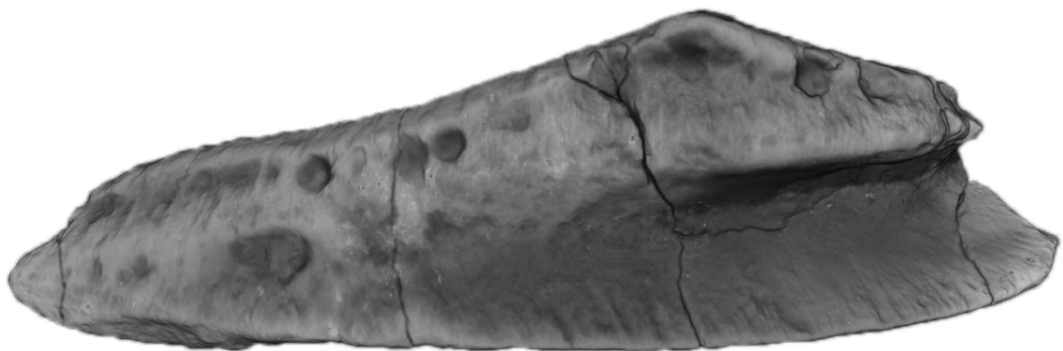


Master Thesis, Department of Geosciences

**Remains of *Omphalosaurus*
from the Early Triassic,
Marmierfjellet, Spitsbergen**

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UNIVERSITY OF OSLO

FACULTY OF MATHEMATICS AND NATURAL SCIENCES

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Discipline: Palaeontology

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May 2016

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This work is published digitally through DUO – Digitale Utgivelser ved UiO

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It is also catalogued in BIBSYS (<http://www.bibsys.no/english>)

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Acknowledgments

On a study trip during elementary school we went to The Natural History Museum in Oslo, and I brought with me a fossil I'd collected during a holiday in Germany. The people that met me showed an interest unknown to me, of what for most people would be just another rock. I came back several times with my treasures, always met with fascination no matter how small or common the fossil truly was. By triggering the interests of fossils in a little girl, they created a lifelong fascination of prehistoric creatures. I think it is reasonable to say that this thesis would not even exist, if it were not for the wonderful staff through the years at The Natural History Museum.

This thesis would also not exist without Jørn Hurum, who gave me the unique opportunity to study *Omphalosaurus* and also be a part of the Spitsbergen Mesozoic Research Group. Thank you for being an exceptional supervisor and inspiration. Lene Liebe Delsett, thank you for being patient every time I came to your office with silly questions and for all the suggestions regarding my thesis.

Great thanks to Martin Sander and Tanja Wintrich at the University of Bonn, who guided me and shared interesting ideas of our beloved *Omphalosaurus*. This thesis would definitely not be what it is without you.

To all wonderful members of the Spitsbergen Mesozoic Research Group; thank you for helping me collect the material for this thesis. I'm truly grateful for having shared two weeks on Svalbard with such amazing people. Jørn, Bjørn, Øyvind, Stig, Lena, Lene, Achim, Aubrey, Ole Frederik, Victoria and Inghild, thank you! A special thanks to Achim Reisdorf for logging help!

Great thanks to May-Liss Knudsen Funke and Bjørn Lund for always being helpful during preparation of the fossils in the lab. This would not have been possible without you. And thank you Janne Bratvold, for all the hours we shared sieving sediments.

To all the people working at the museum, thank you! Thank you Gro Synnøve Lindgaard and Wenche Hafsahl Johansen in the library, for being extremely helpful and providing all the articles I could not find myself. Thank you Hans-Arne Nakrem for sharing your exceptional knowledge of photography and picture editing.

Thank you, Anette Sjøberg, for taking the time to read through my thesis, even though you probably have enough writing your own.

To my best friend Maria Sandsmark, thank you for sharing this everlasting winter with me. Thank you for always being supportive and encouraging, patiently listening to my problems considering marine reptiles. You are the best.

Mom and dad, thank you for always being my biggest fans.

Christina

Oslo, May 2016

Abstract

In this study, tooth-bearing bones and vertebrae of *Omphalosaurus* from the Early Triassic of Spitsbergen have been examined to better understand the morphology, lifestyle and systematic affinities of this enigmatic marine reptile. The tooth-bearing bones consist of 18 dentaries, 7 premaxillae and 30 bones with uncertain position in the jaw. In total 337 vertebrae were collected, together with more than 400 vertebrae fragments. Only the best preserved bones are described in this thesis. The material was collected at Marmierfjellet from the Grippia Niveau and Lower Saurian Niveau, Vikinghøgda Formation, Vendomdalen Member, dated as Spathian. The *Omphalosaurus* material described from Spitsbergen is unique in the amount of material, size range and 3D preservation.

Even though ichthyopterygian affinity of *Omphalosaurus* has been controversial, such an association is proposed here based on the vertebral column described for the first time in this study. Four of the characters by Ji et al. (2015) used to define the ichthyopterygia is suggested present in *Omphalosaurus*; nasal anteriorly extending beyond external naris, neural spine articulation in tail present, caudal peak present and tail stem count $\frac{1}{2}$ or more that of the presacral count.

Omphalosaurus is probably more derived than the most basal ichthyopterygians, due to the presence of discoidal vertebrae centra and a caudal peak. Based on the vertebral column it is suggested as a possible transition between anguilliform and thunniform swimming mode, adapted to an open marine environment.

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1. Introduction

Triassic marine reptiles from the Svalbard archipelago were first collected during expeditions by the Royal Swedish Academy of Sciences in 1864 and 1868, led by Adolf Erik Nordenskiöld (Wiman 1910). The material collected by Nordenskiöld was examined by Hulke (1873) who assigned the material to two new ichthyosaur species *Ichthyosaurus nordenskiöldii* and *Ichthyosaurus polaris*. In 1908, another expedition to Spitsbergen was led by G. De Geer, where the student Bertil Högbom and three of his friends was brought along to collect paleontological material (Wiman 1910). Several ichthyosaurs were described from the fossils collected, which were examined by the Swedish paleontologist Carl Wiman (Wiman 1910). One of them, *Pessopteryx nisseri* Wiman 1910, had tooth-bearing bones recognized by Merriam (1911) as similar to *Omphalosaurus nevadanus* Merriam 1906 (Merriam 1906).

Omphalosaurus is a marine reptile that inhabited the shallow seas in the Eastern Pacific, the Boreal sea and Western Tethys. It is only known from enigmatic jaw fragments and a few vertebrae, from late Early to Middle Triassic (Sander & Faber 1998, 2003). The size of *Omphalosaurus* has been interpreted differently, from “small to medium sized” (Sander & Faber 1998), “moderately large” (Motani 2000) and minimum 3.5 meter long (Tichy 1995). It has been described as rather plump, based on the relatively short and robust snout (Motani 2000).

The most characteristic feature of *Omphalosaurus* is the rounded teeth found in the massive jaw bones, where replacement teeth fill up large parts of the bone. The morphology of the teeth indicates hard-shelled or abrasive food, which easily wears the teeth so that a large number of replacement teeth were needed. The teeth of *Omphalosaurus* is dome-shaped with an enamel surface showing an uneven pattern of small pits, much like the peel of an orange (Sander & Faber 2003). The tooth enamel shows a unique microstructure that can be used to distinguish *Omphalosaurus* from other marine reptiles. The microstructure differs between the replacement teeth and the functional teeth, suggesting enamel maturation from the dental lamina towards the occlusion surface (Sander 1999). The genus was erected based on the unique dentition and new specimens are commonly identified as *Omphalosaurus* based on the presence of these peculiar tooth-bearing bones (Merriam

1906). Tooth-bearing bones are therefore present in all specimens identified as *Omphalosaurus*.

The few vertebrae described belong to the anterior part of the trunk and are deeply amphicoelous anterior and posterior, being nearly notochordal at the center. The atlas has a convex anterior face and a deeply amphicoelous posterior face (Sander & Faber 2003). Vertebra centra from the posterior half of the trunk are so far not described.

An interesting feature is the general lack of compact bone that can be observed in cranial and postcranial bones of *Omphalosaurus*. The cancellous bone seems to be of primary origin and show cyclic growth, a combination uncommon in marine reptiles (de Buffrenil & Mazin 1990; Sander & Faber 2003).

The genus *Omphalosaurus* was erected by Merriam (1906) from a fragmentary skull and two associated vertebrae from the Middle Triassic of Nevada. The holotype was named *Omphalosaurus nevadanus* and placed in the family Omphalosauridae, since Merriam (1906) did not observe any resemblance between *Omphalosaurus* and other marine reptiles known at that time. Merriam (1906) did not explain the etymology of the name *Omphalosaurus*, but the word *omphalos* means navel in Greek. An omphalos is also a religious stone artifact, where in Greek lore the omphalos marked the “navel” of the world.

When Wiman (1910) described the Spitsbergen material collected in 1908, one of his species, *Pessopteryx nisseri*, showed *Omphalosaurus*-like dentition together with ichthyosaur postcranial bones. This was recognized by Merriam (1911), who suggested that the cranial material of *P. nisseri* belonged to *Omphalosaurus*, which Wiman (1916) agreed.

The systematic affinity of *Omphalosaurus* has been discussed for more than a century, where some claim it to be ichthyopterygian (Mazin 1983; Tichy 1995; Sander & Faber 1998, 2003) while others doubt any ichthyopterygian affinities (Maisch & Matzke 2000; Motani 2000).

The first to consider *Omphalosaurus* being an ichthyosaur was (Kuhn 1934), who placed *Omphalosaurus* and *Pessopteryx* in the family Omphalosauridae, within the order Ichthyosauria, for unknown reasons. This view was followed by Huene (1951) and Cox and Smith (1973). Mazin (1983) discussed *Omphalosaurus* remains from Spitsbergen and was the first to give arguments for *Omphalosaurus* belonging within the Ichthyopterygia. Later

Mazin (1986) re-interpreted the holotype from Nevada and concluded that *Omphalosaurus* was a primitive durophagous ichthyosaur, most closely related to *Grippia*.

A new species, *O. nettarhynchus*, was described by Mazin and Bucher (1987) based on an anterior part of a mandible from the Early Triassic of Nevada. This species is interpreted to have had a spatulate snout, which is not observed in other species of *Omphalosaurus* or any known ichthyopterygian (Mazin & Bucher 1987).

