits on the forelimb.

The results comparing numbers of phalanges in the longest digit in the front limb compared to body length and limb length for the whole ichthyosaur dataset do not show any significant relationships. The α values are very low showing that only a fraction of the variance in numbers of phalanges relate to total body length or forelimb length. However, the results for *Stenopterygius* alone show stronger relationships. When numbers of phalanges in the longest digit in the front paddle are compared to total body length, the results show that 44% of the variance in numbers is related to total body length and that 37% of the variance is related to forelimb length. This indicates that numbers of ossified phalanges could be used to help estimate relative ages in *Stenopterygius*. Addition of ossified elements after birth has previously been observed in pachypleurosaurs (Hugi & Scheyer, 2012). It has been observed that there is a clear continuous proximal to distal ossification sequence in *Stenopterygius* (Caldwell, 1997) and the results presented here support this. Further studies into other genera is required in order to see if this is applicable to other genera or a genus-specific feature of *Stenopterygius*. This work is outside the scope of this project.

4.5.3: Comparison of vertebral results with other organisms

Studies of numbers of presacral vertebrae have previously been conducted, but these have tended to focus on phylogenetic trends in vertebral count evolution, rather than ontogeny (Romer, 1956; Müller *et*. *al*., 2010). During ontogeny of the individual, the number of presacral vertebrae remains more or less the same. For this reason, numbers of presacral vertebrae are used more in taxonomic identifications than for estimating relative ages of the individual (Romer, 1956). McGowan & Motani (2003) report 55 or more presacral vertebrae for *Cymbospondylus*, a Triassic genus, and >41 presacral vertebrae for the Jurassic *Ichthyosaurus communis*. It is possible that this relates to changes in swimming styles between Triassic (anguilliform) and Jurassic forms (thunniform) (Romer, 1956; Motani, 2005). In sauropterygians, the trunk remains stable in length, but there is wide variation within neck length, which therefore increases the total presacral count. Forty is the characteristic number of presacral vertebrae for nothosaurs, but elasmosaurs may have as many as 105. As the numbers of presacral vertebrae for most Mesozoic marine reptiles are standard and used for taxonomic assignment, it is not surprising that no statistically significant results were found for presacral numbers in ichthyosaurs. The numbers of presacral vertebrae in other organisms appears to be well constrained within a species compared to the variability observed in ichthyosaurs (Rieppel, 1993; Hugi & Scheyer, 2012).

Despite some variation, the numbers of presacral vertebrae are still used for taxonomic assignment in ichthyosaurs, but do not relate to ontogeny.

Many reptiles (e.g. alligators, turtles, plesiosaurs) have all of the vertebrae ossified at the time of birth or hatching. In the case of pachypleurosaurs, ossification of the vertebrae is complete at the neonate stage and no more are added with increasing size of the individual (Hugi & Scheyer, 2012). The results shown above indicate that the numbers of postflexural vertebrae do change with size in ichthyosaurs. It is not possible to compare numbers of postflexural vertebrae to other marine reptiles of the Mesozoic due to the lack of a tail bend (with the exception of some derived mosasaurs and crocodilians (Massare, 1994)). However, it would be possible to compare total numbers of vertebrae. Ichthyosaurs are not the only Mesozoic marine reptiles that had a mainly tail-driven form of locomotion. The tails of plesiosaurs are relatively short and are not used for locomotion as the limbs fulfil this role (Halstead, 1989). The tail provides the driving force of movement in crocodilians and pachypleurosaurs. The tails of these organisms are straight and do not feature the down turn in the vertebral column that is observed in ichthyosaurs, which forms the anterior part of the semi-lunate tail. In alligators, the anguilliform swimming style results in the straight tail being moved from side to side, which results in the tail providing thrust. The same swimming style is inferred for pachypleurosaurs. Furthermore, modern marine tetrapods, such as whales and dolphins, that have a tail with a similar shape to ichthyosaurs, do not have vertebrae in either part of the tail. It is instead, entirely cartilagenous (Fordyce & Barnes, 1994). Consequently, modern marine tetrapods cannot be used as a comparison with ichthyosaurs for changes in numbers of postflexural vertebrae.

4.5.4: Comparison of limb ontogeny with other organisms

Studies of limb ontogeny in other organisms show that the numbers of digits remain constant after birth. Müller and Alberch (1990) show that the digits in the forelimb ossify in a sequence from digit 5 to 1 in *Alligator mississippiensis*. However, all digits are present at birth and the numbers do not change further with age. Therefore, with the exception of assessing embryonic maturity, the numbers of digits do not vary with age after birth. This is similar to the results shown for ichthyosaurs showing that digit numbers are more closely related to taxonomy than ontogeny.

Limb ossification patterns have also been examined in pachypleurosaurs (Hugi & Scheyer, 1012). The material from Switzerland and Italy provides an ontogenetic series that allows the timing of the onset of osteogenesis and compaction in bone to be observed, as well the timing of when these processes stop. The authors show that limb osteogenesis occurred in two steps; (i) developmental ossification of bone during embryology and in early neonate stages and (ii) periosteal compaction of bone during neonate ontogeny. The results of this analysis show that the forelimb ossifies before the hindlimb in all the pachypleurosaurids included in the study. Furthermore, the ossification of the mesopodial and phalangeal regions ossify during neonate ontogeny, after birth. The order of digital ossification can vary slightly within the pachypleurosaur group. In two of the species studied, the digits ossify in order through digit 1 to digit 5. However, in others the digits ossify in order through digit 1 to digit 3 and then digit five ossifies before digit 4 (Hugi & Scheyer, 2012). The changing order of digit ossification could be of use for taxonomic assignment, but only if the specimen is preserved at the neonate stage. The numbers of digits do not change with age much after the neonate stage. This is similar to that of ichthyosaurs and is a taxonomic feature rather than an ontogenetic feature. However, ichthyosaurs show hyperphalangy (Fedak & Hall, 2004) which is rare in tetrapods. Consequently, it is difficult to make a comparison to other organisms.

4.6: CONCLUSIONS

Ichthyosaurs are unusual amongst amniotes in having plasticity in the numbers of presacral vertebrae. However, the variability observed here does not relate to ontogeny and this feature is of more use to taxonomy. The postflexural vertebrae increase with size, and therefore relative age, while all other repeated elements analysed showed no statistically significant change.

Future work could focus on comparing the numbers of postflexural vertebrae to other ichthyosaur genera in order to observe if this feature can be used for all ichthyosaurs or just for genera found in the Lower Jurassic.

5: SEXUAL DIMORPHISM IN ICHTHYOSAURS

5.1: INTRODUCTION TO SEXUAL DIMORPHISM

Sexual dimorphism is a well-known phenomenon and can result in members of the same species appearing very different from each other, both in fossils and in extant organisms (Johnson *et*. *al*, 2009). Sexual dimorphism is the physical difference between males and females of the same species and evolved as the result of sexual selection. The differences can be in size of soft parts and skeletal elements as well as in ornamentation or colour (see section 5.2). Soft parts are rarely preserved in the fossil record so other forms of evidence are required to identify gender. Ichthyosaurs provide a rare opportunity to study sexual dimorphism in fossils as direct evidence of gender is preserved by the presence of embryos in, or in very close association with, the remains of the mother (Cheng *et*. *al*., 2004). Physical differences between male and female ichthyosaurs could call some taxonomic assignments into question. Ichthyosaur remains could have been assigned to a different or new species where in fact they could be a male or female of a known species. If this were the case, subsequent research into evolution, diversity or geographical distribution would be flawed. Furthermore, previous estimations of age in the published literature have been based on total body length, or a proxy for size of an individual. Previous results show that other features such as skull length compared to body length as well as orbital diameter can be used to assess relative ages in ichthyosaurs (Chapters 3 and 4). If there are large size differences between males and females then the smaller gender could be misinterpreted as a juvenile of a species.

Direct proof of gender in the fossil record is very rare. It is only observed in the fossil record when embryos or eggs are preserved with the remains, or when specimens are preserved copulating and gender can be discerned based on position (see section 5.2 for more details). Pregnancy provides an opportunity to examine sexual dimorphism in ichthyosaurs. This chapter aims to investigate whether or not there are any physical differences between pregnant female specimens and non-pregnant individuals and if so, which features might indicate males and which females.

Sexual dimorphism has been suggested in ichthyosaurs (McGowan, 1979) but no rigorous analysis has been conducted despite pregnant specimens being known for almost a century. Differences in the prenarial ratio and sclerotic ratio, total digit count and the number of primary digits were identified in seven specimens of *Eurhinosaurus longirostris* McGowan 1994 (McGowan, 1979) which were suggested to be features of sexual dimorphism. However, gravid females are not known for this species so this hypothesis cannot be tested. Sexual dimorphism has also been suggested in *Shastasaurus tangae* Cao & Luo, 2000 (Shang & Li, 2013) based on characteristics of the hind limb. Sixteen specimens were analysed and the results showed that, in one type (type A), the hind limb is relatively long and thin with no preaxial accessory digit developed. The distal tarsal, metatarsal and proximal one or two phalanges of digit II are small or absent. By contrast, the type B hind limb tends to be relatively wider and with a well developed preaxial accessory digit. The metatarsal and proximal phalanges of digit II are similar in size to digits III and IV. These differences are identified by the authors are suggested to be sexually dimorphic. However, there are no gravid females to test the theory (Shang & Li, 2013).

5.2: SEXUAL DIMORPHISM IN TETRAPODS

An overview of sexual dimorphism and gender recognition is provided for modern and fossil tetrapods. Section 5.2.5 outlines the implications for the potential identification of sexually dimorphic features in ichthyosaurs.

5.2.1: Amphibian sexual dimorphism

Shine (1979) analysed published literature on amphibian sexual dimorphism for (i) adult body size and (ii) secondary sexual characteristics (any sexual dimorphic feature other than size) such as the presence of oral 'tusks' or spines on the body. The analysis was restricted to anurans (frogs and toads), (589 species) and urodeles (salamanders and newts) (79 species). Body size was based on a snout-vent length. Female-biased sexual size dimorphism is apparent in 61% of urodeles and 90% of anurans. However, species in which adult males equal or exceed the females in size tend to be the species in which physical combat between adult males is recorded. Overall, males are as large as, or larger than, the females in 41% of the 32 anuran species known to show male combat. In comparison, males are larger than females in only 9% of 557 non-combative species. Similarly, males equal or exceed female body size in 87% of the 15 urodele species that show male combat but in only 28% of the 64 non-combative forms (Shine, 1979). Shine (1979) also concluded that secondary sexual characteristics such as oral tusks, spines on the prepollex, breast or arms are common among the anuran species known to exhibit male combat. Furthermore, male spines and tusks are also more common among species in which the males are equal in size, or larger than the females. Despite this result, Shine (1979) goes on to say that this could be explained by chance. Gender can be readily identified in the amphibia. Despite this, there is not a single 'rule' for identifying gender in a particular group. Therefore, knowledge of gender traits for each species would be required in order to distinguish gender in an individual specimen.

Female-biased sexual dimorphism has also been observed by Woolbright, (1983) in some amphibians. Howard (1981) examined secondary sexual characteristics and studied data collected on male mating success in bullfrogs between 1975 and 1978. Data on body length was also collected based on a measurement of snout-ischium. The results showed that females are significantly larger than males, despite that fact that males aggressively defend territories. The defence of the territories leads to other features of sexual dimorphism as shown by Peters & Aulner (2000) who analysed the forearm muscles (abductor indicus longus; flexor carpi radialis; extensor carpi ulnaris) of 18 male and 16 female Bullfrogs. The results of the analysis show that the wet mass and the cross-sectional area of the muscle are larger in males compared to the females for all the muscles analysed (Peters & Aulner, 2000).

Schäube (2004) analysed 1680 specimens of *Limnodynastes tasmaniensis* Günther, 1858 and 646 specimens of *L. peronii* Duméril & Bibron, 1841, two species of frogs. The identification of males and females was based on secondary sexual characteristics. Males were identified by the presence of nuptial pads (both species) or bony excrescences (*L. peronii*) on the fingers and darkened throat patches. Females were identified based on presence of fleshy flanges on the fingers or eggs in the body cavity. Several measurements were obtained for morphometric analyses; (i) snout-urostyle length, measured from the tip of the snout to the posterior tip of the urostyle bone; (ii) head width; (iii) jaw length and (iv) tibia length. Females are larger than males in *L. tasmaniensis*. The sexual dimorphism is small and there is considerable overlap in the size ranges of males and females. In contrast, males are larger than females in *L. peronii* and there is limited overlap between the genders. These results follow a trend for females to be larger than males in smaller species and males to be larger in the large species. Furthermore the results of study showed significant geographical variation in the extent of sexual dimorphism. The results showed that the extent of the body size dimorphism increases along a north-south latitudinal cline for *L. tasmaniensis* (Schäube, 2004).

In the majority of anurans, females are larger than males (Shine, 1979; Katsikaros & Shine, 1997). Despite this, there are species that do not follow that trend (Katsikaros & Shine, 1997). In the tusked frog *Adelotus brevis*, the males grow larger than females and also have larger heads relative to body size. Males also have a pair of projections (tusks) in the lower jaw. These are rare traits among anurans (Katsikaros & Shine, 1997). Tusks are also observed in fanged ranid frogs of the family Ranidae, from Southeast Asia (Emerson, 1998).

Colour can be sexually dimorphic in many organisms and has been inferred in fossil amphibians (Werneburg, 2007). Although original colour cannot be discerned, patterns on amphibian skin can be identified based on colour patterns on the rock (Werneburg, 2007).

The published literature shows that females are larger than males in the majority of species in the amphibia. Secondary sexual characteristics are present in the forms of tusks in the jaw or spines on the hands. These features could be identified in the fossil record as the skeletons and the tusks and spines would be readily preserved (Carroll, 1977). However, in some cases, the presence of eggs was used to identify females. As amphibian eggs are soft, unlike reptilian or avian eggs, they are unlikely to be preserved in the fossil record. Amphibian eggs have not been found in the fossil record and therefore they cannot be used to identify gender.

5.2.2: Reptilian sexual dimorphism

Cox *et*. *al*. (2007) analysed a large dataset of measurements of adult sexual size dimorphism for 1314 populations representing 832 different species of modern reptiles. The species comprised 479 lizards, 277 snakes and 76 turtles.

Size was determined in lizards as a measurement of length (snout-vent length) and the results show that the males are larger than females in the majority of lizard species. Despite this, female-biased (females larger than males) sexual size dimorphism is observed in some lizards and occurs in nearly every family. In some cases the sexual size dimorphism can be extreme with males being 50% longer than females. This is the case for polychrotid anoles (*Anolis*), tropidurids (*Tropidurus*), marine iguanas (*Amblyrhynchus*) and varanid monitor lizards (*Varanus*). However, female length can exceed male length by 20% in some polychrotids (*Polychrus*), skinks (*Mabuya*) and pygopodids (*Aprasis*). Secondary sexual characteristics (sexually dimorphic features other than size differences) in lizards have also been observed in some species. Ribeiro *et. al*. (2010) observed differences in ventral colour patterns in Striped Lava Lizards (*Tropidurus semitaeniatus* Spix, 1825). Eight three lizards (62 adults and 21 juveniles) were collected and analysed in the study. The results show that males display coloured patches on the thighs and precloacal flap while females lack this colouration (Fig. 5.1). This feature can be used to easily identify gender in specimens regardless of size.

Skin patterns have been identified in the fossil record in reptiles (Lingham-Soliar & Plodowski, 2010). Colour is inferred in reptiles based on preservation of colour bearing organelles (Lingham-Soliar & Plodowski, 2010; Zhang *et*. *al*, 2010) such as melanosomes as well as integumental structural proteins. Colour in reptiles has been identified on scales of an exceptionally preserved ceratopsian (Lingham-Soliar, 2010) where high-powered digital imaging was used to analyse the tubercles and fragments of preserved colour. However, reconstruction of colour is not simple as a variety of factors can affect the preservation of colour such as the sediment the fossil is preserved in, burial temperatures, fluid flow and subsurface weathering (McNamara, 2013). The colour is inferred based on the shape of the organelle. It is plausible that the shape of an organelle could be distorted during burial which could lead to misinterpretation of the colour. In some cases, the original pigment can be preserved as in *Archaeopteryx* (Manning *et*. *al*., 2013).

Despite male-biased sexual size dimorphism in lizards, there is still overlap in body size in sexually mature specimens of both genders. Watkins (1996) analysed sexual size dimorphism in the iguanian lizard *Microlophus occipitalis* Peters, 1871, which displays strong male-biased sexual size dimorphism where the males are larger than the females. Data was collected on body length data (based on snout-vent length) in 512 adult male and 543 adult female specimens. Watkins (1996) shows that size at sexual maturity for males is 66.0 ± 15.7 mm while the size at maturity was 55.1 ± 7.5 mm in females. Therefore, the minimum snout-vent length for sexually mature males is 47.3 mm and the maximum snout-vent length for a sexually mature female would be 62.6 mm in length, which shows a potential overlap of 15.3 mm (Watkins, 1996). Madsen and Shine (1993) also show an overlap in body size of sexually mature male and female snakes.

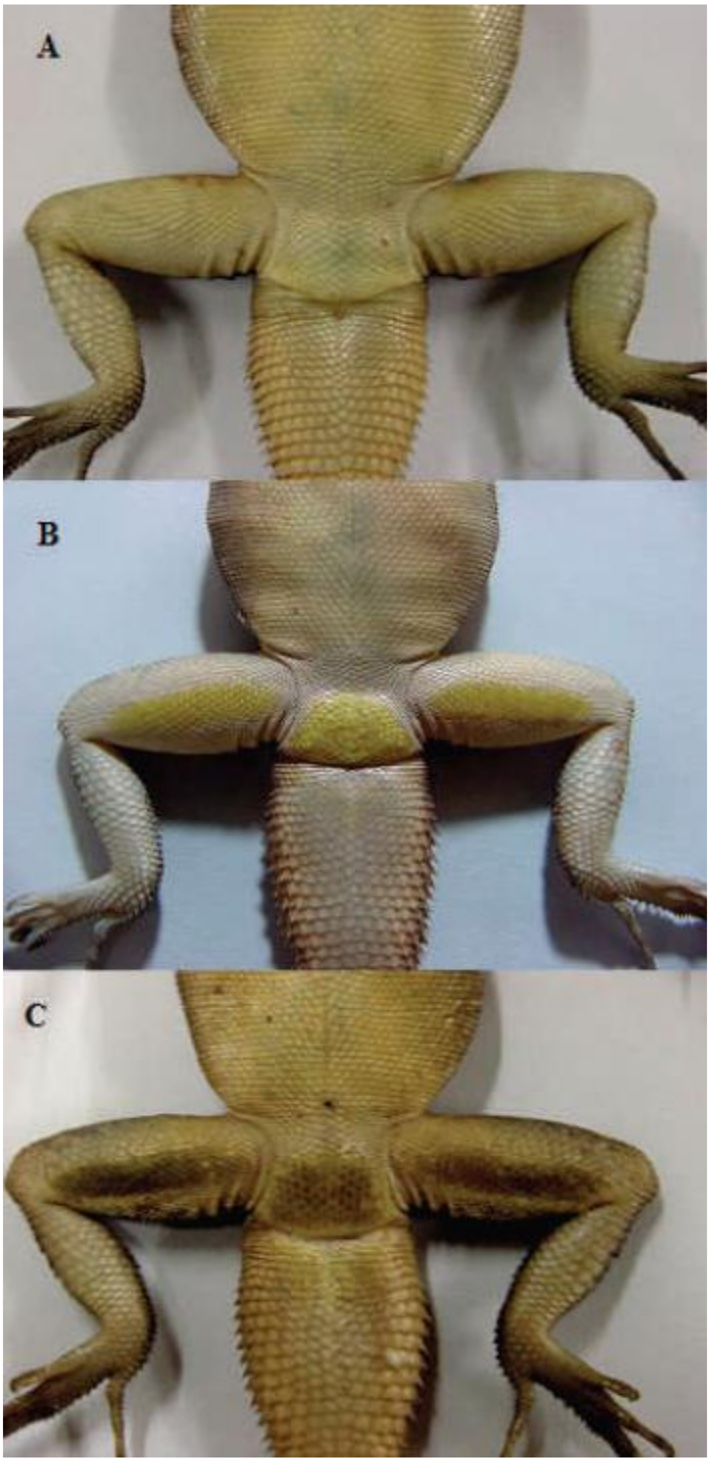


Fig. 5.1: Ventral view of *Tropidurus semitaeniatus* (A) female showing a lack of coloured patches; (B) male with yellow ventral patches on thighs and precloacal flap; (C) male with yellow and black patches on thighs and precloacal flap (from Ribeiro *et*. *al*., 2010).

Size was also determined using snout vent length in snakes. However, unlike lizards, snakes demonstrate female-biased sexual size dimorphism where the females are larger than males in the majority of species (Cox *et*. *al*, 2007). Furthermore, female-biased sexual size dimorphism is the rule for many lineages such as Natricinae, Xenodontinae, Boidae and Scolecophidia. There is only one family (Viperidae) that is characterised by ubiquitous male-biased sexual size dimorphism. As with lizards, the size differences between the genders can be pronounced with females being larger than males by up to 50% in some natricine water snakes (*Nerodia*), xenodontines (*Farancia*), elapid sea kraits (*Laticauda*), boids (*Morelia*) and scolecophidian blind snakes (*Ramphotyphlops*). A previous study on snakes (Shine, 1994), based on published and original data for 374 species from eight different families, showed that generally females are larger than males. However, Shine (1994) showed that in species in which males use combat to compete for females, the males are typically of equal size, or larger than the females. Furthermore, he also showed that viviparity results in more pronounced female-biased sexual size dimorphism. As with the paper by Cox *et*. *al*. (2007), only sexual size dimorphism is taken into account and other features that relate to sexual dimorphism are not mentioned. Other studies have reported sexual dimorphism in snakes. Bonnet *et*. *al*. (2011) analysed 690 tiger snakes over a period of 12 years by recapture. As with previous studies, size was based on snout-vent length. Both genders experienced similar growth rates but at maturity the males were larger than the females. This is likely due to the physical requirements of vitellogenesis and gestation slowing the growth rates of the females (Bonnet *et*. *al*., 2011).

Length in turtles was based on carapace or plastron length (Cox *et*. *al*., 2007). The results of the analysis showed that females tend to be larger than males in the majority of species. Female-biased sexual size dimorphism is the trend for several families including Emydidae, Geoemydidae and Trionychidae. However, there are some families that display male-biased sexual size dimorphism such as Testudinidae and Kinosternidae. Female-biased sexual size dimorphism has been shown in turtles in other studies. Gibbons & Lovich (1990) examined sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta* Schoepff, 1792) and reported female-biased sexual size dimorphism. Forsman & Shine (1995) also demonstrated female-biased sexual size dimorphism in one group of turtles (Testudines) based on previously published data. The extent of the size dimorphism increases with the clutch size of the species.

Gender can also be identified in the fossil record in extremely rare circumstances where exceptional preservation shows behaviour. The Eocene deposit in Messel, Germany is well known for its exceptional preservation (Franzen, 1985). Several pairs of turtles

(*Allaeochelys crassesculpta* Harrassowitz, 1922) have been preserved in the act of copulating (Fig. 5.2). These are the only known vertebrate fossils known to be preserved in the act of mating. The position of the couples demonstrates behaviour as well as helping to identify the genders. Freshwater turtles typically mate in the water with the males mounting the females from the rear. This information can be used to infer gender in copulating pairs. Joyce *et*. *al*. (2012) also states that the male has a longer, more prehensile tail than the females. This confirms the genders of the mating pair (Joyce *et*. *al*., 2012).

Fig. 5.2: Dorsal view of copulating turtles with the male on the right. Scale measures 10cm. (from Joyce *et*. *al*., 2012. Online supplement).

Other features of sexual dimorphism have been identified in turtles. Length of the tail has been reported as sexually dimorphic in some species (White & Murphy, 1973; Wibbels, 2003; Casale *et*. *al*., 2005; Joyce *et*. *al*., 2012). Casale *et*. *al*. (2005) reported that tail length is the main secondary sexual characteristic of adult sea turtles (Loggerhead turtles, *Caretta caretta* Linnaeus, 1758). Size of the tail is defined as the distance from the cloacae to the posterior margin of the carapace. 2631 specimens were investigated and the results show that the males have a larger and muscular prehensile tail whereas the females have a much smaller and less manoeuvrable tail. However, this feature can only be used to identify gender once sexual maturity is reached and can only be used to identify gender in specimens with a plastron length greater than 75cm, the size at which sexual maturity can be safely inferred for both males and females (Casale *et*. *al*. 2005). This approach is of no use for gender identification in hatchlings and juveniles.

The large dataset used in Cox *et*. *al*. (2007) suggests that the results are very robust and they are also supported by other publications (see above). However, sexual dimorphism is only analysed by Cox (2007) in terms of size. Sexual dimorphism can be expressed in features other than size, such as pigmentation, ornamentation or other skeletal features which are not mentioned within the paper by Cox *et*. *al*. (2007).

Sexual dimorphism in pachypleurosaurs, an extinct group of reptiles, has been reported by several authors (Sander, 1989; Rieppel, 1989; Lin & Rieppel, 1998). Rieppel (1989) and Sander (1989) observed some differences in the humerus of some pachypleurosaurs that were attributed to sexual dimorphism. Rieppel (1989) stated that sexual dimorphism affects overall size as well as the relative size of forelimb elements. The dimorphism is most pronounced in the relationship between the minimal width and distal width of the humerus, due to the difference in the size of the epicondyle. However, there was no direct evidence of which gender is which. Sander (1989) suggested that the sex with the larger forelimbs (sex *y*) was female as he inferred that they would have to use the forelimbs to move on land to lay eggs. This is in accordance with Rieppel's (1989) suggestion that sex *x* in *Serpianosaurus* Rieppel, 1989 is the male. However, a more recent analysis by Cheng *et*. *al*. (2004) reported viviparity in a species of pachypleurosaur *Keichousaurus hui* Young, 1958, which contradicts the conclusions of Sander (1989). The discovery of a gravid specimen provides direct evidence of gender and thus allows a more detailed study of sexual dimorphism. Lin and Rieppel (1998) distinguished the gender in this species based on the length ratio between the humerus and the femur as well as structural complexity of the former. In one morph (sex *x*), the humerus is nearly as long as the femur and is structurally simple. In contrast, the other morph (sex *y*) the humerus is much longer than the femur and is structurally massive. The humeri of the gravid females are similar in length to the femur and lack complicated structure. Therefore, in *K. hui* sex *x* represents the female and *y* represents the male. Dimorphism in small European pachypleurosaurs such as *Neusticosaurus* Seeley, 1882 and *Serpianosaurus* is closely comparable and it is therefore now possible to determine gender in these taxa (Cheng *et*. *al*., 2004). There are other forms of extinct Mesozoic reptiles that are known to give birth to live young. In marine examples, viviparity has been proven in mosasaurs (Caldwell & Lee, 2001), plesiosaurs (O'Keefe & Chiappe, 2011) and nothosaurs (Renesto *et*. *al*., 2003). However, those studies used isolated finds (one specimen) and gravid specimens are more common in ichthyosaurs. Renesto *et*. *al*., (2003) only reported nothosaur embryos and inferred viviparity as no gravid specimens have been found. These few specimens may provide some insights into sexual dimorphism but low specimen numbers prevent statistical analysis.

Bennett (1992) examined sexual dimorphism in pterosaurs and more specifically in *Pteranodon* Marsh, 1876. It was shown that two morphs were evident. One morph was larger with a much enlarged cranial crest while the other was smaller with a much more reduced cranial crest (Fig. 5.3). It was hypothesized that the larger morph is more likely to be male. This is supported by further evidence as the size and shape of the pelvis in the smaller morph is relatively larger and deeper which would be more suited for egg laying (Bennett, 1992). This further suggests the smaller morph is indeed the female.

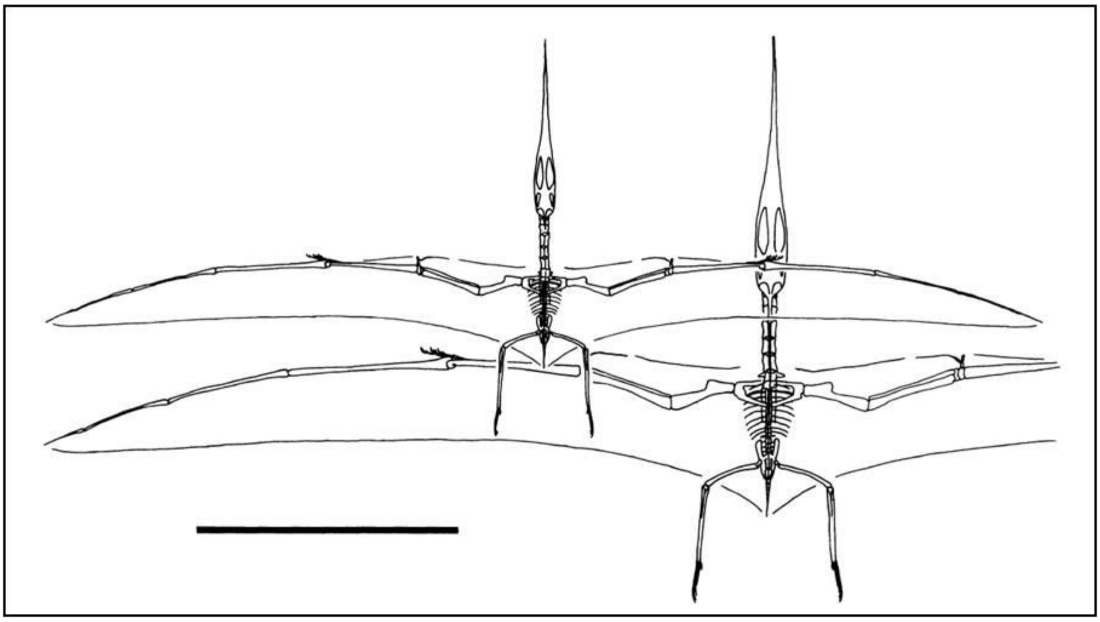


Fig. 5.3: Skeletal reconstruction of a male (larger) and female (smaller) *Pteranodon* superimposed to show size difference (Bennett, 1992). Scale measures 1 metre.

In prosauropod dinosaurs, slight dimorphism occurs in the dimensions of the femur. This results in slightly different loadings of the hind legs (Weishampel & Chapman, 1990). Differences in the proximal end of the femur were also reported the Stegosaurian dinosaur *Kentrosaurus* Hennig, 1915 that were unrelated to size (Bardet & Maidment, 2011). The authors attributed the variation to sexual dimorphism but concluded that there is insufficient data to identify gender in the study. Some sauropod dinosaurs show fusion in some of the caudal vertebrae (Rothschild & Berman, 1991; Rothschild, 1994). It is hypothesised that these fused vertebrae are present in the female to help support the enormous weight of the male during copulation as well as to help keep the tail elevated.

Compared to the sauropods, there are a lot more features in theropod dinosaurs that have been suggested as sexual dimorphic features. These include the presence of crests, rugosites and horns in the nasal and postorbital portion of the skull; the presence of possible gracile and robust forms, the possible presence of medullary bone and possibly the presence or absence of the first caudal chevron in some species (Chapman *et*. *al*., 1997; Schweitzer *et*. *al*., 2005). Bakker (1986) suggested that snout crests in *Allosaurus* Marsh, 1877, *Ceratosaurus* Marsh, 1884 and tyrannosaurs were used for intraspecific combat in males. He noted that it was unlikely that these features were used in hunting as other weapons the animals possessed are more suitable to that task. Other new species that possess crests could support this theory (Zhao & Currie, 1993; Hammer & Hickerson, 1994). However, despite this evidence, dimorphism has not been shown as the numbers of specimens that preserve this feature are insufficient for statistical studies into allometry, ontogeny and sexual dimorphism and any results would not be robust. Medullary bone is unique to female birds and is hypothesised to be unique to female dinosaurs. Schweitzer *et*. *al*. (2005) identified endo-osteally derived bone tissue lining the interior marrow cavities of portions of hind-limb elements, showing that gender can be shown in *Tyrannosaurus rex*.

Robust and gracile morphs have been reported for a number of extinct reptilian species (Colbert, 1990; Carptenter, 1990; Covey, 1993). Carpenter’s study on *Tyrannosaurus rex* Osborn, 1905 showed a difference in the robustness of elements in the neck and the hip (Fig. 5.4). He asserted that the more robust form is the female as the ischia are more divergent and would therefore allow the passage of large eggs. Larson (1994) built on this observation and based further research on modern crocodiles where the first caudal chevron is present only in males and is used as an anchor for the muscles that control the intromittent organ (penis). This feature could be present in *T. rex* also but has so far only been tested in a single gracile specimen (Fig. 5.5). The chevron is a small bone and it may not be preserved in all specimens. Gracile and robust morphs as a means of identifying gender are not accepted by everyone. For example, Padian & Horner (2011) argued that the gracile and robust forms are ontogenetic features related to the maturity of the individual rather than a sexual dimorphic characteristic.

