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Abstract

Presented here is an analysis of 37 vertebrae, 1 complete humerus and 7 humeral fragments of small-sized ichthyosaurs from the Lower Saurian bone bed of the Early Triassic Vendomdalen Member in the Vikinghøgda Formation of Marmierfjellet, Spitsbergen, providing more insight into material from the expeditions by the Spitsbergen Mesozoic Research Group in the field seasons of 2014 and 2015. Comparison with other specimen of both Early- and Middle Triassic ichthyosaurs find that 5 of the fragmented humeri are referred to the family Mixosauridae, based on the unique proximal end of the taxa’s humeri, making these humeri the oldest mixosaurids yet known. The complete humerus is referred to the genus *Utatsusaurus* sp. based on its shape. The discovery of an Early Triassic Mixosauridae indicates that the recovery of marine predators after the Permo-Triassic mass extinction happened faster than previously thought, as Mixosauridae is seen as an intermediary between the anguilliform ichthyopterygians more common in the Early Triassic and the truly thunniform ichthyosaurs of the Jurassic and onward. This discovery is also evidence of a less rapid replacement of Early Triassic ichthyosaurs by the ones of the Middle Triassic, showing instead a period of coexistence in the Late Olenekian. The coexistence between Mixosauridae and *Utatsusaurus* sp. is discussed, especially with regards to the generalist diets of the taxa, as well as the possibility of Mixosauridae being a significantly more derived taxon than its Early Triassic contemporaries.

Sammendrag

Her presenteres en analyse av 37 vertebrae, 1 komplett humerus og 7 brukne humeri fra små ichthyosaurer fra Tidlig Trias i Nedre Saurie-laget i Vendomdalenleddet fra Vikinghøgdaformasjonen, Marmierfjellet, Spitsbergen og gir mer innsikt i materiale gravd opp av Spitsbergen Mesozoic Research Group under feltsesongene i 2014 og 2015. Ved hjelp av sammenligninger med andre fossiler fra både Tidlig- og Mellom-Trias finner vi at 5 av humeriene tilhører familien Mixosauridae, basert på den unike formen på den proximale delen av humerusen, som betyr at disse humeriene er de eldste fossilene etter Mixosauridae som er beskrevet. Den komplette humerusen tilhører *Utatsusaurus.* Oppdagelsen av Mixosauridae i Tidlig Trias indikerer at ichtyosaurer utviklet seg raskere enn antatt etter den Permo-Triassiske masseutryddelsen, ettersom Mixosauridae er et mellomledd i utviklingen av ichthyosaurer, mellom de anguilliforme ichthyopterygiene i Tidlig Trias til de thunniforme ichthyosaurene fra Jura og videre. Denne oppdagelsen gir også bevis på en mindre umiddelbar utskifting fra Tidlig Triasiske til Mellomtriasiske ichthyopterygier og heller en overgangsfase mot slutten av Olenekian. Koeksistensen mellom Mixosauridae og *Utatsusaurus* sp. diskuteres også, med spesielt fokus på at begge taxa var generalister og muligheten for at Mixosauridae var en mer effektiv svømmer enn sine samtidige i Tidlig Trias.

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1 Introduction

The Permian-Triassic extinction event, around 252 Ma was without a doubt the largest extinction event to ever have occurred on this planet. Almost all marine life went extinct, opening the seas for brand new species to evolve and take over. Among the first of the greater marine predators were the ichthyopterygians, who evolved a multitude of forms in the Early Triassic, shortly after the PTME, such as Grippia, Utatsusaurus or the large Cymbospondylus. Not every species that evolved in the immediate aftermath of this extinction is known however, as a direct consequence of the taphonomic process and a fair bit of sheer chance in whether fossilised remains are found or not. The Middle Triassic saw even greater diversification of the Ichthyopterygians, with the family Mixosauridae spreading across the entire northern hemisphere e.g. (Jiang, Schmitz, Motani, Wei-Cheng, et al., 2007; Silvio Renesto et al., 2020; Sander et al., 1990; Økland et al., 2018). In here we present several Early Triassic ichthyosaurian remains from the Lower Saurian niveau of the Early Triassic Botneheia Formation, Svalbard. The remains were excavated between 2014 and 2016 by researchers at the Natural History Museum of Oslo (NHM). The material included herein consists largely of small vertebral centra of somewhat inconclusive origin, due to little previous discussion of the topic, but there are also several humeri, bearing more diagnostic characters.

1.1 Anatomical traits of Mixosauridae

Mixosauridae were a clade of Triassic ichthyosaurians, recognized as an intermediate form between the Early Triassic forms such as *Utatsusaurus* or *Grippia* and the later and more fish-shaped clades like *Opthalmosaurus (Motani, 2005).* The mixosaurids were relatively small in size, between one and two metres in length. The cranium is immediately recognisable by a large, almost completely circular orbit and a distinct sagittal crest that extends from above the orbit and reaches the nasal (Motani, 1999c). The axial skeleton contains approximately 120 vertebrae, with the caudals slightly outnumbering the precaudals (Silvio Renesto *et al.,* 2020). The dorsal neural spines of Mixosauridae are very tall and straight, with continuously reduced zygapophyses posteriorly, until contact is lost around the 14th vertebra (Schmitz *et al.,* 2004). In the caudal region, the vertebrae become highly laterally compressed and form a ventrally oriented bend for the caudal fin. The caudal fin also includes a soft tissue dorsal portion that was discovered in 2020, along with a soft tissue dorsal fin (Silvio Renesto *et al.*, 2020). Apart from the cranium, the appendicular skeleton of Mixosauridae contains the most diagnostic material, especially in the humerus. The proximal end of the humerus has a distinct head on the posterior side that protrudes from the rest of the face, with the anterior portion forming a shelf beneath the head. The posterior border of the humerus is concave, whereas the anterior border contains the large, convex, flattened anterior flange. The posterior distal facet is shorter and wider than the anterior one.

1.2 History of mixosaurid discoveries

Since the original description by Hulke (1873), to more recently (Silvio Renesto *et al.*, 2020), many specimens of mixosaurid ichthyosaurs have been described from several localities. Georg Baur coined the family Mixosauridae and its first genus, *Mixosaurus*, in 1887 (G. Baur, 1887), though the first mention of what would later become *M. nordenskioldii* was published by John W. Hulke in 1873 (Hulke, 1873), then under the genus *Ichthyosaurus*. Since its original description, there has been several new additions to the family. A new genus, *Phalarodon*, with two species was erected in 1910 by John C. Merriam (1910) Mixosauridae remains have been recovered from most of the Northern hemisphere, including Svalbard, Central Europe, North America and China as the most common areas of occurrence.

1.2.1 Svalbard

Svalbard has yielded a large number of ichthyopterygians over the years, since the first description in 1873 (Hulke, 1873) to the present. The most productive formations have been the Vikinghøgda and Botneheia formations, both of Triassic age, but Early and Middle respectively (Vigran *et al.*, 2014). The second description of mixosaurids from Svalbard is a paper from 1910 by Wiman, which renamed the previously described *Ichthyosaurus nordenskioldii* (Hulke, 1873) as *Mixosaurus nordenskioldii* (C. Wiman, 1910). Wiman's description included several interclavicles and an entire pelvic girdle, all of which was found from the Upper Saurian niveau, fossiliferous shale ranging from the Ladinian to the latest Carnian, in what is now part of the Botneheia Formation (Maxwell *et al.*, 2013; C. Wiman, 1910). Wiman's discoveries were further elaborated upon in 1911 by Merriam, who transferred some of Wimans specimens to the newly erected genus *Phalaradon* (Merriam, 1910), based on morphological similarities. Both genera (*Mixosaurus* and *Phalaradon*) are in the family Mixosauridae and from the Middle and Late Triassic (Merriam, 1911). Later, Wiman made a comparison between the then known Triassic ichthyosaurs of Svalbard, Europe and western North America (C. Wiman, 1916). The article agrees with the reclassifications from Merriam 1911 with regards to mixosaurids (Merriam, 1911; C. Wiman, 1916). More material was recovered in the Cambridge expeditions between 1961 and 1973. Among the findings were cranial fragments with dentition characteristic to mixosaurids (Cox *et al.*, 1973). It should be noted that these were originally referred to the genus *Mixosaurus* by Cox and Smith, but this has been contested in later publications, instead referring the specimens to *Phalarodon*, within the same family (Maxwell *et al.*, 2013; Schmitz, 2005). Cox and Smith also describe ichthyosaur remains from a large variety of localities on Svalbard, ranging from Early Triassic to the latest Triassic, (Cox *et al.*, 1973). The article names one specimen of *Mixosaurus*, B1557, which is of Middle Triassic age and compares well with the contemporary *Mixosaur* sp. fossils from Central Europe (more on those later). Maxwell and Kear (2013) reassessed the ichthyopterygian discoveries from Svalbard. They found evidence of *Phalarodon sp.* from the Anisian Botneheia Formation, and the *Phalarodon* species *P. fraasi* and *P. callawayi* from the Ladinian, largely based on cranial elements including dentition (Maxwell *et al.*, 2013). They also note a dorsal section of the skeleton from the Lower Saurian niveau that is comparable to mixosaurids, with no further details (Maxwell *et al.*, 2013). The latest mixosaurid to come out of Svalbard was described in 2016, when a new species of *Phalarodon* was discovered from the Middle Triassic Botneheia Formation, named *Phalarodon fraasi* (Økland *et al.*, 2018).

In summary, no Early Triassic Mixosauridae has conclusively been recovered from Svalbard previously.

It is evident then, that no member of the family Mixosauridae has so far been conclusively recovered from the Early Triassic of Svalbard.

1.2.2 Tethys Ocean

The Besano Formation in Monte San Giorgio have yielded numerous mixosaurids, including a recent find with a complete dorsal fin (Silvio Renesto *et al.*, 2020). Georg Baur (1887) erected the genus *Mixosaurus* and its family Mixosauridae based on museum specimens from the Besano Formation. In 1895, W. Dames (Dames, 1895) reviewed the varied Triassic ichthyopterygians of the Lombardy area of his time. A discovery was made during an expedition in 1957 to the Besano Formation proved that mixosaurids were viviparous, when a pregnant *Mixosaurus* was discovered from the Late Anisian of the Grenzbitumenzone of Monte San Giorgio (Brinkmann, 1996). In 1998, he erected the mixosaurid genus *Sangiorgiosaurus*, based on a peculiar dentition in the lower jaw (Brinkmann, 1998). Another genus was erected in 1998 under the name *Contectopalatus* (Maisch *et al.*, 1998). Maisch and Matzke published further discoveries of the genus and other genera in the family Mixosauridae over the following years (Maisch *et al.*, 2000, 2001, 2005; Maisch *et al.*, 2006). Two specimens of *Mixosaurus cornalianus* were described in 2020 from the Middle Triassic Besano Fm., with preserved soft tissue that showed a dorsal fin and a triangular lobe on the caudal fin, neither of which had previously been described for the genus, making *Mixosaurus* the oldest amniote with a dorsal fin (Silvio Renesto *et al.*, 2020) The one major through line of the body of work to come from the central European region regarding Mixosauridae, is that all are of Middle Triassic age.

