

**A revision of *Temnodontosaurus crassimanus* (Reptilia: Ichthyosauria) from
the Lower Jurassic (Toarcian) of Whitby, Yorkshire, UK**

**A thesis submitted to The University of Manchester for the degree of Master of
Philosophy (MPhil) in the Faculty of Science and Engineering**

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ABSTRACT

The University of Manchester

Emily J. Swaby

The Degree of Master of Philosophy (MPhil)

A revision of *Temnodontosaurus crassimanus* (Reptilia: Ichthyosauria) from the Lower Jurassic (Toarcian) of Whitby, Yorkshire, UK

2019

Temnodontosaurus is known from the Lower Jurassic (Hettangian – Toarcian) of England, Germany, France and Belgium and is the largest Jurassic ichthyosaur known from complete remains, with the total body length of the largest *Temnodontosaurus* exceeding 12 m. Six different species are presently identified: *Temnodontosaurus platyodon* (Conybeare, 1822), *T. trigonodon* (Theodori, 1843), *T. crassimanus* (Blake, 1876), *T. eurycephalus* McGowan 1974a, *T. acutirostris* (Owen, 1840), and *T. azerguensis* Martin et al. 2012. In the UK, Lower Jurassic ichthyosaurs have been collected extensively from many localities, primarily in Lyme Regis and Charmouth, Dorset; Street and Strawberry Bank, Somerset; and Whitby, North Yorkshire. The Yorkshire coast is of historic interest in being one of the earliest British localities to be exploited for fossil marine reptiles, and has produced many well-preserved specimens of plesiosaurs, ichthyosaurs and marine crocodilians. During the 19th century, the Yorkshire coast was extensively quarried for the manufacture of alum, which yielded many specimens of marine reptiles during its operation, including a large, partially-complete, three-dimensionally preserved specimen (YORYM 497) – the holotype of *Temnodontosaurus crassimanus*. While the holotype still remains on display at the Yorkshire Museum, it has remained largely understudied and the validity of the species has long been questioned. Through re-examination of YORYM 497, the study highlighted several morphological features of the postcranial skeleton and determined that *T. crassimanus* differs sufficiently from other species of *Temnodontosaurus*, specifically *T. trigonodon*, in possessing several distinct characteristics. These defining characters include a large, robust humerus that is proximodistally longer than the scapula (scapula length vs humerus length ratio: ~ 0.68); forefins which are significantly longer but less than twice the length of the hindfin (forefin length vs hindfin length ratio: ~ 1.51); and notching of the anterior facet of at least five leading edge elements (digit II) of both the fore- and hindfins. Several additional specimens, previously tentatively assigned to *T. crassimanus*, were located and examined, but none could confidently be assigned to the species. Furthermore, the species was incorporated into a phylogenetic analysis, and results confirm the temnodontosaurid affinities and close relationship with *T. trigonodon*. To understand further the relationship of *T. crassimanus* within Ichthyopterygia, a thorough taxonomic revision of the genus *Temnodontosaurus* and the associated species is greatly required, but this is beyond the scope of the present study. Additionally, this study further highlights the need for a complete re-examination of all the Yorkshire Lias ichthyosaur material, in order to understand better the variety and abundance of marine reptiles from the coastline during the Toarcian. This study has helped to lay the foundations for this future research to be undertaken.

DECLARATION

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

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Dedications

This research is dedicated to my family, including my parents (Graham and Kim Swaby), nan (Betty Ellis), sister (Charlotte Swaby), soon-to-be brother-in-law (Joseph Hodgetts), newly arrived niece (Olivia Grace Hodgetts), boyfriend (Jacob Drury), the Drury's (Ian, Ruth and Daniel); and good friends (Cariad Williams, Megan Jones and Ryan Heath) for their continued encouragement over the past year. Without your support, none of my success would be possible – I hope to continue making you all proud.

Institutional abbreviations (in alphabetical order): **CAMSM**, Sedgwick Museum, Cambridge University, UK; **MANCH**, Manchester Museum, UK; **NHUK**, The Natural History Museum, London, UK; **PB**, Petrefaktensammlung, Banz, Germany; **SMNS**, Staatliches Museum für Naturkunde (Stuttgart State Museum of Natural History), Stuttgart, Germany; **WHITM**, Whitby Museum, UK; **YORYM**, Yorkshire Museum, UK.

1. ACKNOWLEDGEMENTS

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2. INTRODUCTION

Ichthyosaurs were a highly successful group of superficially dolphin-like marine reptiles of the Mesozoic, with an abundant and well-studied fossil record (Maisch and Matzke, 2000; McGowan and Motani, 2003; Cleary et al., 2015; Ji et al., 2016). Spanning from the late Early Triassic to the early Late Cretaceous, these reptiles were fundamental components of Mesozoic marine ecosystems, and were successful major predators (McGowan and Motani, 2003; Motani, 2009; Lomax et al., 2018). Their diversity and variance peaked during the Triassic and Jurassic, when ichthyosaurs ranged in length from < 1 m to possibly more than 25 m, and varied in morphology from long and slender, to deep-bodied (Thorne et al., 2011; Lomax et al., 2018). These tetrapods evolved a distinctive limb structure specifically adapted for marine life, in which their fore and hind fins were used to steer and balance, and their tails to swim (Massare, 1988; Motani, 1999). They had particularly large eyes that allowed them to search for prey at significant depths (Motani et al., 1999). Several ichthyosaur genera have been found with preserved stomach contents reflecting the ichthyosaurs' last meal, including many specimens from the Lower Jurassic strata of Lyme Regis, Dorset; Street, Somerset; Whitby, Yorkshire (UK) and Holzmaden, Germany (Pollard, 1968; Dick et al., 2016). Gastric contents most commonly include fish scales and small cephalopod hooklets, signifying their preferred source of food (Pollard, 1968; Massare, 1987; Lomax, 2010; Valente et al., 2010; Dick et al., 2016). Furthermore, although unusual among reptiles, viviparity (live birth) is well documented in ichthyosaurs, with the remains of embryos preserved in the body cavities of many specimens of *Stenopterygius* discovered from the Toarcian of Holzmaden, southern Germany (Figure 1) (Maisch and Matzke, 2000). Other viviparous specimens have been found elsewhere in the world, as reviewed by Boyd and Lomax (2018). Additional similarities between ichthyosaurs and modern cetaceans were highlighted through the study of preserved soft tissue layers in an exceptionally preserved specimen of the Early Jurassic ichthyosaur *Stenopterygius* (Lindgren et al., 2018). Evidence of a fatty layer beneath the skin demonstrated that *Stenopterygius* possessed blubber and provides further confirmation that ichthyosaurs were able to maintain elevated body temperatures and were extremely active swimmers (Bernard et al., 2010; Motani, 2010; Lindgren et al., 2018).

Ichthyopterygia is the large group (superorder) that includes basal ichthyosaurs such as the Early Triassic *Chaohusaurus* and *Utatsusaurus* and all later members of the order Ichthyosauria (Ji et al., 2016). The name 'ichthyosaur' is applied to all of these members. Ichthyosaurs are widely distributed among various international localities and are particularly well represented from many Lower Jurassic localities in the UK. The study of ichthyosaurs has an extensive history and they have been known to the scientific community for over 200 years (McGowan and Motani, 2003; Evans, 2010). Lyme Regis is often regarded as the historical birthplace of ichthyosaurs, on account of one of the greatest fossil collectors, Mary Anning (1799 – 1847) (Torrens, 1995). During the 19th century, the late Georgian and early Victorian palaeontologist contributed many important specimens to the scientific community, including the first ichthyosaurs and plesiosaurs, in addition to the first pterosaur found outside Germany (Torrens, 1995). In 1811-12, Mary, together with her brother Joseph, discovered the first

ichthyosaur brought to the attention of science, consisting of a well-preserved skull and an incomplete partial postcranial skeleton composed of a small number of cervical and dorsal vertebrae. Although initially identified as a crocodile by Home (1814), it was later recognised as an ichthyosaur, now identified as *Temnodontosaurus platyodon*, and essentially became the catalyst for future ichthyosaur research (McGowan and Motani, 2003).



Figure 1. An embryo-bearing specimen of *Stenopterygius* (SMNS 6293) from the Toarcian of Germany, highlighting how ichthyosaur young were typically born tail-first. Photograph courtesy of Dr Erin Maxwell.

Lower Jurassic ichthyosaurs have been collected extensively in the UK, primarily from Lyme Regis and Charmouth, Dorset; Street and Strawberry Bank, Somerset; and Whitby, North Yorkshire (McGowan and Motani, 2003), with the abundance of these specimens considerably enhancing our understanding of these reptiles from this time interval (Lomax and Gibson, 2015). Lower Jurassic ichthyosaurs are currently represented by ten genera; *Ichthyosaurus*, *Protoichthyosaurus*, *Leptonectes*, *Eurhinosaurus*, *Excalibosaurus*, *Suevoleviathan*, *Stenopterygius*, *Hauffiopteryx*, *Temnodontosaurus* and most recently *Wahlisaurus*, and all but *Suevoleviathan* have been documented from the UK (Lomax, 2016). The primary focus of this work is based on one of the largest known ichthyosaurs of the Early Jurassic, *Temnodontosaurus*, which may have exceeded 12 m in length (Figure 2) (Maisch and Matzke, 2000). *Temnodontosaurus* belongs to the family Temnodontosauridae McGowan, 1974a, and is thought to be represented by at least six species, including *T. platyodon*, *T. eurycephalus*, *T. trigonodon*, *T. acutirostris*, *T. crassimanus* and *T. azerguensis* (McGowan and Motani, 2003; Martin et al., 2012; Ji et al., 2016). The genus is known from various localities in Europe, from the Lower Jurassic (Hettangian - Toarcian) of England, including Dorset, North Yorkshire (Lomax, 2019a) and Nottinghamshire (Lomax and Gibson, 2015); Germany (Maisch and Matzke, 2000); Belgium and northern France (Martin et al., 2012). Despite the fact that the genus is widely recognised and specimens are well known, detailed research on UK material has not been undertaken at great length since McGowan (1974a); but see McGowan and Motani (2003) for an overview.

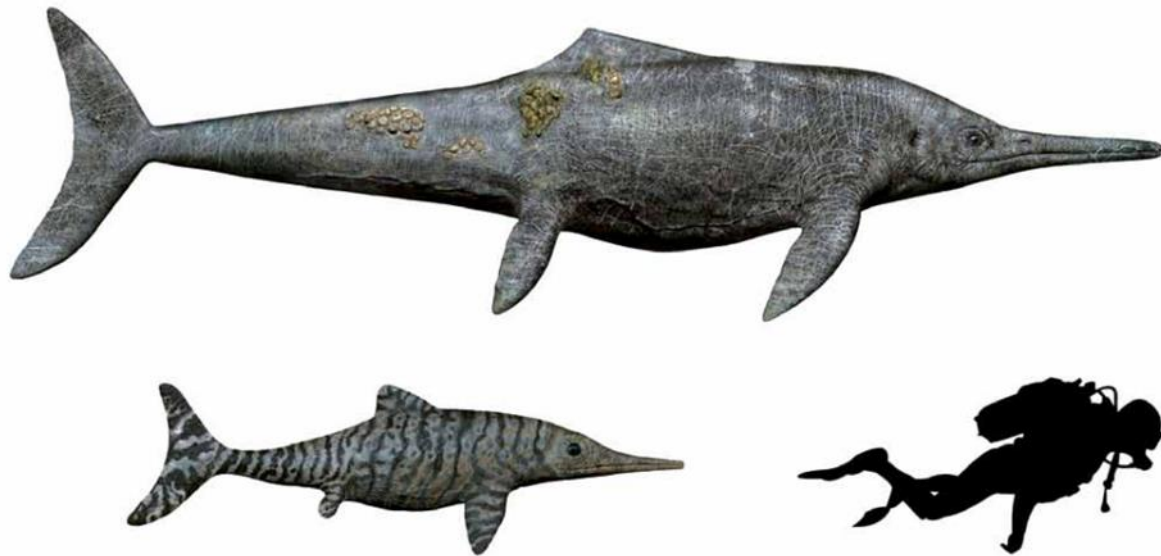


Figure 2. Digital restoration of the large *Temnodontosaurus* alongside the smaller *Stenopterygius*, in comparison to a scuba diver (~ 2 m) as a scale by Fabio Manucci (Insacco et al., 2014).

The aim of this study is to provide a re-examination of the holotype specimen of *Temnodontosaurus crassimanus* from the Lower Jurassic of Whitby, Yorkshire, to determine the validity of this species. This research will focus primarily on the near-complete holotype (YORYM 497) held in the collections of the Yorkshire Museum, in addition to further examples that may belong to this species that were located as part of this research. A cladistic analysis incorporating the holotype of *T. crassimanus*, the first time the species will be included in a phylogenetic analysis, will not only help determine the validity of the species but will potentially highlight the relationship of this species within *Temnodontosauridae*. Although a review of the genus is beyond the scope of this study, this research will help to lay the foundations for a thorough revision of *Temnodontosaurus*.

3. MATERIALS AND METHODS

The holotype of *Temnodontosaurus crassimanus* (YORYM 497) is currently on display at the Yorkshire Museum. The specimen is a large, three-dimensionally preserved partial skeleton including a skull and almost complete postcranial skeleton, with the anterior portion of the rostrum and a portion of the posterior caudal region missing. In part, the skeleton is somewhat poorly preserved and some elements are taphonomically distorted, which somewhat restricts the description. For example, as discussed below, with assistance from my co-supervisor (Dean Lomax), we determined that the hindfins of YORYM 497 had been reversed and were on the opposite side of the mounted skeleton. Within the description, the fins will be described in their correct anatomical position. Where possible, accurate morphological data and measurements were recorded, and photographs were taken.

Measurements were recorded with digital calipers for dimensions less than 10 cm, and were recorded to the nearest 0.1 mm. A tape measure was used for measuring larger features, including the total length of the specimen, and the value was recorded to the nearest 1 cm where possible. Detailed photographs were taken of the studied specimen (camera model: Canon Powershot SX510 HS), although refer to chapter 11.2 for photographic limitations. Additional information on the preservation of the specimen was also recorded where necessary. The software used for the cladistic analysis was the Willi Hennig Society edition of the program TNT version 1.5 (Goloboff et al., 2008; as further discussed in chapter 10).

As part of this study, specimens that have previously been tentatively assigned to *T. crassimanus* by McGowan and Motani (2003) were studied, which includes WHITM: SIM2546 and WHITM: SIM5. Additionally, several other Yorkshire *Temnodontosaurus* specimens were located and examined, including MANCH: L. 1688 and MANCH: LL. 16096, and were then subsequently compared with the holotype of *T. crassimanus*. For species comparison, several specimens of *T. trigonodon* from the Posidonia Shale of Holzmaden, Germany, were also examined, including SMNS 15950, SMNS 50000 and SMNS 17560.

Skull length	Distance between tip of snout and posterior edge of articular surface of quadrate.
Skull width (posterior), in dorsal view	Distance between tip of the posterior edge of articular surface of quadrates.
Skull width (in front of orbit), in dorsal view	Maximum skull width anterior to the orbit.
Jaw length	Distance between tip of mandible and posterior edge of surangular.
Preorbital length	Distance between the anterior edge of orbit to anterior end of premaxilla.
Upper temporal fenestra (UTF) length	Maximum internal length of UTF.
Upper temporal fenestra (UTF) width	Minimum and maximum internal width of UTF.
Premaxillary length	Distance between tip of snout and anterior tip of maxilla.
Prenarial length	Distance between tip of snout and anterior boundary of external naris.
Orbital height	Maximum internal height of orbit.
Orbital length	Maximum internal diameter of orbit.
Orbital ratio	Orbital diameter divided by jaw length.
External naris height	Maximum internal height of external naris.

External naris length	The distance between anterior and posterior boundaries of the external naris.
Basioccipital condyle width	Maximum width of the basioccipital condyle, in posterior view.
Basioccipital condyle height	Maximum height of the basioccipital condyle, from the posterior to the anterior.
Extracondylar area width	Maximum mediolateral width of the extracondylar area.
Extracondylar area height	Maximum height of the extracondylar area, from the posterior to the anterior.
Exoccipital proximal width	Maximum width of the exoccipital at the proximal end.
Exoccipital distal width	Maximum width of the exoccipital at the distal end.
Exoccipital shaft width	Maximum width of the shaft of the exoccipital.
Exoccipital length	Distance between the proximal and distal end along the axis of the exoccipital.
Quadrate length	Distance between the proximal and distal end along the axis of the quadrate.
Quadrate shaft width	Maximum width of the shaft of the quadrate.
Tooth width	Maximum width of the tooth.
Tooth height	Distance between tip of the crown to the posterior edge of the root.

Table 1. Skull measurements and definitions of features. Modified from McGowan (1974a) and McGowan and Motani (2003).

Length of fore- and hindfins	Distance between distal end of propodial and distal edge of most distal phalanx.
Width of fore- and hindfins	Maximum width of the preserved fin, at widest point.
Forefin length ratio	Forefin length of <i>specimen a</i> divided by forefin length of <i>specimen b</i> .
Forefin width ratio	Forefin width of <i>specimen a</i> divided by forefin width of <i>specimen b</i> .
Forefin length vs total estimated body length ratio	Forefin length divided by the total estimated body length.
Forefin length vs hindfin length ratio	Forefin length divided by hindfin length.

Hindfin length ratio	Hindfin length of <i>specimen a</i> divided by hindfin length of <i>specimen b</i> .
Hindfin width ratio	Hindfin width of <i>specimen a</i> divided by hindfin width of <i>specimen b</i> .
Notching	Elements in leading edge of fin that possess a single notch in the middle of their anterior margin.
Number of primary digits	The maximum number of primary digits.
Total digital count	Total number of digits, including accessories.
Number of elements in longest digit	Count commences with epipodials, extending to distal-most phalanx.
Humeral length	Total length from the point between radial-ulnar facets to top of head, along the longitudinal axis.
Humeral proximal width	Maximum width of the humerus at the proximal end.
Humeral distal width	Maximum width of the humerus at the distal end.
Humeral shaft width	Maximum width of the shaft of the humerus.
Humerus length ratio	Humerus length of <i>specimen a</i> divided by humerus length of <i>specimen b</i> .
Humerus proximal width ratio	Humerus proximal width of <i>specimen a</i> divided by humerus proximal width of <i>specimen b</i> .
Humerus distal width ratio	Humerus distal width of <i>specimen a</i> divided by humerus distal width of <i>specimen b</i> .
Humerus distal width vs proximal width ratio	Humerus distal width divided by proximal width.
Humerus length vs femur length ratio	Humerus length divided by femur length.
Radius and ulna width	Maximum anteroposterior width of the elements.
Radius and ulna length	Distance between tip of anterior edge, to the posterior edge of both elements i.e. maximum proximodistal length.
Radiale, ulnare and intermedium width	Maximum anteroposterior width of the elements.
Radiale, ulnare and intermedium length	Distance between tip of anterior edge, to the posterior edge of all individual elements i.e. maximum proximodistal length.
Femur length	Total length from the point between facets to top of head, along the longitudinal axis.
Femur proximal width	Maximum width of the femur at the proximal end.
Femur distal width	Maximum width of the femur at the distal end.
Femur shaft width	Maximum width of the shaft of the femur.
Femur proximal width ratio	Femur proximal width of <i>specimen a</i> divided by femur proximal width of <i>specimen b</i> .

Femur distal width ratio	Femur distal width of <i>specimen a</i> divided by femur distal width of <i>specimen b</i> .
Femur distal width vs proximal width ratio	Femur distal width divided by proximal width.
Femur length ratio	Femur length of <i>specimen a</i> divided by femur length of <i>specimen b</i> .
Tibia and fibula width	Maximum anteroposterior width of the elements.
Tibia and fibula length	Distance between tip of anterior edge, to the posterior edge of both elements i.e. maximum proximodistal length.
Tibiale, fibulae and intermedium width	Maximum anteroposterior width of the elements.
Tibiale, fibulae and intermedium length	Distance between tip of anterior edge, to the posterior edge of all individual elements i.e. maximum proximodistal length.

Table 2. Fore- and hindfin measurements and definitions of features. Modified from McGowan (1974a) and McGowan and Motani (2003).

Precaudal length	Vertebrae anterior to where the rib attachments merge (identifying the first caudal vertebra) or the position of the pelvis if rib attachments are not exposed/poorly preserved.
Preflexural length	Vertebrae lying anterior to the apex of the tailbend.
Total length	Entire length from tip of snout to tip of tail, measured along the vertebral column.
Vertebrae width	Maximum width of the vertebrae.
Vertebrae length	Distance between tip of anterior edge, to the posterior edge of the vertebrae.
Vertebrae height	Maximum height of the vertebrae.
Length of longest preserved rib	Distance between tip of the rib head, to the distal end of the rib, measured along the ribs curvature.

Table 3. Axial skeleton measurements and definitions of features. Modified from McGowan and Motani (2003).

Scapula length	Distance between tip of proximal end, to the distal end along the longitudinal axis.
Scapula proximal width	Maximum width of the scapula at the proximal end.
Scapula distal width	Maximum width of the scapula at the distal end.
Scapula length vs humerus length ratio	Scapula length divided by humerus length.
Clavicle length	Distance between tip of proximal end, to the distal end of the clavicle.
Clavicle shaft width	Maximum width of the shaft of the clavicle.
Pubis length	Distance between tip of proximal end, to the distal end of the pubis.
Pubis length vs femur length ratio	Pubis length divided by femur length.
Pubis proximal width	Maximum width of the pubis at the proximal end.
Pubis distal width	Maximum width of the pubis at the distal end.
Ischium length	Distance between tip of proximal end, to the distal end of the ischium.
Ischium proximal width	Maximum width of the ischium at the proximal end.
Ischium distal width	Maximum width of the ischium at the distal end.
Ilium length	Distance between tip of proximal end, to the distal end of the ilium.
Ilium proximal width	Maximum width of the ilium at the proximal end.
Ilium distal width	Maximum width of the ilium at the distal end.
Ilium length vs femur length ratio	Ilium length divided by femur length.

Table 4. Pectoral and pelvic measurements and definitions of features. Modified from McGowan and Motani (2003).

4. GEOLOGICAL BACKGROUND

Yorkshire is a historic county located in northern England, and home to one of the most spectacular sections of coastline (Figure 3), stretching from the mouth of the River Tees in the north, to Flamborough Head in the south (Lomax, 2011). The geology of the Yorkshire coast has been well-studied, while the Lower Jurassic strata have been central to many significant palaeoenvironmental and sedimentological studies (Howarth, 1962; Morris, 1979) throughout the 20th century (Rawson and Wright, 2000; Swaby, 2018). Like Lyme Regis, Dorset, this coastline is of historic interest in being one of the earliest British localities to be exploited for fossil marine reptiles (Benton and Spencer, 1995). The strata have produced many well-preserved specimens of plesiosaurs, ichthyosaurs and marine crocodilians (as discussed in chapter 5), some of which are unique to Yorkshire, in addition to various invertebrate fossils including a rich ammonite fauna (Howarth, 1962; Benton and Taylor, 1984).

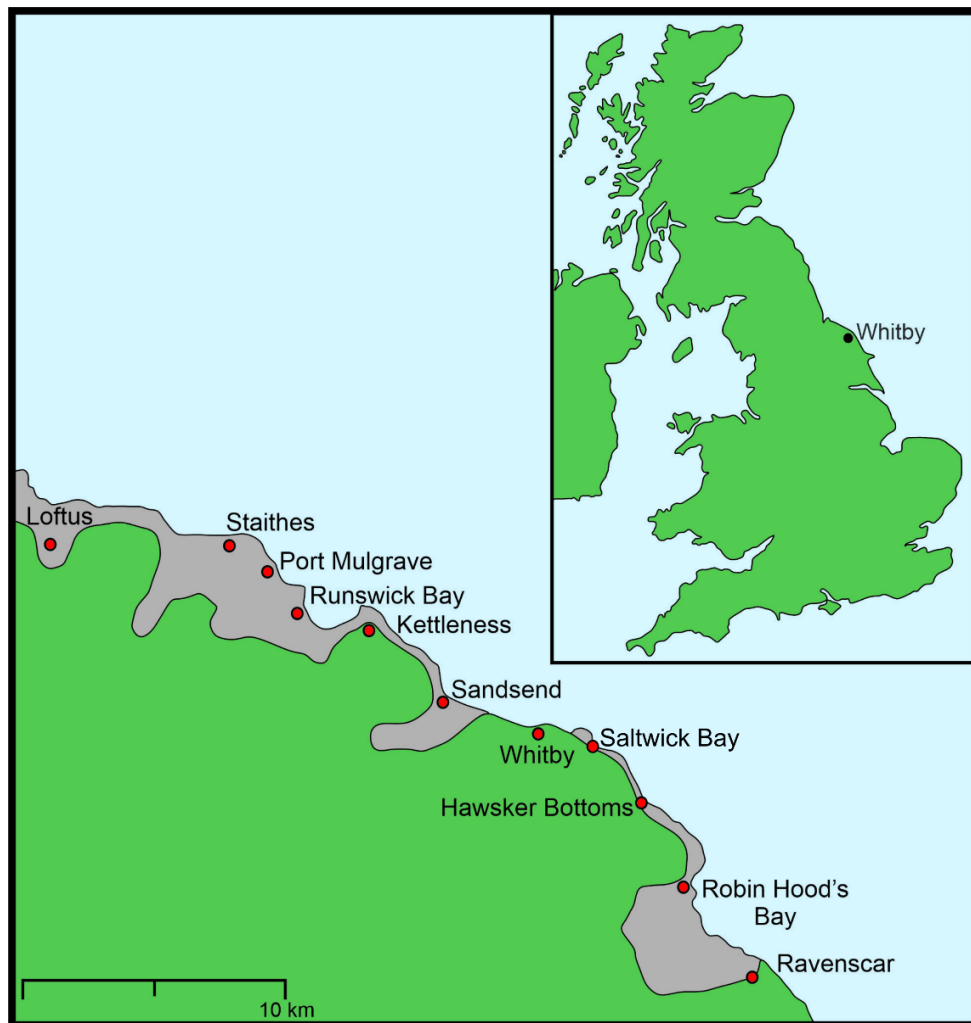


Figure 3. Map of the UK and of the Yorkshire coast, highlighting the location of Whitby and several other coastal localities, the majority of which are important ichthyosaur-bearing locations. Grey shaded areas represent Lower Jurassic rocks, including foreshore exposures. Modified from Benton and Taylor (1984) and Howarth (2002).

While the coastline of North Yorkshire provides exposures of strata ranging from the Hettangian to Aalenian, this study is primarily focused on the Toarcian-aged sediments referred to as the Whitby Mudstone Formation (WMF). These sedimentary deposits, which accumulated in the Cleveland Basin, were deposited in fully marine conditions below the storm wave-base (Caswell et al., 2009). The WMF is divided into five distinct members; The Grey Shale Member, Mulgrave Shale Member, Alum Shale Member, Peak Mudstone Member and the Fox Cliff Siltstone (Rawson and Wright, 2000). However, it is the Mulgrave Shale and Alum Shale members that have yielded the remains of some of the best Upper Lias marine reptiles in the world, and are therefore undoubtedly the most significant members to this study.

The Mulgrave Shale Member is an 8 m sequence of finely-laminated, sulphur and organic-rich dark grey shales, which were deposited in response to an increase in the depositional and preservational rates of organic carbon during the Early Toarcian Oceanic Anoxic Event (T-OAE) (Jenkyns, 1988; Ghadeer and Macquaker, 2012). The lower shales, informally referred to as the 'Jet Rock Member', are composed of well-cemented, often bituminous grey or brown shales, which are subdivided by lateral interbedded bands of calcareous concretions of varying size, referred to as 'doggers'. Within the upper section, known as the 'Bituminous Shales', laminations are less pronounced, and shales are instead interbedded with pyritic concretionary bands (Benton and Spencer, 1995). As discussed below (see chapter 5.1), the Mulgrave Shale Member is comparable to many fine-grained siliciclastic mudstone dominated successions deposited across northwestern Europe during the Toarcian, including the Lower Jurassic Posidonia Shale of southwestern Germany (Ghadeer and Macquaker, 2012). The Alum Shale Member is a 37 m sequence of poorly-laminated, soft, medium to dark grey mudstones, interbedded by irregular lateral bands of scattered calcareous concretions and sideritic mudstone layers (Howarth, 1962). The Alum Shale Member has three informal divisions, the Hard Shales, the Main Alum Shales and the Cement Shales (Howarth, 1962). Both members represent individual shale facies, and are also divided by distinct ammonite zones and sub-zones (Figure 4). Coastal exposures of the above members can be observed at various localities along the coastline (Figure 3), including Port Mulgrave, Runswick Bay and Kettleness (Howarth, 1962), in addition to outcrops on the wave-cut platforms around the vicinity of Saltwick Bay (Benton and Spencer, 1995).

During the 19th century, the Lower Jurassic rocks of the Yorkshire coast were extensively quarried for the manufacture of alum. Although inland quarries were occasionally in operation, larger companies, including the Kettleness Alum Works dominated the coastline, exposing sections in both the Mulgrave Shale and Alum Shale members, which in turn revealed the remains of many marine reptiles (Benton and Taylor, 1984; Osborne and Bowden, 2005). Although ichthyosaurs appear to have been collected from various horizons within the WMF, there is much confusion over the precise stratigraphic location of many historic specimens, as discussed later (see chapter 5.1). Within the formation, marine reptiles are found ranging from isolated fragments, to complete skeletons (Lomax, 2019a). Most specimens discovered from within the strata are found to be well preserved in an articulated state with only minimal damage, as the prevalent anoxic conditions assisted in preventing scavenging, and partial skeletons and fragments are thought to have been broken up prior to burial or by recent weathering.

(Benton and Spencer, 1995). Although focus often resides on the Upper Lias exposures, the Lower Lias outcrops of the Yorkshire coast have also yielded marine reptiles, including from the Redcar Mudstone Formation (Hettangian – Pliensbachian) which underlies the WMF. This formation is well exposed at Robin Hood’s Bay, Staithes, Saltburn and Redcar, but specimens from this strata are much rarer (Benton and Taylor, 1984; Benton and Spencer, 1995; Massare et al., 2015; Lomax, 2019a).

System	Stage	Form.	Member	Division	Bed No.	Zone	Subzone	Facies Morris (1979)
LOWER JURASSIC	TOARCIC	WHITBY MUDSTONE FORMATION	Alum Shale Member	Cement Shales	65 - 72	<i>Hildoceras bifrons</i>	<i>Zugodactylites braunianus</i>	
				Main Alum Shales	60 - 64		<i>Peronoceras fibulatum</i>	
					51 - 59		<i>Dactylioceras commune</i>	
				Hard Shales	49 - 50			Restricted
			Mulgrave Shale Member	Ovatum Band	48	<i>Harpoceras falciferum</i>	<i>Harpoceras falciferum</i>	Bituminous
				Bituminous Shales	41 - 47			
				Jet Rock	33 - 40		<i>Harpoceras exaratum</i>	
			Grey Shale Member	Grey Shales	28 - 32	<i>Dactylioceras tenuicostatum</i>	<i>Dactylioceras semicelatum</i>	
					20 - 27		<i>Dactylioceras tenuicostatum</i>	
					18 - 19		<i>Dactylioceras clevelandicum</i>	Normal
					3 - 17		<i>Protogrammoceras paltum</i>	
					1 - 2		<i>Pleuroceras hawskerense</i>	

Figure 4. A stratigraphic column of the lower three divisions of the Whitby Mudstone Formation, which yield many of the marine reptiles from Whitby (Swaby, 2018). The term ‘Liassic’ was formerly used within older literature to refer to the Lower Jurassic, however the word is now technically abolished and ‘Lias’ is used instead.