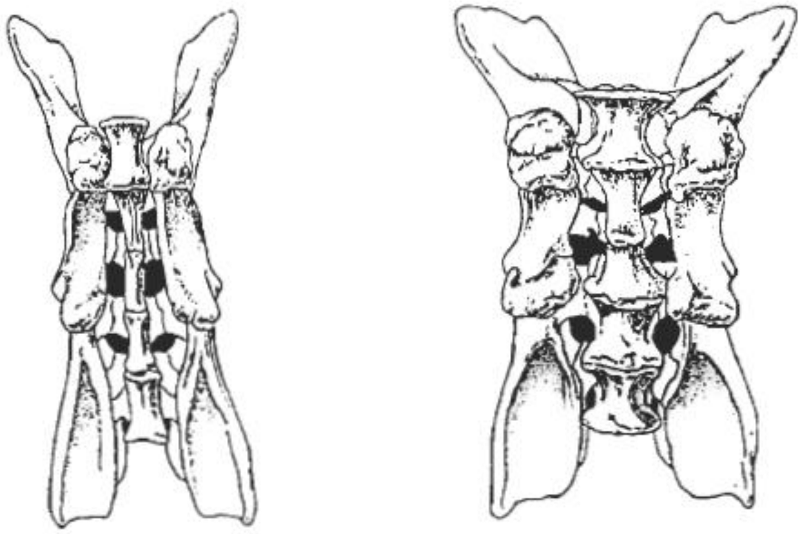


Fig. 5.4: Illustration of the gracile, inferred male morph (left) and the robust, inferred female morph of *Tyrannosaurus* pelves (right) from Chapman *et*. *al*. (1997). Scale not provided.

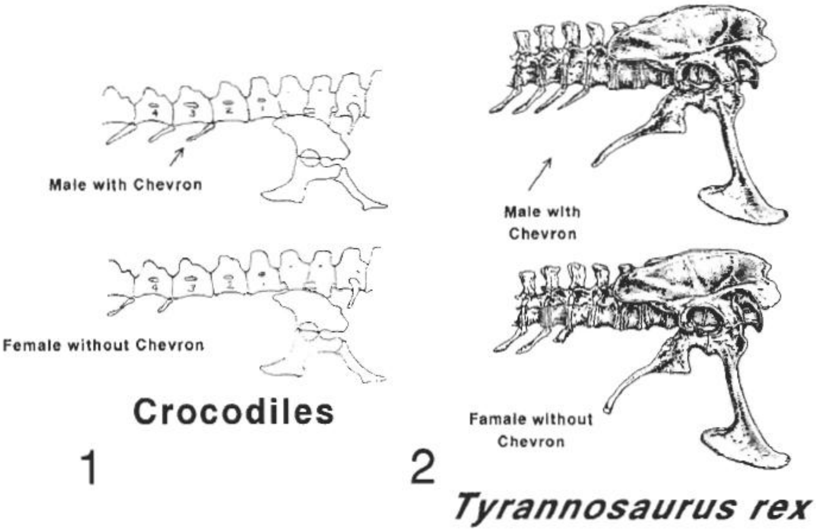


Fig. 5.5: Illustration of sexual dimorphism where first caudal chevrons are present in males and absent in females. 1 represents crocodiles and 2 represents *T. rex* (from Larson, 1994). Scale not provided

5.2.3: Avian sexual dimorphism

Extant species of birds have many different forms of dimorphism including size dimorphism and plumage colour dimorphism. Owens & Hartley (1998) report some examples of avian dimorphism and state that male and female corn buntings (*Miliaria calandra* Linnaeus, 1758) have nearly identical plumage but males are commonly 40% heavier than females. By contrast, male and female superb fairy-wrens (*Malurus cyaneus* Ellis, 1782) are similar in size but the males have an iridescent blue plumage that is not seen in the females. Some species have an integration of size and colour dimorphism such as the red-winged blackbird (*Agelaius phoeniceus* Linnaeus, 1766) while others can be almost identical in both size and colour such as the European swift (*Apus apus* Linnaeus, 1758) (Metz & Weatherhead, 1991; Owens & Hartley, 1998). Some birds, such as birds of paradise, have many secondary sexual characteristics. Møller and Pomiankowski (1993) reported that the male Lawes' parotia (*Parotia lawesii* Ramsay, 1885) have (i) six wire-like, racket-tipped head plumes, (ii) an iridescent breast shield and (iii) dense flank plumage (Fig. 5.7). There are many different species, such as the dark-eyed junco (*Junco hyemalis carolinensis* Brewster, 1886), in which the males have a more showy plumage compared to that of the females (Hill *et*. *al*., 1999).

Colour can be inferred in extinct birds based on the preservation of colour bearing organelles from fossilised feathers (Zhang *et*. *al*., 2010; Li *et*. *al*., 2010) such as integumental structural proteins and melanosomes. Li *et*. *al*. (2010) used this technique to analyse feather colour pattern in a single specimen of *Anchiornis huxleyi* Xu & Zhou, 2009, a species of Late Jurassic basal paravian theropod dinosaur (discussed in this section as the colours are in feathers, rather than on skin). Quantitative comparisons in melanosome shape and density between the fossil and extant birds indicate that the body was grey and dark and the face had rufous (red/brown) speckles while the long limb feathers were white (Li *et*. *al*., 2010). Feathers are also preserved in the fossil bird *Confuciusornis sanctus* Hou *et*. *al*., 1995 and these have also been analysed by Wogelius *et*. *al*. (2010). The authors used synchrotron x-ray techniques in order to map and characterise chemical residues of melanin pigments. The results show that trace metals, such as copper, are present in fossils as organometallic compounds most likely derived from the original eumelanin. The different chemical elements represent the concentration of the original melanin, and thus the darkness, but not colour, of the feathers. The results show a high concentration of trace elements in the downy body feathers which gradually reduces towards the flight feathers indicates a dark body that gets lighter in colour towards the wings (Fig. 5.6). The large distal flight feathers show very little or no elements indicating that these feathers were either white, or the trace elements were not preserved.

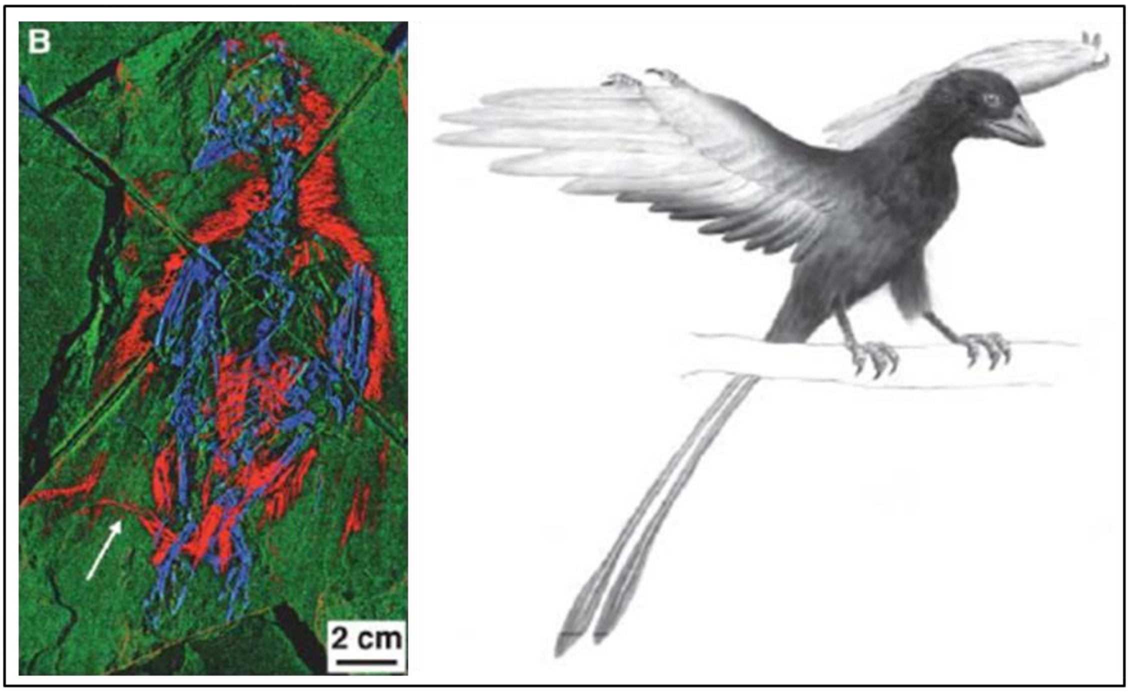


Fig. 5.6: False colour image (left) of *C. sanctus (*where green is the rock, red indicates Cu and blue indicates Ca) and an artist's reconstruction (right) (adapted from Wogelius *et*. *al*., 2010). Scale measures 2 cm.

It is possible to examine sexual size dimorphism in extinct birds (Bunce *et*. *al*., 2003) as size is represented in skeletal measurements. It is also possible to study secondary characteristics of sexual dimorphism due to exceptional preservation (Chiappe *et*. *al*., 2008; Peters & Peters, 2009 & 2012). The three described species of the extinct moa *Dinornis* Owen, 1843 from New Zealand are markedly different in size (1-2m height at back) and exhibit an estimated mass range from 34-242 kg (Bunce *et*. *al*., 2003). Ancient mitochondrial DNA (525 base pairs, 32 specimens) was analysed from these 3 species and the results showed that they were genetically indistinguishable. Molecular data was used to identify females as females have a female specific W-chromosome. Furthermore, tests of the DNA primer pair 112f and 267r consistently produced a 180-bp product in female but not male rhea, ostrich and kiwis. A similar product was produced in the larger specimens of *Dinornis* (Bunce *et*. *al*., 2003). It is therefore possible to conclude that the larger specimens are female and that *Dinornis* displays female-biased sexual dimorphism. This female-biased sexual dimorphism is extreme with the largest females being roughly 150% the height and 280% the weight of the males (Bunce *et*. *al*., 2003). Rather than the three initial species, the results show a juvenile stage, an adult male stage and an adult female stage.

Fig. 5.7: Painting of male (above) and female (below) of *P. lawesii* by Richard Bowdler Sharpe from Stavenga *et. al*. (2011)

Another example of avian sexual dimorphism in the fossil record is *Confuciusornis sanctus* Hou *et*. *al*., 1995 (Chiappe *et*. *al*., 2008; Peters & Peters, 2009 & 2012). *C. sanctus* is a Mesozoic bird found in the Early Cretaceous (125-120 Ma) Yixian and Jiufotang Formations of China. Preservation is exceptional where feathers and stomach contents are preserved and some fossils show two specimens preserved in the same block showing different morphology. One specimen on the block displays long, stiff tail feathers (Fig. 5.8) whereas the other does not. One hypothesis is that this is the earliest example of sexual dimorphism in birds, with the male possessing the long tail feathers for display (Chiappe *et*.

al., 2008). Chiappe *et*. *al.* (2008) investigated sexual dimorphism by using multivariate analyses of morphometric datasets from a sample of 106 skeletons of *C. sanctus*. The maximum lengths of 5 limb bones (humerus, ulna, radius, femur and tibiotarsus) were obtained. The results of the analysis showed that there is no correlation between size and presence of the long tail feathers. Therefore, if the tail feathers are sexual characteristics, they are not related to sexual size dimorphism (Chiappe *et*. *al*., 2008). There are species of extant birds that have very different feather patterns between the genders while the size remains the same (*P. lawaesii*). The paper by Chiappe *et*. *al*. (2008) does not conclusively show whether the long tail feathers are sexually dimorphic features or not although gender is inferred.

Fig. 5.8: Image of *C. sanctus* showing the elongate tail feathers in the inferred male (left) and a inferred female (right) on the same block. *C. sanctus* is approx. the same size as a Rook (from Benton & Harper, 2009).

Peters & Peters (2009; 2010) analysed the length of long bones from previously published data demonstrating a trimodal distribution, unlike the bimodal distribution of the specimens showed by Chiappe *et*. *al*. (2008). Peters and Peters (2009) concluded that the trimodal distribution related to a single juvenile stage and two separate adult stages and rejected the theory that the long tail feathers are a male sexual characteristic based on a comparison with extant birds (Peters & Peters, 2009). Peters and Peters (2010) addressed the size differences in the inferred adult stages and concluded that sexual size dimorphism is the most consistent explanation for the size differences observed. Despite the exceptional preservation and relatively large numbers of specimens it was still unclear at the time the paper was published whether sexual dimorphism can be shown in *C. sanctus*.

A recent study into gender identification of *C. sanctus* uses a different angle of investigation. Chinsamy *et. al.* (2013) examined bone histology from the left humerus, tibia and ulna from a single specimen and showed the presence of medullary bone in the humerus. The deposition of avian medullary bone is unique to females as it is directly linked to the maturation of the ovarian follicles before egg-laying. It also acts as a calcium reservoir for the production of eggshells. This provides absolute proof of gender for that specimen and is the first case of gender identification in a Mesozoic bird. The specimen containing the medullary bone did not possess any ornamental rectrices (elongate ornamental tail feathers). This supports the theory that specimens containing the long tail feathers are males and those that lack it are females (Chinsamy *et. al.*, 2013). The result from Chinsamy *et. al.* (2013) cannot be disputed; however, the results only come from a single specimen. If bone histology of specimens with and without ornamental tail feathers all showed results that agree with the above conclusion, the results would be better supported.

5.2.4: Mammalian sexual dimorphism

There are several different features in mammals that are sexually dimorphic. In terms of body size dimorphism, adult males are usually larger than adult females, but there are several matriarchal species where the reverse is observed, and many species without any dimorphism. Size is typically based on a measurement of skeletal length, but can also be based on a weight measurement in extant species (Myers, 1978; Moors, 1980; McPherson & Chenoweth, 2012). In some species, there is a marked difference in body size between males and females, such as in elephant seals, sea lions (Fig. 5.9), whales and kangaroos (Ralls & Mesnick, 2002). Furthermore, size differences tend to be greater in polygamous mating systems. This could be due to males fighting with other males and protecting females as larger males will be more successful (McPherson & Chenoweth, 2012). However, in some ungulates, body size can be related to the ratios of males and females within a population or geographical area, with a larger size difference when there are more males (Pérez-Barbería *et. al.*, 2002; McPherson & Chenoweth, 2012). Again, it is most likely that this is related to male competition as larger males are likely to defeat smaller males and secure mates. The size difference between males and females can only be analysed and compared with sexually mature individuals rather than individuals of the same age (McPherson & Chenoweth, 2012). This is because females typically become sexually mature before males. Despite the overall pattern for males to be larger, there are species where females are larger than males. This is related to competition for resources with other females as well as for defending offspring. Myers (1978) studied 14 different species of vespertilionid bats. 19 skin and skull measurements were taken and forearm length was chosen to represent size. Sexual size dimorphism was recognised in every species with the female being larger than the male. Myers (1978) goes on to say that it is likely that females are larger in forearm length, which allows for larger wings to provide the extra lift needed in order to fly whilst carrying young.

Fig. 5.9: Sexual size dimorphism in sea lions with the larger male (top) and the smaller female (bottom) (Ralls & Mesnik, 2002).

There are other size differences between mammalian males and females apart from overall body size. Males tend to have larger and more muscular head, neck and shoulder regions than females (Schulte-Hostedde *et*. *al*., 2001; McPherson & Chenoweth, 2012). There are size differences internally as well as externally. Females have a wider pelvis for the purpose of giving birth to young. Human males have a longer leg length as well as a larger bone mass. Human females tend to have larger brains than males, as do horses and rats. Female mammals also tend to have larger livers, thymus and spleens. However, males tend to have larger hearts and lungs (McPherson & Chenoweth, 2012). Schulte-Hostedde *et*. *al*. (2001) analysed muscle mass in small mammals (bushy-tailed wood rats (*Neotoma cinerea* Ord, 1815), deer mice (*Peromyscus maniculatus* Wagner, 1845), and red-backed voles

(*Clethrionomys gapperi* Vigors, 1830). 40 males and 22 female wood rats, 83 male and 21 female deer mice and 66 males and 20 female red-backed voles were included in the study. The result showed that male muscle mass was larger than that of females in each species examined.

Another feature of sexual dimorphism in mammals is the presence of features that can be used as either weapons or for display such as horns, antlers, tusks or enlarged canines. These features are typically enlarged in the males and reduced or absent in the female of the species (Kunz *et*. *al*., 1996; Emlen, 2008).

Colouration of fur and skin as well as the amount of fur can also be different between males and females within the same species. Generally, males tend to be more brightly coloured than females, although this is to a lesser extent than in birds. Males can often display larger amounts of hair in some areas of the body such as large manes in lions and mandrills (Setchell, 2005). Pigmentation in the skin is less common but still does occur in mammalian species. For example, male Mandrills can have pink faces and buttocks and bright blue snouts and scrotums. It is thought that the more vibrant the colour, the more dominant the individual is. The vibrant colour makes it more likely that females will choose them as a mate (McPherson & Chenoweth, 2012).

Furthermore, there are a few behavioural differences. This is mainly based on vocalisation where males tend to be more vocal than females. It is likely that this is used to attract mates and announce territory. Therefore, the male with the largest voice would attract more mates and be able to have a larger territory (McPherson & Chenoweth, 2012).

Another method for identifying gender in extinct and extant mammals is the presence or absence of the baculum, or penis bone. The baculum is only present in males and is present in the penis, used to maintain stiffness and aid the male during intercourse. Many, but not all mammals have a baculum such as bears (Abella *et*. *al*., 2013), some primates (Dixson, 1987), rodents (Burt, 1936), as well as in major clades such as carnivores, pinnipeds and bats (Dixson, 1995). The presence of a baculum in the fossil record would be direct evidence of gender. However, it is not commonly preserved as it is easily broken and it is also easily mistaken for ribs (Abella *et*. *al*., 2013).

Exceptional preservation in the Eocene oil shales at Messel in Germany preserves pregnant specimens of early horses, thus showing absolute proof of gender (Franzen, 2006).

This proof of gender provides an opportunity to study any potential sexual dimorphism in early horses.

There are several features of marine mammal sexual dimorphism. As with reptiles, the most striking characteristic is overall size difference, where males tend to be larger than females. The difference is most extreme in sperm whales, killer whales, bottlenose whales and belugas (Ralls & Mesnik, 2002). There are other features in some species that can be used to distinguish between males and females. Male killer whales have a large, erect dorsal fin which can be as large as 1.8m. By comparison, females tend to have much shorter dorsal fins, up to about 0.7m and the shape is distinctly falcate rather than upright (Clark & Odell, 1999; Ralls & Mesnik, 2002).

There can also be differences between males and females in the dentition. This is very obvious in narwhals, where the males have the large, forward pointing tooth or tusk that extends beyond the front of the head. Furthermore, male Blainville's beaked whales have a single pair of teeth or tusks in the lower jaw that the females do not possess. These are likely used either for display or as weapons when males fight and compete for females with which to mate. Another sexual dimorphic feature that relates to male competition is bone density. Species that ram one another with their heads can develop thicker and denser bones. This feature is seen in Bottle-nosed whales where males have much thicker and denser bones around the skull (Ralls & Mesnik, 2002). There are some other body differences that also relate to sexual dimorphism. In Eastern Spinner dolphins, adult males tend to have a post-anal hump. The dorsal fin is curved forwards and the tips of the flukes point upwards (Fig. 5.10).

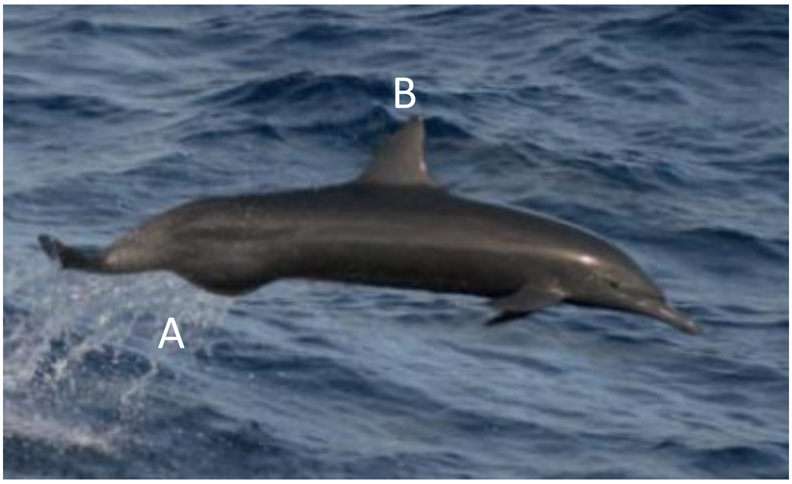


Fig. 5.10: Photo of an eastern Spinner dolphin showing (A) a post anal hump and (B) a forward curved dorsal fin (Ralls & Mesnik, 2002).

5.2.5: Implications for the study of ichthyosaurs

There are many different forms of sexual dimorphism discussed in sections 5.2.1 - 5.2.4 that could be relevant to the investigation into sexual dimorphism and gender identification in ichthyosaurs. One of the main features of sexual dimorphism is size difference observed in many groups of reptiles, amphibians, birds and mammals. This can be analysed in ichthyosaurs using a skeletal measurement for size, such as total body length. A proxy for size could also be used, such as humerus length, which would then allow incomplete or disarticulated specimens to be included into an analysis.

Soft part preservation is extremely rare for Mesozoic marine reptiles. An isolated specimen of a lepidosaur (*Pontosaurus*) (Caldwell & Dal Sasso, 2004) has been reported to have soft body preservation as well as an isolated mosasaur (Lindgren *et*. *al*., 2013). Ichthyosaurs are the only Mesozoic marine reptiles that preserve body outlines in any number (McGowan & Motani, 2003). However, the number of specimens that preserve this type of detail is small and the results from any analyses would not be robust. Furthermore, orientation at the time of death and compaction of the specimen could also alter size and shape of the soft part outline. Limb size shows sexual dimorphism in ocean dwelling mammals, such as whales, and it is possible that this is also the case in ichthyosaurs. Body outlines of ichthyosaurs could be examined, despite the low numbers, to see if these are dimorphic. Investigation into the sizes of internal organs or genitalia is not possible in ichthyosaurs as these are not preserved.

Sexual dimorphism in fur and feathers (e.g. in colour) occurs in mammals and birds. Ichthyosaurs do not possess fur or feathers so these features could not be used for investigation into ichthyosaur sexual dimorphism. Ornamentation such as those seen in mammals like horns, tusks or antlers would potentially preserve in fossils as they are hard parts. Ichthyosaurs are smooth and streamlined (McGowan & Motani, 2003), similar to modern dolphins and do not posses these features so they cannot be used to help identify gender. The features discussed above for dinosaurs are not comparable in ichthyosaurs as ichthyosaurs do not possess the crests, rugosites and horns that are observed on the snouts of some of the dinosaurs (McGowan & Motani, 2003). The presence or absence of a first caudal chevron, as seen in crocodiles, has not been previously studied in ichthyosaurs. However, some, but not all, of the pregnant female ichthyosaurs as well as some non-pregnant specimens studied here do possess the first caudal chevron. Therefore, this approach cannot be used to help identify gender in ichthyosaurs. Furthermore, ichthyosaurs do not possess a baculum as seen in the males of many forms of mammals so ichthyosaur sexual dimorphism cannot be analysed in this manner.

Colour is another feature of sexual dimorphism that has been shown in the skin of some fossil reptiles and amphibians. In amphibians, colour patterns on the matrix can relate to original colour from the skin. It is unlikely that any colour organelles or pigmentation have been preserved in ichthyosaurs as the body outline is typically a preserved bacterial mat (Motani, 2005). Therefore, the shape of the colour cells may not be preserved and colour could not be inferred. However, one study disputes this (Lindgren *et*. *al*., 2014) and shows preservation of eumelanin in the dark body outline of an ichthyosaur. The results indicate that an ichthyosaur would have been completely black or dark grey. However, the size and shape of eumelanin and bacteria are very similar so further study is needed to conclusively determine this. No sexually dimorphic colour patterns have been shown but this could be an area for further study.

Robust and gracile pelves were identified in *Tyrannosaurus* with the wider pelvis allowing movement of eggs, thus indicating a female. The hind limbs in ichthyosaurs are reduced and, in some cases, not connected to the spine so neither robust nor gracile morphs are observed. This approach to gender identification cannot be used in ichthyosaurs.

Ichthyosaurs are one of the very few groups in the fossil record that show direct evidence of gender (along with one fossil turtle, single specimens of other marine reptiles, some pachypleurosaurs & one extinct form of horse, discussed above). It is much easier to do this in mammals as there are more living relatives. Consequently, more is known about mammalian dimorphism, especially in more recently extinct mammals. In ichthyosaurs, sufficient numbers of pregnant females exist to allow an investigation into sexual dimorphism. This study quantitatively analyses sexual size dimorphism in ichthyosaurs. Total body size, as well as a number of proxies for size will be compared between pregnant and non-pregnant specimens to identify significant differences (see Materials & Methods).

5.3: MATERIALS AND METHODS

The specimens used in this chapter are the same as those used in Chapter 3 (see section 3.2 for full details), but reduced in number in order to be reasonably sure that all specimens included are sexually mature. All specimens that are smaller than the smallest pregnant specimen have been removed from the main set of analyses. Sexual maturity is required for specimens in the study as sexual dimorphism typically is expressed as size differences, shape differences or both. Using specimens inferred to be sexually mature, based on large size, will reduce the errors of ontogeny. Subsequently, some analyses were repeated using specimens of all sizes as it is possible that mature males are significantly smaller than females. The analyses were also conducted on *Stenopterygius* only as this is the best-represented genus in the dataset as well as the genus with the largest number of pregnant specimens. This also removes natural size differences between different genera.

The data collected comprises total body length, skull length, the length and width of the humerus, length and width of the manus and the orbital diameter (Table 1). These measurements were selected as they (i) have been used to help identify age previously in the literature; and (ii) have been identified as features that vary with ontogeny earlier in this study (Chapters 3 and 4). Females were definitively identified as those specimens that had an embryo preserved either in the remains of the parent or in very close proximity to the specimen and these are identified as pregnant specimens.

One statistical method that is used in this chapter to analyse various skeletal elements in order to establish whether sexual dimorphism in ichthyosaurs is apparent is discriminant analysis. The purpose of this approach is to project a multivariate dataset down to one dimension in a way that maximises separation between two groups. This method uses a bivariate or multivariate dataset that is typically comprised of linear measurements. The items used in the analysis are divided into two groups that are defined *a priori* (Hammer

& Harper, 2006). For this analysis, one group was defined as females that included all the pregnant specimens. The other group was defined as non-pregnant specimens. Once the specimens are plotted into one dimension a new axis (discriminant axis) is created through the dataset that maximises the difference. This axis is then rotated to be horizontal. The data points are projected onto the horizontal axis, which creates a histogram of the groups. This creates a visual representation of where the data lies on the axis (Fig. 5.11). Furthermore, discriminant analysis can show whether the predefined groups are statistically dissimilar enough to be classed as two distinct groups. A p(same) value is calculated and any value lower than 0.05 is considered statistically significant, indicating dimorphism For further information on this analysis see Methodology chapter (Chapter 2).

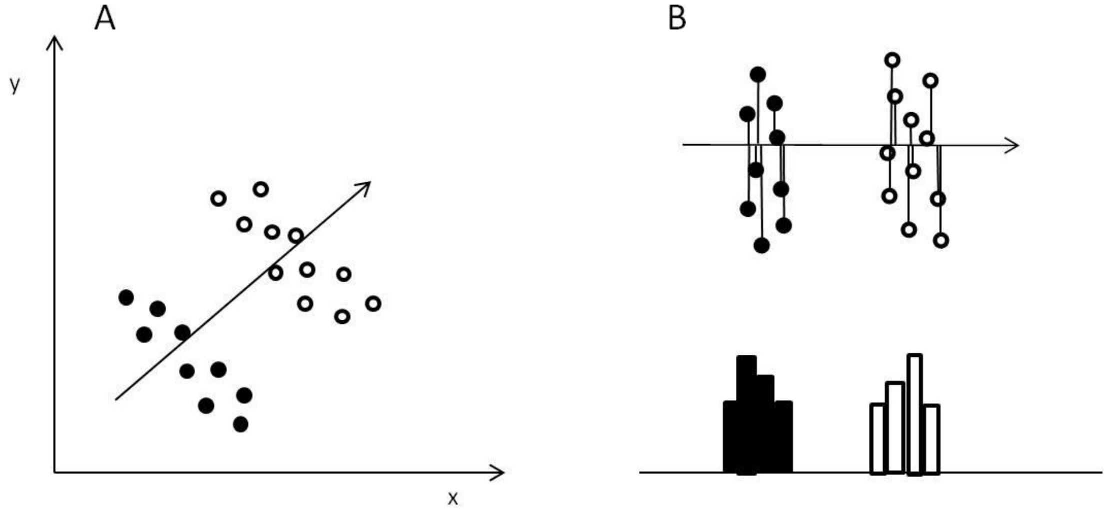


Fig. 5.11: Discriminant analysis with variables *x* and *y*. (A) The data points are plotted in the coordinate system spanned by the original variables. The discriminant axis (arrow) is the direction along which separation between the two predetermined groups is maximised. (B) The datasets are projected onto the discriminant axis, which creates the histogram (modified from Hammer & Harper, 2006).

Mann-Whitney tests were also performed with the data. This tests whether two univariate samples are taken from populations with equal medians (Hammer & Harper, 2006). The two samples are pooled together and sorted into ascending order. The ranks are positioned in the sorted sequence so that the smallest number has rank 1. If the medians of the two samples are almost equal, values from the two samples would be intermingled within the ranked sequence. The mean rank can be calculated for each specimen and compared allowing the p(same) value to be calculated (Hammer & Harper, 2006). In this study, the dataset for each measurement was split into two samples, pregnant specimens and non-pregnant specimens. The hypothesis tested is that the data is drawn from populations with the same median values. The results of this test will show if there is dimorphism within the dataset or not. If the medians are the same, then there is no dimorphism. However, if the medians are significantly different then dimorphism is shown for that variable.

Specimen Number	14846	56856	55748	50963	55934	7402	54816	54027	17500	54064	51142	15033	5792	3375	57532	56584	51552	6.14	6.43	6.38	6.41
Skull length	620		497	528	454	504	432	513	625	458		492		456		475	611	472.1	423	403	475.5
Orbital diameter	125	76.5	112.3	120	98.3	113.9	108	165.3	140.4	110.4	112	107.8				112.9	153.6	114.8	101.5	91.4	
Length of longest digit	202	180	194	189		216	116.2	169	424		209	210	253	179	325	181	116.6	174	155.1	178	162.6
Width of paddle	115	91	111	102	63.1	114	88.9	93.5	157		110	131.8	123.6	101.7	133.7	93.9	93.4	116	81.2	91.1	89.5
Length of humerus	95.9	69	97.2	98.2	56.7	94.2	86.9	83.5	127.5	88.9	106	104.4	121.2	92.5	130.1	88.2	75.1	102.5		68	90.1
Width of humerus	40.2	25.5	39.7	32.1	25	43.3	28.3	34.4	58.2	28.9	29.4	41	48.5	29.4	43.4	31.9	31.9	35.4	25.8	25	28.9
Total body length	3374	2175	3188	2998	2068	2565	2614	2667	3710	2364	3386	3147	3327	2804	3337	2598	2989	3018	2097	2125	2805.6
Number of presacral vertebrae	43		44	46	42	44	43	46	43	42	48	43	42	45	38	47		44	43	38	
Number of dorsal vertebrae	37		38	42	37	38	38	36	41	39	44	39	38	42	33	42		39	40	35	
Number of caudal vertebrae	118	114	113	117	95	55	107	86	116	93	98	115	115	99	113	111		119	113	102	
Number of preflexural vertebrae	36	32	34	30	37	33	36	29	35	32	39	30	33	35	33	36		31	34	32	
Number of postflexural vertebrae	76	82	79	87	58		71	55	81	61	59	85	82	64	80	75		88	79	70	
Pregnant				1	1	1	1			1								1	1	1	1

Table 5.1: Table of data for the large, inferred sexually mature, specimens used in most analyses. All measurements in millimetres. See appendix 1 sheet 2 for the data for all *Stenopterygius* specimens

Any discriminant results that show a statistically significant difference between pregnant and non-pregnant specimens in the inferred adult dataset will be subjected to a further discriminant analysis using size corrected data in order to establish whether the results are a false positive due to size differences between species. Residuals, gained from a Major Axis Regression, will be plotted instead of the original data.

5.4: MANN-WHITNEY RESULTS FOR LARGE SPECIMENS

The results for the Mann-Whitey tests show that some of the measurements are dimorphic while others are not (Table 2). Total body length, skull length, humerus width and width of manus have a p(same) value below 0.05. The difference between pregnant and non-pregnant specimens is statistically significant which shows that there is dimorphism for these measurements.

Measurement	n (total)	n(non pregnant)	mean rank	n (pregnant)	mean rank	p(same)	Dimorphic?
Total body length	21	12	8	9	3	0.001164	Yes
Skull length	17	8	5.588	9	3.412	0.03038	Yes
Humerus width	21	12	7.714	9	3.286	0.0358	Yes
Width of paddle	20	12	7.65	8	2.85	0.0409	Yes
Orbital Diameter	17	9	5058	8	3.412	0.1939	No
Humerus length	20	12	7.2	8	3.3	0.177	No
Length of longest digit	19	12	7.474	7	2.526	0.0692	No

Table 5.2: Results for the Mann-Whitney test showing whether or not each measurement displays dimorphism. A p(same) value lower than 0.05 indicates dimorphism.

However, orbital diameter, humerus length and length of the longest digit have p(same) values higher than 0.05. There is therefore no significant statistical difference between pregnant and non-pregnant specimens, indicating no dimorphism for these variables.

5.5: DISCRIMINANT ANALYSIS RESULTS

5.5.1: Results for all measurements of large specimens (see Table 5.1)

There is significant overlap between pregnant females and non-pregnant specimens (Fig. 5.12). Furthermore, the p(same) is 0.3437 which shows there is no significant difference between the two groups.

