The first recovered ichthyosaur from the Middle Triassic of Edgeøya, Svalbard

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The Blanknuten Member of the Botneheia Formation preserves ichthyopterygians of various body-sizes. Due to the fragmentary nature of their remains, their systematic positions are controversial. The most complete skeleton of a mixosaur from Svalbard (PMO 219.250) described in this paper adds new data to the *Phalarodon-Mixosaurus* controversy, which is directly connected to the Svalbard taxa, starting with the description of *Ichthyosaurus nordenskioeldii* by Hulke in 1873. The ratios of the posterior dorsal vertebrae to the mid caudal vertebrae are a mixture of what is stated to be typical for *P. callawayi*, *M. nordenskioeldii* and *M. cornalianus*. We conclude that PMO 219.250 most likely should be assigned to the genus *Phalarodon*, but refrain from further assignment to a species.

Key Words: Ichthyosaurs, Mixosauridae, Ichthyopterygia , Triassic, Edgeøya, Svalbard.

Introduction

The earliest discoveries of vertebrate fossils from the Triassic of the Svalbard archipelago were made by the Nordenskiöld expeditions in 1864 and 1868 (Hulke, 1873), and the Russian-Swedish expedition in 1898 (Yakowlew, 1903). Expeditions in the early 20th century added more material (Wiman on the de Geer expedition in 1908; Stensiö and Wiman in 1912-1918; the Hamberg Swedish Expedition 1927; for history see Buchan et al., 1965 and Hagström, 2007). The ichthyopterygians found on these expeditions were thoroughly described by Carl Wiman in a series of papers (Wiman, 1910, 1916 a, b, 1928, 1933). In 1969 the Musée Nationale d'Histoire Naturelle, Paris conducted an expedition to Spitsbergen to collect fossil vertebrates from the Lower and Middle Triassic. The ichthyopterygians from this collection were described by Mazin (1981a, b, 1983a, 1984) and Maisch and Matzke (2002). More material has been collected randomly by different geological expeditions to Svalbard over the years but the Wiman collection has remained the

core collection and has been redescribed several times (for historical background see Maxwell and Kear, 2013). Even so, Maxwell and Kear concluded (2013:9): *"The persistent nomenclatural issues surrounding the Svalbard Triassic ichthyopterygians cannot be solved without the discovery of more diagnostic material."*

Most collections of Triassic ichthyopterygians from the Svalbard archipelago have so far been focused on the Isfjorden area. Vertebrate fossils from the Triassic of Edgeøya are less studied, mainly due to the island's remote location. A list of fossils was given by Cox and Smith (1973), who also briefly mentioned a jaw of *Pessosaurus*. Lock et al. (1978) reported large numbers of vertebrate fossils, but did not carry out any further investigations.

The Svalbard archipelago, being a late Mesozoic and Cenozoic uplifted area of the Barents Sea shelf, is a unique location for studying the sedimentology and development of the northern Barents Sea. For several
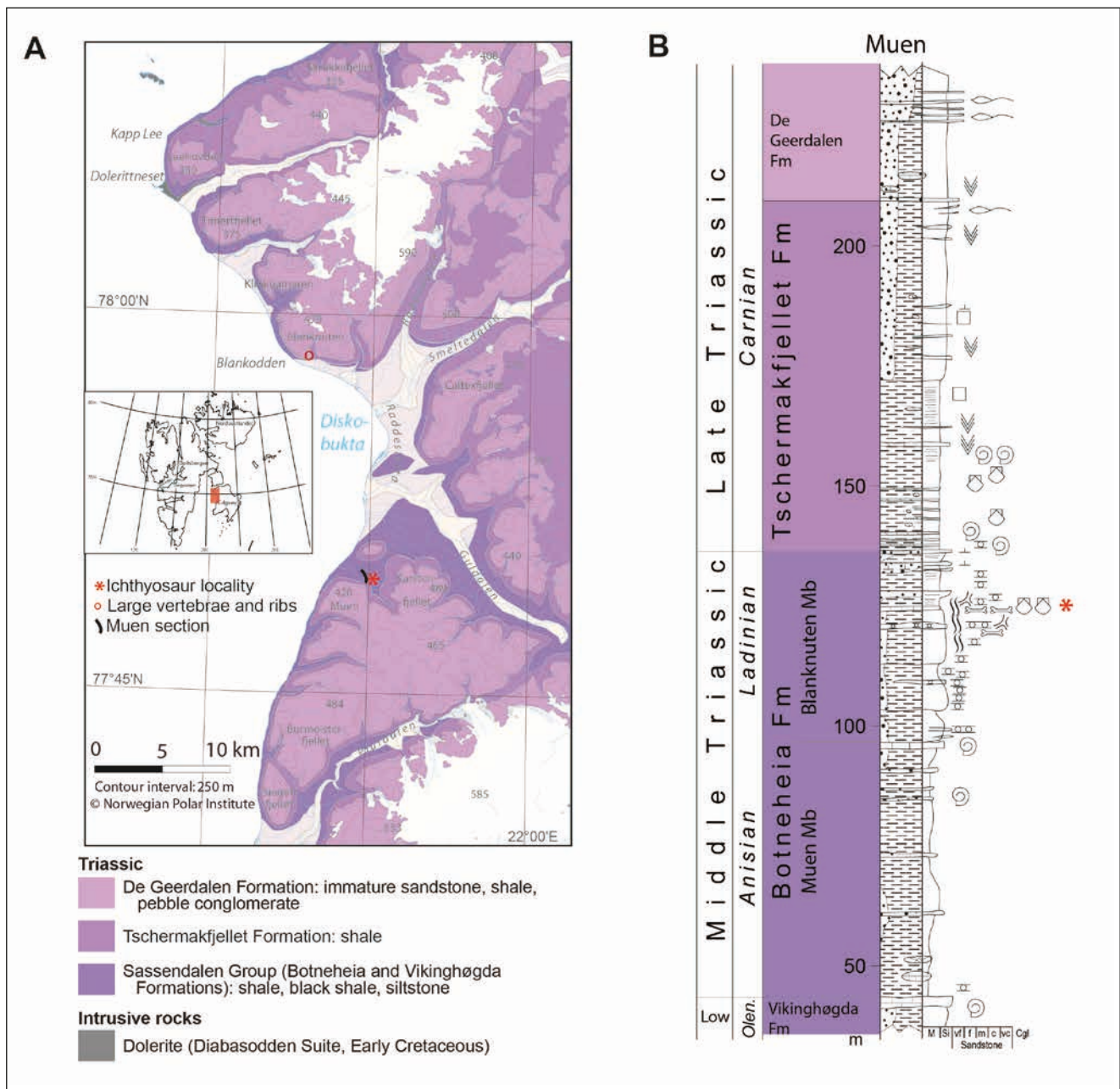
Figure 1. **A.** *Geologic map of studied area at Edgeøya.* **B.** *Stratigraphic column of the Muen Section.*

years, the Norwegian Petroleum Directorate (NPD) has worked on the geological sections as part of understanding of the Barents Sea area, in cooperation with Russian colleagues from VNIIOkeangeologia (All-Russia Research Institute for Geology and Mineral Recourses of the World Ocean) and the Geological Institute, Russian Academy of Science on terrestrial and marine geology and geophysics. SINTEF Petroleum Research has participated as scientific and logistic supervisor. Other academic institutions have also been invited on the yearly expeditions (since 2006) and have contributed to the interpretation of results.