The first mixosaurid to be found in China, or the East Tethys sea, was first described in 1960, but then as a plausible nothosaurian from the Lower Middle Triassic of the Guanling Formation (C.-C. Young, 1960). The specimens were rediscribed by the same author some years later and reassigned to mixosauridae, but as a new species, *Mixosaurus maotaiensis*, establishing that Mixosauridae had a presence in the Eastern Tethys ocean (C.-C. Young, 1965). Another new species was added to the *Mixosaurus* genus in 2006, *M. panxianensis*, again from the Guanling Formation (Jiang *et al.*, 2006). The first Chinese member of Mixosauridae's other genus, *Phalarodon*, was described the year after from the formation as the previous (Jiang *et al.*, 2007). Another *Mixosaurus* skull was described in 2011, from the Anisian of the Guanling Formation (Liu *et al.*, 2011). Two years later Liu et.al. published the first description of a *Phalarodon atavus* from China, from the lower Carnian, Upper Triassic which is also the first published complete specimen of *P. atavus* (Liu *et al.*, 2013).

As with the western Tethys ocean, the East Tethys also contains numerous mixosaurids from the Middle Triassic.

1.2.3 North America

On the other side of the world, in Nevada, a mixosaurid was described all the way back in 1910. The description concerns two specimens from an 1895 expedition, both of cranial origin with retained dentition and both from the Middle Triassic of the West Humboldt Range, Nevada. Both specimens were identified as *Phalarodon fraasi* (Merriam, 1910). More mixosaurids were described from the Sulphur Mountain Formation in British Columbia, Canada. One specimen from this expedition consists of an array of highly fragmentary skull pieces, and is dated as Olenekian in age. The other mixosaurids are of Middle Triassic, Ladinian age and consists of series of caudal vertebrae (Callaway *et al.*, 1989). Another series of vertebrae was discovered from the Middle Triassic of Nevada the year after, with complete articular facets and articulated neural spines (Sander *et al.*, 1990). Up to 1999 there had been a discussion on the relationship between *Mixosaurus* and *Phalarodon* (Christopher McGowan, 1972; Merriam, 1910; Sander *et al.*, 1990), but this was more or less concluded by the discovery of a Middle Triassic *Phalarodon* skull associated with distinctly mixosaurid-like postcranial material, conclusively placing the two genera within a single family, Mixosauridae (Elizabeth L. Nicholls *et al.*, 1999). Not long after this, a new mixosaurid species was erected from material recovered from the Middle Triassic Favret Formation in Nevada, based on a three-dimensional skull, the cervical and large portions of anterior appendicular skeleton, presented along with almost complete postcranial skeleton from *M. nordenskioldii* (Schmitz *et al.*, 2004). Though Callaway's findings from 1989 might indicate the presence of a Lower Triassic *Mixosaurus*, it must be noted that almost all subsequent publications on the family refer to Mixosauridae as a purely Middle Triassic taxon e.g.(Houssaye *et al.*, 2014; Kolb *et al.*, 2011; Motani, 2005; Schmitz, 2005; Økland *et al.*, 2018). Whatever the case may be, up to now, Callaway's findings are the only clear indication of a an Early Triassic *Mixosaurus* (Callaway *et al.*, 1997; Økland *et al.*, 2018)

2 Materials and methods

2.1 Institutional abbrevations

PMO = Paleontological Museum Oslo, the University of Oslo, Oslo, Norway.

2.2 Excavation and collection

The Spitsbergen Mesozoic Research Group collected a large array of ichthyosaur remians during the fieldwork seasons of 2014 and 2015 to the Isfjorden area of central Spitsbergen. The material was collected from both the Vikinghøgda and Botneheia formations, spanning the Early to Middle Triassic. This thesis presents small ichthyosaurian remains from the Lower Saurian bonebed in the Olenekian (Spathian) Vendomdalen Member of the Vikinghøgda Formation, recovered by the aforementioned expeditions.

2.3 Preparation

As this study only concerns small ichthyosaurs from the Early Triassic, shark- and fish material was sorted out, as was large-sized ichthyosaur remains (see Engelschiøn *et al.* (2018) for the large-sized ichthyosaur remains). Most of the fossils were already completely free of matrix when they were collected or were prepared by other researchers and collection technicians at the Natural History Museum, Oslo. An exception was the ichthyopterygian vertebra PMO 231.013, which was partially covered by matrix, most of which was then removed with an air scribe. Some matrix was left as it did not impede study, and as further preparation could damage the bone.

All specimens were photographed using the focus stacking function on a Nikon D850, with an AF-S Micro NIKKOR 60mm 1:2.8 G ED lens (20 pictures per stack, focus step width adjusted for the individual specimens). The raw files were converted to DNG format for use in Adobe Photoshop using the Adobe DNG converter, as the default RAW format of the camera was incompatible with Photoshop, where temperature, exposure and contrast were adjusted. The files were then stacked and made black and white using the existing commands in Photoshop CS6 (64 bit). The final step was to remove the background and insert a scale bar, which was done in Corel Painter Essentials 7, a simplified version of the program Corel Painter 7.

2.4 Analysis

The vertebrae were compared morphologically with each other to ascertain anatomical position in the vertebral column, and were also compared with previous publications on both Early- and Middle Triassic ichthyosaurs to determine taxonomical affinity. The humeri were compared with each other and with material from previous publications to ascertain taxonomic affinity. The vertebrae were measured on dorsoventral height, anteroposterior length and mediolateral width. All measurements were taken at the longest, tallest or widest point, respectively.

3 Geological setting

In the Triassic Period, there was a large embayment of the Panthalassa Ocean on the northern rim of Pangea, known as the Boreal Ocean (Lundschien *et al.*, 2014). This ocean, at approximately 45°N, was a large, low-relief, open marine shelf with mainland Pangea to the south, east and north. Following the shelf that makes up the Boreal Ocean south, one finds what is today the Wapiti lake and the Vega-Phroso siltstone member in the Sulphur Mountain Formation, British Colombia, Canada, where *Utatsusaurus* has previously been recovered (Fig. 1) (Robin S Cuthbertson *et al.*, 2014).

The specimens described herein were recovered from the Lower Saurian niveau, upper Vendomdalen Member (Spathian age), of the Vikinghøgda Formation in Sassendalen, central Spitsbergen, during expeditions in the summers of 2014 and 2015 (Fig . 2) (Engelschiøn *et al.*, 2018). The Lower Saurian niveau is an approximately 95 cm thick section consisting of shale and siltstone, with vertebrate remains scattered throughout (Fig. 3) (see Engelschiøn et al. 2018 for a more detailed description).

4 Results

4.1 Axial skeleton

Owing to a lack of description of axial material of other Early Triassic ichthyopterygians present in the Lower Saurian Niveau, no vertebra could be diagnosed with more specificity than “small, Early Triassic Ichthyopterygian”. Some vertebrae do fit previous descriptions of Mixosauridae, but without proper comparisons with other ichthyopterygians from the time period, they cannot in good faith be designated as such. There are some synapomorphies of the vertebrae in the family Mixosauridae that have previously been used to diagnose the family, but naturally only in the context of the Middle Triassic and as such not with comparisons with Early Triassic taxa such as Utatsusauridae or Gripiidae (Schmitz, 2005; Schmitz *et al.*, 2004). As such, the vertebrae presented herein are designated Ichthyopterygia indet., but share several morphotypical traits and can probably be seen a single morphotype.

All the vertebral centra described herein share the trait of being dorsoventrally taller than anteroposteriorly long, with no centrum having a lower height-length ratio (henceforth abbreviated H-L ratio) than 1.36, observed in PMO 230.763.

Anterior dorsal vertebrae (PMO 230.775, PMO 230.783, PMO 230.897)

These vertebrae (Figure 3) are classified by their hexagonal shape, the presence of both diapophyses and zygapophyses anteroventrally and relatively low levels of lateral compression, when compared to the other vertebrae morphotypes presented herein. These traits are based on previous descriptions of mixosaurid vertebrae (Elizabeth L. Nicholls *et al.*, 1999; Schmitz *et al.*, 2004; Økland *et al.*, 2018).

In anterior and posterior view, the vertebrae display a distinctly rounded hexagonal shape that is slightly elongated in the dorsal half of the centra. Both rib articular facets are visible in anterior view as they protrude out laterally from the anterior margin, the diapophyses at the dorsoventral midpoint and the zygapophyses at the ventral-most point of the lateral anterior margin. The ventral portion of the anterior margin is a straight line from zygapophysis to zygapophysis, whereas the dorsal margin curves inward medially to accommodate the neural canal. The only major difference between the anterior and posterior margins is that the flat posterior ventral margin does not connect with the zygapophyses.

In lateral view, the lateral surface is deeply anteroposteriorly concave, making the anterior and posterior faces bulge out from the anteroposterior middle. The diapophyses are situated dorsoventrally medial on the bone, fused with the anterior margin and are of a slightly oval, small knob-like outline. The zygapophyses are smaller than the diapophyses, situated much more ventrally, fused to the anterior margin.

Dorsal vertebrae (PMO 231.160, PMO 231.022, PMO 231.076, PMO 213.013)

The following vertebral centra (Figure 4) are referred to the dorsal section of the ichthyosaur body based on a rounded hexagonal outline, single rib articular facet on either lateral, situated close to the anterior border, medially to just ventral of medial, and are slightly raised rounded protrusions, as described by previous literature (Sander *et al.*, 1990; Schmitz *et al.*, 2004).

In anterior and posterior view, these vertebrae are of a rounded hexagonal outline with a notochordal pit that is filled with matrix in most specimen. The neural canal is visible from both the anterior and posterior views, as a deepening of the margin between the articular facets for the neural arch.

In anterior view in PMO 231.160, the diapophysis protrudes laterally slightly out from the rest of the anterior border at the widest point. The facets for the neural arch are visible as raised points on either side of the neural canal, followed by a straight to slightly concave portion until the border bends away to the lateral portion.

In posterior view, the facets for the neural arch are visible as raised points on either side of the neural canal and no diapophyses are fused with the border. It is otherwise quite identical to the anterior face.

The lateral surface is concave, making the anterior and posterior margins seem bulging in comparison. The tallest point of the lateral surface is a ventromedial ridge posterior to the diapophysis. In shape, the diapophysis is a raised oval knob that is longer anteroposteriorly than dorsoventrally. Anteriorly it is fused with the anterior margin, whereas it posteriorly gently curves in toward the centre of the vertebra. This inward curve forms part of the lateral ventromedial ridge mentioned earlier.

In dorsal view, the vertebrae have distinct, very slim grooves for neural arch facets. The grooves are much longer anteroposteriorly than their lateral expanse, covering about half the anteroposterior length from where they fuse with the anterior border.

The ventral surface is concave in both anteroposterior and lateral directions and is bordered on either lateral by a slight ridge following from the lateral surface. The ridge spans the gap between small reinforcements of the corners of the ventral anterior and posterior margin. These reinforcements occupy the same space as the zygapophyses of the anterior and posterior dorsal vertebrae, but the reinforcements are much smaller, less pronounced, more ventrally oriented and are situated on both the anterior and posterior side, so it must be concluded that they are not articular surfaces for ribs.