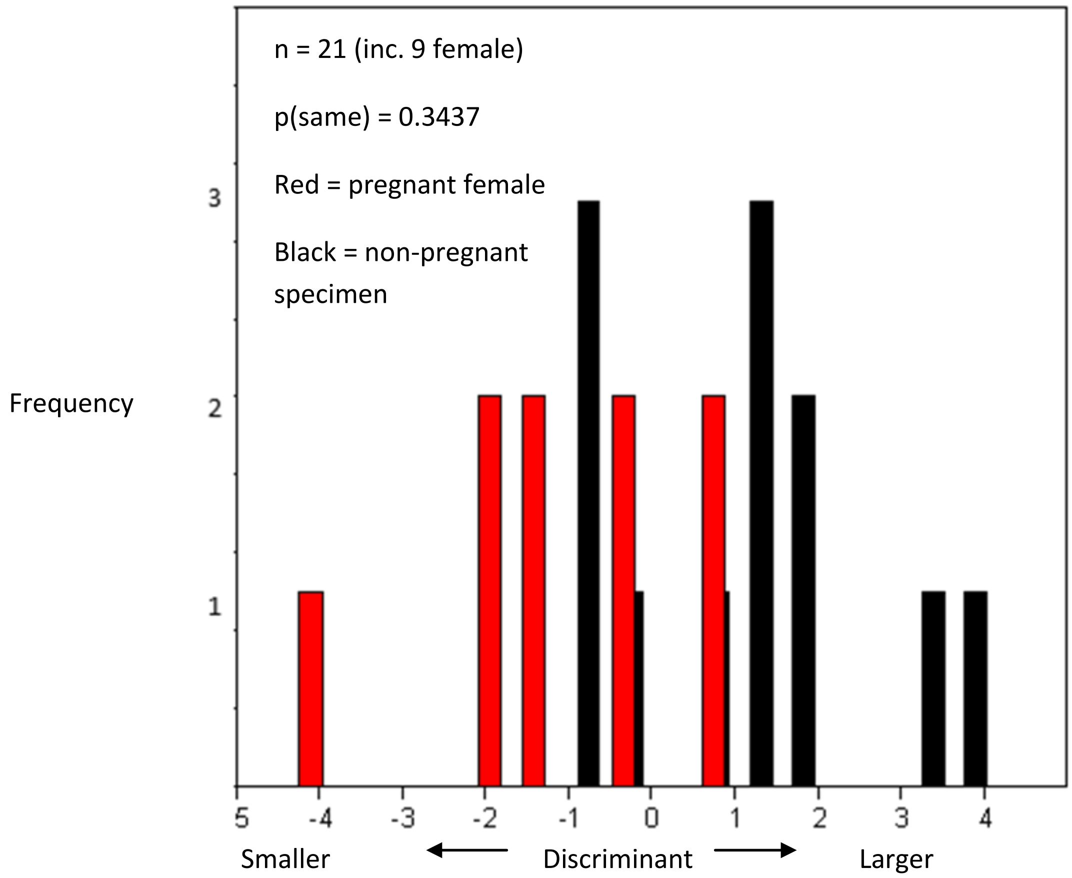


Fig. 5.12: Discriminant analysis for all the measurements showing no dimorphism.

5.5.2: Results for the manus (length of longest digit and width) of large specimens

There is significant overlap between the two predefined groups. This shows that the manus are very similar between pregnant females and non-pregnant specimens. Furthermore, the p(same) value is 0.2299 which shows there is no significant difference between the two groups (Fig. 5.13). Therefore there is no evidence for dimorphism within theforelimbs of ichthyosaurs. These results are consistent with the results shown in the Mann-Whitney tests for manus width and length of longest digit.

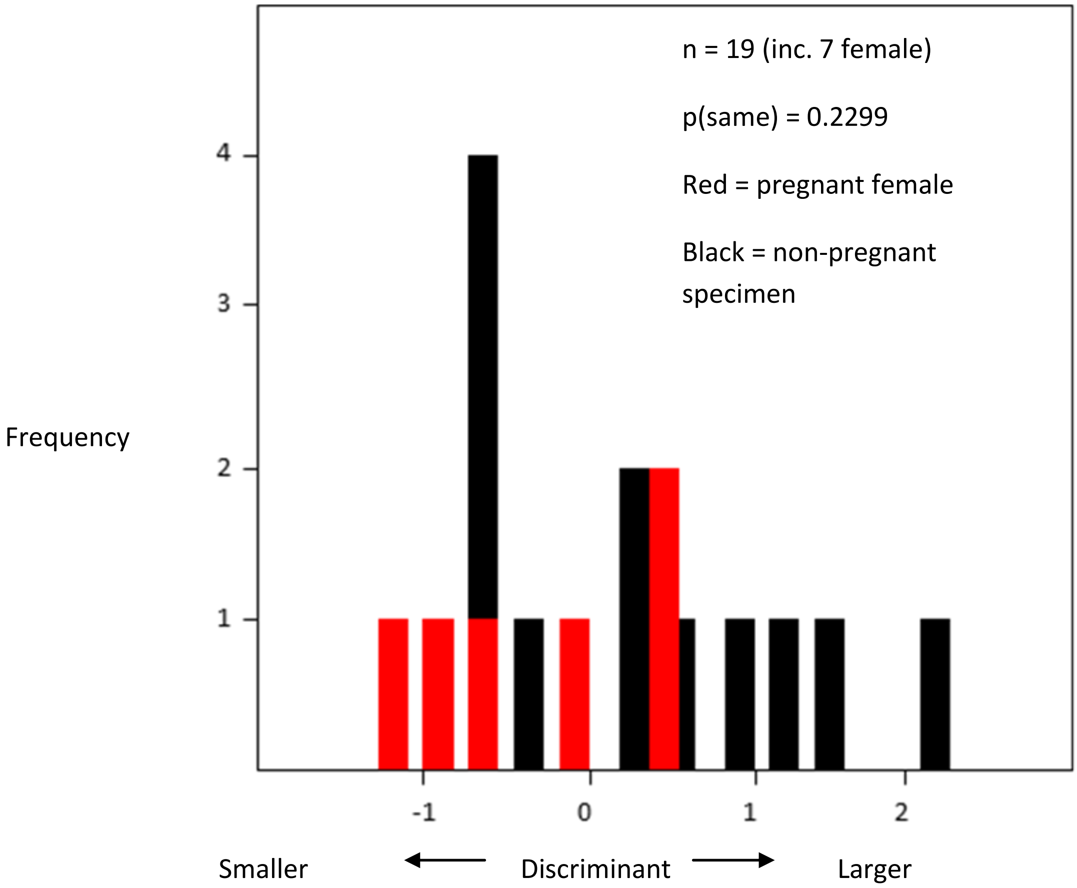


Fig. 5.13: Discriminant analysis of length of longest digit and manus width showing no dimorphism

5.5.3: Results for the humerus (length and width) of large specimens

The length and width of the humerus were examined as humeri are sexually dimorphic in pachypleurosaurs (Sander, 1989; Rieppel, 1989; Lin, 1998) and might also be in ichthyosaurs.

The results do not show a significant separation between known females and non-pregnant specimens (Fig. 5.14). There is some overlap between the pregnant females and the non-pregnant specimens. The p(same) value is 0.1261, which shows that there is no statistically significant difference between the two groups. The result shown for the discriminant analysis is consistent with the Mann-Whitney result for humerus length. However, the Mann-Whitey result showed that the humerus width is dimorphic.

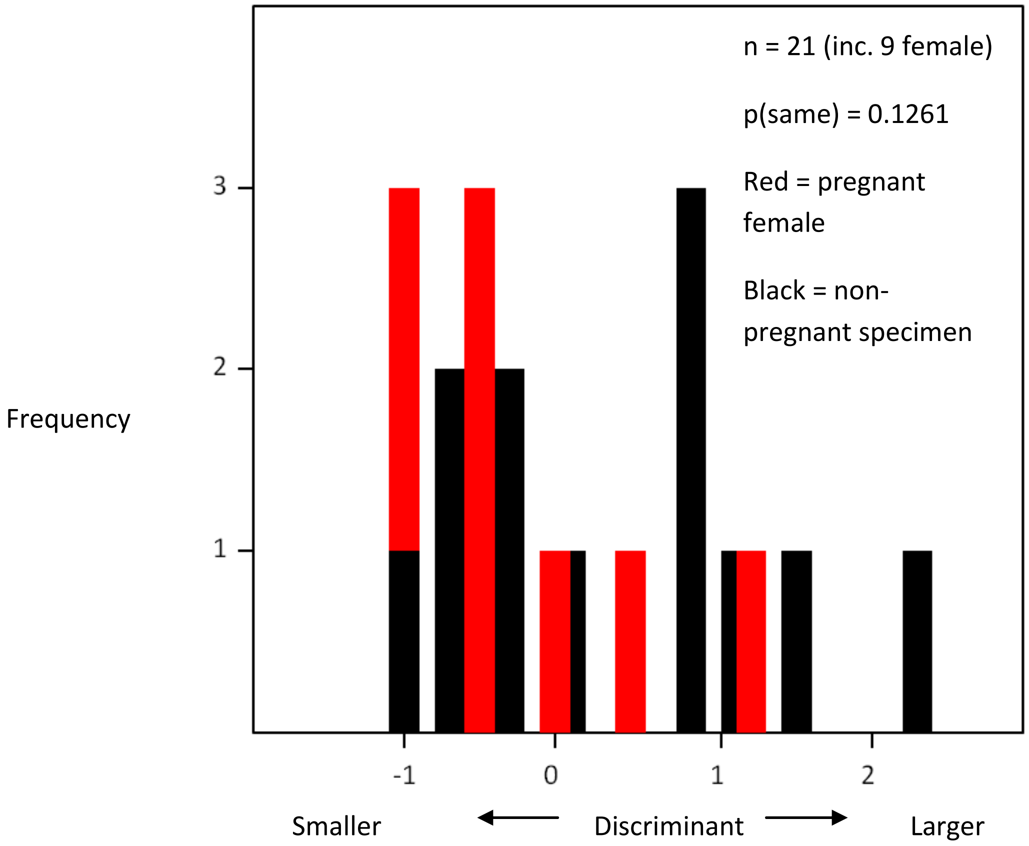


Fig. 5.14: Discriminant analysis for the humerus showing no dimorphism

5.5.4: Results for skull length and body length of large specimens

Skull length showed some variability in relative size during ontogeny (Chapter 3) when compared to the total body length of the individual. Inferred younger, immature specimens displayed a larger skull length compared to total body length. The skull length displays negative allometry and therefore becomes smaller with age relative to total body length. Therefore, the same measurements are being examined here to show if there is any difference at sexual maturity between pregnant females and non-pregnant specimens.

The results for this analysis indicate that there are two distinct groups, with the pregnant females being generally smaller than the non-pregnant specimens. The p(same) value is 0.027, which shows that there is a statistically significant difference between the two predefined groups (Fig. 5.15). These results are consistent with the results shown in the Mann-Whitney tests for skull length and total body length.

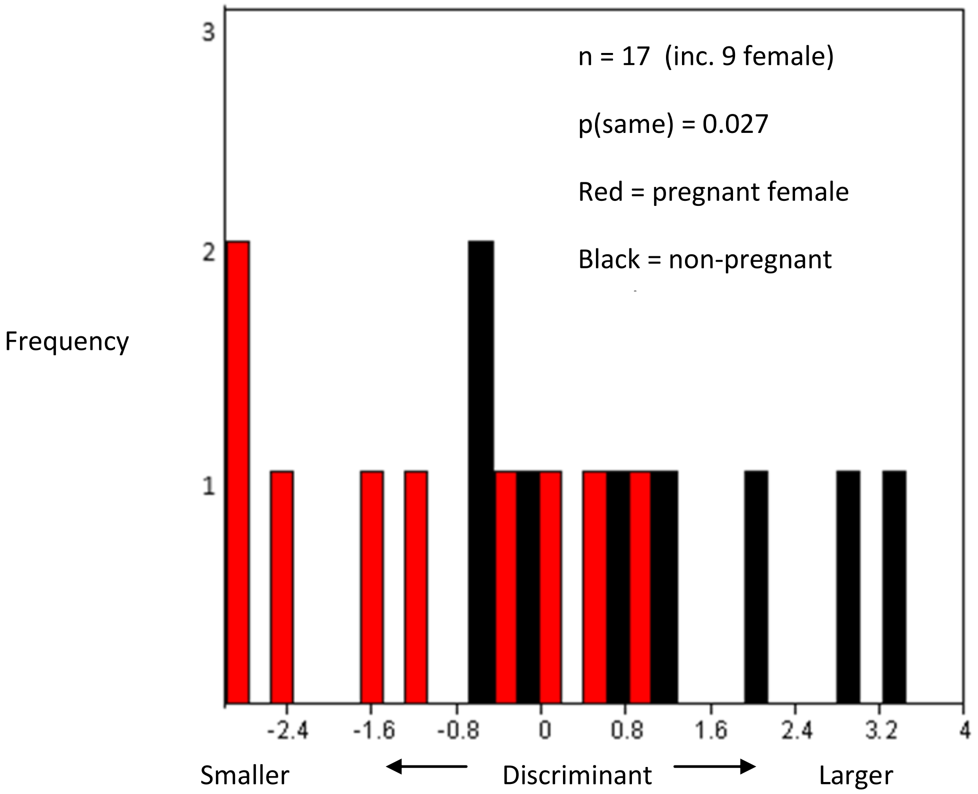


Fig. 5.15: Results for discriminant analysis of total body length vs. skull length showing dimorphism with pregnant females being smaller than non-pregnant specimens.

5.5.5: Results for orbital diameter and skull length of large specimens

The diameter of the orbit showed relative size change during ontogeny (Chapter 3), with inferred juveniles showing a large orbital diameter compared to inferred adults when compared to skull length. Orbital diameter displays negative allometric growth resulting in relatively smaller eyes in older individuals. For this reason, orbital diameter and skull length are compared here to detect any differences at sexual maturity between known females and non-pregnant ichthyosaurs.

The results of the discriminant analysis indicate that there are two distinct groups. As with the results for skull length and body length, the pregnant females are predominantly positioned on the left (Fig. 5.16) indicating that they are smaller than non-pregnant specimens. The p(same) value is 0.025, which means that there is statistically significance difference between the two predefined groups showing that pregnant females tend to have relatively smaller skulls and orbits compared to non-pregnant specimens. The results for the discriminant analysis are consistent with the Mann-Whitney result for skull length but not for orbital diameter.

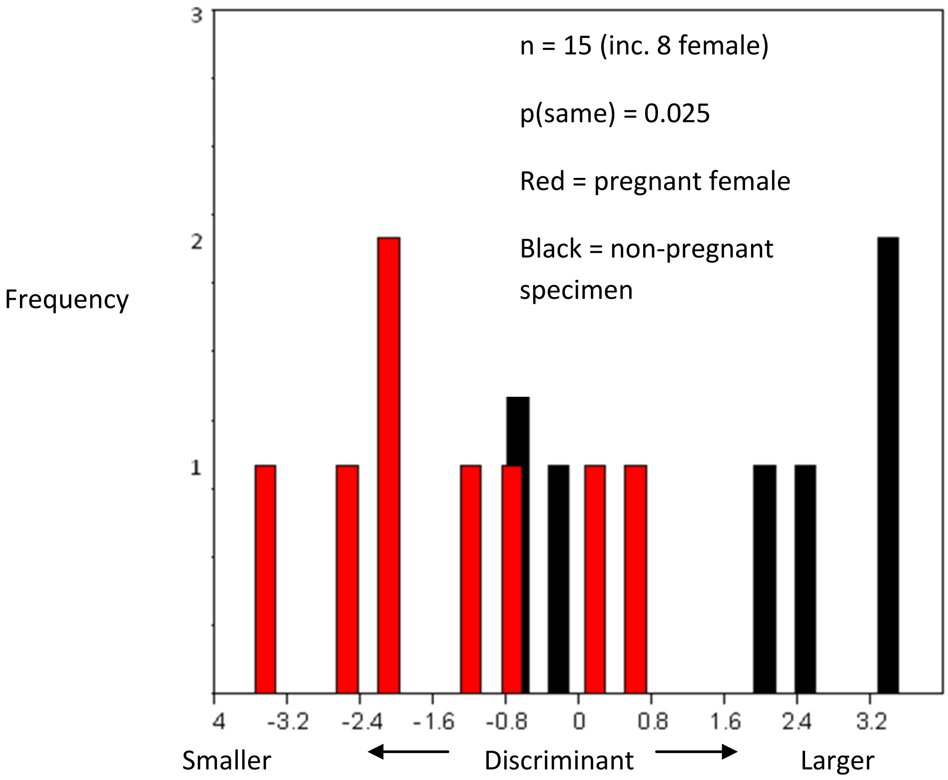


Fig. 5.16: Discriminant analysis for orbital diameter and skull length showing dimorphism with females being generally smaller than non-pregnant specimens

5.5.6: Size corrected results for large specimens

The results that are statistically significant for sexual dimorphism (skull length and orbital diameter) could be false positives, with the analysis highlighting differences between species. To test this, the data has been scaled with size and the residual data has been used in new discriminant analyses. The discriminant analysis results for size corrected data for total body length and skull length (p(same)= 0.990) and total body length and orbital diameter (p(same)=0.6534) are not significant. This suggests that there are no allometric size differences between pregnant and non-pregnant specimens but there is isometric size difference between pregnant and non-pregnant specimens. Therefore, a discriminant analysis was conducted on total body length alone (p(same)= 0.033) and the result was statistically significant. Therefore, it can be concluded that sexual dimorphism is present in ichthyosaurs but purely in size, with no allometric differences between pregnant and non-pregnant specimens.

5.5.7: Extreme size reduction in males tested using all specimens

It is possible, although unlikely, that icthyosaur males are much smaller than the females. This trait is observed in some fish, such as the angler fish (Vollrath, 1998). If this is the case all specimens in the previous analyses (sections 5.5.1 – 5.5.6) could have been female. Males could have been excluded from the original discriminant analyses by only selecting specimens larger than the smallest pregnant females. Therefore, the discriminant analyses have been repeated including all available specimens of *Stenopterygius*. This approach has the added advantage of increasing the numbers of specimens that can be included in the analyses (see appendix 1, sheet 2 for a list of all specimens included). For all the measurements no additional specimens could be added to the previous analysis (Fig. 5.12). The new results for the other discriminant analyses are given below.

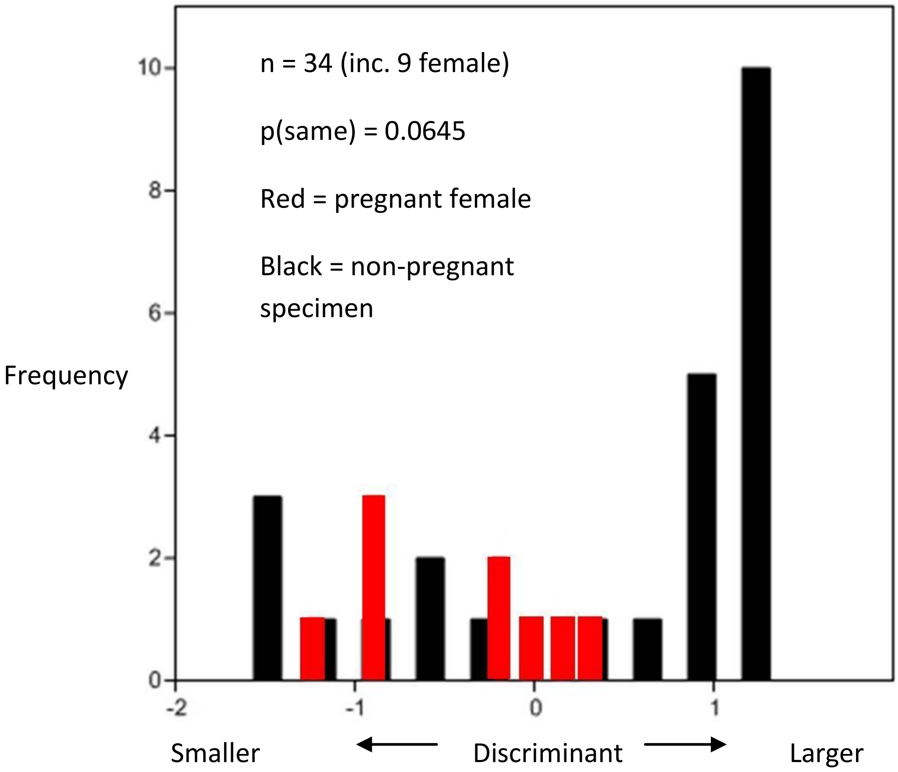


Fig. 5.17: Discriminant analysis for skull length and body length showing no dimorphism.

The result for skull length and body length show overlap between pregnant females and non-pregnant specimens. The p(same) value of 0.0645 also shows that there is no significant dimorphism observed in these features (Fig. 5.17), which is contrary to the result from the analysis only using the large specimens. However, the p(same) value is very close to the dividing value (0.05) which would indicate a statistically significant result.

The results for digit length and width of manus also showed no significant difference between pregnant females and non-pregnant specimens. The p(same) value of 0.275 further supports this observation (Fig. 5.18), which is consistent with the previous analysis.

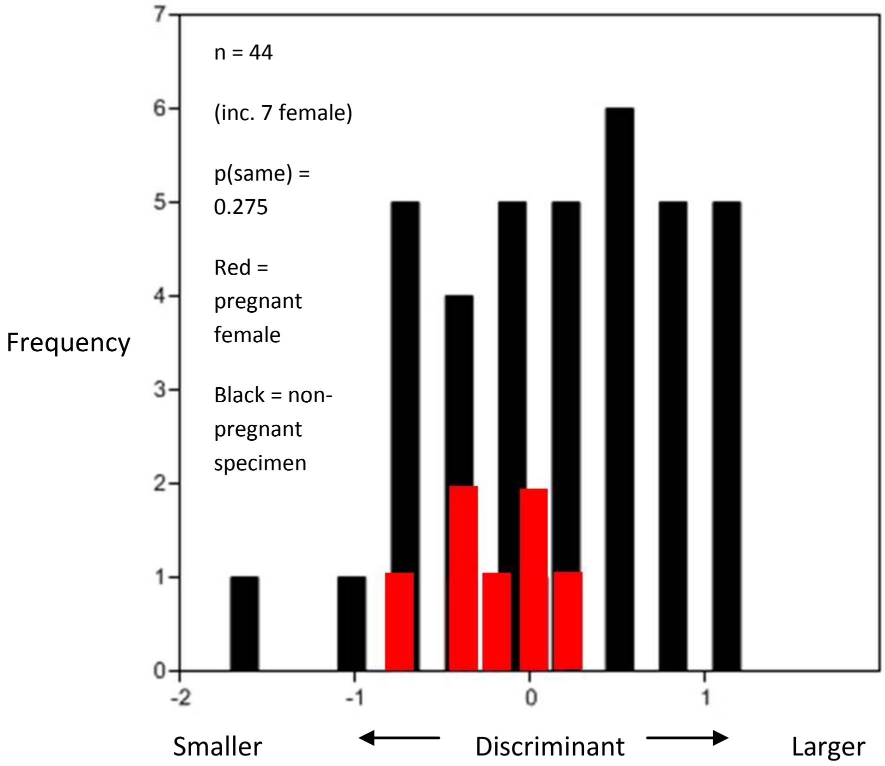


Fig. 5.18: Discriminant analysis for length of longest digit and manus width showing no dimorphism.

The result for humerus length and humerus width shows overlap in the graph. However, the p(same) value of 0.0136 indicates that there are statistically significant differences between pregnant females and non-pregnant specimens (Fig. 5.19). Consequently, size and shape of the humerus could be used to help identify gender in individual specimens of *Stenopterygius*.

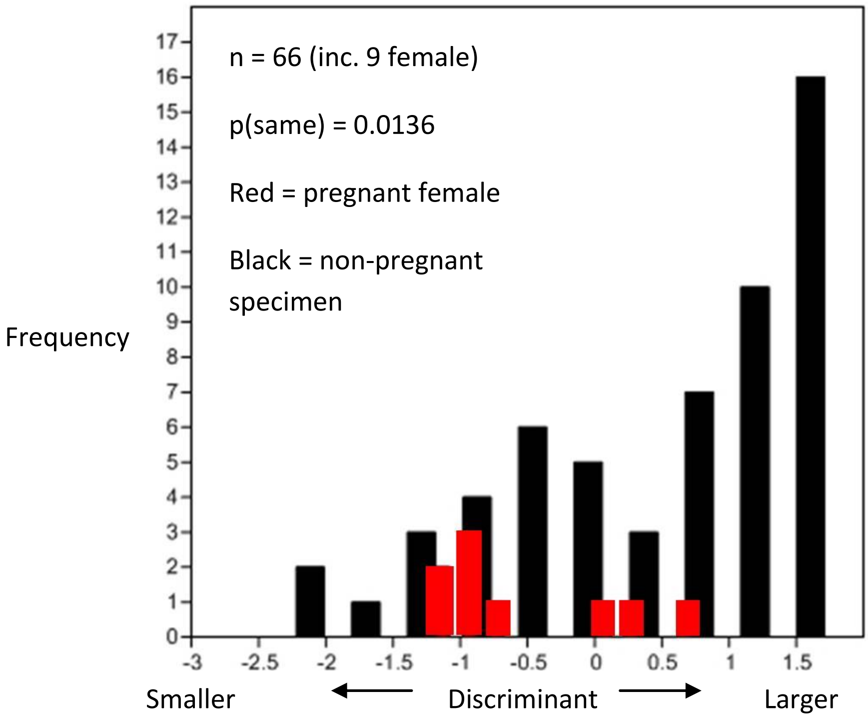


Fig. 5.19: Discriminant analysis for humerus length and width showing statistically significant differences between pregnant females and non-pregnant specimens.

The result for orbital diameter and skull length shows some overlap in the graph. Furthermore, the p(same) value of 0.0753 indicates that there is no significant difference between pregnant females and non-pregnant specimens (Fig. 5.20). However, this value is very close to the dividing value for significant results.

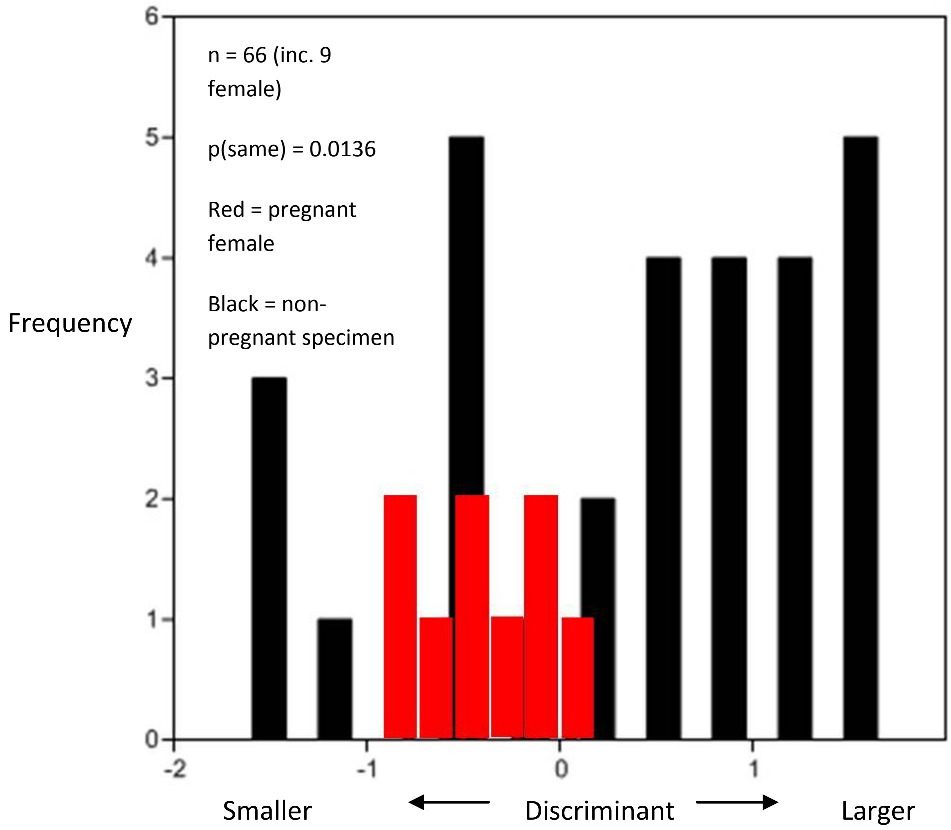


Fig 5.20: Discriminant analysis for orbital diameter and skull length showing no dimorphism.

5.6: DISCUSSION

5.6.1: Limitations of the data

Stenopterygius was used for the analyses of sexual dimorphism as it is the best-represented genus within the dataset with the highest number of pregnant females. A single genus was also selected to remove confounding size differences between the genera. However, several species may be included in the dataset resulting in interspecific variations influencing the results. It is possible that the results shown here are related to taxonomic differences rather than sexually dimorphic difference. It is equally possible that a taxonomic signal could obscure more subtle, sexually dimorphic features. However, there are insufficient numbers if specimens for a single species and hence this issue cannot be avoided.

Any specimen smaller than the smallest pregnant specimen was excluded from the initial study in order to exclude most, if not all, immature specimens. Numbers were further reduced as the measurements analysed are not available in every specimen. The tip of the snout is slender and easily broken (pers. obs.) meaning that skull length and total body length cannot always be measured consistently. The skull can also be distorted by compaction as most specimens are preserved in two dimensions. This means that orbital diameter cannot always be measured. Therefore, the maximum number of specimens that could be used in the analyses is 21. However, the subsequent analyses, which included smaller specimens (section 5.5.7), did increase the sample size for some analyses, with the largest being 66. Other studies (see section 5.2) use much higher numbers of specimens, in some cases many hundreds of specimens (e.g. Cox *et*. *al*., 2007) thus providing very robust results. Cox *et*. *al*. (2007) analysed many extant genera which also helps increase the sample size whereas this study examines a single extinct genus. Numbers of ichthyosaur specimens could have been increased as more specimens do exist. However, these are located in several different museums, mainly in Germany and visiting them all would have been too costly. Despite the low numbers of specimens in the study on ichthyosaurs, it is still a worthwhile investigation to provide an indication of features that could show sexual dimorphism. As no previous publications on ichthyosaurs examine sexual dimorphism, any new insights can provide a greater understanding of ichthyosaurs and can indicate direction for future work. There is also some absent data (see gaps in Table 5.1) within the dataset for the Discriminant analysis and Mann-Whitney test. This should not affect the results.

The subsequent discriminant analyses (section 5.5.7) were conducted as it is possible, although unlikely, that mature males were much smaller than mature (pregnant) females. Therefore, all specimens of *Stenopterygius* were included in these analyses The results show an increase in numbers of specimens larger than the largest pregnant female. The original dataset (Table 5.1) was based on total body length in order to infer sexual maturity based on size larger than smallest pregnant female. This excluded specimens for which a total body length was not known. In the subsequent analyses, larger specimens, for which total body length was not known, were included along with additional smaller specimens.

The purpose was to increase the number of smaller specimens in the analysis and while some smaller specimens have been added, the majority of new specimens are larger. It is likely that this reflects a bias in the collections towards larger specimens. Additional data from smaller specimens is required to further analyse potential dimorphism in smaller specimens.

5.6.2: Is there dimorphism in ichthyosaurs?

The results show statistically significant dimorphism in skull length and body length for ichthyosaurs, with non-pregnant specimens being larger than pregnant specimens. Two specimens in the analyses consistently plot at the ends of the two groups. SMNS 17500 a non-pregnant specimen of *Stenopterygius crassicostatus*, a moderately-sized species, plots as one of the two largest specimens in each analysis while SMNS 643, a pregnant female specimen of *Stenopterygius quadriscissus*, a smaller species, plots as one of the two smallest specimens in each analysis. These facts demonstrate consistent dimorphism in the sample. Overlap between the two groups is discussed below (section 5.6.3). By contrast, the subsequent analyses which included smaller specimens, did not show statistically significant dimorphism. However, the p(same) value was very close to the cut-off point (0.05). It has been shown that immature specimens display a larger skull compared to body length (Chapter 3). Consequently, it is possible that the additional immature specimens have ’overprinted’ the results with an ontogenetic feature rather than a sexually dimorphic feature. It is likely that this is the cause for contradictory results for the humerus length and width.

In some cases, for the large inferred sexually mature specimens, the results for the Mann-Whitney analysis contradict the results for the discriminant analysis (humerus width, manus width, orbital diameter). This is likely because the Mann-Whitney analysis is a univariate test while the discriminant analysis is bivariate or multivariate analysis. Orbital diameter is shown to not be dimorphic in a Mann-Whitney test, but is shown to be dimorphic in the discriminant analysis. This is probably because orbital diameter is combined with skull length in the discriminant analysis. The latter is dimorphic and it is this result that ‘dominates’ the discriminant analysis.

5.6.3: Is there sexual dimorphism in ichthyosaurs?

Males tend to be larger than females in some modern reptile groups (see section 5.2.1) and the results for the larger, inferred sexually mature ichthyosaurs are consistent with male-biased sexual size dimorphism. Larger size in male ichthyosaurs is also consistent with that in extant members of the same guild such as dolphins (see section 5.2.4). The results from all specimens (section 5.5.7) are similar to to the original discriminant analysis and it is therefore unlikely that mature males are much smaller than pregnant females.

The group of smaller pregnant female ichthyosaurs is well constrained as only pregnant specimens are included in that group. However, there is overlap between the pregnant and non-pregnant specimens in all the histograms from the discriminant analysis. This overlap could be explained by the presence of non-pregnant females in the dataset, which would have been incorporated into the non-pregnant group. If females are smaller these would plot on the smaller end of the non-pregnant group and contribute to the overlap. It is also possible that smaller, possibly immature, male specimens have been included in the sample as maturity was inferred based on size of the smallest pregnant female. Smaller male specimens would also plot on the small side of the non-pregnant group and contribute to the overlap. A PCA analysis (see Chapter 3 for details) was run for all specimens of *Stenopterygius* for which all measurements were known in order to see if the specimens larger than the smallest pregnant female were distinct from other specimens (Fig. 5.21). The results show that all the larger, inferred sexually mature specimens plot at the higher end of PC1 (98% of variance), which represents size.