5. LITERATURE REVIEW

5.1 A HISTORY OF ICHTHYOSAURS FROM THE YORKSHIRE COAST

The Lower Jurassic strata of the Yorkshire coast have yielded many significant palaeontological discoveries over the past 200 years and have produced some of the best Upper Lias fossil reptiles in the world (Benton and Taylor, 1984; Benton and Spencer, 1995). The collection of Yorkshire reptiles extends back to 1758, following the discovery of the first fossil reptile, a marine ‘crocodile’ (crocodyliform), recorded from near Whitby (Benton and Taylor, 1984). Described by William Chapman (1758) as being discovered in the sea-shore approximately half a mile from Whitby, the specimen (NHMUK R1088) was concluded to have been collected from the Alum Shale Member at The Scar, a small promontory in the Alum Shale Member approximately 700 m east of Whitby harbour mouth (Benton and Spencer, 1995). The specimen was later named *Teleosaurus chapmani* (now *Steneosaurus bollensis*) (Buckland, 1836; Benton and Taylor, 1984; Benton and Spencer, 1995). In 1819, the first recorded Yorkshire ichthyosaur was also collected from The Scar, in which the skeleton was reported to lay imbedded within the Alum Shale Member, presumably the same locality and horizon as the previously discovered crocodilian (Benton and Spencer, 1995). This specimen was comprised of a skull and partial skeleton, and was the third fossil reptile to be recorded from the coastline (Benton and Taylor, 1984). Subsequently, a second, more complete ichthyosaur skeleton was collected from the same locality in 1821, and although these specimens cannot be traced, figures suggest that they may be examples of *Leptopterygius* (*Leptonectes*) *acutirostris*, now tentatively referred to *Temnodontosaurus* (McGowan and Motani, 2003; but see Maisch, 2010).

The first Yorkshire plesiosaurs were reported in 1822, with the best documented specimen collected in 1841 from the Lias cliffs of Saltwick Bay (Benton and Taylor, 1984). This specimen (CAMSM J35182) was comprised of an articulated skeleton approximately 4.5 m long with a 0.2 m long skull and was initially referred to the Lower Lias species *Plesiosaurus dolichodeirus* (Benton and Taylor, 1984), until Seeley (1865) described it as the holotype of *P. macropterus*, now referred to *Microcleidus* (Watson, 1911). While the Lower Jurassic strata of Yorkshire yield a diverse assemblage of ichthyosaurs, plesiosaurs and marine crocodilians, pterosaurs have also been recorded. Although Lower Jurassic pterosaurs are best known from Dorset, England (Benton and Spencer, 1995), one of the best-preserved specimens, a three dimensional near-complete skull (BGS GSM 3166), was collected from the Toarcian Whitby Mudstone Formation of Loftus, North Yorkshire (Newton, 1888; O’Sullivan and Martill, 2017). It should also be noted that very rare dinosaur bones have also been found in the Yorkshire Lias, which include a single posterior dorsal vertebra referred to the genus *Streptospondylus*, and a partial femur, although both specimens are considered ‘lost’ and thus their validity cannot be confirmed (Lomax and Tamura, 2014; Lomax, 2019b).

Young and Bird (1828) stated that over 40 ichthyosaur specimens were collected from the Whitby area during the early 19th century, many of which were acquired for private collections and have not been located (Benton and Spencer, 1995). However, many ichthyosaurs from the Lower Jurassic

strata of Yorkshire are present within various institutional collections around the UK (and elsewhere), but still require detailed examination and taxonomic revision (Massare et al., 2015; Lomax, 2019a). As previously mentioned (see chapter 4), the majority of Whitby ichthyosaurs derive from the Whitby Mudstone Formation and appear to have been recorded from various horizons within the strata. Specimens vary from isolated material, including isolated and articulated vertebrae, rib sections and isolated fore- and hindfins, to partial skeletons and isolated skulls (Lomax, 2011; 2019a). Many of the early discoveries were most likely collected from the Main Alum Shales along the coastline section between Whitby and Saltwick Bay (Benton and Taylor, 1984). However, as discussed in the geological background above, due to insufficient study, there is much confusion over the accurate localities and zones for many of the Yorkshire specimens (Benton and Taylor, 1984; Benton and Spencer, 1995). Since the 19th century, the majority of specimens collected from the coastline were simply recorded as ‘from Whitby’, even if the original location was some distance from the coastal town (Massare et al., 2015). These early discoveries were mostly found during the quarrying of the Alum Shale, and so could have been collected from several Lower Jurassic localities along the coastline or even from inland alum quarries. The lack of collection data has created uncertainty on the provenance of many specimens collected from the area, although recent discoveries tend to be accompanied with more precise and reliable collection information.

Although the ichthyosaurs from the Upper Lias of Whitby are undoubtedly the best examples from the UK, specimens from the coeval Lower Jurassic Posidonia Shale of southwestern Germany are not only more abundant with better preservation and greater variety, but are significantly better understood. The Posidonia Shale (*Posidonienschiefer*) of Holzmaden has produced several thousand ichthyosaur specimens, many of which are relatively complete, but apparently yields comparatively fewer specimens of crocodylians and plesiosaurs (Benton and Spencer, 1995). Ichthyosaurs from the Posidonia Shale fall into five recognized genera varying from the larger *Temnodontosaurus*, *Eurhinosaurus* and *Suevoleviathan*, to the small to mid-sized *Hauffiopteryx* and *Stenopterygius*, with the latter being the most abundant genus by far (Maxwell, 2012). While several species of marine reptiles are shared between Yorkshire and Germany, only three of the five genera here are known from the Yorkshire Lias, which includes *Temnodontosaurus*, *Eurhinosaurus* and *Stenopterygius*. The extensive study of the German specimens, in comparison to the Yorkshire material, has resulted in the collection and description of more abundant and better-preserved specimens. This has led to a detailed insight of the fauna and also represents a greater species diversity from this time interval, although this may be due to the lack of understanding of the material (Lomax, 2019a).

Furthermore, while the Posidonia Shale has also yielded over one hundred embryo-bearing specimens of *Stenopterygius*, only one gravid female is known from the Yorkshire Lias. Boyd and Lomax (2018) described the youngest occurrence of ichthyosaur embryos in the UK, from the remains of several ichthyosaur embryos situated within a fragment of the rib-cage of an adult ichthyosaur. The limestone boulder was observed to enclose between six to eight embryos, each represented by various skeletal elements including vertebral centra, associated ribs and possible skull material (Figure 5). The specimen (YORYM: 2016.316) was discovered *ex situ* on the beach at Sandsend,

North Yorkshire, and derives from the *bifrons* Biozone of the Toarcian Whitby Mudstone Formation (Boyd and Lomax, 2018). Although the specimen cannot be assigned to a particular taxon, it does, however, represent the first occurrence of ichthyosaur embryos recorded from Yorkshire, despite the historical richness of these Lower Jurassic rocks.

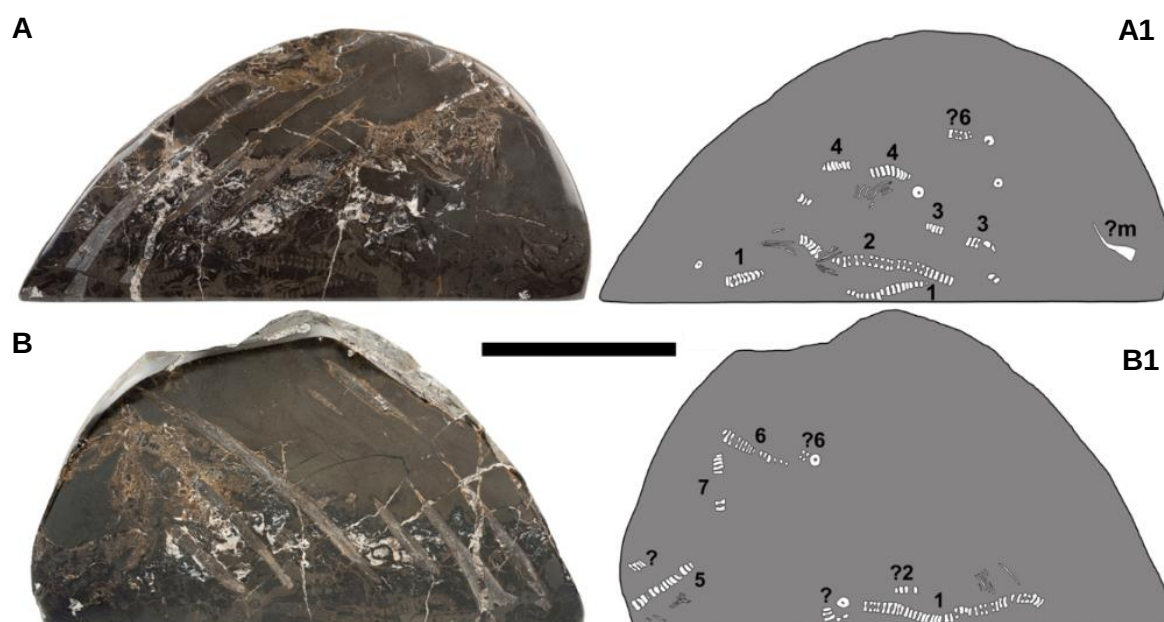


Figure 5. YORYM: 2016.316; a cut and polished boulder (Block A and B) containing between six and eight ichthyosaur embryos, accompanied by illustrations of the identifiable sections of embryos (Block A1 and B1). Scale bar equals 10 cm (Boyd and Lomax, 2018, fig. 1).

The earliest revision of ichthyosaurian material from the Jurassic of Yorkshire was undertaken by Young and Bird (1828), in which they stated that the majority of specimens could be assigned to *Ichthyosaurus communis*, in addition to '*I. platyodon*' and '*I. tenuirostris*' (McGowan and Motani, 2003). Following further revision by Blake (1876), the taxonomy of these Lower Jurassic ichthyosaurs was reviewed by McGowan (1974a) during a revision of the longipinnate ichthyosaurs of the English Lias. Benton and Taylor (1984) briefly but extensively discussed all marine reptiles from the Toarcian of the Yorkshire coast, and concluded that there were two valid species, represented by the 69 ichthyosaur specimens that they had observed. However, the authors highlighted that it was important for the Yorkshire Lias material to be revised and studied in further detail, as confusing views had been expressed on ichthyosaur taxonomy. Further revision by Benton and Spencer (1995) later stated that approximately seven species of marine reptiles described from the Whitby area may be valid, including only two ichthyosaur species recognised by McGowan (1974a): *Eurhinosaurus longirostris* and *Stenopterygius acutirostris*. Later, McGowan and Motani (2003) concluded that only *Temnodontosaurus crassimanus* and *Eurhinosaurus longirostris* could be recognised from the Yorkshire Lias, but suggested that *Temnodontosaurus acutirostris* and *Stenopterygius* sp. are also

possibly found in the area. The most recent taxonomic revision of the ichthyosaurs of the Yorkshire coast was undertaken by Lomax (2019a), in which the taxonomic validity of 5 species was discussed. However, this was purely a review on what had previously been done, hence further revision of Yorkshire ichthyosaurs, including a thorough reassessment of the taxonomy and description of new material, is necessary.

Unless stated otherwise, the following descriptions are based on the most recent review by Lomax (2019a) and McGowan and Motani (2003), but have been expanded upon.

5.2 ICHTHYOSAUR SPECIES FROM YORKSHIRE

5.2.1 *Eurhinosaurus longirostris* (Mantell, 1851)

In 1851, Mantell briefly described a partial ichthyosaur skeleton collected from the Upper Lias of Whitby, Yorkshire, referred to as *Ichthyosaurus longirostris*, which was subsequently followed by Jäger (1856) who described three additional specimens from the Upper Lias of Germany as also belonging to the same species. The unusual shortness of the mandible, which extended only half the length of the skull, observed on Jäger's specimens, warranted the erection of a new genus, in which Abel (1909) proposed the name *Eurhinosaurus* (see discussion in McGowan, 1994). The genus *Eurhinosaurus* is arguably one of the most specialized Lower Jurassic ichthyosaurs, unique for its long, elongated rostrum and abbreviated mandible, which superficially resembles the modern swordfish, *Xiphias* (McGowan, 1986). The shortened mandible produces a significant overbite, a characteristic also shared with other Lower Lias ichthyosaurs (in the family Leptonectidae), including *Excalibosaurus* (McGowan and Motani, 2003). While the holotype material is from the Toarcian of Whitby, *Eurhinosaurus* has a wide distribution, with the majority of the material found in Holzmaden, southern Germany, in addition to France and Switzerland (Reisdorf et al., 2011; Ji et al., 2016).



Figure 6. The practically complete specimen of *Eurhinosaurus longirostris* (SMNS 14931) from the Upper Lias of Germany. Photograph courtesy of Dr Erin Maxwell.

Eurhinosaurus longirostris is a large, swordfish-like ichthyosaur, reaching a total adult length in excess of 7 m (Lomax, 2019a). It possesses an incredibly long and slender rostrum and is unusual in having a mandible which is less than 60% of the total skull length (Figure 6). The pelvic girdle is tripartite without fusion between the pubis and the ischium. Both the fore- and hindfins are long and slender, with the number of elements in the longest digit exceeding 17. The forefins are composed of four or five digits with notching either absent or occurring in fewer than four elements of the leading edge. Notching also usually occurs in the hindfin (Lomax, 2019a). Although first figured by Owen (1881), *Ichthyosaurus longirostris* was first noted by Mantell in 1851, after observing the specimen on display within the old British Museum, in which he described a partial skeleton of an ichthyosaur from Whitby, approximately six feet in length. The holotype specimen, now identified as NHMUK PV OR 14566, is from the Upper Lias of Whitby, North Yorkshire and is comprised of a dorsoventrally compressed skull, partial vertebral column, and several ribs, in addition to a partial forefin (McGowan, 1994). As the skull of the specimen was only exposed in a dorsal view, Mantell would have been unable to determine that the mandible was greatly abbreviated, and was only revealed to be the case following subsequent preparation in the early 1990s (McGowan, 1994). The skull of the holotype specimen is approximately 86 cm in length, and the abbreviated mandible approximately 17.2 cm, with the majority of the bone remaining embedded within the original matrix (McGowan, 1994).

Lomax (2019a) suggested the possibility of a further two specimens (YORYM: 2005.2407 and YORYM: 2012.36), which may also belong to *E. longirostris*, but the specimens have not been described. Although the holotype specimen is the only example definitely known from the Yorkshire Lias, based on the Holzmaden material, *Eurhinosaurus longirostris* is certainly the most well-defined ichthyosaur documented from the coastline, in contrast to other Yorkshire taxa. This species occurs within the Upper Lias, Lower Jurassic (Toarcian) Alum Shale Member (most likely *bifrons* Biozone), of the Whitby Mudstone Formation.

5.2.2 ?*Temnodontosaurus acutirostris* (Owen, 1840)

Temnodontosaurus is a genus of large non-thunnosaurian neoichthyosaur, represented by at least six species (McGowan and Motani, 2003; Martin et al., 2012; Ji et al., 2016). Although the genus was first erected by Lydekker (1889), *Ichthyosaurus platyodon* (now referred to as *T. platyodon*) was first scientifically reported by De la Beche and Conybeare (1821) from remains collected from the Lower Lias of Lyme Regis, Dorset. In addition to *T. platyodon*, McGowan (1974a) later highlighted three additional species referable to a single genus, including *T. longirostris*, *T. risor* and *T. eurycephalus*, which were subsequently referred to the genus *Temnodontosaurus*. As discussed previously, the genus is known from the Lower Jurassic (Hettangian - Toarcian) of England, including Lyme Regis, Dorset, Whitby, North Yorkshire, Nottinghamshire, England, Holzmaden, southern Germany, Belgium and northern France (McGowan and Motani, 2003). While *T. trigonodon* is well documented from the vicinity of Holzmaden, southern Germany, only one isolated forefin (YORYM: 1994.1799.53) from the Yorkshire Lias may possibly belong to this species (Lomax, 2019a). Apart from the work of McGowan

(1974a), generally, the genus is generally poorly known from the English Lower Jurassic and is most commonly represented by incomplete specimens (McGowan, 1996; McGowan and Motani, 2003). The remains of large-bodied ichthyosaurs from the Yorkshire Lias are often referred to *Temnodontosaurus*, but could possibly belong to various species of this taxon or another as-of-yet unidentified taxon (e.g. see McGowan, 1996).

Temnodontosaurus acutirostris was originally described by Owen (1840) and is a moderately large ichthyosaur with a skull length of < 1 m. The skull itself possesses a large orbit, and a long, slender snout, probably tapering to a sharp point. The snout is often depicted down-curved, and although this is a feature of some specimens (NHMUK PV OR 15500a; Figure 7), it has been suggested to be a possible result of dorsoventral compression. Teeth are numerous, with no tendency towards reduction in overall size or number. The forefins are elongate and slender, with the number of elements in the longest digit possibly exceeding 30. Notching is most likely restricted to proximal elements including the radius and subsequent elements (McGowan and Motani, 2003). The type specimen (NHMUK PV OR 14553) is comprised of a skull, a complete forefin, elements of the other fin, a coracoid, other components of the pectoral girdle, and numerous ribs. Owen (1881) further described and figured the skull of *I. acutirostris* (plate 28, fig. 2), which was also redrawn by McGowan and Motani (2003, fig. 78); note that the scale for this figure is incorrect.

Following Owen's original description, the specimen was transferred to the present site of the NHMUK and was subsequently recorded as 'probably lost' by McGowan (1974a). The specimen was later relocated in the collections of the NHMUK, but was found to have lost the anterior section of the rostrum and a portion of the lower part of the left forefin (Doyle and Chapman, 2002). Additionally, Owen made no reference to the extremely long and slender forefin of this specimen in any of his descriptions or figures, resulting in the authenticity of the forefin, which has never been described in detail, being questioned (Doyle and Chapman, 2002; McGowan and Motani, 2003; Maisch, 2010). However, the forefin was considered valid by Doyle and Chapman (2002) and was subsequently figured by Lomax (2019a; fig. 20.7).

Two additional specimens from Whitby have also been tentatively assigned to *T. acutirostris*; a nearly complete skull with a down-curved snout in dorsal view (NHMUK PV OR 15500a; Figure 7), and a large, three-dimensional partial skull (CAMSM J35176) (McGowan and Motani, 2003; Lomax, 2019a). The latter specimen was originally described as *Ichthyosaurus zetlandicus* by Seeley (1880), but was later synonymized with *T. acutirostris*. Furthermore, Maisch (2010) argued that it remains unclear whether *Temnodontosaurus acutirostris* is a temnodontosaurid, and that a detailed review of the Whitby material is required to assess its validity, but suggested that it was likely a different genus; this species had previously been referred to *Stenopterygius* by McGowan (1974a). The holotype (NHMUK PV OR 14553) was collected from the section of coastline between Whitby and Saltwick Bay, whilst Benton and Spencer (1995) noted that CAMSM J35176 was collected from the same horizon, but from the Loftus Alum Quarries, North Yorkshire. This species occurs within the Lower Jurassic (Toarcian) Alum Shale Member (most likely *bifrons* Biozone) of the Whitby Mudstone Formation.



Figure 7. A nearly complete skull in dorsal view of *Temnodontosaurus acutirostris* (NHMUK PV OR 15500a) from the Upper Lias of Whitby, Yorkshire. Scale bar equals 10 cm.

5.2.3 *Temnodontosaurus crassimanus* (Blake, 1876)

Temnodontosaurus crassimanus is one of only four species positively confirmed from the Upper Lias of Yorkshire, and is based on the holotype specimen (YORYM 497), a near complete, three-dimensionally preserved skeleton. Aside from the holotype, two partial skeletons (WHITM: SIM2546 and WHITM: SIM5) have also been cautiously assigned to this species. As this study aims to provide a thorough description of this taxon, further, more detailed information will be presented later (see chapter 7 - 9).

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

Ichthyosaurus is one of the most speciose genera of parvipelvic ichthyosaurs and is currently represented by six species; *Ichthyosaurus communis*, *I. breviceps*, *I. conybearei*, *I. anningae*, *I. larkini* and *I. somersetensis* – all of which are distinguished predominantly by skull and humerus features (Massare and Lomax, 2017). *Ichthyosaurus* was the first genus of ichthyosaur to be recognised scientifically (De la Beche and Conybeare, 1821) and is the most common genus of Lower Jurassic ichthyosaur to be found in the UK (Lomax et al., 2017a). Well over a thousand specimens are present in various institutional collections across the world, particularly in the UK. Ichthyosaurs collected during the 19th century were mostly assigned to the genus *Ichthyosaurus* and by 1900, more than 50 species of *Ichthyosaurus* had been described (McGowan and Motani, 2003). The genus has definitively been reported from the Lower Lias of England (Hettangian – Pliensbachian), but it has also been suggested that some specimens of *Ichthyosaurus* in historical collections are possibly from

the Rhaetian (see McGowan and Motani, 2003; Massare and Lomax, 2017). Many specimens have been collected from Dorset and Somerset, with *I. communis* being the most abundant species of ichthyosaur collected from Lyme Regis, accounting for approximately half of the known skeletons (Massare and Lomax, 2017). Aside from Dorset and Somerset, in Britain, *Ichthyosaurus* has been reported from localities in Nottinghamshire, Leicestershire, Gloucestershire, Worcestershire, Devon, Warwickshire, Yorkshire, Northern Ireland and South Wales (Massare and Lomax, 2017), but has not been reported from Toarcian strata (McGowan and Motani, 2003; Massare et al., 2015).

I. communis is a small to medium sized ichthyosaur species, with a maximum total body length of approximately 2 m (Lomax and Sachs, 2017). The forefins are wide and have no fewer than five digits with numerous and closely-packed phalanges and a digital bifurcation always occurring anteriorly. The humerus has nearly equal width proximally and distally, with a slight constriction in the shaft. The pelvic girdle is tripartite, without fusion between the pelvic elements. Notching on both the fore- and hindfins is never present in this species, but is observed in other species of *Ichthyosaurus* (Massare and Lomax, 2017).



Figure 8. Skull of *Ichthyosaurus communis* (SMNS 13111) from the Lower Lias of Yorkshire. Scale bar equals 5 cm. Modified from Massare and Lomax (2017, fig. 5C).

Rare *Ichthyosaurus* specimens have been identified from the Yorkshire Lower Lias (Figure 8), but are mostly from undetermined localities along the Whitby coastline. Benton and Taylor (1984) discussed the description of skeletons belonging to the species *I. intermedius* made by Owen (1840) in a review of British ichthyosaurs, which were stated to have been described ‘in the Lias near Whitby and Scarborough’. However, due to the lack of Lias exposures in Scarborough, this most likely referred to where Owen examined the specimens in the collections (Benton and Taylor, 1984). Blake (1876) discussed several specimens from the Lower Lias, in addition to a supposedly poorly preserved skeleton of *I. intermedius* from Robin Hood’s Bay, one of the few Lower Lias reptiles documented from the coastline. However, these specimens have yet to be located in any collections.

Maisch (1997) described a well-preserved, isolated skull (SMNS 13111), most likely collected from the Upper Sinemurian, *oxynotum* Biozone, Redcar Mudstone Formation, exposed at Robin Hood's Bay, and was identified as belonging to *I. intermedius*. However, Massare and Lomax (2017) reviewed both *I. intermedius* and *I. communis* and determined that *I. intermedius* must be considered a synonym for *I. communis*, agreeing with the work of McGowan (1974b) and McGowan and Motani (2003). Subsequently, SMNS 13111 was determined to have many similarities with *I. communis*, and was therefore assigned to that species (Massare and Lomax, 2017), the only definite example of the species from Yorkshire. Massare et al. (2015) described a large, incomplete forefin most likely from the Redcar Mudstone Formation of the Lower Jurassic of Yorkshire which was determined to have the largest humerus known from the genus *Ichthyosaurus*. The specimen (YORYM 2005.2411) could be assigned to the genus on the basis of the humerus shape, two digits originating from the intermedium, and an anterior digital bifurcation. Regression analyses suggest that the individual had a total body length around 3 m and therefore (at that time) represented the largest *Ichthyosaurus* described from the UK (Massare et al., 2015), but see Massare and Lomax (2017) and Lomax and Sachs (2017) for revised estimations. In addition, a fragmentary skeleton (YORYM: 2015.618) collected from the Upper Sinemurian, *obtusum* Biozone, Redcar Mudstone Formation at Robin Hood's Bay was donated to York Museum in 2015, and is the only other identifiable *Ichthyosaurus* specimen from Yorkshire (Lomax, 2019a).

5.2.5 *Stenopterygius* sp.

As well as *Ichthyosaurus*, *Stenopterygius* is one of the most well-known Lower Jurassic ichthyosaurs and is widely known from the Lias of Western Europe (Motani, 2005; Maxwell, 2012). The genus is primarily concentrated in the Toarcian Posidonia Shale of southwestern Germany (Figure 9), but is also known from the Toarcian of France, Belgium, Luxembourg, Switzerland and England (Maisch, 2010; Maxwell, 2012). In addition to being the most abundant ichthyosaur genus in the Posidonia Shale, many of the specimens demonstrate exceptional preservation. This includes the retention of soft tissue and gastric contents, in addition to embryonic preservation inside the body cavity, demonstrated by over one hundred embryo-bearing examples (McGowan, 1979; Maxwell, 2012). Following the erection of the genus by Jaekel (1904), *Stenopterygius* (initially identified as *Ichthyosaurus*), is now thought to be represented by four species following the most recent taxonomic analysis, which include *S. quadriscissus*, *S. triscissus*, *S. uniter* and *S. aaleniensis* (Maxwell, 2012; Maxwell et al., 2012). *Stenopterygius* is a small to medium sized ichthyosaur, with a total body length between approximately < 4 to 6 m (McGowan and Motani, 2003; Maxwell, 2012). The skull possesses a moderately long and slender snout packed with slender teeth which lack enamel ornamentation (Maxwell, 2012). The pelvic girdle is bipartite, comprised of an ischium and pubis fused to form a single element and a separate ilium. Forefins are fairly long and slender, and are at least twice the length of the hindfins. The forefins possess four to five digits with tightly packed individual elements; notching is present in some elements of the leading edge. Hindfins are comprised of three to four digits, with notching present in some anterior elements (Maxwell, 2012).



Figure 9. Practically complete skeleton of *Stenopterygius* (SMNS 17500) from the Toarcian Posidonienschiefer, Lower Jurassic, Upper Lias. Photograph courtesy of Dr Dean Lomax.

Despite the high concentrations in the coeval Posidonia Shale of southwestern Germany, very little material found from the Yorkshire Lias has been confidently assigned to *Stenopterygius*, or indeed any species of the genus. A single Whitby specimen, WHITM: SIM876S, which includes a pelvic girdle (a fused pubis and ischium), teeth, and a preflexural vertebral count of approximately 78 was tentatively referred to as *Stenopterygius quadrischissus* by McGowan and Motani (2003). Motani (2005) also discussed two partial skulls from the Toarcian of Whitby (NHMUK/PV R729 and WHITM: SIM 876.2), that were determined to belong to *Stenopterygius longifrons* (now synonymized with *S. trischissus* and *S. uniter*) (Maisch, 2008; Maxwell, 2012). However, as these specimens have been referred to this species tentatively, they should be considered as *Stenopterygius* sp. until further examination of the material is undertaken. The genus occurs along the Yorkshire coast from the Toarcian Whitby Mudstone Formation in the Upper Lias; however, specific biozones have yet to be determined. As highlighted by Lomax (2019a), recently collected specimens, including partial skeletons, isolated skulls and forefins that belong to *Stenopterygius*, are currently stored in private collections and are therefore unavailable for study. As a result, the remains of *Stenopterygius* from the Yorkshire Lias have received insufficient study and are in need of taxonomic revision.

5.2.6 Other Ichthyosaurs

As highlighted by Lomax (2019a), Blake (1876) described a few specimens referred to as *Ichthyosaurus tenuirostris* (now *Leptonectes tenuirostris*) from the Lias of Whitby, including isolated jaws from the York Museum (YORYM) and other specimens housed in the British Museum (now NHMUK), preserved with portions of the skeleton. However, specimen numbers or illustrations were not provided by Blake, and the specimens have not been located. Furthermore, McGowan (1974b)

mentioned a specimen (NHMUK PV OR 36876) that was collected from the Upper Lias of Whitby that could also belong to the species *L. tenuirostris*, but stated that the specimen was too fragmentary and could not be confidently assigned to this taxon. Although this species occurs at various localities in the UK, predominantly Somerset and Dorset, but also Leicestershire, Gloucestershire and Nottinghamshire, *Leptonectes* has never been reported from the Lias of the Yorkshire coast or from the Toarcian (McGowan, 1996).

6. COMPARATIVE MATERIAL

In this study, YORYM 497 was compared with several contemporaneous specimens of *Temnodontosaurus trigonodon* from Holzmaden, southwestern Germany. *Ichthyosaurus trigonodon* (now *T. trigonodon*) was first erected by Theodori (1843) following the description of a large near-complete skull and partial postcranial skeleton, currently on display at the Banz Castle Museum (see chapter 6.1) (McGowan, 1996). As previously discussed (see chapter 5.1), the Lower Jurassic Posidonia Shale of Holzmaden is broadly coeval to the Whitby Mudstone Formation of North Yorkshire, in which several species of marine reptiles are shared between the two strata (Lomax, 2019a). Although many specimens of this large Toarcian ichthyosaur have been discovered from the Lower Jurassic of southwestern Germany, in addition to the Upper Lias of northern France (McGowan and Motani, 2003), *T. trigonodon* has yet to be described from the Yorkshire coast. Nevertheless, as discussed below (see chapter 7), *T. crassimanus* has previously been synonymized with *T. trigonodon* (Lydekker, 1889; Woodward and Sherborn, 1890; Fox-Strangways and Barrow, 1915), therefore in addition to a redescription of the holotype specimen of *T. crassimanus*, a detailed comparison between the two species is essential and long overdue. Furthermore, while *Temnodontosaurus platyodon* is well-known from the Lower Jurassic of England, predominantly from Lyme Regis, Dorset, this species was not included in the following comparison with *T. crassimanus*. The stratigraphic range of *T. platyodon* is from the Hettangian – Sinemurian, which is stratigraphically older than the Toarcian Whitby Mudstone Formation of North Yorkshire, which yielded the holotype of *T. crassimanus*. Additionally, the species diagnosis of *T. platyodon* is also rather poor, with the most recent species diagnosis by McGowan and Motani (2003) stating the following characteristics: 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. Whilst a taxonomic revision for *T. platyodon* is also greatly required, it is beyond the scope of this study.

The following includes a list and a discussion of several specimens of *T. trigonodon* from the Posidonia Shale of Holzmaden, Germany, which were referenced and/or examined as part of this study to aid in species comparison. The descriptions below are brief, as more detailed comparisons are made between these specimens within the redescription of the holotype below (see chapter 8). All specimens of *T. trigonodon* observed at the SMNS can be assigned to the species on the basis of: forefin notching in most elements of leading edge; forefin long; number of elements in longest digit probably > 17; presacral vertebrae probably > 48; rostrum relatively long, snout ratio usually > 0.65 (McGowan and Motani, 2003). The genus diagnosis for *Temnodontosaurus* is presented in chapter 8.

6.1 SPECIMEN PB 1

Temnodontosaurus trigonodon

Posidonienschiefer Formation, Toarcian; Unnersdorf, Germany.