Middle caudal vertebrae (PMO 230.651, PMO 231.027)

The caudal vertebrae (Figure 5) are recognizable in their laterally deeply compressed, hexagonal outline, with knob-like diapophyses, but no parapophyses.

In anterior view, the caudal vertebrae have a dorsoventrally elongated hexagonal outline, with deep notochordal pits and rounded diapophyses slightly protruding at the dorsoventrally widest point of the bone, at the anterior margin.

Posterior caudal vertebrae (PMO 230.660, PMO 230.622, PMO 230.661, PMO 230.922, PMO 231.132, PMO 231.143, PMO 231.044)

These vertebrae (Figure 6) are laterally compressed from life, lack diapophyses and bear facets for chevrons. They have an H-L ratio between 1.44 (PMO 230.622) and 1.81 (PMO 231.044). In anterior or posterior view, they are elongated hexagonal to almost square due to the lateral compression in outline with faces that bulge out from the lateral surfaces.

The lateral surfaces do not bear any rib articular facets or traces thereof and are concave, with a slight expansion at the dorsoventral midpoint that follows the expansion of the anterior and posterior margins in the same area, giving the specimens their hexagonal shape.

The dorsal surface has two anteroposteriorly elongated grooves for neural arch facets, as is typical of this morphotype. The ventral surface has a pair of chevron articular facets at the anterior and posterior border.

4.2 Appendicular skeleton

PMO 229.783

PMO 229.783 (Figure 7 A) is a complete humerus. The proximal head is almost completely flat anteroposteriorly, with slight proximal bulging on the anterior and posterior facet surfaces. The deltopectoral crest makes the anterior portion of the facet slightly wider than the posterior in proximal view. There is a ridge (from this point termed the deltopectoral ridge) running from the deltopectoral crest postero-distally, about halfway down the humerus. The posterior margin is somewhat concave, whereas the anterior margin consists of a convex, flattened anterior flange. The posterior portion of the humeral shaft is laterally constricted distally to the deltopectoral ridge. The distal facet for the ulna is short, wide and concave, while the facet for the radius is longer, slimmer and straight. The two facets meet at an angle of approximately 140°. The proximal and distal ends of this humerus are almost parallel. Proximally to the ulnar facet is a third, small, triangular facet, a trait that is also present in Motani's description of an *Utatsusaurus* humerus (Motani, 1997). This small facet is not present in Mixosauridae (Schmitz *et al.*, 2004). It is clearly longer than wide, which would run contrary to descriptions of *Grippia*, whose humeri were as long as wide (Motani, 1998). In overall shape, PMO 229.783 does not match any depiction of a mixosaurid humerus, as PMO 229.783 does not have the proximally expanded humeral head described in Mixosauridae (Schmitz *et al.*, 2004), as well as a much straighter posterior border (Kolb *et al.*, 2011) and a relationship between the radial and ulnar facets more in line with the *Utatsusaurus* descriptions by Motani (1997), than with mixosaurid descriptions (Motani, 1999a; Schmitz *et al.*, 2004). Overall, PMO 229.783 is almost identical to the one described by Motani (1997), with the exception that the proximal facet of PMO 229.783 is completely ossified.

This humerus is referred to *Utatsusaurus sp.* based on the pronounced anterior flange, the almost straight proximal facets, parallel and equal in length proximal and distal ends, the placement of the deltopectoral crest at the anteroproximal end and the presence of a third, small, triangular facet postero-distally, posterior to the ulnar facet.

Proximal humeri pieces (PMO 229.786, PMO 229.788, PMO 229.789, PMO 230.185, PMO 230.186)

These humeri are all referred to Mixosauridae based on the following traits: The posterior portion of the proximal facet is raised proximally beyond the anterior portion of the same facet, with the anterior portion forming a anteroposteriorly flat shelf, wider anterior portion of the proximal facet compared to the posterior, the anterior flange beginning after a slight distal dip in the anterior portion of the proximal surface or traces of said flange, as well as a pronounced deltopectoral crest and deltopectoral ridge going postero-distally from the crest. This shape differs from that of other similar Triassic Ichthyopterygians, in that the proximally raised head is not present in members of Utatsusauridae or Grippiidae, who all display flatter proximal facets than that of Mixosauridae (Motani, 1997, 1998, 1999a).

PMO 229.786

PMO 229.786 (Figure 9 A) is a portion of a humerus, conserving the proximal facets, portions of an anterior flange and approximately half of the body of the bone. The posterior portion of this facet is proximally xpanded beyond the anterior portion, forming a pronounced head. The anterior portion of the facet is flat and somewhat shelf-like. The anterior flange contacts slightly below the shelf-like anterior facet, and looks to be anteriorly convex, but not much of it is preserved. The remaining portion of the posterior border of the humerus is concave, but as the bone is broken it is impossible to say exactly what shape the posterior border would have had. In proximal view, the facet is widest at the anteriormost point and slimmest at the posterior end. The ventral border of the facet is nearly straight, whereas the dorsal widens at the apex of the facet to from the deltopectoral crest, though the apex of the crest and the deltopectoral ridge are missing from this specimen. In terms of osteology, PMO 229.786 displays a slightly rough surface on the undamaged portions, and the proximal facet is well formed, though more porous than the surface and facet of PMO 229.788. It is however difficult to ascertain the age of the individual for certain due to a lack of comparative material, but pictures in Figure 2 of Kolb et.al. (2011), especially C and F, give an inkling of different stages of mixosaurid humerus ossification and the shape at different stages, which would probably put PMO 229.786 somewhere in the middle of the range, based on the shape of the posterior proximal facet being closer to F and the roughness of the surface being more in line with C in figure 2 of Kolb et.al. (2011).

PMO 229.788

PMO 229.788 (Figure 9 B) is the largest of the proximal humerus pieces. It is broken partway down distally along the shaft in a similar fashion to other specimen of this section. The head is more eroded than in PMO 229.786 and 230.186, especially at the posterior end. The anterior flange is visible as a flat expansion of the bone along the anterior border with a well preserved surface, but is otherwise missing. The proximal surface is much wider anteriorly, owing to a large deltopectoral crest and ridge. The deltopectoral ridge goes postero-distally from the crest. The posterior portion of the proximal surface is thinner than the anterior, and is proximally raised in a similar fashion to the humeri of this section. This bone also displays the smoothest ventral surface of the proximal humerus pieces, and its anterior portion of the proximal facet and deltopectoral crest is better ossified than the other proximal humeral pieces, especially at the deltopectoral crest itself. The posterior portion of the proximal facet is however difficult to say much about, as it is badly eroded on much of the posteriormost parts. The dorsal side is pockmarked across most of the surface, though at least some this is attributable to erosion, and the surface approaching the anterior flange is much smoother. Considering the size and ossification of the surface of PMO 229.788, it is here considered the most adult of the bones.

PMO 229.789

PMO 229.789 (Figure 8 B) is smaller than PMO 229.788, but otherwise quite similar, particularly at the anterior portion of the proximal facet, both of which are wider at the deltopectoral crest than the other humeri described herein. The deltopectoral crest and ridge almost doubles the width of the anterior portion of PMO 229.789. A portion of the bone posterior to the apex of the deltopectoral ridge is eroded in a proximodistally directed cavity that terminates slightly distally of halfway down the bone, where another piece postero-distally, and connected with the cavity, is eroded away. The anterior flange is missing, save for a piece of the most proximal portion, situated distally to the proximal surface. The surface of the anterior proximal facet is wide and evenly convex dorsoventrally, but slopes sharply down to the anterior flange and is flat posteriorly, similar to the shelf-like shape of the anterior proximal surface of the rest of these humeral fragments. The posterior portion of the proximal surface curves further proximally and becomes slimmer, forming the posterior head. The exact height of the head cannot be discerned due to erosion on the posterior proximal surface and along the posterior surface of the shaft. The surface of the deltopectoral ridge is the smoothest of all the humeri described herein, whereas the deltopectoral crest is slightly rougher than PMO 229.788.

PMO 230.186

PMO 230.186 (Figure 9 C) is nearly identical to PMO 229.786, except PMO 230.186 is slightly larger, the anterior flange is worse preserved, though present, and the posterior portion of the facet is slightly flatter. The deltopectoral crest of PMO 230.186 is better preserved than in PMO 229.786, being only slightly chipped at the dorsal peak. The surface of PMO 230.186 is less rough than that of the smaller PMO 229.786, but also rougher than that of PMO 229.788 and PMO 229.789, which fits with the size gradient between these humeri, assuming the humeri would grow with age in the species.

PMO 230.185

In proximal view, PMO 230.185 (Figure 8 A) is similar to PMO 230.186, but the preservation is worse. This fossil is the most eroded out of all the humeri presented herein, but some characteristics are still present. The posterior portion of the proximal facet is both slimmer and taller than the anterior, though the apex of the fossil is missing. The deltopectoral crest and the deltopectoral ridge are both present, but deeply weathered. The anterior surface retain only traces of an anterior flange and the posterior lacks most of the bone surface. The surface is vary weathered, making a definitive comment on the ossification of the surface difficult.

Distal humerus fragments (PMO 229.792 and PMO 230.790)

PMO 229.792 (Figure 7 B) and PMO 230.790 (Figure 7 C) are both distal portions of humeri and are almost identical with the exception of the shape of the broken surface proximally and PMO 230.790 being 1.6 times as long as PMO 229.792. The distal surface is divided between the two articular facets for the radius and ulna, with the radius articulating anteriorly and the ulna posteriorly. The radial facet is flat, thin and long, at approximately two times the length anteroposteriorly and 0.75 of the dorsoventral width of the ulnar facet. The ulnar facet is concave dorsoventrally and the border between the ulnar and radial facet is a straight dorsoventral ridge clearly dividing the two. The posterior border of the shaft is concave, protruding distally to meet the ulnar facet. There is a tuberosity proximal to the ulnar facet, referred to as the postero-distal tuberosity in the literature (Chris Mcgowan *et al.*, 1999; Motani, 1999a). Anterior to the radial facet, the bone thins into the anterior flange. The length of the radial facet compared to the ulnar hints towards these fossils being of mixosaurid origin rather than the utatsusaurid humerus PMO 229.783, based on the comparison done by Motani (1998).