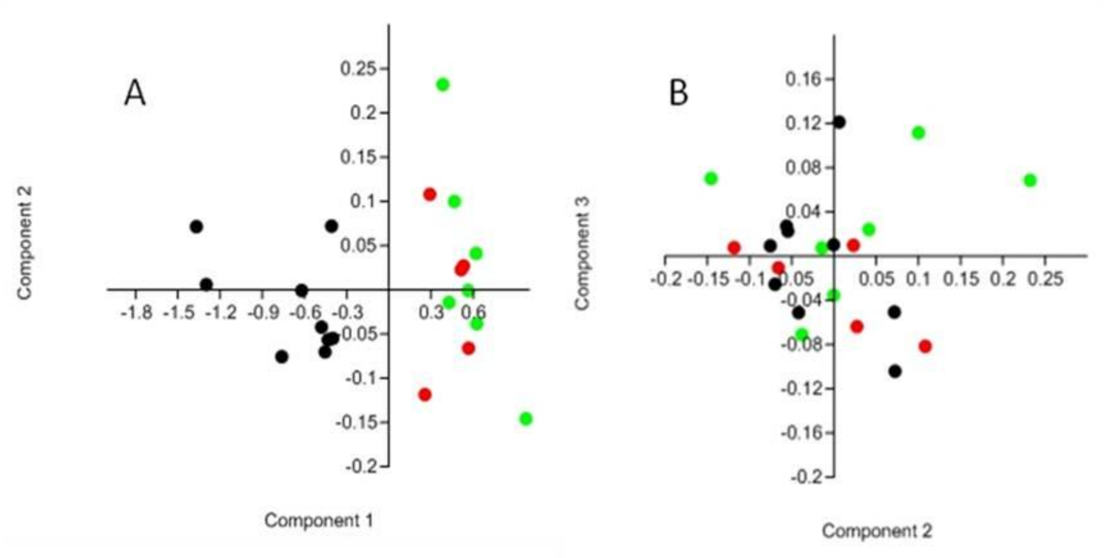


Fig. 5.21: PCA scatter plot; (A) showing that the larger, inferred sexually mature specimens (red and green) form a discrete cluster and are larger than other specimens (black) of *Stenopterygius*, and therefore are indeed likely to be mature. PC1 represents size [body length]): (B) PC2 and PC3, shows overlap between all the specimens showing that gender cannot be further discriminated by these components. Measurements are total body length, skull length, humerus length, humerus width, length of longest digit, width of manus and orbital diameter (Appendix 1). Red = pregnant female, green = non-pregnant specimen of larger inferred sexually mature specimens, black = other specimens. Out of a possible 81 specimens, only 21 showed all six measurements hence only 21 could be used in the PCA. PC1 covers 96.9% of the variance, PC2 covers 1.59% and PC3 covers 0.78%.

Furthermore, there are two discrete clusters with no overlap between the inferred sexually mature specimens (red and green dots in Fig. 5.21) and other specimens (black dots in Fig. 5.21). This supports the idea that the larger specimens are likely to be sexually mature and strengthens the argument for sexual dimorphism. It is not possible to show whether the other specimens (black dots) are male or female as pregnancy is still the best indicator of gender. However, specimens with absent data cannot be included in PCA. As a consequence of this, the sample size is reduced to 21 specimens (9 not used in previous analyses, 12 pregnant female and inferred mature non-pregnant specimens). Despite the low numbers, the indication of a group of mature specimens is still strong with no overlap (Fig. 5.21A). A PCA analysis was also conducted for only the larger, inferred sexually mature individuals (Fig. 5.22). The results of this analysis show overlap between the pregnant females and the non-pregnant specimens therefore providing no further means for discrimination between male and female specimens.

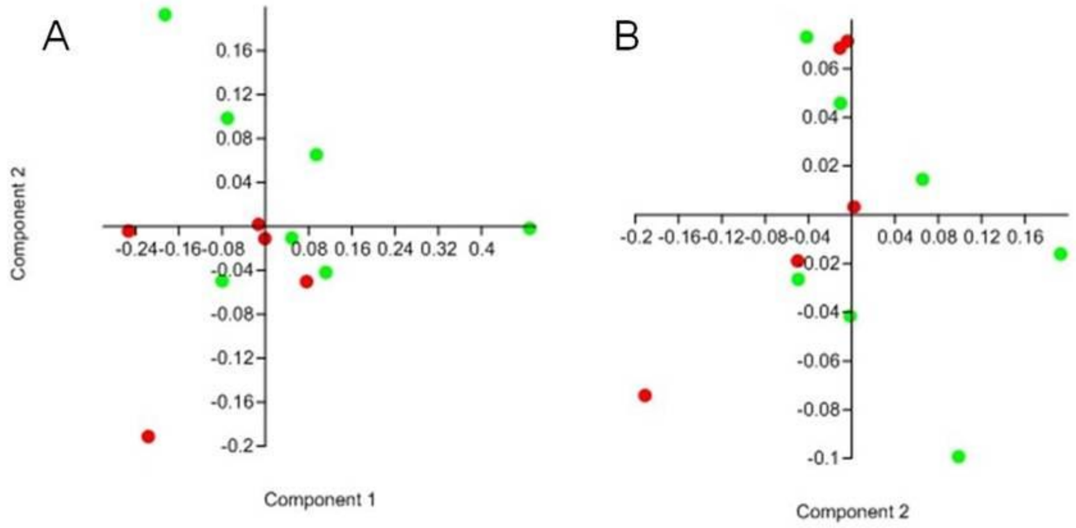


Fig. 5.22: PCA analysis for large, inferred sexually mature specimens of *Stenopterygius* showing some separation and some overlap between pregnant (red dots) and non-pregnant specimens (green dots). (A) shows PC1 (representing size [body length]) and PC2 and (B) shows PC2 and PC3. Measurements include total body length, skull length, humerus length, humerus width, length of longest digit, width of manus and orbital diameter (Table 1). Out of the 21 specimens in the sexual dimorphism analyses, only 12 showed all seven measurements necessary for the PCA. PC1 covers 73.1% of the variance, PC2 covers 16.3% and PC3 covers 6.15%.

The relative time at which each gender becomes sexually mature could also affect the results of the discriminant analysis. In mammals, females typically reach sexual maturity before males. If this is the case with ichthyosaurs, then individuals of the same size could be at different levels of maturity, which would mean that immature males are included in the inferred sexually mature non-pregnant specimen group. If immature specimens are included in the sample, this would contribute to overlap in the Discriminant analysis and potentially hide subtle sexually dimorphic features.

Overlap in body size of sexually mature males and females is observed in some extant frogs, lizards and snakes (see section 5.2). It is plausible that this overlap is typical for reptile groups, both extinct and extant. Although figure 5.21A shows no overlap between inferred mature and probable immature specimens, there is still overlap between sexually mature pregnant females and non-pregnant specimens. Figure 5.21B shows that it is not possible to further separate these groups. The overlap seen in ichthyosaurs is consistent with some extant reptiles.

The results for the discriminant analysis of large, inferred sexually mature specimens shows that two specimens consistently plot as one of the two largest, or one of the two smallest specimens, in every analysis. The larger of the two specimens (SMNS 17500) belongs to the species *S. crassicostatus* while the smaller of the two specimens belongs to the species *S. quadriscissus* (Fig. 5.23). Therefore, it is possible that the dimorphism shown in the discriminant analysis is caused by taxonomic differences between the species. However, *S. quadriscissus* is defined as a medium-sized ichthyosaur with a body length of <3.5 m (McGowan & Motani, 2003). *S. cassicostatus* (treated as a subspecies of *S. hauffianus*) is also defined as a moderately-sized species with a total body length of <3.5 m (McGowan & Motani, 2003). As the total body length is similar between these two species, it is unlikely that the size dimorphism shown is related to differences between the species despite *S. quadriscissus* tending to plot on the smaller side and *S. hauffianus*, *S. longifrons* and *S. crassicostatus* tending to plot at the larger end of the plot.

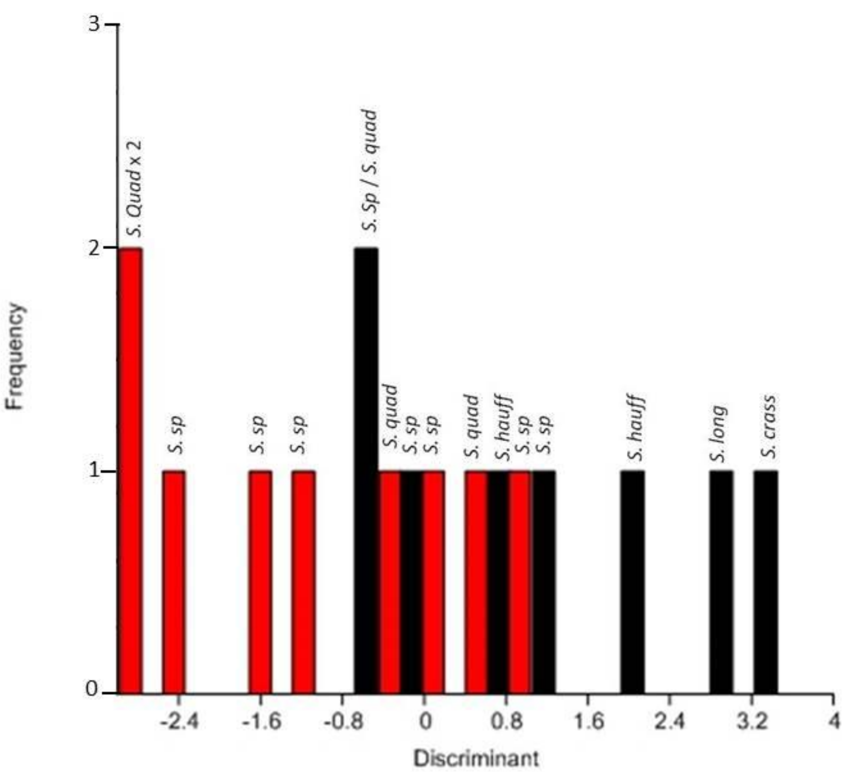


Fig. 5.23: Discriminant analysis for total body length and skull length from Fig 5.15 annotated with species where known for each specimen. Abbreviations are; *S. quad* = *S. quadriscissus*; *S. hauff* = *S. hauffianus*; *S. long* = *S. longifrons*; *S. crass* = *S. crassicostatus*; *S. sp* = unidentified species of *Stenopterygius*.

Overall, it seems likely that the dimorphism shown is sexual size dimorphism, especially for end member specimens outside the area of overlap. This interpretation is not conclusive because of the overlap between groups and the uncertainties associated with the non-pregnant specimens discussed above. As a consequence the size differences cannot be used to identify gender in a non-pregnant specimen and pregnancy remains the only conclusive proof of gender. For a given species, a specimen significantly larger than the largest pregnant female is more likely to be male than female.

5.6.4: Comparisons with other organisms

Many gender specific features observed in extant organisms are not observed in ichthyosaurs (see section 5.2) and therefore cannot be used to identify gender. Furthermore, a comparison of the results for ichthyosaurs with other forms of extinct marine reptiles is difficult because pregnant specimens, or other absolute proof of gender, are required as one gender needs to be determined beyond reasonable doubt. In mosasaurs (Caldwell & Lee, 2001), pleisosaurs (O'Keefe & Chiappe, 2011) and nothosaurs (Renesto *et*. *al*., 2003) only a single gravid specimen is known for each group.

It is also difficult to compare ichthyosaurs to other animals from the same guild, which exploit the same niche in the same way. Whales and dolphins are typically fast swimming, open ocean pursuit predators that give birth to live young at sea. This is the same ecological niche that ichthyosaurs exploited in the Jurassic. There are no modern reptiles in the same guild as ichthyosaurs making a comparison to niche equivalent modern reptiles impossible. Although fish and mammals are very different animals to reptiles, it is possible to compare the guilds. Males are typically the larger gender in the majority of mammalian marine pursuit predators such as whales and dolphins (see section 5.2.4), which is consistent with the results for ichthyosaurs. Some whales and dolphins also exhibit sexual dimorphic features in the shape of the flukes and dorsal fins. Some ichthyosaurs have body outlines preserved so it could be possible for these features to be studied in the future. Other features such as enlarged tusks and teeth are also present in some whales and dolphins, however these features are not observed in ichthyosaurs (McGowan & Motani, 2003).

5.6.5: Future work

The results in this chapter indicate dimorphism, and potential sexual dimorphism, in ichthyosaurs. However, none of the results show a conclusive indicator of gender in a non-pregnant specimen. A larger sample size, including more pregnant specimens, could provide further insights. However, even though pregnant females are more numerous than in all other Mesozoic marine reptile fossil groups, they are still not common. Larger sample sizes could be used in future by basing the specimen selection criterion on a feature other than total body length. For example, all specimens with a humerus larger than that of the smallest pregnant female could be chosen. This would allow the inclusion of specimens for which a measure of total body length is not known and hence increase the sample size.

The shape of some soft parts, such as dorsal fins and flukes, can vary between the genders in dolphins (see section 5.2.4). There is a possibility of studying some of the soft parts in ichthyosaurs as body outlines are occasionally preserved, primarily in material from the Posidonia shale, near Holzmaden in Germany. Data on the soft parts was not collected as the numbers were too low in the specimens that were available for this project (approximately 10). Additional specimens with body outlines would be required to make this line of study viable. Care should be taken when measuring soft body outlines as it is possible that some have been fabricated, or had the external margin ‘tidied’ during preparation. Only genuine, unaltered body outlines should be included in such a study.

5.7: CONCLUSIONS

Dimorphism has been shown in larger, inferred sexually mature ichthyosaurs in terms of total body length, skull length and orbital diameter where the inferred males (non-pregnant specimens) tend to be larger than the females, as is consistent with examples of modern reptiles. However, there is overlap between pregnant female specimens and non-pregnant specimens, making it impossible to confirm that this dimorphism is due to gender. The inclusion of several species is unavoidable adds further uncertainty as to whether the dimorphism observed relates to gender. There are two specimens that consistently plot as one of the largest and one of the smallest (a pregnant female) respectively (Fig. 5.23). These belong to similarly sized species so this supports the interpretation of sexual dimorphism.

Although these results can be used to help indicate the gender of ichthyosaur specimens it is not conclusive. Smaller, sexually mature males and larger non-pregnant females are likely preserved and this would lead to confusion when attempting to identify gender or make it impossible. The features that tend to be larger in males can be used as an indicator of the gender of a specimen, however there are currently no features (such as antlers in mammals), which can prove gender other than pregnancy in ichthyosaurs.

6: BODY SIZE EVOLUTION IN ICHTHYOSAURS

6.1: INTRODUCTION TO BODY SIZE EVOLUTION

Invasion of the open-ocean by tetrapods represents a major evolutionary transition that occurred independently in cetaceans, mosasauroids, chelonids (sea-turtles), plesiosaurs and ichthyosaurs (Benson & Druckenmiller, 2012) as well as pinnipeds (Liwanag *et al*., 2012), sirenians (Fitzgerald *et al*., 2013), placodonts (Neenan *et al*., 2013) and mesosaurs (Piñeiro *et al*., 2012). Ichthyosaurs invaded the pelagic, open-ocean environment after the Permo-Triassic extinction event (McGowan & Motani, 2003) and became the top predator in the Triassic. Ichthyosaur remains are found globally (with the exception of Africa) and range from the Olenekian (251Ma) to the end Cenomanian (93.9Ma). These readily available fossils provide an opportunity to examine body size evolution that can potentially give insights into macroevolutionary processes and the diversification of ichthyosaurs throughout the Mesozoic.

Body size evolution examines the changes in overall size of an adult organism using a direct measure of body size or a proxy for size, such as body mass, length of a composite body part, length of an individual skeletal element or an estimate of body size. This measure of total body size, or a proxy, can remain constant, increase or decrease through phylogeny and/or geological time. Such size changes can relate to macroevolutionary changes in metabolism, population ecology, locomotion and reproduction (Hone *et*. *al*., 2008; Carrano, 2006) as well as changes in lifestyle such as trophic level and habitat.

Ichthyosaur remains exhibit a wide variety of body sizes (McGowan & Motani, 2003). Despite this, body size evolution has not previously been examined in ichthyosaurs. This study aims to address this gap in our knowledge and to determine if there are any trends or patterns in ichthyosaur body size through the Mesozoic. This could lead to insights into ichthyosaur evolution, diversity and extinction.

6.2: BODY SIZE EVOLUTION IN TETRAPODS

6.2.1: General trends in body size evolution

General trends observed in organisms, not specific to any group, are outlined below. The subsequent sections will examine specific groups of tetrapods in more detail.

Research shows that resource availability is a significant factor in the body size evolution of terrestrial organisms. Burness *et*. *al*. (2001) analysed body size data and food requirements of the top terrestrial herbivores and carnivores over the past 65000 years from oceanic islands and continents. Body mass (proxy for body size) and food requirements were plotted against land area. The results showed that the body mass of the top species (largest herbivore and carnivore) increases with increasing land area. For a given land area, the body size of the top species decreased in the sequence: ectothermic herbivore > endothermic herbivore > ectothermic carnivore > endothermic carnivore (Burness *et*. *al*., 2001).

Body size can increase or decrease in island populations. Island dwarfism, where organisms become smaller compared to their ancestors, is likely due to limited land area and limited food resources (Lomolino, 2005) such occurred with the extinct dwarf elephant *Elephas falconeri* Busk, 1867 (Raia et. al., 2003). This phenomenon is consistent with the analysis by Burness *et al*. (2001). Island gigantism is the opposite of island dwarfism and results in organisms becoming larger than their ancestors. This is likely to a lack of natural predators on an island setting which allows organisms to become larger (such as the extinct Haast's Eagle (*Harpagornis moorei* Haast, 1872) of New Zealand (Scofield & Ashwell, 2009) and the possibility of filling a different ecological niche (Lomolino, 2005). However, it is unlikely that ichthyosaurs were affected in such a manner as habitat is not as limited in the marine realm. Trends in marine tetrapods are given in section 6.2.3.2.

6.2.2: Reptilian body size evolution

6.2.2.1: Mesozoic marine reptiles

Very little research has been conducted into body size evolution in Mesozoic marine reptiles. However, Benson *et al*. (2012) analysed body size evolution in plesiosaurs (Reptilia, Sauropterygia), a group of extinct marine reptiles that are distantly related to ichthyosaurs (Chapter 1). Trunk length (defined as the distance between the anterior surface of the anterior-most vertebra with an elongate 'dorsalised' rib and the posterior surface of the posterior-most sacral vertebra) was used as an overall proxy for body size. Data were collected from 31 taxa. Only measurements from the largest individuals were included in the analysis. Taxa known only from juveniles (based on rounded, incompletely fossilised margins of slowly ossified bones such as the limb girdles) were excluded. The results showed that both maximum and minimum body size increased with time during the Jurassic (Fig. 6.1). However, the authors did not state whether the results are statistically significant or merely an artefact of the data (Benson *et al.*, 2012). Statistical tests that assess the apparent changes in body size are required to resolve this issue. The overall increase in size among plesiosaurs was substantial (an increase of 1.5m), which suggests that this could be significant. However, it is not possible to state this without any statistical support.

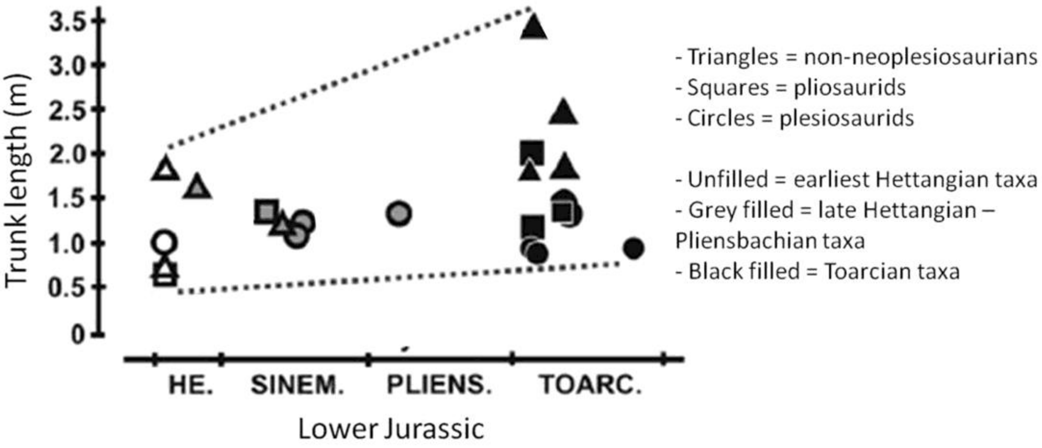


Fig. 6.1: Graph showing an increase in minimum and maximum body size for plesiosaurs during the Lower Jurassic. He = Hettangian (201.3-199.3Ma); Sinem = Sinemurian (199.3-190.8Ma); Pliens = Pliensbachian (190.8-182.7Ma); Toarc = Toarcian (182.7-174.1Ma). Dashed line represents the inferred minimum and maximum body size. Modified from Benson *et al*. (2012).

6.2.2.2: Archosauriforms

Archosauria is arguably one of the most successful groups of amniotes. Extant archosaurs include the crocodilians and birds. Extinct archosaurs include non-avian dinosaurs, pterosaurs and pseudosuchians (the remainder of the clade that includes modern crocodilians). The first large (>1m) diapsids appeared after the Permian-Triassic extinction and a subset of diapsids, the archosauriforms, expanded their maximum body size soon after the early Middle Triassic (Turner & Nesbitt, 2013).

Turner & Nesbitt (2013) analysed 128 specimens representing 128 archosauriform taxa in order to examine body size evolution across the Triassic-Jurassic boundary. Femoral length was used as a proxy for body size (Fig. 6.2). The results show a general size increase throughout the Triassic, the majority of which occurred early in the Triassic. Non-archosaurian archosauriformes (specifically phytosaurs) increased in maximum body size in the Early and Middle Triassic. Pseudosuchian maximum body size also increased through the Early and Middle Triassic, but then decreased in maximum body size towards the end of the Triassic and into the Jurassic. Ornithodirans (the group including dinosaurs, pterosaurs and birds) were initially dwarfed by the pseudosuchians in the mid-Triassic but their maximum body sizes were similar by the mid-Carnian (~224Ma). Furthermore, the largest archosauriforms in the Triassic, the sauropodomorphs, continued to increase in maximum body size during the Jurassic. Femoral length was used as a proxy for size and is generally considered an appropriate measurement as it grows isometrically in many extant reptiles. This measurement is easily obtainable in complete and disarticulated specimens. Furthermore, a large number of taxa can be sampled this way. The large dataset collected by Turner & Nesbitt (2013) allowed the results to be analysed for statistically significant results. However, Turner & Nesbitt (2013) only had one specimen for each taxon and it is possible that some of the femora measured did not come from adult specimens. Therefore, it is possible that there is some error in the results. Additional information on mean body size for five archosaur clades that survived the Triassic-Jurassic boundary shows that the Crocodylomorpha decrease in size across the boundary while the Sauropodomorpha, Pterosauria ,Theropoda and Ornithischia all increase in average body size across the Triassic-Jurassic boundary (Turner & Nesbitt, 2013) (Fig. 6.2). However, the results for the Pterosauria are based on very few specimens and, as such, these results are less reliable.

Dinosaurs have been studied in detail as a result of the enormous range of sizes seen in the group (Fig. 6.3). Carrano (2006) collected data on three size proxies (femoral length; femoral anteroposterior diameter; femoral mediolateral diameter) in order to examine body size evolution in non-avian dinosaurs. 1640 non-avian dinosaur specimens were measured, representing all major ingroup clades and nearly every taxon for which limb length is known (Carrano, 2006).

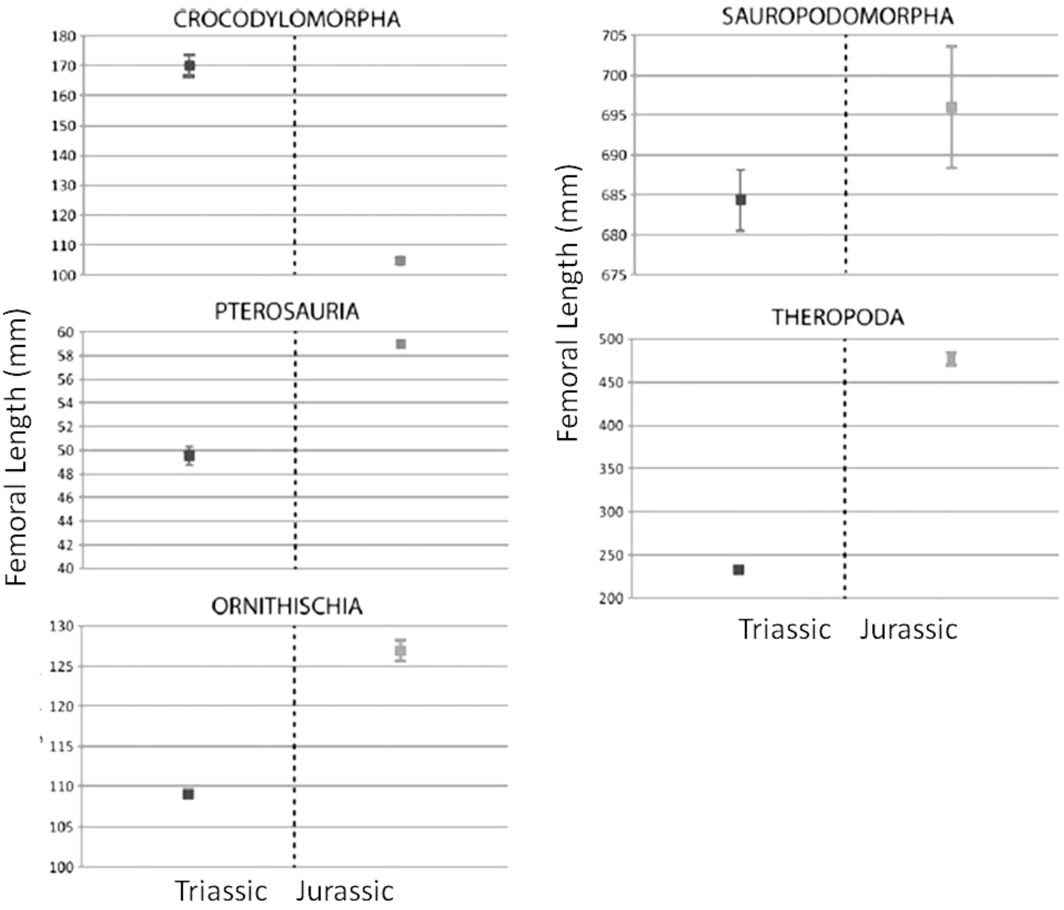


Fig. 6.2: Mean femoral length with 95% confidence intervals (where applicable) for the five archosaur sub-clades summarising the difference between the Triassic and Jurassic (modified from Turner & Nesbitt, 2013). The number of taxa included in each plot was not provided by the authors.

Taxa represented by juvenile limbs only were excluded from the analysis, but the author did not specify which features were used to establish ontogenetic stage. The analysis uses a composite phylogeny where 11 of the measured taxa were omitted because their relationships were uncertain. The results of the analysis showed that dinosaur evolution was characterised by a marked, pervasive pattern of maximum and minimum body size increase through the Mesozoic. This is consistent with the results of Turner and Nesbitt (2013). Body size increase is evident in most of the major ingroup clades. However, two clades (Macronaria and Coelurosauria) showed a decrease in maximum body size. Benson *et al.* (2014) examined body mass (used as a proxy for size) for avian dinosaurs. Data on 'limb robustness' (stylopodial circumference) was collected for 441 taxa. The data were inputted into a scaling equation derived from modern tetrapods that provides a value for body mass. The results show a rapid increase in body mass from the Late Triassic onward: for example, masses of 0.99kg (*Sinosauropteryx prima* Ji & Ji., 1996) to 7700kg (*Tyrannosaurus rex* Osborn, 1905) in non-maniraptoran theropods and from 8.5kg (*Pampadromaeus barberenai* Cabreira *et*. *al*., 2011) to 90000kg (*Argentinosaurus huinculensis* Bonaparte & Coria, 1993) in sauropods. Furthermore, feathered maniraptoran dinosaurs (including Mesozoic birds) sustain rapid evolution of and increases in body mass from the Middle Jurassic onward rising from a mass of 0.14kg (*Parvicursor remotus* Karhu & Rautian, 1996) to 3100kg (*Suzhousaurus megatherioides* Daqing *et*. *al*., 2007) (Benson *et*. *al*., 2014).

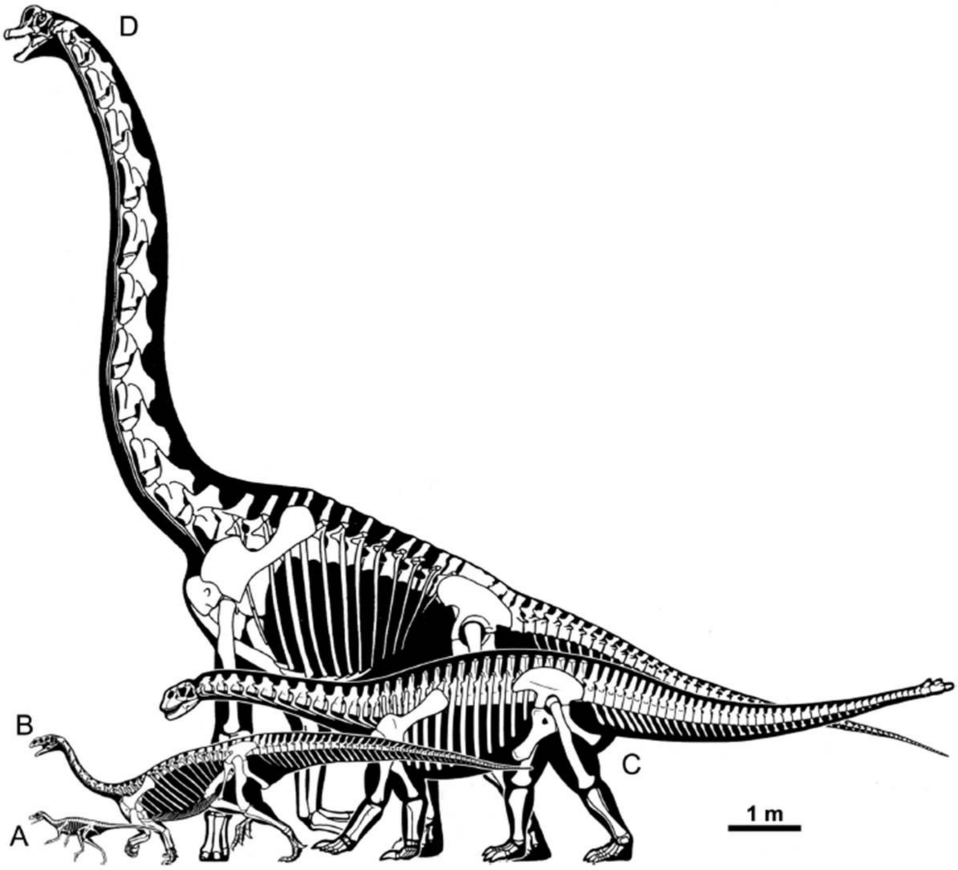


Fig. 6.3: Diagram illustrating the varying body sizes in a basal saurischian and several sauropodomorphs. (A) basal saurischian *Eoraptor* from the Late Triassic; (B) basal sauropodomorph *Plateosaurus* from the Late Triassic; (C) basal eusauropod *Shunosaurus* from the Middle Jurassic; (D) basal macronarian *Brachiosaurus* from the Late Jurassic. Modified from Rauhut *et al*., 2011.

Butler *et al*. (2010) described a new, very small, adult ornithischian dinosaur with an estimated body length of 65-75 cm (*Fruitadens haagarorum*), altering the lower size limit considered by Carrano (2006). However, the age estimate for the new material (*F. haagarorum*) suggests that the material was from a young adult, estimated to be in the 5th year of development (Butler *et al*., 2010). This indicates that the species could have potentially increased in body size with age, which would result in an inaccurate lower body size estimate for the group as specimens included in the analysis must be mature. The discovery of larger *F. haagarorum* specimens could be used to help correct this error.

Crocodylomorpha is another archosaur group that has been studied in detail. Young *et al*. (2011) studied Metriorhynchidae, a group of fossil crocodylomorphs that returned to the oceans and evolved a fully marine lifestyle from the Middle Jurassic to the Early Cretaceous (~171-136Ma). Young *et al*. (2011) collected data on basicranial length and femoral length. A regression equation, based on five complete metriorhynchid specimens, was then used to estimate total body length, which was then plotted against time. The results indicate two major trends in metriorhynchid body size evolution. The trend among metriorhynchine metriorhynchids shows a decrease in maximum body size, whereas the opposite is true for the geosaurine metriorhynchids that show an increase in maximum body size. However, these trends oversimplify body size evolution. The geologically youngest metriorhynchid species have larger body sizes than the oldest species and in the geosaurines the genus with the smallest maximum body size is the geologically youngest. Both of these examples show the reverse of the general trend for their subclades. As a consequence, the authors concluded that there is no clear pattern in body size evolution across metriorhynchid phylogeny (Young *et al*., 2011).