PB 1, on display at the Banz Castle Museum, is the holotype of *T. trigonodon*, which is comprised of a largely complete skull and partial postcranial skeleton. The holotype was not examined as part of this study, but it is included here due to the importance of the specimen. The large skull, which displays excellent osteological detail and individual bone sutures (Figure 10), was estimated to measure approximately 1.8 m in length, and the total body length of the individual was believed to have exceeded 9 m (McGowan, 1996).



Figure 10. The nearly complete skull of the holotype specimen of *Temnodontosaurus trigonodon* (PB 1), on display at the Banz Castle Museum. Photograph courtesy of Dr Erin Maxwell.

Aside from the initial description by Theodori (1843), the skull has been discussed and figured various times (see Theodori, 1854; Fraas, 1891; Huene, 1922; Figure 11), but most recently by Maisch (1998), in which the narial region was illustrated and the specimen was discussed in context with *T. burgundiae* material (now referred to *T. trigonodon*). While it was determined that the total skull length of the holotype was significantly larger than other referred specimens of *T. burgundiae*, Maisch (1998) determined it did not greatly exceed their size range; the skull of the largest referred specimen of *T. burgundiae* (now *T. trigonodon*), SMNS 50000 (as discussed below), was only 14 % smaller than the skull of the holotype (McGowan and Motani, 2003). While most of the features were consistent with those observed on the former *T. burgundiae*, Maisch (1998) highlighted that the only characteristic of the holotype which appeared to vary from other referable *Temnodontosaurus* specimens was a small ventral extension of the lacrimal, which overlies both the premaxilla and jugal (McGowan and Motani,

2003). However, Maisch (1998) stated that the use of this small osteological difference to maintain both *T. trigonodon* and *T. burgundiae* as two different species was insufficient; McGowan also later regarded this feature as not taxonomically useful (McGowan and Motani, 2003). Subsequently, Maisch (1998) stated that all specimens of the Toarcian *Temnodontosaurus burgundiae* from southwestern Germany belong to *Temnodontosaurus trigonodon*.

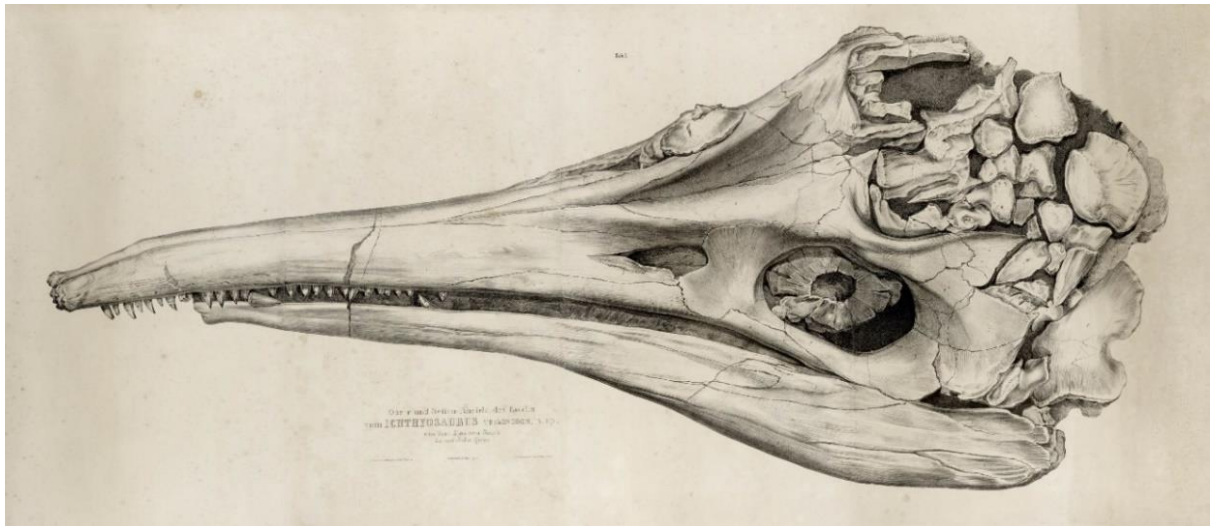


Figure 11. An early illustration of the skull of the holotype specimen of *Temnodontosaurus trigonodon* (PB 1) (Theodori, 1854).

6.2 SPECIMEN SMNS 15950

Temnodontosaurus trigonodon

Posidonienschiefer Formation, Toarcian; Holzmaden, Germany.

SMNS 15950 is described further in comparison to *T. crassimanus* below (see chapter 8), whilst measurements of the specimen are presented in appendix A.



Figure 12. A nearly complete skeleton of *Temnodontosaurus trigonodon* (SMNS 15950). Scale bar equals ~ 160 cm.

SMNS 15950 is a virtually complete and largely articulated specimen, exposed in left lateral view (Figure 12). The specimen is comprised of a well-preserved skull, both forefins, pectoral girdle elements, both hindfins, pelvic elements, ribs, and a largely articulated vertebral column. The total preserved length of the specimen, measured along the vertebral column and including the skull, is approximately 777.1 cm, whilst the preflexural length (including the skull) is 646.5 cm. The estimated vertebral precaudal count is 51, based on the position of the pelvis (see McGowan, 1996). Additionally, while the preserved tail bend on this specimen is prominent, this could potentially be preservational and may not represent the true tail bend of the individual. The skull of the specimen is well-preserved, whilst the majority of the cranial bones and individual sutures are well-defined. The preserved skull measures approximately 160 cm (including the recreated rostrum), while the preserved jaw length is 164.9 cm. In addition to possessing a relatively long rostrum, McGowan and Motani (2003) stated that this specimen possesses a small overbite, as the tip of the snout extends beyond the mandible. However, this could be due to severe taphonomic compression, as the tip of the snout appears to have been damaged and slightly displaced. The teeth on this specimen are reconstructed, therefore measurements were not taken. The orbit, which is noticeably longer than high, appears to be slightly compressed and a partial sclerotic ring is preserved. The external naris is overall relatively large in size, and dorsoventrally 'pinches' anteriorly. Due to the preservational angle of SMNS 15950, posterior skull elements are not exposed.

While the pectoral girdle is well-preserved, the majority of elements are either partially covered by overlying ribs or by other associated pectoral elements, preventing accurate measurements. Both humeri are exposed, with both possessing a rounded head, a constricted shaft and a widely expanded distal end, being almost as anteroposteriorly wide as they are proximodistally long. The elements also possess two prominent distal facets for the radius and the ulna. Whilst the right forefin is partially obscured by overlying vertebrae and ribs, the left forefin is particularly well-preserved; both forefins are moderately long and particularly slender. The forefins have 3 primary digits (II, III, IV; Motani, 1999), in addition to an accessory digit, whilst there are 12 elements in the longest digit (digit II, left forefin). Notching is present on the leading edge of all elements in digit II on both forefins, with the exception of the radius and radiale on the left forefin and the radiale on the right. Additionally, both ulnae also appear to possess a proximal notch on the preaxial margin; although whilst unlikely, this could potentially be due to damage. The closely packed distal carpals, metacarpals and phalanges range from polygonal to oval distally and the accessory digit elements are rounded in shape. The pelvic girdle, particularly the elements presumably from the left, are well-preserved. The ischia are robust elements with widely expanded proximal and distal ends, whilst the left ischium appears partially fused distally to the pubis and overlain by the associated ilium. While the preserved elongate femora are somewhat similar in length to the above humeri, the distal end of the elements are considerably less expanded in comparison to the humeri; no distal facets are present on either femora. Like the forefins, both hindfins are well-preserved, moderately long and particularly slender. The hindfins are composed of 3 primary digits (II, III, IV), whilst the longest digit is composed of 16 elements (digit IV, left hindfin). The closely packed distal tarsals, metatarsals and phalanges of both hindfins range from polygonal to oval distally. Notching is again present on the leading edge of all

elements in digit II on both hindfins, except for the last three phalanges on the left hindfin, and one phalanx on the right forefin; however, it appears that in both instances, these un-notched phalanges are most likely displaced from digit III. Furthermore, as discussed by Pardo-Pérez et al. (2018), the specimen also displays various pathologies, including improperly healed ribs bearing pseudarthroses and cranial injuries to the upper jaw.

6.3 SPECIMEN SMNS 50000

Temnodontosaurus trigonodon

Posidonienschiefer Formation, Toarcian; Ohmden, Germany.

SMNS 50000 is described in further detail below, compared with *T. crassimanus* below (see chapter 8), whilst measurements of the specimen are presented in appendix A.

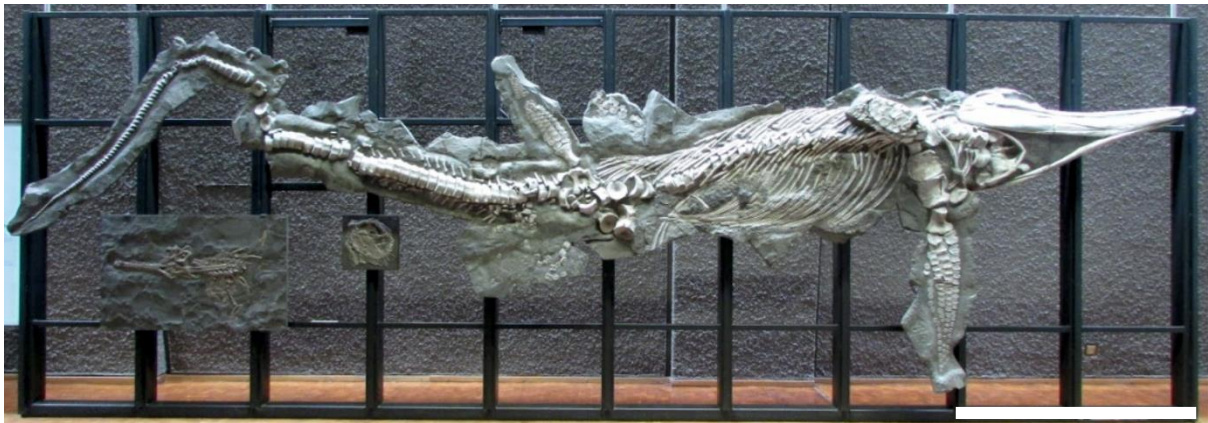


Figure 13. The nearly complete skeleton of *Temnodontosaurus trigonodon* (SMNS 50000). Scale bar equals ~ 170 cm.

SMNS 50000 is a large, nearly complete, and somewhat largely articulated specimen, primarily exposed in ventral view (Figure 13). The specimen is comprised of a somewhat well-preserved skull, both forefins, pectoral girdle elements, a hindfin, pelvic elements, ribs, and a vertebral column that is disarticulated in parts. The total preserved length of the specimen, measured along the vertebral column, and including the skull, is approximately 916 cm, whilst the preflexural length could not be determined due to disarticulation. Numerous vertebrae in the pectoral region are buried by overlying ribs and are poorly exposed, therefore meaning that they could not be counted; however McGowan (1996) estimated the precaudal count to the pelvis to be approximately 50. Similar to SMNS 15950, the preserved tail bend appears rather ‘prominent’; however this is most likely due to the preservation of the specimen, rather than representing the original tail bend. Although best exposed in ventral view, the majority of the right side of the skull is exposed and rather well-preserved, with

individual elements and cranial sutures being well-defined. The preserved skull of SMNS 50000 measures approximately 153 cm, and like SMNS 15950, McGowan and Motani (2003) stated that this specimen also possesses a small overbite, as the tip of the snout extends beyond the mandible; however, this could be again due to taphonomic distortion or the preservation of the individual. The orbit, which is noticeably longer than high, appears to have been slightly crushed, whilst the upper section of the sclerotic ring is preserved.

Although somewhat disarticulated, the pectoral girdle is well-preserved, including both coracoids, the right scapula, partial left scapula and a clavicle. The coracoids, in particular, are clearly exposed and each possess a prominent anterior notch, whilst both elements are mediolaterally wider than anteroposteriorly long. Although both humeri are exposed, the humerus of the left forefin is undoubtedly the best preserved. The humerus possesses a rounded head, a constricted shaft and a widely expanded distal end; being almost as anteroposteriorly wide as they are proximodistally long. The element also possesses two slight prominent distal facets for the radius and ulna. While the right forefin is somewhat poorly preserved and disarticulated, the left forefin is well-preserved and has previously been figured in the literature (see McGowan, 1996; McGowan and Motani, 2003); the fin is moderately long and particularly slender. The forefin has three primary digits (II, III, IV), in addition to what might be an accessory digit or digit V, and there are at least 17 elements in the longest digit (digit II); however some distal elements may be missing, meaning this figure could potentially be higher. Notching is present on the leading edge of all elements in digit II on the left forefin, although it is not possible to determine for the right forefin. Whilst the ulna is slightly overlaid by the humerus, the element appears to possess a proximal notch on the preaxial margin; although it is unlikely, this could again be due to damage. As observed on the previous specimen (SMNS 15950), the closely packed distal carpals, metacarpals and phalanges of the left forefin range from polygonal to oval distally, and the accessory digit elements are also rounded in shape.

While the pelvic girdle of the specimen is disarticulated, the ischium appears partially fused distally to the pubis. The preserved elongate femur is considerably shorter and more slender in comparison to the humerus, with the distal end of the element being considerably less expanded than that of the left humerus; no distal facets are preserved on the femur. Only the right hindfin is preserved, while several disarticulated isolated elements of the left hindfin are also exposed. Like the left forefin, the hindfin is mostly well-preserved, moderately long and particularly slender; however the total length of the fin cannot be measured due to disarticulation. The hindfin is composed of three primary digits (II, III, IV), in addition to what might be an accessory digit, whilst the number of elements in the longest digit cannot be determined due to the partial disarticulation of the fin. Additionally, notching appears to be present on the leading edge of all elements in digit II.

6.4 SPECIMEN SMNS 17560

Temnodontosaurus trigonodon

Posidonienschiefer Formation, Toarcian; Schömburg, Germany.

SMNS 17560 is described in further detail below, compared with *T. crassimanus* below (see chapter 8), whilst measurements of the specimen are presented in appendix A.



Figure 14. A three-dimensional mounted skeleton of *Temnodontosaurus trigonodon* (SMNS 17560). Scale bar equals ~ 70 cm.

SMNS 17560 is a three dimensionally mounted skeleton, composed of a replica skull and authentic fore- and hindfins, accompanied by a mostly reconstructed skeleton (with the exception of some vertebrae) (Figure 14); the original skull is displayed elsewhere. All of the authentic material associated with SMNS 17560 is from a single individual, thus the specimen is not a composite (E. Maxwell, 2019, pers comm.). The skull of the specimen is mostly well-preserved, with the exception of minor restoration work to the rostrum, whilst the majority of the cranial bones and individual sutures are well-defined. The preserved skull measures approximately 150.2 cm in length, whilst the

preserved jaw length is 154.3 cm; the rostrum is relatively long. The orbits, which are noticeably longer than high, appear to be partially damaged/distorted, whilst a large portion of the sclerotic ring is preserved in each opening. The external nares are relatively large in size and appear to dorsoventrally pinch anteriorly, although the right naris is damaged. The posterior of the skull is significantly well preserved, with individual elements including the basioccipital, exoccipitals and quadrates being very prominent. Although somewhat poorly preserved, there are approximately 116 original teeth preserved in the rostrum; approximately 67 teeth on the left side of the jaw and 49 teeth on the right side. The best-preserved tooth, situated on the left side of the jaw, measures 34.5 mm in length and 14.7 mm in width. They are relatively robust and possess heavily grooved roots, with smooth striations and lineation between the root and the crown.

Both humeri are preserved and possess rounded heads, constricted shafts and widely expanded distal ends; being almost as anteroposteriorly wide as they are proximodistally long. As highlighted on the right humerus, the element also possesses two slight distal facets for the radius and the ulna. Both forefins are well-preserved and are long and somewhat slender. The forefin has three primary digits (II, III, IV), in addition to what might be an accessory digit or digit V, and there are at least 11 elements in the longest digit (digit II, on both forefins); however some distal elements may be missing. In both forefins, notching is present on the leading edge of all elements, in addition to a proximal notch on the preaxial margin of both ulnae; whilst unlikely, this could potentially be due to damage. It is also worth noting that both ulnae, especially apparent on the left ulna, possess a notch on the posterior margin, although this could be due to damage. As observed on both of the previous specimens (SMNS 15950 and SMNS 50000), the closely packed distal carpals, metacarpals and phalanges of the forefins range from polygonal to oval distally, with the accessory digit elements also being rounded in shape. Although the left femur is a cast, the right femur is well-preserved and is similar in length to the preserved humeri. The proximal end of the element is less expanded compared to the widely expanded distal end of the humerus. The hindfins are well-preserved, moderately long and noticeably more slender than the forefins. The hindfins are composed of three primary digits (II, III, IV), whilst the number of elements in the longest digit is approximately 16 (digit IV, right hindfin); however some distal elements may be missing, particularly on the left hindfin. The closely packed distal tarsals, metatarsals and phalanges of both hindfins range from polygonal to oval distally. Additionally, on both hindfins, notching appears to be present on the leading edge of all elements in digit II.

7. THE HISTORY OF *TEMNODONTOSAURUS CRASSIMANUS*

During the 19th century, the Yorkshire coast was extensively quarried for the manufacture of alum, which in turn revealed the remains of many marine reptiles (Benton and Taylor, 1984; Osborne and Bowden, 2005). Kettleness Alum Works, north of Whitby, exposed sections in the Mulgrave Shale and Alum Shale members and produced many specimens during operation, including YORYM 497 (Benton and Taylor, 1984). The specimen was discovered in 1857 during quarrying and was reported to have been found within a few yards of the type specimen of the plesiosaur *Rhomaleosaurus cramptoni*, but 15 or 16 feet higher in the Main Alum Shales (Carte and Baily, 1863; Benton and Taylor, 1984). YORYM 497 was donated to the Yorkshire Museum by the Rev. D. R. Roundell in 1857, where it has remained on display (Figure 15). The specimen was initially considered to be *Ichthyosaurus platyodon* (see discussion in Melmore, 1930). In 1858, the specimen was examined by Owen who recognised it to be distinct from *I. platyodon* and therefore considered it to be a new species, *I. crassimanus*; however he never described the species (Melmore, 1930). Following a brief reference by Phillips and Etheridge (1875, p. 272), YORYM 497 was formally described by Blake (1876), albeit briefly, in which the similarities it shared with *I. platyodon* were noted. However, the specimen was suggested to differ from *I. platyodon* by the relative size of the fins, as *I. crassimanus* was described to possess larger forefins in comparison to the hindfins, while the fins of *I. platyodon* were of equal size (McGowan and Motani, 2003). This was also reiterated further by Simpson (1884, p. 12). Nevertheless, Lydekker (1889a) later expressed the opinion that there was no reason to separate *I. crassimanus* and *I. trigonodon* (as discussed in Melmore, 1930). Woodward and Sherborn (1890) briefly mentioned *I. crassimanus*, in which they included the species as a query under *I. trigonodon*, which was further supported by Fox-Strangways and Barrow (1915, p. 20) who considered both species to be synonymous.

Subsequently, the holotype specimen was redescribed by Melmore (1930), which was the most detailed description of the specimen. Although Melmore determined that the relative snout length and the size of the skull and its openings were similar in both *I. crassimanus* and *I. trigonodon*, a number of characters were proposed which apparently showed sufficiently that the two ichthyosaurs should be regarded as distinct and valid species. In particular, it was suggested that the tooth crown of *I. crassimanus* was conical, not trigonal; the vertebrae were longer, while the costal tubercles possessed a distinct concavity; both the humerus and femur were thinner relative to their length; the femur was proportionally shorter when compared to the humerus; and the radius was proportionally shorter in relation to the humerus, when compared to *I. trigonodon* (Melmore, 1930). McGowan (1974a) later proposed that only *I. platyodon*, *I. acutirostris* and *I. longirostris*, along with the new species *T. risor* and *T. eurycephalus* from the Lower Jurassic of England were valid and suggested that *I. crassimanus* was a junior synonym of *I. acutirostris* (*Stenopterygius acutirostris*). Subsequently, it was determined that there were no major inconsistencies between YORYM 497 and WHITM: SIM2546S, which was also referred to as *S. acutirostris*, and as they were both reported to be from the same locality and horizon, it was assigned to that species by McGowan (1974a). However,

McGowan and Motani (2003) later suggested that the holotype of *T. crassimanus* appeared to differ from *T. platyodon* and *T. trigonodon* sufficiently to warrant retention of the taxon, but implied that further research could question its validity. They stated that due to the lack of complete skeletons of any *Temnodontosaurus* species, it is difficult to determine whether the differences between the relative lengths of the fore and hindfins are consistent, therefore, deeming Blake's (1876) distinguishing feature as currently of little taxonomic use. McGowan and Motani (2003) also provided a diagnosis for *T. crassimanus* and stated that it is distinguished from other Toarcian ichthyosaurs by a combination of characters including the fact that forefin notching probably does not include more than four elements and certainly does not involve most of the elements of the leading edge and that the presacral vertebrae number fewer than 48.

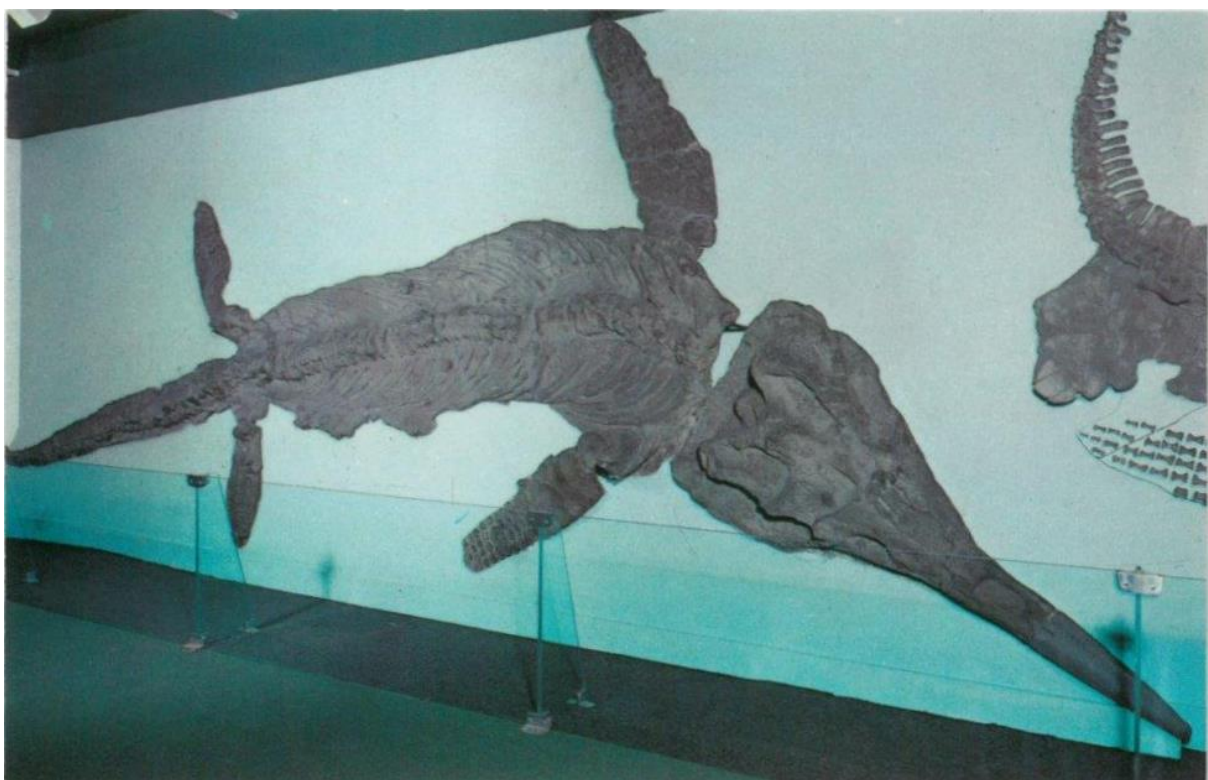


Figure 15. The three-dimensional mounted skeleton of *Temnodontosaurus crassimanus* (YORYM 497) wall-mounted during the 1970s, in addition to the original recreated rostrum. Photograph courtesy of York Museums Trust :: <http://yorkmuseumstrust.org.uk/> :: Public Domain.

In the following, a detailed redescription of the holotype of *T. crassimanus* (YORYM 497) is presented. The following also includes comparisons to several contemporaneous specimens of *Temnodontosaurus* from both Yorkshire, including WHITM: SIM2546, WHITM: SIM5, MANCH: L.1688, MANCH: LL. 16096, and several similar-sized specimens of *T. trigonodon* from Germany, including SMNS 15950, SMNS 50000 and SMNS 17560 (see chapter 6), which have previously been mentioned and described in various studies (e.g. McGowan, 1996; Pardo-Pérez et al., 2018). The

Yorkshire specimens mentioned here are discussed further below in the assessment of possible additional specimens (see chapter 9). Furthermore, although isolated remains of large-bodied ichthyosaurus from the Yorkshire Lias are often referred to as *Temnodontosaurus* sp., and may perhaps belong to *T. crassimanus* (Lomax, 2019a), the comparative material used in this study focused exclusively on complete or partial skeletons and isolated skulls.

8. REDESCRIPTION OF THE HOLOTYPE OF *TEMNODONTOSAURUS CRASSIMANUS* AND COMPARISON WITH *TEMNODONTOSAURUS TRIGONODON*

SYSTEMATIC PALAEOLOGY

Ichthyosauria de Blainville, 1835

Parvipelvia Motani, 1999b

Temnodontosauridae McGowan, 1974a

***Temnodontosaurus* Lydekker, 1889b**

Type species: Temnodontosaurus platyodon (Conybeare, 1822); Hettangian – Sinemurian, Lower Jurassic of England, UK.

Genus diagnosis – Modified from McGowan and Motani (2003); Martin et al. (2012) and Ji et al. (2016): large nonthunnosaurian usually 7 – 12 m in length; long and robust snout, with a ratio usually < 0.65 but > 0.59 ; nasal-parietal contact lateral to frontal present; maxilla with long anterior process, extending as far as the nasal anteriorly; 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; forefin probably < 5 digits; ulnare smaller than intermedium; at least two notches in anterior-most elements of leading edge of forefin and hind fin, sometimes involving most elements; forefin and hind fin composed of numerous roughly hexagonal elements; phalanges may be well spaced distally; constricted humerus; distal end of humerus markedly wider than proximal end, probably with prominent preaxial facet; anterodistal margin of femur slightly enlarged; pubis and ischium separate but may be partially fused; preflexural vertebrae probably > 80 .

***Temnodontosaurus crassimanus* (Blake, 1876)**

Ichthyosaurus crassimanus Blake, 1876: 253

Stenopterygius acutirostris Owen; McGowan, 1974a: fig. 11A

Temnodontosaurus crassimanus McGowan and Motani, 2003: 87

Holotype – YORYM 497, a large, three-dimensionally preserved partial skull and an associated incomplete skeleton comprising pectoral girdle elements, both forefins and hindfins, pelvic elements, ribs, and a largely articulated, although incomplete vertebral column.

Referred material – No additional material could be confidently assigned to this species (see below).

Previous species diagnosis – Forefin notching probably does not involve more than four elements and certainly does not involve most of the elements of the leading edge; presacral vertebrae probably > 48 (McGowan and Motani, 2003).

Emended species diagnosis – Large-bodied temnodontosaurid ichthyosaur with the following characters: humerus proximodistally longer than scapula (scapula length vs humerus length ratio: ~ 0.68); forefin significantly longer but less than twice the length of the hindfin (forefin length vs hindfin length ratio: ~ 1.51); forefins large relative to total body length (forefin length vs estimated total body length ratio: ~ 0.12), anteroposteriorly wide fore- and hindfins; number of elements in the longest digit probably > 15; notching of the anterior facet of at least five leading edge elements (digit II) of both fore- and hindfin, but most likely does not involve all of the elements of the leading edge.

8.1 COMPARATIVE DESCRIPTION

General preservation. YORYM 497 is a large, three-dimensionally preserved partial skeleton including a skull and postcranial skeleton, best exposed in dorsal view (Figure 16). It is mostly embedded in the original matrix, with the exception of some of the elements of the right forefin and right hindfin, which have been reset in plaster. These elements, comprised mostly of the phalanges, are in a ‘random orientation’, indicated by the presence of notching facing posteriorly (incorrectly). The majority of vertebrate specimens discovered from Whitby and the surrounding areas during the 19th century were prepared by hand, which may have led to ‘artificial improvements’ made to certain specimens (Benton and Spencer, 1995). This can be observed on YORYM 497, as several ‘teeth’ in the jaws of the holotype appear to have been carved in to the original matrix during preparation, giving the appearance of a more-complete dentition. The skull is poorly-preserved and has suffered taphonomic deformation, with the right side bearing more damage than the left. The lower jaw is also slightly disarticulated with respect to the upper. In addition to the poor preservation, the skull is also heavily pyritized, dense and bears a significant amount of chisel marks from the original preparation, which has all contributed to the poor condition of the specimen.

Additionally, it was determined that the hindfins had been reversed and were placed on the opposite side of the mounted skeleton, as demonstrated by the presence of notching and the articulation with preserved pelvic bones; this had previously gone unnoticed in other studies (e.g. Melmore, 1930), although it is possible that the confusion may have occurred more recently. The specimen represents a large individual with a total preserved length, from the tip of the incomplete skull to the last preserved caudal vertebra, of approximately 730.5 cm and a preflexural length of approximately 560 cm. While the anterior portion of the rostrum and a portion of the posterior caudal region is missing, with the body being incomplete beyond the tail bend, the total length of YORYM 497 is estimated at approximately 9 m, based on an estimated 70 cm missing from the skull and > 1 m missing in the caudal region. The last preserved mid-caudal vertebrae are also disarticulated from the vertebral column, forming an isolated block.



Figure 16. The three-dimensional skeleton of *Temnodontosaurus crassimanus* (YORYM 497) showcased in the new Yorkshire's Jurassic World exhibition at the Yorkshire Museum. Note that it is now impossible to photograph the complete skeleton due to the specimen being on permanent display.

Ontogenetic stage. Limited research has been conducted on the ontogeny of ichthyosaurs (Johnson, 1979; Deeming et al., 1993), and while it is not the case for some genera, juvenile specimens of *Temnodontosaurus* have been described. McGowan (1995) examined three specimens formerly referred to as *T. risor*, in addition to a previously undescribed, three-dimensionally preserved specimen collected from the Black Ven, east of Lyme Regis, to determine the validity of the species. The skull of the latter specimen was significantly larger compared with the post-cranial skeleton and both fore- and hindfins were noticeably smaller, relative to the skull length. The skull also possessed a distinctly curved rostrum, similar to the specimens formerly referred to as *T. risor*, in which it was determined that the new specimen belonged to the same species. This work concluded that *T. risor* represents an immature stage and McGowan (1995) suggested that the former is a juvenile of *T. platyodon*, and forms part of a growth series for that species (McGowan, 1995).

Although it is widely accepted that an increase in age accompanied by an increase in size could determine relative age, Johnson (1979) highlighted how osteological features associated with sexual maturity or immaturity can be used to estimate relative age in ichthyosaurs, irrespective of their size. The study focused on the pectoral girdle and forefin of 26 specimens of *Stenopterygius*, in addition to gravid females, all of which were collected from the Lower Jurassic of Germany. Specimens were arranged relative to size based on humeral length to establish a growth series and the material was then compared with a neontological model of growth, based on descriptions of reptilian epiphyseal

and long bone ontogeny (Johnson, 1979). Results highlighted that four characters of the forefin were observed to differ consistently between ontogenetic stages and could collectively be used as reliable measure of relative age, including;

(i) The shape of the proximal articular surface of the humerus appears flat in immature specimens and convex in sexually mature specimens.