5 Discussion

The humeri described in this thesis represent two taxa of Early Triassic Ichthyopterygians, namely the genus *Utatsusaurus* sp. and the family Mixosauridae. The genus *Utatsusaurus* could be decided as there is currently only one member of its family (Utatsusauridae), whereas Mixosauridae contains at least the two genera *Mixosaurus* and *Phalarodon* from Svalbard (Merriam, 1911; Økland *et al.*, 2018), and neither genus is remarked in the literature for diagnostic humeri. Therefore, the humeral fragments here referred to Mixosauridae cannot be more specific, but they are doubtlessly of mixosaurid origin, given the distinct shape of the proximal area of mixosaurid humeri when compared with other Early and Middle Triassic taxa. The presented vertebrae are more difficult to attribute to a specific taxon with any large degree of certainty, given that there is little material discussing the vertebrae of small sized Early Triassic ichthyopterygians and that

Ichthyopterygians described from the Olenekian have been characterized by their small body size and their morphological basality, manifest in their slender bodies with relatively long necks and more anguilliform locomotion, compared to the gradually more streamlined and heavyset bodies with more thunniform locomotion seen in later taxa (Moon *et al.*, 2020; Motani, 2005). Notable small bodied genera of the Olenekian are *Grippia* (C Wiman, 1929), *Chaohusaurus* (C. Young *et al.*, 1972), *Utatsusaurus* (Shikama *et al.*, 1978), *Thaisaurus* (Mazin *et al.*, 1991), *Parvinitator* (Nicholls *et al.*, 1995) and *Isfjordosaurus* (Motani, 1999b), though *Isfjordosaurus* and *Thaisaurus* have not been used in later phylogenetic analyses, as they are too incomplete (Moon, 2019; Motani, 1999b). Of these small ichthyopterygians, only *Grippia* has thus far been seen as prevalent in the Olenekian, Early Triassic on Svalbard (Maxwell *et al.*, 2013).

The Middle Triassic saw a change in the ichthyopterygian fauna, with the family Mixosauridae largely replacing the aforementioned small-sized and an increased prevalence of larger forms (Engelschiøn *et al.*, 2018; Liu *et al.*, 2011; Liu *et al.*, 2013; Elizabeth L Nicholls *et al.*, 1999; Silvio Renesto *et al.*, 2020; Schmitz *et al.*, 2004; Økland *et al.*, 2018). By the Middle Triassic, Mixosauridae had reached a fully global distribution, with fossils having been recovered from both sides of the Tethys Ocean, in today's Svalbard and several locations in North America (Georg Baur, 1887; Jiang *et al.*, 2007; Motani, 1999c; Elizabeth L Nicholls *et al.*, 1999; Schmitz *et al.*, 2004; Økland *et al.*, 2018).

The Early Triassic Ichthyopterygians are recognized as more primitive than their Middle and Later Triassic counterparts, for instance in the difference between *Grippia* and *Mixosaurus* (Motani, 2005). A defining feature of this distinction has been the development of the caudal fin towards a more dorsoventral lunate shape and the development of a dorsal fin, along with a shorter neck and a more streamlined body (Moon *et al.*, 2020; Motani, 2005; Silvio Renesto *et al.*, 2020). The tail of Mixosauridae is defined by a ventral bend of the tail slightly posterior to the pelvic area, with taller neural spines at the bend and a high degree of lateral compression in the caudal vertebrae, who are at their tallest at the bend, with a dorsal protrusion of soft tissue. These traits show a clear development toward the caudal fins of later forms (Gutarra *et al.*, 2019; Silvio Renesto *et al.*, 2020; Schmitz *et al.*, 2004). The presence of a dorsal fin has been confirmed in an Anisian, Lower Middle Triassic *Mixosaurus cornalianus*, making this the oldest family of amniotes with such a fin (Silvio Renesto *et al.*, 2020). With these traits, Mixosauridae approaches a more thunniform outline and mode of transportation than the more anguilliform bodies of e.g. *Utatsusaurus* or *Grippia* (Motani, 2005). The disarticulated nature of the material presented here can neither confirm nor deny whether or not these traits existed in Mixosauridae in the late Olenekian, Early Triassic, but given the relatively short time span between the Olenekian and Anisian, this thesis will employ the assumption that any differences would be minor. As such, Mixosauridae will still be treated as a morphological intermediary between anguilliform and thunniform ichthyosaurian forms. The overall more thunniform body plan of Mixosauridae, when compared to Olenekian contemporaries puts Mixosauridae as a more efficient and faster swimmer than e.g. *Utatsusaurus*. This advantage likely contributed to Mixosauridae largely outcompeting the other small forms by the Middle Triassic (Maxwell *et al.*, 2013), as a more efficient body plan naturally lends itself to more efficient hunting and also to more efficient use of energy. Moon *et al.* (2020) illustrate the importance of the intraspecific competition in the replacement of basal taxa by the intermediary ones, as they write that the intermediary taxa did not exploit new ecospaces, but rather continued to use the older ones, implying that they could coexist for long, which they did not. This does not mean that Mixoasuridae and other intermediary taxa (e.g. *Cymbospondylus*) immediately replaced the former Early Triassic forms, but rather that there was a period of temporal overlap between the more basal and the intermediary forms (Engelschiøn *et al.*, 2018; Reeves *et al.*, 2021). In the Middle Triassic, Mixosauridae occupied a highly similar ecosapce to *Chaohusaurus* of the Early Triassic (Moon *et al.*, 2020), with *Cymbospondylus* and *Besanosaurus* occupying niches for more large-sized animals (Engelschiøn *et al.*, 2018). The overlap in ecospace occupation between Mixosauridae and other small-sized Early Triassic Ichthyopterygians shows that the transition between basal and intermediary small-sized forms did not mean an immediate transition to new morpho- and ecospace, but rather a gradual shift as new areas emptied after the PTME were explored (Moon *et al.*, 2020).

5.1 Rapid diversification

Moon *et.al.* (2020) described the early evolution of ichthyopterygians as a rapid process following an EB (Early Burst) model, defined by an early high rate of evolution and diversification, followed by a tapering off of the rate later in the evolutionary history. This description includes an assumption that Mixosauridae evolved and diversified during the Middle Triassic (Moon *et al.*, 2020). The discoveries herein of Early Triassic mixosaurids substantiate the claim that the EB-model as the most appropriate fit for explaining ichthyosaur evolution, but imply that either the rate of evolution or the origin of the ancestral taxon must be revised, as this discovery increase the Early Triassic diversity. Seeing as the diversity of Early Triassic ichthyopterygians, though impressive in considering the proximity to the world’s most devastating extinction event, is still of such a size that moving Mixosauridae to the Early Triassic most likely has a statistically significant impact on the evolutionary history of Triassic ichthyopterygians as laid out by Moon *et al.* (2020).

As the PTME wiped out nearly 90% of marine life, the ecosystem was forever changed as the old ecological niches were either destroyed or vastly reduced. The Triassic saw a very high rate of evolution as species evolved to fill the gaps and new taxa evolved to take advantage of these. Ichthyosaurs became abundant during the Early Triassic, Grippiidae as a possible durophagous animal based on their dentition and crania, and Utatsusauridae as a generalist, again based on dentition and crania. The addition of Mixosauridae to the families present in the Early Triassic, along with Grippiidae, Utatsusauridae and Cymbospondylidae implies a more rapid recovery of the marine predators after the PTME, as these taxa approached the new niches opened up after the extinction.

Another possibility is that Early Triassic mixosaurids not necessarily means a faster rate of evolution, but rather an earlier date of origin for the ichthyosaur clade. Moon *et al.* (2020) calculated the clades root age as between 256.1 to 254.8 Mya, meaning that already a Late

Permian (Lopingian) origin is a possibility, but the presence of Mixosauridae reinforces the idea that the earlier suggested date might be more appropriate.

5.2 Mixosauridae as a more advanced form

Middle Triassic mixosaurids are consistently recovered with a more advanced caudal fin than Early Triassic ichthyosaur taxa, and a body shape that is seen as an intermediary between the thunniform mode of transportation of Jurassic ichthyosaurs and the anguilliform movement of the Early Triassic forms (Motani *et al.*, 1998). Not much can be said in regards to any differences in body plan between these Olenekian specimen and the ones from the Middle Triassic, as the specimen presented here consist o

Based on the disarticulated nature of the material described here, not much can be said on whether or not the Early Triassic Mixosauridae had the more developed tail fin or dorsal fin described elsewhere as more advanced traits than for instance *Utatsusaurus* (Motani *et al.*, 1998; Silvio Renesto *et al.*, 2020). This thesis will employ an assumption that the Early Triassic Mixosauridae were somewhat more adapted, or at the very least more adaptable, to the area than the other taxa of the region. This is because Mixosauridae became the dominant small-sized ichthyosaurian taxon in the region by the Middle Triassic, whereas *Grippia* and *Utatsusaurus* both went extinct, which would not happen were the other taxa better adapted. Though neither the presence of the tail bend or dorsal fin can be ascertained by these fossils, the assumption must still stand that Mixosauridae was more adapted to its marine environment than its contemporaries, simply because it still existed in the Middle Triassic, whereas *Grippia* and *Utatsusaurus* did not.

5.3 Coexistence of small ichthyosaur generalists

Robin S Cuthbertson *et al.* (2014) showed evidence of *Utatsusaurus* inhabiting an area West South West of where the remains of this thesis where located, on the same marine shelf. The paper shows that *Utatsusaurus* was able to disperse from the East Tethys to the West, with the most likely migration route taking them across the Boreal Ocean, which would certainly increase the likelihood of a member of the genus fossilising in the region. With an established presence relatively close to modern day Svalbard and not separated by major geographical obstacles like more open waters or land, migration or drift between the locations is not unimaginable. The areas are relatively close latitudinally (see Figure 2 in Geological Setting), putting them in similar temperature zones (Péron *et al.*, 2005), which further strengthens the hypothesis that *Utatsusaurus* could travel from the Wapiti Lake area to Spitzbergen area of the Panthalassa Ocean. Furthermore, Mixosauridae is known from the Wapiti Lake area in the Middle Triassic in the form of *Phalarodon fraasi* from British Columbia (Elizabeth L Nicholls *et al.*, 1999). With this in mind, it is not improbable that *Utatsusaurus* should end up in Svalbard.

The question then becomes whether or not such cohabitation is ecologically feasible. Coexistence between these taxa would imply that they were sufficiently different or adaptable to overcome the competition that naturally arises if two species of similar niche interact (Velzen, 2020). It might be considered that the *Utatsusaurus* sp. humerus might not be related to a stable population but rather a singular dispersal event, such as between the East and West Tethys, like the migration proposed by (Robin S Cuthbertson *et al.*, 2014). However, given the low rate of fossilization, it seems more apt to assume that there was a relatively stable population in the region.

The heterodont dentition of both Mixosauridae and *Utatsusaurus* implies they were both generalists, as was the norm for the Triassic ichthyopterygians (Walker *et al.*, 2002). Generalists are known to often coexist for periods of time, such as modern day crows (*Corvus corone*) and magpies (*Pika pika*) in many cities. These generalist coexistences are however seldom stable over the long term, as evolutionary pressure in most cases favour either one generalist or several specialists in one system (Orlando *et al.*, 2015). As Mixosauridae is regarded as a more derived form of ichthyopterygian than the previously known Early Triassic forms, it is likely that it would out-compete its contemporary forms in the late Olenekian and early Anisian, thus explaining the absence of these more basal forms by the Middle Triassic.