A third species, *Omphalosaurus wolfi*, was described by Tichy (1995) from the Middle Triassic in the Northern Alps of Germany. In this specimen the anterior part of the trunk is preserved together with the skull, which makes it the most complete specimen of *Omphalosaurus* described so far (Sander & Faber 2003). The anterior trunk show ribs, gastralia and vertebra centra including the atlas, but unfortunately more detailed morphological features is hard to observe due to the poor preservation of the specimen (Sander & Faber 2003). Tichy (1995) also suggested ichthyopterygian affinities of *Omphalosaurus*, which was followed by Sander and Faber (1998). The material of *O. wolfi* was re-described by Sander and Faber (2003), where similarities between *O. nevadanus* and *O. wolfi* were discussed. They concluded that no anatomical differences existed, and the two species could not be differentiated on morphological grounds (Sander & Faber 2003). Since both specimens are poorly preserved and incomplete, *Omphalosaurus* cf. *O. nevadanus* was used for the Alpine specimen (Sander & Faber 2003).

The first find of *Omphalosaurus* from the Germanic Basin was described by Maisch and Lehmann (2002), who erected the new species *Omphalosaurus peyeri* from the Middle Triassic of Germany. It was described from one left maxilla, with only one tooth row and few replacement teeth. This specimen has later turned out to be a placodont and not *Omphalosaurus*, by examination of the tooth enamel in SEM (Sander, pers. comm, March 7th, 2016).

Sander and Mazin (1993) discussed the affinities between the questionable ichthyopterygian *Tholodus* Von Meyer (1851) and *Omphalosaurus*, suggesting different genera with a close relationship. The affinities between *Omphalosaurus* and *Tholodus* has previously been discussed by several authors (Woodward 1932; Peyer 1939; Huene 1956; Romer 1956) and a synonymy between the two was suggested by Romer (1966). Still the differences are greater than the similarities, where the shape, size and arrangement of the teeth in the jaw can easily be distinguished between the two (Dalla Vecchia 2004).

Omphalosaurus also lacks plicidentine, which is present in *Tholodus* (Sander & Mazin 1993; Dalla Vecchia 2004; Arkhangelsky et al. 2016) and has a micro-unit enamel that differs from the enamel of *Tholodus* (Sander & Faber 1998; Sander 1999). In a comprehensive study of the microstructure of reptilian tooth enamel, Sander (1999) studied the enamel of *Omphalosaurus* and categorized it as a durophagous Ichthyosaur.

Motani (2000) argued against *Omphalosaurus* being an ichthyopterygian due to lack of basal synapomorphies identified for the Ichthyopterygia. Maisch and Matzke (2000) supported this and referred to *Omphalosaurus* as an “enigmatic ichthyosaur-like reptile” (Maisch & Matzke 2000).

Further arguments for assigning *Omphalosaurus* to the Ichthyopterygia was given by Sander and Faber (2003), as well as new information on bone histology and CT scans of jaw fragments. An extensive study of the dentition of *Omphalosaurus* was also made, discussing the implantation of the teeth, arrangement, replacement and wear patterns (Sander & Faber 2003). Sander and Faber (2003) stated that many of the characters observed in *Omphalosaurus*, like bone mass reduction and shortened vertebrae, is associated with a strong adaption to an aquatic environment and can be found in several groups of marine amniotes other than ichthyopterygians. Still, these groups occurred much later than late Early Triassic. It is therefore more likely that *Omphalosaurus* is ichthyopterygian rather than one of the earlier members in a later occurring group like plesiosaurs, mosasaurs or marine turtles (Sander & Faber 2003).

McGowan and Motani (2003) followed the view of Motani (2000) and considered *Omphalosaurus* to be non-ichthyosaurian. Maisch (2010) erected a new species for the *Omphalosaurus* material described by Wiman (1910), *Omphalosaurus merriami*, and chose a lectotype from the material (Maisch 2010). Maisch (2010) listed the family Omphalosauridae as questionable ichthyosaurs, with *Omphalosaurus*, *Tholodus* and *Xinminosaurus* as genera within the family, *Xinminosaurus* being a possible junior subjective synonym of *Tholodus*.

A new specimen of *Omphalosaurus* sp. from Poland was described in the BSc thesis of Wintrich (2014), collected in the Lower Muschelkalk of Middle Triassic age.

Omphalosaurus and *Tholodus* are not included in the most recent phylogeny of the Ichthyopterygia by Ji et al. (2015), while *Xinminosaurus* is moved to the Cymbospondylidae within the Ichthyosauria.

In this study a large amount of new material from Spitsbergen is examined to reveal information on the enigmatic *Omphalosaurus*. Tooth-bearing bones are studied in detail to better understand the morphology and function of the peculiar skull. An attempt to reconstruct the vertebral column is made, to better understand the lifestyle of this animal, as well as its systematic position. This is the first time *Omphalosaurus* is described from the Grippia Niveau, making it the stratigraphically oldest material of *Omphalosaurus* ever described from Spitsbergen. *Omphalosaurus* remains of Spathian age is only known from Spitsbergen and Nevada (Mazin & Bucher 1987), and the material described therefore represents some of the oldest remains of *Omphalosaurus* known worldwide.

1.1 Geological setting

The Svalbard archipelago is located in the northwest of the Barents Sea, between mainland Norway and the North Pole, at latitudes 74-81° N and 10-35° E (Fig. 1). In the Early Triassic, Svalbard represented a large embayment located northwest of the supercontinent Pangea (Lundschien et al. 2014). During Permian the collision between Laurentia and Siberia had formed the Uralian Mountains in the south-east and closed the previous seaway between the equatorial Tethys Ocean and the Boreal Seas (Dallmann 2015). Entering the Triassic, boreal communities had replaced the Permian warm water ecosystems (Dallmann 2015). The erosion of the Uralian Mountains, the basement rock of Norway and the Kola Peninsula, filled the basin with sediments (Lundschien et al. 2014).

The material examined in this study are from the Early Triassic deposits of Marmierfjellet, central Spitsbergen, Svalbard (Fig. 1). It was found in the Sassendalen Group, Vikinghøgda Formation, Vendomdalen Member, which is dated as Spathian (Mørk et al. 1999). The formation is interpreted as being deposited in a moderately deep shelf environment (Lundschien et al. 2014) dominated by silty shale (Mørk et al. 1999).

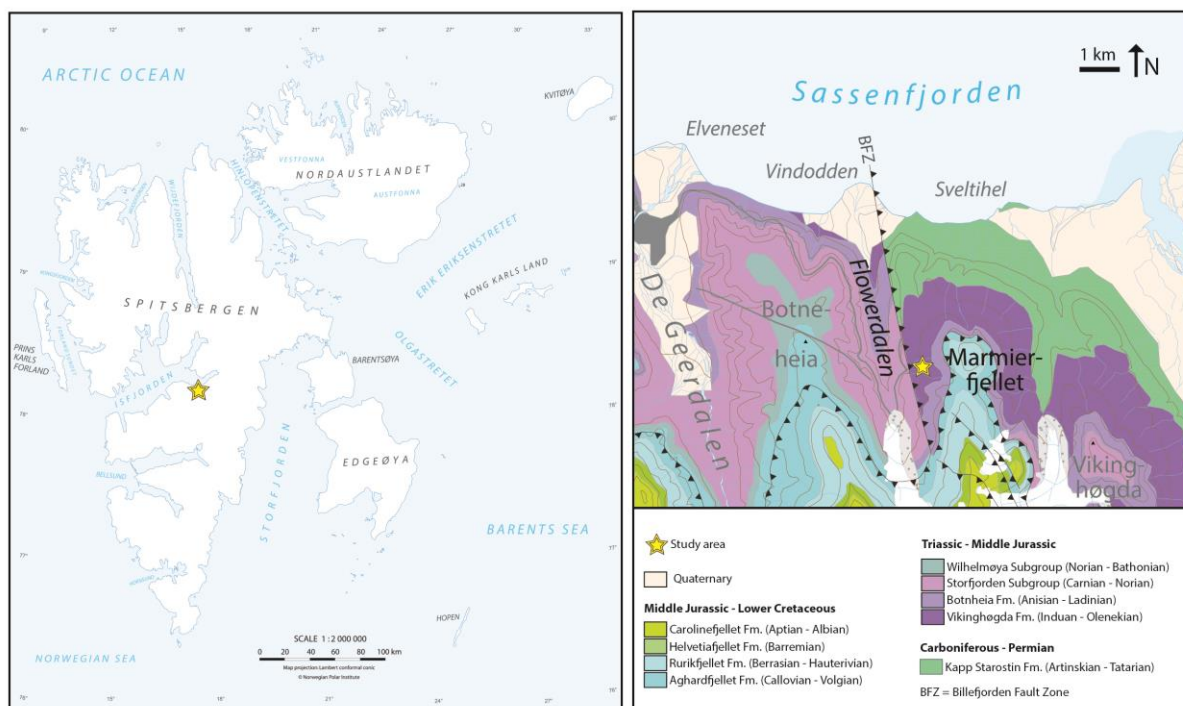


Figure 1: Overview of Svalbard and geological map of the study area in central Spitsbergen. The star marks the site where the material was collected. Modified from Dallmann (2015).

The Vendomdalen Member is the uppermost of three members in the Early Triassic Vikinghøgda Formation, which is overlain by the Botneheia Formation (Mørk et al. 1999). Together, the two formations form the Sassendalen Group, which earlier was introduced and divided into the Vardebukta, Sticky Keep, and Botneheia Formations by Buchan et al. (1965).

At Marmierfjellet (Fig. 1) the Vendomdalen Member consists of 94 meter thin to medium bedded silty, dark grey, laminated mudstone, where yellow weathering dolomite beds and nodules are common (Fig. 2) (Mørk et al. 1999). The depositional environment is interpreted to be distal shelf, below wave base, with a high accumulation of organic material in a low oxic environment (Mørk et al. 1999). Each of the members in the Vikinghøgda Formation are thought to represent transgressive-regressive successions (Lundschien et al. 2014), where the Vendomdalen Member represents a transgressive sequence, observed by a reduction in terrestrial palynodebris, increase in marine plankton, decreased sedimentation rate and current indicators (Mørk et al. 1999). The organic carbon content is measured to generally above 1% and the member is interpreted as a mixed type II/III kerogen (Mørk et al.