Trends in archosauriform body size evolution broadly show an increase in maximum body size with time in each of the groups mentioned above. However, this oversimplifies the data as several subgroups do decrease in size or maintain a constant body size while other subgroups show no clear patterns in body size evolution.

6.2.3: Mammalian body size evolution

6.2.3.1: General trends

Mammals exhibit a vast diversity in body size from the minute bumblebee bat to the African elephant and blue whale. They have evolved to fill every niche and can swim, fly, burrow, climb, and run. They first appear in the fossil record during the Late Triassic (Alroy, 1999).

Alroy (1999) examined the fossil record of North American mammals. 4385 mammalian fossil localities ranging from ~98Ma (early Late Cretaceous) to 0.1Ma (late Pleistocene) were analysed. Data were compiled from published measurements for 19363 lengths from lower first molars. These length data were inputted into regression equations based on a modern equivalent (separate equations were used for each of the major mammalian orders) in order to obtain a body mass estimate (used as a proxy for size), which was then plotted against time.

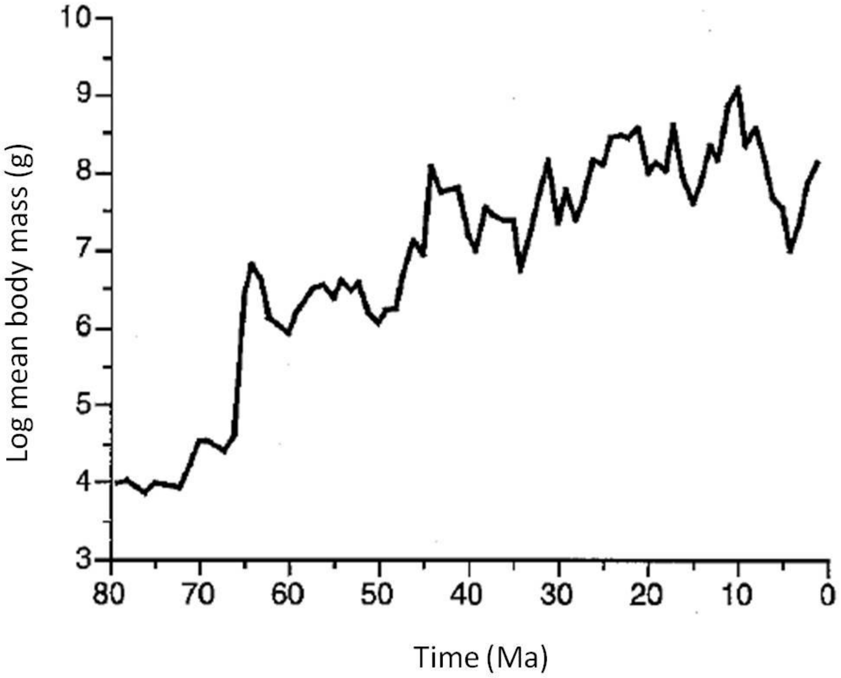


Fig. 6.4: Plot showing the increase in mean body mass with time in mammals. n=19363. Time bins=1Ma. (Alroy, 1999).

The results show that Cretaceous mammals were on average small and occupied a narrow range of body sizes (masses). After the Cretaceous–Paleogene (K-Pg) boundary, there was a rapid and permanent increase in the mean maximum body size (mass) (Alroy, 1999) (Fig. 6.4).

These results are well-supported because the dataset used is very large (n=19363) and covers a wide size range of mammals, from shrews to mammoths. However, the analysis did not take into account any physical size differences caused by sexual dimorphism, geographical variation or within-species anagenetic change. The comparatively small differences in sexual dimorphism would likely not affect the results (Alroy, 1999).

Gingerich (1980) analysed tooth size in 10 lineages of mammals and also documented an overall increase in maximum mammalian body size (mass) after the K-Pg boundary. However, a more detailed analysis shows that of a total of 22 lineage segments, 10 (45%) showed an increase in maximum body size (mass), eight (36%) a decrease and four (18%) were unchanged (Gingerich, 1980). These results show that the overall body size (mass) increase oversimplifies a variety of underlying trends in body size evolution.

In some mammal groups, there is a short interval of dwarfism, with species decreasing in maximum and minimum body size across the Paleocene-Eocene boundary (Gingerich, 2003; Gingerich, 2006; Smith *et*. *al*., 2006). Gingerich (2003) used data on tooth surface area to estimate body weight for three separate genera (*Ectocion* Cope, 1882; *Copecion* Gingerich, 1989; *Hyracotherium* Owen, 1841) across the Paleocene-Eocene boundary (Fig. 6.5). The maximum and minimum body weight returns to background values relatively quickly after the Paleocene-Eocene boundary in the genera *Ectocion* and *Copecion*. In the genus *Hyracotherium* maximum body weight increases after the boundary to reach a maximum at ~54Ma followed by a decrease to ~53.6Ma.

These studies show that mammalian body size evolution is not a simple case of maximum body size increasing with time. There are examples of short term dwarfing and of dwarfing lineages.

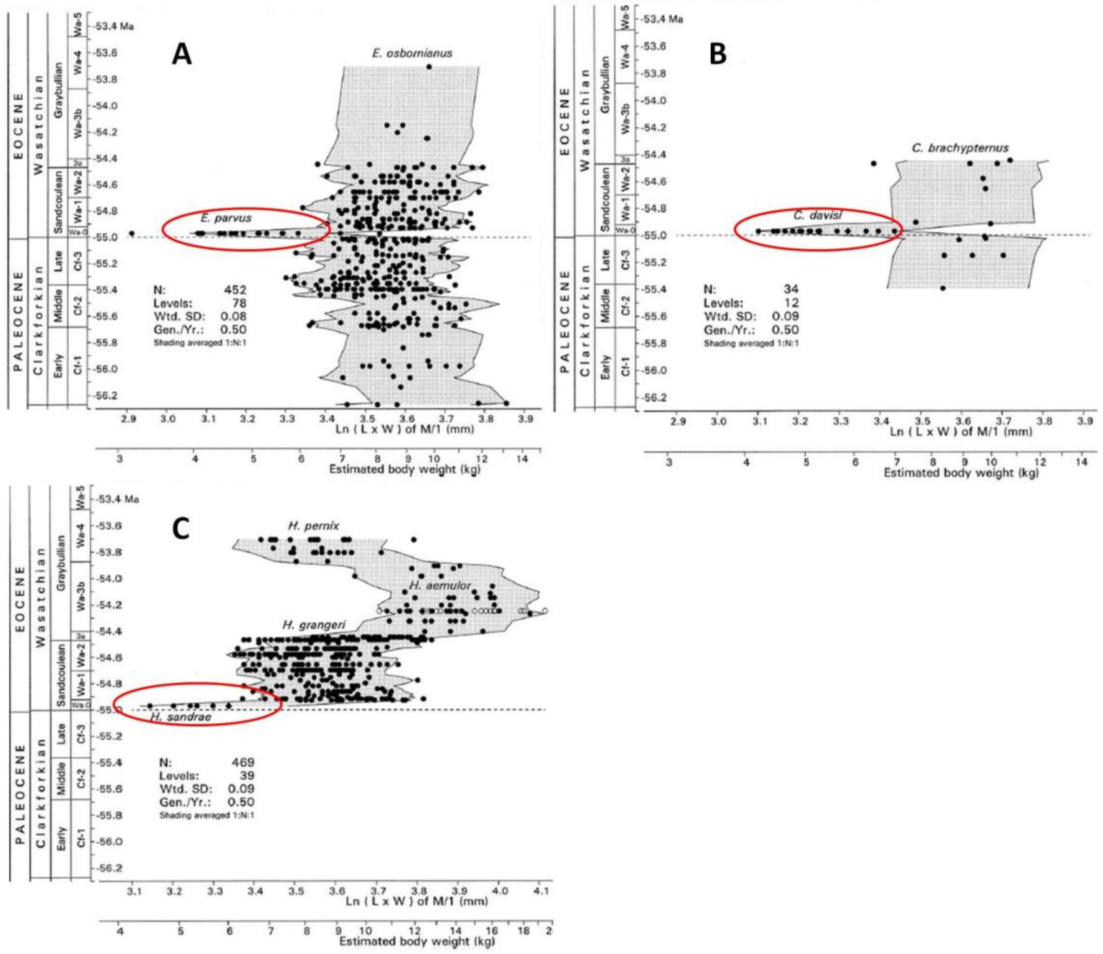


Fig. 6.5: Stratigraphic record of tooth surface area and estimated body weight for the genera *Ectocion* (A); *Copecion* (B); *Hyracotherium* (C) showing a large reduction in maximum and minimum body weight across or near the Paleocene-Eocene boundary (as shown by the dashed line) (highlighted in red circle). Modified from Gingerich (2003).

6.2.3.2: Cetaceans

Cetaceans (whales and dolphins) are of particular interest in this study as they are niche equivalents to ichthyosaurs. As with ichthyosaurs, cetaceans are secondarily adapted tetrapods that evolved a pelagic lifestyle. However, as cetaceans are mammals and ichthyosaurs are reptiles, comparisons must be made with caution.

Cetacea is a diverse group of secondarily adapted marine mammals. There is a large range of body size, with the smallest extant cetacean measuring 1.4m in length (*Phocoena sinus* Norris & MacFarland, 1958) and the largest, the Blue Whale (*Balaenoptera musculus Linnaeus, 1758),* measuring up to 33m (Thewissen & Williams, 2002). Studying body size evolution in fossil cetaceans is difficult as complete fossils are rare, despite isolated or fragmentary fossils being relatively common. Also, the large size and fragile nature of the material results in fossils being hard to collect and preserve (Fordyce & Barnes, 1994).

Early protocetids, at the base of the cetacean radiation were small, although probably larger than the smallest extant odontocetids. Early Oligocene cetaceans include large species but a general reduction in maximum body size led to smaller species in the late Oligocene. There was a period of gigantism among the basilosaurids of the late Eocene. There is little evidence for large species in the early Miocene but one late Miocene balaeontopterid was comparable in size to the modern blue whale (Thewissen & Williams, 2002).

Generally, the maximum body size of cetaceans has increased over time with the extant blue whale representing the upper limit of this size evolution. However, the lower size limit may have decreased as the smallest extant odontecetids were probably smaller than the earliest protocetids.

6.2.3.3: Equidae

Equid (horse) evolution has been examined by many authors (Haldane, 1949; Simpson, 1953; Stanley, 1979, 1985; Gingerich, 1982, 1983; MacFadden, 1985, 1992; Shoemaker & Clauset, 2014). MacFadden (1986) conducted a detailed study on horse evolution from the entire fossil record of horses from 57Ma to the present. A suite of seven characters from the upper dentition and skull were collected as well as head-body length where available from 628 individual specimens representing 21 genera and 45 species. These measurements were subsequently inputted into a regression equation based on an extant species of *Equus* in order to establish a measure of body mass (used as a proxy for body size). The results of the analysis showed a period of stasis in body size (mass) before a rapid increase in maximum body size with time. This is consistent with other reports on body size evolution in Equidae (Haldane, 1949; Simpson, 1953; Stanley, 1979, 1985; Gingerich, 1982, 1983; MacFadden, 1985) and is also consistent with Cope's rule. However, Cope's rule suggests a gradual increase in maximum body size over time while the results indicate that the first half of horse evolution (57-25Ma) was characterised by size stasis. This was followed by a diversification of body size in the early to middle Miocene. The late Miocene and early

Pleistocene are characterised by a continual increase in maximum body size (Fig. 6.6), as well as extinction of smaller species (Gingerich, 1986).

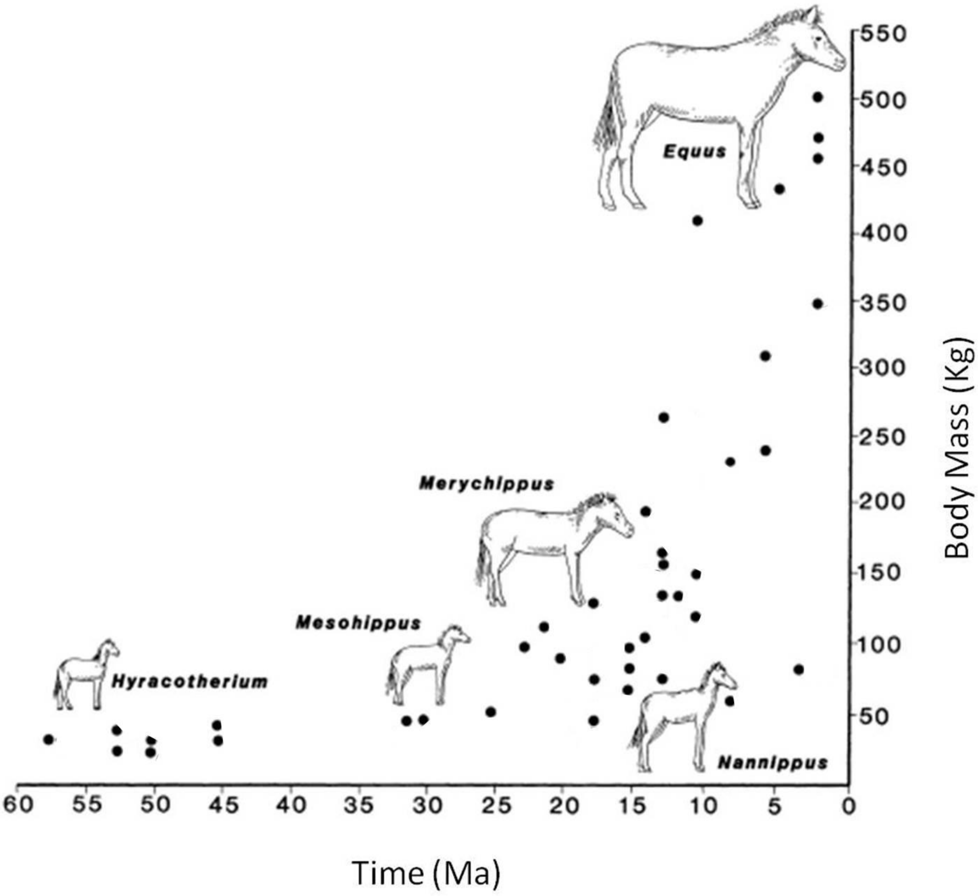


Fig. 6.6: Graph of the distribution and increase in body mass for 40 species of fossil horses, showing initial stable size followed by a relatively rapid increase with some dwarf lineages, modified from MacFadden (1986).

However, using the same data, MacFadden (1986) noted several dwarf lineages, where the descendant is smaller than the ancestor, resulting in a decrease in maximum body size over time. MacFadden (1986) examined 24 ancestral-descendant species pairs (using the same measurements). Nineteen showed an increase in maximum body size over time while five lineages were characterised by dwarfism, including *Nannippus* Matthew, 1926. MacFadden, 1986).

Tooth measurements are very suitable proxies for mammalian body size as research has shown that teeth grow isometrically with the overall size of the individual (MacFadden, 1992). This, combined with the large number of specimens included in the analysis, suggests that the results are robust

Guthrie (2003) examined body size changes in Pleistocene Alaskan horses. Metacarpal lengths were analysed as a proxy for body size. The data were plotted against time, based on radiocarbon dating. The results showed a rapid decline in maximum body size prior to their extinction. It is likely that other factors affected the body sizes. Guthrie (2003) analysed Alaskan horses while Gingerich (1986) analysed North American horses in general. Alaska became much colder than the rest of North America, which would have resulted in a reduction in food availability. It is likely that food reduction, and low temperatures (that were better suited to smaller-sized animals) resulted in dwarfism. The majority of North America did not suffer from these environmental constraints, which might have allowed maximum body size to continue to increase in other regions (pers. obs.).

Dwarf lineages of horses have also been reported across the Paleocene-Eocene boundary (Gingerich, 2003). Secord *et al*. (2012) used area of the first lower molar in *Hycracotherium* in a high-resolution analysis. This showed a size decrease of ~30% over the first ~130000 years of the Paleocene-Eocene thermal maximum (PETM), followed by a ~76% increase in the recovery phase of the PETM. These results are consistent with the results of Gingerich (2003). These results show that body size evolution in Equidae is not entirely consistent with Cope's Rule and some lineages do decrease in maximum body size despite the overall trend for maximum body size increase.

D'Ambrosia *et al*. (2014) examined dwarfism in mammals during the Eocene in relation to changing temperature and CO_2 levels. Data was collected on teeth (total crown area) from mammals in the Bighorn Basin, Wyoming. The results showed that during times of increased mean temperature, body size was reduced, leading to dwarfism. *Hyracotherium* exhibited the largest change during a temperature increase with a decrease in body size of ~19%. Total body size returned to 'normal' when the temperature fell. This is consistent with dwarfism around the Paleocene-Eocene thermal maximum (PETM) where body size decreased by ~30%. Similar results were observed in *Diacodexis* (an artiodactyl) and *Cantius* (a primate) that experienced decreases in body size of 22% and 7.7%, respectively. This suggests that mammalian dwarfism is a common evolutionary response to increasing CO_2 levels and/or increasing temperatures (D'Ambrosia *et al*., 2014). It is likely that the dwarfism observed across the Paleocene-Eocene boundary (Gingerich, 2003; Secord *et al*., 2012) is also linked the increased temperature at the PETM.

6.2.3.4: Summary of mammalian body size evolution

Generally, mammals increased in maximum body size with time (Alroy, 1999) and this is consistent with Cope's Rule. However, more detailed studies have shown that body size evolution is not as simple as the steady increase suggested by Cope's Rule. Gingerich (1980) showed that some groups of mammals have a body size that remains constant while others decrease in maximum body size. A detailed study of the Equidae shows that body size remains constant during the early phase of equid evolution before rapidly increasing in maximum body size for many species, while other species experience reduction in maximum body sizes resulting in dwarf lineages (MacFadden, 1986). Tooth measurements are very suitable proxies for mammalian body size as research has shown that teeth grow isometrically with the size of the individual (MacFadden, 1992) and teeth are abundant and easy to identify. Maximum body size also increases in Cetacea (Thewissen & Williams, 2002), but minimum body size also decreased.

6.2.4: Avian body size evolution

Birds are a very diverse clade with extant species that exhibit a wide range of body sizes and masses, from the bee hummingbird (*Mellisuga helenae* Lembeye, 1850) with a body mass of 2g to the ostrich (*Struthio camelus* Linnaeus, 1758) with a 100Kg body mass. However, the mass distribution across living Aves is severely right-skewed, even on a logarithmic scale, with the median extant bird mass being 37.6g (Blackburn & Gaston, 1994). Flight requires a certain size to mass ratio, beyond which it is not feasible to have a wing large enough to create sufficient lift. Due to this constraint, the heaviest extant flying bird is the great bustard (*Otis tarda* Linnaeus, 1758), which is roughly 1m long but weighs only 16kg. It is possible that some extinct flying birds could have been heavier. This indicates that body mass is not synonymous with size when comparing birds with and without the ability to fly. Therefore, the body size evolution of flying birds and terrestrial birds must be studied separately.

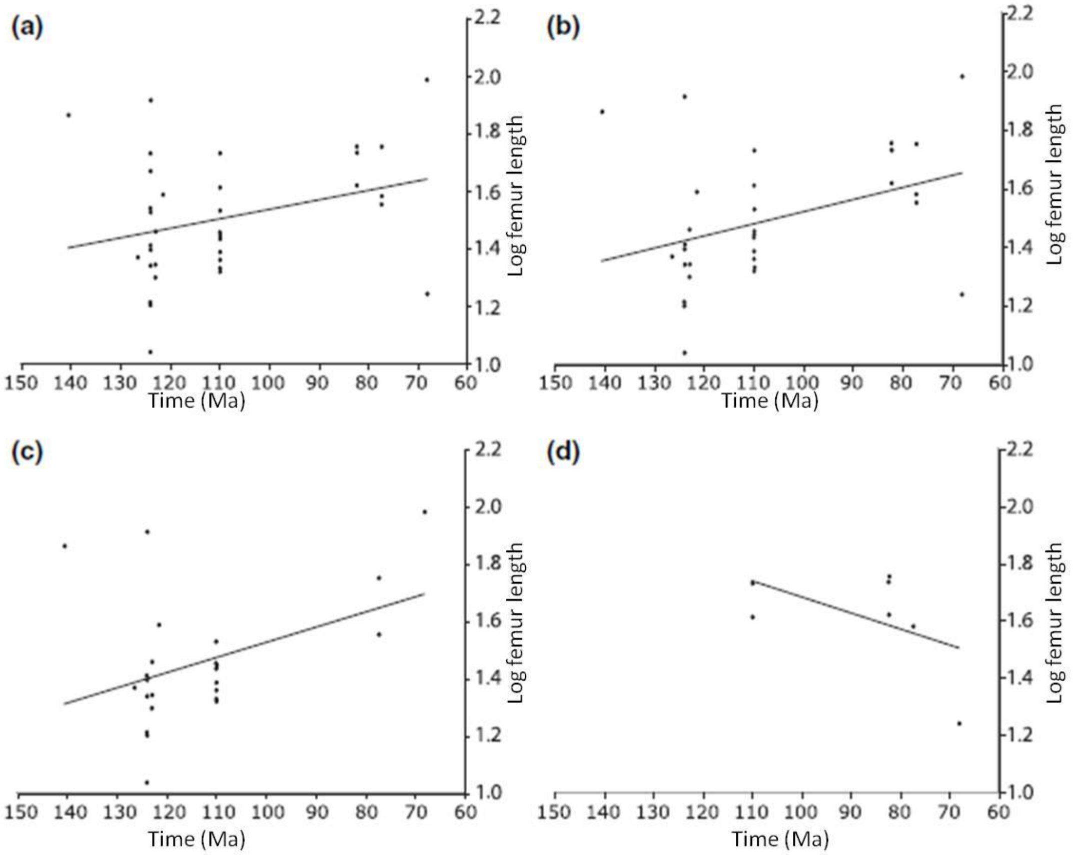


Fig. 6.7: Log femur length (proxy for body size) plotted against time showing an increase in maximum body size with time for (a) Pygostylia; (b) Ornithothoraces; (c) Enantiornithes, and a decrease in (d) Ornithomorpha with each point representing a single species. (Hone *et al*., 2008).

Hone *et al*. (2008) examined the evolution of body size in Mesozoic flying birds. Length measurements were collected for fore and hind limb bones from the literature. The dataset contains 117 bird specimens representing 47 distinct species that covered more than 95% of the known diversity of Jurassic and Cretaceous birds (up to 2006). Body mass was estimated using limb bones and allometric scaling equations. The authors did not state what the scaling equations were based on. The analysis shows an overall increase in avian maximum body size through the Jurassic and Cretaceous (Fig. 6.7). The clades Pygostylia and Ornithothoraces both showed strong positive trends with an increase in maximum body size (Fig. 6.7a,b). The Enantiornithes (Fig. 6.7c) also showed maximum body size increase, but at a slightly increased rate. In contrast, the Ornithomorpha exhibited a trend towards decreasing size (Hone *et al*, 2008) (Fig. 6.7d).

However, Butler & Goswami (2008) disputed the results of Hone *et al*. (2008). Hone *et al*. (2008) used a series of least-squared regressions of log-femur length against stratigraphic age to examine trends in body size evolution (Fig. 6.7). Butler & Goswami (2008) noted that this approach increases type 1 errors and cannot resolve whether any identified increase in body size is a result of selection within or among lineages. Also, Hone *et al*. (2008) did not report significance values for any of their regressions, but did suggest that they were 'significant'. Furthermore, Shapiro-Wilk's tests on the data used by Hone *et al*. (2008) showed that the original data were not normally distributed, and therefore, the parametric methods that they used cannot assess statistical significance. Butler & Goswami (2008) re-examined the data of Hone *et al*. (2008) using more appropriate non-parametric tests. The results of the non-parametric tests showed that only one clade, Ornithothoraces, showed a significant trend for increasing body size. The non-parametric tests show no evidence of significant trends in avian body size evolution overall (Butler & Goswami, 2008).

The ratites (Aves: Dinornithiformes) range from the size of an extant turkey to the extinct, 3m tall *Dinornis* weighing up to an estimated 300kg. Extant members of the ratite lineages include the ostrich (Africa), emu, cassowary (Australia & New Guinea), rhea (South America) and kiwi (New Zealand) while extinct ratites include the giant elephant birds (Madagascar) and moa (New Zealand) (z). Several ratites, such as the extinct elephant bird and extant ostrich, became very large due to flight not limiting size. There has been no study of body size evolution in flightless birds, but there has clearly been an increase in maximum body size with time. However, the largest forms (such as the elephant birds and moa) are extinct with the largest extant form being the ostrich. This suggests that there has been a subsequent decrease in maximum body size.

6.2.5: Implications for study of ichthyosaurs

Several different analyses are discussed in sections 6.2.1 - 6.2.4 that could be relevant to the investigation of body size evolution in ichthyosaurs. Many of the studies use a proxy for body size instead of a direct measurement of overall size as many fossil specimens are rare or incomplete. This approach could also be used for ichthyosaurs, as many specimens are incomplete. However, the element used would have to be present in every species included in an analysis.

As an alternative to direct use of a size proxy, several authors applied regression equations in order to estimate body size or body mass from a length measurement of an individual skeletal element, such as the femur. Such equation must be based on either a modern or fossil analogue, but a fossil analogue must be a complete specimen. Typically an extant analogue is used, such as the modern horse *Equus* in analyses of equid evolution. The most suitable modern reptile as an analogue for ichthyosaurs would be a crocodile, but this is a not a particularly appropriate analogue as crocodilian lifestyles are semi-aquatic and their limbs are retained for terrestrial locomotion. The closest niche equivalent would be an extant member of the Cetacea. However, cetaceans are also inappropriate as they are mammals. Complete fossil specimens would also be needed for each genus and species in the regression. As there is no appropriate modern analogue, and there are too few complete fossil specimens, this approach cannot be used to investigate ichthyosaur body size evolution.

Several studies have used tooth size as a proxy for body size. This is an appropriate measurement in mammals as tooth size scales isometrically with body size. This is not the case with ichthyosaurs. Furthermore, ichthyosaurs have a range of tooth sizes and shapes (Massare, 1987). Consequently, tooth size is not a suitable proxy for size in ichthyosaurs.

Several of the studies dealt with changes to minimum body size as well as changes to maximum body size. Body size evolution is based on mature specimens. In ichthyosaurs, the moment at which an individual is sexually mature cannot be determined exactly (Chapter 5), and the only evidence of minimum body size would be the size of the smallest pregnant individual. There are insufficient ichthyosaur species that preserve pregnant female specimens for minimum body size to be studied.

The large numbers of included specimens used in many of the analyses summarised above, typically in the region of hundreds or thousands, are not possible in ichthyosaurs. Authors studying groups including extant species, or better represented fossil species, are able to sample a far greater number of specimens than those examining fossilised remains, as not every individual would be preserved.

6.3: MATERIALS AND METHODS

Length measurements were collected from the literature for ichthyosaur genera throughout the Mesozoic. Total maximum body length (direct measure of the body length of the largest specimen, measured from the tip of the snout, along the spine to the tip of the tail) data were collected where possible; however proxies for body size were also collected. These were, estimated body length (estimated maximum body length), humerus length (maximum length of the humerus) and femur length (maximum length of the femur). Data were obtained in a variety of ways. Direct measurements (total body length, humerus length and femur length) were taken from direct reports of measurements in the published literature (e.g. tables of measurements), or measured from published figures using ImageJ (Hoffman *et al*., 2013). Direct measurements were also obtained from the dataset for the whole project. The dataset for this chapter is provided in Table 6.1 (see end of chapter). Estimated maximum body lengths were only taken from publications where the author has estimated the body length and these data, with reasons where provided, are given in Table 6.2 (see end of chapter). The estimated body lengths are an estimate of the maximum size of a species so these are typically larger than the largest known specimen of a well-represented species where complete specimens are known, such as *Stenopterygius quadriscissus*. It is not possible to state how much each species is over-estimated.

Minimum body size estimates cannot be obtained for ichthyosaurs because the exact point at which in individual ichthyosaur becomes mature is still a matter of debate (Chapters 3 & 4). The only direct evidence for maturity in ichthyosaurs is the presence of embryos in pregnant specimens and these are only known for a limited number of genera.

The latest complete phylogeny (Fig. 6.8), that of Thorne *et al*. (2011), was used as a framework for selecting the genera to be included, with the addition of *Thalattoarchon* Fröbisch *et al*., 2013. Species within the genera were selected from McGowan and Motani (2003) as this is the most recent analysis at species level. The size data were plotted on a timescale at the earliest occurrence of that particular species. A least-squares regression was conducted on the data and the slope value (α) used to assess the strength of any relationships. An α value of -1 shows a strong negative relationship between body size and time while an α value of 1 shows a strong positive relationship. Values between -0.5 and 0.5 indicate a weak relationship or no relationship in the dataset.

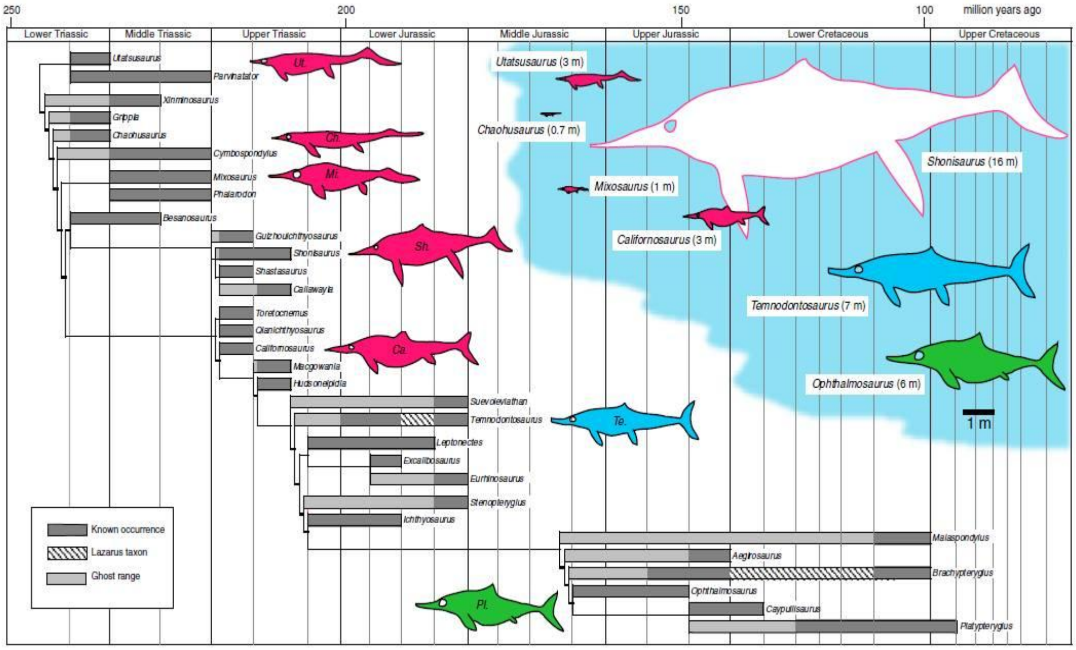


Fig. 6.8: Phylogeny of ichthyosaurs plotted against geological time. Silhouette outlines (Ca = *Californosaurus*; Ch = *Chaohusaurus*; Mi = *Mixosaurus*; Pl = *Platypterygius*; Sh = *Shonisaurus*; Te = *Temnodonotosaurus*; Ut = *Utatsusaurus*) indicate major body morphologies in Triassic (Red), Early Jurassic (Blue) and mid-Jurassic to Cretaceous (Green) (Thorne *et al*., 2011).

6.4: RESULTS

The results for estimated body length (n=34) and humerus length (n=40) are presented below as these were the best-represented measurements in the dataset. The results for femoral length (n=24) are not presented here due to insufficient numbers.

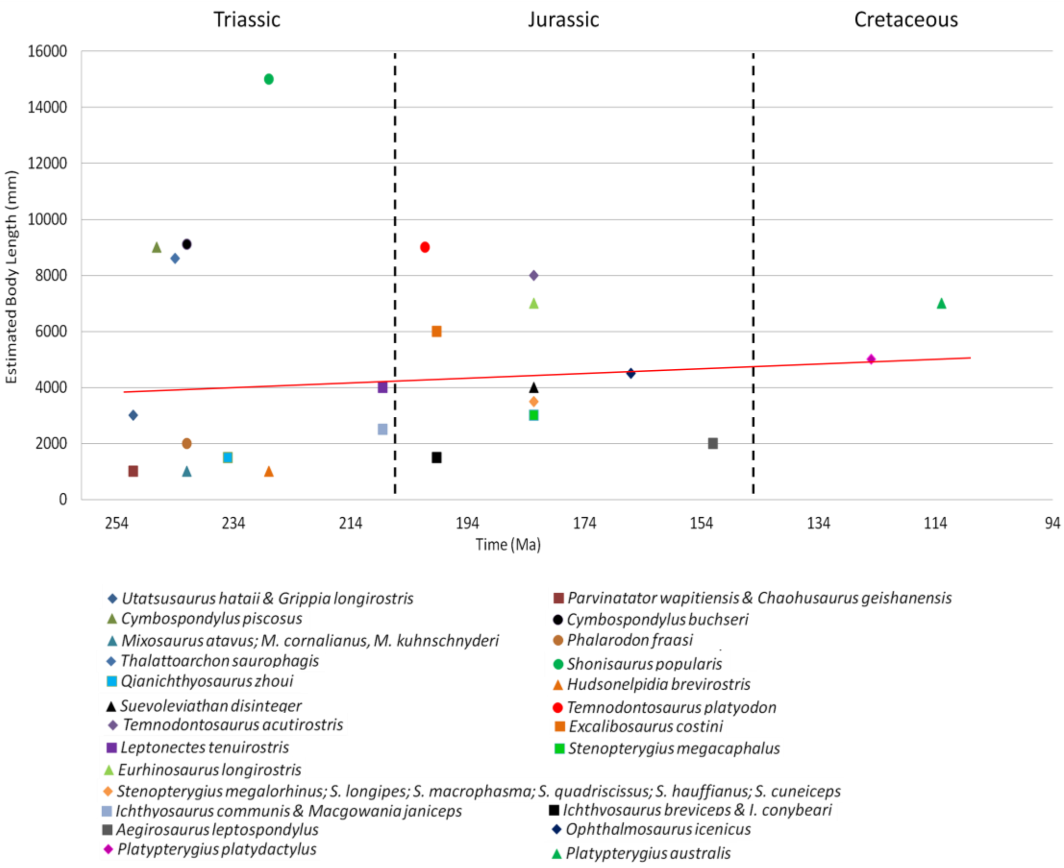


Fig. 6.9: Results for estimated body length against time showing no clear pattern with large and small taxa coexisting from the start (n=35). Red line of best fit from linear regression (α=0.008: r^2=0.0083: y=-0.0078*x* + 5.6812: p(uncorr)=0.522). The following taxa have no estimated body length but are included in the humerus length analysis:- *Besanosaurus leptorhynchus*; *Brachypterygius extremus*; *B. cantabrigiensis*; *Caypullisaurus bonapartei*; *Leptonectes moorei*; *Mixosaurus maotaiensis*; *M. solei*; *Platypterygius americanus*; *P.hauthali*; *Shastasaurus neoscapularis*; *Temnodontosaurus trigonodon*; *T. crassimanus*; *Toretocnemus zitteli*; *Xinminosaurus catcates*.