(ii) The surface texture of the shaft of the humerus is textured in immature specimens, while in sexually mature specimens this surface is smooth.

(iii) The sutures between the proximal fin elements in immature specimens are open, while in adults, the sutures between articulating members are closed.

iii) For species in which notching of the leading edge of the elements of the first digit is a characteristic feature of the adults, notching was rudimentary or absent in the immature specimens.

While the above characteristics were concluded from specimens of *Stenopterygius*, these criteria could prove useful in estimating relative age in other fossil reptiles (Johnson, 1979). On YORYM 497, the shape of the proximal articular surface of the right humerus appears convex, while the surface texture of the shaft appears smooth, which are both considered to be indicators of maturity in *Stenopterygius* (Johnson, 1979). However, while a convex humeral head was suggested to be indicative of a sexually mature individual, McGowan (1995) suggested that the angle at which the humerus is observed can affect the convexity of the humeral head. Additionally, approximately four and five elements of digit II of the left and right forefins respectively of the specimen are notched, and the sutures between articulating proximal fin elements are closed on YORYM 497, further suggesting an adult (Johnson, 1979). YORYM 497, similar to other species of *Temnodontosaurus* (McGowan, 1996), has a large total preserved length of 730.5 cm, with a total estimated length of approximately 9 m, thus representing a large individual. Additionally, Fernández et al. (2005) explored how the relative size of the sclerotic ring and orbits can be used in estimating relative age in some ichthyosaurs, and determined that in juvenile parvipelvic ichthyosaurs, the sclerotic ring almost completely filled the entire orbit, while in mature individuals, it fills significantly less of the orbit. Despite this juvenile characteristic being present in several *Temnodontosaurus* specimens observed as part of this study (e.g. NHMUK R.792; Figure 17), unfortunately, no sclerotic rings are preserved in the orbits of YORYM 497. While age-related criteria have not currently been determined specifically for *Temnodontosaurus*, YORYM 497 possesses several characteristics, which in addition to the large total body size, suggests that this is likely to be a fully mature individual.



Figure 17. A partial skull of ?*Temnodontosaurus acutirostris* (NHMUK PV R.792) from the Upper Lias of Whitby, in right lateral view. Note how the sclerotic ring almost completely fills the entire orbit. Scale bar equals 5 cm.

Cranium and mandible. Measurements of the skull are presented in Table 5. The skull is preserved in three dimensions, but best preserved in dorsal view (Figure 18). As originally highlighted by Melmore (1930), due to the deformation and preservation, as mentioned above, the robust skull generally only provides information on its general proportions and on the size of the openings. Individual cranial sutures are difficult to distinguish, with the majority of bones also being difficult to identify, resulting in a limited assessment and description of skull elements. Furthermore, the skull is missing a significant section of the anterior portion of the rostrum (Figure 19), meaning the full length of the skull and jaw cannot be determined.



Figure 18. The three-dimensional skull of *Temnodontosaurus crassimanus* (YORYM 497) in dorsal view. Scale bar equals 10 cm.

SMNS 50000, SMNS 15950 and SMNS 17560 (*T. trigonodon*) all have similar sized skulls to YORYM 497 (see appendix A for measurements) and are therefore used for comparison below. The preserved skull of YORYM 497 measures 137 cm long, while the preserved jaw length is approximately 154 cm. The missing portion of the snout was originally reconstructed in plaster (McGowan, 1974a), and the rostrum has also since been partially repaired. The estimated skull length for YORYM 497 (~ 1.7 m) is only marginally smaller than large skull of the holotype of *T. trigonodon* (PB 1; Figure 20), which measures approximately 1.8 m in length (McGowan, 1996).

The orbits are slightly deformed, probably due to crushing, particularly noticeable on the right, and as previously discussed, no sclerotic rings are preserved. However, the left orbit is less distorted, and appears oval in shape, being longer (33 cm) than tall (18 cm). Although the length of the orbits may potentially be exaggerated due to taphonomic compression, the orbits of YORYM 497 are significantly larger than the slightly crushed orbit of SMNS 50000 (length = 26.5 cm, height = 14.2 cm), despite the skulls of both specimens being of similar size. The jugal, postfrontal and postorbital are partially visible; however, individual sutures are difficult to distinguish, and it is not possible to describe their morphology. In lateral view, seen best on the left side, although damaged, it is clear that the nasal makes up most of the dorsal margin of the external naris, whereas the supranarial process of the premaxilla makes up a small portion of the anterior margin of the naris. The external nares of YORYM 497 are large, oval and appear to dorsoventrally 'pinch' posteriorly, unlike in SMNS 15950 and SMNS 17560 where the nares pinch anteriorly. Both nares on YORYM 497 are longer (15.5 cm and 13cm) than tall (8 cm and 9 cm) (left and right naris respectively), and are of similar size to the external naris of SMNS 15950. In dorsal view, the nasals are wide posteriorly, although sutures are difficult to follow, but anteriorly, they end abruptly in a narrow pinch ~ 20 cm anterior to the external naris; this feature was also observed in specimens of *T. trigonodon*, including SMNS 17560 and SMNS 15950. In lateral view, some of the maxilla is exposed, but badly damaged, and appears to be a dorsoventrally low element that extends anteriorly well beyond the external naris; a feature which is typical of *Temnodontosaurus*, including *T. trigonodon* (as observed on SMNS 17560).



Figure 19. The three-dimensional skull of *Temnodontosaurus crassimanus* (YORYM 497) in dorsolateral view, highlighting the absence of the anterior portion of the rostrum.

Scale bar equals 10 cm.

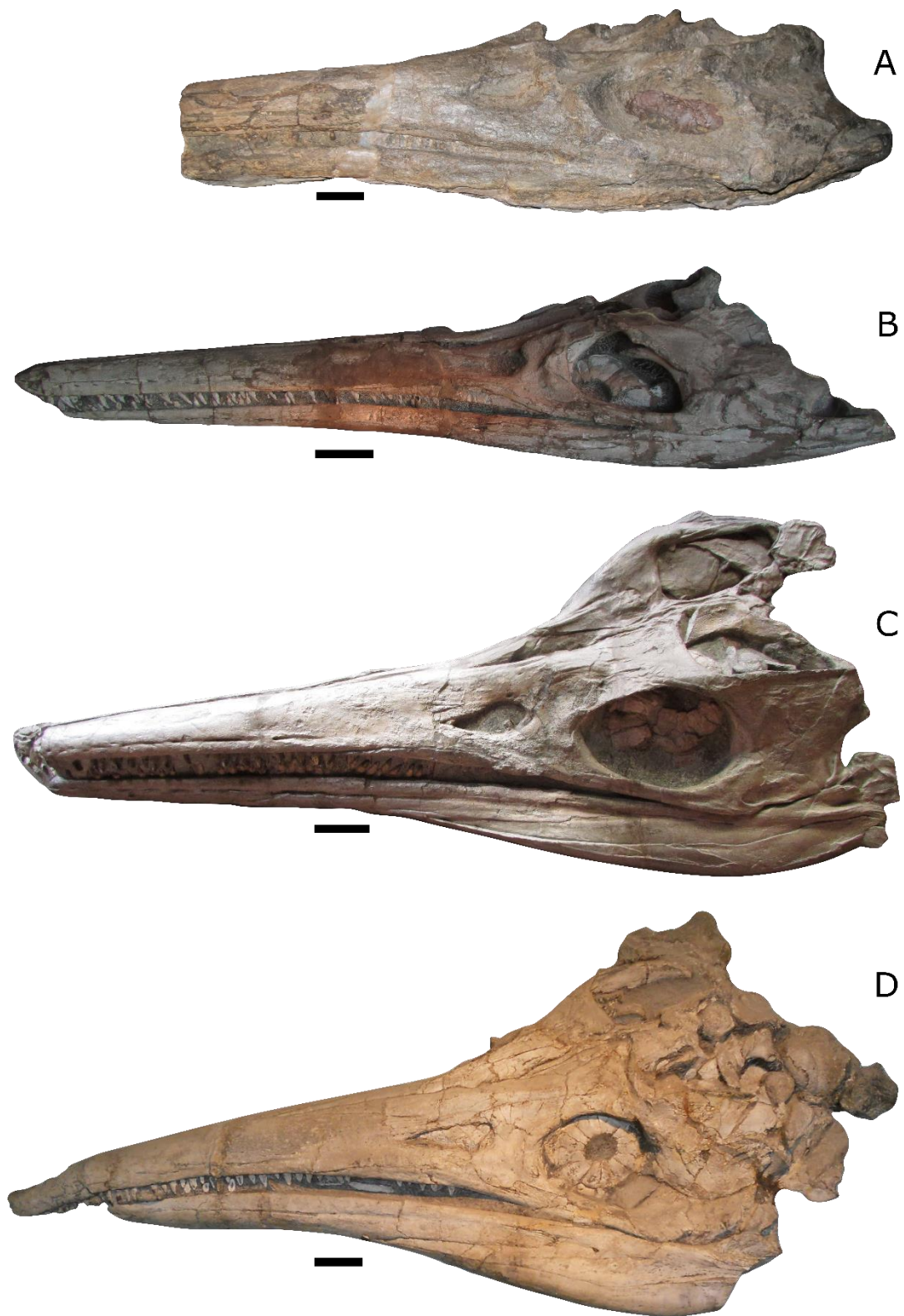


Figure 20. Skull comparison of similarly sized *Temnodontosaurus* **(A)** Partial skull of *T. crassimanus* (YORYM 497) in left lateral view. **(B)** Skull of *T. trigonodon* (SMNS 17560) in left lateral view. **(C)** Skull of *T. trigonodon* (SMNS 15950) in left dorsolateral view. **(D)** Skull of the holotype of *T. trigonodon* (PB 1) in left lateral view. Scale bars equal 10 cm.

As previously noted by Melmore (1930), the basioccipital condyle in YORYM 497 is clearly exposed (Figure 21) and is an extremely robust element, measuring approximately 12 cm wide and 10 cm high, similar in proportion to the condyle of SMNS 17560. The extracondylar area is also partially exposed and wide, and measures approximately 18 cm wide and 12 cm high. The paired exoccipitals are preserved dorsal to the dorsal surface of the basioccipital and, although they are partially covered by matrix, they are longer, with a larger shaft width, in comparison to SMNS 17560. The elements are slender and strongly expanded at both the proximal and distal ends, appearing markedly hourglass-shaped (Figure 22).

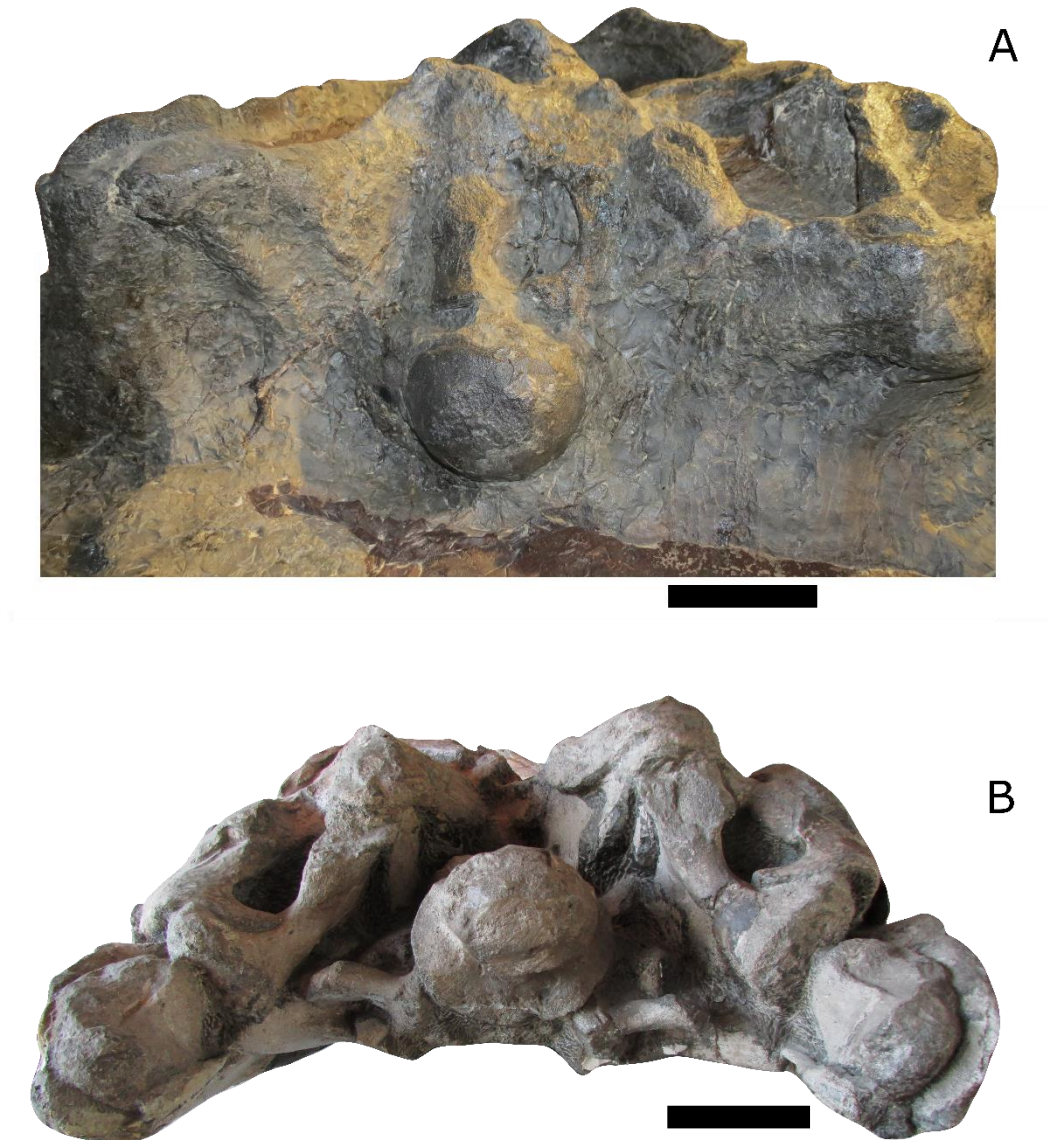


Figure 21. Comparison of posterior skull elements **(A)** Three-dimensional skull of *T. crassimanus* (YORYM 497) in posterior view. **(B)** Three-dimensional skull of *T. trigonodon* (SMNS 17560) in posterior view. Note the large basioccipital condyle and extensive extracondylar area of both species. Scale bars equal 10 cm.



Figure 22. Close up of the basioccipital condyle, extracondylar area and paired exoccipitals of *T. crassimanus* (YORYM 497) in posterior view. Scale bar equals 5 cm.

Only the left quadrate is preserved, which is a large and robust element exposed on the posterior surface of the left side of the skull (Figure 23). In posterior view, the quadrate appears crescent-shaped and possesses a strong lateral curve to the shaft. The element is greatly expanded laterally, although the articular condyle is buried. Despite the distal end being partially obscured, the quadrate has a preserved dorsoventral length of approximately 23 cm, and a shaft width of 6.5 cm; the right quadrate of SMNS 17560 is relatively shorter than that of YORYM 497, in addition to the quadrate shaft width SMNS 17560 which is less than half the size of the shaft width of the holotype of *T. crassimanus*. Other elements of the skull are preserved, notably the parietal, but other than noting its presence very little can be said about sutural contacts and extent of elements given the poor preservation. Similarly, a portion of what is probably a large pineal foramen is also preserved, but its morphology and placement cannot be determined, although it appears to be between the frontals and parietal, as in other *Temnodontosaurus* (McGowan and Motani, 2003, fig. 69).



Figure 23. The robust left quadrate of *T. crassimanus* (YORYM 497) in posterior view.
Scale bar equal 10 cm.

Dentition. Ignoring the reconstructed teeth from the surrounding matrix, approximately 21 original teeth are preserved in the rostrum. The teeth are poorly preserved, and the majority are covered by matrix, meaning that limited measurements and comparisons can be made, contrary to Melmore (1930) who suggested that the tooth morphology was unusual in comparison to *T. trigonodon*. They are relatively robust, with smooth striations and lineation between the root and the crown, although a complete crown is not present. As the teeth are embedded in the matrix, the full circumference of the teeth are obscured. The best-preserved tooth, situated on the left side of the jaw, measures 21.1 mm in height, and 10.4 mm in width, but the root and crown of this tooth is buried (Figure 24). Although somewhat poorly preserved, the largest tooth, situated on the right side of the jaw, measures 32.5 mm in total height and 16.4 mm in total width.



Figure 24. The best-preserved tooth of *T. crassimanus* (YORYM 497), situated on the left side of the jaw, in left lateral view. Scale bar equals 1 cm.

Features	(cm)
Skull length	137*
Skull width (posterior)	88*
Skull width (in front of orbit)	42
Skull width (proximal most point)	14
Jaw length (left)	154
Jaw length (right)	152
Right UTF length	34
Right UTF width at widest point	11
Right UTF width at narrowest point	7
Left UTF length	38
Left UTF width	15.5
Parietal width	15
Parietal length	25
Basioccipital condyle width	12
Basioccipital condyle height	10

Extracondylar area width	18
Extracondylar area height	12
Right exoccipital length	10.2*
Right exoccipital distal width	4
Left exoccipital length	9
Left exoccipital distal width	5
Left exoccipital proximal width	5
Left exoccipital shaft width	4
Left preorbital length	76
Right preorbital length	77.3
Left preaural length	52
Right preaural length	53.5
Right orbit length	32*
Right orbit height	18
Left orbit length	33
Left orbit height	18
Left external naris length	15.5
Left external naris height	8
Right external naris length	13
Right external naris height	9
Left quadrate length	23
Left quadrate shaft width	6.5

Table 5. Measurements of the skull elements of YORYM 497.

**Denotes an estimate as the bone is damaged, or elements are missing/not preserved.*

Axial skeleton. Measurements of the axial skeleton are presented in Table 6. Due to the estimated total length of YORYM 497, SMNS 50000 was the most suitable specimen for morphological comparison due to the relative size of both specimens.

A partially complete, largely articulated vertebral column preserves 84 centra, with at least 45 precaudal centra preserved, however the atlas-axis are not exposed, and it is possible that at least two or three vertebrae could be missing at the back of the skull. In the most recent diagnosis for *T. crassimanus*, McGowan and Motani (2003) proposed that the species probably possesses >48 presacral vertebrae, similar to *T. trigonodon*, which is supported by the above precaudal count. The total preserved length of YORYM 497, measured along the vertebral column and, including the incomplete skull, is 730.5 cm. Excluding the skull, the specimen has a precaudal length (measured along the vertebral column) of approximately 333 cm, and a preflexural length of approximately 560 cm, although this is an estimate. The majority of the preserved centra exceed a diameter of 15 cm,

with the dorsal centra having an average width of 15.4 cm and average length of 6.2 cm (Table 6; Figure 25). However, the size of some centra are difficult to determine as some portions of the vertebral column are buried, displaced or disarticulated, which hindered measurements. Although the width of many centra could not be measured, the average length of the dorsal centra of SMNS 50000 was 5.4 cm, smaller than the average length recorded from YORYM 497.

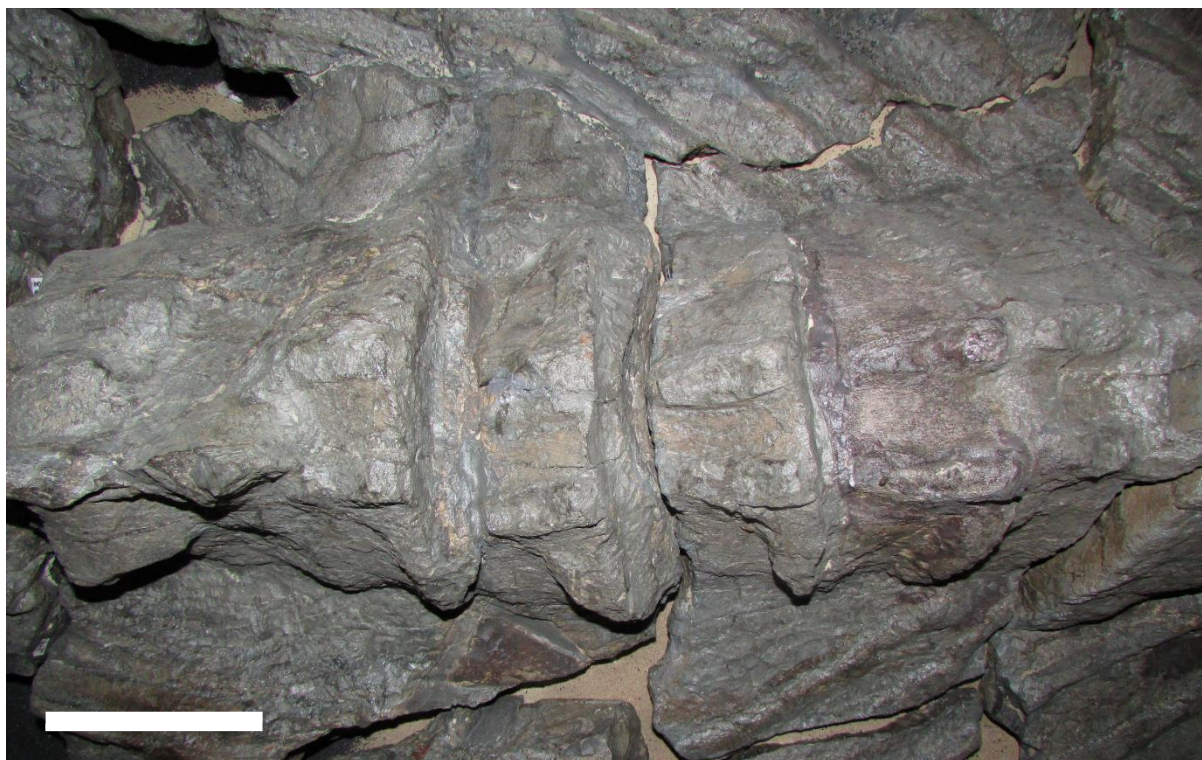


Figure 25. Articulated mid-dorsal vertebrae of *T. crassimanus* (YORYM 497) in dorsal view, highlighting the poor, fragmentary preservation of the specimen. Scale bar equals 10 cm.

Vertebral centrum width increases along the vertebral column to an average width of 16.5 cm and average length of 5.9 cm for the preflexural vertebrae. Overall, centrum width slowly increases to centrum 48, followed by an overall gradual decrease in width from centra 49 – 84. Centrum length demonstrates less variation, with a gradual increase from centra 1 – 18, followed by a slow decrease through the tail stock. The majority of vertebrae are exposed in dorsal view, so the height of the articulated centra could not be determined. Although rib attachments are buried, based on the position of the hindfins, the last precaudal vertebrae of YORYM 497 is estimated to be centrum 45, although see comments above regarding atlas-axis and possible missing vertebrae. As discussed (see chapter 6.3), numerous vertebrae in the pectoral region of SMNS 50000 are buried by overlying ribs and are poorly exposed, meaning that the count to the last precaudal vertebrae at the pelvis was difficult to determine. However McGowan (1996) estimated the precaudal count to the pelvis to be approximately 50, in addition to estimating the vertebral count to the pelvis of SMNS 15950 to be 51.

The vertebral count of both specimens of *T. trigonodon* are marginally higher than the precaudal count of 45 from YORYM 497; however, this discrepancy could be justified by the absence of approximately at least three or more vertebrae, including the atlas/axis, at the back of the skull.

Following the precaudal count, there are 39 caudal vertebrae to the last preserved vertebra on YORYM 497, although beyond here, the rest of the caudal region is missing. Centra 78 – 84 are detached from the remaining vertebral column and are articulated together in an isolated block, in addition to centrum 77 which is also isolated (Figure 26). Based on the size dimensions of these vertebrae, it is likely that the isolated block of caudal vertebrae does not articulate with the vertebral column and that additional vertebrae are missing from this section. The last articulated vertebra (centrum 76) measures a width of 13.5 cm, a height of approximately 11.4 cm and a length of 4.4 cm, while the next isolated vertebrae (centrum 77) measures 12 cm wide, 10.6 cm in height and 4 cm in length, demonstrating an unusual reduction in size that further suggests vertebrae are missing in this portion of the column.

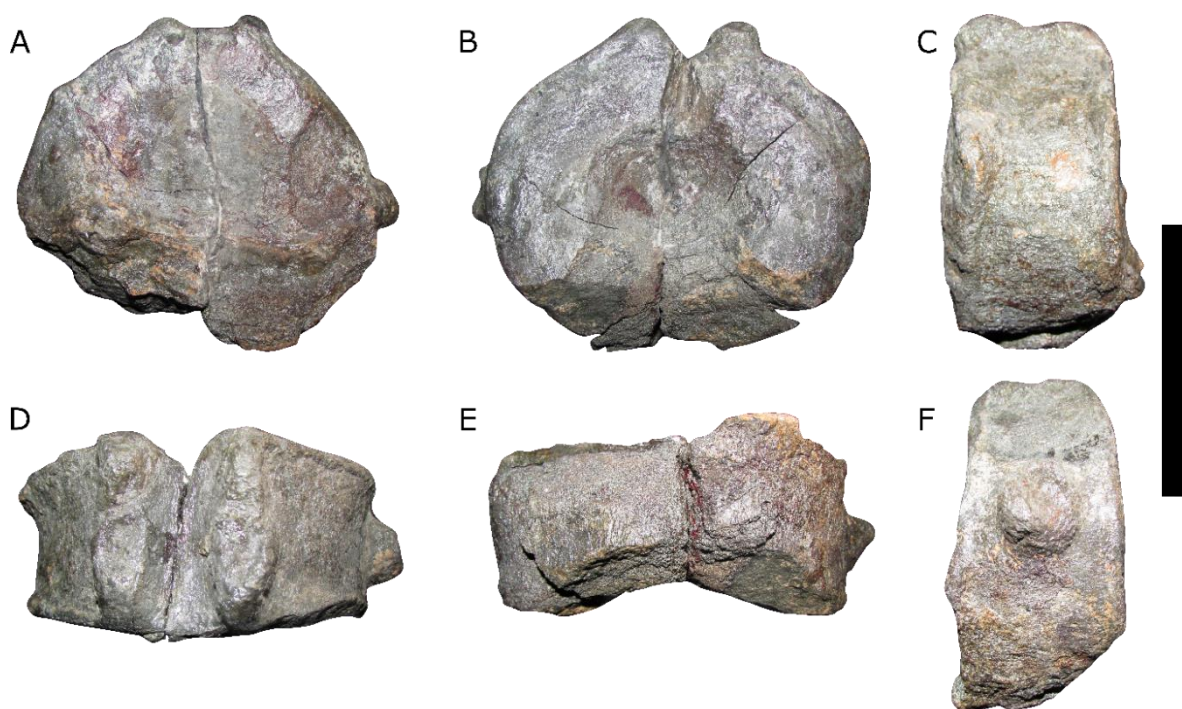


Figure 26. An isolated vertebra (centrum 77) of *T. crassimanus* (YORYM 497). **(A)** Anterior view; **(B)** posterior view; **(C)** left lateral view; **(D)** dorsal view; **(E)** ventral view; **(F)** right lateral view. Scale bar equals 10 cm.

No neural arches are visible on YORYM 497 and the preservation of the neural spines is poor, although the base of the neural spine on centrum 49 is well preserved. Many large rib fragments are present, but no individual rib is complete. The longest preserved rib measures 66.5 cm along its curvature, but the distal end is partially buried, and the majority of the preserved ribs are fragmented.

In comparison, the longest rib of SMNS 50000 and SMNS 15950 is 83.5 cm and 90.5 cm respectively. Ribs overall decrease in thickness along the vertebral column, and a rib cross-section is not visible. The first caudal rib of YORYM 497 is associated with vertebrae 46. No gastralia are preserved.

Vertebra No. (As preserved)	Vertebra width (cm)	Vertebra length (cm)	Vertebra height (cm)
1	13	-	
2	14	5	
3	12.5	4	
4	14	5.5	
5	15	5.5	
6	14.5	6	
7	14	5.5	
8	15*	6	
9	16*	6*	
10	16.5*	5.5*	
11	-	-	
12	-	-	
13	14.5*	5.3*	
14	15*	5.5*	
15	15*	-	
16	14	-	
17	15	6	
18	15*	7.5	
19	16.5	7	
20	15.5*	5*	
21	15	7	
22	15.5	7	
23	15*	6.3	
24	14.5	7	
25	15.5	7	
26	15.5	6.5*	
27	-	5.5	
28	-	-	
29	-	-	
30	-	-	
31	15.5	6	
32	16	6.2	

33	15	5.5	
34	16	7	
35	16*	5.5	
36	16	6	
37	16	6.5	
38	16	7	
39	16	5*	
40	-	-	
41	-	-	
42	-	6.5	
43	-	-	
44	-	6	
45	-	-	
46 **	17	6	
47	18	5.8	
48	18	6.5	
49	17	6	
50	17.5	6.5	
51	17.5	6.6	
52	17.5	6.5	
53	17.5*	6*	
54	-	6.5	
55	17.5	6	
56	17	6.2	
57	17.5	6.5	
58	17.5	6.5	
59	16.5	5.8	
60	17	6	
61	17	5.3	
62	15	5.8	
63	15.5	6.5	
64	17	5.6	
65	16.5*	5.5*	
66	17.5	-	
67	17.5	6.4	
68	16.5	6.5	
69	15.5	5.5	
70	15	5.5	
71	16.5	-	

72	15.5	-	
73	15.7	4.8*	
74	15	5	
75	13.5	5.6	
76	13.5	4.4	11.4*
77	12	4	10.6
78	10.7	5	-
79	11.9	3.8	9
80	10.1	4.2	9.7
81	9.5	3.4	9
82	9	3.4	8
83	7.6	3.7	7.3
84	7.3	3.6	7.6

Table 6. Measurements for the preserved vertebral column of YORYM 497. *Denotes an estimate as the bone is damaged, or elements are missing/not preserved. **Denotes the first caudal vertebrae.

Pectoral girdle. Measurements of the pectoral girdle are presented in Table 7. Most of the pectoral girdle is poorly preserved and elements are also either obscured by matrix, or only partially exposed. However, the right scapula is preserved and visible in dorsal and lateral view (Figure 27). The scapula is laterally compressed and along the long-axis, the preserved length of the element is 21 cm. Although it appears complete, the proximal end could be marginally damaged with a portion missing (although < 3/5 cm). When compared with the humerus length, the scapula length vs humerus length ratio is approximately 0.68 (Table 7; Table 8), whereas the right scapula of the similarly sized *T. trigonodon*, SMNS 50000, measures 28.9 cm along the long-axis, and possesses a scapula length vs humerus length ratio of approximately 1.42. Similarly, the left scapula of SMNS 15950 measures 27.6 cm and has a scapula length vs humerus length ratio of approximately 1.28; therefore the humerus is much longer than the scapula in *T. crassimanus*, whereas this feature is reversed in *T. trigonodon* and is unique. On YORYM 497, the scapula shaft is relatively thick, while this robust element also possesses a strong curve. In SMNS 50000, the distal end of the scapula appears rather flared and expanded, and is considerably wider than the distal end of the scapula of YORYM 497, which appears more rounded in shape; however, the preservation and preparation could account for this difference in shape. A portion of the clavicle is also preserved and exposed in dorsal view, but is broken. The preserved length of the clavicle is approximately 14 cm, with a shaft width of 3 cm.