During the 2007 expedition, the team worked on a plateau at Muen, a mountain on western Edgeøya (Fig. 1), and discovered several bluish bones of ichthyosaurs. An articulated skeleton was found by the two Russian geologists Andrey Fedyaevskiy and Pavel Luner and the Polish geologist Krzysztof P. Krajewski (photo in Krajewski, 2008, fig. 9E). Further skeletons and articulated bones were also discovered by other members of the group, and were GPS marked for possible excavation the following summer. As a co-operation between NPD, The Natural History Museum of Oslo and SINTEF Petroleum Research, permission from the Governor of Svalbard (Sysselmannen) was granted

to collect the skeletons. In 2008, one of us (HAN), with assistance from the remainder of the field group (AM and JAS) excavated the ichthyosaur. The skeleton described in this paper was collected together with several other parts of ichthyosaurs and other fossils (bivalves and ammonoids).

Triassic ichthyopterygians from Svalbard

Ichthyopterygians, the group including the less inclusive clade Ichthyosauria and their Early and Middle Triassic ancestors, were a group of globally distributed marine reptiles which thrived during the Mesozoic (Motani, 1999a). Ichthyopterygians evolved from a group of terrestrial diapsid amniotes, which adapted towards aquatic lifestyle during the Permian/Triassic transition and were fully marine by the Early Triassic (Sander, 2000; Maisch and Matzke, 2002). The Triassic ichthyosaurs show great variability in body shape and size (Sander, 2000; Motani, 2005). Although some species of Triassic ichthyosaurs show traces of their terrestrial heritage, they developed a mosaic of increasingly specialized adaptions to marine life through the Triassic (Motani et al., 1996).

The Triassic ichthyopterygian assemblages of Svalbard were recently summarized and discussed by Maxwell and Kear (2013). Of the numerous named ichthyopterygian taxa from the Triassic of Svalbard, Maxwell and Kear (2013) only regard *Grippia longirostris*, *Pessopteryx nisseri*, *Quasianosteosaurus vikinghoegdai*, *Omphalosaurus* sp., *Isfjordosaurus minor*, *Phalarodon* cf. *callawayi* and *Phalarodon* cf. *fraasi* as potentially valid. However they also recognized some additional morphologically differentiated specimens such as *Cymbospondylus* (Sander, 1992), the toretocnemid reported by Maisch and Blomeier (2009) and the shastasaurid formerly recognized as *Pessosaurus polaris* (sensu Sander and Faber, 1998).

The ichthyopterygian fossils from Svalbard are found in beds which span the Early to earliest Late Triassic and can be stratigraphically divided into six horizons, with age estimates from Mørk et al. (1999). Only selected papers are listed here; for a more complete publication list see Maxwell and Kear (2013).

1. "Fish Niveau" " Lusitaniadalen Member, Vikinghøgda Formation, early Olenekian (Smithian): only isolated material (Wiman, 1933).
2. "Grippia Niveau" Vendomdalen Member, Vikinghøgda Formation, late Olenekian: *Quasianosteosaurus vikinghoegdai* Maisch and Matzke, 2003 and *Grippia longirostris* Wiman, 1928, Motani (1998, 2000).
3. "Lower Saurian Niveau" Vendomdalen Member, Vikinghøgda Formation, late Olenekian: *Pessopteryx nisseri* Wiman, 1910, *Isfjordosaurus minor* Motani, 1999a, and *Omphalosaurus* sp. (Wiman, 1910). Based on a tooth, the presence of a mixosaurid was reported

from core 7327/07-U-04 by Mørk and Elvebakk (1999) from the Svalis Dome, in the central Barents Sea. This core is dated as late Olenekian (late Spathian) (Vigran et al., 1998).
4. Lower Botneheia Formation (Anisian): a toretocnemid reported by Maisch and Blomeier (2009), *Phalarodon* sp. (Maxwell and Kear, 2013).
5. "Upper Saurian Niveau" Blanknuten Member, uppermost Botneheia Formation and the boundary beds to the Tschermakfjellet Formation, late Ladinian–early Carnian: *Phalarodon* cf. *callawayi* and *Phalarodon* cf. *fraasi*. (Hulke, 1873; Merriam, 1910; Wiman, 1910; Schmitz, 2005; Schmitz et al., 2004), a shastasaurid formerly recognised as *Pessosaurus polaris* (sensu Sander and Faber, 1998) and *Cymbospondylus* sp. (Sander, 1992).

The Mixosauridae of Svalbard

The most common Middle Triassic ichthyosaurs are those belonging to the family Mixosauridae (Baur, 1887). The family Mixosauridae is diagnosed primarily on differences in limb and tooth structure (see systematic palaeontology section). Mixosaurids had a wide distribution including Canada, China, France, Germany, Timor, New Zealand, Poland, Russia, Svalbard (Norway), Switzerland, Turkey and the United States (McGowan, 1978; Mazin, 1983a, b; 1988; Zammit, 2010; Callaway and Massare, 1989; Sander and Mazin, 1993). Most mixosaurids are of Middle Triassic age, although undiagnostic fragments of *Mixosaurus* sp. have been reported from the Early Triassic of Canada (Callaway and Brinkmann, 1989). They are seen as an intermediate between the primitive Triassic and the more derived Jurassic body forms (Motani, 2005). Despite retaining several primitive morphological characters, mixosaurids show evidence of viviparous behavior (Brinkman, 1996). Until recently, Mixosaurids were the earliest indication of such a trait in ichthyopterygians. The recent discovery of embryos in the 248 million year old basal ichthyopterygian *Chaohusaurus geishanensis*, has pushed the evolution of this behavior back even further (Motani et al., 2014). Some of the first ichthyosaurs from the Triassic worldwide were collected by the Nordenskiöld expeditions in 1864 and 1868. The fossils, from what is now known as the Blanknuten Member of the Botneheia Formation, were described by Hulke in 1873. Hulke assigned the very fragmentary material to two new species, a large form named *Ichthyosaurus polaris* and a smaller one *Ichthyosaurus nordenskioeldii*. The two vertebral series of *Ichthyosaurus polaris* have a long history of different affinities since the first description are now recognized as material belonging to *Shastasauridae* indet (see discussion and references in Sander and Faber, 1998, and Maxwell and Kear, 2013). Dames (1895) referred the smaller species, *Ichthyosaurus nordenskioeldii*, to *Mixosaurus*. The better material found in 1908 and 1909 and described by Wiman in 1910 was also attributed to *Mixosaurus nordenskioeldii*, but Merriam in the following year identified jaw

fragments of *Phalarodon fraasi* among the specimens figured (Merriam, 1911). In 1916 Wiman summarized the findings and agreed with Merriam (Wiman, 1916 b). Several mixosaurid species have been described and these have been synonymized and reinstated over the years (Callaway, 1997; McGowan and Motani, 2003; Jiang et al., 2006). The review by McGowan and Motani (2003) recognized five species: *M. avatus* (Quenstedt, 1852), *M. nordenskioeldii* (Hulke, 1873), *M. cornalianus* (Bassani, 1886), *M. fraasi* (Merriam, 1910) and *M. kuhnschnyderi* (Brinkmann, 1998). In Jiang et al. (2006) and Liu et al. (2013) there is a disagreement on the genera and species definitions, but they both separate the family Mixosauridae into two genera, *Mixosaurus* and *Phalarodon*. Jiang et al. (2006) propose that the genus *Mixosaurus* contains three species; *M. cornalianus*, *M. kuhnschnyderi* and *M. panxianensis*. The second genus *Phalarodon* is often synonymized with *Mixosaurus* (see e.g. Schmitz et al., 2004), but proposed as a separate genus by Jiang et al. (2006) and later discussed in detail by Liu et al. (2013), with three species *P. avatus*, *P. callawayi* (Schmitz et al., 2004) and *P. fraasi* (Merriam, 1910).