The results do not show any consistent pattern of change in estimated maximum body size (Fig. 6.9). Large and small taxa coexist from their earliest occurrences in the fossil record. The largest size range appears in the Triassic with a maximum estimated body length of 15m. The range is slightly lower during the Jurassic with a maximum body size of 9m, with a decrease to 7m in the Cretaceous. The result for the least squares analysis gives a slope value (α) of 0.008 and an r^2 value of 0.0083 which also indicates no pattern of estimated body length change within the dataset. Furthermore, the p(uncorr) value of 0.522 shows that there is no significant correlation between estimated maximum body size and stratigraphic age (p(uncorr)=0.05 to be a significant correlation).

Humerus length is the best represented measurement in the dataset and was used as a proxy for size. The results (Fig. 6.10) do not show a clear pattern. As with estimated body length, the largest size range is in the Triassic. The size range is reduced in the Jurassic and further reduced in the Cretaceous.

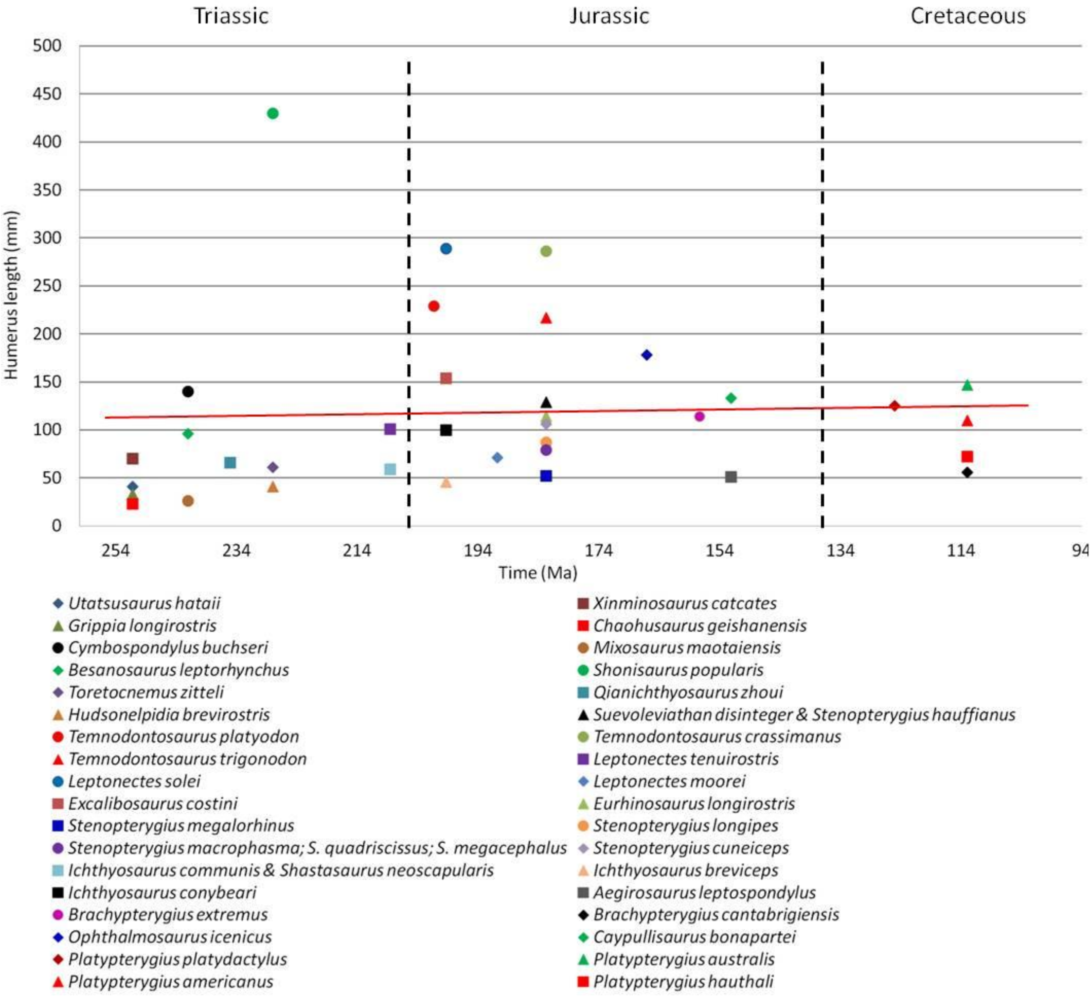


Fig. 6.10: Results for humerus length against time showing no clear pattern with large and small taxa coexisting from the start (n=40). Red line of best fit from linear regression (α=0.192: r^2=0.0089; y=-0.1924*x* + 148.82: p(uncorr)=0.5608). The following taxa have no humerus length but are included in the estimated body length analysis; *Cymbospondylus piscosus*; *Macgowania janiceps*; *Mixosaurus atavus*; *M. cornalianus*; *M. kuhnschnyderi*; *Parvinatator wapitiensis*; *Phalarodon fraasi*; *Thalattoarchon saurophagis*.

The results for the least squared analysis gives a slope value (α) of 0.192 and an r^2 value of 0.0089, which also indicates no clear pattern of changes in humerus length with time within the dataset. Furthermore, the p(uncorr) value of 0.5608 shows that there is no significant correlation between humerus length and stratigraphic age.

The Jurassic has the largest number of taxa. Therefore, a least squares regression analysis was conducted on these taxa alone (humerus length) in order to establish whether or not any significant trends could be seen. The results (α=1.0321; r^2=0.0439; y=1.0321x-58.435; n=20) show that there is no statistically significant trend for humerus length during the Jurassic. Due to the Cretaceous specimens being underrepresented in both the analyses, further OLS analyses were conducted with the Cretaceous taxa, and the *Shonisaurus* outlier omitted. The results for the estimated maximum body size (α=9.8773: r^2=0.0130: y=-9.8773x+5789.4: p(uncorr)=0.5336) show no significant correlation between estimated maximum body size and stratigraphic age. The results for the humerus, omitting the Cretaceous taxa and the *Shonisaurus* outlier, (α=0.8457: r^2=0.1381: y=-0.8475x+275.32: p(uncorr)=0.03046) which does show a correlation between humerus length and stratigraphic age in ichthyosaurs with an increase in size between the Triassic and the Jurassic.

6.5: DISCUSSION

6.5.1: Apparent trends in ichthyosaur body size and possible causal factors

Although there are no statistically significant trends in ichthyosaur body size evolution, there are still some trends visible in the results. Estimated maximum body size in ichthyosaurs increases to a peak in the Middle Triassic and then decreases throughout the Jurassic into the Cretaceous. Furthermore, the minimum body size steadily increases from the Triassic to the Cretaceous. The amount of variation in body sizes (standard deviation) also decreases steadily from the Triassic to the Cretaceous.

The earliest ichthyosaurs are initially small in the Triassic but estimated maximum body size increases rapidly in the Early Triassic with large species appearing, including the extremely large *Shonisaurus popularis* that plots as an outlier (Fig. 6.9, 6.10). However, the removal of this outlier only slightly affects the results (α=15.51: r^2=0.047: y=-15.512x+7027.3: p(uncorr)=0.216) but still does not show any statistically significant results. However, smaller species are still abundant throughout the Jurassic. Estimated maximum body size subsequently decreases in the Jurassic, with the smaller species remaining constant. Maximum body size stabilised at a medium size (5-7m) in the Cretaceous, while the largest and smallest taxa are extinct by this stage. The range of body sizes was highest in the Triassic with the largest species (*Shonisaurus popularis*) having an estimated body length of 15m and the smallest species measuring only 1m, a difference of 14m. The range of body sizes is reduced in the Jurassic with the largest species (*Temnodontosaurus platyodon*) estimated to be 9m long and the smallest species (*Ichthyosaurus breviceps* & *I. conybeari*) measuring 1.5, a difference of 7.5m. The trend of reducing the range in estimated body size continues in the Cretaceous with the largest species (*Platypterygius australis*) measuring 7m and the smallest (*P. platydactylus*) measuring 5m. However, there are large gaps in the estimated maximum body size between taxa that could indicate that many taxa of intermediate size are missing from this analysis (particularly where the Cretaceous record is so incomplete) and the apparent trends are not an accurate representation of the changes in maximum body size in the Mesozoic.

There are some inconsistencies between the datasets for estimated body size and humerus length. In the Early Triassic, there is a relatively large gap in estimated maximum body length between small taxa such as *Parvinatator wapitiensis* and *Utatsusaurus hataii* and larger taxa such as *Cymbospondylus piscous*, *Thalattoarchon saurophagis* and *Cymbospondylus buchseri* (Fig. 6.9). However, the results for the humerus length are inconsistent with this pattern and show various sizes of humerus up to 140mm and then a large gap to the *Shonisaurus* outlier (Fig. 6.10). This can be partly explained as *T. saurophagis* and *Cymbospondylus piscosus* are not represented in the analysis of humerus length as no humerus has been reported for these species. Furthermore, more species for this time interval, namely *Xinminosaurus catcates*, *Besanosaurus leptorhynchus*, *Toretocnemus zitteli*, *Mixosaurus maotaiensis* and *M. solei* are represented in the humerus analysis providing the intermediates that are absent from the estimated body length analysis.

The results also show that humerus length tends to be markedly larger in the Jurassic compared to that of the Triassic, with the exception of the *Shonisaurus* outlier. However, the removal of this outlier from the analysis only slightly affects the results ($\alpha=0.3846$: $r^2=0.0579$: $y=-0.3846x+177.19$: $p(\text{uncorr})=0.1397$) and still shows no statistical significant results. This pattern is not observed when estimated body length is analysed. It is possible that this related to a change in swimming style from the ‘eel-like’ anguilliform swimming inferred in Early Triassic taxa to a ‘tuna-like’ thunniform swimming style inferred for species that survived across the Triassic-Jurassic boundary (Motani, 2005). The pectoral fins adapt with time to become rigid hydrofoils as swimming style changes. Another reason for this pattern could be sampling bias, with more taxa included from the Jurassic than the Triassic or Cretaceous. The 'Jurassic Coast', located on the south coast of England, and the Holzmaden 'Posidonia' Shales, located in Germany, are two of the best sites for preserving ichthyosaurs. Both of these are Lower Jurassic in age and the majority of ichthyosaurs used in the dataset come from these sites. Furthermore, these sites often preserve many complete or nearly completely articulated specimens, as exceptional preservation is common in the Posidonia shales. Due to a lack of comparable localities in the Triassic and Cretaceous, it is possible that species with larger humeri are not preserved, or that the humeri are absent from known species. It is currently not known why there is a size discrepancy between humerus length in the Jurassic compared to the Triassic and Cretaceous.

Many authors have investigated the Triassic-Jurassic extinction event, where 50% of known species became extinct (Hautmann *et al*., 2008; Thorne *et al*., 2011; Kelley *et al*., 2014). However, none of the observed patterns in ichthyosaur body size appear to reflect the extinction event. Kelley *et al*. (2014) examined the effects of sea level change (using the composition of seawater strontium [^{87}Sr/^{86}Sr] as a proxy) on the diversity of marine reptiles. The results indicate that the proportional abundance of marine reptiles adapted towards a diet of shelled prey rose during times of rapid sea level rise and fell during sea level fall. However, marine reptiles adapted to open water, such as ichthyosaurs were less affected (Kelley *et al*., 2014). Thorne *et al*. (2011) also examined the affect on the Triassic-Jurassic boundary on ichthyosaur diversity. They used a data matrix for ichthyosaurs consisting of 38 genera and 105 characters. Thorne *et al*. (2011) concluded that ichthyosaurs passed through an evolutionary bottleneck at, or close to, the Triassic-Jurassic boundary which reduced their diversity to as few as three or four lineages. Diversity bounced back in the Jurassic to some extent but disparity remained 10% of pre-extinction levels (Thorne *et al*., 2011). However, the evolutionary bottleneck and reduction in disparity is not reflected in the results of the body size evolution analyses presented here.

The patterns observed in ichthyosaur body size evolution could be related to competition with other organisms. Ichthyosaurs appear in the fossil record as fully adapted to marine life and quickly evolve. This rapid evolution would have allowed ichthyosaurs to fill many niches such as large top predators feeding on large organisms (large body size), to pursuit predators feeding on smaller prey items such as fish and squid (intermediate and small body size). The research by Thorne *et al*. (2011) indicates that ichthyosaurs go through an evolutionary bottleneck at the Triassic-Jurassic boundary, which reduces the amount of variation (standard deviation) in body sizes and lineages. This allows other organisms to occupy niches previously occupied by ichthyosaurs. The Plesiosauria (Reptilia: Sauropterygia) evolve from more basal sauropterygians just before the Triassic-Jurassic boundary (O'Keefe, 2002). Within the Plesiosauria, the long-necked, small headed plesiosaurs and the short-necked large headed pliosaurs evolved. The predatory pliosaurs were among the largest creatures to inhabit the oceans, some reaching lengths greater than 15 m. Fossils from this subclade are known from the Lower Jurassic (Hettangian) to the Upper Cretaceous (Turonian) (Smith & Dyke, 2008) and likely replaced ichthyosaurs as the top predators, resulting in ichthyosaurs not increasing their proportions to those seen in the Triassic. Furthermore, the smaller plesiosaurs also evolved to fill the smaller, pursuit predator sized, niches, increasing the competition with ichthyosaurs. In addition, the sharks (Lamniformes) began to radiate in the Jurassic (Kriwet *et al*., 2009) and into the Cretaceous providing further competition with ichthyosaurs resulting in the further reduction in variety of sizes. The competition caused by the evolution and radiation of these and other organisms, could have resulted in the steady decline of the ichthyosaurs from the Jurassic onwards. This decline is reflected in the decrease of body size and the decrease in the variety of sizes as lineages became extinct.

Bardet (1992) stated that the extinction of ichthyosaurs is poorly understood, both in terms of time and causation. Ichthyosaur extinction may be tentatively correlated with the Cenomanian-Turonian boundary events. During this interval, biological factors such as a break in the food chain attested by severe extinction in marine invertebrates, especially belemnites, may have led to the extinction of ichthyosaurs. It is possible that a decline in readily available prey items is also linked to the reduction in ichthyosaur body size (Bardet, 1992). However, this is unlikely as ichthyosaurs probably had a varied diet and did not rely solely on one source of food (Massare, 1987). Lingham-Soliar (2003) suggested a biological explanation for the extinction of ichthyosaurs and refuted the suggestion of Bardet (1992). Lingham-Soliar (2003) examined the feeding strategy of modern day dolphins and whales and compared that with ichthyosaurs. He concluded that the reduction in abundance of one prey item would not be sufficient to result in the extinction of ichthyosaurs. Lingham-Soliar (2003) observed that monopoly on fast, thunniform swimming by ichthyosaurs has gone by the end of the Jurassic with the emergence of fast-swimming hydrodynamic fishes placing new energetic costs on ichthyosaurs as predators and prey (Lingham-Soliar, 2003). This new competition, combined with competition from other organisms, would lead to the reduction in size observed in ichthyosaurs from the Jurassic onwards until their extinction in the Cretaceous.

6.5.2: Limitations of the data

Due to the nature of the fossil record, it was not always possible to collect the data required so some species or specimens are not represented in the analyses. These missing data could represent particularly large or small examples as well as intermediate-sized forms. The inclusion of these missing data would enable a more comprehensive view of ichthyosaur body size evolution.

Estimated body length and humerus length were used as these are the most frequent measurements in the dataset. However, body length estimates are based on a number of different observations. For well-known and well-represented genera, such as *Stenopterygius* and *Ichthyosaurus*, it seems that the estimated maximum body length has been gained by rounding up the largest known body length to the nearest half metre but these authors provide no reasoning for this. Due to the large numbers of specimens, many incomplete, the maximum body size estimation is likely to be inaccurate. However, not all genera and species are so well represented; some are represented by single or fragmentary specimens. *Shonisaurus popularis* is a species with a maximum estimated body length of 15m (Camp, 1980) but there are no complete specimens. The maximum body size estimate is based on a composite skeleton constructed from skeletal fragments. In order to produce the composite skeleton, the numbers of presacral and caudal vertebrae were estimated. Kosch (1990) initially disagreed with the reconstruction of Camp (1980) saying that (i) the skull was too large; (ii) the dorsal length was too short creating a ‘pot-bellied’ appearance; (iii) the tail was too long; and (iv) the limbs are too long. The reconstruction by Kosch (1990) provides a body size estimation of 13.6m (Fig. 6.11). Despite this new reconstruction, Kosch (1990) also observes that there are larger elements known for *S. popularis* that indicate a maximum body size of 15m is possible (Fig. 6.9). In other cases, species where isolated elements are known have been compared to better-known genera with similarly-sized elements. A justification for the maximum body size estimate has not been provided for several species such as *Platypterygius ochevi* Arkhangelsky *et al*., 2008 and *Chaohusaurus* *geishanensis* Young & Dong, 1972. *Thalattoarchon saurophagis* Fröbisch *et al*., 2012 is a newly erected genus and species with an estimated body length of >8.6m based on a partial skeleton comprising part of the skull and axial skeleton, part of the pelvic girdle and parts of the hind fins. The preserved skull length is around 930mm but the entire rostrum is missing. The authors assume that the preserved skull length is similar but slightly shorter than the postnarial skull length. They use *Cymbospondylus petrinus* as a comparison, which has a total skull length of 1170mm with a postnarial skull length of ~530mm (57% of the same in *T. saurophagis*). Therefore, a conservative estimate for skull length in *T. saurophagis* is 1200mm. Furthermore, Fröbisch *et*. *al*. (2012) estimate postcranial length of 6745mm based on an estimation of the partial prepared presacral and caudal vertebrae. Therefore, the estimated length of the skull, presacral and caudal vertebrae measure 8600mm in total, which the authors consider a conservative estimate.

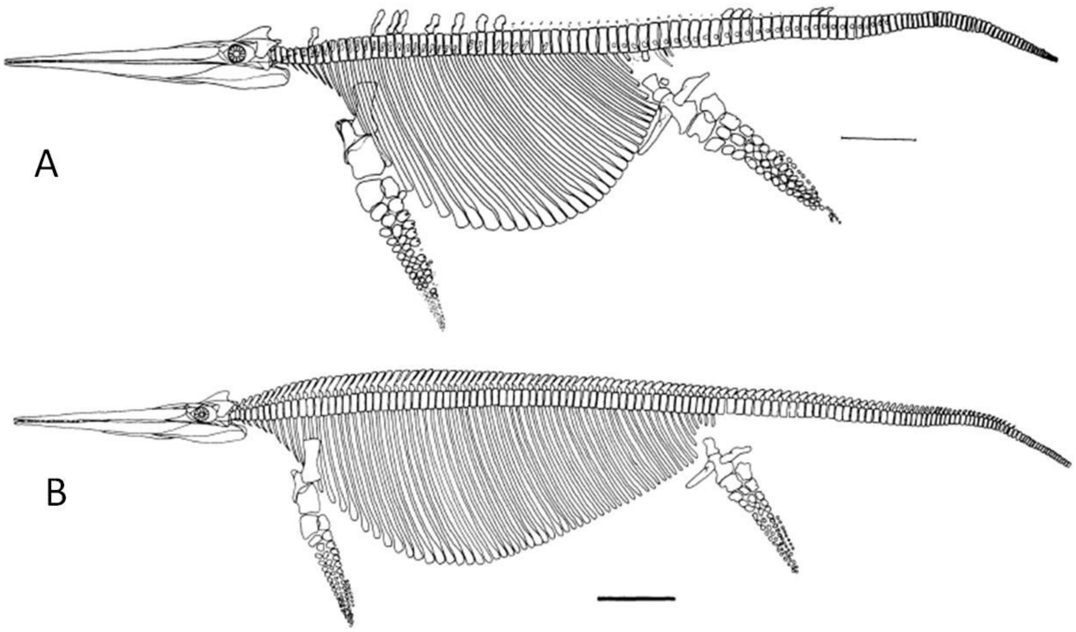


Fig. 6.11: Skeletal reconstructions of *Shonisaurus popularis* by (A) Camp, 1980 and (B) Kosch, 1990. Scale bar measures 1m.

There is little uncertainty in estimated maximum body sizes where many well preserved specimens are known. However, there is a large amount of uncertainty in genera and species where this is not the case. The length of the rostrum in ichthyosaurs can vary dramatically between species. *I. breviceps* and *L. mooeri* both have unusually short snouts while *Eurhinosaurus longirostris* and *Excalibosaurus costini* both show remarkable elongate rostra with extreme overbites. As total body length is defined as the distance between the tip of the snout and the tip of the tail measured along the vertebral column (McGowan & Motani, 2003), differences in rostrum length can greatly increase or decrease the body length. Furthermore, numbers of vertebrae can vary in ichthyosaurs, particularly caudal vertebrae (McGowan & Motani, 2003). This study also shows that the numbers of post-flexural vertebrae can vary with ontogeny (Chapter 4). The changing numbers of vertebrae in both the presacral and caudal regions can affect the measure of body length. Therefore, maximum body length cannot be determined definitively in species where complete specimens are unknown. Consequently, a large amount of uncertainty is involved in the estimation of maximum body size and results of analyses using these measurements should be regarded with caution.

There are also taxonomic issues due to disagreements over which species are valid in some genera, as exemplified by *Stenopterygius* (Fig. 6.12). There are four published schemes for the taxonomy of *Stenopterygius* (Maxwell, 2012). The first was established by von Huene (1922, 1931, 1939, 1949) who recognised 11 species (*S. quadriscissus*; *S. S. megacephalus*; *S. megalorhinus*; *S. crassicostatus*; *S. hauffianus*; *S. banzensis*; *S. uniter*; *S. eos*; *S. incessa*; *S. longifrons*; *S. incessa*) as well as three subspecies. These species were erected based on body proportions and vertebral counts as well as on features of the pectoral girdle. McGowan (1979) and McGowan and Motani (2003) attempted to consolidate the work of von Huene and considered eight species of *Stenopterygius* valid (*S. quadriscissus*; *S. hauffianus*; *S. megacephalus*; *S. macrophasma*; *S. cuneiceps*; *S. longipes*; *S. megalorhinus*; *S. longifrons*). Godefroit (1994) further reduced the numbers of species and considered only three taxa valid (*S. quadriscissus*; *S. longifrons*; *S. hauffianus*) based on bivariate analysis of allometric growth. Maisch (1998) also analysed the taxonomy of *Stenopterygius* and considered four species valid (*S. quadriscissus*; *S. hauffianus*; *S. megalorhinus*; *S. longifrons*) based on analysis of perfectly preserved specimens (Maxwell, 2012). The conclusions of McGowan & Motani (2003) were followed in this analysis as it is the most comprehensive study of the genus. However, the use of McGowan & Motani (2003) adds uncertainty to the results as some of the taxa they consider valid are not considered valid by Maisch (1998). This could mean that taxa are represented that did not really exist. This would result in species of *Stenopterygius* being over represented. In contrast, von Huene considered more taxa valid than McGowan and Motani (2003). This would mean that *Stenopterygius* is under represented in the analyses above. The addition or subtraction of species would affect the n value in the analyses which could affect the correlations. However, it is unlikely that any alteration to the correlation would result in statistically significant results as all the species of *Stenopterygius* have a total body length of 3–3.5m, and plot as a small to intermediate size. Therefore, the addition or subtraction of species that would result from using a different interpretation of the taxonomy would not alter the overall results of this study. Furthermore, taxonomic issues such as this are not common in ichthyosaurs and, as such, taxonomic issues are unlikely to affect the overall results.

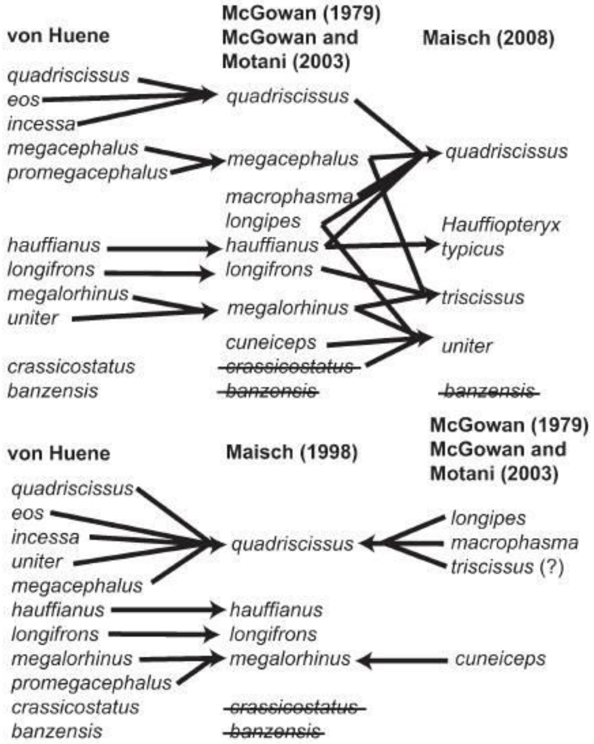


Fig. 6.12: Diagram illustrating the taxonomic disagreements between authors with regard to the species of *Stenopterygius*. Names considered *nomen dubia* are indicated by a strike-through, those followed by a question mark are considered species inquirenda (doubtful) by the author in question (Maxwell, 2012).

As a result of the issues highlighted above, of a possible 32 genera and 60 species from the Mesozoic (based on McGowan & Motani, 2003 and Thorne *et*. *al*., 2011), only 40 species (53%) are represented in the humerus length analysis. It is possible that a species not represented plots between *Shonisaurus popularis* and *Mixosaurus* species where there is currently a size gap of 404mm. Furthermore, the large proportion of missing species could contain particularly large or small species as well as intermediate species. Therefore, as an insufficient proportion of known ichthyosaurian taxa are represented, the results should be viewed with caution. Future work could focus on addressing some of these issues which in turn could produce more reliable results.

6.5.3: Are there trends in body size evolution in ichthyosaurs?

The results of the analyses presented herein show that large and small taxa coexisted almost from the earliest occurrence of ichthyosaurs in the fossil record. This is unlike the trends of body size evolution observed in other organisms (section 6.2), which tend to show a change in body size with time. Furthermore, there are large gaps in size between the represented ichthyosaur taxa. Gaps like these are not observed in other groups. One possible explanation is that ichthyosaurs are not sufficiently represented in the fossil record. However, it could be that ichthyosaurs had specific size categories that best suited a particular mode of life or habitat for that particular time and there were no intermediate sized species not represented in the fossil record. The discovery of new species would demonstrate whether this is the case or not.

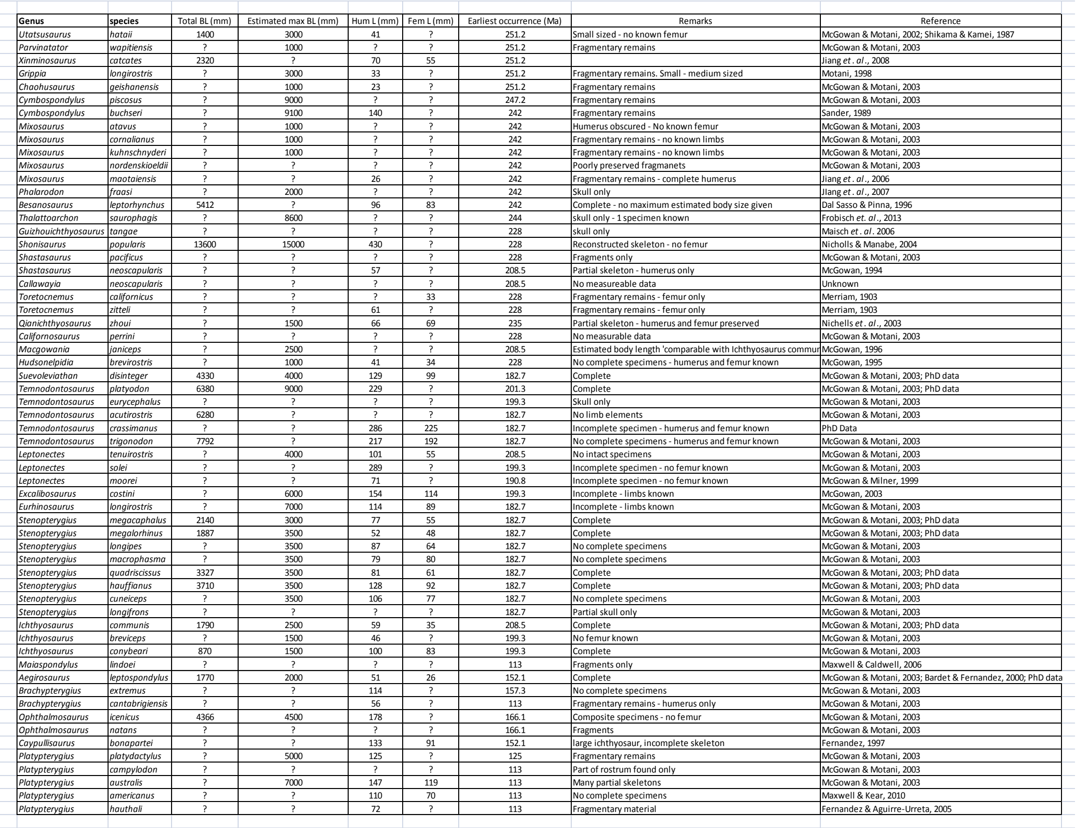
Furthermore, there are problems with the estimates for maximum body size, as different authors have used several different measurements (section 6.5.2) (Table 6.2). Therefore, the results should be regarded as preliminary as many taxa could be smaller or larger than shown in the analysis.

In a major review of ichthyosaurs, Motani (2005) stated that no clear pattern occurs in ichthyosaur body size evolution due to the co-existence of large and small ichthyosaurian species from the Early Triassic onward. However, no detailed analyses of ichthyosaur body size evolution have previously been conducted and these statements were likely based on general observations of size. The new results presented herein confirm his conclusions that small and large taxa coexisted since the earliest occurrence of ichthyosaurs and that there are no statistically significant trends, despite the apparent decrease in maximum body size evolution. This conclusion is further supported by the results of the linear regressions that also indicate no relationship between size and geological time. The largest recorded estimated body size decreases from the *Shonisaurus* outlier in the Triassic at 15m to *Temnodontosaurus platyodon* in the Jurassic at 9m and further decreases to *Platypterygius australis* at 7m (Fig. 6.9). Humerus length shows a similar, but slightly more pronounced, trend of decreasing size with time (Fig. 6.10). Such graphical trends have previously been used by other authors to (e.g., Fig. 6.1; Fig. 6.7). However, when appropriate tests are applied to the data in Figs 6.9 and 6.10, no significant relationship is found between ichthyosaur body size and geological time. This could be an accurate result, showing that ichthyosaur body size did not change and there is no relationship, or it could be due to the issues discussed above resulting in inadequate data that does not enable any reliable conclusions to be drawn. Only 53% of species are represented in the most complete humerus length dataset and the estimated maximum body length may be incorrect for a number of taxa. Focussing on new discoveries and better-preserved taxa may result in sufficient data for this analysis in the future. Due to lack of adequate data and the uncertainties discussed above, these results cannot be considered definitive.