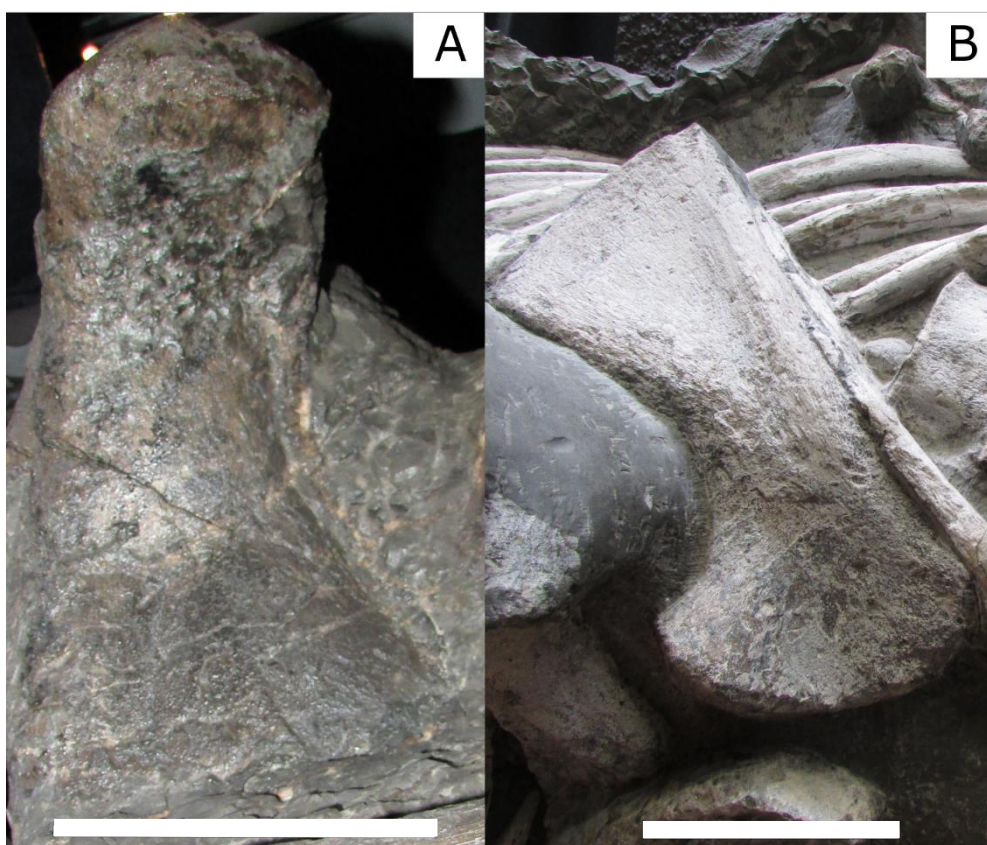


Figure 27. Scapula comparison of two similarly sized *Temnodontosaurus*. **(A)** Right scapula of *T. crassimanus* (YORYM 497) in lateral view. **(B)** Scapula of *T. trigonodon* (SMNS 50000) in lateral view. Scale bars equal 10 cm.

Features	(cm)
Scapula length	21
Scapula proximal width	12.5
Scapula distal width	7.8*
Partial clavicle length	14*
Partial clavicle shaft width	3

Table 7. Measurements for the pectoral girdle of YORYM 497.

*Denotes an estimate as the bone is damaged, or elements are missing/not preserved.

Ratio	YORYM 497	SMNS 50000	SMNS 15950	SMNS 17560
Scapula length vs humerus length	0.68	1.42	1.28	1.42
Humerus length vs femur length	1.24	1.25	1.16	1.26
Forefin length vs hindfin length	1.51	*	1.30	1.20
Forefin length vs total estimated body length	0.12	0.07	0.09	*

Table 8. Notable ratios calculated for both *T. crassimanus* (YORYM 497) and *T. trigonodon* specimens (SMNS 50000, SMNS 15950, SMNS 17560), as discussed in the following.

**Denotes ratios that could not be determined.*

Forefins. Measurements of the forefins are presented in Table 9 and 10. Both forefins are preserved in dorsal aspect, and although they are incomplete, they are both well-preserved (Figure 28). While the individual elements of the right forefin are better preserved than the elements of the left forefin, the majority of the phalanges of the right forefin have been reset in plaster in a random orientation, identified by the presence of notching facing posteriorly, the incorrect direction. To aid with description, the left forefin is described first.

The left humerus is not exposed and thus the description of the humerus is based on the right, described below. There are three primary digits (II, III, IV) in addition to what is probably an accessory digit, or alternatively digit V (although see Motani, 1999a) as observed in *T. trigonodon*. Excluding the humerus, the fin has a preserved length of at least 106 cm (from the proximal tip of the radius) and a maximum preserved width of 37 cm (at the widest point). Including the radius, radiale, distal carpal 2 and metacarpal two, there are 15 elements in the longest digit (digit II), which also has the largest elements of the four preserved digits. In *T. trigonodon*, the number of elements in the longest digit usually exceeds 17 (Motani, 1999a; McGowan and Motani, 2003), as seen in SMNS 50000. However, due to the preservation of YORYM 497, the forefins are incomplete, meaning that the proposed number of elements in the longest digit of *T. crassimanus* may be underestimated and could be higher, similar to *T. trigonodon*. The radius and ulna are wider than long, with the radius both longer and wider than the ulna. The radius (14 cm wide and 11.5 cm long) and ulna (13 cm wide and 8 cm long) are wider than long, with the radius both longer and wider than the ulna, although only marginally wider. The radiale and intermedium are approximately equal in size, while the ulnare is longer but smaller in width than either of the two elements (Table 9). The ulnare also appears to be overlapped by distal carpal 4, but this might be due to the displacement or deformation. The distal carpals, metacarpals and phalanges range from sub-rectangular to oval distally; the polygonal, closely packed carpals and metacarpals of YORYM 497 are comparable to those of other *Temnodontosaurus*

species, including *T. trigonodon*. At least four elements of digit II, including distal carpal 2 and three phalanges are notched on the leading edge. The radius also appears notched; however the damage and preservation makes this difficult to confirm.

Regarding the right forefin, the humerus is a large, robust element that is 31 cm long, and noticeably wider distally than proximally (27 cm and approximately 12 cm, respectively; Table 10), being almost as distally wide as the element is long. The humerus is also clearly constricted mid-shaft. The proximal end possesses a rounded head and the humerus dorsal process is prominent and largely centrally located. The humerus bears minor damage to the proximal end; however, what appears to be a broken edge anteroproximally, is distinctly sloped and is in fact original and not the result of damage. When compared with *T. trigonodon*, the preserved humerus of YORYM 497 is remarkably longer (proximodistally) than all observed specimens (Figure 29) which is clearly highlighted when compared to specimens of similar total body length (e.g. the left humerus of SMNS 50000 is 20.4 cm in length). The humerus length ratio of YORYM 497 vs SMNS 50000 is approximately 1.52. The humerus proximal width of the holotype is only marginally larger than all observed specimens of *T. trigonodon*. However, while the humeri of both specimens are wider distally than proximally, the humeral distal width of YORYM 497 is considerably larger than the distal width of *T. trigonodon*, as demonstrated by SMNS 50000, with a ratio of approximately 1.42. Additionally, the humeral distal width vs proximal width ratio of YORYM 497 is approximately 2.25, whereas the ratio of SMNS 50000 is approximately 1.73. This difference is also observed in SMNS 15950, as the left humeral distal width vs proximal width ratio is approximately 1.74, highlighting that the humeral distal width of YORYM 497 is significantly wider than that of *T. trigonodon*, when compared to the proximal width. As with the left forefin, there are three primary digits (II, III, IV) in addition to an accessory digit (or what might be digit V), and the fin has a preserved length of approximately 107 cm (excluding the humerus) and a maximum preserved width of 33 cm (at the widest point); the total length of the right forefin is estimated as the distal elements are set in plaster. The radius and ulna are wider than long, while both elements are approximately equal in size. The radius is approximately 14 cm wide and 10 cm long, while the ulna is approximately 14.5 cm wide and 10 cm long; the intermedium is wider than both the radiale and ulnare (Table 10). The distal carpals, metacarpals and phalanges range from sub-rectangular to oval distally, and the accessory digit elements are rounded. However, digit II has eight distal elements reset in random orientation in plaster, demonstrated by some notched elements facing the wrong direction, so the morphology of this part of the fin cannot be considered accurate. Approximately five elements of digit II, including the radius (Figure 30) and distal carpal 2 appear notched on the leading edge, in addition to three phalanges that are reset in plaster; however the damage and preservation makes this difficult to confirm.

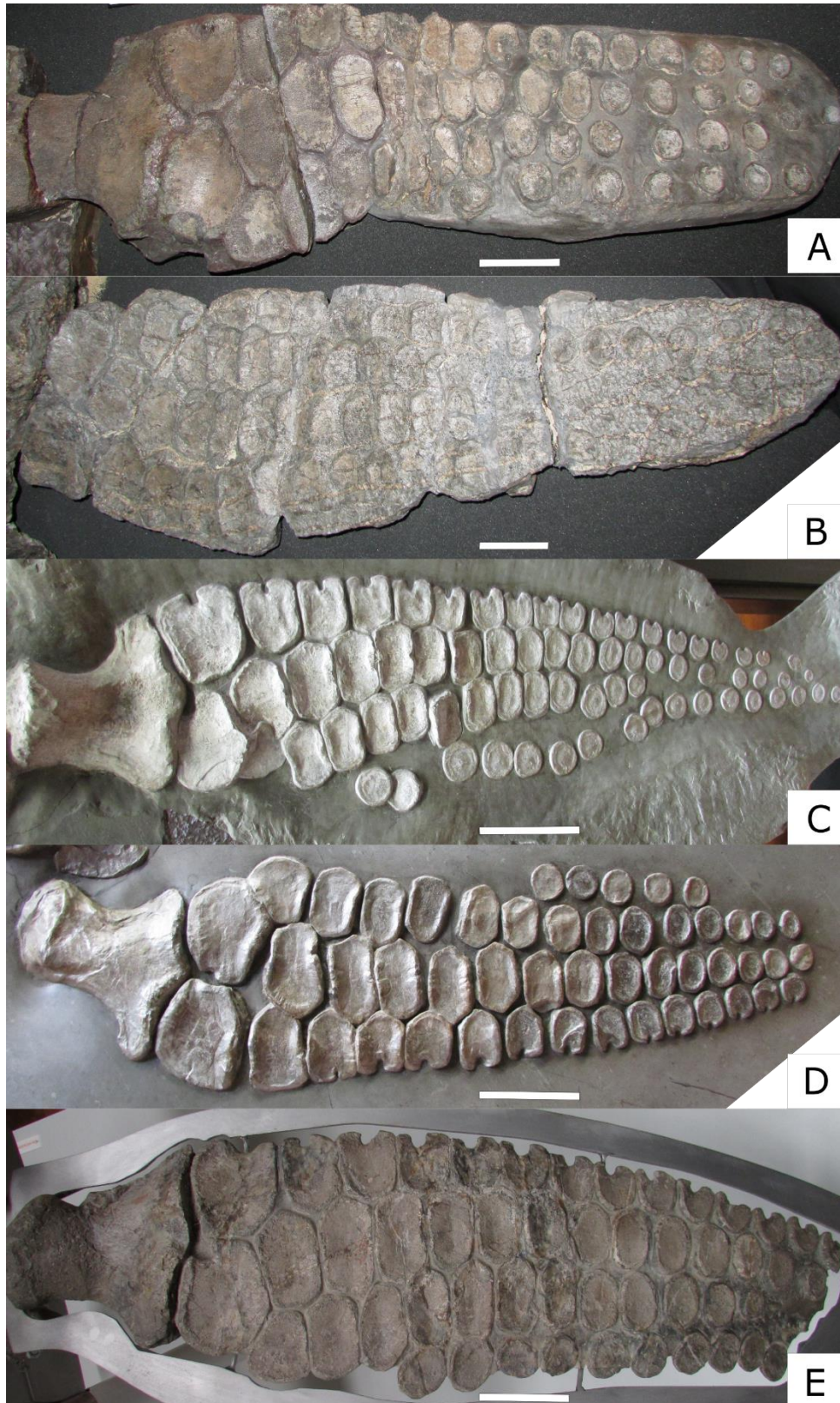


Figure 28. Forefin comparison **(A)** Right forefin of *T. crassimanus* (YORYM 497) in dorsal view. **(B)** Left forefin of *T. crassimanus* (YORYM 497) in dorsal view. **(C)** Left forefin of *T. trigonodon* (SMNS 50000) in ventral view. **(D)** Left forefin of *T. trigonodon* (SMNS 15950) in dorsal view. **(E)** Left forefin of *T. trigonodon* (SMNS 17560) in dorsal view. Scale bars equal 10 cm.

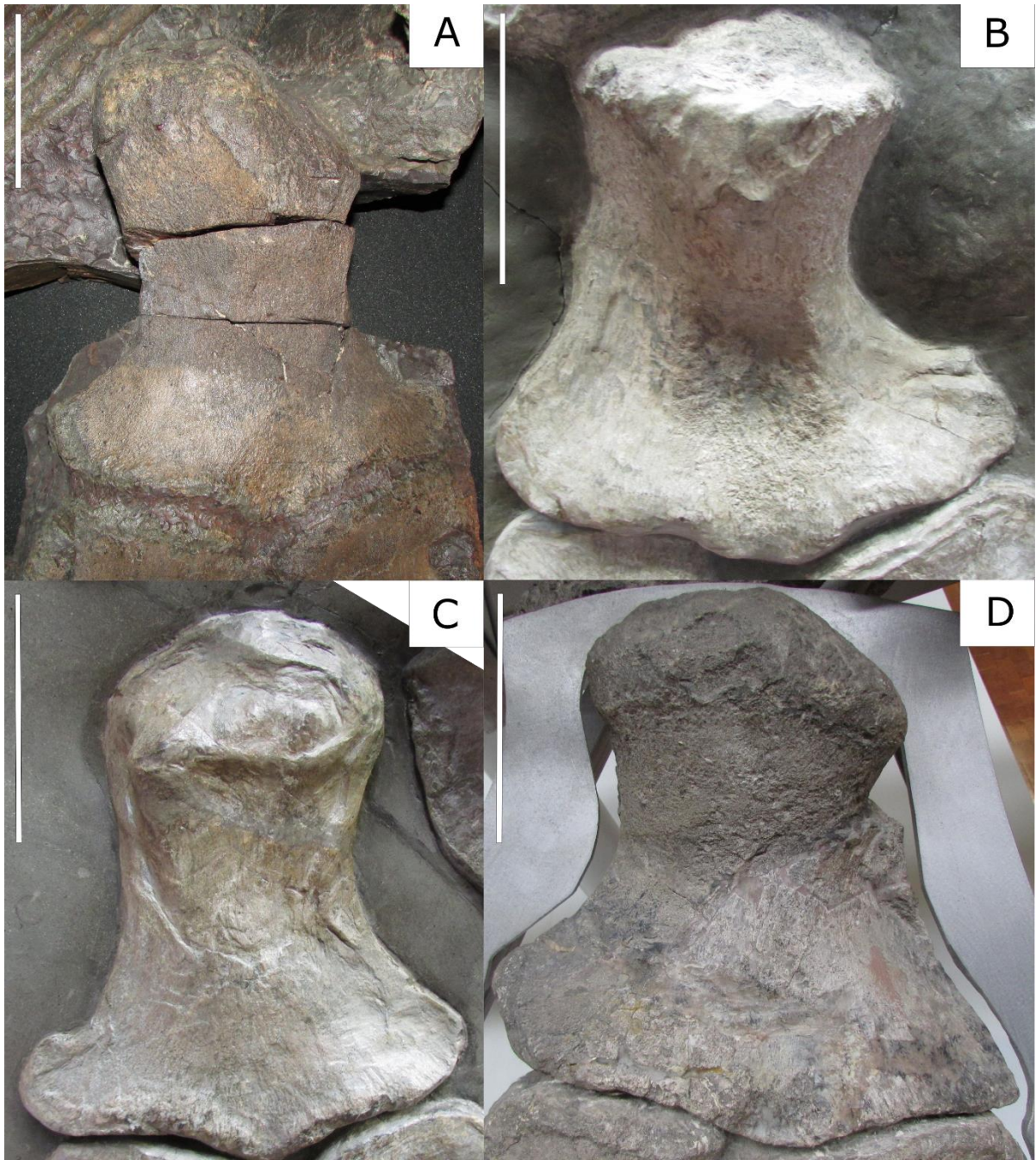


Figure 29. Humeral comparison **(A)** Right humerus of *T. crassimanus* (YORYM 497) in dorsal view. **(B)** Left humerus of *T. trigonodon* (SMNS 50000) in ventral view. **(C)** Left humerus of *T. trigonodon* (SMNS 15950) in dorsal view. **(D)** Right humerus *T. trigonodon* (SMNS 17560) in dorsal view. Scale bars equal 10 cm.

The initial description of YORYM 497 by Melmore (1930) states that none of the elements on the leading edge were notched, and that instead two elements, including the radius, possess a 'conical depression near the anterior margin' (Melmore, 1930). However, McGowan and Motani (2003) later proposed that forefin notching of *T. crassimanus* probably does not involve more than four elements and certainly does not involve most of the elements of the leading edge. While not all of the elements on digit II of the forefins of YORYM 497 are notched, it is evident that at least four fin elements of the anterior digit (digit II) on the left forefin are notched, as are at least five on the right forefin (Figure 28; Figure 30). In contrast, as previously stated, forefin notching is observed to be present in most elements of the leading edge in *T. trigonodon*, as seen on SMNS 50000, SMNS 15950 and SMNS 17560, and therefore seemingly distinct from YORYM 497. However, it is possible that more elements of digit II may be notched, although the somewhat poor preservation of the forefins of the holotype means that this is difficult to confirm and thus assess the taxonomic utility of this character in *T. crassimanus*; it does, however, appear to be different to *T. trigonodon*.



Figure 30. Distal end of right humerus with articulated radius and ulna of YORYM 497, *Temnodontosaurus crassimanus*. Note the notched radius in dorsal view, highlighted by the red arrow. Scale bar equals 10 cm.

Blake (1876) originally noted that the forefin length of YORYM 497 was approximately twice the length of the hindfin and was unusual when compared with other specimens of *Temnodontosaurus*, including *T. platyodon*. While the hindfin length of YORYM 497 is somewhat comparable with specimens of *T. trigonodon*, the preserved total forefin length of the specimen is significantly larger, despite the incompleteness of the fins (Figure 28). Due to the distal elements being set in plaster on the right forefin, only the left forefin of YORYM 497 was used in fin comparisons. As discussed above, the left forefin of YORYM 497 measures 106 cm in length (excluding the humerus), in comparison to the left forefin of SMNS 50000 which is 65.6 cm in length (excluding the humerus), resulting in a forefin length ratio of approximately 1.61. Additionally, the left forefin of SMNS 15950 measures 73.1 cm in length (excluding the humerus), resulting in a forefin length ratio for YORYM 497 vs SMNS 15950 of approximately 1.50; overall, this demonstrates a seemingly distinct and significant difference in forefin length between both species. Furthermore, the forefins are much larger relative to total body length in *T. crassimanus*, than in *T. trigonodon*. The forefin length vs total estimated body length ratio of YORYM 497 is approximately 0.12, whereas this ratio for SMNS 50000 is approximately 0.07. Additionally, the forefins of *T. trigonodon* appear more slender when compared to the anteroposteriorly wider forefins of YORYM 497; the left forefin of YORYM 497 is 37 cm wide, compared to a width of 23.4 cm for the left forefin of SMNS 50000, resulting in a forefin width ratio of approximately 1.60 and therefore further highlighting a difference in forefin morphology. However, McGowan and Motani (2003) stated that it has yet to be determined whether there are any consistent differences between the relative lengths of the fore- and hindfins among species of *Temnodontosaurus*, so this characteristic and the above ratios should be used with caution when comparing specimens. Nevertheless, it is clear that there is a difference in overall forefin size and length in *T. crassimanus* and *T. trigonodon*.

Features	(cm)
Radius width	14
Radius length	11.5
Ulna width	13
Ulna length	8*
Radiale width	11.5
Radiale length	7
Intermedium width	11.5
Intermedium length	7
Ulnare width	10.5
Ulnare length	9
Width of preserved forefin (at widest point)	37
Length of preserved forefin	106

Table 9. Measurements for the left forefin of YORYM 497.

*Denotes an estimate as the bone is damaged, or elements are missing/not preserved.

Features	(cm)
Humerus length	31
Humerus proximal width	12*
Humerus distal width	27
Humerus shaft width	14
Humerus distal width vs proximal width ratio	2.25
Radius width	14
Radius length	10
Ulna width	14.5
Ulna length	10
Radiale width	11
Radiale length	7.2
Intermedium width	13
Intermedium length	7
Ulnare width	8
Ulnare length	7.5
Width of preserved forefin (at widest point)	33
Length of preserved forefin	107*

Table 10. Measurements for the right forefin of YORYM 497.

**Denotes an estimate as the bone is damaged, or elements are missing/not preserved.*

Pelvic Girdle. Measurements of the pelvic girdle are presented in Table 11. The pelvis is poorly preserved, and the majority is obscured by matrix, heavily fractured or not preserved. The left pubis, ilium and ischium are preserved in lateral view. The ilium is a long, narrow element with a slightly flared proximal end, and has the longest preserved length of all the pelvic elements, although this could be due to the damage affecting the relative lengths of the pubis and ischium. The ilium length vs femur length ratio is approximately 0.68. The ilium is broken into two, with the proximal end preserved with the associated pubis and ischium, and the distal end preserved with the femur of the associated fin. Melmore (1930) originally described the identified ilium as the pubis and stated that in addition to the bone being greatly foreshortened, the fragment of the bone remained near to its natural position, situated on top of the head of the femur. With the exception of this fragment, Melmore (1930) did not describe any other pelvic bones, suggesting that the pelvic girdle of YORYM 497 was not recognised and therefore accounting for the mis-identification of the ilium; however, this may have been missed due to the confusion between the left and right hindfins (as discussed above, see chapter 3). The ischium is an elongate and robust bone and is the widest of the preserved pelvic elements. It appears to be expanded proximally and distally, although both ends of the ischium are damaged. The pubis appears the shortest of the pelvic elements and curves slightly posteriorly, but is partially obscured by

matrix, limiting further observations and measurements. The pelvic girdle of *T. trigonodon* specimen SMNS 15950 is well-preserved and seems morphologically similar to the preserved pelvic elements of YORYM 497 (Figure 31). However, the pubis and ischium of SMNS 15950 are partially fused distally, whereas the two elements of YORYM 497 look to be separate; however, this could potentially be due to the poor preservation of the pelvic girdle.

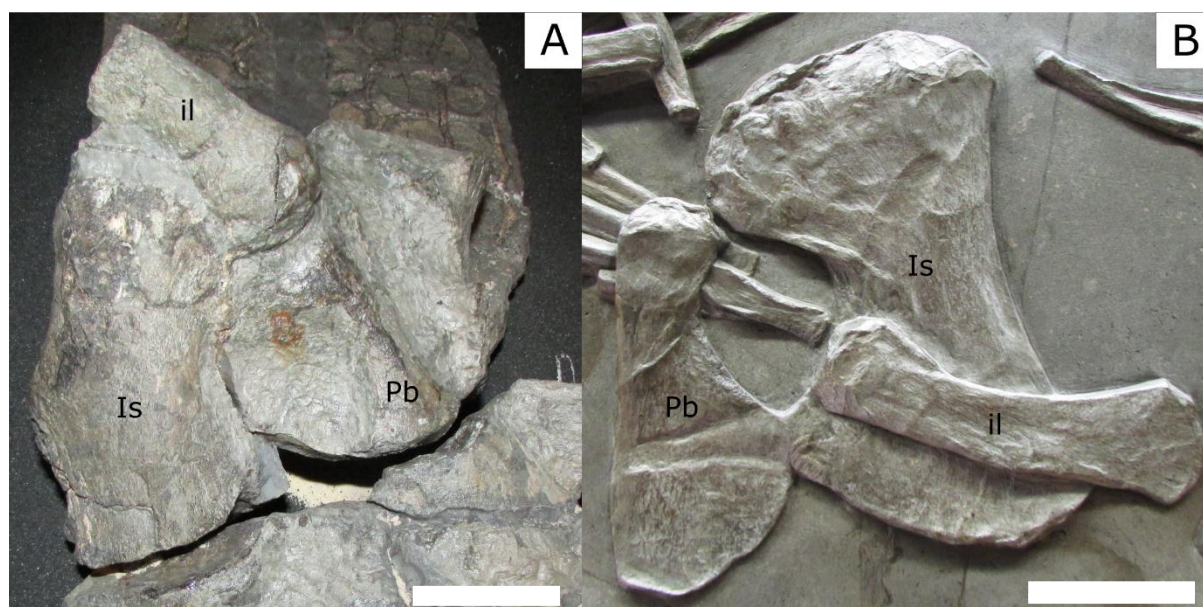


Figure 31. Pelvic comparison **(A)** Preserved pelvic girdle of *T. crassimanus* (YORYM 497) in lateral view. **(B)** Pelvic girdle of *T. trigonodon* (SMNS 15950) in lateral view. Abbreviations: Is, ischium; Pb, pubis; il, ilium. Scale bars equal 5 cm.

Features	(cm)
Pubis length	14.5
Ischium length	16.5
Ilium length	17
Ilium distal width	6
Ilium proximal width	5.5
Ilium depth	6.7
Ilium length vs femur length ratio	0.68

Table 11. Measurements for the pelvic girdle of YORYM 497.

Hindfins. Measurements of the hindfins are presented in Table 12 and 13. Both hindfins are preserved in dorsal aspect and, although they are incomplete, are at large well-preserved. As discussed previously (see chapter 3), it was determined that the hindfins had been reversed and were articulated

on the opposite side of the mounted skeleton. Only a partial femur is exposed on the right hindfin, thus the description of the femur is based on the left.

The femur is a large, elongate, robust element with a rounded head, a dorsal process that is offset anteriorly, a constricted shaft and is noticeably wider distally than proximally (20 cm and approximately 10.5 cm, respectively; Table 12). The element is 25 cm in length and resembles the humerus in being noticeably longer (proximodistally) than the femur of all observed specimens of *T. trigonodon* (Figure 32); the femur length ratio of YORYM 497 vs SMNS 50000 is approximately 1.53, in addition to the ratio of YORYM 497 vs SMNS 15950 being approximately 1.34. Melmore (1930) originally proposed that the femur of YORYM 497 is proportionally shorter in relation to the humerus than when compared with specimens of *T. trigonodon*. For YORYM 497, the humerus length vs femur length ratio is approximately 1.24, whereas on SMNS 15950, the humerus length vs femur length ratio is approximately 1.16, demonstrating that the elements of *T. trigonodon* are more in proportion. However, this was proven not always to be the case, as the humerus length vs femur length ratio of SMNS 50000 is approximately 1.25, and therefore proportionally shorter in comparison to YORYM 497, highlighting that this does not appear to be a reliable character. Like the humerus, the proximal width of the femur is only marginally larger than all observed specimens of *T. trigonodon*. While the femora of both species are wider distally than proximally, the distal width of YORYM 497 is larger than the femur distal width of all observed *T. trigonodon* specimens; the femur distal width ratio of YORYM 497 and SMNS 50000 is approximately 1.51, whilst the ratio of YORYM 497 and SMNS 17560 is approximately 1.32. Furthermore, the femur distal width vs proximal width ratio of YORYM 497 is approximately 1.90, whereas the femur distal width vs proximal width ratio of SMNS 50000 and SMNS 17560 is approximately 1.60 and 1.73 respectively, therefore highlighting that the femur distal width of YORYM 497 is somewhat wider than that of *T. trigonodon*.

The left hindfin possesses three primary digits (II, III, IV; Figure 33). Excluding the femur, the fin has a preserved length of 70 cm (from the proximal tip of the tibia) and a maximum width of 23 cm (at the widest point). The tibia and fibula are wider than long, while the fibula is slightly wider than the tibia. The tibia is approximately 9 cm wide and 7 cm long, while the fibula is approximately 10 cm wide and 7 cm long. The intermedium is both longer and wider than distal tarsal 2 (Table 12). The distal tarsals, metatarsals and phalanges range from sub-rectangular to somewhat oval distally. At least four elements of digit II, including the tibia, distal tarsal 2, metatarsal ii and a phalanx, are notched on the leading edge; however, like the forefins, the damage and preservation of the fin makes it difficult to confirm if additional elements are notched.



Figure 32. Femoral comparison **(A)** Left femur of *T. crassimanus* (YORYM 497) in dorsal view. **(B)** Right femur of *T. trigonodon* (SMNS 50000) in ventral view. **(C)** Left femur of *T. trigonodon* (SMNS 15950) in dorsal view. **(D)** Right femur of *T. trigonodon* (SMNS 17560) in dorsal view. Scale bars equal 10 cm.

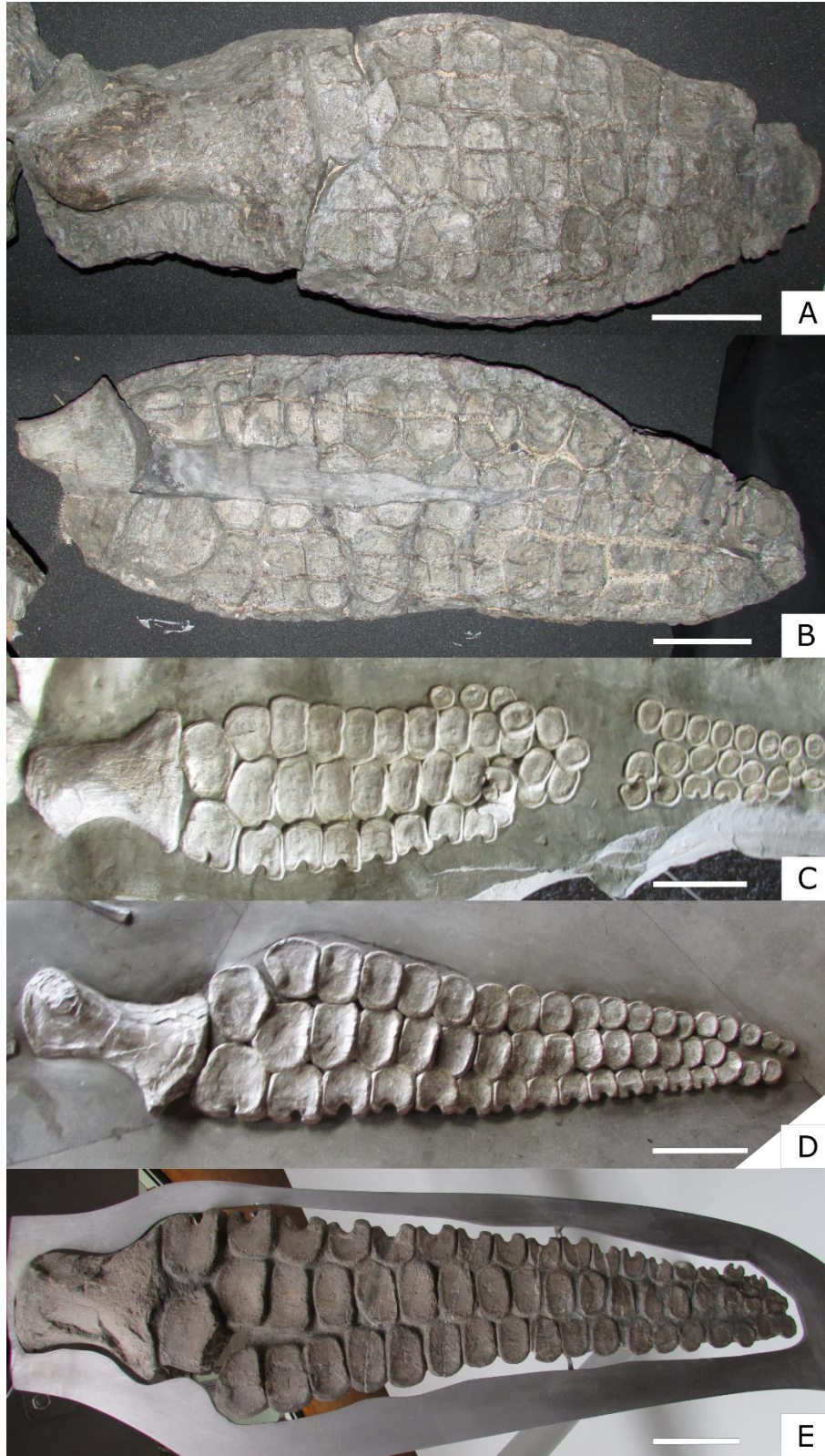


Figure 33. Hindfin comparison **(A)** Left hindfin of *T. crassimanus* (YORYM 497) in dorsal view. **(B)** Right hindfin of *T. crassimanus* (YORYM 497) in dorsal view. **(C)** Right hindfin of *T. trigonodon* (SMNS 50000) in ventral view. **(D)** Left hindfin of *T. trigonodon* (SMNS 15950) in dorsal view. **(E)** Right hindfin of *T. trigonodon* (SMNS 17560) in dorsal view. Scale bars equal 10 cm.