The validity of *Mixosaurus nordenskioeldii* has been debated for many years and this is now considered a nomen dubium, due to non-diagnostic type material (see discussion in Schmitz, 2005). Schmitz (2005) attributed all Svalbard mixosaurids to *Phalarodon fraasi* and *P. callawayi*, on the basis of differing height to length ratio of vertebrae centra. This attribution was later followed by Maisch (2010). Maxwell and Kear (2103)

noted inconsistencies in the dentition between the type material of *P. fraasi* from Nevada and the Svalbard material, but regarded the Svalbard material of *P. fraasi* and *P. callawayi* to be potentially valid; we briefly discuss the problematic taxonomy of *Mixosaurus nordenskioeldii* in this paper.

Geological setting

The exposed strata on Edgeøya consist entirely of rocks of Triassic age (Fig. 1) from the Sassendalen and Kapp Toscana groups, except for two small areas eroded down into the top Permian. Falcon (1928) named the dark shales at the island the Oil Shale member (now the Botneheia Formation) with its overlying Purple shale (Tschermakfjellet Formation). Detailed fieldwork in 1969 resulted in a map and short description (Flood et al., 1971), which extended the Triassic stratigraphic nomenclature from Spitsbergen with minor modifications. A more thorough description, based on the same work, was later used to define a local stratigraphy for Barentsøya and Edgeøya (Lock et al., 1978). This scheme was further modified by Mørk et al. (1982) as they focused on the similarities of these two islands with the surrounding islands. In the revision of Svalbard's post Caledonian succession, Mørk et al. (1999) coordinated these earlier stratigraphical schemes to demonstrate the similarities and differences between the different areas of Svalbard (Fig. 2).

The Sassendalen Group of Early to Middle Triassic

Figure 2. A correlation of the stratigraphic formations and groups of the Triassic of Svalbard (modified from Mørk et al., 1999).
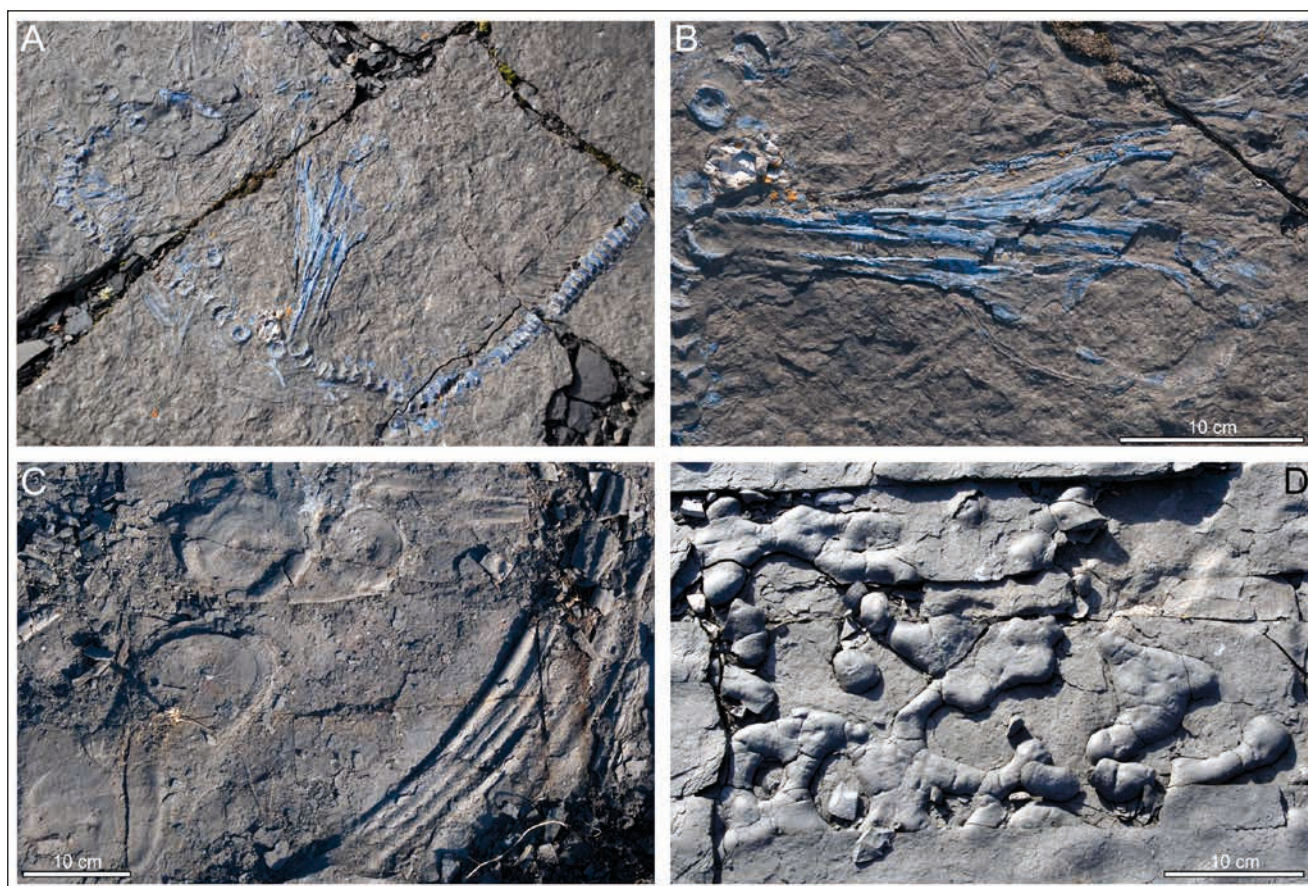
*Figure 3. A. Specimen PMO 219.250 before excavation. B. Skull of PMO 219.250 before excavation with abundant bivalves around (*Daonella*). C. Ribs and imprints of vertebrae from a large ichthyopterygian from the same level (not excavated). D. Typical trace fossils from the level of the skeletons (*Thalassinoides*).*

age is dominated by dark grey and black shales, and therefore Lock et al. (1978) grouped these units in the Barentsøya Formation. This scheme was retained by Mørk et al. (1982). During the total revision of the Mesozoic stratigraphy of Svalbard Mørk et al. (1999) again separated out the Botneheia Formation, as a practical mapping unit that also can be followed offshore. For Edgeøya and Barentsøya, Krajewski (2008) has given a thorough description of the formation, redefined type localities, and erecting the lower Muen Member overlain by the revised Blanknuten Member, and this subdivision is followed herein.