Another question then is that of a third genus, *Grippia*, another taxon that has been recovered from the Olenekian, Early Triassic of the Spitsbergen area (Motani, 1998). A simple answer here is to say that, since no definitive remains of *Grippia* have been recovered in this material, it did not inhabit this area. It could be that *Grippia* was extirpated from the region at this time. If not, then it too must have existed alongside Mixosauridae and *Utatsusaurus*. The coexistence of three generalists is somewhat unlikely, favouring the hypothesis of extirpation of *Grippia*, especially considering that Mixosauridae was the dominant species by the Middle Triassic. If *Grippia* was not extirpated, and its lack of specimen in this thesis is the result of either oversight or happenstance, it would imply such an abundance of food as to support three populations in relative proximity. As the Lower Saurian bone bed stretches over several kilometres, this might be, but cannot be said with certainty.

6 Conclusion

Material gathered from the Lower Saurian bone bed (Spathian age) of the upper Vendomdalen Member in the Spitsbergen area of Svalbard, has yielded the first definitive evidence of members of the family Mixosauridae in the Early Triassic. The proximal humeri elements (Figure 8, Figure 9) are undoubtedly mixosaurid, as the proximal potion of the mixosaurid humerus is not seen in any other ichthyosaurian taxon. The distal humeral elements (Figure 7 B and C) can not be designated more specifically than ichthyopterygian, as their shape is seen in several taxa. The complete humerus (Figure 7 A) is designated *Utatsusaurus* sp., as it is more similar to other humeri of this genus than others are. The vertebrae could unfortunately not be designated further than ichthyosauria indet. though they resemble mixosaurid vertebrae form the Middle Triassic, but no comparative material was found in the work of this thesis. Further work on this is encouraged.

The discovery of several mixosaurid humeri in the Early Triassic indicates that the family evolved earlier than previously believed, as the family up to now has been described as a purely Middle to Late Triassic taxon. As Mixosauridae is considered an intermediary taxon between more basal Early Triassic form such as *Grippia* or *Utatsusaurus* and later forms like *Stenopterygius*, this discovery indicates both a faster and less linear evolution of Triassic ichthyosaurs than what was previously thought. Previous theories on Triassic ichthyosaur evolution shows a neat transition between Early Triassic ichthyopterygians like *Grippia* and *Utatsusaurus*, to intermediary forms like *Mixosaurus* or *Cymbospondylus* emerging in the Middle Triassic, with very little temporal overlap between the taxa. Here it is shown that there was a substantial temporal overlap between the taxa.

The existence of Mixosauridae in the Early Triassic indicates that the overall evolution of Triassic ichthyosaurs either happened faster than what has been indicated previously, or that the group evolved before the PTME. This discovery should be used in future analyses of the rate of evolution or temporal origin of ichthyosaurs.

7 Appendices

7.1 Appendix A: Figures

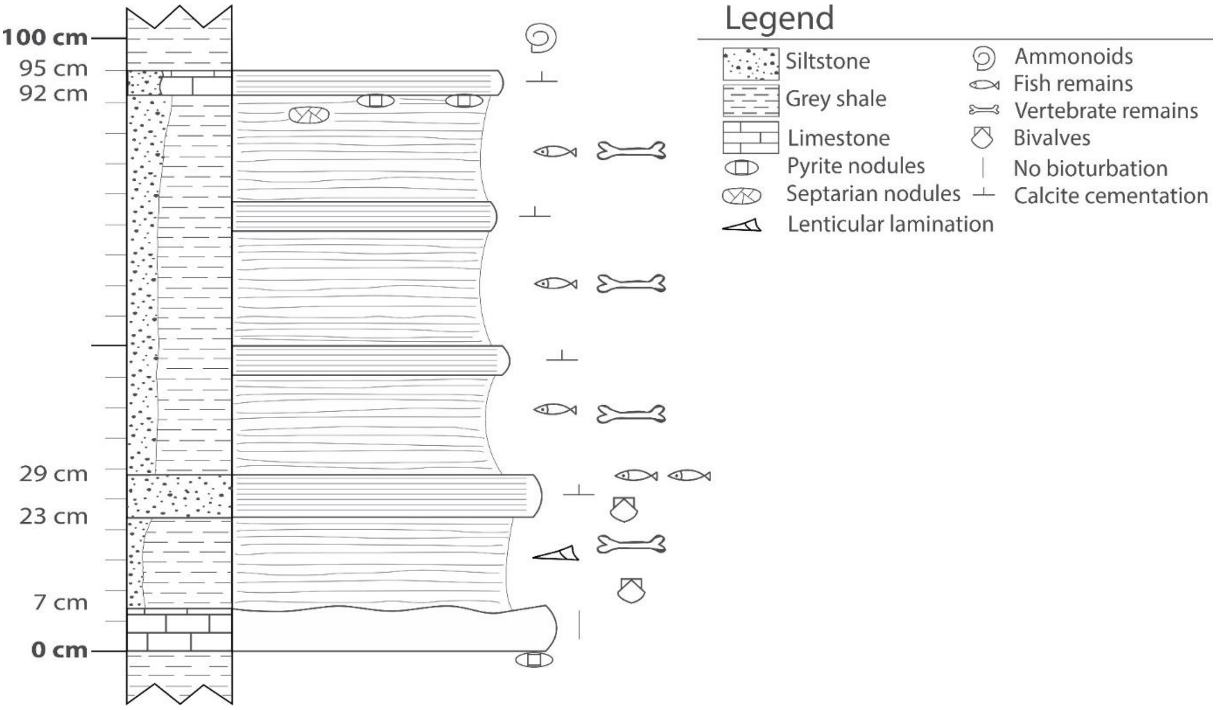

Figure 1:

Reprinted from "Large-sized ichthyosaurs from the Lower Saurian niveau of the Vikinghøgda Formation (Early Triassic), Marmierfjellet, Spitsbergen" by V. S. Engelschiøn et.al., 2018, *Norwegian Journal of Geology 98*, p. 241. Copyright V. S. Engelscjiøn, L. L. Delsett, A. J. Roberts & J. H. Hurum.

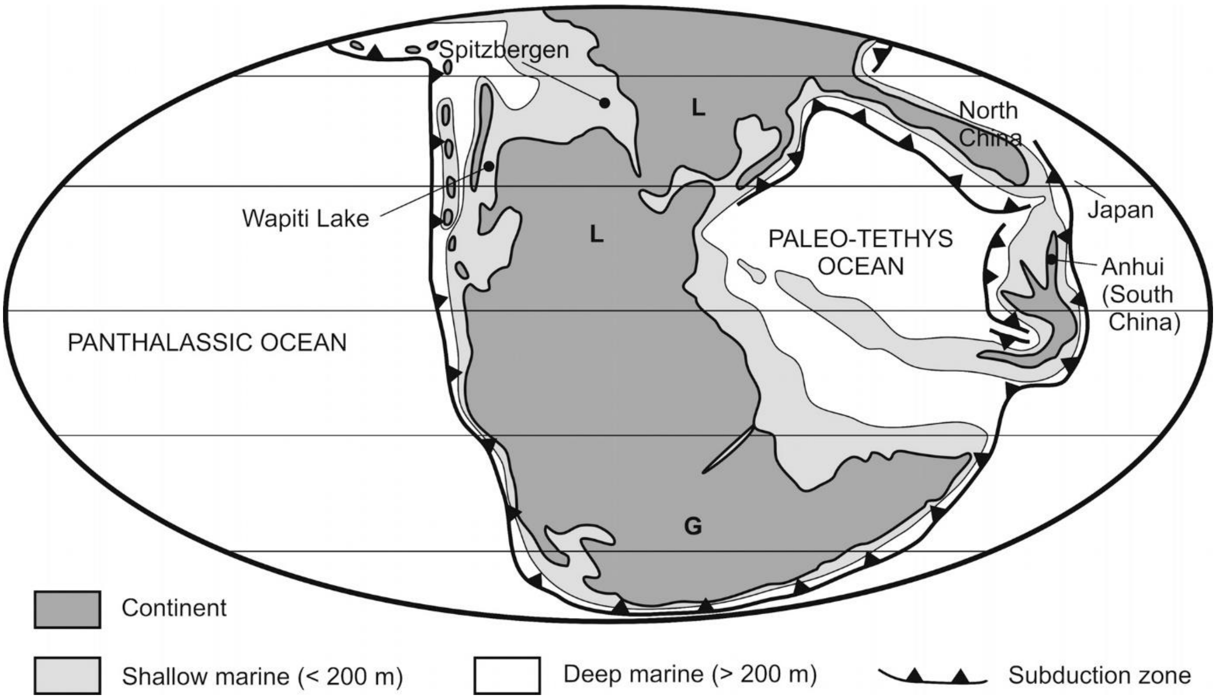

Figure 2:

Map of Pangea in the Early Triassic from Robin S. Cuthbertson *et al.* (2013), displaying the locations Wapiti lake and Spitsbergen. Robin S Cuthbertson *et al.* (2014) described specimen of *Utatsusaurus* from the Wapiti Lake region, and this thesis describes one *Utatsusaurus* sp. humerus from the Spitsbergen region. The map shows that these locations are within sufficient distance to enable migration between them, and in similar enough environments to allow this, being on the same shelf and not too far apart longitudinally. Reprinted from "Cranial morphology and relationships of a new grippidian (Ichthyopterygia) from the Vega-Phroso Siltstone Member (Lower Triassic) of British Columbia, Canada" by R. S. Cuthbertson et.al., 2013, *Journal of Vertebrate Paleontology, 33,* p. 854, Copyright 2013 by the Society of Vertebrate Paleontology.