The right hindfin is somewhat poorly preserved and has been partially repaired with plaster (Figure 33), therefore limiting description and measurements. There are three primary digits (II, III, IV), and the fin has a preserved length of 75.5 cm (including the partial distal end of the femur) and a maximum width of 26 cm, at the widest point. The forefin length vs hindfin length ratio of YORYM 497 is approximately 1.51, whereas the forefin length vs hindfin length ratio of SMNS 17560 and SMNS 15950 is approximately 1.20 and 1.30 respectively; demonstrating that the fore- and hindfins of *T. trigonodon* are more in proportion, compared to *T. crassimanus*. While the hindfin length of YORYM 497 is somewhat comparable with *T. trigonodon*, like the forefins, the hindfins are significantly wider than the noticeably narrower, elongated hindfins of *T. trigonodon*; the hindfin width ratio of the left hindfin of YORYM 497 vs the right hindfin of SMNS 50000 is approximately 1.40. Furthermore, the hindfin width ratio of the left hindfin of YORYM 497 vs the left hindfin of SMNS 17560 is approximately 1.30, further highlighting a difference in forefin morphology.

As previously discussed, the distal end of the femur is partially preserved, with a width of approximately 18 cm (Table 13). Individual measurements of the fin elements were not recorded due to the poor preservation and incompleteness of the repair work; however it is worth noting that at least five elements of digit II, including the tibia, distal tarsal 2, metatarsal ii and at least two phalanges are notched on the leading edge. Therefore, it is evident that while not all of the elements on digit II are notched in *T. crassimanus*, at least four fin elements are notched on the left hindfin, and at least five on the right hindfin. In comparison, like the forefins, hindfin notching is observed to be present in most, if not all elements of the leading edge in *T. trigonodon*, as observed on SMNS 50000, SMNS 15950 and SMNS 17560. Due to the preservation of the fore- and hindfins, it is difficult to confirm whether the more distal elements are notched in YORYM 497.

Features	(cm)
Femur length	25
Femur proximal width	10.5
Femur distal width	20
Femur shaft width	11
Femur distal width vs proximal width ratio	1.90
Tibia width	9
Tibia length	7
Fibula width	10*
Fibula length	7
Tibiale width	7
Tibiale length	6
Intermedium width	8.5
Intermedium length	6.5
Width of hindfin at widest point	23

Length of hindfin	70
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Table 12. Measurements for the left hindfin of YORYM 497.

**Denotes an estimate as the bone is damaged, or elements are missing/not preserved.*

Features	(cm)
Partial femur length	13.5
Femur distal width	18
Width of hindfin at widest point	26
Length of hindfin	62

Table 13. Measurements for the right hindfin of YORYM 497.

9. ASSESSMENT OF POSSIBLE ADDITIONAL SPECIMENS OF *TEMNODONTOSAURUS CRASSIMANUS*

Two specimens have been tentatively assigned to *Temnodontosaurus crassimanus* (WHITM: SIM2546.S and WHITM: SIM5) by McGowan and Motani (2003). These specimens are discussed below, in addition to other *Temnodontosaurus* specimens from the Upper Lias of Yorkshire that might belong to the same species (MANCH: LL. 16096 and MANCH: L. 1688). The following specimen descriptions are focused on the elements that are also preserved on YORYM 497 for comparative analysis, therefore not all features preserved on the individual specimens are discussed in detail.

9.1 SPECIMEN WHITM: SIM2546.S

Measurements of WHITM: SIM2546.S are presented in appendix B.

WHITM: SIM2546.S is a large, partial skeleton that was excavated from the Hawsker cliff in the 1860's during jet mining and was subsequently acquired by the Whitby Museum, where it has remained on display (Figure 34) (Benton and Taylor, 1984). The specimen was apparently excavated 'from the bed above the Jet Rock, Hawsker, No. 6 Simpson's division of the Upper Lias' and was most likely collected from the bituminous shale near to the Jet Rock workings at Hawsker Bottoms (Benton and Taylor, 1984). Like YORYM 497, WHITM: SIM2546.S was assigned to *I. acutirostris* (*Stenopterygius acutirostris*) by McGowan (1974a), after he proposed that only *I. platyodon*, *I. acutirostris* and *I. longirostris* from the Lower Jurassic of England were valid, in addition to *T. risor* and *T. eurycephalus*, suggesting that *I. crassimanus* was a junior synonym for *T. acutirostris*. McGowan and Motani (2003, p. 87) later proposed that YORYM 497 and WHITM: SIM2546S, in addition to WHITM: SIM5 (see below), appear to differ sufficiently from *T. platyodon* and *T. trigonodon*, and were therefore all tentatively assigned to *T. crassimanus* (Lomax, 2019a).

Preservation. WHITM: SIM2546.S is a somewhat complete, largely articulated but poorly preserved specimen, exposed in ventral view. The specimen is comprised of a poorly preserved skull, both forefins, partial pectoral girdle elements, both hindfins, pelvic elements, ribs, and a largely articulated vertebral column. However, the left fore- and hindfins of the specimen are composites, with the individual elements set in plaster in a latipinnate configuration (four primary digits) (McGowan, 1974a); the right fore- and hindfins appear authentic and have a longipinnate configuration (three primary digits) (McGowan, 1974a). The total preserved length of the specimen, measured along the vertebral column and, including the skull, is approximately 769 cm.



Figure 34. The large, poorly-preserved, partial skeleton of WHITM: SIM2546.S.
Scale bar equals 45 cm.

Skull, mandible and dentition. Due to the poor preservation and disarticulation of the skull, no measurements could be taken, except for limited data for the dentition. Approximately 23 isolated teeth are exposed among the disarticulated skull elements, and are poorly preserved, with the majority covered by matrix; therefore, limited comparisons can be made. The teeth are robust with heavy striations. As the teeth are embedded in the matrix, the full circumference of the teeth are obscured. The best-preserved tooth measures 55.2 mm in length, and 15 mm in width, which is larger than the longest preserved tooth (32.5 mm) of YORYM 497.

Axial skeleton. The mostly complete, largely articulated vertebral column is comprised of 115 centra, and similar to YORYM 497, preserves at least 46 precaudal centra (based on the position of the hindfins). However, the atlas-axis is not exposed, and it is possible that at least two or three vertebrae could be missing at the back of the skull, as also observed in YORYM 497. The estimated precaudal length (including the incomplete skull), measured along the vertebral column, is approximately 440 cm, while McGowan (1974a) stated that the vertebral count to the pelvic girdle of WHITM: SIM2546.S was between 48 and 50. The majority of the preserved centra exceed a diameter of 11 cm, which are noticeably smaller in comparison to the centra of YORYM 497. However, the size of some centra are difficult to determine due to the vertebral column being buried, displaced or disarticulated in various places, which hindered measurements. Most vertebrae are exposed in ventral view (Figure 35), so the height of the centra could not be determined. No neural arches are visible. Similar to YORYM 497, the

longest preserved rib measures approximately 60 cm along its curvature; however the majority of the preserved ribs are heavily fragmented and/or partially buried. No gastralia are preserved.

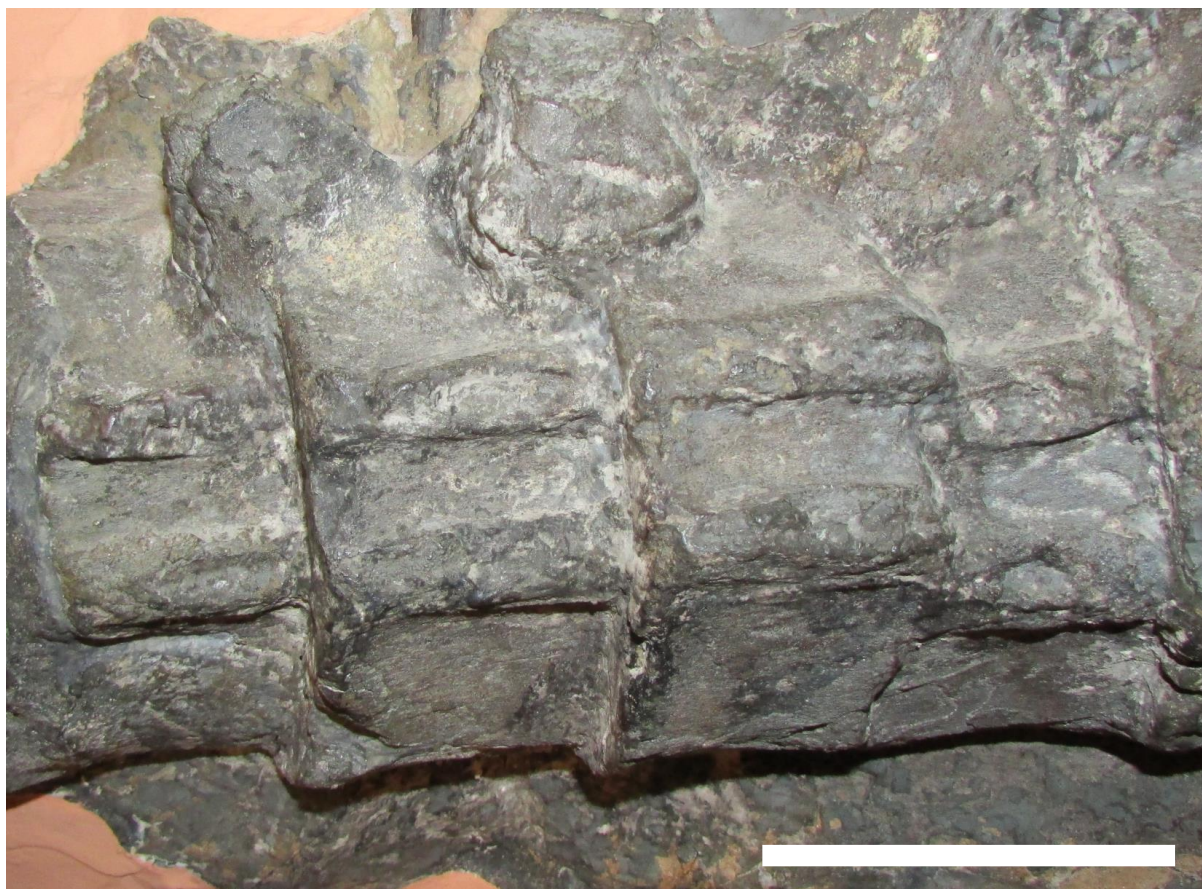


Figure 35. Articulated dorsal and caudal vertebrae of WHITM: SIM2546.S in dorsal view. Scale bar equals 10 cm.

Pectoral girdle and forefins. Most of the pectoral girdle is poorly-preserved and elements are also either obscured by matrix and overlaying ribs, or only partially exposed. A possible partial scapula is preserved, although measurements could not be taken due to the poor preservation. While both humeri are exposed, they are poorly preserved, therefore resulting in a limited assessment and description of these elements and unfortunately meaning that comparison with the humerus of YORYM 497 cannot be made. As the left fore- and hindfin of the specimen are composites, the descriptions focus on the right forefin, which possesses three primary digits (II, III, IV), in addition to what might be a pre-axial accessory digit (McGowan, 1974a), and there are at least 14 elements in the longest digit, marginally less than the number of elements in the longest digit of YORYM 497. However, individual elements in the forefin are poorly preserved, with some also partially covered by matrix (Figure 36). Like YORYM 497, the forefin may also be incomplete and some distal elements may be missing, meaning that the number of elements in the longest digit and the total forefin length of WHITM: SIM2546.S may be higher.



Figure 36. The partial, poorly-preserved humeri and forefins of WHITM: SIM2546.S in ventral view; **(A)** right (uppermost) forefin, **(B)** left (lowermost) forefin. Note the left forefin of the specimen is a composite, with individual elements set in plaster. Scale bars equal 10 cm.

As observed on the holotype, notching appears to be present in approximately five elements on the leading edge (digit II) including distal carpal 2; however some of these elements are displaced and it is difficult to confirm if the notching is genuine or a result of damage. The ulna also appears to have a slight proximal notch on the preaxial margin, although this is likely to be due to damage. The radius and ulna are wider than long, with the radius longer but marginally narrower than the ulna. The radius is approximately 10.9 cm wide and 8.5 cm long, while the ulna is approximately 10.3 cm wide and 8.8 cm long. The intermedium is wider than both the radiale and the ulnare but is shorter than the latter elements. The distal carpals, metacarpals and phalanges range from sub-rectangular to oval distally. The preserved forefin is long but somewhat wide, measuring approximately 63.5 cm in length (from the tip of the radius) and approximately 24.5 cm in width (at the widest point); however, these measurements are estimated due to the slight disarticulation of the fin.

McGowan (1974a) highlighted that the right forefin of WHITM: SIM2546.S is considerably smaller in comparison to the left forefin of YORYM 497; in fact, the forefin length ratio of YORYM 497 vs WHITM: SIM2546.S is approximately 1.67. The forefin of WHITM: SIM2546.S is also significantly narrower in comparison to the left forefin of the holotype, demonstrated by a forefin width ratio for

YORYM 497 vs WHITM: SIM2546.S of approximately 1.51. Additionally, the forefins of YORYM 497 are also much larger relative to the total estimated body length, than in WHITM: SIM2546.S; the forefin length vs total estimated body length ratio of YORYM 497 is approximately 0.12, whereas the ratio for WHITM: SIM2546.S is approximately 0.08. However, McGowan (1974a) suggested that the relative size of the fore- and hindfin is a variable character, and that size ranges can occur in species. Furthermore, evaluating fore and hindfin length is also debatable, as distal fin elements may not have been preserved, therefore effecting the total preserved length of the fin and thus obscuring measurements.

Pelvic girdle and hindfins. The pelvic girdle of the specimen, like the pectoral girdle, is poorly-preserved. The only identifiable pelvic element is a somewhat well-preserved possible pubis, exposed in lateral view dorsal to the left hindfin (Figure 37). The possible pubis measures 17.5 cm in length and is a robust element that appears to curve slightly anteriorly. The pubis is flared proximally, with a proximal width of 8.5 cm and a distal width of 9.4 cm; the shaft of the element is thinner, with a width of 5.3 cm. The pubis length vs femur length ratio is approximately 0.95.



Figure 37. The somewhat well-preserved possible pubis of WHITM: SIM2546.S, exposed in lateral view. Scale bar equals 5 cm.

While the right femur is better preserved than both humeri, the femur of the left hindfin is clearly a composite, and therefore measurements were not taken (Figure 38). The femur of the right hindfin is a large, elongate, robust element with a somewhat constricted shaft and which unlike YORYM 497, appears only marginally wider distally than proximally (11.8 cm and approximately 10.9 cm, respectively). The element is 18.5 cm in length and noticeably shorter than the femur of the holotype; in fact, the femur length ratio of YORYM 497 vs WHITM: SIM2546.S is approximately 1.35. Although the femur proximal width of WHITM: SIM2546.S is marginally larger than that of the holotype, it is not the case for the distal width. The femur distal width of the holotype is significantly wider than the distal width of WHITM: SIM2546.S, demonstrated by a femur distal width ratio of approximately 1.69. Furthermore, the femur distal width vs femur proximal width ratio of YORYM 497 is approximately 1.90, whereas this ratio for WHITM: SIM2546.S is approximately 1.1, highlighting that the femur distal width of YORYM 497 is significantly wider than that of this specimen, in contrast to the proximal width.

The right hindfin is composed of three primary digits (II, III, IV), although the number of elements in the longest digit could not be determined due to some of the distal elements being set in plaster and the slight disarticulation of the fin (Figure 38). The tibia is longer than the fibula, while the width could not be determined for both elements due to poor preservation; the tibia is 6 cm long and the fibula is 5.4 cm long. The remaining elements could not be accurately measured due to poor preservation and slight disarticulation of the hindfin. The distal tarsals, metatarsals and phalanges range from sub-rectangular to somewhat oval distally. While not as defined as that observed in YORYM 497, notching may be present in at least 1 element on the leading edge (digit II); however it is difficult to confirm if notching is present and not just damage. Like the forefin, the hindfin is long and wide, measuring approximately 51 cm in length (from the tip of the tibia) and 21 cm in width (at the widest point); however, these measurements are somewhat estimated due to the slight disarticulation of the fin. The right hindfin of WHITM: SIM2546.S appears considerably smaller in comparison to the left hindfin of YORYM 497; in fact, the hindfin length ratio of YORYM 497 vs WHITM: SIM2546.S is approximately 1.40. Nevertheless, the hindfin width of WHITM: SIM2546.S is of similar size to the holotype, with a hindfin width ratio for YORYM 497 vs WHITM: SIM2546.S of approximately 1.1. Furthermore, the right fore- and hindfin of WHITM: SIM2546.S are more in proportion, compared to left fore- and hindfin of the holotype specimen; the forefin length vs hindfin length ratio of YORYM 497 is approximately 1.51, whereas the ratio of WHITM: SIM2546.S is approximately 1.25. However, it can again be argued that the relative size of the fore- and hindfin is a variable character (McGowan, 1974a), and that it is difficult to evaluate fore and hindfin length, as distal fin elements may not have been preserved, therefore effecting the total preserved length of the fin. McGowan and Motani (2003) stated that it has yet to be determined whether there are any consistent differences between the relative lengths of the fore- and hindfins among species of *Temnodontosaurus*, and therefore this characteristic should be used with caution.

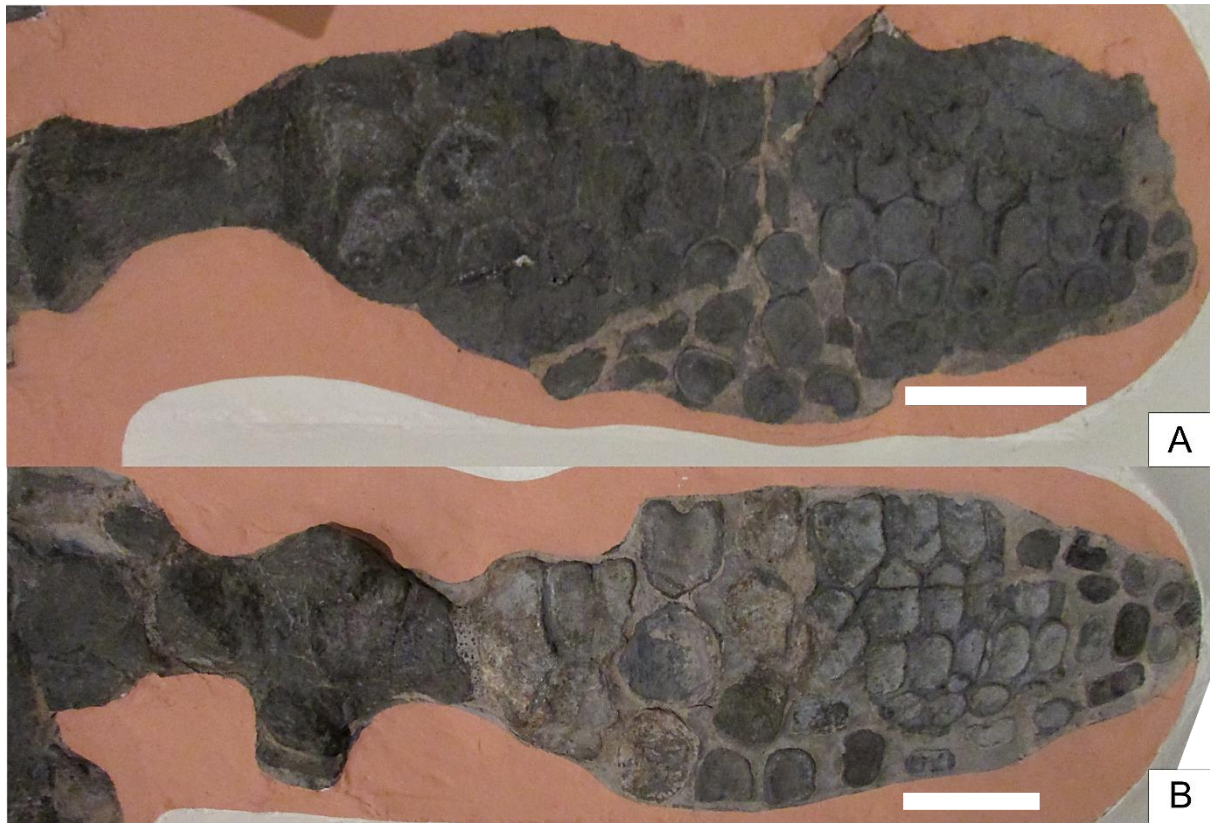


Figure 38. The elongate femora and partial, poorly-preserved hindfins of WHITM: SIM2546.S in ventral view; **(A)** right (uppermost) hindfin, **(B)** left (lowermost) hindfin. Note the left hindfin of the specimen is a composite, with individual elements set in plaster. Scale bars equal 10 cm.

Species assessment. Although WHITM: SIM2546.S displays features comparable to those observed on YORYM 497, including similar estimated precaudal counts and possible fore and hind fin notching, in addition to a large total body length, the somewhat poor preservation of the specimen means that it does not display enough characters, including a well-preserved humerus and scapula for reliable identification. While it is possible that WHITM: SIM2546.S may belong to the genus *Temnodontosaurus*, without the relevant characters to assess, there is no confidence in assigning WHITM: SIM2546.S to *T. crassimanus*.

9.2 SPECIMEN WHITM: SIM5

WHITM: SIM5 is a moderately large, partial skeleton, including the skull and postcranial elements, that was excavated from the Upper Lias Loftus Alum Quarries by Mr Louis Hunton (Simpson, 1884). The specimen was subsequently acquired by Whitby Museum, where it has remained on display (Figure 39). WHITM: SIM5 was briefly described by Simpson (1884, p. 12), in which the specimen was referred to as *Ichthyosaurus platyodon* (now *Temnodontosaurus platyodon*). As previously discussed, along with YORYM 497 and WHITM: SIM2546.S, WHITM: SIM5 was later assigned to *I. acutirostris* (*Stenopterygius acutirostris*) by McGowan (1974a), but McGowan and Motani (2003, p. 87) later proposed that WHITM: SIM5 could be tentatively assigned to *T. crassimanus*. (Lomax, 2019a). In comparison to the previous specimen, WHITM: SIM5 could not be easily accessed to examine, due to how it is displayed, and therefore no measurements were collected, and the specimen was only photographed. Refer to Simpson (1884) and McGowan (1974a), the most recent studies of WHITM: SIM5, for measurements of this specimen.



Figure 39. The moderately large, partial skeleton of WHITM: SIM5, figured by McGowan (1974a) in right lateral view. Scale bar equals 45 cm.

Preservation. WHITM: SIM5 is a rather complete and largely articulated specimen, exposed in lateral view. The specimen is comprised of a somewhat poorly preserved skull, both forefins, partial pectoral girdle elements, ribs, and a largely articulated vertebral column. The skeleton itself is poorly preserved, and has suffered from pyrite decay, which has especially affected the mudstone between the jaws and the area around the pectoral girdle and forefin (Andrew, 1999). The total length of the specimen, including the skull, is approximately 5 m (Simpson, 1884; Benton and Taylor, 1995), considerably smaller than the estimated length of YORYM 497 and the smallest of all the studied skeletons.

Skull, mandible and dentition. The skull of WHITM: SIM5 is rather poorly preserved, predominately due to pyrite decay (Figure 40); therefore the majority of the cranial bones and individual sutures are somewhat difficult to identify. Simpson (1884) determined the skull length to be approximately 1.2 m, while McGowan (1974a) highlighted that the snout of the specimen appeared slightly recurved. In contrast to YORYM 497, while the orbit of WHITM: SIM5 is poorly preserved, it is large in comparison to the skull and appears circular in shape, with limited deformation. No sclerotic ring is preserved.

Numerous original teeth are preserved in the rostrum, with the majority either poorly preserved or covered by the original matrix. The teeth are described as robust, conical and striated, which are said to flatten at the tip (Simpson, 1884).



Figure 40. The partial skeleton of WHITM: SIM5, highlighting the large, poorly-preserved skull in right lateral view. Scale bar equals ~ 60 cm.

Postcranial skeleton. Simpson (1884) discussed that the largely articulated vertebral column is comprised of 86 vertebrae, with the majority of the presacral vertebrae concealed under the overlaying, fragmented ribs so that the precaudal count could not be determined. The atlas-axis is also not exposed. The diameter of the largest vertebrae are approximately 6.9 cm, and 4.4 cm in length (Simpson, 1884). The forefins are generally poorly preserved, with the left (lower) forefin being the better of the two; therefore the description focuses on the left forefin. It is comprised of three primary digits (II, III, IV) in addition to what is probably an accessory digit, or perhaps digit V, as observed in YORYM 497 (Figure 41). McGowan (1974a) stated that the maximum number of elements in the longest digit of WHITM: SIM5 was estimated at 14, marginally fewer than the number of elements in the longest digit of YORYM 497. Notching appears to be present on at least two phalanges; however, the poor preservation of the specimen means that it can be difficult to confirm if notching is actually present, as opposed to damage. The ulna also appears to have a slight proximal notch on the preaxial margin, although this could again be due to damage. The right forefin was determined to measure approximately 50 cm in length and 15 cm in width (Simpson, 1884); however, the right forefin of WHITM: SIM5 does appear slightly incomplete and is likely that some distal elements may well have not been preserved. Furthermore, the width of the forefins are noticeably different between the two specimens, as the right forefin of WHITM: SIM5 is significantly narrower in comparison to the left forefin of the holotype, demonstrated by a forefin width ratio for YORYM 497 vs WHITM: SIM5 of approximately 2.50; this might suggest it is a composite specimen. Additionally, the forefins of YORYM 497 are also larger relative to total estimated body length, than in WHITM: SIM5. Although originally referred to as a femur by Simpson (1884), the right humerus measures approximately 15 cm in length and is therefore noticeably shorter than the humerus of the holotype, with a humerus length ratio for YORYM 497 vs WHITM: SIM5 of approximately 2.10. McGowan

(1974a) also highlighted that the humerus of WHITM: SIM5 appears to possess three distal facets, which is a distinctive feature and not observed on YORYM 497. A partial pectoral girdle is also preserved on the specimen, in which two coracoids are somewhat well-exposed; the coracoids were described as fairly thick and robust, with an anterior notch present (McGowan, 1974a).



Figure 41. Close up of the partial right forefin, in addition to the paired coracoids and fragmented ribs of WHITM: SIM5 in right lateral view. Scale bar equals ~ 15 cm.

Species assessment. WHITM: SIM5 appears to display limited comparable features to those observed on YORYM 497 and does not possess some of the key features that were used to define *T. crassimanus*. However, the specimen instead seems to possess elements that appear distinct from YORYM 497, e.g. a humerus that may possess three distal facets (McGowan, 1974a). Therefore, there is nothing to suggest that WHITM: SIM5 can reliably be assigned to *T. crassimanus*.

9.3 SPECIMEN MANCH: LL. 16096

Measurements of MANCH: LL. 16096 are presented in appendix B.

MANCH: LL. 16096 is a moderately large, three-dimensionally preserved partial skull that was supposedly collected from the Lower Lias of Port Mulgrave, North Yorkshire by fossil collector Mr Howard Turner. Following repair and preparation, the specimen was donated to Manchester Museum in 2013, where it currently remains on display. Although identified as *Ichthyosaurus crassimanus* (*Temnodontosaurus crassimanus*), a formal description has yet to be undertaken for this specimen, hence the inclusion within this study.



Figure 42. The large, partial skull of MANCH: LL. 16096 in left lateral view. Scale bar equals 15 cm.

Preservation. MANCH: LL. 16096 is a partially complete skull, best exposed in lateral view (Figure 42). The specimen is embedded in the original matrix and is composed of two blocks which have been repaired. Although incomplete, the skull has only minor deformation and has a total preserved length of approximately 76 cm.

Skull, mandible and dentition. Individual skull elements and cranial sutures are rather difficult to identify due to the preservation of the specimen. However, several elements that form the orbits are visible, including the jugal, prefrontal, lacrimal and postorbital. Although damaged, it is clear that the nasal makes up most of the dorsal margin of the external naris, whereas the supranarial process of the premaxilla makes up a small portion of the anterior margin of the naris. Additionally, a portion of the maxilla is exposed, and appears to be a dorsoventrally low element that extends well beyond the external naris, as frequently observed in *Temnodontosaurus*, including YORYM 497. The dentary and surangular are exposed but poorly preserved and not much can be described. The orbit is partially preserved, in addition to an incomplete sclerotic ring that appears to fill the majority of the opening.

The large external naris, as observed on YORYM 497, is considerably longer (14.6 cm) than tall (5 cm). In dorsal view, the nasals are wide posteriorly, but anteriorly they appear to come to an end anterior to the external naris; this was also observed in YORYM 497 and in other *Temnodontosaurus* specimens, including *T. trigonodon*. Only three original teeth are preserved in the rostrum and are poorly preserved and partially covered by matrix (Figure 43), meaning that limited measurements and comparisons can be made. In comparison to the skull, the preserved teeth are small in size, with the best-preserved tooth measuring 12.5 mm in length, although the root of this tooth is buried; the preserved teeth are significantly smaller than the teeth of YORYM 497, although both specimens only have a few teeth for comparison. They are relatively robust, with smooth striations, however no roots are exposed.



Figure 43. The small, poorly-preserved teeth of MANCH: LL. 16096, situated in the rostrum in left lateral view. Scale bar equals 2 cm.

Postcranial skeleton. A partial rib is preserved posteriorly, measuring 15.5 cm in length and 1.6 cm in width, in addition to what appears to be a possible rib head above; however, no other postcranial material is preserved.

Species assessment. While several elements of MANCH: LL. 16096 appear to be characteristic of *Temnodontosaurus*, due to the poorly preserved skull of YORYM 497 and lack of readily preserved characters for comparison, it is impossible to assign this specimen to *T. crassimanus* with any degree of confidence.

9.4 SPECIMEN MANCH: L. 1688

Measurements of MANCH: L. 1688 are presented in appendix B.