The ichthyopterygians recovered in 2008 on Edgeøya are found in the uppermost part of the Botneheia Formation (Figs. 1, 2). Lock et al. (1978) were the first to report the presence of vertebrate remains in this unit on Edgeøya, noting mainly ichthyosaur vertebrae. Fish fossils also occur in the laterally equivalent Bravaisberget Formation, and are irregularly dispersed throughout the Sassendalen Group (Mørk et al., 1982). All the articulated specimens described herein are from one level high in the Botne-heia Formation (Figs. 1, 3). Most specimens have relatively small vertebrae, but a specimen found by AM in 1979 at Blanknuten has several large ribs and vertebrae ca. 10 cm in diameter. Large vertebrae were also observed by JAS just

above the specimen described in this paper (Fig. 3C). The association of fossils in the upper part of the Botneheia Formation demonstrates a special taphonomic environment. Very high organic content, from 8 to 12 % organic material for the upper part of the Blanknuten Member, was demonstrated by Mørk and Bjorøy (1984), and Brekke et al. (2014). Vigran et al. (2008) have shown that much of this organic material is derived from algae, mainly *Tasmanites*. The high organic content in the sediment, abundant *Thalassinoides* and a rich benthic fauna of bivalves (*Daonella*) indicate alternating anoxic and oxic conditions, as suggested by Mørk and Bromley (2008). Similar variations in bottom conditions have also been suggested by Krajewski et al. (2007) for the time equivalent unit along western Spitsbergen, and for Edgeøya by Krajewski (2008).

Material and methods

Fieldwork

An application from the Natural History Museum, University of Oslo, was sent to the Governor of Svalbard in 2008 to obtain permission to collect and conserve the ichthyopterygian fossils. Permission was granted (2008/00489-3 a.512).

The collection and field conservation of the fossils met two major challenges: frost weathering causing congelifraction made the fossilized bones rather brittle, and the compaction of the shale beds during diagenesis had also compressed and fractured them.

The commonly used vertebrate paleontological excavation technique to embed the bones and surrounding sediments in field jackets made of plaster and burlap was selected, in order to reduce further breakage during transport from the field to the laboratory. The studied specimen, occupying approximately 1.4 m x 1.1 m, was split in seven parts to make it possible to carry it from the field to the expedition ship. It was mainly split along natural fractures or using a knife. The bed housing the fossils is 5-10 mm thick.

The collected material comprises:
Specimen 1. The main specimen, PMO 219.250 (described in this paper, Figs. 3A, B, 4).
Specimen 2. A vertebral column and a collection of weathered ribs and gastralia.
Specimen 3. A long vertebral column (33 vertebrae and 39 imprints of eroded vertebrae).
Specimen 4. Scattered vertebrae and bones from the shoulder and lower jaw.
Specimen 5. A vertebral column and heavily weathered skull and (jaw) bones with eroded teeth.

All specimens, in part split, were embedded in plaster and enforced with bandage and metal rods.

The main specimen (PMO 219.250), nick-named "ODa", was selected for subsequent laboratory preparation and description. This is an acronym for Oljedirektoratet (The Norwegian name of the Norwegian Petroleum Directorate) which supported the excavation and preparation of the specimen.

Laboratory work

The main specimen was prepared at the Löwentor Museum in Stuttgart, Germany, by technician May-Liss Knudsen Funke (NHM, Oslo) under the supervision of Dr. Rainer Schoch and technician Isabell Rosin. The slabs were strengthened with polyester and fibre glass on their back side before being transported to Germany. The fossil and surrounding shale was very fragile and it was decided to use a sandblasting technique to remove rock matrix from the bones. Iron particles smaller than 0.2 mm were used and the work carried out under a Leitz Wild M3Z binocular microscope. A vibrotool was used in places where the sandblasting was unsuccessful. The bones were reinforced with "pioloform" (polyvinylbutyral) after the mechanical preparation.

The characteristic blue colour of the bones, caused by surface mineralization of vivianite, a hydrated iron phosphate, during years of frost weathering was lost during the sandblasting process (Figs. 3A, B and 4 for comparison before and after treatment).

Institutional abbreviations:
FMNH   Field Museum of Natural History, Chicago, USA.
PMO   Palaeontological museum, Natural History Museum, University of Oslo, Norway.
PMU   Palaeontological Museum, University of Uppsala, Sweden.

Description

Systematic Palaeontology

Family Mixosauridae Baur, 1887
Subfamily Mixosaurinae Baur, 1887

Specimen PMO 219.250 is a partially articulated medium-sized mixosaurid ichthyosaur from the Middle Triassic of Edgeøya, Svalbard (Fig. 4). It is flattened laterally and is in a curled up position as the skull is disarticulated from the rest of the axial skeleton. It is preserved in seven slabs labeled 1-7. Slab 1 (PMO 219.250/1) consists of vertebrae, a partial femur, and an impression of a femur with a partial paddle and numerous rib fragments. Slab 2 (PMO 219.250/2) consists of tail vertebrae along with several neural arches. Slab 3 (PMO 219.250/3) consists of articulated and disarticulated tail vertebrae. Slab 4 (PMO 219.250/4) consists of the skull, vertebrae, neural arches, ribs and gastralia. Slab 5 (PMO 219.250/5) consists of rib fragments and part of forefin. Slab 6 (PMO 219.250/6) consists of individual ribs and possible gastralia (not figured). Slab 7 (PMO 219.250/7) contains a partial pectoral girdle, two partial forefins, vertebrae and ribs. The articulated skeleton is estimated to have been 170-180 cm long, based on skull length and the vertebral column compared to other well known mixosaurids (see e.g. Sander, 2000; Maisch and Matzke, 2000; McGowan and Motani, 2003; Schmitz et al., 2004; Jiang et al., 2006; Liu et al., 2013).

Skull
The skull has undergone ventral-lateral compaction, resulting in a flattening of all elements of the cranium and mandible. The right lateral and ventral side of the skull is visible, although most of the individual elements are in too poor condition to be described. See Table (1) for individual skull measurements.

Dermatocranium - The premaxilla is the dominant rostrum element, terminating posteriorly at the ventral and anterior border of the external naris. It bears small teeth with enamel ridging throughout the entire length, with little room between the individual teeth. It overlaps the maxilla in line with the external naris. The dorsal process of the maxilla is eroded, but it appears to exclude the lacrimal from the external naris, forming the posterior border. It bears large conical teeth, larger