7.2 Appendix B: Vertebrae plates

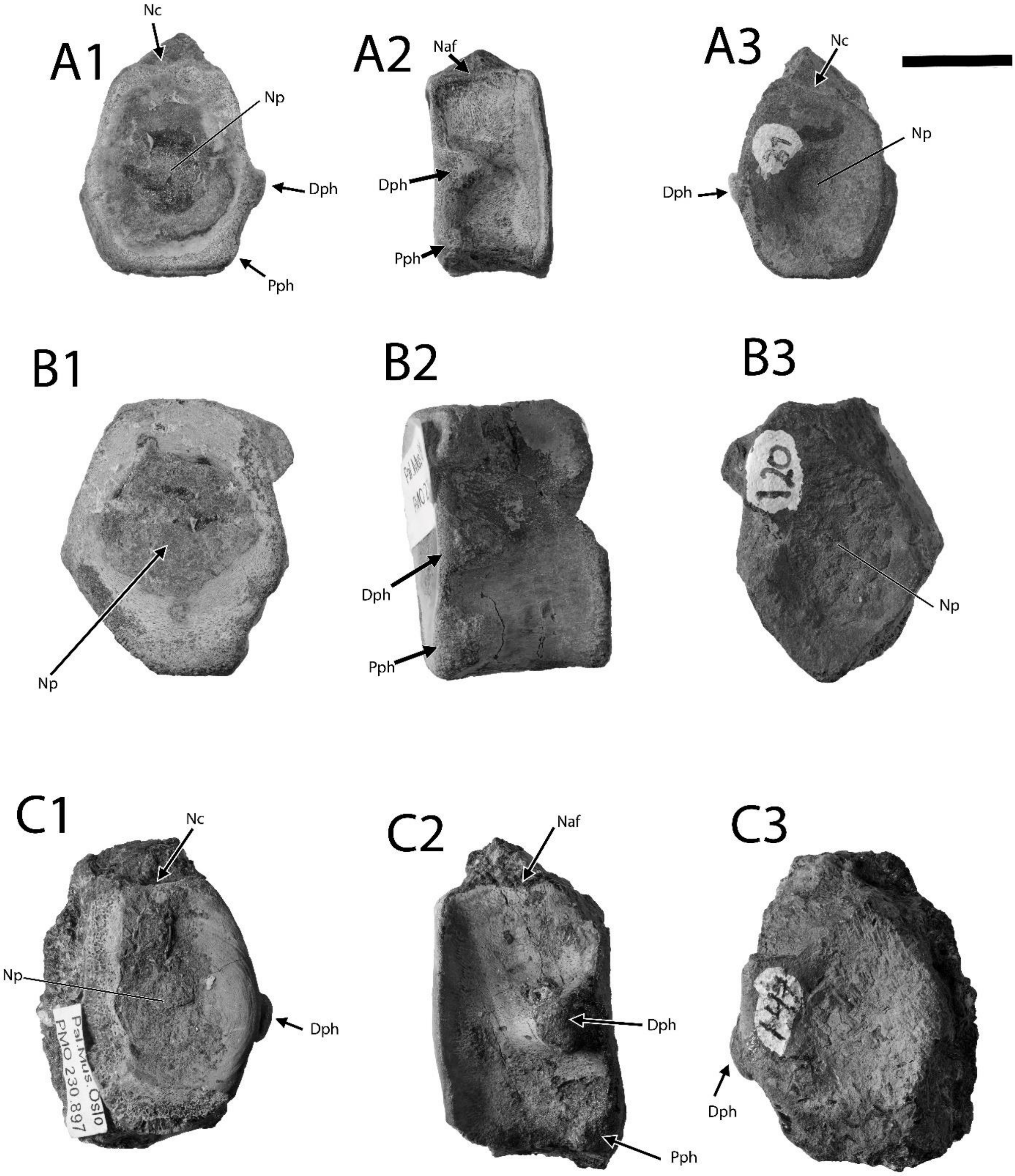

Figure 3: Anterior dorsal vertebrae of uncertain, Early Triassic ichthyopterygian origin. A: Anterior dorsal vertebra PMO 230.775 in A1: anterior view, A2: left lateral view, A3: posterior view. B: Anterior dorsal vertebra PMO 230.783 in B1: anterior view, B2: left lateral view, B3: posterior view. C: Anterior dorsal vertebra PMO 230.897 in C1: anterior view, C2: right lateral view, C3: posterior view. Abbreviations: Dph = diapophysis, Naf = neural arch facet, Nc = neural canal, Np = notochordal pit, Pph = parapophysis. Scale = 1 cm

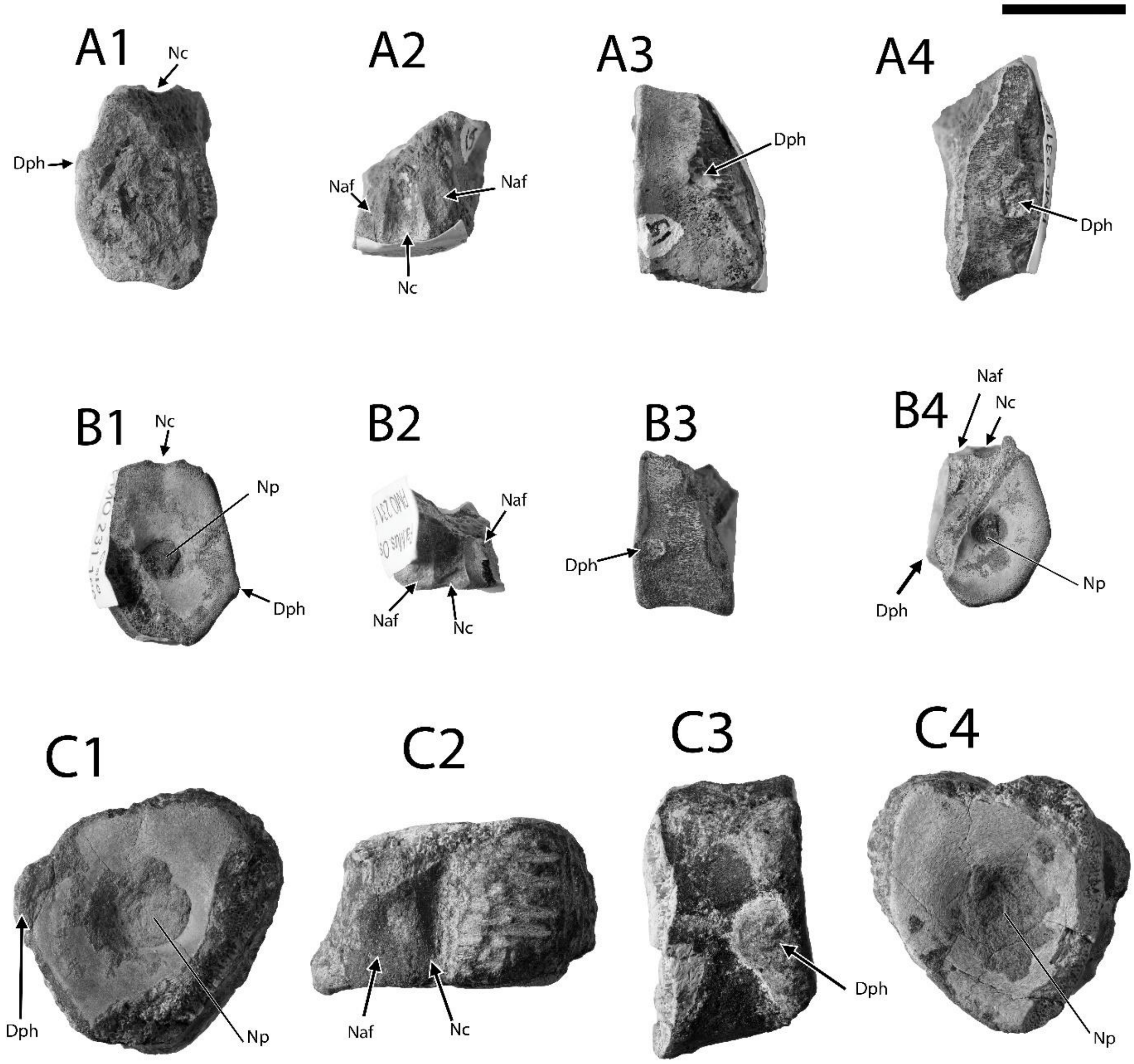

Figure 4: Dorsal vertebrae of uncertain, Early Triassic ichthyopterygian origin. A: Dorsal vertebra PMO 231.021 in A1: posterior view, A2: Dorsal view, A3: left lateral view, A4: right lateral view. B: Dorsal vertebra PMO 231.160 in B1: Anterior view, B2: dorsal view, B3: right lateral view, B4: posterior view. C: Dorsal vertebra PMO 231.013 in C1: anterior view, C2: dorsal view, C3: right lateral view, C4: posterior view. Abbreviations: Dph = diapophysis, Naf = neural arch facet, Nc = neural canal, Np = notochordal pit, Pph = parapophysis. Scale = 1 cm.

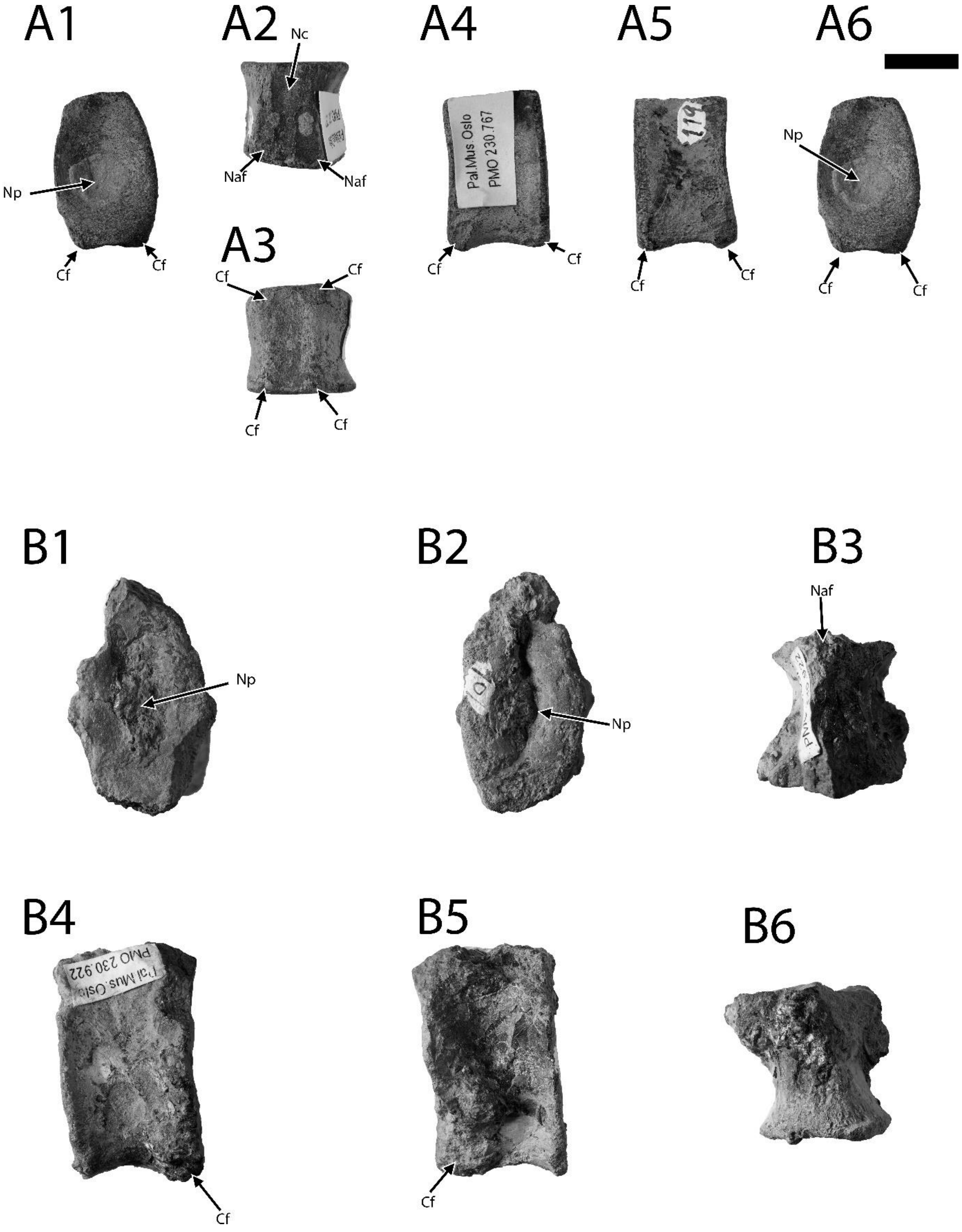

Figure 5: Middle caudal vertebrae of uncertain, Early Triassic ichthyopterygian origin. A: Caudal vertebra PMO 230.767 in A1: anterior, A2: dorsal, A3: ventral, A4: left lateral, A5: right lateral, and A6: posterior view. B: Caudal vertebra PMO 230.922 in B1: anterior, B2: posterior, B3: dorsal, B4: right lateral, B5: left lateral, and B6: ventral view. Abbreviations: Cf = chevron facet, Naf = neural arch facet, Nc = neural canal, Np = notochordal pit. Scale = 1 cm