MANCH: L. 1688 is a moderately large, three-dimensionally preserved partial skeleton, including a skull and postcranial elements, that was excavated from the Kettleness Alum Works, Marquis of Normanby quarry in Whitby, North Yorkshire in 1847 by James Heywood and George Hadfield (Benton and Taylor, 1984; K. Sherburn, 2019, pers. comm.). Carte and Baily (1863, p. 162) discussed two ichthyosaur specimens collected from the *bifrons* Zone at the Kettleness Alum Works, most likely referring to YORYM 497 and MANCH: L. 1688 (Benton and Taylor, 1984), with the latter acquired by Manchester Museum in 1893 from Mr Hadfield, where it remains on display (Figure 44). MANCH: L. 1688 was originally figured as *Ichthyosaurus crassimanus* by Eagar and Preece (1977, p. 15), and is currently ‘assigned’ to *Stenopterygius acutirostris* (now *T. acutirostris*) according to the specimen information displayed in the museum; however, Lomax (2011) referred to the specimen as *Temnodontosaurus* sp.



Figure 44. Archive photograph of the partial skeleton of MANCH: L. 1688. Photograph courtesy of Manchester Museum.

Preservation. MANCH: L. 1688 is a mostly complete and largely articulated specimen, exposed best in lateral view. The specimen is comprised of a partially preserved skull, two forefins, pectoral girdle

elements, a hindfin, ribs, and a largely articulated vertebral column. However, the skull is missing a portion of the rostrum, which has since been partially reconstructed with plaster. The total preserved length of the specimen, measured along the vertebral column (including the skull and recreated rostrum), is approximately 599 cm, therefore smaller than YORYM 497. The specimen was also partially behind glass, which hindered taking measurements and photographs, particularly of the fore- and hindfins (Figures 48 and 49). In addition to the poor preservation, the specimen is also heavily pyritized, dense and bears a significant amount of chisel marks from the initial preparation, as also observed on YORYM 497.

Skull, mandible and dentition. The skull is preserved in three dimensions, but best exposed in dorsal and lateral view. Like YORYM 497, MANCH: L. 1688 is missing a significant section of the anterior portion of the rostrum, but has since been reconstructed with plaster so that the full, accurate length of the skull and jaw cannot be determined (Figure 45). The preserved skull measures approximately 145 cm (including the recreated rostrum) while the preserved jaw length is 153.5 cm.



Figure 45. The three-dimensional skull of MANCH: L. 1688 in left lateral view, accompanied by the reconstructed rostrum. Note how the glass hindered accessibility when photographing the specimen. Scale bar equals 20 cm.

Compared with YORYM 497, the skull is better preserved and appears to have suffered less deformation; the majority of the cranial bones and individual sutures are identifiable. The maxilla is a dorsoventrally low element that extends well beyond the external naris. Several elements that form the orbit are visible, including the jugal and prefrontal. The jugal is a thin, elongate element that forms the ventral margin of the orbit. The jugal expands dorsally to meet the poorly preserved postorbital, while the anterior contact with the maxilla and the lacrimal is difficult to distinguish. The prefrontal is a relatively robust but sculpted element that forms the anterodorsal margin of the orbit and contacts the nasals in the skull roof. Like the holotype, it is clear that the nasal makes up most of the dorsal margin

of the external naris, whereas the supranarial process of the premaxilla makes up a small portion of the anterior margin of the naris. The preorbital length of the specimen is approximately 124 cm. The orbit is longer (33 cm) than tall (25.5 cm), and while approximately the same length as YORYM 497, the orbit of MANCH: L. 1688 is significantly taller, although this is likely due to crushing in the holotype. Additionally, a small fragment of the sclerotic ring is preserved. The orbital ratio of MANCH: L. 1688 is approximately 0.21, characteristic of *Temnodontosaurus*. The large external naris of MANCH: L. 1688 is considerably longer (19 cm) than tall (3.5 cm) and is noticeably longer than the holotype. In contrast to the oval and posteriorly dorsoventral 'pinch' in the external naris of YORYM 497, the naris of MANCH: L. 1688 is elongated and pinches anteriorly. In dorsal view, similar to the holotype, the nasals are wide posteriorly, but anteriorly, they end abruptly anterior to the external naris. Elements present in the posterior portion of the skull are not exposed due to the preservation of the specimen, so comparisons between the specimens cannot be made here. Ignoring the teeth in the recreated rostrum, approximately 19 original teeth are preserved; however some are covered by matrix. The teeth are relatively robust and the roots are coarsely striated, with smooth striations and lineation between the root and the crown, although a complete crown is not present (Figure 46). The best-preserved tooth measures 26.1 mm in length, and 12.8 mm in width.



Figure 46. The original, robust teeth of MANCH: L. 1688, highlighting the coarsely striated roots in left lateral view. Scale bar equals 2 cm.

Axial skeleton. The poorly articulated vertebral column is comprised of 69 centra, noticeably fewer than the total vertebral count of the holotype; however, some vertebrae are displaced or missing.

Furthermore, beyond the 26th centrum, the vertebrae have been set in plaster, and therefore may not reflect the original vertebral arrangement and could possibly even indicate a composite. Similar to YORYM 497, the atlas-axis is not exposed, and numerous vertebrae are missing or are not exposed at the back of the skull; therefore the precaudal count could not be determined. The majority of the preserved centra exceed a diameter of 10 cm, significantly smaller than the centra of YORYM 497; however, as the vertebral column is buried, displaced and disarticulated in various places (Figure 47), the size of the majority of the centra are difficult to determine, which limited measurements. Furthermore, most vertebrae are exposed in lateral view, so the full height of the centra could not be determined. The longest preserved rib measures approximately 34.5 cm along its curvature, although the majority of the preserved ribs are heavily fragmented and/or partially buried.



Figure 47. Close up of the displaced and disarticulated vertebral column of MANCH: L. 1688, exposed in dorsal view. Scale bar equals 5 cm.

Pectoral girdle and forefins. While the majority of the pectoral girdle is poorly-preserved, the coracoids are well-exposed, with the uppermost (right) coracoid being better preserved than the lowermost (left). Although damaged, the elements are spherical in shape, with no anterior notches and are marginally mediolaterally wider than anteroposteriorly long. A possible partial scapula is also preserved; however measurements could not be taken as it is poorly exposed. While two humeri are preserved, there is a

distinct difference between these two elements, suggesting they may either be from different individuals or preserved in different orientations which could alter their appearance (Figure 48). Additionally, as the elements of the lower forefin are set in plaster, it is difficult to determine which is the true left and right forefin; therefore, the forefins, and their associated humeri will be referred to the lowermost and uppermost. Regarding the lowermost humerus, the element measures approximately 18 cm in length, and is noticeably wider distally than proximally (15.5 cm and approximately 9 cm, respectively), in addition to also being almost as distally wide than the element is long. While the robust humerus is large in size, it is significantly shorter than the humerus of YORYM 497. Although the humerus proximal width of the holotype is only somewhat larger than MANCH: L. 1688, the humerus distal width of YORYM 497 is significantly wider than that of MANCH: L. 1688, with a humeral distal width ratio of approximately 1.74. Furthermore, the humerus distal width vs humerus proximal width ratio of YORYM 497 is approximately 2.25, whereas the ratio for MANCH: L. 1688 is approximately 1.72; highlighting that the humeral distal width of YORYM 497 is significantly wider than that of this specimen, in contrast to the proximal width. The humerus also possesses a rounded head and a constricted shaft. In comparison, the uppermost humerus is again large but somewhat less robust, with a slightly smaller proximal and shaft width. The humerus measures 19.5 cm in length, and possesses a slightly damaged, rounded head, and a constricted shaft; the dorsal process is centrally located. It is again noticeably wider distally than proximally (18.5 cm and approximately 7.9 cm, respectively), being almost as distally wide than the element is long. While this element possesses a larger distal width than the lowermost humerus, the humerus of YORYM 497 is again significantly longer than the upper humerus of MANCH: L. 1688.

The lowermost forefin is composed of individual elements set in plaster and appears to have four digits (Figure 48); therefore limited measurements were taken, and attention was focused on the uppermost forefin. While the upper fin appears authentic and has three primary digits, like YORYM 497, it is poorly preserved (Figure 48). The elements, including the distal carpals, metacarpals and phalanges, appear more rounded in shape, in comparison to the more sub-rectangular elements of the lower fin of YORYM 497. The radius and ulna are wider than long, while the radius is overall larger in size. The radius is approximately 10.8 cm wide and 9 cm long, while the ulna is approximately 9.6 cm wide and 8.6 cm long. The intermedium is wider than both the radiale and ulnare; however the latter element is the longest. In contrast to YORYM 497, no elements of the forefin appear notched, although the poor preservation and the overlying matrix makes this difficult to confirm. The fin has a total preserved length of approximately 36 cm (from the tip of the radius) and a maximum preserved width of 21.5 cm (at the widest point); however, these measurements are estimated due to the possible incompleteness of the fin. Due to the lower forefin being set in plaster, only the upper forefin of MANCH: L. 1688 was used in fin length comparison. The upper forefin of MANCH: L. 1688 is considerably smaller in comparison to the left forefin of YORYM 497. There is also a clear difference in the width of the forefins, as the left forefin of the holotype is considerably wider than the upper forefin of MANCH: L. 1688, demonstrated by a forefin width ratio of approximately 1.72. The forefins of YORYM 497 are also much larger relative to total estimated body length, than in this specimen.



Figure 48. The robust humeri and partial, poorly preserved forefins of MANCH: L. 1688 in dorsal view; **(A)** lowermost forefin, **(B)** uppermost forefin. Note the more robust humerus and sub-rectangular fin elements of the lowermost forefin, in contrast to the more elongate, slender humerus and rounded elements of the uppermost forefin. Scale bars equal 10 cm.

Pelvic girdle and hindfins. No pelvic elements are preserved on the specimen. Additionally, only one hindfin is preserved (Figure 49). Like YORYM 497, the femur is a large, elongate, robust element with a somewhat constricted shaft and is wider distally than proximally (9.9 cm and approximately 6.5 cm, respectively). The element is approximately 14.5 cm in length, and noticeably shorter than the femur of the holotype. The femur proximal width of YORYM 497 is also larger than that of MANCH: L. 1688, and the femur distal width of the holotype is significantly wider than the distal width of MANCH: L. 1688. For YORYM 497, the humerus length vs femur length ratio is approximately 1.24, whereas for MANCH: L. 1688, the uppermost humerus length vs femur length ratio is approximately 1.34 and the lowermost humerus length vs femur length ratio is approximately 1.24; demonstrating that the elements of this specimen are less in proportion than the holotype and thus may suggest a composite specimen. The hindfin is composed of three primary digits (II, III, IV), and there are seven elements in the longest digit; however, the rest of the hindfin is poorly preserved and it is clear that some elements are missing. The tibia is marginally wider (5.9 cm) than long (5.8 cm), while the fibula could

not be measured due to damage. The intermedium is wider than both tarsal 2 and the fibulare, but the latter element is the longest. As observed on YORYM 497, notching is present in at least four elements of the leading edge (digit II), including distal tarsal 2; however it is difficult to confirm if notching is present in any of the other elements. The hindfin has a preserved length of approximately 25.7 cm (from the tip of the tibia) and a maximum preserved width of 15.8 cm (at the widest point); however, these measurements are estimated due to the possible incompleteness of the fin. Like the forefins, the hindfin of MANCH: L. 1688 is considerably smaller in contrast to the left hindfin of YORYM 497. There is a clear difference in the width of the hindfin, as the hindfin of MANCH: L. 1688 is much narrower than the left hindfin of the holotype. Furthermore, the upper forefin and hindfin of MANCH: L. 1688 are slightly more in proportion, in comparison to left fore- and hindfin of the holotype specimen; as previously mentioned, the forefin length vs hindfin length ratio of YORYM 497 is approximately 1.51, whereas the ratio of MANCH: L. 1688 is approximately 1.40.



Figure 49. The preserved femur and partial, poorly preserved hindfin of MANCH: L. 1688 in dorsal view, highlighting the prominent notching of at least four elements of digit II. Scale bar equals 10 cm.

Species assessment. While MANCH: L. 1688 does display various features comparable to those observed on YORYM 497, including the humerus distal width being almost as long as the humerus length, the specimen does not possess enough of the key characteristics that were used to define *T. crassimanus* and therefore it is not possible to assign WHITM: SIM5 to *T. crassimanus* with any degree of confidence.

10. PHYLOGENETIC ANALYSIS

In order to explore the relationships of *Temnodontosaurus crassimanus*, *T. trigonodon*, and other Lower Jurassic ichthyosaurs, a phylogenetic analysis was undertaken. Prior to this study, *T. crassimanus* has only been included in one other phylogenetic analysis, by Moon (2017), however the position of the species remained unresolved. For example, in Moon (2017) Fig. 5, *T. crassimanus* was found to be with *T. nuertingensis*, *Macgowania janiceps* and *Ichthyosaurus conybeari*, although in his Fig. 8., *T. crassimanus* was found to be with *T. azerguensis* and *T. eurycephalus*. Again, in Figs 4, 6 and 7 the position was once again different, sometimes grouped even with *Ichthyosaurus*, or on a single branch. Therefore, *T. crassimanus* position is unstable in Moon's analysis and is not consistently grouped with other species of *Temnodontosaurus*, most likely because *T. crassimanus* could not be coded for many of the characters used by Moon (2017) as this species is poorly known and not enough characters are preserved. This current study, however, has found additional characters and identified new features of *T. crassimanus* and has presented the most detailed comparison of that and other *Temnodontosaurus* species ever offered. Therefore, this research presents the most complete view of the species and offers more insights into its temnodontosaurid relationships and affinities than is presented by Moon (2017).

Although there were many suitable datasets available (e.g. Maxwell et al., 2012; Ji et al., 2016; Moon, 2017), *T. crassimanus* was added into the data matrix of Fischer et al. (2013) as this matrix is the largest dataset that focuses on parvipelvian ichthyosaurs and includes the majority of Lower Jurassic taxa at species level. The character list of Fischer et al. (2013) was modified and four new characters were added (characters 67 – 70; Appendix C); therefore all taxa were subsequently coded for these additional characters (Appendix E). In total, the character list was comprised of 70 characters, which included data from various character matrices including: Mazin (1982); Motani (1999a); Maisch and Matzke (2000); Sander (2000); Fernández (2007); Druckenmiller and Maxwell (2010); Fischer et al. (2011); Fischer et al. (2012); Ji et al. (2016) and Lomax et al. (2017b). *T. crassimanus* and *T. trigonodon* were coded based on personal observations as part of this study, with the exception for character 44 for *T. trigonodon* which was based on the data from Fischer et al. (2013). Coding for *T. crassimanus* was based only on the holotype (YORYM 497) (as described above, see chapter 8), and the majority of coding for *T. trigonodon* was based on specimens held in collections (PB1, SMNS 15950, SMNS 50000 and SMNS 17560; discussed in chapter 6). One issue, however, was the incompleteness and preservation of YORYM 497 which unfortunately meant that data was either absent or difficult to interpret, meaning that the potential taxonomic differences between specimens may not be fully represented or resolved in any matrix. However, 40 of the 70 characters (57 %) were preserved in the holotype of *T. crassimanus*, whereas *T. trigonodon* could be coded for all 70 characters (100 %). Apart from the modifications mentioned above, the coding provided by Fischer et al. (2013) was retained for all other species.

10.1 RESULTS

The phylogenetic analysis was performed using the cladistics program TNT version 1.5 (Goloboff et al., 2008), in which a new technology search with default settings was conducted. Six most parsimonious trees (MPTs) of 152 steps (consistency index (CI) = 0.507; retention index (RI) = 0.753) were found. As there was more than one tree, a strict consensus calculation was then performed on the MPTs. The strict consensus tree showed that *T. crassimanus* closely related to *T. trigonodon* (Figure 50), as would be expected as they shared 36 characters. However, the analysis demonstrated that these two species, in addition to *Leptonectes tenuirostris*, were united on the basis of two 'synapomorphies': no lunate tailfin (character 34; although uncertain in *T. crassimanus*) and manual digit V lost or reduced to small floating elements (character 55); of course, the latter is not preserved in *T. crassimanus*, so this does not provide any useful information. *T. crassimanus* is distinct from *T. trigonodon* in only three characters included in the matrix: the relative size of the fore and hindlimbs (forelimb/hindlimb ratio; character 56), the absence of a spatium interosseum between the tibia and fibula (character 64), and the humerus which is proximodistally longer than the scapula (character 70). In reality, *T. crassimanus* possesses other additional characters that distinguishes it from *T. trigonodon* as discussed above (see chapter 8). To assess the data matrix further, a second analysis was conducted, in which a new technology search with default settings was run, with the results again revealing six trees. The matrix was then bootstrapped with 1,000 replicates and the results found that the relationships among the species were different, with *T. crassimanus* and *L. tenuirostris* united, albeit over one character; forelimb longer but less than twice as long as hindlimb (forelimb/hindlimb ratio, character 56; see appendix D). A third analysis was also run with implicit enumeration; however due to the relatively large data matrix, the analysis did not complete; Goloboff et al. (2008) recommended implicit enumeration for mainly small data sets.

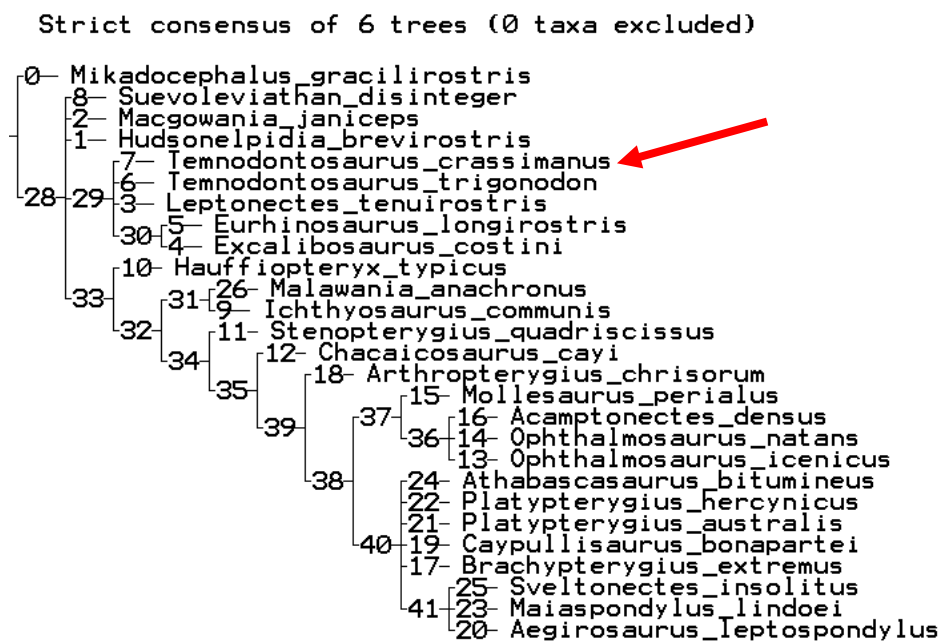


Figure 50. The strict consensus tree from the species-level cladistic analysis, highlighting the position of *T. crassimanus*.

11. DISCUSSION

11.1 COMPARISON, TAXONOMIC IDENTIFICATION AND INTERPRETATION

Whilst a detailed taxonomic revision of the genus *Temnodontosaurus* is greatly required, it is beyond the scope of this study. The most recent genus diagnoses found in the literature, including McGowan and Motani (2003), Martin et al. (2012) and Ji et al. (2016), were used to establish a revised diagnosis for both *Temnodontosaurus* and *T. crassimanus* in this study (presented above, see chapter 8).

Although YORYM 497 is incompletely exposed and poorly-preserved in part, this study has determined that *T. crassimanus* possesses many characters shared with *Temnodontosaurus*, and therefore can be assigned to the genus with confidence. The large size of the individual (estimated at 9 m in length), lies within the size range (7 – 12 m) for an adult *Temnodontosaurus*, as proposed by Ji et al. (2016). It possesses probably > 80 preflexural vertebrae, as highlighted by McGowan and Motani (2003). In addition to a long and robust snout (unlike *T. eurycephalus*, *T. azerguensis* and *T. acutirostris*), *T. crassimanus* also possesses a dorsoventrally low maxilla with a long anterior process, that extends as far as the nasal anteriorly, a feature which is typical of all *Temnodontosaurus* (Martin et al., 2012; Ji et al., 2016). The nasals are wide posteriorly, but anteriorly they end abruptly anterior to the external naris. *T. crassimanus* also possesses a large basioccipital condyle with an extensive extracondylar area (McGowan and Motani, 2003). *T. crassimanus* possesses both a constricted humerus and elongate femur (shared with *T. trigonodon* and *T. azerguensis*), where the distal end of both elements is markedly wider than the proximal end. Characteristic of *Temnodontosaurus*, the forefins of the species are composed of three primary digits (II, III, IV Motani, 1999a), in addition to what is probably an accessory digit or possibly digit V, as observed in *T. trigonodon*. As with *T. crassimanus*, proximally the fore- and hindfin of other *Temnodontosaurus* are composed of numerous closely packed roughly hexagonal elements, in addition to the phalanges which are oval in shape and well-spaced distally (McGowan and Motani, 2003; Ji et al., 2016).

Temnodontosaurus possesses at least some notching in the anterior-most elements of the leading edge of the forefin and hindfin, sometimes involving most elements. As discussed above (see chapter 8), while Melmore's (1930) initial description of YORYM 497 states that none of the elements on the leading edge were notched, it is evident that at least four fin elements of the anterior digit (digit II) on the left forefin are notched, and at least five on the right forefin. Notching in either the fore- or hindfin occurs in the majority of Lower Jurassic parvipelvian ichthyosaurs (McGowan and Motani, 2003), in which fin elements of the anterior digit (digit II) display a distinct C-shaped indentation on the leading edge (Maxwell et al., 2014; Massare and Lomax, 2016). Various hypotheses have been proposed to explain the presence of notching in limb elements of ichthyosaurs, in which the structure has been suggested to protect nerves and blood vessels (Johnson, 1979; Caldwell, 1997) or inferred to be a primitive feature homologous to the shafts in long bones of terrestrial tetrapods (Huene, 1922; Motani, 1999a). Most recently, Maxwell et al. (2014) observed microstructures created by stresses on the anterior digit, through examination of the bone histology associated with notching in *Stenopterygius* –

suggesting that notching could highlight hydrodynamic stresses, and therefore be important for fin locomotion and manoeuvrability in ichthyosaurs (Maxwell et al., 2014; Massare and Lomax, 2016). While notching displays a high variability, this characteristic can sometimes be used to distinguish between species (Massare and Lomax, 2016), as observed in the genus *Temnodontosaurus*. For example, *T. platyodon* displays forefin notching, but it is restricted to the radius and one or two of the consecutive elements, while *T. trigonodon* displays notching in most elements of the leading edge (McGowan and Motani, 2003). However, this character can vary and in other species has no significance taxonomically (Maxwell et al., 2014). Furthermore, whilst YORYM 497 may possess more notched elements on the right forefin than the left forefin, Maxwell et al. (2014) highlighted that in certain species, e.g. *Stenopterygius quadriscissus*, left-right asymmetry in the number of notches is very common, although this difference is never greater than one. Left-right asymmetry can be observed on some specimens of *T. trigonodon* (e.g. SMNS 15950), as notching is present on the leading edge of all elements in digit II on both forefins of this specimen, with the exception of the radius and radiale on the left forefin and the radiale on the right. However, the left-right asymmetry observed on YORYM 497 is most likely the result of preservation. Overall, as stated previously, it is currently difficult to assess the taxonomic utility of notching in *T. crassimanus*.

In comparison with other temnodontosaurids, including *T. trigonodon*, this study revealed that YORYM 497 possesses several unusual features, suggesting *T. crassimanus* is a valid taxon with distinct characters. *T. crassimanus* differs not just from all temnodontosaurids, but all Lower Jurassic ichthyosaurs in possessing a humerus which is proximodistally longer than the scapula (scapula length vs humerus length ratio: ~ 0.68). In Blake's (1876) initial description of the species, he discussed that the forefins of *T. crassimanus* were approximately twice the length of the hindfin (McGowan and Motani, 2003); however this study found this not to be the case. In contrast to *T. trigonodon* and *T. platyodon*, the forefins of *T. crassimanus* are significantly longer although less than twice the length of the hindfin (forefin length vs hindfin length ratio: ~ 1.51); additionally, both the fore- and hindfins are wide in comparison to the slender fins of *T. trigonodon*. The forefins of *T. crassimanus* are also large relative to total body length (forefin length vs estimated total body length ratio: ~ 0.12). The large robust humerus and elongate femur are considerably larger than the elements of other temnodontosaurids, when compared with similarly sized specimens of *T. trigonodon*; the distal ends of both elements are also significantly larger than their corresponding proximal ends (in dorsal view), than observed in *T. trigonodon*. Additionally, the distal width of both elements is only marginally less than their proximodistal length. As discussed, *T. crassimanus* possesses notching of the anterior facet of at least five leading edge elements (digit II) of both the fore- and hindfin, but most likely does not involve all of the elements of the leading edge; this is in contrast to *T. trigonodon* that almost always has notching on all elements of digit II. Overall, these characteristics, suggests that YORYM 497 warrants the retention of the taxon *T. crassimanus*, and that this species is valid.

11.2 LIMITATIONS

During the progression of this research, a number of limiting factors were encountered. The holotype of *Temnodontosaurus crassimanus* (YORYM 497) is incomplete and somewhat poorly preserved, particularly the skull; therefore some data is absent or difficult to determine for the species. Consequently, YORYM 497 does not provide a full representation of all the taxonomic characters of *T. crassimanus*, and therefore limits the comparisons that can be made between other species of *Temnodontosaurus*, making comparisons particularly difficult. This also limits the ability to assign other specimens confidently to this species. Ultimately, while distinct differences can be recognised between this species and other temnodontosaurids, there are no other known specimens that can be confidently assigned to *T. crassimanus* to determine fully the characteristics of the species. Aside from the holotype, this study also focused on locating and examining additional specimens of *Temnodontosaurus* in museum collections, which have been tentatively assigned to *T. crassimanus* (WHITM: SIM2546.S and WHITM: SIM5), or those that might belong to the same species (MANCH: LL. 16096 and MANCH: L. 1688). Following the examination of these individuals (see chapter 9), the study was unable to assign any of these specimens confidently to *T. crassimanus*. As highlighted by McGowan and Motani (2003), the material collected from the Yorkshire coast as a whole is poorly preserved, demonstrated by the specimens included in this study. This makes it difficult to assign specimens to a taxon based on a poorly preserved holotype, when additional specimens are also incomplete and poorly preserved. Despite McGowan (1974a) originally assigning YORYM 497, WHITM: SIM2546.S and WHITM: SIM5 to the same species (*T. acutirostris*), in addition to McGowan and Motani (2003) who also tentatively referred these specimens to *T. crassimanus*, it is difficult to determine whether the latter specimens share the key characteristics that were used to define *T. crassimanus* in this study. Therefore, none of these specimens can be assigned to *T. crassimanus*, but instead should be regarded as *Temnodontosaurus* sp.

Further difficulties arose during the examination of the holotype, as the specimen is displayed within a glass case of limited height, reducing access to the specimen. YORYM 497 is also considerably heavy and unable to be moved freely, preventing closer examination of individual elements and their orientations. Additionally, lack of lighting in the dark exhibition meant that it was difficult to assess certain cranial features and take clear photographs of the specimen, further contributing to the challenges posed when examining this specimen.

12. CONCLUSION

The main objective of this study was to provide a revision of the holotype of *Temnodontosaurus crassimanus* (YORYM 497) from the Lower Jurassic (Toarcian) of Whitby, Yorkshire. The re-examination of the species has resulted in the identification of several unique morphological features of the postcranial skeleton. *T. crassimanus* differs sufficiently from other species of *Temnodontosaurus*, specifically *T. trigonodon*, in possessing several distinct characteristics including a large, robust humerus that is proximodistally longer than the scapula (scapula length vs humerus length ratio: ~ 0.68 ; the opposite relationship is seen in *T. trigonodon*); humerus distal width which is almost as long as the humerus length; forefins which are significantly longer but less than twice the length of the hindfin (forefin length vs hindfin length ratio: ~ 1.51); and notching of the anterior facet of at least five leading edge elements (digit II) of both the fore- and hindfins. Although additional specimens that were previously tentatively assigned to *T. crassimanus* were located as part of this study, it was determined that none of these specimens can be assigned to *T. crassimanus*, and thus were referred to as *Temnodontosaurus* sp. The species was also incorporated into a phylogenetic analysis to explore its relationships with other Lower Jurassic ichthyosaurs and was found to be a sister taxon with *T. trigonodon* in some trees. The affirmation of the taxon has resulted in the species becoming better defined and adds to the currently six valid taxa of *Temnodontosaurus*, including *T. platyodon*, *T. eurycephalus*, *T. trigonodon*, *T. acutirostris*, *T. azerguensis* and *T. crassimanus*.

Furthermore, although the associated ammonites preserved on YORYM 497 are unfortunately unidentifiable, as highlighted in various literature (Carte and Baily, 1863; Benton and Taylor, 1984; Lomax, 2019a), the holotype of *T. crassimanus* most likely originated from the *bifrons* ammonite zone, and hence shared the same period of time as other large Toarcian temnodontosaurids (Figure 51) including *T. trigonodon* and *T. azerguensis* (Martin et al., 2012). *Temnodontosaurus* is often described as a classic example of a large-bodied predatory ichthyosaur from the Lower Jurassic, characterised by their skulls and jaws which often exceed 1 m in length, and with a total body length estimated at up to 12 m (Ji et al., 2016); associated gastric contents also indicate predation on other ichthyosaurs and cephalopods (McGowan and Motani, 2003; McGowan, 1996; Pardo-Pérez et al., 2018). Although stomach contents are not preserved with YORYM 497, the large total body length of the individual (~ 9 m), in addition to the large estimated skull length (~ 1.7 m) suggests that *T. crassimanus* most likely occupied the apex predator niche. In conclusion, *T. crassimanus* is one of only four species positively confirmed from the Upper Lias of Yorkshire, and this research has helped to lay the foundations for long overdue assessments of both the genus *Temnodontosaurus* and all of the Yorkshire Lias ichthyosaurs.

Toarcian	<i>aalensis</i>	
	<i>pseudoradiosa</i>	
	<i>dispansum</i>	
	<i>thouarsense</i>	
	<i>varibilis</i>	
	<i>bifrons</i>	
	<i>serpentinum</i>	
	<i>tenuicostatum</i>	
Pliensbachian	<i>spinatum</i>	<i>T. trigonodon</i> <i>T. azerguensis</i> <i>T. crassimanus</i>
	<i>margaritatus</i>	
	<i>davoei</i>	
	<i>ibex</i>	
	<i>jamesoni</i>	
Sinemurian	<i>raricostatum</i>	<i>T. platyodon</i> <i>T. eurycephalus</i>
	<i>oxynotum</i>	
	<i>obtusum</i>	
	<i>turneri</i>	
	<i>semicostatum</i>	
	<i>bucklandi</i>	
Hettangian	<i>angulata</i>	
	<i>lasicus</i>	
	<i>planorbis</i>	

Figure 51. Stratigraphic distribution of *T. platyodon*, *T. eurycephalus*, *T. trigonodon*, *T. azerguensis*, with the addition of *T. crassimanus* (highlighted in red) at the level of the ammonite zones during the Early Jurassic (stratigraphic ranges of *Temnodontosaurus* are based on Maisch and Matzke (2000), McGowan and Motani (2003) and Lomax (2019a). Modified from Martin et al. (2012).