1999). At the mountain Vikinghøgda (Fig. 1), the Vendomdalen Member has been dated by ammonoids to be of Spathian age by Mørk et al. (1999), where the lower part is identified as the *Bajarunia euomphala* Zone, above this the *Keyserlingites subrobustus* Zone and the upper part as the *Parasibirites grambergi* Zone. The section is also dated with palynomorphs by Vigran et al. (2014), where the lower part of the section is assigned to the *Pechorosporites disertus* Composite Assemblage Zone, early Spathian age, and the upper part to the *Jerseyiaspora punctispinosa* Composite Assemblage Zone of late Spathian age.

Wiman (1910) named distinct fossiliferous horizons in the Triassic successions of Svalbard based on the vertebrate content, namely the “Fish Niveau”, “Lower Saurian Niveau” and “Upper Saurian Niveau”. Another horizon was described by Wiman (1928) which was named the “Grippia Niveau” due to *Grippia* being the most abundant taxon in this level (Maxwell & Kear 2013). The Grippia Niveau had earlier been observed by Stensiö (1921), where he mentioned a fossiliferous horizon located as proximately 33 meter above the “Fish Niveau”. Until 1965, the niveaus of Wiman was used as the stratigraphic terminology of the Triassic of Svalbard, but was then replaced by the terminology suggested by Buchan et al. (1965). Still, the terms have been used in vertebrate paleontology but they were not correlated with new stratigraphical terminology until Maxwell and Kear (2013) did a revision of the different ichthyopterygian assemblages of the Triassic deposits of Svalbard.

The material described in this work were collected at the western side of Marmierfjellet, in the hills of Flowerdalen (Fig. 1). The bones are collected from both the Grippia Niveau and the Lower Saurian Niveau, where the Grippia Niveau is located just below the middle of the Vendomdalen Member and the Lower Saurian Niveau in the top of the Vendomdalen Member. The Grippia Niveau is estimated as 247.5 Ma, and the slightly younger Lower Saurian Niveau as 247.2 Ma. In the Lower Saurian Level the bones appear as floating material scattered over a large area. At the Grippia level the bones are also occurring as floating material, but in a much smaller extent than for the Lower Saurian level. One bonebed was located for the Grippia Niveau. The material described represents both weathered surface material and bones that was preserved in situ in the excavated bonebed.

Even though the material are from two niveaus, the main focus of this study will be on the Grippia Niveau, where this paper provides the very first description of an *Omphalosaurus* bonebed.

The Grippia bonebed (Fig. 3) is a thin layer with a pebbly appearance, consisting of bones, fish remains and coprolites. XRD analysis of the Spitsbergen material shows that bones, coprolites and shark teeth are composed mainly of apatite. Overall in appearance the Grippia bonebed is almost identical to the Late Triassic “Rhaetic bonebeds” common in Rhaetian marine sediments of NW and central Europe (Suan et al. 2012). The Vendomdalen Member (Fig. 2) is like the Rhaetic bonebeds assumed to represent a transgressive sequence (Mørk et al. 1999; Korneisel et al. 2015). The Rhaetic bonebeds have been suggested as a result of a disturbance in the carbon and phosphorous cycles in the ocean, caused by major environmental changes (Suan et al. 2012). Increase of phosphate in shallow waters caused anoxic conditions, followed by phosphorous regeneration, so that vertebrate hard parts in coastal areas were well preserved (Korneisel et al. 2015).

The bones, teeth, fish remains and coprolites in the Grippia bonebed show a size range of a few μm up to 20 cm, where the bones are in various states of wear. The bonebed consists of bones in all conditions, from compressed and heavily eroded to perfect preservation in 3D. Common in the bonebed are shark teeth, fish remains, ichthyopterygian remains and *Omphalosaurus*. A surprising find was a fragment of a lungfish tooth-plate, since lungfishes are assumed mainly freshwater (Richter & Toledo 2008) and the Grippia bonebed is deposited in an open water environment (Mørk et al. 1999). This and the different weathering and size of the bones suggests that the Grippia bonebed is composed of distal transported material, brought from shallow to open water by storm events. This probably caused the mix of shallow water species together with more open water species as *Omphalosaurus*. Except for one small bivalve there are no invertebrates present in the Grippia bonebed and no signs of burrows from any benthic organism. This highly suggests that the conditions on the sea bottom were unfavorable for bottom life. The lack of pelagic vertebrates with aragonitic shells could be due to dissolution or replacement by phosphate. Bottom currents might have winnowed the material continuously, so that thin shelled fragments were crushed, while bones were only slowly eroded.

Stratigraphical log of Marmierfjellet, Spitsbergen

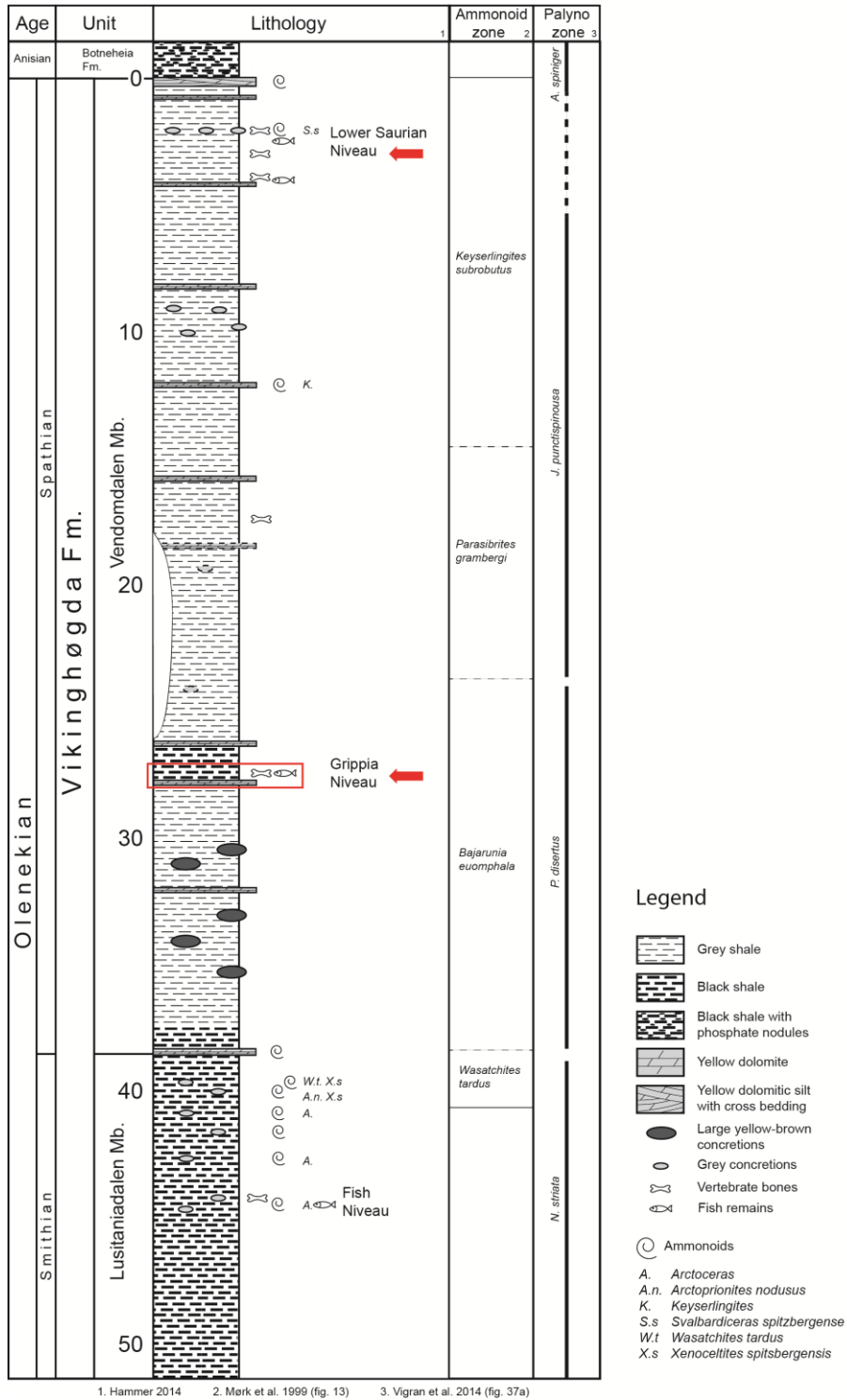


Figure 2: Stratigraphical log for the Vikinghøgda Formation at Marmierfjellet. The red box marks the position of the detailed log in Fig. 3.

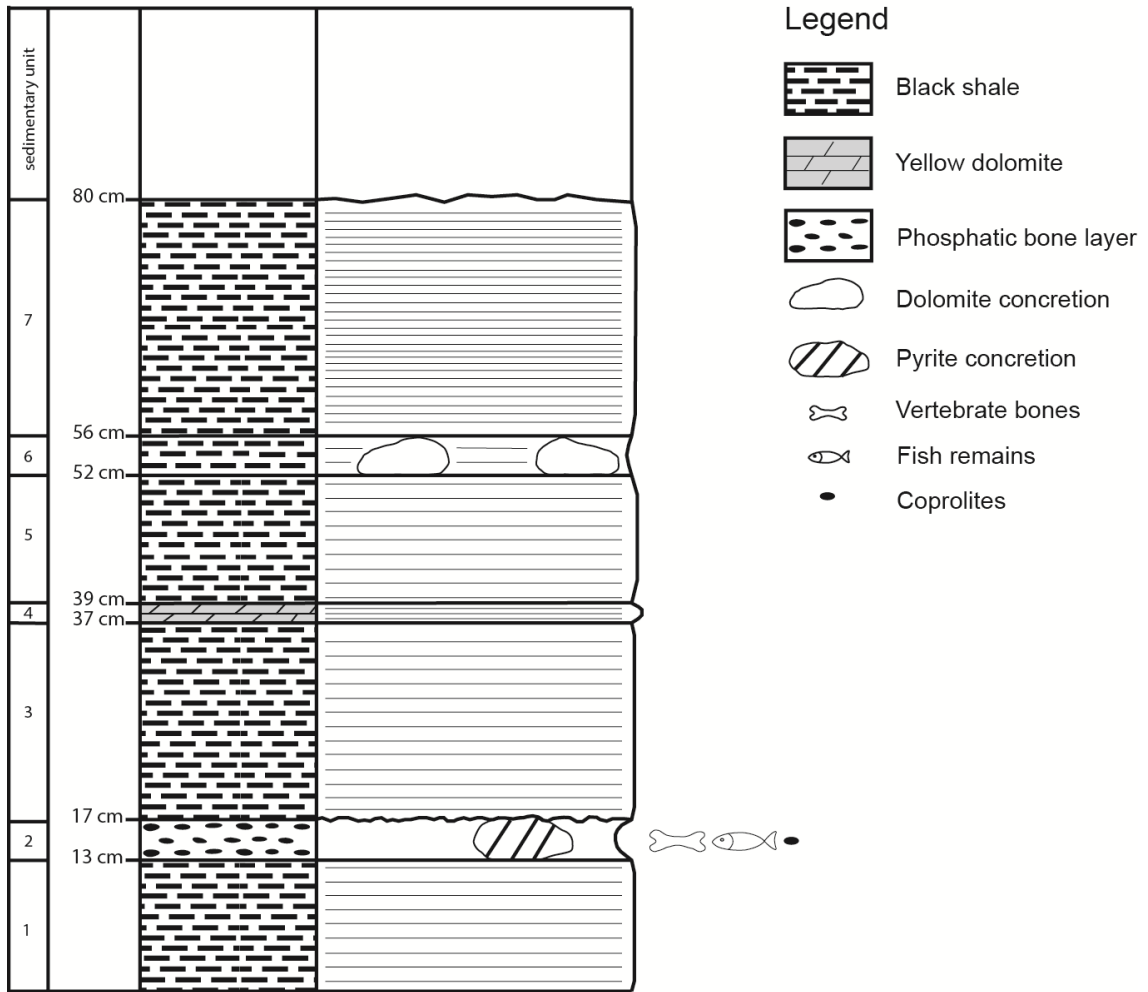


Figure 3: Detailed sedimentological log of the Grippia bonebed and surrounding sediments. Grippia bonebed is represented by sedimentary unit 2.