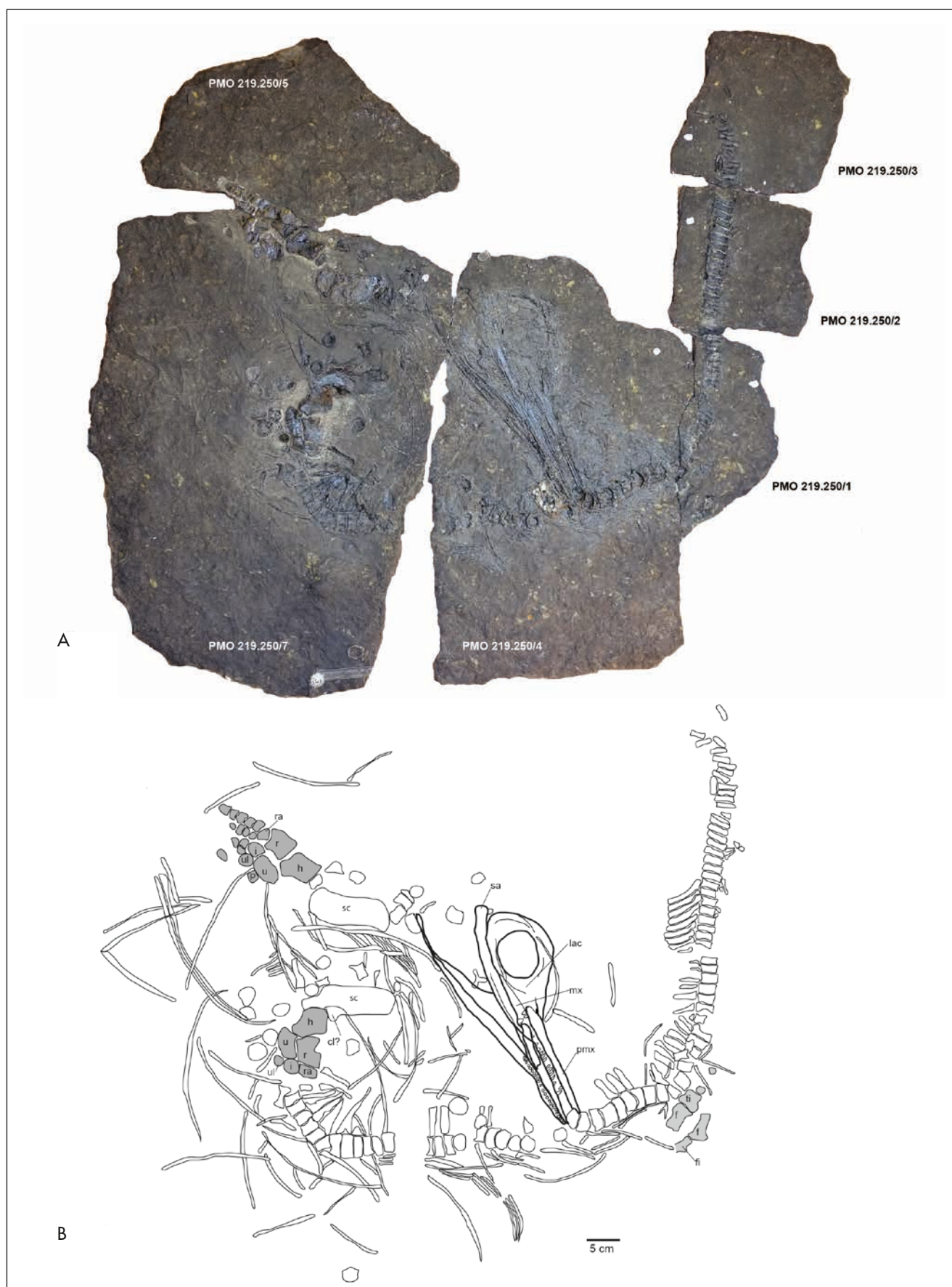***Figure 4.*** *The specimen PMO 219.250.* **A.** *prepared skeleton on slabs 1-5 and 7. Slab 6 is not figured as only a few disarticulated ribs were present.* **B.** *Schematic drawing of the skeleton. Abbreviations: cl-clavicula, f-femur, fi-fibula, h-humerus, i-intermedium, lac-lacrimal, mx-maxilla, pmx-premaxilla, r-radius, ra-radiale, sa-surangular, sc-scapula, ti-tibia, u-ulna, ul – ulnare.*

Table 1. *Selected skull element measurements of PMO 219.250.*

Selected skull element measurements	mm
Preserved skull length (Postorbital to preserved anterior of premaxilla)	280
Anteroposterior length of orbit	66
Maximum dorsaventral hight of orbit	58
Anteroposterior length of postorbital bar	21
Preserved length of lower jaw (right)	310
Jugal length	~70
Maximum height of the posterior ramus	9
Articular anteroposterior length	12

than the teeth present in the premaxilla. There are significantly fewer teeth in the maxilla than in the premaxilla. Posteriorly it contacts the jugal, just ventral to the lacrimal. The lacrimal forms the anteroventral border of the orbit. It is small and somewhat eroded, missing the dorsal edge. There is no contact with the external naris. The external naris is anteroposteriorly longer than dorsoventrally high, measuring 21 mm in length and 3 mm in maximum height. The nasal is severely eroded and only the part in line with the external naris is preserved. However, there is a possible trace of a nasal terrace present. The prefrontal is almost entirely eroded and only the posterodorsal part is preserved, forming part of the orbital rim. There is no frontal preserved. The jugal is present as a gracile bar, forming the ventral part of the orbital rim. It articulates with the lacrimal anterodorsally and the maxilla anteriorly. The posterior terminal end articulating with the postorbital is missing. However, an impression is present and appears broad. The postfrontal is present although partially eroded, forming the posterodorsal border of the orbital rim. The postorbital appears to be a broad element, covering the other elements in the postorbital region. It is overlapped by the postfrontal anterodorsally and an eroded element which is either the squamosal or the supratemporal posterodorsally. An element possibly representing part of the parietal is present in the posterodorsal region of the skull. A disarticulated imprint of the basioccipital is also present, posterior to the skull.

Mandible - The dentary stretches along the rostrum and terminates posteriorly in line with the external naris, although it is partially covered by the splenial due to the ventral-lateral compaction. The element bears small conical teeth, set in sockets, throughout the entire length of the rostrum. There is little to no room between the individual teeth, except in the posteriormost region. The surangular is a robust element, dominating the mandible, appearing to extending anteriorly past the level of the bony nasal aperture. The surangular appears to form the posterior ramus of the lower jaw with the angular, however it is difficult to interpret how much is due to

the preservation. There is no sign of a coronoid process. The angular is a small element in comparison to the surangular, making up the posteroventral region of the mandible. An articular is also preserved disarticulated posterior to the mandible, which is rounded in shape laterally.

Appendicular skeleton

Pectoral girdle - There are several pectoral girdle elements preserved in Slab 7. The element in partial articulation with the left forefin represents a scapula. It appears to have been twisted 180 degrees. A second scapula impression is present in the proximity of the right forefin. The scapula bears two long extensions, one towards the anterior, the other posterior with a short glenoid process in between. A small element which could represent part of the clavicle is present, but due to the poor preservation this is equivocal.

Forefin - Two forefins are preserved in PMO 219.250, in slabs 5 and 7 (Fig. 4). They appear to be in ventral view. The left forefin is lying close to the articulated vertebral column. The right forefin is split between slabs 5 and 7. See Table 2 for selected forefin and hind fin measurements.