13. FUTURE RESEARCH

To understand further the relationships of *Temnodontosaurus crassimanus* in Ichthyopterygia, a thorough taxonomic revision of *Temnodontosaurus* and the associated species, particularly *T. platyodon* is greatly required. At present, *Temnodontosaurus* is difficult to distinguish definitively and the genus is currently used to associate a selection of large Lower Jurassic neoichthyosaurs from various localities in Europe (McGowan and Motani, 2003; Ji et al., 2016); it is essentially a wastebasket taxon. Despite several diagnoses for *Temnodontosaurus* being proposed (discussed above, see chapter 8 and 11.1), better characters that unite the species have yet to be described and published, and it is likely that the individuals have been arbitrarily grouped together based simply on the fact that the specimens are 'large and from the Lower Jurassic', and not on the basis of their shared derived characters. If an in-depth review of the genus is undertaken, the additional specimens examined in this study (WHITM: SIM2546.S, WHITM: SIM5, MANCH: LL. 16096 and MANCH: L. 1688) could possibly be assigned to a species, and not just limited to *Temnodontosaurus* sp. By locating additional specimens and utilizing those currently inaccessible in museum collections (e.g. WHITM: SIM5), it would allow for more detailed data to be collected and gain a better understanding for the genus as a whole. The study of additional specimens should aid in helping to further understand and define the genus and species therein, resulting in the recognition of distinct characters. One of the unique characters of *T. crassimanus* highlighted within this study, the scapula length vs humerus length ratio, requires further research to determine its validity and whether similar features are found in other Lower Jurassic ichthyosaurs. Additionally, the forefins of *T. crassimanus* were determined to be significantly longer but less than twice the length of the hindfin, in contrast to *T. trigonodon* and *T. platyodon*. However, further research needs to be undertaken to determine whether there are any consistent differences between the relative lengths of the fore- and hindfins in *Temnodontosaurus* and the relevance of this character, as suggested by McGowan and Motani (2003). The biomechanical implications of these features observed in this species also require further analysis.

This study has also reinforced that whilst the ichthyosaurs from the Upper Lias of Yorkshire are undoubtedly among the best examples from the UK (others being from Strawberry Bank, Somerset; Caine and Benton, 2011) and therefore important to the scientific community, the material has been inadequately studied. The Lower Jurassic Posidonia Shale of southwestern Germany yields an abundance of well-preserved, relatively complete ichthyosaurs, of various species. The extensive study of these specimens, in comparison to the Yorkshire material, has resulted in a mostly well-understood and thoroughly described collection. In contrast, ichthyosaurs from the coeval Upper Lias of Yorkshire are poorly understood, mainly due to the limited collection data with historical specimens, lack of descriptions and overall poorly preserved specimens. Consequently, in addition to a review of the genus *Temnodontosaurus*, a complete re-examination and revision of all the Yorkshire ichthyosaur material is required to determine the variety and abundance of taxa and to provide a better understanding of the fauna during the Toarcian. While beyond the scope of this study, this thesis has helped to lay the foundations for this future research to be undertaken.

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15. APPENDICES

APPENDIX A

Measurements for *Temnodontosaurus trigonodon* specimens

Below are individual tables of all measurements for each *Temnodontosaurus trigonodon* specimen (SMNS 50000, SMNS 15950 and SMNS 17560) referred to within this study. *Denotes an estimate as the bone is damaged, or elements are missing/not preserved.

Table A1.	
Measurements for the preserved cranial and postcranial elements of SMNS 50000 (<i>T. trigonodon</i>).	
Features	(cm)
Total preserved length of specimen	916
Skull length	153
Preorbital length	112
Prenarial length	86.8
Right orbit length	26.5
Right orbit height	14.2
Right external naris length	15.6
Right external naris height	4.6
Right coracoid length	18.2
Right coracoid width	25
Left coracoid length	19
Left coracoid width	23.1
Scapula length	28.9
Scapula proximal width	12.5
Scapula distal width	13.1
Scapula shaft width	7.2
Scapula length vs left humerus length ratio	~ 1.42
Partial clavicle length	48*
Partial clavicle shaft width	3.6
Right humerus length	15.5*
Right humerus distal width	18
Right humerus shaft width	8.4
Right radius width	10.4
Right radius length	7.6
Right ulna width	10
Right ulna length	8.6
Width of preserved right forefin (at widest point)	24

Length of preserved right forefin	60*
Left humerus length	20.4
Left humerus proximal width	11
Left humerus distal width	19
Left humerus shaft width	10
Left humerus distal width vs proximal width ratio	~ 1.73
Left radius width	9.8
Left radius length	8.6
Left ulna width	10.6
Left ulna length	8.5
Left radiale width	8.3
Left radiale length	6.1
Left intermedium width	9
Left intermedium length	6.5
Width of preserved left forefin (at widest point)	23.4
Length of preserved left forefin	65.6
Pubis length	14.3
Pubis proximal width	4.7
Pubis distal width	8.1
Pubis shaft width	2.7
Ischium length	18.2
Ischium proximal width	11.0
Ischium distal width	8.3
Ischium shaft width	3.5
?Ilium length	7.9
?Ilium shaft width	2.6
Right femur length	16.3
Right femur proximal width	8.3
Right femur distal width	13.2
Right femur shaft width	7.1
Left humerus length vs right femur length ratio	~ 1.25
Right femur distal width vs proximal width ratio	~ 1.60
Right tibia width	6.2
Right tibia length	5.5
Right fibula width	70.6
Right fibula length	5.5
Right tibiale width	5.4
Right tibiale length	4.4
Right intermedium width	5.6

Right intermedium length	5.2
Width of right hindfin at widest point	16.5
Length of preserved right hindfin	78.4*
Length of longest preserved rib	83.5
Total number of preserved/exposed vertebrae	185

Table A2.	
Measurements for the preserved cranial and postcranial elements of SMNS 15950 (<i>T. trigonodon</i>).	
Features	(cm)
Total preserved length of specimen	777.1
Preflexural length (including the skull)	646.5
Skull length	160
Jaw length	164.9*
Premaxilla length	113.8
Maxilla length	53.1
Extent of maxilla under orbit	8
Right UTF length	21.9
Right UTF width	12
Left UTF length	25.4
Left UTF width	10.9
Preorbital length	106.3
Prenarial length	99
Orbit length	27.9
Orbit height	18
External naris length	14
Left external naris height	5.7
Width of preserved coracoid	19
Left scapula length	27.6
Left scapula proximal width	11.3
Left scapula distal width	10.6
Scapula length vs humerus length ratio	~ 1.28
Right humerus length	21.1
Right humerus proximal width	10.9
Right humerus distal width	18.5
Right humerus shaft width	9.6
Right radius width	10.1
Right radius length	9.1

Right ulna length	9.4
Right radiale width	8.9
Right radiale length	6.5
Right intermedium width	10.6
Right intermedium length	6.2
Width of preserved right forefin (at widest point)	20*
Length of preserved right forefin	70.4*
Left humerus length	21.6
Left humerus proximal width	10.9
Left humerus distal width	19
Left humerus shaft width	9.3
Left humerus distal width vs proximal width ratio	~ 1.74
Left radius width	10.8
Left radius length	9.2
Left ulna width	11.0
Left ulna length	9.7
Left radiale width	9.2
Left radiale length	6.1
Left intermedium width	10.2
Left intermedium length	6.3
Left ulnare width	7.4
Left ulnare length	7.0
Width of preserved left forefin (at widest point)	25.2
Length of preserved left forefin	73.1
Left pubis length	13
Left pubis proximal width	3.2
Left pubis distal width	7.9
Left pubis shaft width	2.8
Left ischium length	17
Left ischium distal width	10
Left ischium proximal width	9.5
Left ischium shaft width	5.2
Left ilium length	12.8
Left ilium proximal width	3.4
Left ilium distal width	4.2
Left ilium shaft width	2.4
Right femur length	18
Right femur proximal width	5.4
Right femur distal width	12.1

Right femur shaft width	6.3
Right tibia width	4.8
Right tibia length	7.0
Right fibula width	7.9
Right fibula length	6.7
Right tibiale width	5.6
Right tibiale length	5.2
Right intermedium width	7.4
Right intermedium length	5.6
Right fibulae width	5.6
Right fibulae length	5.4
Width of right hindfin at widest point	17.6
Length of preserved right hindfin	61.5
Left femur length	18.6
Left femur proximal width	8.9
Left femur distal width	12.8
Left femur shaft width	6.3
Left humerus length vs left femur length ratio	~ 1.16
Left tibia width	7.3
Left tibia length	6.4
Left fibula width	7.7
Left fibula length	6.2
Left tibiale width	5.7
Left tibiale length	5.0
Left intermedium width	7.0
Left intermedium length	5.8
Left fibulae width	6.2
Left fibulae length	5.3
Width of left hindfin at widest point	18
Length of preserved left hindfin	58
Left forefin length vs left hindfin length ratio	~ 1.30
Length of longest preserved rib	90.5
Total number of preserved/exposed vertebrae	178

Table A3.	
Measurements for the preserved cranial and postcranial elements of SMNS 17560 (<i>T. trigonodon</i>).	
Features	(cm)
Skull length	150.2

Jaw length	154.3
Right UTF length	12.9
Right UTF width	7.4
Left UTF length	15.7
Left UTF width	8.4
Right orbit length	22.7
Right orbit height	12.1
Left orbit length	22.3
Left orbit height	12.8
Right external naris length	10.3*
Right external naris height	4.2
Left external naris length	7.5
Left external naris height	4.7
Basioccipital condyle width	10.6
Basioccipital condyle height	9.4
Extracondylar area width	14.8
Extracondylar area height	9.7
Left exoccipital length	6.3
Left exoccipital shaft width	1.7
Right quadrate length	19
Right quadrate shaft width	3.0
Left quadrate length	17.8
Left quadrate shaft width	3.0
Length of best preserved tooth (right side)	2.9
Width of best preserved tooth (right side)	1.3
Length of best preserved tooth (left side)	3.4
Width of best preserved tooth (left side)	1.4
Left coracoid length	20.7
Left coracoid width	25.5
Right coracoid length	20.5
Right coracoid width	24
Left scapula length	32
Left scapula proximal width	11.5
Left scapula distal width	14
Left scapula shaft width	9.2
Right humerus length	21.5
Right humerus proximal width	11.8
Right humerus distal width	22.2
Right humerus shaft width	11.9

Right radius width	11.0
Right radius length	9.2
Right ulna width	11.9
Right ulna length	10.1
Right radiale width	8.8
Right radiale length	6.4
Right intermedium width	10.3
Right intermedium length	6.4
Right ulnare width	7.5
Right ulnare length	6.8
Width of preserved right forefin (at widest point)	27.4
Length of preserved right forefin	76
Left humerus length	22.6
Left humerus proximal width	11.7
Left humerus distal width	20.6
Left humerus shaft width	11.1
Left radius width	10.2
Left radius length	9.2
Left ulna width	11.1
Left ulna length	9.6
Left radiale width	7.9
Left radiale length	6.4
Left intermedium width	10.4
Left intermedium length	6.4
Left ulnare width	6.9
Left ulnare length	5.6
Width of preserved left forefin (at widest point)	26.2
Length of preserved left forefin	75.6
Right femur length	18
Right femur proximal width	8.7
Right femur distal width	15.1
Right femur shaft width	8.4
Right femur distal width vs proximal width ratio	~ 1.74
Right tibia width	6.9
Right tibia length	6.7
Right fibula width	8.1
Right fibula length	8.3
Right tibiale width	5.2
Right tibiale length	4.6

Right intermedium width	6.1
Right intermedium length	5.3
Right fibulae width	6.2
Right fibulae length	4.6
Width of right hindfin at widest point	17.1
Length of preserved right hindfin	63.4
Left forefin length vs right hindfin length ratio	~ 1.2
Left tibia width	7.2
Left tibia length	6.8
Left fibula width	7.9
Left fibula length	6.4
Left tibiale width	5.5
Left tibiale length	4.6
Left intermedium width	6.5
Left intermedium length	4.9
Left fibulae length	5.5
Width of left hindfin at widest point	18.3
Length of preserved left hindfin	56.3

APPENDIX B

Measurements for additional *Temnodontosaurus* specimens

Below are individual tables of all measurements for the additional *Temnodontosaurus* sp. specimens (WHITM: SIM2546.S, MANCH: LL. 16096 and MANCH: L. 1688) referred to within this study. Data for WHITM: SIM5 is not presented here, as no measurements were able to be taken. *Denotes an estimate as the bone is damaged, or elements are missing/not preserved.

Table B1.	
Measurements for the preserved cranial and postcranial elements of WHITM: SIM2546.S.	
Element	(cm)
Total preserved length of specimen	769
Precaudal length	440*
Best preserved isolated tooth length	5.5
Best preserved isolated tooth width	1.5
Right humerus distal width	19.5*
Right radius width	10.9
Right radius length	8.5
Right ulna width	10.3
Right ulna length	8.8
Right radiale width	7.1
Right radiale length	6.5
Right intermedium width	9.6
Right intermedium length	5.9
Right ulnare width	7.3
Right ulnare length	6.4
Width of preserved right forefin (at widest point)	24.5
Length of preserved right forefin	63.5
Left humerus length	21*
Preserved pubis length	17.5
Pubis proximal width	8.5
Pubis distal width	9.4
Pubis shaft width	5.3
Pubis length vs femur length ratio	~ 0.95.
Right femur length	18.5
Right femur proximal width	10.9
Right femur distal width	11.8

Right femur shaft width	6.3
Right femur distal width vs proximal width ratio	~ 1.1
Right tibia length	6.0
Right fibula length	5.4
Right intermedium width	6.2
Right intermedium length	5.1
Width of right hindfin at widest point	21
Length of preserved right hindfin	51
Right forefin length vs right hindfin length ratio	~ 1.25

Table B2.	
Measurements for the preserved cranial elements and postcranial elements of MANCH: LL. 16096.	
Element	(cm)
Total preserved length of specimen	76*
Width across naris	21*
Left external naris length	14.6*
Left external naris height	5.0
Best preserved tooth length	1.2
Partial clavicle length	15.5
Partial clavicle shaft width	1.6*

Table B3.	
Measurements for the preserved cranial and postcranial elements of MANCH: L.1688.	
Element	(cm)
Total preserved length of specimen	599
Skull length	145*
Jaw length	153.5
Preorbital length	124*
Prenarial length	88.5
Premaxilla length	125.5
Maxilla length	68*
Left UTF width (narrowest point)	6.4
Left UTF width (widest point)	12
Left orbit length	33
Left orbit height	25.5

Left external naris length	19
Left external naris height	3.5
Length of best preserved tooth	2.6
Width of best preserved tooth	1.2
Right coracoid length	14.5
Right coracoid width	16
Left coracoid length	13.5*
Left coracoid width	18
?Scapula shaft width	3.3
Lowermost humerus length	18*
Lowermost humerus proximal width	9
Lowermost humerus distal width	15.5
Lowermost humerus shaft width	8*
Lowermost humerus distal width vs proximal width ratio	~ 1.72
Uppermost humerus length	19.5
Uppermost humerus proximal width	7.9
Uppermost humerus distal width	18.5
Uppermost humerus shaft width	7.7
Uppermost humerus distal width vs proximal width ratio	~ 2.34
Uppermost radius width	10.8
Uppermost radius length	9.0
Uppermost ulna width	9.6
Uppermost ulna length	8.6
Uppermost radiale width	6.1
Uppermost radiale length	5.2
Uppermost intermedium width	7.1
Uppermost intermedium length	5.4
Uppermost ulnare width	6.2
Uppermost ulnare length	5.6
Width of preserved uppermost forefin (at widest point)	21.5
Length of preserved uppermost forefin	36
Lowermost femur length	14.5*
Lowermost femur proximal width	6.5
Lowermost femur distal width	9.9
Lowermost femur shaft width	6.0
Uppermost humerus length vs femur length ratio	~ 1.34

Lowermost humerus length vs femur length ratio	~ 1.24
Femur distal width vs proximal width ratio	~ 1.52
Lowermost tibia width	5.9
Lowermost tibia length	5.8
Lowermost tibiale width	4.0
Lowermost tibiale length	4.1
Lowermost intermedium width	4.9
Lowermost intermedium length	4.2
Lowermost fibulae width	4.2
Lowermost fibulae length	4.7
Width of lowermost hindfin at widest point	15.8
Length of preserved lowermost hindfin	25.7*
Uppermost forefin length vs hindfin length ratio	~ 1.40

APPENDIX C

List of phylogenetic characters for cladistic analysis (Fischer et al., 2013)

Characters with an asterisk (*) denotes characters that have been modified/added.

1. Crown striations: presence of deep longitudinal ridges (0); crown enamel subtly ridged or smooth (1) (Druckenmiller and Maxwell, 2010: character 25).
2. Base of enamel layer: poorly defined, invisible (0); well defined, precise (1) (Fischer et al., 2011: character 2).
3. Root cross-section in adults: rounded (0); quadrangular (1) (Fischer et al., 2011: character 3, modified).
4. Root striations: present (0); absent or subtle (1).
5. Overbite: absent or slight (0); clearly present (1) (Motani, 1999: character 33).
6. Processus postpalatinis pterygoidei: absent (0); present (1) (Maisch and Matzke, 2000: character 38).
7. Maxilla anterior process: extending anteriorly as far as nasal or further anteriorly (0); reduced (1) (Fischer et al., 2011: character 7).
8. Descending process of the nasal on the dorsal border of the nares: absent (0); present (1). (Fernández, 2007: character 2).
9. Processus narialis of the maxilla in lateral view: present (0); absent (1) (Fischer et al., 2011: character 9, inverted coding).
10. Processus supranarialis of the premaxilla: present (0); absent (1) (Maisch and Matzke, 2000: character 10).
11. Processus narialis of prefrontal: absent (0); present (1) (Fischer et al., 2011: character 11).
12. Anterior margin of the jugal: tapering, running between lacrimal and maxilla (0); broad and fan-like, covering large area of maxilla ventrolaterally (1) (Druckenmiller and Maxwell, 2010: character 6).
13. Sagittal eminence: present (0); absent (1) (Fernández, 2007: character 5, inverted coding Fischer et al., 2011).

14. Processus temporalis of the frontal: absent (0); present (1) (Fischer et al., 2011: character 14).
15. Supratemporal-postorbital contact: absent (0); present (1) (Sander, 2000: character 27, inverted coding Fischer et al. 2011).
16. Squamosal shape: square (0); triangular (1); squamosal absent (2) (Fischer et al., 2011: character 16, inverted coding Fischer et al., 2011).
17. Quadratojugal exposure: extensive (0); small, largely covered by squamosal and postorbital (1) (Maisch and Matzke 2000: character 30, modified Fischer et al., 2011).
18. Lower temporal arch between jugal and quadratojugal: present (0); lost (1) (Sander, 2000: character 25, modified).
19. Basispterygoid processes: short, giving basisphenoid a square outline in dorsal view (0); markedly expanded laterally, being wing-like, giving basisphenoid a marked pentagonal shape in dorsal view (1) (Fischer et al., 2011: character 18).
20. Extracondylar area of basioccipital: wide (0); reduced but still present ventrally and laterally (1); extremely reduced, being nonexistent at least ventrally (2) (Fernández, 2007: character 10, modified Fischer et al., 2011).
21. Basioccipital peg: present (0); absent (1) (Motani 1999: character 29, modified Fischer et al., 2011).
22. Ventral notch in the extracondylar area of the basioccipital: present (0); absent (1) (Fischer et al., 2012: character 19).
23. Shape of the paroccipital process of the opisthotic: short and robust (0); elongated and slender (1) (Fischer et al., 2012: character 20).
24. Stapes proximal head: slender, much smaller than opisthotic proximal head (0); massive, as large or larger than opisthotic (1) (Sander, 2000: character 34, modified Fischer et al., 2011).
25. Angular lateral exposure: much smaller than surangular exposure (0); extensive (1) (Motani, 1999: character 32, inverted coding Fischer et al., 2011).
26. Posterior dorsal/anterior caudal centra: 3.5 times or less as high as long (0); four times or more as high as long (1) (Maxwell, 2010: character 15, inverted coding Fischer et al., 2011).
27. Tail fin centra: strongly laterally compressed (0); as wide as high (1) (Maxwell, 2010: character 16).

- 28.** Neural spines of atlas-axis: completely overlapping, may be fused (0); functionally separate, never fused (1) (Druckenmiller and Maxwell, 2010: character 26).
- 29.** Chevrons in apical region: present (0); lost (1) (Sander, 2000: character 72).
- 30.** Rib articulation in thoracic region: predominantly unicapitate (0); exclusively bicapitate (1) (Maisch and Matzke, 2000: character 53).
- 31.** Rib cross-section at mid-shaft: rounded (0); '8'-shaped (1) (Sander, 2000: character 73, modified).
- 32.** Ossified haemapophyses: present (0); absent (1) (Maisch and Matzke, 2000: character 63).
- 33.** Tail as long or longer than the rest of the body (0) distinctly shorter (1) (Maisch and Matzke, 2000: character 65).
- 34.** No lunate tailfin (0) well developed lunate tailfin (1) (Maisch and Matzke, 2000: character 66).
- 35.** Glenoid contribution of the scapula: extensive, being at least as large as the coracoid facet (0); reduced, being markedly smaller than the coracoid facet (1) (Fischer et al., 2012: character 27).
- 36.** Prominent acromion process of scapula: absent (0); present (1) (Fischer et al., 2011: character 28).
- 37.** Anteromedial process of coracoid and anterior notch: present (0); absent (1) (Fischer et al., 2011: character 29, modified).
- 38.** Plate-like dorsal ridge on humerus: absent (0); present (1) (Motani, 1999: character 56).
- 39.** Protruding triangular deltopectoral crest on humerus: absent (0); present (1); present and very large, matching in height the trochanter dorsalis, and bordered by concave areas (2) (Fischer et al., 2011: character 31, modified).
- 40.** Humerus distal and proximal ends in dorsal view (thus regardless of the size of the dorsal and ventral processes): distal end wider than proximal end (0); nearly equal or proximal end slightly wider than distal end (1) (Motani, 1999: character 55, modified Fischer et al., 2011).
- 41.** Humerus anterodistal facet for accessory zeugopodial element anterior to radius: absent (0); present (1) (Godefroit, 1993: character 10, modified Fischer et al., 2011).
- 42.** Humerus with posterodistally deflected ulnar facet and distally facing radial facet: absent (0); present (1) (Fischer et al., 2011: character 34, modified).

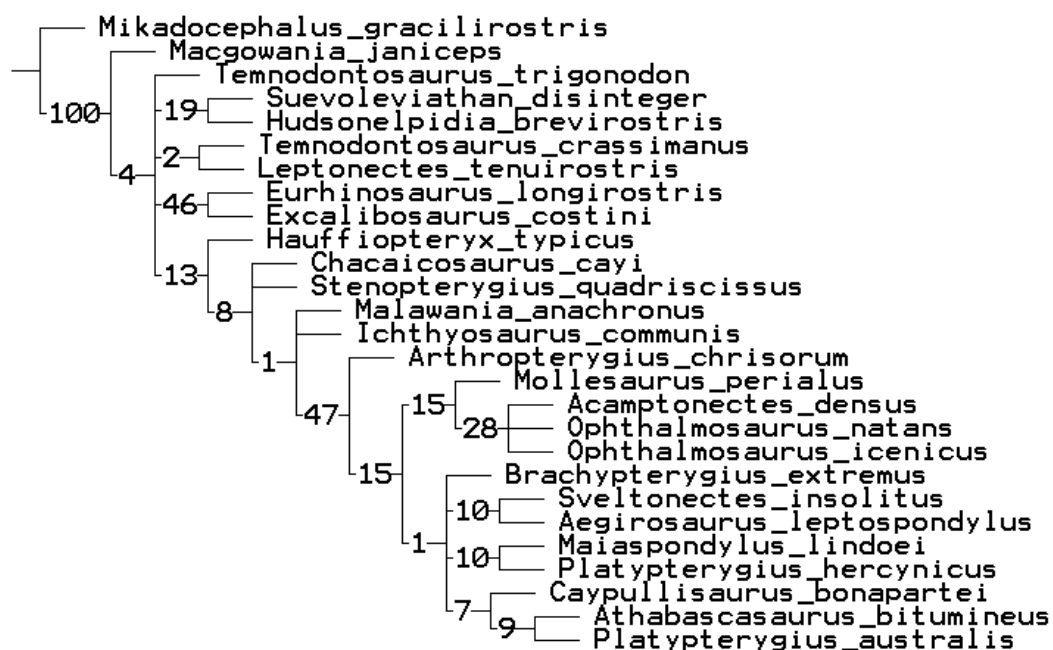
43. Humerus/intermedium contact: absent (0); present (1) (Fernández, 2007: character 15).
44. Anterodistal extremity of the humerus: prominent leading edge tuberosity (0); acute angle (1).
45. Shape of the posterior surface of the ulna: rounded or straight and nearly as thick as the rest of the element (0); concave with a thin, blade-like margin (1) (Fischer et al., 2012: character 36).
46. Radio-ulnar foramen: present (0); absent (1) (Maisch and Matzke, 2000: character 84, modified).
47. Manual pisiform: absent (0); present (1) (Motani 1999: character 67, inverted coding Fischer et al., 2011).
48. Notching of anterior facet of leading edge elements of forefin in adults: present (0); absent (1) (Motani 1999: characters 59 and 65, modified Fischer et al., 2011).
49. Posterior enlargement of forefin: number of postaxial accessory 'complete' digits: none (0); one (1), two or more (2) (Maisch and Matzke 2000: character 89, modified Fischer et al., 2011).
50. Preaxial accessory digits on forefin: absent (0); present (1) (Maisch and Matzke, 2000: character 91).
51. Longipinnate or latipinnate forefin architecture: one (0); two (1) digit (s) directly supported by the intermedium (Fischer et al., 2011: character 40).
52. Zeugo- to autopodial elements flattened and plate-like (0); strongly thickened (1) (Maisch and Matzke, 2000: character 94).
53. Tightly packed rectangular phalanges: absent, phalanges are mostly rounded (0); present (1) (Maisch and Matzke, 2000: character 102, modified Fischer et al., 2011).
54. Digital bifurcation: absent (0); frequently occurs in digit IV (1) (Fischer et al., 2011: character 43).
55. Manual digit V: lost or reduced to small floating elements (0); present (1) (Motani, 1999: character 73, modified).
56. *Forelimb/hindlimb ratio: (0) nearly equal or hindlimb longer; (1) forelimb longer but less than twice as long as hindlimb; (2) forelimb at least twice as long as hindlimb (Motani, 1999; Ji et al., 2016).

57. Ischium-pubis fusion in adults: absent or present only proximally (0); present with an obturator foramen (1); present with no obturator foramen (Mazin, 1982: character 13, modified Fischer et al., 2011).
58. Ischium or ischiopubis shape: plate-like, flattened (0); rod-like (1) (Motani, 1999: character 87, modified Fischer et al., 2011).
59. Iliac antero-medial prominence: present (0); absent (1) (Motani, 1999: character 81).
60. Prominent, ridge-like dorsal and ventral processes demarcated from the head of the femur and extending up to mid-shaft: absent (0); present (1) (Fischer et al., 2011: character 46).
61. Wide distal femur blade: present (0); absent, the proximal and distal extremity of the femur being sub-equal in dorsal view (1).
62. Astragalus/femoral contact: absent (0); present (1) (Maxwell, 2010: character 33).
63. Femur anterodistal facet for accessory zeugopodial element anterior to tibia: absent (0); present (1) (Fischer et al., 2011: character 48).
64. Spatium interosseum between tibia and fibula: present (0); absent (1) (Maisch and Matzke, 2000: character 114, modified).
65. Hind fin leading edge element in adults: notched (0); straight (1) (Motani, 1999: character 92, modified).
66. Postaxial accessory digit: absent (0); present (1) (Fischer et al., 2011: character 50).
67. *Radius with anterior notch: present (0); absent (1) (modified from Fischer et al., 2013: character 48; Lomax et al., 2017b).
68. *Tibia with anterior notch: present (0); absent (1) (modified from Fischer et al., 2013: character 65; Lomax et al., 2017b).
69. *Femur distal and proximal ends in dorsal view (thus regardless of the size of the dorsal and ventral processes): distal end wider than proximal end (0); nearly equal or proximal end slightly wider than distal end (1) (Motani, 1999: character 55, modified Fischer et al., 2011, modified Fischer et al., 2013: character 40).
70. *Humerus proximodistally longer than the scapula: yes (0); no (1).

APPENDIX D

Results of second cladistic analysis (new technology search with default settings, matrix bootstrapped with 1,000 replicates).

GC values, 1000 replicates, cut=1 (tree 0) - Standard Bootstrap



APPENDIX E

Individual species character coding used with the cladistic analysis

The following includes the individual coding for all of the species used in the cladistic analysis, in addition to the number and percentage of characters coded for each species. A '?' highlights a character that is either unknown in that species due to the poor preservation, lack of material or that the feature is absent in the specimen. Characters coded as [01] or B/[12] represents that both character states have been observed for that species. Refer to Appendix C for the phylogenetic characters used in the cladistic analysis and their individual descriptions.

[illegible]

<i>Acamptonectes densus</i>	11?1???1???1???111111100?1?[01]???0101111101111?1?0???????????????1
<i>Brachypterygius extremus</i>	01110?0110?1????11211?1????????101?1001101111111001????????1???
<i>Arthropterygius chrisorum</i>	????????????????0201?1?11?1?????0111110101?1?0???????0?0???1???
<i>Caypullisaurus bonapartei</i>	????0?00100???0001?????10???????111121100101112101101121?110?111111
<i>Aegirosaurus leptospondylus</i>	00010?111111?11111?????1???????11??1?100110111111?101121??1001111111
<i>Platypterygius australis</i>	01110000000101120112110110111??11?011121100101112101101220?1101111101
<i>Platypterygius hercynicus</i>	01100?101?01111[01]11?2?1?1??1?111???011121100101112101101????111011?1101
<i>Maiaspondylus lindoei</i>	?110??1?11?1?????0?????0??????????1?10011011?1?0?101?????10???????
<i>Athabascasaurus bitumineus</i>	10?1??0001?1101001?2???110?1????????????????????????2001?????????
<i>Sveltonectes insolitus</i>	10110?11111111???10211?1100?1?11??1101210001?1?11111101?21?1101111111
<i>Malawania anachronus</i>	????????????????????????????1??00??11000101?0001?001??????????1??1

Species	No. of characters coded	% of characters coded
<i>Mikadocephalus gracilirostris</i>	36	51
<i>Hudsonelpidia brevirostris</i>	30	43
<i>Macgowania janiceps</i>	25	36
<i>Leptonectes tenuirostris</i>	57	81
<i>Excalibosaurus costini</i>	45	64
<i>Eurhinosaurus longirostris</i>	64	91
<i>Temnodontosaurus trigonodon</i>	70	100
<i>Temnodontosaurus crassimanus</i>	40	57
<i>Suevoleviathan disinteger</i>	52	74
<i>Ichthyosaurus communis</i>	69	99
<i>Hauffiopteryx typicus</i>	51	73
<i>Stenopterygius quadriscissus</i>	69	99
<i>Chacaicosaurus cayi</i>	18	26
<i>Ophthalmosaurus icenicus</i>	70	100
<i>Ophthalmosaurus natans</i>	40	57
<i>Mollesaurus perialus</i>	12	17
<i>Acamptonectes densus</i>	32	46
<i>Brachypterygius extremus</i>	36	51
<i>Arthropterygius chrisorum</i>	23	33
<i>Caypullisaurus bonapartei</i>	46	66
<i>Aegirosaurus leptospondylus</i>	48	69
<i>Platypterygius australis</i>	66	94
<i>Platypterygius hercynicus</i>	54	77
<i>Maiaspondylus lindoei</i>	25	36
<i>Athabascasaurus bitumineus</i>	23	33
<i>Sveltonectes insolitus</i>	57	81
<i>Malawania anachronus</i>	20	29