2. Material and methods

In this study, isolated bones of *Omphalosaurus* collected during fieldwork in 2014 and 2015 by the Spitsbergen Mesozoic Research Group have been examined. The material was collected from the Grippia Niveau and the Lower Saurian Niveau, Vendomdalen Member, at Marmierfjellet in central Spitsbergen. The bones are kept at the Natural History Museum, University of Oslo.

Material

Of all the material collected, 240 vertebrae centra was recognized as belonging to *Omphalosaurus* and could be placed within the different regions of the vertebral column. The centra was placed in the column based on the morphological trends in the well-known vertebrae column of the ichthyopterygian *Cymbospondylus* (Merriam 1908). 101 additional centra were identified as *Omphalosaurus*, but could not be placed in the vertebral column due to poor preservation. In addition more than 400 fragments of vertebrae centra are assumed to belong to *Omphalosaurus*. Of the tooth-bearing material, 18 dentaries and 7 premaxillae could be identified as *Omphalosaurus*, in different states of wear. More than 30 fragments of tooth-bearing bones were recognized as *Omphalosaurus*, but could not be identified as premaxilla or dentary.

The figured material consists of 17 vertebrae, 5 dentaries and 4 premaxillae, where 1 premaxilla and 2 dentaries are from the Lower Saurian Niveau, the remaining collected from the Grippia Niveau. Due to the large amount of material from this locality, only the best preserved bones are described in detail. For simplicity, the “Grippia bonebed” will be used for the material excavated from the bonebed while the niveaus will be used as reference for the floating material collected.

All premaxillae described were collected during fieldwork in 2014, where PMO 229.921, PMO 229.923 and PMO 229.924 are from the Grippia Niveau and PMO. 220.922 is from the Lower Saurian Niveau.

Of the dentaries, PMO 229.917 and PMO 229.919 are from the Lower Saurian Niveau, the first collected in 2014 and the latter in 2015. PMO 229.918 and PMO 229.920 are from the Grippia Niveau. PMO 229.918 was collected in 2014 and the rest in 2015. PMO 229.916 was excavated from the Grippia bonebed (Fig. 3).

Of the vertebrae PMO 229.908 and PMO 229.910 were collected in 2014 from the Grippia Niveau. PMO 229.903, PMO 229.904, PMO 229.905, PMO 229.906, PMO 229.907, PMO 229.909, PMO 229.911, PMO 229.912, PMO 229.913, PMO 229.914, PMO 229.915, PMO 230.135, PMO 230.136, PMO 230.137 and PMO 230.138 were collected in 2015 from the Grippia bonebed.

Dentaries and premaxillae were used in this study since they are the best recorded and easiest identifiable material of *Omphalosaurus*. Identification of the tooth-bearing bones are based on the Alpine specimen (MBG 1500) which is the only specimen described until now with complete premaxillae and dentaries in articulation (Sander & Faber 2003). For this thesis only teeth in the identifiable bones will be described and compared with teeth from the equivalent bone in other specimens.

The vertebrae were recognized as belonging to *Omphalosaurus* due to the very porous bone structure described by Sander and Faber (2003) which can be observed on fractured bone surfaces by using a hand lens. The cervicals and dorsals are deeply amphicoelous, as the vertebrae of the Alpine specimen described by Sander and Faber (2003).

Caution must be made when comparing the material, especially since the bones are collected from two different niveaus. What makes the material special are the great size range of the bones, as well as morphological differences between the specimens, which could be due to different species of *Omphalosaurus* or different ontogenetic stages. It must be taken into account that fish, amphibians and other ichthyopterygians and marine reptiles are found

within these niveaux. Therefore the material could be misinterpreted due to the unknown morphology of *Omphalosaurus*. Some material collected are heavily weathered and compressed, which could affect size measurements and interpretation of shape. The cancellous nature of the bones of *Omphalosaurus* is also worth considering, and the extreme concavity of some of the vertebrae could be due to collapse of the centra during compaction of the sediments. It is worth noting that the identified tooth-bearing bones could represent maxilla, vomers or palatines, as already discussed by Sander and Faber (2003). Since the Spitsbergen material is identified based on description and personal observation of the Alpine specimen (MBG 1500), premaxilla and dentaries will be used when describing the tooth-bearing bones. Other possibilities of tooth-bearing bones will be mentioned in the discussion. A study of the tooth enamel in SEM is needed to verify that, especially the smaller jaw fragments, belongs to *Omphalosaurus* and not another animal with similar dentition. SEM analysis and enamel microstructure description is beyond the scope of this thesis.

Fieldwork

The bones were collected as surface material for both the Grippia Niveau and the Lower Saurian Niveau. Additionally for the Grippia Niveau 7x1 meter of the bonebed was extracted, for study of both micro and macro fauna. The GPS-coordinates of the excavation site are UTM: N78.30521 E016.60118. Since the Grippia Niveau at this locality consists of bones, coprolites and fish remains held in a loose matrix of shale, the bonebed was collected systematically in quadrates of 1x1 meter in large plastic bags for further sieving at the lab.

Three plaster jackets were made to study the taphonomy of the bonebed as well as protecting large, fragile bones. A field jacket is made by removing the shale on top of the fossil, as well as around and below so that a “lip” can be formed for the plaster to fasten. Wet toilet paper is applied directly on the fossil to prevent that the plaster fasten to the bone, then plaster, burlap and metal rods is applied to strengthen the jacket. When the plaster is set the jacket is undercut and chisels are driven through the shale underneath to separate the jacket from the shale. The jacket is then flipped and the same process with toilet paper, plaster and burlap is applied to the underside.

Laboratory work

The preparation of the three small plaster jackets took place at the Natural History Museum, University of Oslo. The bonebed was exposed by removing the shale with a tweezer and a brush (Fig. 3). Bones and fish remains were freed from the matrix and cleaned with an ultrasonic cleaner and abrasive blasting with sodium bicarbonate. Broken pieces were glued together with the cyanoacrylate Paleobond (type Jurassic gel).

The material collected in bags was sieved through the fractions 2 mm, 1 mm, 0.5 mm, 0.25 mm and 0.06 mm, where only the material larger than 2 mm were used for this study. After drying, bones and fish remains were collected from the sieved material and broken pieces were glued.



Figure 4. One of the three plaster jackets collected from the Grippia bonebed at Marmierfjellet, Spitsbergen (Spathian). The larger piece is the right dentary PMO 229.916. Scale bar 5 cm, the bonebed is prepared from above.

Terminology

For the vertebral column, the different vertebral regions defined by Romer (1956) have been used for this study. The vertebrae centra are identified and placed in the vertebral column based on *Cymbospondylus* described by Merriam (1908). Otherwise, the terminology by McGowan and Motani (2003) has been used for the morphological descriptions of the vertebrae centra, jaw fragments and teeth.

Measurements

The different bones were measured and compared to each other and previously described specimens. Since the Alpine Specimen is the only preserved specimen with dentaries and premaxillae, the measurements was taken according to measurements by Sander and Faber (2003). The length was measured along the medial face from anteriormost to posteriormost, while the width was measured perpendicular to it from the lateralmost point to the medial face (Figs. 4C, 4D). The height of the premaxillae was measured perpendicular to the medial face, from the dorsalmost point on the triangular point to the medial surface (Fig. 4E).

The width and height of the vertebrae was measured as maximum values in anterior view, where the width is the lateral maximum and the height is the dorsoventrally maximum (Fig. 4A). The length is measured in lateral view, in the middle of the ventral and dorsal surface parallel to the notochordal foramen (Fig. 4B). All the measurements were taken with a caliper.