Table 2. *Selected fore- and hind fin measurements of PMO 219.250.*

Humeral measurements	Left in mm	Right in mm
Maximum proximodistal length	44	49
Maximum anteroposterior width, proximal end	?	29
Maximum anteroposterior width, distal end	~42	?
Length of ulnar facet	16	18
Length of radial facet	~26	?
Maximum height of the posterior ramus	9	9
Articular anteroposterior length	12	12
Autopodium measurements	Left in mm	Right in mm
Anteroposterior width of radiale	31	?
Proximodistal length of radiale	19	?
Anteroposterior width of intermedium	20	?
Proximodistal length of intermedium	20	23
Anteroposterior width of ulnare	14	18
Proximodistal length of ulnare	15	19
Femoral measurements	Left in mm	Right in mm
Maximum proximodistal length	35	36
Maximum anteroposterior width, proximal end	~17	12
Maximum anteroposterior width, distal end	?	26
Length of tibial facet	19	?
Length of fibular facet	?	10

The left forefin includes a humerus, with distally articulating radius and ulna and several autopodium elements. Details of the proximal end are not available due to coverage by scapula. The right forefin includes a humerus, distally articulating radius and ulna, proximal carpal elements and several phalanges. The humerus is proximodistally longer than anteroposteriorly wide. There is an extensive unnotched anterior flange (see Jiang et al., 2005). The humeri bear deltopectoral crests on the anteroventral surface, starting at the proximal margin and twisting posteriorly down the shaft. The distal surface bears two facets for the radius and ulna, the latter of which is the smaller (Table 2). The two facets are offset and enclose an angle of approximately 115 degrees. The radius and ulna are preserved in partial articulation with the humerus and distal elements. The proximal edge of the radius forms a straight facet to meet the humerus. The anterior edge is straight, ending in a point distally. The anterior edge bears a notch close to the proximal end. It is unlikely that the radius and the ulna had any proximal contact, due to the edge of the humerus separating the two facets. The posterior edge of the radius appears to be straight. There is a small spatium interosseum between the two elements, not as large as in other mixosaurids (see e.g. Maisch and Matzke, 2000), as only the ulna bears a concave edge. The distal surface of the radius bears a long straight facet for the radiale and a significantly smaller posterior facet for the intermedium. The proximal edge of ulna forms a straight facet for the posterodistal humeral facet. The ulna is concave anteriorly and convex posteriorly. The distal end bears two facets of similar size for the intermedium and ulnare. The posteroproximal part of the ulna is drawn out into a point-like projection.

The carpal series in the right forefin are near complete, lacking only the fifth metacarpal series and the most distal elements. There are three proximal carpals, the radiale, the intermedium and the ulnare and four preserved distal carpals although a fifth seems likely. The autopodium elements are better preserved in the left forefin and are less flattened. Individual measurements of the proximal elements are available in Table 2. The radiale is preserved on both fore fins. It is rectangular in shape, but with a small notch-like facet posterodistally. The radiale is anteroposterally wider than the intermedium and the ulnare and has two distal facets for the first and second carpals. The intermedium is polygonal with two proximal facets for the radius and ulna. The intermedium separates the ulna and radius by having a small proximal point between the two elements. It has two clear distal facets for third and fourth distal carpal. A small anteroproximal notch is present in the intermedium. The ulnare is rounder in shape than the other proximal carpals. The pisiform is rather large and square. It has two distal facets for the fourth and fifth carpals. The distal carpals are of similar size and square in shape. The first metacarpal series is the most complete, with five phalanges.

Hind fin - Two partial hind fins are preserved in specimen PMO219.250 in slabs 1 and 4, comprising mainly impressions and partial fragments of elements (Table 2). The hind fin furthest from the vertebral column in the bottom right of Fig. 4 consists of a single femur. An element which could represent the tibia was located distally to this femur, but was lost during excavation (see Fig. 4). This femur is the more complete of two, and based on a partially eroded mid-centered process appear to be exposed on its ventral side. The distal end of the femur has two facets for the tibia and fibula. As the anteriormost facet is the tibia, this femur is interpreted to be the left. The hind fin closest to the vertebral column is therefore interpreted to be the right. The right femur comprises of a fragment and an impression of the remaining part of the femur spread on both slabs (1 and 4). The element articulating to the right femur, which also comprises a partial impression and fragments, is interpreted to be the tibia, because the articular surface is broad and contacts the largest femoral facet, as well as on the basis of its size and the general morphology. There is another preserved element articulating distally to the tibia. This element is rectangular in shape and is significantly smaller than the tibia. A fibula is present articulating to the left femur, represented partially by bone and impressions. It appears to have an anterior notch along its anterior margin, proximal from the astragalus facet.

Axial skeleton

Vertebrae - The preserved vertebral column consists of 86 complete to partial vertebrae (See Table 3 for details). One was removed during preparation to expose more of the forefin. Six impressions of vertebrae were also observed, giving a total of 92 vertebrae. There are 48 presacral vertebrae preserved (including the impressions and the removed vertebra). The vertebrae anterior to the pectoral girdle are all disarticulated, and some of the cervical vertebrae, including the atlas-axis,

Table 3. *Number of vertebrae identified on slab 1-7 of PMO 219.250.*

Slab	Vertebral count	Vertebral impressions
PMO 219.250/6	0	0
PMO 219.250/7	27	0
PMO 219.250/5	0	0
PMO 219.250/4	19	1
PMO 219.250/1	13	0
PMO 219.250/2	15	2
PMO 219.250/3	11	3
Removed during prep. from PMO 219.250/7	1	0
Total	86	6
Sum	92	

Table 4. Measurements of all vertebrae.			
Vertebrae number from pectoral region	Dorsal-ventral height	Anterior-posterior length	Height/length
1	2.20	1.30	1.69
2	2.30	1.40	1.64
3	2.30	1.30	1.77
4	2.20	1.20	1.83
5	2.20	1.20	1.83
6	2.20	1.50	1.47
7	2.50	1.50	1.67
8	2.70	1.50	1.80
9	2.50	1.60	1.56
10	2.50	1.60	1.56
11	?	?	?
12	?	?	?
13	?	?	?
14	?	?	?
15	2.00	1.20	1.67
16	?	?	?
17	2.50	1.30	1.92
18	2.50	1.40	1.79
19	?	?	?
20	2.20	?	?
21	2.30	?	?
22	2.40	?	?
23	2.20	?	?
24	2.30	1.60	1.44
25	2.20	1.30	1.69
26	2.10	1.30	1.62
27	2.40	1.30	1.85
28	2.20	1.30	1.69
29	?	?	?
30	2.30	?	?
31	?	?	?
32	?	?	?
33	?	1.30	?
34	?	1.20	?
35	?	?	?
36	?	1.10	?
37	2.10	1.10	1.91
38	?	1.20	?
39	2.20	1.20	1.83
40	2.10	1.20	1.75
41	2.00	1.20	1.67
42	2.00	1.20	1.67

appear to be missing. This number is consistent with the estimates by Sander (2000) of 45-50 presacral vertebrae for mixosaurids. There are 44 postsacral vertebrae preserved (including the impressions), but the posteriormost caudal vertebrae are missing (See Table 4 for vertebrae measurements). By measuring the distance between slabs, it was estimated that there are at least three vertebrae missing between slabs 5 and 7 and three missing between slabs 2 and 3. Depending on how many of the posteriormost caudal vertebrae and the anteriormost cervical vertebrae are missing, between 10-20 vertebrae are estimated to be lost based on the estimate of Sander (2000).

Each articulated vertebra was measured at its maximum dorsal-ventral height at the anterior end, and the measurements plotted in a graph using PAST (Hammer et al., 2001). The results are presented in Fig. 5). Vertebrae that could not be measured due to erosion and vertebrae missing between slabs were taken into account to give a more correct picture of the dorsal-ventral height change throughout the vertebral column. The figure clearly illustrates a higher dorsal-ventral height in mid-caudal region as is common for mixosaurids (Sander, 2000).