6.6: CONCLUSIONS

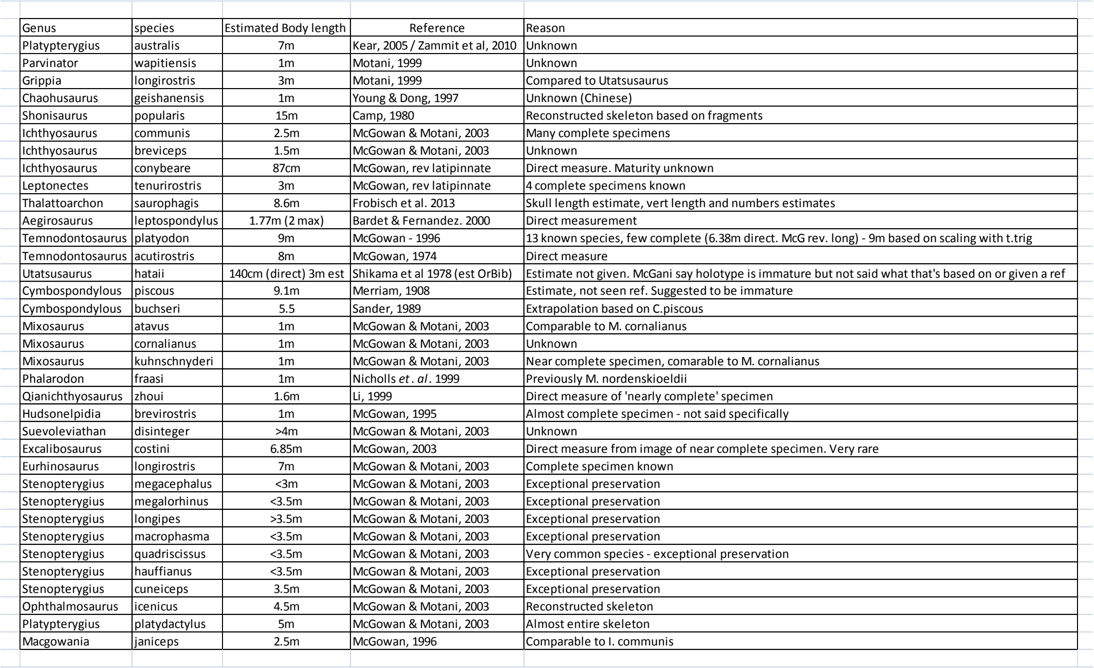
There are no statistically significant relationships shown in either estimated maximum body length or humerus length. However, the pattern shows that maximum body size increases to a peak in the Middle Triassic and then steadily decreases into the Cretaceous while minimum body size appears to increase steadily throughout the Mesozoic. However, it is possible that ichthyosaur maximum body size did not change throughout the Mesozoic, but it is not possible to demonstrate this definitively because many taxa cannot be represented in the analyses. Humerus length is known for the largest number of taxa (n=40) but this only represents 53% of the total number of ichthyosaur species (n=34 for estimated body length). Data on other proxies for body size were collected but these are even less well representative of ichthyosaur species (n=24 for femoral length; n=16 for body length). Furthermore, disagreements between authors with regards to taxonomy, potential errors in estimation of body length and different approaches to body length estimation all add to uncertainty in interpretation. Possible changes in minimum body size were not examined as adult specimens are required and the time at which an individual becomes mature is not currently known in ichthyosaurs.

Therefore, it is currently not possible to show whether ichthyosaurs increased or decreased in maximum body size during the Mesozoic. It is also not possible to say with confidence that maximum ichthyosaur body size did not change throughout the Mesozoic.



Genus	**species**	Total BL (mm)	Estimated max BL (mm)	Hum L (mm)	Fem L (mm)	Earliest occurrence (Ma)	Remarks	Reference
Utatsusaurus	*hataii*	1400	3000	41	?	251.2	Small sized - no known femur	McGowan & Motani, 2002; Shikama & Kamei, 1987
Parvinatator	*wapitiensis*	?	1000	?	?	251.2	Fragmentary remains	McGowan & Motani, 2003
Xinminosaurus	*catcates*	2320	?	70	55	251.2		Jiang *et . al*., 2008
Grippia	*longirostris*	?	3000	33	?	251.2	Fragmentary remains. Small - medium sized	Motani, 1998
Chaohusaurus	*geishanensis*	?	1000	23	?	251.2	Fragmentary remains	McGowan & Motani, 2003
Cymbospondylus	*piscosus*	?	9000	?	?	247.2	Fragmentary remains	McGowan & Motani, 2003
Cymbospondylus	*buchseri*	?	9100	140	?	242	Fragmentary remains	Sander, 1989
Mixosaurus	*atavus*	?	1000	?	?	242	Humerus obscured - No known femur	McGowan & Motani, 2003
Mixosaurus	*cornalianus*	?	1000	?	?	242	Fragmentary remains - no known limbs	McGowan & Motani, 2003
Mixosaurus	*kuhnschnyderi*	?	1000	?	?	242	Fragmentary remains - no known limbs	McGowan & Motani, 2003
Mixosaurus	*nordenskioeldii*	?	?	?	?	242	Poorly preserved fragmanets	McGowan & Motani, 2003
Mixosaurus	*maotaiensis*	?	?	26	?	242	Fragmentary remains - complete humerus	Jiang *et . al*., 2006
Phalarodon	*fraasi*	?	2000	?	?	242	Skull only	JIang *et . al*., 2007
Besanosaurus	*leptorhynchus*	5412	?	96	83	242	Complete - no maximum estimated body size given	Dal Sasso & Pinna, 1996
Thalattoarchon	*saurophagis*	?	8600	?	?	244	skull only - 1 specimen known	Frobisch *et. al*., 2013
Guizhouichthyosaurus	*tangae*	?	?	?	?	228	skull only	Maisch *et . al*. 2006
Shonisaurus	*popularis*	13600	15000	430	?	228	Reconstructed skeleton - no femur	Nicholls & Manabe, 2004
Shastasaurus	*pacificus*	?	?	?	?	228	Fragments only	McGowan & Motani, 2003
Shastasaurus	*neoscapularis*	?	?	57	?	208.5	Partial skeleton - humerus only	McGowan, 1994
Callawayia	*neoscapularis*	?	?	?	?	208.5	No measureable data	Unknown
Toretocnemus	*californicus*	?	?	?	33	228	Fragmentary remains - femur only	Merriam, 1903
Toretocnemus	*zitteli*	?	?	61	?	228	Fragmentary remains - femur only	Merriam, 1903
Qianichthyosaurus	*zhoui*	?	1500	66	69	235	Partial skeleton - humerus and femur preserved	Nichells *et . al*., 2003
Californosaurus	*perrini*	?	?	?	?	228	No measurable data	McGowan & Motani, 2003
Macgowania	*janiceps*	?	2500	?	?	208.5	Estimated body length 'comparable with Ichthyosaurus commur	McGowan, 1996
Hudsonelpidia	*brevirostris*	?	1000	41	34	228	No complete specimens - humerus and femur known	McGowan, 1995
Suevoleviathan	*disinteger*	4330	4000	129	99	182.7	Complete	McGowan & Motani, 2003; PhD data
Temnodontosaurus	*platyodon*	6380	9000	229	?	201.3	Complete	McGowan & Motani, 2003; PhD data
Temnodontosaurus	*eurycephalus*	?	?	?	?	199.3	Skull only	McGowan & Motani, 2003
Temnodontosaurus	*acutirostris*	6280	?	?	?	182.7	No limb elements	McGowan & Motani, 2003
Temnodontosaurus	*crassimanus*	?	?	286	225	182.7	Incomplete specimen - humerus and femur known	PhD Data
Temnodontosaurus	*trigonodon*	7792	?	217	192	182.7	No complete specimens - humerus and femur known	McGowan & Motani, 2003
Leptonectes	*tenuirostris*	?	4000	101	55	208.5	No intact specimens	McGowan & Motani, 2003
Leptonectes	*solei*	?	?	289	?	199.3	Incomplete specimen - no femur known	McGowan & Motani, 2003
Leptonectes	*moorei*	?	?	71	?	190.8	Incomplete specimen - no femur known	McGowan & Milner, 1999
Excalibosaurus	*costini*	?	6000	154	114	199.3	Incomplete - limbs known	McGowan, 2003
Eurhinosaurus	*longirostris*	?	7000	114	89	182.7	Incomplete - limbs known	McGowan & Motani, 2003
Stenopterygius	*megacaphalus*	2140	3000	77	55	182.7	Complete	McGowan & Motani, 2003; PhD data
Stenopterygius	*megalorhinus*	1887	3500	52	48	182.7	Complete	McGowan & Motani, 2003; PhD data
Stenopterygius	*longipes*	?	3500	87	64	182.7	No complete specimens	McGowan & Motani, 2003
Stenopterygius	*macrophasma*	?	3500	79	80	182.7	No complete specimens	McGowan & Motani, 2003
Stenopterygius	*quadriscissus*	3327	3500	81	61	182.7	Complete	McGowan & Motani, 2003; PhD data
Stenopterygius	*hauffianus*	3710	3500	128	92	182.7	Complete	McGowan & Motani, 2003; PhD data
Stenopterygius	*cuneiceps*	?	3500	106	77	182.7	No complete specimens	McGowan & Motani, 2003
Stenopterygius	*longifrons*	?	?	?	?	182.7	Partial skull only	McGowan & Motani, 2003
Ichthyosaurus	*communis*	1790	2500	59	35	208.5	Complete	McGowan & Motani, 2003; PhD data
Ichthyosaurus	*breviceps*	?	1500	46	?	199.3	No femur known	McGowan & Motani, 2003
Ichthyosaurus	*conybeari*	870	1500	100	83	199.3	Complete	McGowan & Motani, 2003
Maiaspondylus	*lindoei*	?	?	?	?	113	Fragments only	Maxwell & Caldwell, 2006
Aegirosaurus	*leptospondylus*	1770	2000	51	26	152.1	Complete	McGowan & Motani, 2003; Bardet & Fernandez, 2000; PhD data
Brachypterygius	*extremus*	?	?	114	?	157.3	No complete specimens	McGowan & Motani, 2003
Brachypterygius	*cantabrigiensis*	?	?	56	?	113	Fragmentary remains - humerus only	McGowan & Motani, 2003
Ophthalmosaurus	*icenicus*	4366	4500	178	?	166.1	Composite specimens - no femur	McGowan & Motani, 2003
Ophthalmosaurus	*natans*	?	?	?	?	166.1	Fragments	McGowan & Motani, 2003
Caypullisaurus	*bonapartei*	?	?	133	91	152.1	large ichthyosaur, incomplete skeleton	Fernandez, 1997
Platypterygius	*platydactylus*	?	5000	125	?	125	Fragmentary remains	McGowan & Motani, 2003
Platypterygius	*campylodon*	?	?	?	?	113	Part of rostrum found only	McGowan & Motani, 2003
Platypterygius	*australis*	?	7000	147	119	113	Many partial skeletons	McGowan & Motani, 2003
Platypterygius	*americanus*	?	?	110	70	113	No complete specimens	Maxwell & Kear, 2010
Platypterygius	*hauthali*	?	?	72	?	113	Fragmentary material	Fernandez & Aguirre-Urreta, 2005

Table 6.1: Data table used for the analyses listing all taxa. ? = measurements unavailable.



Genus	species	Estimated Body length	Reference	Reason
Platypterygius	australis	7m	Kear, 2005 / Zammit et al, 2010	Unknown
Parvinator	wapitiensis	1m	Motani, 1999	Unknown
Grippia	longirostris	3m	Motani, 1999	Compared to Utatsusaurus
Chaohusaurus	geishanensis	1m	Young & Dong, 1997	Unknown (Chinese)
Shonisaurus	popularis	15m	Camp, 1980	Reconstructed skeleton based on fragments
Ichthyosaurus	communis	2.5m	McGowan & Motani, 2003	Many complete specimens
Ichthyosaurus	breviceps	1.5m	McGowan & Motani, 2003	Unknown
Ichthyosaurus	conybeare	87cm	McGowan, rev latipinnate	Direct measure. Maturity unknown
Leptonectes	tenurirostris	3m	McGowan, rev latipinnate	4 complete specimens known
Thalattoarchon	saurophagis	8.6m	Frobisch et al. 2013	Skull length estimate, vert length and numbers estimates
Aegirosaurus	leptospondylus	1.77m (2 max)	Bardet & Fernandez. 2000	Direct measurement
Temnodontosaurus	platyodon	9m	McGowan - 1996	13 known species, few complete (6.38m direct. McG rev. long) - 9m based on scaling with t.trig
Temnodontosaurus	acutirostris	8m	McGowan, 1974	Direct measure
Utatsusaurus	hataii	140cm (direct) 3m est	Shikama et al 1978 (est OrBib)	Estimate not given. McGani say holotype is immature but not said what that's based on or given a ref
Cymbospondylous	piscous	9.1m	Merriam, 1908	Estimate, not seen ref. Suggested to be immature
Cymbospondylous	buchseri	5.5	Sander, 1989	Extrapolation based on C.piscous
Mixosaurus	atavus	1m	McGowan & Motani, 2003	Comparable to M. cornalianus
Mixosaurus	cornalianus	1m	McGowan & Motani, 2003	Unknown
Mixosaurus	kuhnschnyderi	1m	McGowan & Motani, 2003	Near complete specimen, comarable to M. cornalianus
Phalarodon	fraasi	1m	Nicholls *et . al*. 1999	Previously M. nordenskioeldii
Qianichthyosaurus	zhoui	1.6m	Li, 1999	Direct measure of 'nearly complete' specimen
Hudsonelpidia	brevirostris	1m	McGowan, 1995	Almost complete specimen - not said specifically
Suevoleviathan	disinteger	>4m	McGowan & Motani, 2003	Unknown
Excalibosaurus	costini	6.85m	McGowan, 2003	Direct measure from image of near complete specimen. Very rare
Eurhinosaurus	longirostris	7m	McGowan & Motani, 2003	Complete specimen known
Stenopterygius	megacephalus	<3m	McGowan & Motani, 2003	Exceptional preservation
Stenopterygius	megalorhinus	<3.5m	McGowan & Motani, 2003	Exceptional preservation
Stenopterygius	longipes	>3.5m	McGowan & Motani, 2003	Exceptional preservation
Stenopterygius	macrophasma	<3.5m	McGowan & Motani, 2003	Exceptional preservation
Stenopterygius	quadriscissus	<3.5m	McGowan & Motani, 2003	Very common species - exceptional preservation
Stenopterygius	hauffianus	<3.5m	McGowan & Motani, 2003	Exceptional preservation
Stenopterygius	cuneiceps	3.5m	McGowan & Motani, 2003	Exceptional preservation
Ophthalmosaurus	icenicus	4.5m	McGowan & Motani, 2003	Reconstructed skeleton
Platypterygius	platydactylus	5m	McGowan & Motani, 2003	Almost entire skeleton
Macgowania	janiceps	2.5m	McGowan, 1996	Comparable to I. communis

Table 6.2: A list of the species with estimated body length with the references and the reason for the estimation where it is provided

7: DISCUSSION

7.1: GROWTH IN ICHTHYOSAURS

The growth of ichthyosaurs, summarised below, was interpreted using a variety of methods. In this chapter, the implications of these new results for ichthyosaur biology and ecology are considered, the uniqueness of ichthyosaurs is discussed, and the benefits and difficulties associated with these analyses are examined. The impact of preservation and collection biases in the ichthyosaur fossil record is evaluated and the data collected for the project are appraised critically.

7.1.1: Overview of ichthyosaur growth

Juvenile and neonate ichthyosaurs were small but had large skulls and eyes in comparison to their total body length (Chapter 3). Juveniles also had fewer post-flexural tail vertebrae than adults (Chapter 4). The skulls and eyes show negative allometry, becoming smaller compared to body length as an ichthyosaur matured. Growth became isometric at sexual maturity and no other features examined in this study changed with age (Chapter 3). However, males grew to larger body sizes than females, either due to a faster growth rate in males or a reduced growth rate in females during (Chapter 5). It would not be possible to distinguish between slower growth rates in females in general or due to pregnancy. As gender cannot be determined, with the exception of pregnancy, a comparison between pregnant and non-pregnant females is not currently possible. The point at which any given individual reached sexual maturity cannot currently be identified as growth quickly becomes isometric. Pregnancy is the only indication of sexual maturity in an individual specimen (Chapters 3 & 4). Gender cannot currently be determined using consistent growth-related criteria and pregnant females are the only individuals that can be sexed accurately (Chapter 5). Determining the pattern of body size evolution within Ichthyosauria suffers from many uncertainties, particularly relating to estimated body sizes and missing taxa. Although the analyses showed that body size does not increase or decrease through geological time, only 53% of known taxa were included. Therefore, it is currently not possible to accurately study ichthyosaur body size evolution. Small- and large-bodied taxa coexisted throughout the Mesozoic (Chapter 6).

7.1.2: Influence of body size on changing ichthyosaur behaviour

There is no evidence for extended parental care in ichthyosaurs, nor any indication that they fed their young, so it seems likely that neonates would have had to acquire prey soon after birth. Features that may relate to behaviour changes are discussed below.

The large eyes of ichthyosaurs allowed good vision in low light levels (Motani *et al*., 1999; Motani, 2005), which made deep diving for prey a possibility Avascular necrosis has been observed in bones of ichthyosaurs (Motani *et al*., 1999). This damage is often caused as a result of rapid change in depth and is indicative of 'the bends' and hence further supports deep diving behaviour in ichthyosaurs. However, this feature is not unique to ichthyosaurs but has also been documented in mosasaurs, sauropterygians and turtles from the Middle Jurassic to Late Cretaceous (Rothschild *et al*., 2012). This indicates that other groups were capable of deep diving but may not have had as acute vision at depth as ichthyosaurs. Furthermore, jaws needed to be large enough to grasp and hold onto prey, such as soft-bodied squid (Pollard, 1968). It seems likely that juvenile ichthyosaurs would have been able to hunt and provide food for themselves as they were born with relatively large heads, and jaws complete with erupted teeth, and large eyes to allow them to locate prey (Chapter 3).

Despite these advantages, juvenile ichthyosaurs could easily have been preyed upon by many larger reptiles, such as pliosaurs, crocodylians or larger ichthyosaurs, as well as sharks. Although stomach contents are known for some of these predators (Taylor *et* al., 1993; Shimada, 1997), ichthyosaur remains in stomach contents are rare. However, their small size would have allowed them to swim in shallower water and thus avoid larger predators that could become beached in the shallows. However, there is no evidence for this. The remains of an ichthyosaur had previously been reported as stomach contents in the body cavity of a plesiosaur (O'Keefe *et al*., 2009). However, the remains are those of an ichthyosaur embryo, which the authors conclude to be a voided embryo rather than a neonate. If this is the case, it is more likely that the embryo was ingested due to scavenging activity rather than predation (O'Keefe *et al*. 2009). The disadvantage (risk of predation) of small size would not have lasted long as studies of the bone histology in the long bones of ichthyosaurs show large amounts of highly vascularised fibrolamellar bone, which suggests high growth rates in all ichthyosaurs (Buffrénil & Mazin, 1990; Kolb *et al*., 2011; Houssaye *et al*., 2014).

Small size could have been a disadvantage to juvenile ichthyosaurs in other ways besides risk of predation. Their small stature might imply that their swimming capabilities may not have been equal to those of fully mature individuals. Juvenile muscles would have been smaller, meaning that swimming may not have been as fast or sustained for the same amount of time. Morphological and physiological changes through ontogeny have been shown to affect swimming capabilities in bottlenose dolphins, a mammalian niche equivalent (Noren *et al*., 2006). Video footage of three mother and calf pairs, two juveniles and one additional adult was used to collect data on mean and maximum swim speed (swim performance data) and stroke amplitude and tail beat frequency (swim effort). Swim performance was significantly lower in 0–1 month-old calves and only approached that of adults after 1 year. Size specific stroke amplitude was also smaller in younger specimens (0–3 months-old, 23-26% of body length) compared to more mature specimens (10+ months-old, 29-30%). Therefore, individuals aged 10-12 months have a greater swimming capability than those <10 months (Noren *et al*., 2006). Furthermore, lungs would have been smaller in juveniles and it is highly likely that they could not have remained submerged for the same amount of time as the larger adults. Research into changing diving capabilities with ontogeny has been conducted on Australian sea lions, a modern, semi-aquatic mammalian tetrapod (Fowler *et al*., 2006; Fowler *et al*., 2007). The results show that both the duration and depth of dives increased with age (Fig. 7.1).

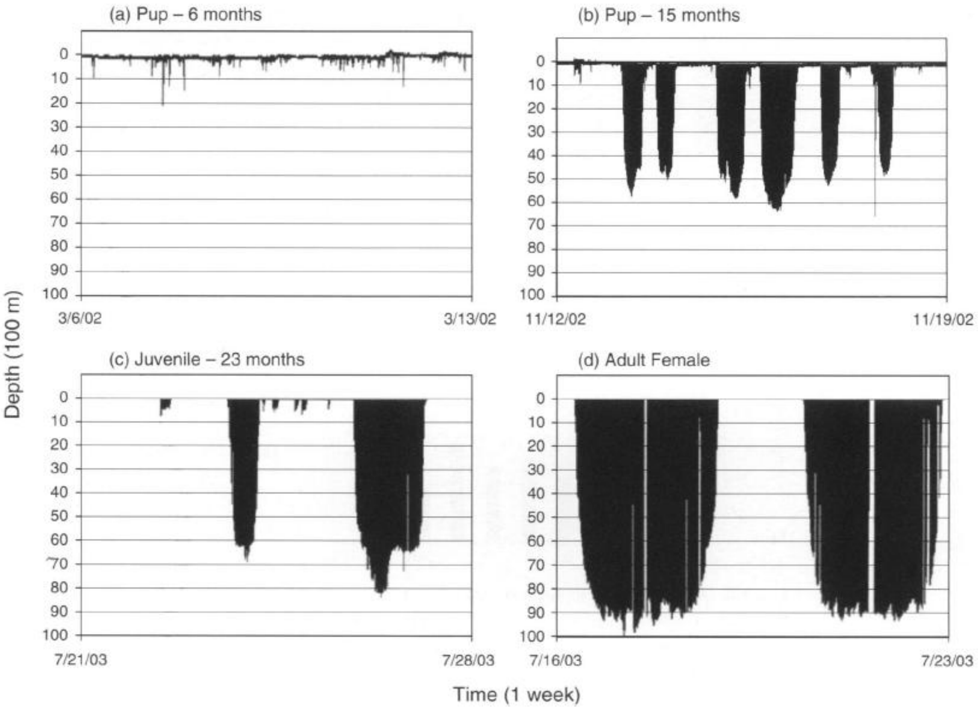


Fig. 7.1: Graphs showing increasing dive depth and duration with age in Australian sea lions: (a) 6 month old pup; (b) 15 month old pup; (c) 23 month old juvenile; (d) adult (Fowler *et al.*, 2006).

Similar studies have been conducted on aquatic and semi aquatic reptiles such as leatherback turtles (Salmon *et al.*, 2004) and marine iguanas (Bartholomew *et al.*, 1976). In both studies, both swimming and dive performance was shown to improve with increasing age. It is plausible that a similar pattern would be shown by a growing ichthyosaur.

For a deep diving organism, variation in dive depth could have affected prey preference through ontogeny. Although there is currently no evidence, it is plausible that neonate ichthyosaurs could have been born in shallow waters and supported or cared for by an adult (possibly the mother). Such behaviour is observed in modern whales (Martins *et al.*, 2001). However, there is a specimen of *Stenopterygius quadriscissus* that is preserved in the process of giving birth (Fig. 7.2). The specimen is preserved in very fine grained, dark coloured shale that is indicative of an anoxic, deep marine environment. This would indicate that the individual was giving birth in an open ocean environment, rather than in near-shore, shallow water. An alternative explanation is that the neonate ichthyosaur was forced out of the body, along the birth canal, by decompositional gases after death (McGowan, 1991; Motani, 2005) or the embryo was voided during death. If this was the case, the mother might have died during the act of giving birth, subsequently becoming bloated with decompositional gases and floating out to deeper water, only sinking with the release of the gas.

Fig. 7.2: Neonate ichthyosaur (Lower Jurassic), whose parent died during birth, preserved in a dark shale matrix (SMNS). Scale measures 100mm. Photo by Sam Bennett.

However, this second scenario seems unlikely. A floating carcass would be likely to attract scavengers, there is no evidence of scavenging (such as puncture wounds/tooth marks) and the skeletal remains are articulated. Consequently, it seems more likely that the specimen sank rapidly after death into an anoxic layer before scavengers had an opportunity to feed. This specimen neither proves nor disproves the hypothesis that ichthyosaurs gave birth in shallow, near shore environments. However, the fact that specimens are preserved in deep marine lithofacies shows that ichthyosaurs were capable of giving birth in open water environments, which undermines the shall water hypothesis. Further study into this is required to test these hypotheses.

Inferred male, sexually mature ichthyosaurs tended to be larger than sexually mature females (Chapter 5). Larger male size may have conferred an advantage in gaining a mate. If there were physical competition between males, such as fighting, a larger body size, and therefore greater body strength, would have been a benefit in beating smaller males. Ichthyosaurs had no body parts suited for weaponry, such as enlarged teeth or claws. Therefore, brute force, directly related to size and strength, would have provided an advantage assuming aggressive competition took place (Spitz, *et al*., 2002). Aggressive, intrasexual encounters have been inferred in bottlenose dolphins (Scott *et al*., 2005) after an analysis of tooth-rake marks (Fig. 7.3).

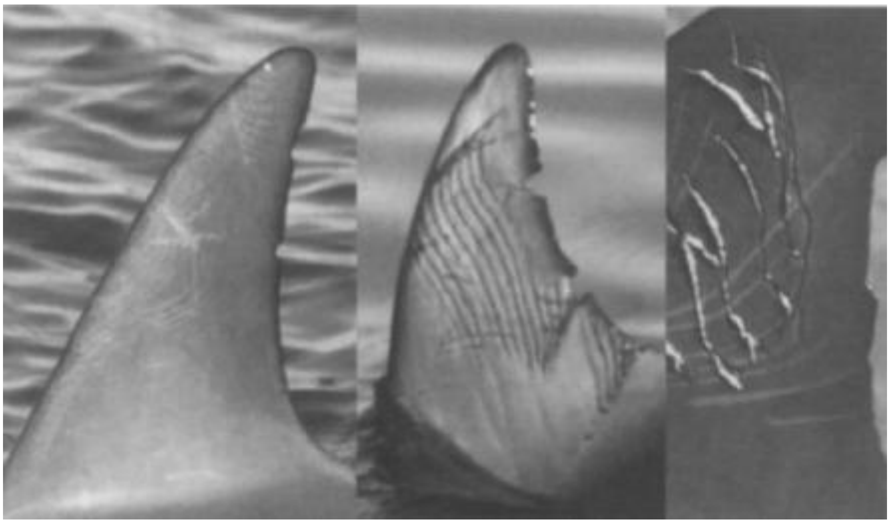


Fig. 7.3: Examples of tooth rake marks on bottlenose dolphins showing faint marks (left); obvious marks (middle); detail of fresh marks (right). From Scott *et al*. (2005). Scale not given

These bottlenose dolphins, in Shark Bay, Australia, have been studied since 1984 and the analysis is based on photo-identification of specific individuals. The tooth rake marks are an indirect measure of received conspecific aggression. Sexually mature males possess significantly more rake marks than mature females. This indicates aggression and competition between males.

However, females also have rake marks on their bodies, with cycling females (those becoming pregnant within 6 months of the photograph being taken) more likely to show fresh rake marks. This indicates male aggression towards females, possibly in order to coerce them into mating (Scott *et al*. 2005).

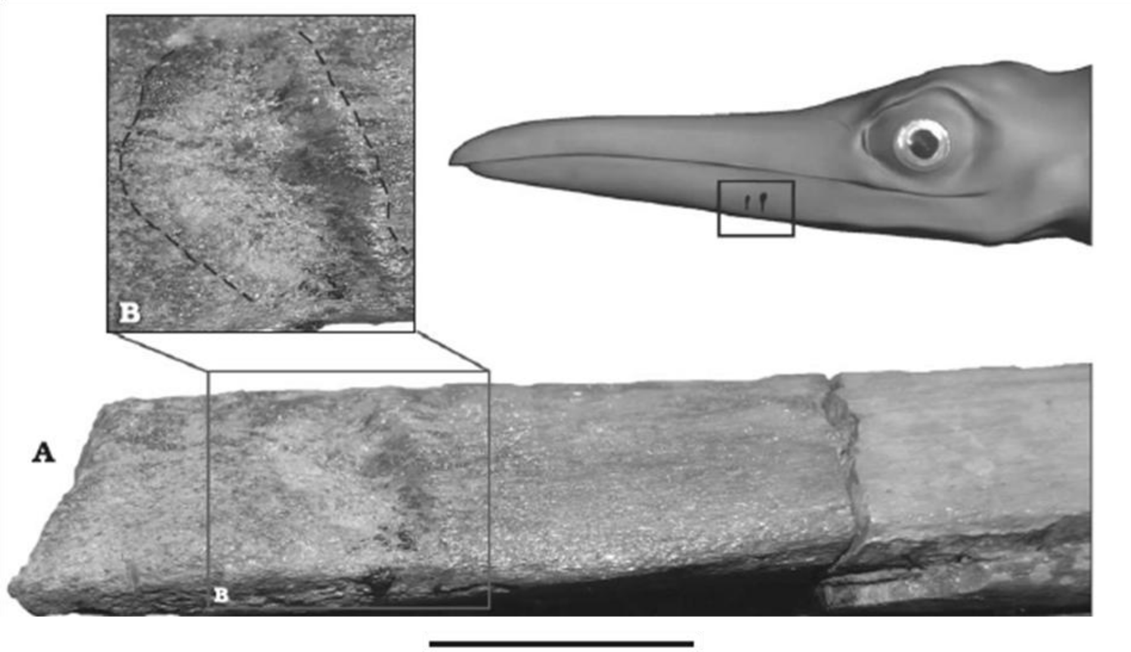


Fig. 7.4: *Platypterygius* with a wound on the jaw bone (A), detail of wound (B) and a reconstruction of the wound (top right). Scale bar measures 30mm. (From Zammit & Kear, 2011).

It is possible that ichthyosaurs exhibited the same or similar behaviour. However, the wounds reported in the study by Scott *et al*. (2005) are superficial and did not mark bone so it may not be possible to infer intraspecific aggression in ichthyosaurs using the same techniques, even where preservation is exceptional. Some ichthyosaurs do preserve soft parts and it is possible that rake marks might be preserved but none have been reported. Some ichthyosaurs do show scoring on the bone (Zammit & Kear, 2011). A large specimen of *Platypterygius* shows healed cuts and gouges on the lower jaw (Fig. 7.4) providing direct evidence of bite force trauma. However, it is impossible to say whether the wound was caused by an attack from a predator or intraspecific interaction (Zammit & Kear, 2011). It is unlikely that the bite mark was from a scavenger as the bone shows signs of healing, and therefore, the ichthyosaur was alive at the time of the wound.

Male aggression is also observed in humpback whales (Tyack & Whithead, 1982). During the breeding season males have enlarged testes and the females ovulate. Tyack & Whithead (1982) observed large groups of wintering humpback whales. They noted that males tended to gather around a central female and proceeded to fight for proximity to the female, presumably for a better chance of mating. Observed fighting behaviour included fluke thrashes, bubble streams and other physical contact that could result in bleeding wounds (Tyack & Whithead, 1982). Furthermore, the aggression is almost always associated with a female: no aggression was observed in single sex groups, which strongly suggests that this behaviour is linked with mating and competition for females.

In the examples outlined above, the larger body size in some male cetaceans (Connor *et al*., 1998) would provide an advantage in fighting off other males in order to gain access to a female as well as in coercing females to mate. It is possible that the larger body size of male ichthyosaurs was used in the same way but there is currently no direct evidence for this behaviour.

It is also possible that females chose larger males with which to mate. Large body size would indicate the strength and success of the individual. If ichthyosaurs were territorial, a larger body size may result in the ability to maintain a larger area of territory, which in turn could have provided a larger male access to a greater number of females. However, there is no current evidence to indicate whether or not males engaged in competition for mates with other males or whether or not ichthyosaurs were territorial. However, it not known if ichthyosaurs were territorial and there is currently no evidence for territorial behaviour in modern cetaceans (Connor *et al*., 1998). However, some crocodilians are territorial of feeding spots and nesting sites (Garrick & Lang, 1977). It is not currently known if ichthyosaurs were territorial or not.

7.1.3: Summary of the behavioural implications of ichthyosaur growth

The small size of neonate and juvenile ichthyosaurs implies that they might not have been able to swim as far, fast or deep as adults. However, bone histology suggests rapid growth so it is likely that this stage of development was short. Comparisons with extant niche equivalents suggest that swimming and diving capabilities would have been comparable to those of adults after approximately one year. The smaller size of neonates would have allowed them to swim in shallow waters that may have helped them to avoid larger predators while relatively large eyes and skulls (including jaws) would allow them to hunt adequately. Growth becomes isometric with sexual maturity but males reach greater body sizes than females. Larger male size is unlikely to have been related to territorial behaviour but might have been an advantage in competition with other males for a mate as well as aiding in coercion of females.

7.2: DISTINCTIVE CHARACTERISTICS OF ICHTHYOSAURS AND THEIR FOSSIL RECORD

Ichthyosaurs possess many unique features among reptiles, such as a lack of bone fusion and a fish-like body plan, which result in the lack of close modern reptilian niche equivalents. The implications of these unique features are discussed in this section. Furthermore, the positive and negative aspects of preservation quality and collection bias are evaluated.

7.2.1: Lack of Modern Reptilian Niche Equivalents

When studying any organism, particularly extinct ones, it is important to have other organisms, ideally closely related to the organism being studied, which can be used for comparison. The Extant Phylogenetic Bracket (EPB) approach is often used to infer features (typically soft tissue) that are absent in the fossil record (Witmer, 1995). This approach makes explicit references to at least the first two extant outgroups of the fossil taxon of interest, and uses these extant organisms to infer features absent from the fossil record. These comparisons can help create hypotheses by providing a model to test, such as for ontogeny or sexual dimorphism, as closely related organisms tend to grow and mature in similar ways.