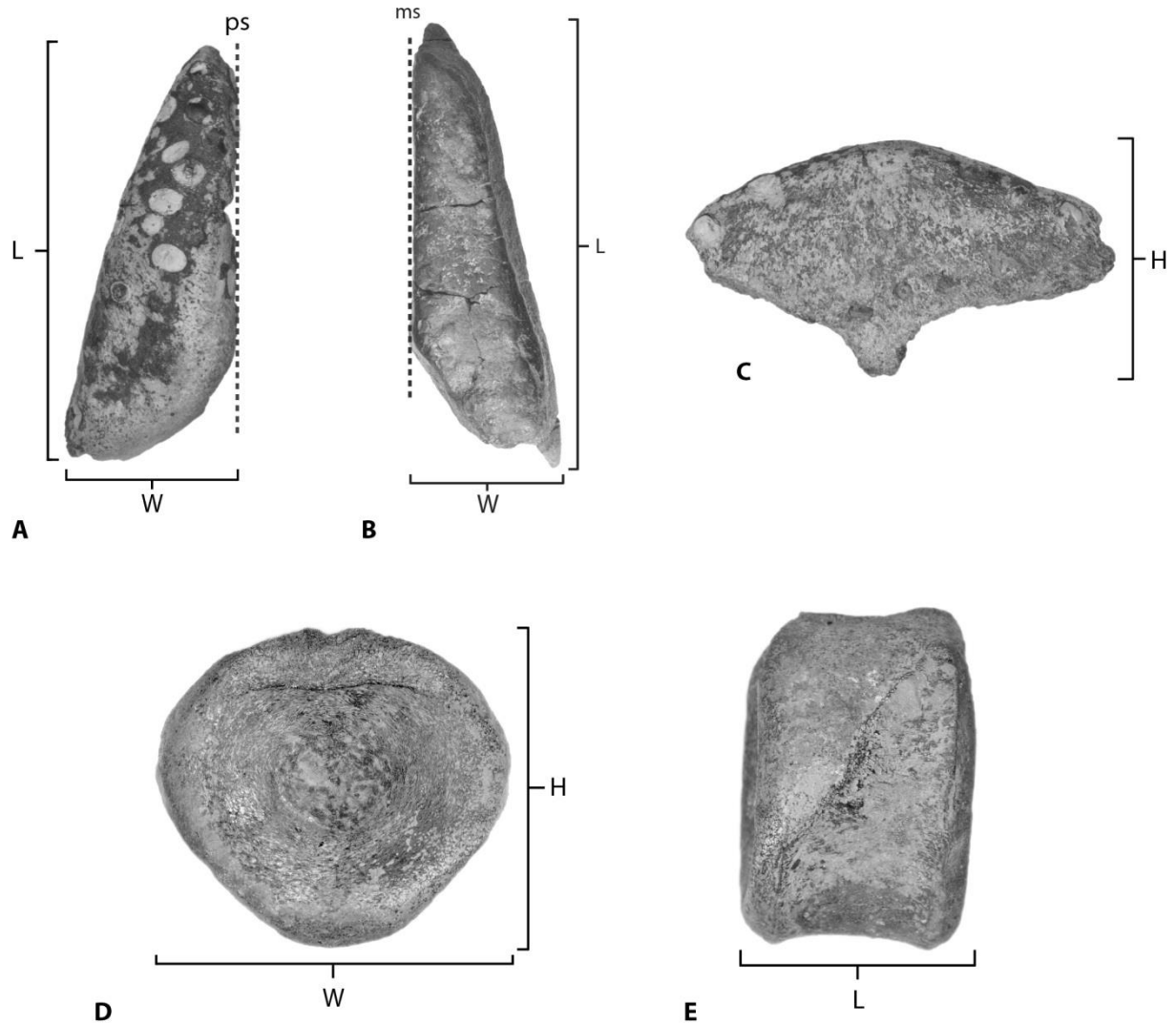


Figure 5. Measurements of the different bones of *Omphalosaurus* collected at Marmierfjellet, Spitsbergen (Spathian). **A**, premaxilla in ventral view. **B**, dentary in dorsal view. **C**, premaxilla in lateral view. **D**, Vertebrae centrum in anterior view. **E**, vertebrae centrum in lateral view. Bones not to scale. **Abbreviations:** **H**, height; **L**, length; **ms**, mandibular symphysis; **ps**, premaxillary symphysis; **W**, width.

Abbreviations used in tables and Figures

ap = anterior process, **aP** = apophysis, **aT** = anterior tooth, **D** = dentine, **dl** = dental laminae, **dP** = diapophysis, **E** = enamel, **em** = embayment, **fNa** = facet for the neural arc, **fNc** = floor of neural canal, **fo** = foramina, **fT** = functional teeth, **gr** = groove, **H** = height, **L** = length, **ms** = mandibular symphysis, **nF** = notochordal foramen, **os** = occlusal surface, **Pc** = pulp cavity, **pP** = parapophysis, **ps** = premaxillary symphysis, **rT** = replacement teeth, **tp** = triangular process, **vc** = vascular canals, **vK** = ventral keel, **W** = width, **Y** = Y-mark.

Institutional Abbreviations

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

PMU = Paleontologiska Museet, Uppsala University, Uppsala, Sweden

MBG = Museum Burg Golling, Golling near Salzburg, Austria

UCMP = Museum of Paleontology, University of California at Berkeley, Berkeley, USA.

3. Description

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758

DIAPSIDA Osborn, 1903

? ICHTHYOPTERYGIA Owen, 1840

OMPHALOSAURIDAE Merriam, 1906

OMPHALOSAURUS Merriam, 1906

Referred material:

Premaxillae: Grippia Niveau: PMO 229.921, PMO 229.923, PMO 229.924. Lower Saurian Niveau: PMO 229.922.

Dentaries: Grippia bonebed: PMO 229.916. Grippia Niveau: PMO 229.918, PMO 229.920. Lower Saurian Niveau: PMO 229.917, PMO 229.919.

Vertebrae centra: Grippia bonebed: PMO 229.903, PMO 229.904, PMO 229.905, PMO 229.906, PMO 229.907, PMO 229.909, PMO 229.911, PMO 229.912, PMO 229.913, PMO 229.914, PMO 229.915, PMO230.135, PMO 230.136, PMO 230.137, PMO 230.138, PMO 230.210. Grippia Niveau: PMO 229.908, PMO 229.910.

Additional material not pictured:

Premaxillae: PMO 230.339-341

Dentaries: PMO 230.342-354

Vertebrae centra: Atlases: PMO 230.358, PMO 230.355. Cervicals: PMO 230.357, PMO 230.800. Dorsals: PMO 230.356, PMO 230.359-414, PMO 230.600-602. Caudals: PMO 230.415-449, PMO 230.451-573.

Locality: West side of Marmierfjellet, northeast of Longyearbyen, Spitsbergen, Svalbard, Norway. Grippia bonebed: UTM: N78.30521 E016.60118

Horizon and stage: Vendomdalen Member, Vikinghøgda Formation, Spathian, late Early Triassic.

3.1 Premaxillae

Of the premaxillae, PMO 229.922 (Figs. 6B) is the most complete, while PMO 229.921 consists of the posterior half of the premaxilla (Figs. 6A). PMO 229.924 (Figs. 6C) and PMO 229.923 (Figs. 6D) are missing the anterior and posterior end, as well as being heavily corroded in ventral view. PMO 229.922 is the only premaxilla described that was collected from the Lower Saurian Niveau, the rest collected from the Grippia Niveau. The characteristics used to identify and differ the premaxillae from the dentaries, are the convex occlusion surface and a triangular ascending process in dorsal view, as described for the Alpine specimen (MGB 1500; Sander and Faber (2003)).

PMO 229.922 (Figs. 6B) was measured 49.5 mm anteroposteriorly long and 17.8 mm mediolaterally wide, with 29.4 mm in dorsoventral maximum. The only measurable surface of PMO 229.921 (Figs. 6A) is the dorsoventral maximum, being 48.1 mm. If assuming the shape of PMO 229.921 is similar to that of PMO 229.922, this suggests an anteroposteriorly length of approximately 134 mm for PMO 229.921. The right premaxilla of the Alpine specimen (MBG 1500) was measured by Sander and Faber (2003) as 205 mm anteroposteriorly long and 65 mm mediolaterally wide. This is the only specimen described until now with premaxilla complete. The rest of the premaxillae in the Spitsbergen collection are too fragmented to be measured.

In ventral view the premaxilla has an almost elongated triangular shape. The lateral side in ventral view is the anteroposterior longest in the triangle, the posteromedial the shortest. Anteriorly the medial side has an 23° angle to the lateral side in PMO 229.922 (Fig

6B1), while in the other specimens this angle is not possible to measure. The ventral surface is convex and show tooth crowns in various states of wear, as seen in PMO 229.922 (Figs. 6B1, B2, B4). A convex tooth-bearing ventral surface was also described for the Alpine specimen (MBG 1500), which according to Sander and Faber (2003) fits well the concave surface of the tooth-bearing bones in the lower jaw (see below). The teeth are located mainly on the anterior half, while posteriorly only along the lateral margin in PMO 229.922 (Fig 6B1), where in PMO 229.921 (Fig. 6A1) the teeth are covering the entire posteroventral surface.

The tooth-bearing ventral side, including the slopes towards the medial and posteromedial sides, is the only finished surface of the premaxilla, as observed in PMO 229.922 (Figs. 6B1, B2). A finished surface means a smooth periosteum of the bone, which is usually expected on all surfaces except in bone joints and sutures between bones. In *Omphalosaurus* the other surfaces show unfinished porous bone, lacking the periosteum normally covering the outer surface of bone. The same was observed in the Alpine specimen (MBG 1500) by Sander and Faber (2003). Corrosion of finished surfaces was suggested a possibility of this peculiar appearance, but being present in two specimens' corrosion seems unlikely.

The medial surface of the premaxilla show particularly well the convex ventral surface (Figs. 6B2, C2). The premaxillae are at the widest dorsoventrally in the middle, where a triangular process is located, similar to the Alpine specimen (MBG 1500) (Sander & Faber 2003). The process show dorsoventral striations, especially in PMO 229.921 (Fig. 6A2). Anterior and posterior to the process the dorsoventral width is decreasing until reaching minimum width anteriorly and posteriorly, as seen in PMO 229.922 (Fig. 6B2), PMO 229.921 (Fig. 6A2) and PMO 229.924 (Fig. 6C2). Anterior to the process a deep and short embayment is visible, while posterior to the process the embayment is more shallow and longer. From PMO 229.922 (Fig. 6B2) it looks like the embayments are actually the floor where the tooth growth begins in the bone, the dental laminae.

The teeth are exposed in lateral view on the medial surface of the premaxilla, as in the Alpine specimen (MBG 1500). This surface was suggested as an active grinding surface by Sander and Faber (1998), but according to Sander and Faber (2003) it is more likely that

the medial sides of the two premaxillae met in the sagittal plane of the upper jaw. The medial side is best preserved in PMO 229.922 (Fig. 6B2), where the dorsal part of the medial surface has the finished surface described above, where the teeth are grinded down similar to the ventral surface. The rest of the medial face is corroded, the surface is not visible. The finished surface of the dorsal part in medial view indicates that at least parts of this assumed premaxillary symphysis was an active grinding surface, due to the polished cross section of the tooth crowns in lateral view. The medial surface is rather corroded in all other specimens of the Spitsbergen material.

In dorsal view a foramen is observed posterior to the triangular process in PMO 229.921 (Fig. 6A3), PMO 229.922 (Fig. 6B3) and PMO 229.923 (Fig. 6D3). Another foramen is located on the lateral side of the process, which is more prominent in PMO 229.921 (Fig. 6A3) and PMO 229.922 (Fig. 6B3). A ridge runs anteroposterior on the lateral surface in dorsal view, which is connected to the triangular process in the middle, as seen most clearly in PMO 229.922 (Fig. 6B3).