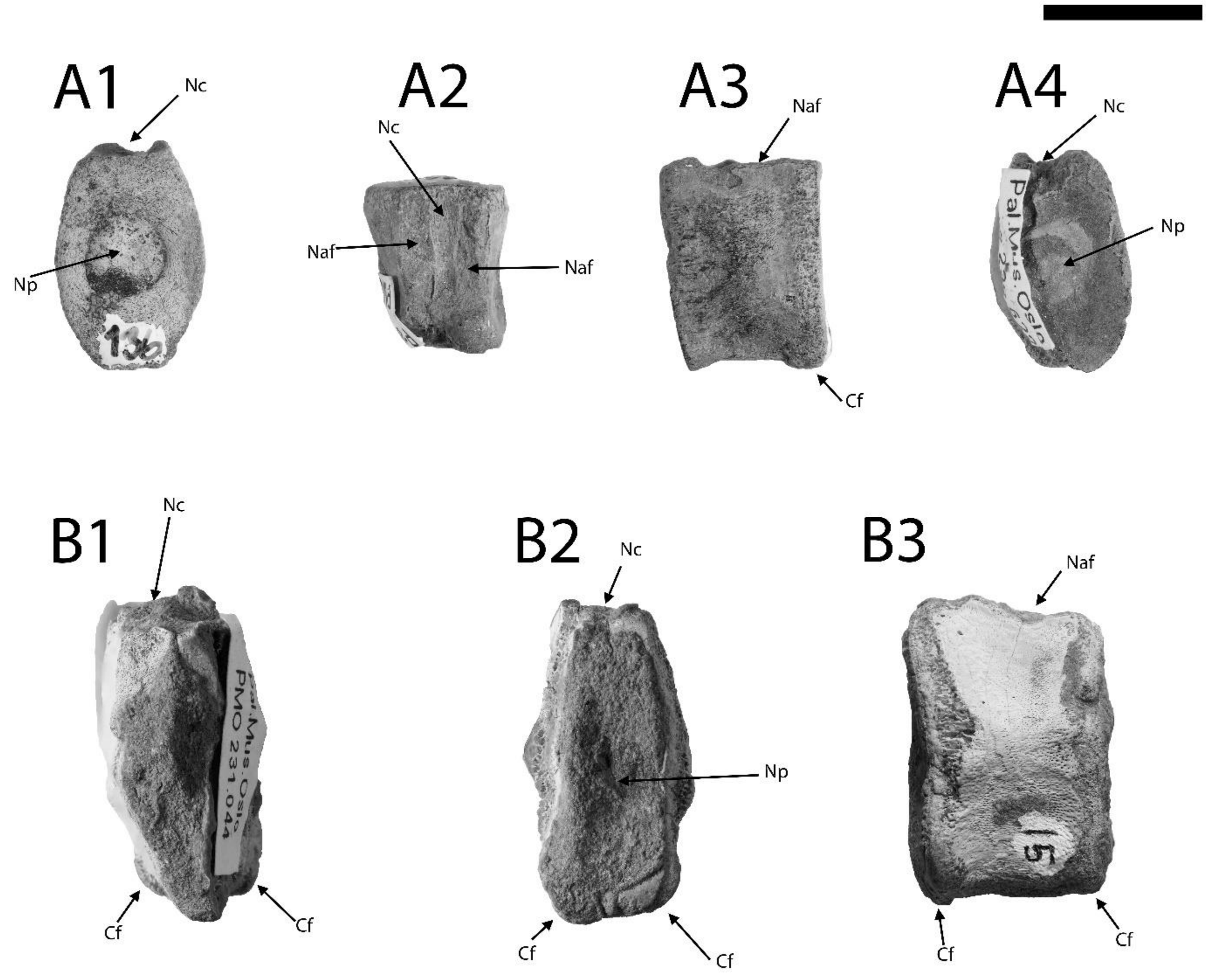

Figure 6:

Posterior caudal vertebrae of uncertain, Early Triassic ichthyopterygian origin. A: Posterior caudal vertebra PMO 230.622 in A1: anterior, A2: dorsal, A3: right lateral, and A4: posterior view. B: Posterior caudal vertebra PMO 231.044 in B1: anterior, B2: posterior, and B3: right lateral view. Abbreviations: Cf = chevron facet, Naf = neural arch facet, Nc = neural canal, Np = notochordal pit. Scale = 1 cm

7.3 Appendix C: Humeri plates

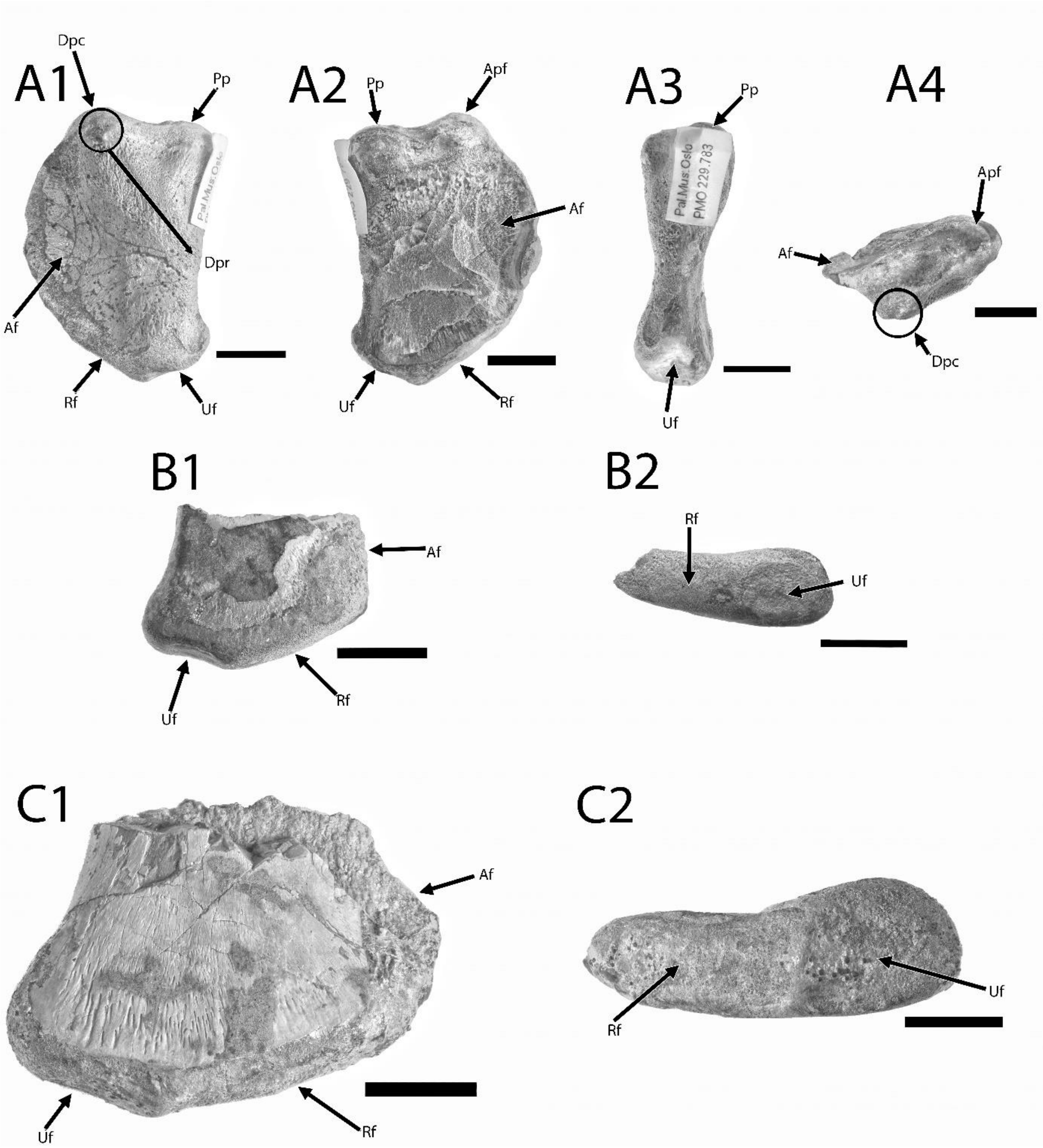

Figure 7:

Humeri of Early Triassic ichthyosaurs. A: Humeris of *Utatsusaurus* sp., PMO 229.783, in A1: dorsal view, A2: ventral view, A3 posterior view, A4: proximal view. B: Small distal portion of an ichthyopterygian humerus, possibly mixosaurid, PMO 229.792, in B1: ventral view, B2: distal view. C: Large distal portion of an ichthyopterygian humerus, possibly mixosaurid, PMO 230.790, in C1: ventral view, C2: distal view. Abbreviations: Af = anterior flange, Apf = anterior proximal facet, Dpc = deltopectoral crest, Dpr = deltopectoral ridge, Pp = posterior process, Rf = radial facet, Uf = ulnar facet. Scale bars = 1 cm.