Although there are many examples of extant niche equivalents for ichthyosaurs such as teleost fish, lamniforme sharksand odontocetid whales, there are no extant reptilian niche equivalents. It is likely that these other groups of organisms, as well as other forms of extinct marine reptiles, replaced the niches filled by ichthyosaurs during their decline and after they became extinct (see discussion in Chapter 6, section 6.5). If an extant, reptilian niche equivalent existed for ichthyosaurs, it would be possible to examine the skeletal features and dimensions at known stages of life (embryo, neonate, juvenile and adult). From there it would be possible to see if similar features and dimensions were observed in ichthyosaurs of varying sizes and use them to infer a relative age. The known gender of the extant equivalents could be used to determine any features relating to sexual dimorphism. These could then be searched for in ichthyosaurs in order to infer gender in individual specimens. Furthermore, it would be possible to examine the behaviour, capabilities and habitats in the living specimens of the niche equivalent in order to see how, if at all, these changed with age. Any features that relate to a particular behaviour or habitat could then be inferred in ichthyosaurs. However, the closest niche equivalents to ichthyosaurs are fish or cetaceans (mammals), which are not ideal comparisons. Fish have a different body plan to reptiles, they typically gain oxygen through gills and, therefore, do not need to surface to breath, they typically do not give birth to live young, and in some groups, the skeleton is cartilaginous (e.g. sharks) (Dean & Summers, 2006) making them unsuitable comparisons. Mammals are a more suitable comparison as they lack some of the disadvantages of fish as analogues as they possess lungs and must breathe at the surface and they give birth to live young. Despite this, they are still not ideal analogues as mammals grow in a different way to ichthyosaurs. The bones in mammals can fuse extensively, especially in the skull, which becomes a single unit and, in dolphins, there are no hind limbs. The morphology of the fluke is also different in mammals. The tail is positioned so that the flukes project laterally and swimming is achieved by dorsal-ventral tail movement. In ichthyosaurs, the flukes project dorsally and ventrally and swimming is achieved by lateral tail movements.

7.2.2: Skeletal anatomy and body plan

7.2.2.1 Body Plan

Ichthyosaurs are diapsids (Massare & Calloway, 1990; Motani *et al*., 1998; Motani, 2000), although their exact relationships are still debated. Consequently, it is difficult to identify close relatives for detailed comparisons of their behaviour and biology. In addition, they are unique among all extinct and extant reptiles in possessing a ‘fish-shaped’ body plan and are the most thoroughly modified marine diapsids and whales are the only other tetrapods that became so completely aquatic (Fig. 7.5), which contributes to the problems with niche equivalents. The tail developed into a semi-lunate shape and became the main form of propulsion. The front limbs are modified as paddles acting as hydrofoils, the hind limbs became vestigial, functionally uncoupled from the vertebral column and were not used for swimming. Most Mesozoic marine reptiles (such as plesiosaurs, pliosaurs and turtles) use their limbs for locomotion (Storrs, 1993). Others, such as pachypleurosaurs and crocodilians (including modern crocodiles and alligators), can use their tails to swim but also have functional limbs that allow them to walk along the bottom in aquatic habitats as well as on land (e.g. modern crocodilians).

The unique features outlined above, and the lack of close living relatives, means that no suitable reptilian niche equivalent can be established. Hence, trends in ontogeny and sexual dimorphism cannot be compared directly to those of closely related reptilian taxa (see section 7.2.2 for details). By comparison, the study of body size evolution in the group is independent of these limitations.

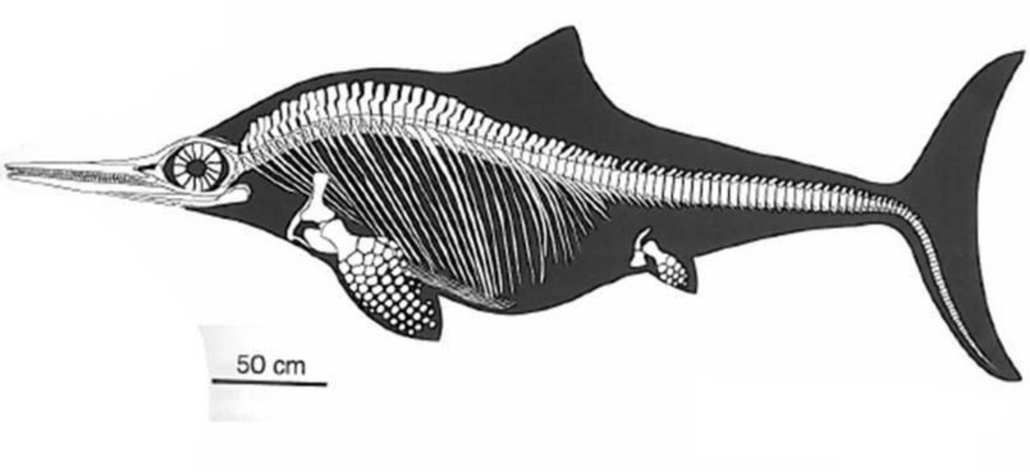


Fig. 7.5: Diagram illustrating the typical body plan of a Jurassic ichthyosaur where the white areas show the skeleton and the shaded areas show a soft body outline. Scale measures 50cm (from McGowan & Motani, 2003).

7.2.2.2 Bone fusion

One of the most remarkable features of ichthyosaur skeletal anatomy is the lack of fusion between bones (with the exception of the atlas-axis complex and the pubis and ischium: McGowan & Motani, 2003), which contributes to the issues with a modern niche equivalent. Fusion between bones is common among other Mesozoic marine reptiles and has been used to study ontogeny in plesiosaurs (Druckenmiller & Russell, 2006; Kear, 2007; Bardet *et al.*, 2008), pachypleurosaurs (Sander, 1989; Hugi & Scheyer, 2012) and crocodilians (Brochu, 1996; Brochu *et al.*, 2002; Buchy *et al.*, 2006) (see Chapter 3). In these taxa, the degree of bone fusion, and the order in which bones fuse, is well known. This can provide an estimate of relative age, independently of size in an individual specimen. The lack of fusion in ichthyosaurs has not prevented the study of ontogeny (Chapter 3 & 4) but it has reduced the number of ways in which it can be investigated. The relative ages, as estimated in the above taxa, cannot currently be identified with confidence in ichthyosaurs, with the exception of pregnant females, whose offspring provide direct and unequivocal evidence of sexual maturity. There are, however, only a limited number of pregnant specimens.

Conversely, the lack of bone fusion in ichthyosaurs does not affect analyses of sexual dimorphism (Chapter 5) or body size evolution (Chapter 6). For example, the atlas-axis complex and the pubis and ischium are fused from birth in some species ichthyosaurs and these characteristics are used as taxonomic features. For example, the pelvic girdle in *Stenopterygius* is bipartite but the ischium and pubis are fused to form a single element. By contrast, in *Temnodontosaurus,* the pubis and ischium are typically separate (McGowan & Motani, 2003).

It is currently not known why bone fusion in ichthyosaurs is rare. It is possible that the lack of fusion is the primitive state for diapsids but, unfortunately, no information seems to be available on bone fusion in Younginiformes, which are basal to ichthyosaurs in diapsid phylogeny (see Chapter 1, section 2.2.1). Alternatively, other marine reptiles (and many other terrestrial taxa) exhibit widespread fusion and the absence of bone fusion in ichthyosaurs might therefore represent a secondary loss of this ability. The main area of fusion in plesiosaurs is located in the pectoral girdle. Plesiosaurs use their paddles as the main form of locomotion and therefore, the muscles need strong attachments provided by the advancement of a rigid, fused pectoral girdle (Halstead, 1989). Ichthyosaurs did not possess the fused pectoral girdle meaning that they would not have had the strength to use the front limbs as a means of propulsion. However, this probably had no deleterious effect on ichthyosaurs as the tails were used for propulsion (Buchholtz, 2001; Motani, 2002).

The lack of bone fusion in ichthyosaurs may have conferred flexibility and manoeuvrability, which would be well-suited for a pursuit predator chasing fast, agile prey, although there is no evidence for this. Conversely, the absence of rigidity may have negatively affected swimming ability as a rigid can provide stronger muscle attachments, enabling stronger swimming. However, larger muscle mass and strong tendons could have compensated for a relative lack of skeletal rigidity, thus reducing the negative impact of un-fused bones. Many of the articular surfaces of the bones in the pectoral girdle of ichthyosaurs show a rugose texture. This indicates the presence of large amounts cartilage between the bones (McGowan & Motani, 2003). Large pressure associated with deep diving puts a lot of strain on an organism. This high pressure could compress the bones together and fully fused bones could break under the increased weight. However, the cartilage between the unfused bones in ichthyosaurs could have acted as a buffer, slowing compression as pressure increases but does not allow the bones to make contact. Therefore, this may have allowed the bones to compress without causing any damage, thus allowing deep diving.

7.2.2.3: Presacral vertebrae

The numbers of presacral vertebrae, particularly dorsal vertebrae, typically remain consistent in all genera and species within a particular group of vertebrates (Richardson *et al*., 1998). By contrast, the numbers of presacral vertebrae vary within and between species of ichthyosaurs (McGowan & Motani, 2003), which contributes to issues with a niche equivalent. However, as the hind limbs become vestigial, the pelvis and hind limbs become detached from the vertebral column, making the junction between the presacral vertebrae and caudal vertebrae difficult to recognise (Fig. 7.6). The lack of a clearly defined boundary between presacral and caudal vertebrae might explain the apparent variation in presacral vertebral counts within a species. However, the variation observed in numbers of presacral vertebrae is often more than one or two, and therefore, it is unlikely that the issue with the boundary adequately explains the variety and there is genuine plasticity in this feature.

The results of the ontogenetic analysis showed no significant change in the numbers of presacral vertebrae present during growth. It is possible that the uncertainty in the numbers of presacral vertebrae prevents an accurate ontogenetic analysis of this region of the spine, and any ontogenetic signal in presacral numbers may be overlooked as result.

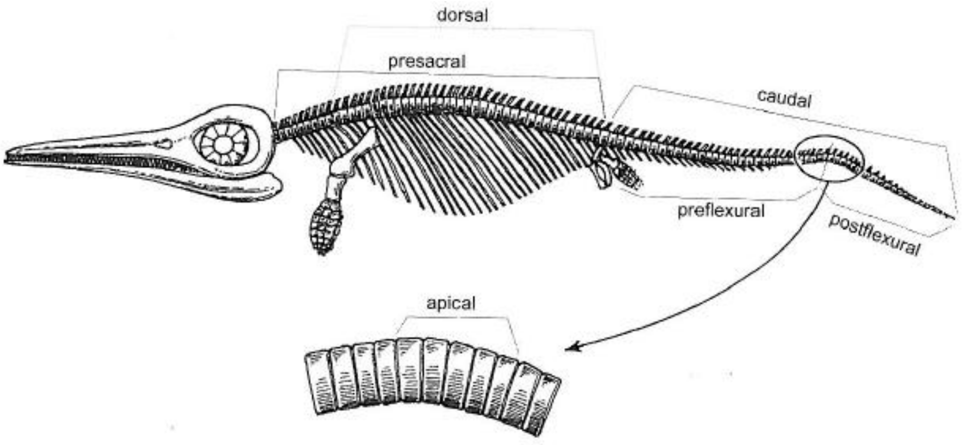


Fig. 7.6: A typical ichthyosaur body plan illustrating the regions of the vertebral column (McGowan & Motani, 2003).

7.2.3: Preservation quality

Ichthyosaurs are known from all over the world on the basis of numerous specimens (Motani, 2005). However, preservation quality can vary greatly between localities and this has affected the work in this thesis in a number of ways. Ichthyosaur specimens are often found missing the tip of the snout and the tip of the tail (approximately 50% in

Ichthyosaurus).

Fig. 7.7: A specimen of *Stenopterygius* showing that, even in exceptional preservation, there is displacement and loss of several distal caudal vertebrae highlighted in the red circle (SMNS: 54026). Scale measures 10cm. Photo by Sam Bennett.

The tip of the snout is typically thin and fragile and is therefore easily broken. The vertebrae at the end of the tail are very small and light and therefore are easily moved by taphonomic processes (van Loon, 2013) (Fig. 7.7). Parts of the skeleton are often absent which means that measurements cannot be obtained (Appendix 1). Preservational problems such as these limit the number of specimens available for use in palaeobiological analyses.

Despite a fragmented skull and the loss and disarticulation of the distal caudal vertebrae (Fig. 7.7), the majority of this *Stenopterygius* skeleton is preserved. This is not the case for all ichthyosaurs, however, and some species have been erected on fragments or partial skeletons meaning, for example, that total body lengths are unknown or based on poorly supported estimates (see Chapter 6, Table 1). Although the low numbers of complete did impact the studies of ontogeny and sexual dimorphism presented herein, it was still possible to extract statistically significant results from the specimens available. However, a lack of suitable specimens meant that ichthyosaur diversity was not fully represented in the body size evolution study with only 53% of known taxa included in the analysis. Therefore, it is currently not possible to show whether ichthyosaurs increased or decreased in maximum body size during the Mesozoic. It is also not possible to say with confidence that maximum ichthyosaur body size did not change throughout the Mesozoic (see Chapter 6).

7.2.4: Preservation and collection bias

Preservation biases can occur in the fossil record where certain geographic regions or certain ages tend to have a larger number of better-preserved specimens or have been better-sampled than others. There is certainly a preservation bias in relation to studies of ichthyosaur evolution and biology. Two of the best locations for ichthyosaur remains in the world are the Posidonia shale, Holzmaden, Germany (hereafter referred to as the Holzmaden shales) and the Jurassic Coast, Dorset, England. The Lower Lias consists of the Blue Lias, the Black Ven Mudstone member, the Stonebarrow Marl member (also known as the Belemnite Marls) and the Seatown Marl member. Both of these locations are Lower to Middle Jurassic in age. Furthermore, each of these locations has been excavated for >200 years. The Holzmaden shales have been excavated since the end of the sixteenth century (Selden & Nudds, 2012) while the first ichthyosaur was found along the Jurassic Coast in the late nineteenth century (Home, 1814). These areas, particularly the Holzmaden shales, show exceptional preservation with many complete, fully articulated specimens known.

Fig. 7.8: Exceptional preservation of a specimen of *Stenopterygius* (SMNS: 56631) from the Holzmaden Shales with the soft body outline still visible. Scale measures 10cm. Photo by Sam Bennett.

In some cases, soft part preservation is known and ichthyosaur body outlines, including the dorsal fin, can be seen. All specimens observed in this study had been expertly prepared and no additional preparation work was required. By comparison, there are no similar sites for Triassic or Cretaceous ichthyosaurs and, therefore, taxa of these ages are not as well known or as well represented. Motani (1999) states that *Mixosaurus cornalianus* is the only Triassic species for which complete specimens are known. Therefore, there is a clear preservation bias in favour of Lower Jurassic specimens and taxa.

This preservation bias has been an advantage for the studies of ichthyosaur ontogeny and sexual dimorphism presented herein, as many Jurassic specimens, the majority of which are complete, were available for the analysis. As with preservation quality (section 7.2.3), the bias has had a severe, negative affect the analysis of body size evolution.

It is also possible that there is a collection bias within the areas where many specimens are known. Many museums and publications focus on specimens that differ from the majority already known for a taxon. This could include specimens that are remarkably large, pregnant, caught in the act of giving birth, or that have extensive soft part preservation. However, all good specimens should be collected and made available for study. The Jurassic Coast in England is a popular tourist area and many tourists find and remove fragmentary ichthyosaur specimens from along the coast. By contrast, professional collectors and museums have tended to preferentially select largely complete specimens. This means that smaller items, such as isolated humeri, could be lost to science. It could also mean that a large, almost complete specimen could have small parts missing due to collection over a long interval of exposure resulting in a potential loss of data. However, unlike the quarries in the Holzmaden shales, it would be impossible for all Jurassic Coast specimens to be collected because material is easily lost through marine erosion. It is possible that such a collection bias affected the studies of ontogeny presented here (Chapter 3 and 4) as smaller specimens may have been under-collected in favour of larger specimens. Additional specimens of all sizes would provide a more comprehensive understanding of growth in ichthyosaurs. Conversely, studies into sexual dimorphism would have benefitted from such a large-specimen collection bias. Large specimens are necessary for this work as inferred sexual maturity is required for inclusion in the analysis. Furthermore, pregnant specimens are essential for the study of sexual dimorphism and collection biases for unusual material would tend to increase the numbers of pregnant specimens available for study. Analyses of body size evolution are also likely to have been affected by a collection bias. A preference for larger specimens would increase the likelihood of collecting data on maximum body size, for example. However, as the point at which a specimen becomes sexually mature cannot be identified with confidence, no attempt was made to study changes in minimum body size through time. The addition of smaller specimens could make this study possible if the point of sexual maturity could be identified.

7.2.5: Ichthyosaur taxonomy

Errors have previously been made where juveniles of one species have been misidentified as separate species (McGowan, 1995). One aim of this thesis was to identify features that may have resulted in similar errors in other ichthyosaurs thus contributing to improving ichthyosaur taxonomy. However, this has not proven possible as the only ontogenetic (and sexually dimorphic) features identified are based on relative sizes of the skeleton that, on their own, are not sufficient for taxonomic identification. Furthermore, the genus with a largest amount of taxonomic uncertainty is *Stenopterygius*. Four authors, each consider different species valid, one as many as eleven and another as low as three (see Chapter 6, section 6.5.2) However, all species of *Stenopterygius* have a similar estimated body size. It is therefore, unlikely that any of the features identified in this study could be used to address taxonomic uncertainties.

7.3: COMMENTARY ON METHODS

This section will discuss the approach to data collection and analysis adopted in this thesis. The suitability of data from different parts of the body will be considered, as well as areas of anatomy that may have been overlooked. The methods used to analyse ontogeny, sexual dimorphism and body size evolution will be evaluated with comments on any changes that could have been made with hindsight.

7.3.1: Statistical approaches

Various statistical tests were used to analyse anatomical changes through ontogeny, sexual dimorphism and body size evolution in ichthyosaurs. Bivariate and multivariate methods were used to explore the data, increasing the reliability of the results compared to using only a single approach. Furthermore, Bootstrap tests and Pearson’s ‘R’ tests were used where applicable to assess the statistical significance of the results. Principal Components Analysis (PCA) and Principal Coordinate Analysis (PCO) were initially used as exploratory methods in order to establish regions of allometric growth in ontogeny (Chapters 3 and 4). These regions were then studied in more detail. Reduced Major Axis Regression (RMA) combined with Pearson’s ‘R’ and Bootstrap tests were used on all measurements against body length to further check for specific areas of allometric growth as well as providing a

95% confidence interval to assess statistical significance. RMA was selected as any errors in the measurements would be present in both axes. A Mann-Whitney test was initially used to test whether there were two distinct groups of specimens in the sample (i.e. pregnant and non-pregnant) and discriminant analysis was used to test for sexual dimorphism (Chapter 5). In order to correct for taxonomic differences and reasonably infer sexual maturity, only specimens larger than the smallest pregnant *Stenopterygius* specimen were included in the analysis of sexual dimorphism. Furthermore, size corrected data was used in order to establish whether any of the results were affected by species differences rather than size per se. Ordinary Least Squared analysis (OLS) was used to test for any potential relationship between body size and geological time. These approaches were applied to the majority of the body regions identified in the skeleton reducing the chance that features of ontogeny were missed and therefore increasing the reliability of the results.

7.3.2: Data collection

Data for this project were gathered in one of two ways; by length measurements or by counting repeated elements. Data were obtained mainly for the skull and limbs (humerus/femur and manus) as well as total body length, which was measured from the tip of the snout, along the spine, to the tip of the tail. These measurements cover the majority of the skeleton. They were selected as they have displayed changes in ontogeny and sexually dimorphic differences in other organisms (Chapters 3, 4 and 5).

A large dataset was required in order to study growth in ichthyosaurs.Consequently, the Lower Jurassic was selected as it contains the largest number of specimens (see section 7.2.4) and museums with a large number of specimens were selected for data collection in the UK (see Chapter 2, section 2.2.1) in order to collect the most data in the least amount of time. Furthermore, one museum (Staatliches Museum für Naturkunde Stuttgart, Germany) was selected due to large numbers of exceptionally preserved specimens including complete or almost complete skeletons, soft body preservation and pregnant females. However, not all of the specimens in these collections were available for study as many (mostly *I. communis*) were on public display in the NHMUK and inaccessible. Measurements could not be taken through the glass sashes covering these specimens, nor could accurate photographs be taken, lowering the number of specimens in this study. If these specimens could have been included (as well as those from many other museums in the UK and elsewhere that could not be visited during the course of this study), the greater numbers may have made it viable to conduct studies into ontogeny and sexual dimorphism on the genus *Ichthyosaurus* alone.

Data from single elements can be obtained from partial and disarticulated specimens as well as from isolated elements. However, measurements based on composite body parts (e.g. skull and limbs) cannot be obtained in disarticulated specimens. If the skull bones are moved then several measurements (skull length, jaw length, snout length, premaxillary length, prenarial length, orbital diameter) cannot be obtained. Furthermore, small elements, such as distal phalanges or the anterior-most post flexural vertebrae are easily lost through taphonomic processes resulting in the loss of data. The tip of the snout is typically a slender and fragile part of the skull and is often lacking resulting in a loss of data for that specimen (Fig. 7.9). The numbers of specimens included in analyses involving total body length are lower still as the lack of data on total body length meant that this feature could not be used in the analysis of body size evolution and estimated body size was used (as well as humerus length as a proxy for body size) instead. In some cases, partial skeletons, and particularly isolated elements could not be identified to genus level and, as a result, could not be included in the analysis.

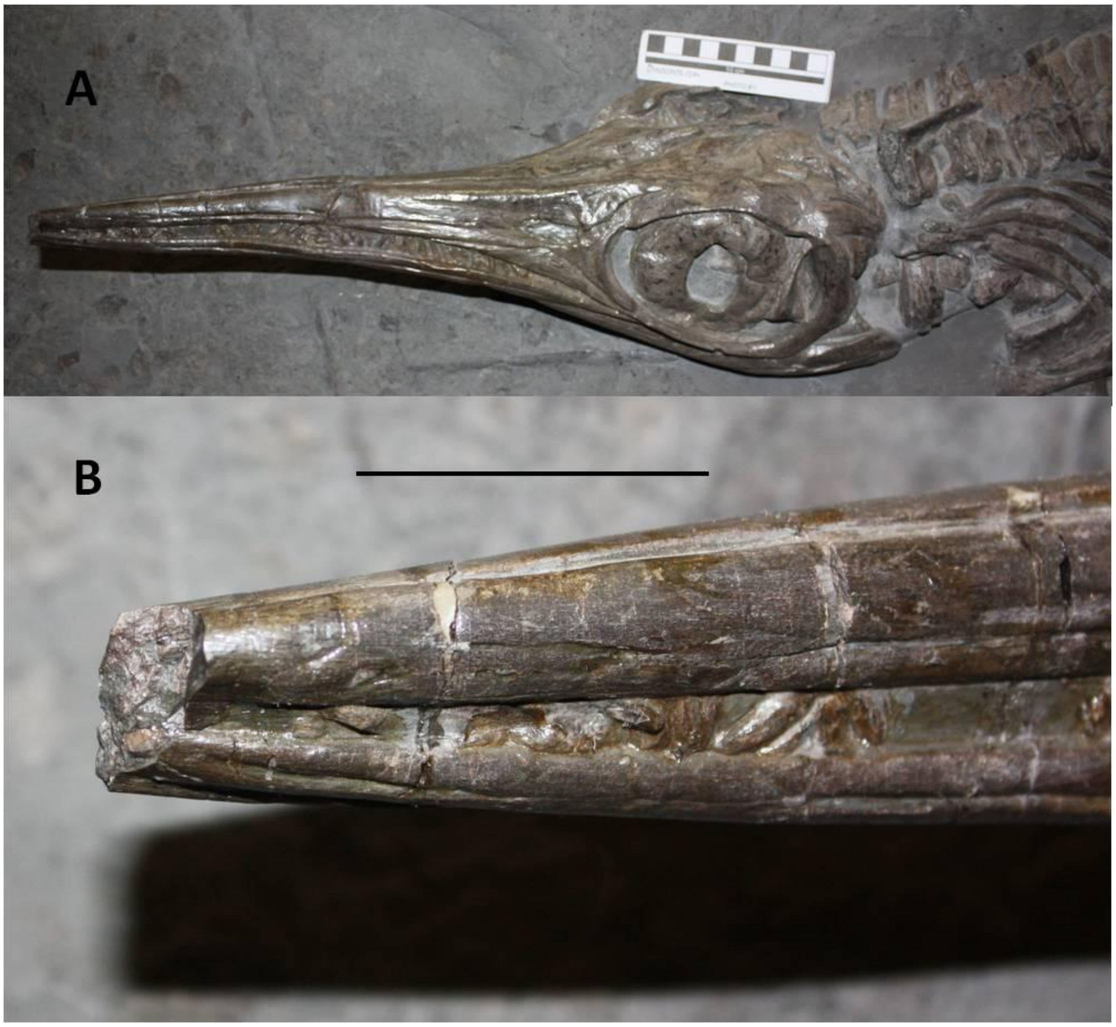


Fig. 7.9: A specimen of *Stenopterygius* (SMNS: 51133) lacking the tip of the snout resulting in a loss of data. (A) The skull. Scale measures 10cm. (B) Broken tip in detail. Scale measures 4cm. Photos by Sam Bennett

The pectoral girdle shows changes during ontogeny in other organisms (Chapter 3). However, these elements were not examined in this study. It is possible that some ontogenetic features of ichthyosaurs were overlooked due to this omission. However, Johnson (1977) examined features of the pectoral girdle in a study of ontogeny in *Stenopterygius* and concluded that there was no ontogenetic change in this region. However, Johnson (1977) does not specify which aspects of the pectoral girdle were examined and his study was confined to a single genus, whereas it is possible other taxa do exhibit some ontogenetic changes in this region.

In this study, the measurements gathered from the skull were all orientated in an anterior-posterior direction with none in a dorso-ventral direction. Consequently, some ontogenetic or sexually dimorphic features may have been overlooked and this is considered under future work (Section 7.5)

7.4: WAS GROWTH THE SAME IN ALL ICHTHYOSAURS?

The dataset used for the investigation into ichthyosaur ontogeny and sexual dimorphism consists of specimens from the Lower Jurassic. It is possible that growth was different in basal, Triassic species and in derived Cretaceous species. If this was the case, then the results cannot simply be extrapolated to all ichthyosaurs. However, histology in the long bones of ichthyosaurs shows large amounts of highly vascularised fibrolamellar bone, which suggests high growth rates in ichthyosaurs from the Middle Triassic (Kolb *et al*., 2011; Houssaye *et al*., 2014) and the Lower to Middle Jurassic (Buffrénil & Mazin, 1990), implying that ichthyosaurs from these intervals grew in a similar manner. However, bone growth rates for Lower Triassic and Cretaceous taxa are currently unknown. Morphometric analyses of Lower Triassic and Cretaceous growth series are needed to demonstrate categorically whether or not ichthyosaur growth remained the same throughout the Mesozoic. However, due to the lack of complete specimens from these time periods, such an analysis is not currently possible.

7.5: FUTURE WORK

The priority of future work would be to increase the sample size for all species of ichthyosaur. A particular focus would be to collect data on Triassic and Cretaceous growth series. A growth series of humeri from the genus *Mixosaurus* (Middle Triassic) has been analysed (Kolb *et al*., 2011; see chapter 1, section 2.2.2). However, a growth series of complete or nearly complete specimens is still unknown. The majority of the species known from the Triassic and Cretaceous are fragmentary with no complete specimens or growth series preserved and it is therefore not currently possible to conduct a similar study on ichthyosaur ontogeny or sexual dimorphism for the Triassic or Cretaceous.

It would be possible to increase the sample by visiting more collections and collecting data on specimens not included in this study. For this study, the Lower Jurassic was selected, as this time period has the largest number of accessible specimens preserved. Use of the Stuttgart collections was also appropriate due to the large numbers of specimens, exceptional quality of preservation and a comparatively large number of pregnant specimens. Some museums, that only house one or two specimens, were not visited due to prioritising museums with a larger number of specimens. Museums such as the National Museum of Ireland, Dublin were considered but the specimens are covered with a black 'tar-like' substance (D. Lomax, pers. comm.) meaning the junctions between bones cannot be identified, reducing the amount of the collectable data. Therefore, this museum was not visited. Visiting and collecting data from the museums that only contain one or two specimens is possible and this would increase the number of Lower Jurassic specimens. However, due to the very fragmentary nature of the fossil record of ichthyosaurs in the Triassic and Cretaceous, it would be harder to obtain any new suitable specimens. In this study, data on Triassic and Cretaceous taxa was gathered from the literature and it is likely that the most known suitable specimens have been published already. The discovery of new specimens (such as are being currently found in China: Li, 1999) is required to increase the sample size rather than visiting additional museums.

Currently, only 53% of the known species of ichthyosaurs could be included in the analysis of body size evolution and the majority of the species absent were from the Triassic and Cretaceous. In order to correct for this, new specimens would have to be discovered and described. Furthermore, if more specimens were discovered, it would be possible to investigate sexual dimorphism in these species. Currently a few pregnant specimens are known from the Triassic (Brinkman, 1996; Sal Sasso & Pinna, 1996) but only embryos the Cretaceous (Maxwell & Caldwell, 2003). This would test whether other ichthyosaurs display the same features of sexual dimorphism as *Stenopterygius*.

A larger number of specimens could allow opportunity for other approaches to be used in the examination of ichthyosaurs, such as landmark and semi-land mark analysis, if enough specimens were preserved in the same orientation. Shape changes could be studied in finer detail and ontogenetic or sexually dimorphic features that have been overlooked in this study might be recognised. Furthermore, CT scanning, as a method of data collection could provide new and valuable insights into ichthyosaur growth and sexual dimorphism, particularly in the region of the skull. Many individual elements in the skull overlap and extend laterally a relatively long way. A CT scan would be able to show the extent of the bones that are not visible at the surface and observe if they change with relative age or between pregnant and non-pregnant specimens.

Studies on the palaeo-facies in which ichthyosaurs are preserved, particularly where pregnant females and inferred neonates and juveniles are found, could provide insights into the hypotheses of a shallow-water nursery for ichthyosaurs. However, scavenging and predation are more common in shallow waters. This would likely break up specimens resulting in disarticulation and isolated elements in the fossil record. Scavenging and predation could also completely remove a specimen from the fossil record. Furthermore, detailed analysis of the lithostratigraphy where many specimens are preserved could help indicate if ichthyosaurs lived in family groups. However, such a study could prove problematic as a group of specimens would have to be preserved on the same horizon in order for a family group to be preserved and it is not always possible to show this. Furthermore, in areas with a slow sedimentation rate, animals that appear to have been preserved on the same horizon could have been deposited at a very different time.

8: CONCLUSIONS

Growth in ichthyosaurs was analysed in a number of ways throughout this project and the conclusions of this study are outlined below.

There are ontogenetic features in ichthyosaurs that could be used to distinguish between neonate, juvenile and adult (sexually mature) specimens. The relative size of the skull and orbit is larger in younger individuals and growth becomes isometric at sexual maturity in Lower Jurassic species. This quantitative study confirms previous comments made in the literature. Furthermore, the post flexural tail vertebrae increase in number with age. This new discovery could be used to help identify the relative age of an individual specimen. These ontogenetic changes have been observed in Lower Jurassic specimens but it is possible that growth was different in Triassic or Cretaceous species. Due to the low numbers of well-preserved specimens in the Triassic and Cretaceous, it is currently not possible to study ontogenetic changes in taxa of these stratigraphic ages.

The point at which sexual maturity is reached cannot be identified in an individual as growth rapidly becomes isometric. Therefore, there is no method of differentiating between a large juvenile and a small, sexually mature individual. With the exception of changing numbers of post-flexural tail vertebrae, no features of the post cranial skeleton exhibited any change during ontogeny in either the relative size of individual elements, relative size of composite body parts or number of repeated elements.

Sexual dimorphism is present in ichthyosaurs but only in the form of size, where non-pregnant specimens tend to be larger than pregnant females. The paddle manus (length of longest digit and manus width) and humerus (length and width of the humerus) showed no differences between pregnant females and non-pregnant specimens. Owing to low specimen numbers, the analysis had to be undertaken at generic level on the single genus *Stenopterygius* and therefore interspecific variation might have influenced the results. It is possible that sexually dimorphic features are expressed in other ichthyosaur genera. In order to study sexual dimorphism, a relatively large number of pregnant specimens are required. Due to issues with preservation it is currently not possible to study sexual dimorphism in Triassic or Cretaceous ichthyosaurs. However, it would be possible to study sexual dimorphism in *Ichthyosaurus* if access was provided to specimens behind glass that were inaccessible during this study. Specimens from museum collections in the UK not visited during this study (due to containing only one or two specimens) could also be included in a subsequent analysis.

Body size, analysed using estimated body length or humerus length (as a proxy for body length), shows no statistically significant trends through the Mesozoic. Estimated maximum body size increases to a peak in the Middle Triassic and then decreases. Minimum body size increases from the Triassic to the Cretaceous. These variations in body size could be related to varying extent of competition from other marine reptiles and fish. However, due to the nature of the fossil record, estimated body length and humerus length were often unobtainable resulting in only 53% of known species being represented in the analysis. Because of this issue, particularly for the Triassic and Cretaceous, it is currently not possible to adequately examine body size evolution in ichthyosaurs.

A suitable focus for future work would be to gather additional data on another taxon in order to compare growth to that of *Stenopterygius*. A suitable genus would be *Ichthyosaurus* as it is well represented in the fossil record and pregnant specimens are known. Furthermore, finding and describing more complete specimens of Triassic and Cretaceous taxa would be beneficial, particularly for understanding body size evolution.

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