The lateral view of the premaxillae shows striations in the bone surface in a fan-like radiation from the convex surface ventrally. This is most prominent in PMO 229.924 (Fig. 6C3). A narrow groove is visible running parallel to the ventral margin, as seen in PMO 229.921 (Fig. 6A4), and barely visible in PMO 229.922 (Fig. 6B4). The groove is not interrupting the fan-like striations from the convex ventral surface. The foramen on the triangular process is also visible in lateral view, where in PMO 229.922 (Fig. 6B4) two more foramina are located posterior to the first one. In PMO 229.921 (Fig. 6A4) a possible foramen is located in the posterior upper corner of the triangle shaped process, creating a groove posterior to the process. This differs from PMO 229.921 (Fig. 6B4) where a smooth bend is visible posterior to the process.

Since PMO 229.922 (Figs. 6B) is assumed to be a nearly complete premaxilla, the ventral surface of the premaxilla has been mirrored to get an idea of the occlusal surface and how the two premaxillae might have met in the sagittal plane (Fig. 7). Even though the Alpine specimen re-described by Sander and Faber (2003) is measured to have an anteroposterior length more than four times longer than this specimen, the shape of the premaxillae looks fairly similar in occlusal view. What differ the most between the two is the arrangement of

the teeth, as well as the Alpine specimen being longer and more slender, the Spitsbergen premaxillae is much wider posteriorly than anteriorly. Length/width ratio of the ventral surface of PMO 229.921 is calculated as 2.8, where for the Alpine specimen a length/width ratio of 3.15 is calculated using the measurements of Sander and Faber (2003).

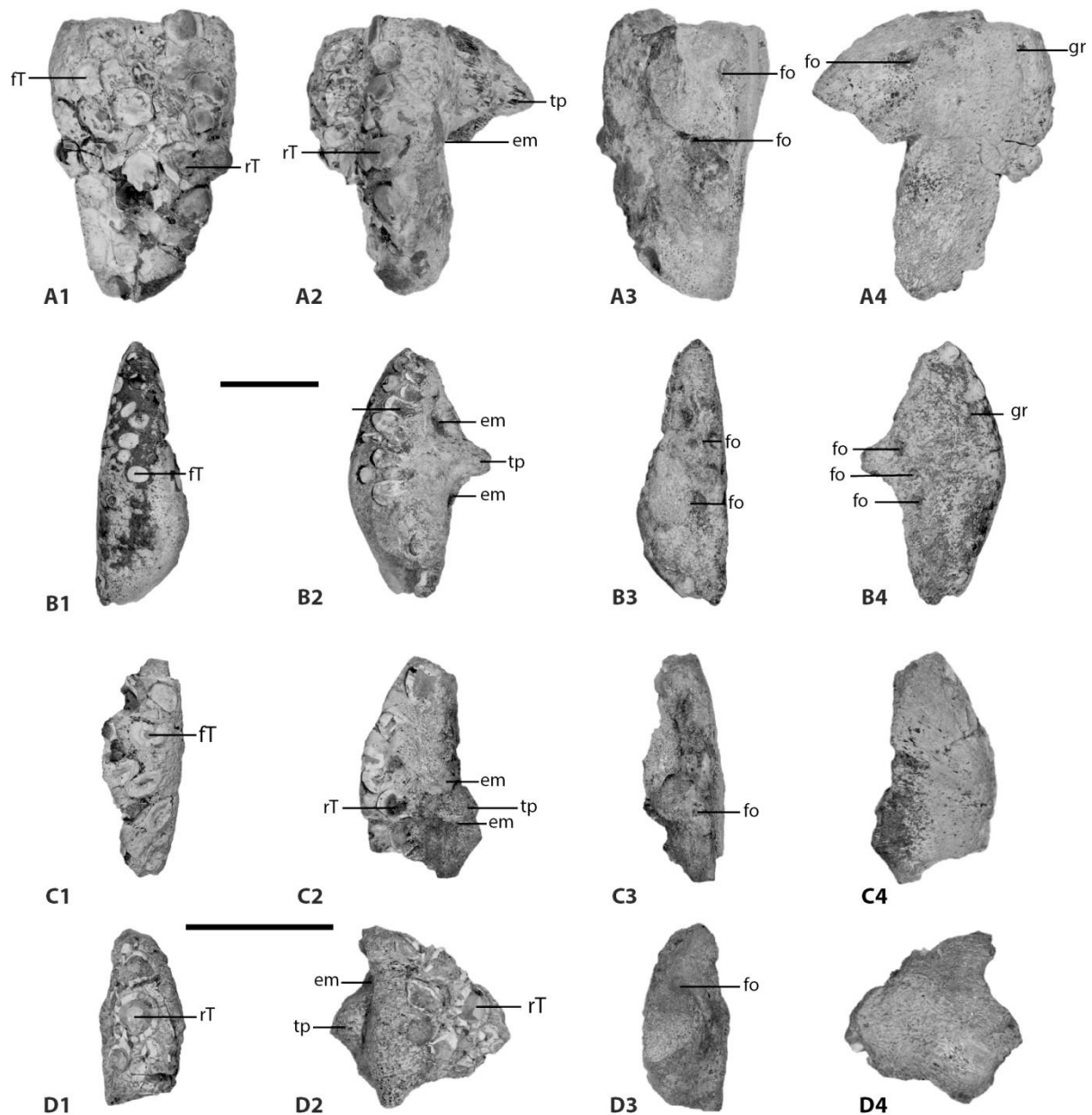


Figure 6: Premaxillae of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, PMO 229.921, left premaxilla. A1. Ventral view, A2. Medial view, A3. Dorsal view and A4. Lateral view. **B**, PMO 229.922, left premaxilla. B1. Ventral view, B2. Medial view, B3. Dorsal view and B4. Lateral view. **C**, PMO 229.924, left premaxilla. C1. Medial view, C2. Dorsal view and C3. Lateral view. **D**, PMO 229.923, right premaxilla. D1. Medial view, D2. Dorsal view and D3. Lateral view. A, B scale bar 2 cm; C, D scale bar 2 cm. Anterior is to the top for all photographs. Only one tooth of each type is marked in the different views of the premaxilla to exemplify. **Abbreviations:** **em**, embayment; **fo**, foramina; **ft**, functional teeth; **gr**, groove; **rT**, replacement teeth; **tp**, triangular process.

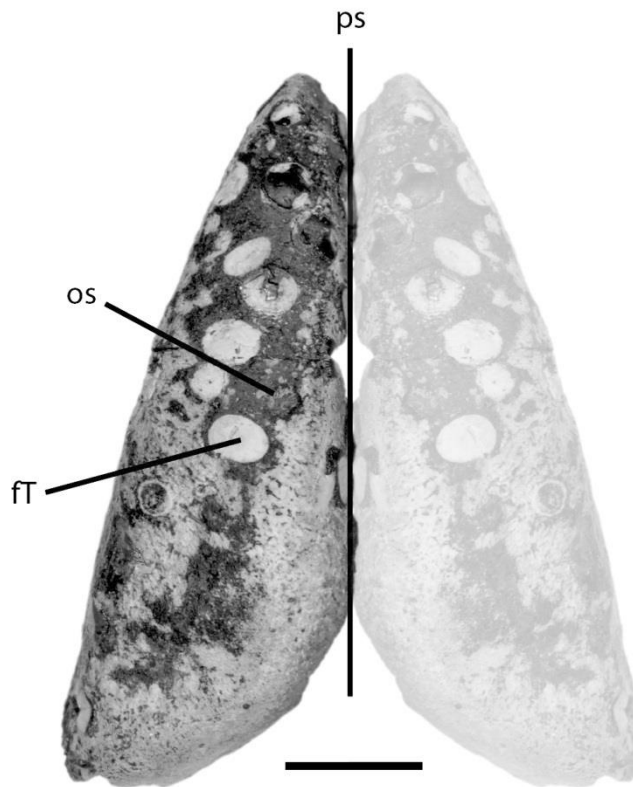


Figure 7. Mirrored ventral view of left premaxilla PMO 229.922 of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). Scale bar 2 cm, anterior is to the top. Only one tooth is marked to exemplify.
Abbreviations: **ft**, functional teeth; **os**, occlusal surface; **ps**, premaxillary symphysis.

3.2 Dentaries

Of the dentaries, PMO 229.916 (Figs. 8) is complete, PMO 229.919 (Figs. 10C) is missing the very anterior and posterior parts, PMO 229.917 (Figs. 9) is complete but heavily weathered, while PMO 229.918 (Figs. 10A) and PMO 229.920 (Figs. 10B) consist of the anteriormost part only. The characteristics used to identify the dentaries is concave dorsal surface with a triangular outline and teeth mainly located along the symphysis, as described for the Alpine specimen (MBG 1500) (Sander & Faber 2003). A single tooth anteriormost on the dentary seems to be a characteristic of the dentaries observed from the Spitsbergen material, and is used to identify the more corroded specimens.

PMO 229.916 (Figs. 8) was measured as 210 mm anteroposteriorly long and 60 mm mediolaterally wide, while PMO 229.017 (Figs. 9) showed an anteroposteriorly length of 157 mm and a mediolaterally width of 79 mm. The smaller PMO 229.919 (Figs. 10C) was measured as 51 mm anteroposteriorly long and 20 mm mediolaterally wide, but this specimen is lacking the anteriormost and posteriormost part, so that the measurement of the length is not as exact as for the other two. In the Alpine specimen (MBG 1500) the right dentary was measured as 285 mm anteroposteriorly long and 85 mm mediolaterally wide, and the left one 287 mm anteroposteriorly long and 80 mm mediolaterally wide (Sander & Faber 2003). Dentaries of *Omphalosaurus* have also been described from the Nevada specimen *O. nettarrhynchus* (Mazin & Bucher 1987) and the holotype *O. nevadanus* (UCMP 8281) (Merriam 1906; Mazin 1986), but are not preserved complete in these specimens.

In dorsal view the dentaries have an elongated, triangular shape, as described for the Alpine specimen and the holotype of *Omphalosaurus* (Merriam 1906; Sander & Faber 2003). Of the sides composing the triangle, the lateral side is the longest, the posteromedial the shortest, while the third side is the entire length of the symphysis. The Alpine specimen (MBG 1500) was first misinterpreted to have a V-shaped arrangement of the dentaries (Sander & Faber 1998) but from comparing it with *O. nevadanus* (UCMP 8281) from Nevada, this was found to be a result of disarticulation of the long, rather loose, symphysis (Sander & Faber 2003). The dorsal surface is concave, which is most prominent in specimen PMO 229.916 (Fig. 8) and PMO 229.919 (Figs. 10C). This concave dorsal occlusion surface is also observed in the Alpine specimen (MBG 1500), and is assumed to have met the convex ventral occlusion surface of the premaxilla (Sander & Faber 2003).