The vertebrae in the mid-caudal region (slab 2) are significantly dorsal-ventrally higher than the preceding vertebrae. These vertebrae also appear to have widely spaced intervertebral joints between the centra of each vertebra, which are now filled with sediment. Some of these intervertebral joints are up to 3.5 mm wide and are prominent in all the mid-caudal vertebrae. There are no clear gaps between the centra at the intervertabral joint in the anterior vertebrae.

Neural arches - Several neural arches are preserved from various regions of the axial skeleton, most being from the anterior region of the axial skeleton. These are distinctively tall compared to the height of the dorsal vertebrae, being approximately twice the height in the trunk region (Table 3). These appear robust at the base of the spine, but thin out towards the terminal end. Impressions of neural arches around the sacral region show the spines are slightly reduced in size and robustness. This is, however, equivocal because of the poor preservation of the neural arches in this region. In the mid-caudal region where the vertebrae increase in dorsal-ventral height, the neural arches also appear to be long, densely packed and thin in comparison to the anterior trunk neural arches.

Ribs - Numerous rib fragments are preserved in specimen PMO 219.250, and several chevrons in the mid-caudal region are complete.

Gastralia - Several small gastralia fragments are present in slab 7; these are about half the thickness of the ribs and appear more rounded. There are also several impressions present in slab 6, which are a third of the thickness of the ribs.
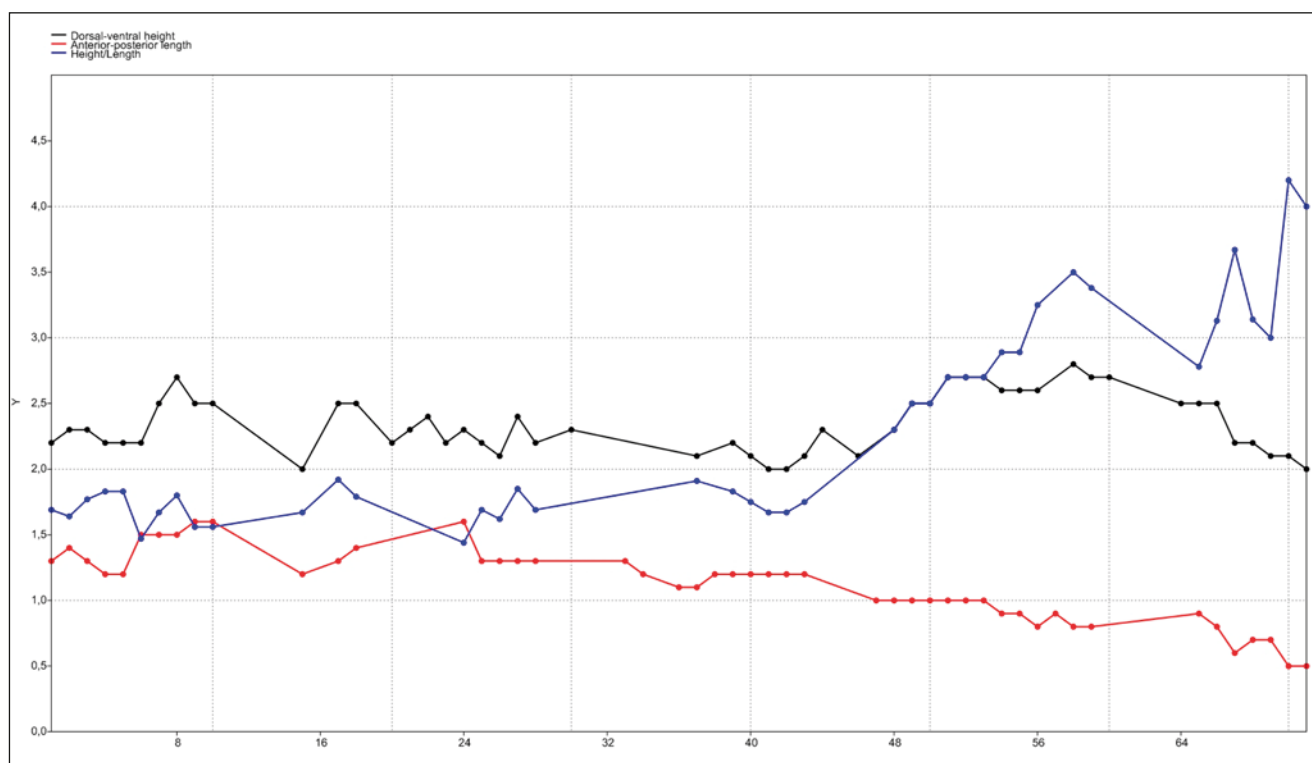
Figure 5. Graph illustrating dorsal-ventral height (black), anterior-posterior length (red) and the height/length ratio of the articulated vertebrae from the pectoral region to the caudal region of PMO 219.250. Vertebrae that could not be measured due to erosion and an estimated number of vertebrae lost between the slabs have been taken into account.

Discussion

PMO 219.250 can be placed confidently in the family Mixosauridae on the basis of the following synapomorphies (taken from Liu et al., 2013 and references therein), which the specimen shares with members of the family:
- The premaxilla is posteriorly pointed.
- Distinctly high and narrow neural spines extend to the caudal peak.
- Mid-caudal vertebral centra have increased size (absent in some specimens of *M. cornalianus*).
- Posterior teeth are more robust than anterior ones (convergent in *Chaohusasaurus* and *Grippia* and absent in *M. cornalianus* and *Phalarodon avatus*).
- Distal carpal 1 is slightly larger than other distal carpals.
- Humeri are relatively short but still retain constricted shafts (Sander, 2000; Maisch, 2010; Maisch and Matzke, 2000; McGowan and Motani, 2003; Schmitz et al., 2004; Jiang et al., 2006; Liu et al., 2013).
- Posterior dorsal and anterior caudal vertebrae are dicephalous (Nicholls et al., 1999).

Other characters that are shared with most mixosaurids are:
- The lacrimal has no contact with the external naris, similar to other Triassic mixosaurids (Schmitz et al., 2004; Jiang et al., 2005; Liu et al., 2013).
- The humerus has an extensive unnotched anterior flange, common in mixosaurids (Jiang et al., 2005).

Skull - The elements of the rostrum of specimen PMO 219.250 are displaced, and in some places covered by palate elements. Identifying the individual elements is therefore challenging. The premaxilla forms the anterior border and anteroventral border of the external naris, as in *P. avatus* and *P. callawayi* (Schmitz et al., 2004). This is different from *M. panxianensis* where although bordering the anterior region, the premaxilla does not form a subnarial process and the maxilla forms the entire ventral border of the external naris (Jiang et al., 2006). As with most mixosaurs, the maxilla excludes the lacrimal from externally bordering the external naris, with a postnarial process (Schmitz et al., 2004; Jiang et al., 2005; Liu et al., 2013). The external naris is located dorsally 50 mm anterior to the orbital rim, which is further anteriorly than most other members of the genus *Phalarodon* (Schmitz et al., 2004; Jiang et al., 2007; Liu et al., 2013). Little of the nasal is preserved on specimen PMO 219.250, so comparison is difficult. However there does appear to be a partial nasal terrace above the external naris, as in *Phalarodon* sp. (Liu et al., 2013). The lacrimal articulates ventrally with the jugal and the maxilla, as in *M. panxianensis* (Jiang et al., 2005, 2007). Even though the posterior region of the skull of PMO 219.250 is poorly preserved, the jugal has a broad articulating ramus to the postorbital similar to *P. fraasi*, but dissimilar to *M. panxianensis* which has a short posteroventral process (Jiang et al., 2005, 2006, 2007).