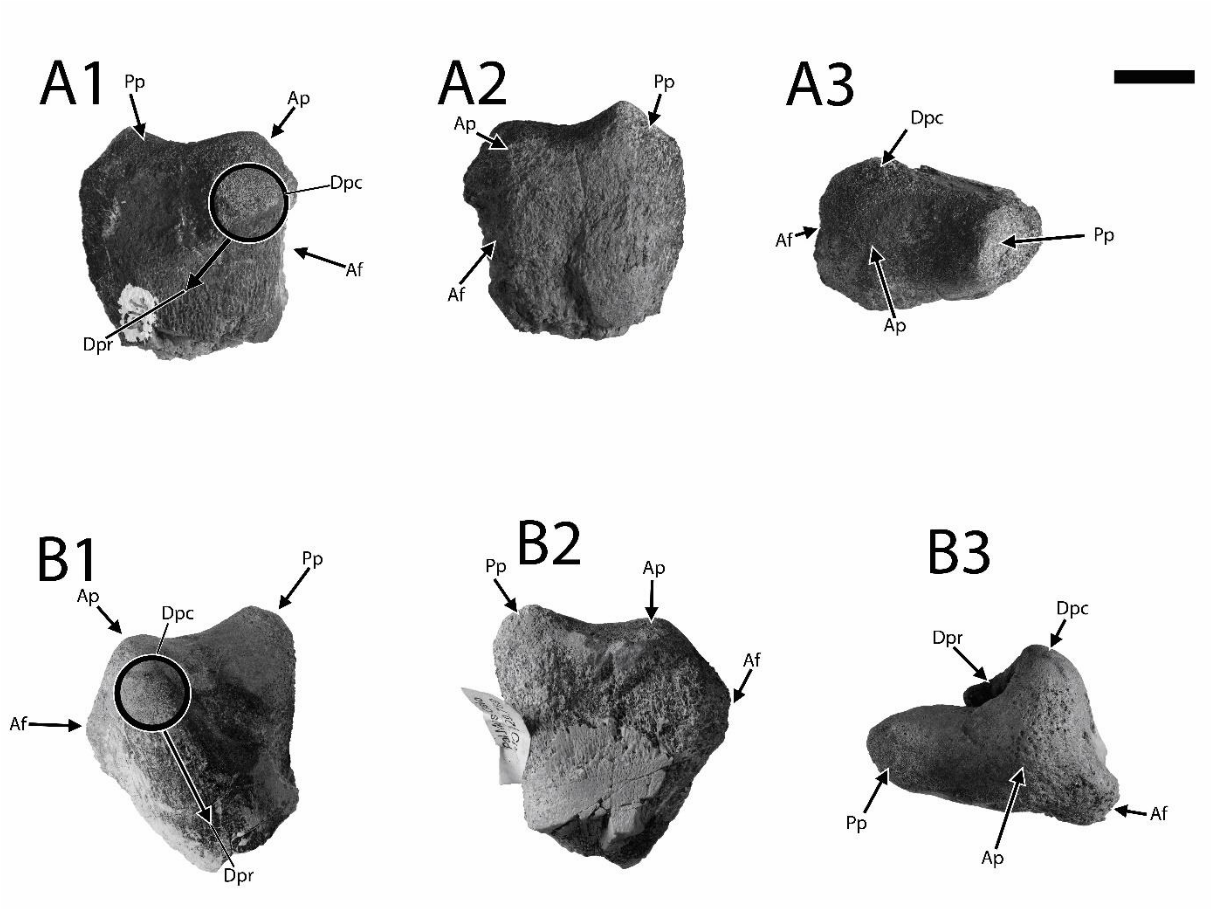

Figure 8:

Proximal portions of mixosaurid humeri. A: PMO 230.185 in A1: dorsal view, A2: ventral view, A3: proximal view. B: PMO 229.789 in B1: Dorsal view, B2: ventral view, B3: proximal view. Abbreviations: Af = anteriorflange, Ap = anterior process, Dpc = deltopectoral crest, Dpr = deltopectoral ridge, Pp = posterior process. Scale = 1 cm.

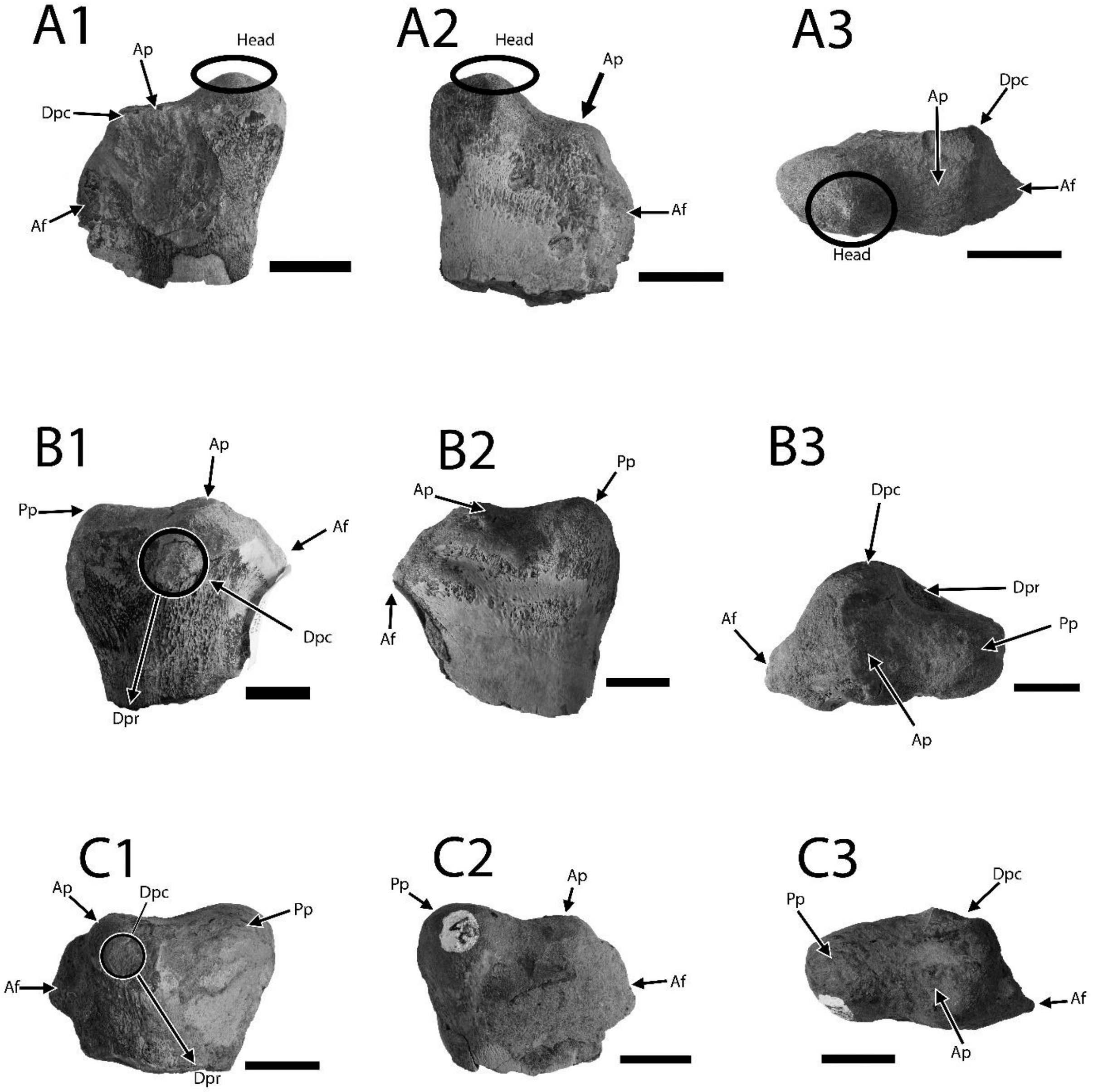

Figure 9:

Proximal portions of mixosaurid humeri. A: PMO 229.786 in A1: dorsal view, A2: ventral view, A3: proximal view. B: PMO 229.788 in B1: dorsal view, B2: ventral view, B3: proximal view. C: PMO 230.186 in C1: Dorsal view, C2: ventra view, C3: proximal view. Abbreviations: Af = anteriorflange, Ap = anterior process, Dpc = deltopectoral crest, Dpr = deltopectoral ridge, Pp = posterior process. Scale = 1 cm.

7.4 Appendix D: Measurements of vertebrae

Table 1: Measurements of vertebrae

PMO	Position	Taxon - family	H-L ratio	Height	Width	Length
230.614	Caudal	Mixosaurid	X	X	X	X
230.622	Caudal	Mixosauridae	1,44	1,3	0,8	0,9
230.651	Caudal	Mixosaurid	X	X	X	X
230.660	Caudal	Mixosaurid	X	1,8	0,9	X
230.661	Caudal	Mixosaurid	X	X	X	X
230.662	Caudal, posterior	Ichthyosauria	2,14	3	1,9	1,4
230.675	Caudal, posterior	Mixosauridae	2,29	3,2	2,3	1,4
230.677		Mixosauridae	2,13	3,2	2,4	1,5
230.716	Dorsal	Mixosauridae	1,53	2	X	1,3
230.748	Anteriormost dorsal	Mixosauridae	1,82	2	1,7	1,1
230.763	Caudal		1,36	1,5	1,1	1,1
230.767	Caudal	Mixosauridae	1,62	2	1,4	1,3
230.775	Caudal	Mixosauridae	1,88	1,7	1,4	0,9
230.777	Dorsal/anterior dorsal	Mixosauridae	1,45	1,6	1,3	1,1
230.783	Posterior dorsal/caudal	Mixosauridae	1,21	2,3	1,9	1,9
230.784	Anterior dorsal	Mixosauridae	1,7	1,7	1,9	1
230.879	Caudal	Mixosauridae	1,4	2,1	1,4	1,5
230.897	Caudal	Mixosauridae	1,57	2,2	1,5	1,4
230.922	Caudal	Mixosauridae	1,5	2,4	1,6	1,6
230.951	Dorsal	Mixosaurid	X	2,5	2,3	X
230.952	Caudal	Mixosauridae	1,85	2,4	1,5	1,3
230.959	Caudal	Mixosauridae	1,53	2,3	1,6	1,5

230.974		Mixosauridae	1,55	1,7	1,2	1,1
230.999	Caudal	Ichthyosauria	2,6	1,2	1	1
231.002	Dorsal	Cymbospondylidae	1,86	1,3	1,2	0,7
231.007	Caudal	Mixosaurid	1,58	1,9	1	1,2
231.013		Mixosaurid	1,67	2	1,1	2,1
231.022	Dorsal	Mixosaurid	1,45	1,6	1,2	1,1
231.027	Caudal	Mixosauridae	1,18	2	1,3	1,7
231.034		Ichthyosauria	3	2,1	2,3	0,7
231.044	Caudal	Mixosaurid	1,69	2,2	1,1	1,3
231.075	Caudal		1,63	2,6	1,8	1,6
231.076	Caudal	Mixosauridae	1,92	2,5	X	1,3
231.132	Caudal	Mixosauridae	1,69	2,2	0,8	1,3
231.143	Caudal	Mixosaurid	1,2	1,8	1,2	1,5
231.160	Dorsal	Mixosaurid	1,88	1,5	1,1	0,8
231.241	Anterior caudal	Mixosauridae	1,55	1,7	1,1	1,1

Notes for table 1: Measurements of all vertebrae analysed for this thesis. Height is measured at the dorsoventrally tallest point, width is measured at the mediolaterally widest point and length is measured at the anteroposteriorly longest point. X marks aspects that could not be reliably measured due to erosion of the bone.

7.5 Appendix E: Measurements of humeri

Table 2: Measurements of humeri

Table 2: Measurements of humeri

PMO	Portion	Juv/Adult	Taxon - family	P/D length	A/P length	D/V length
229.783	Whole	Adult	Utatsusaurus	3,6	2,5	0,8
229.786	Proximal	Juv or eroded	Mixosauridae	X	2,3	0,8
229.788	Proximal	Adult	Mixosauridae	X	3,4	1,9
229.789	Proximal	Adult	Mixosauridae	X	2,9	1,9
229.792	Distal	Juv or eroded	Mixosauridae	X	2,1	0,6
230.185	Proximal	Adult	Mixosauridae	X	2,1	1,2
230.186	Proximal	Adult	Mixosauridae	X	2,6	1,4
230.790	Distal	Adult	Mixosauridae	X	3,8	1,2

Notes for table 2: Measurements of all humeri described herein. P/D = proximodistal, A/P = anteroposterior, D/V = dorsoventral. X indicates lack of measurement, as the Mixosauridae humeri are broken proximodistally. “Portion” indicates which portion of the humerus this PMO is referred to. Juv = juvenile.

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