PMO 229.917 has a slightly convex lateral edge in dorsal view, where PMO 229.916 is more concave. The anterior part of PMO 229.916 is slightly rounded laterally in dorsal view, where in PMO 229.918 (Fig. 10A1) and PMO 229.920 (Fig. 10B1) the lateral side has a 15° angle to the symphysis. The dentary widens mediolaterally from anterior to posterior, until the end of the symphysis where the width is at a maximum perpendicular to the symphysis.

The posteromedial side of PMO 229.916 has a 50° angle from the posterior part of the symphysis towards the posteriormost end. The teeth are concentrated along the

symphysis and the medial posterior margins, as described for the Alpine specimen (MBG 1500) and the holotype from Nevada (UCMP 8281) (Sander & Faber 2003). In medial view of the symphysis the replacement teeth are visible in lateral view, also seen in PMO 229.919 (Fig. 10C2). In the larger dentaries this side is heavily corroded but the articulation surface of the symphysis is visible in PMO 229.916 (Fig. 8B) and PMO 229.918 (Fig. 10A2). In PMO 229.919 (Fig. 10C2) this side shows a smooth surface with stacked teeth, which differs from the other specimens. In PMO 229.916 (Fig. 8B) and PMO 229.918 (Fig. 10A2) the dorsal part of the medial surface is smooth but with dorsoventrally oriented ridges in the bone surface.

The ventral surface is well preserved in PMO 229.916 (Fig. 8C), where a massive ridge runs from the anterior tip along the lateral side towards the posterior end. Posteriorly this ridge slopes into a massive groove, dorsoventrally deepest at the posteriormost end. In the ventral part of the medial side of PMO 229.916 (Fig. 8C) and PMO 229.918 (Fig. 10A4) dorsoventrally striations are visible in the bone, assumed to be vascular canals.

In lateral view the concavity of the dorsal surface is clearly visible. Anteriorly a ventral process makes the anteriormost point of the dentary, also observed in PMO 229.916 (Fig. 8B) and PMO 229.920 (Fig. 10B4). Just dorsal to this process a single tooth is pointing anteriorly. This is present in PMO 229.916, PMO 229.918, PMO 229.920 and PMO 229.917. PMO 229.918 is anteriorly a little more rounded and wider dorsoventrally than PMO 229.916, which might be due to compression.

As for the premaxillae, the dentaries have been mirrored to get an impression of the mandible (Figs. 11). Five different shapes are distinguished in dorsal view of the dentaries. PMO 229.916 (Fig. 11A) is long and slender, similar to the Alpine specimen and the holotype from Nevada, only differing in the posteriormost part which is slightly wider. PMO 229.917 (Fig. 11B) is much wider mediolaterally and shorter anteroposterior compared to PMO 229.916, even though the length of the symphysis is similar. PMO 229.918 (Fig. 11C) and PMO 229.920 (Fig. 11D) is similar in shape and size, being mediodorsally thinner and pointed anteriorly than the other specimens. Still, these specimens consist of the anterior part only, so that the posterior part cannot be compared with the other specimens. PMO 229.919 (Fig. 11E) is much smaller, as well as having sharp and defined edges, especially between

the dorsal and medial surfaces. Compared to PMO 229.916 (Fig. 11A) the lateral side is also much thinner dorsoventrally. Whether these differences are due to different species, individual variation or growth stages are uncertain. It is worth noting that PMO 229.917 and PMO 229.919 are from the Lower Saurian Niveau, while the rest is collected from the Grippia Niveau and the Grippia bonebed. Length/width ratio is measured as 3.5 for PMO 229.916, 2.0 for PMO 229.917 and 2.6 for PMO 229.919. For the Alpine specimen re-described by Sander and Faber (2003) the length/width ratio is 3.6.

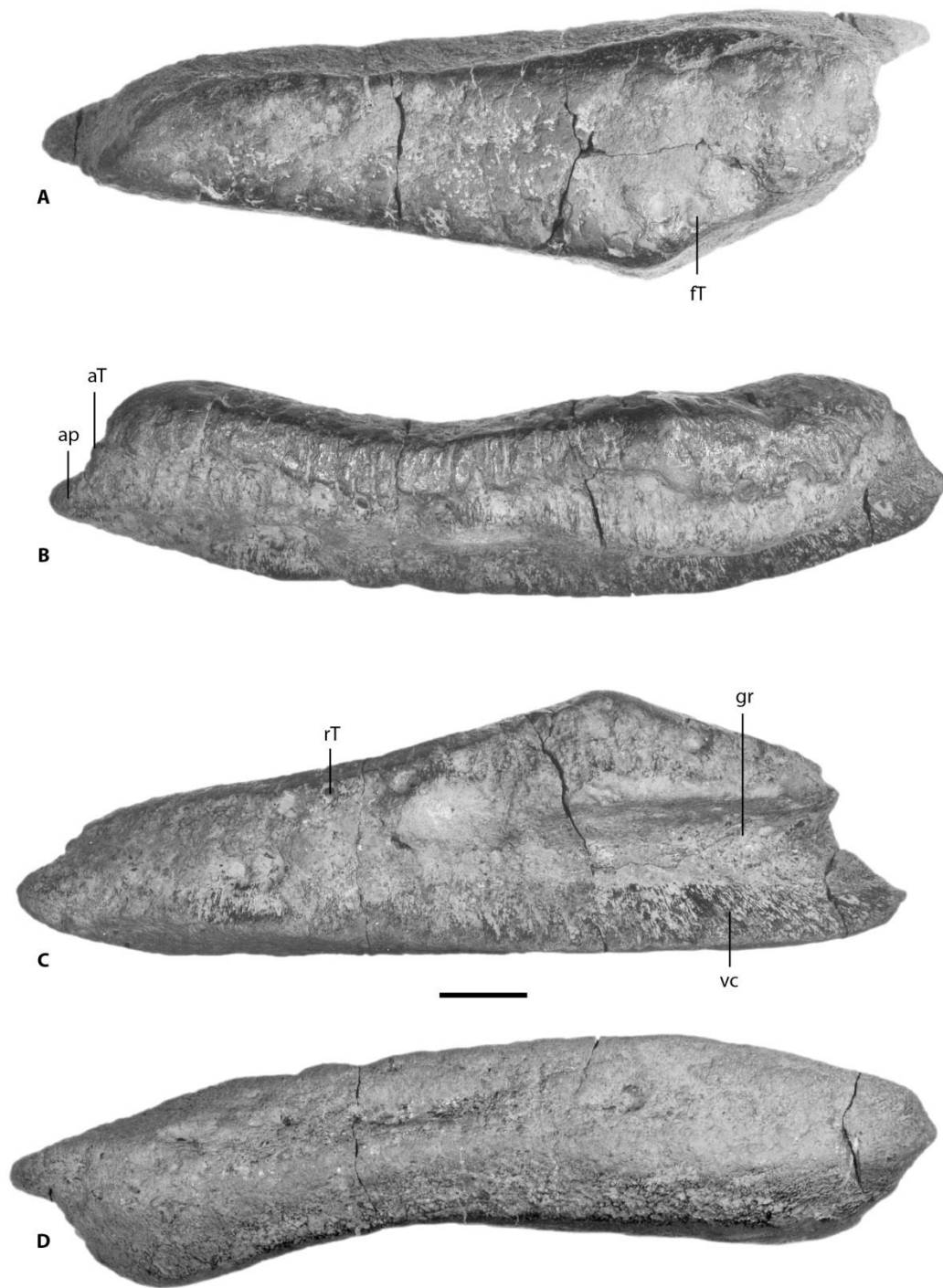


Figure 8. PMO 229.916, right dentary of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A.** Dorsal view. **B.** Medial view. **C.** Ventral view. **D.** Lateral view. Scale bar 2 cm, anterior is to the left for all photographs. **Abbreviations:** **ap**, anterior process; **aT**, anteriormost tooth; **fo**, foramina; **ft**, functional teeth; **gr**, groove; **rT**, replacement teeth; **vc**, vascular canals.