Mandible - The mandible of PMO 219.250 is so crushed and disarticulated that comparison is difficult. The dentary stretches along the rostrum and terminates in-line with the external naris, unlike *P. fraasi* where it ends posteriorly in-line with the anterior region of the orbit (Jiang et al., 2007). As in *P. fraasi* the surangular terminates anteriorly past the last tooth (Jiang et al., 2007). There is no presence of a coronoid process on the surangular as in *P. fraasi*, *M. cornalianus* and *M. kuhnschnyderi*, unlike the prominent coronoid process of *P. callawayi* (Schmitz et al., 2004).

Dentition - Similar to many of the members of the family, the maxilla bears more robust, conical, blunt teeth compared to the premaxilla dentition (Motani, 1997; Jiang et al., 2005; Liu et al., 2013). There is no sign of multiple maxillary tooth rows, but this may be due to poor preservation. The premaxilla bears smaller needle-like teeth, which are closely spaced as in *P. fraasi*, and unlike the widely spaced teeth of *M. panxianensis* and *M. nordenskioeldii* (Schmitz, 2005; Jiang et al., 2006, 2007). The teeth are set in sockets in the premaxilla and dentary similar to in *P. fraasi*, *P. avatus* and *P. callawayi* (Schmitz et al., 2004; Jiang et al., 2007; Liu et al., 2013), unlike *M. panxianensis* and *M. cornalius* where teeth are located in a dental groove (subthecodont) (Maisch and Matzke, 1997; Jiang et al., 2005).

Appendicular skeleton - The humeri are proximodistally longer than anteroposteriorly wide, as in *Phalarodon* (Jiang et al., 2006). There is an extensive anterior flange that lacks evidence of notching similar to *M. panxianensis*, unlike in *P. avatus* which has a weak notch (Jiang et al., 2006; Liu et al., 2013). There are two distal facets for the radius and ulna as in *M. panxianensis*, in contrast to the three distal facets of *P. avatus* (Liu et al., 2013). The anterior edge of the radius bears a notch close to the proximal end, whereas in *M. panxianensis* and *P. callawayi* there are two notches on the leading edge of the shaft (Jiang et al., 2006). The spatium interosseum is smaller than in other mixosaurids, as the posterior edges of radii shafts are straight (Jiang et al., 2005). The posterior margin of the ulna is rounded and convex as in *M. cornalianus*, while it is notched in *P. callawayi* (Motani, 1999b; Schmitz et al., 2004). As in *P. avatus* the ra dius facet of PMO 219.250 of the intermedium is significantly smaller than that for the radial. In contrast the intermedium proximal edge of *M. panxianensis*, has two equal facets for the radius and ulna. A small anteroproximal notch is present in PMO 219.250 and *P. avatus*. There are 5 distal carpals present in the described specimen as in *M. panxianensis*, whereas *P. avatus* has four distal carpals (Jiang et al., 2006; Liu et al., 2013). As in all mixosaurids the first distal carpal is the largest, and there are 5 metacarpal series (Maisch and Matzke, 2000).

The femora of PMO 219.250, as in *M. panxianensis*, *Phalarodon* and material described as *M. nordenskioeldii*

have two wide distal facets, where the tibia facet is the larger (Maisch and Matzke, 2000; Jiang et al., 2006; Liu et al., 2013). The anterior margin of the fibula of PMO 219.250 has an anterior notch as in *P. avatus* and *M. panxianensis* (Jiang et al., 2006; Liu et al., 2013).

Axial skeleton - There are 48 presacral vertebrae preserved in PMO 219.250; for mixosaurids this is rather high, considering that several of the cervical vertebrae are missing. Sander (2000) estimated that 40-50 presacral vertebrae are normal for mixosaurids, but this specimen could have up to 55. This may suggest a more undulatiory movement than in other mixosaurids, as a reduction in this number is considered an adaptation to enhanced caudal propulsion (Motani et al., 1996). There are 44 postsacral vertebrae preserved in the described specimen, although the majority of the postflexural vertebrae are missing. An increase of the post-sacral vertebral count, thereby increasing the intervertebral joint count, increases the flexibility of the column (Buchholtz, 2001). The widely spaced mid-caudal intervertebral joints are not commonly observed, but are also present in the *Mixosaurus* sp. specimen FMNH PR 1804 from the Farvet Formation in the southern Tobian Range (USA) (Sander et al., 1994).

All previously described mixosaurid specimens from the Middle Triassic Blanknuten Member (also known as Upper Saurian niveau) have recently been referred to *Phalarodon callawayi* and *P. fraasi* (Schmitz, 2005; Maxwell and Kear, 2013; Schmitz et al., 2004). Schmitz et al. (2004) used the differing height to length ratio of the vertebral centra to discern between the two species. If we compare our plot (Fig. 5) to the plot made by Schmitz et al. (2004: fig 2), the specimen described here has a ratio of posterior dorsals closely comparable to *Mixosaurus cornalianus* and *M. nordenskioeldii* of 1.5-1.9. However, the mid caudal ratio extends to 4, while in *Mixosaurus cornalianus* and *M. nordenskioeldii* the ratio is about 2.5. The ratio of 3-4 for the mid caudals is between that of *P. callawayi* (up to 5) and the value cited for *Mixosaurus cornalianus* and *M. nordenskioeldii* in Schmitz et al. (2004).

The specimen from Svalbard designated as *P. callawayi* by Schmitz et al. (2004; PMU R 188) and figured by Wiman (1910: plate VI, fig. 1) consists of 59 posterodorsal and caudal vertebrae with a pelvic girdle and one hind fin. In size the specimen PMO 219.250 is similar, but the height to length ratios of the preserved vertebrae are significantly larger in PMU R 188. This could suggest either that PMO 219.250 is new species, or that there is more intraspecific variation in this region than previously anticipated; the latter explanation is considered to be more likely.

This specimen shows clearly the difficulties encountered when combining partial skeletons of mixosaurids and identifying species from partial individuals.

Conclusion

PMO 219.250 resembles species referred to the genus *Phalarodon* (Merriam, 1910), based on the following synapomorphies (Jiang et al., 2007):

- Nasal region with pronounced narial shelf
- Maxillary teeth in sockets
- The premaxilla forms the anterior half of the ventral border of the external naris.

The specimen shares some anatomical traits with the previously described species from Spitsbergen (*P. fraasi* and *P. callawayi*), some of which could be synapomorphies. However, there are a number of differences between PMO 219.250 and the known species of *Phalarodon*, which suggests that the taxonomic relationships within Mixosauridae are more complex and less understood than previously anticipated. We refrain from erecting a new species, awaiting the preparation and description of the rest of the material collected from the site at Edgeøya.

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