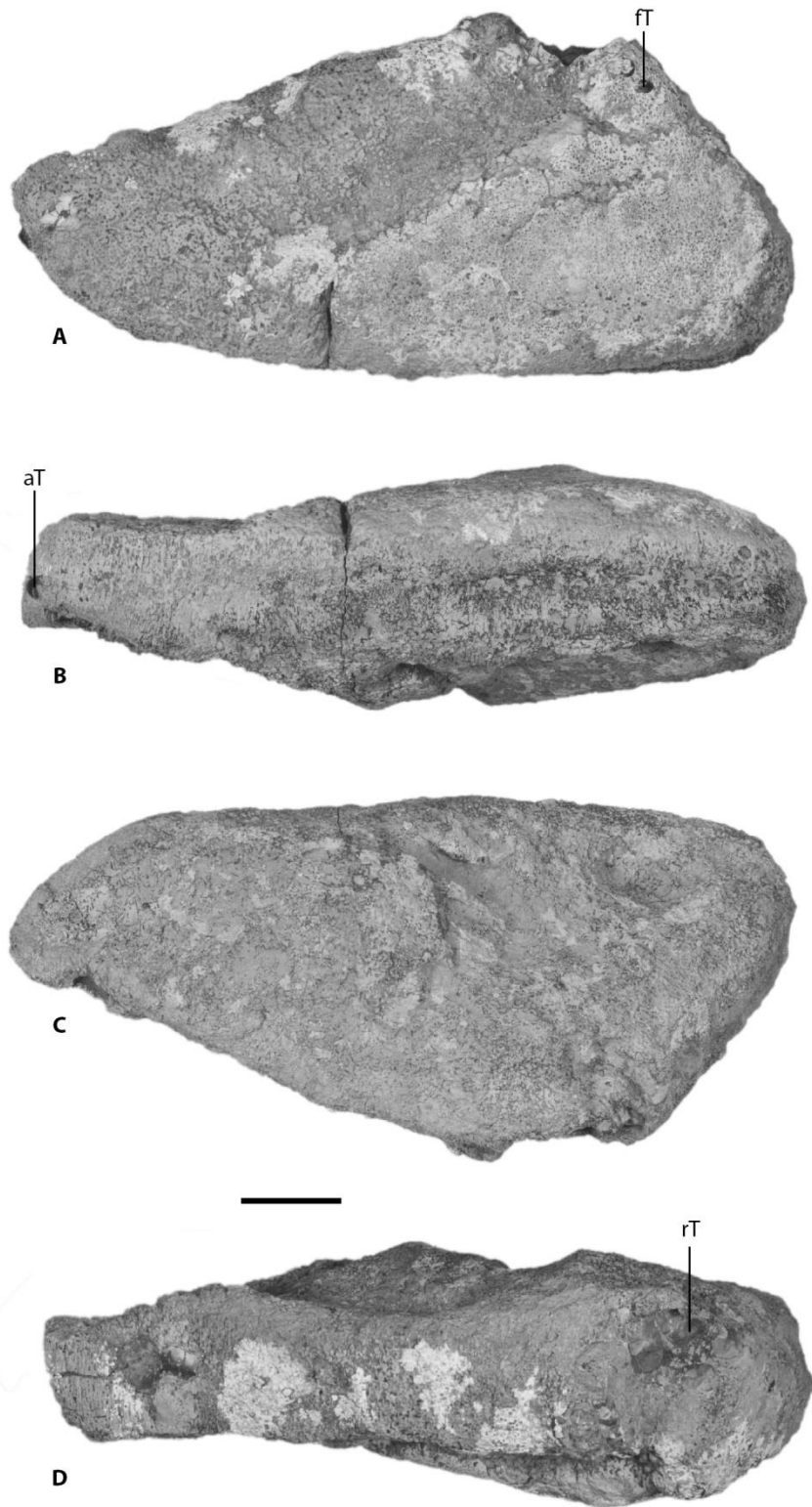


Figure 9. PMO 229.917, left dentary of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, Dorsal view. **B**, Medial view. **C**, Ventral view. **D**, Lateral view. Scale bar 2 cm, anterior is to the left for all photographs. **Abbreviations:** **aT**, anterior tooth; **fT**, functional teeth; **rT**, replacement teeth.

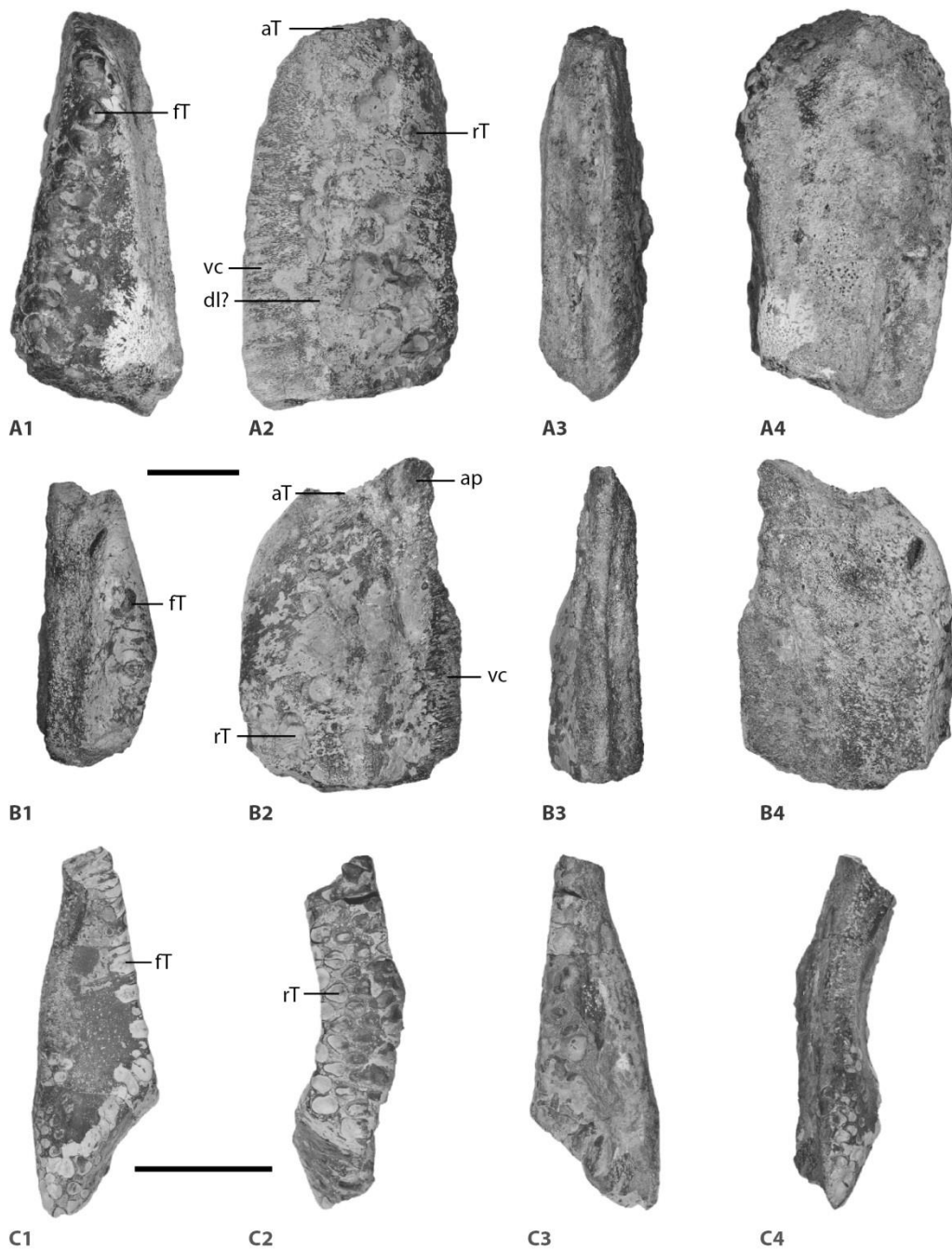


Figure 10. Dentaries of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, PMO 229.918, right dentary. A1. Dorsal view, A2. Medial view, A3. Ventral view and A4. Lateral view. **B**, PMO 229.920, left dentary. B1. Dorsal view, B2. Medial view, B3. Ventral view and B4. Lateral view. **C**, PMO 229.919, left dentary. C1. Dorsal view, C2. Medial view, C3. Ventral view and C4. Lateral view. A, B scale bar 2 cm; C, D scale bar 2 cm. Anterior is to the top for all photographs. **Abbreviations:** **ap**, anterior process; **aT**, anterior tooth; **dl?**, dental laminae; **ft**, functional teeth; **rT**, replacement teeth; **vc**, vascular canals.

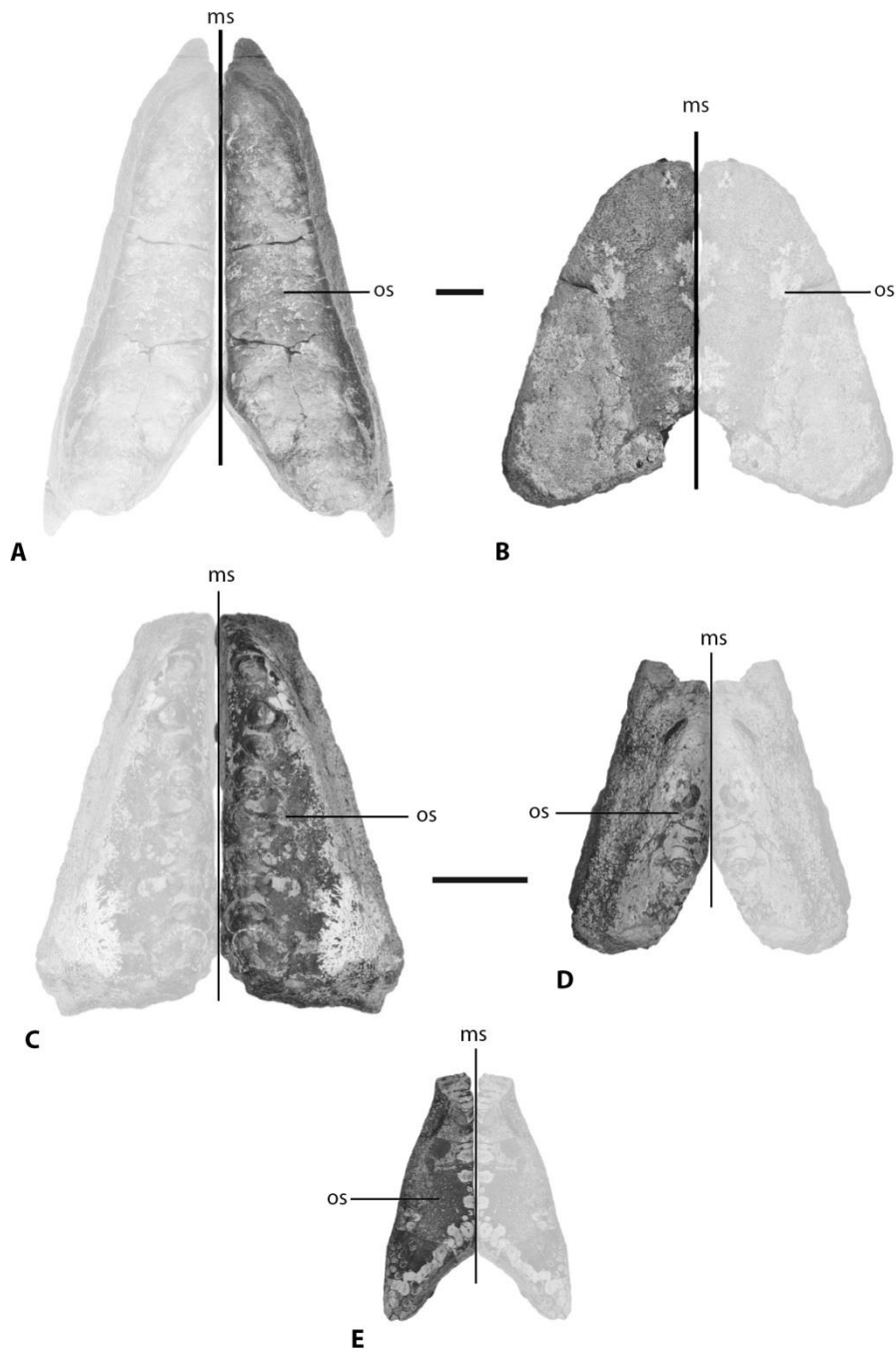


Figure 11. Mirrored dentaries in dorsal view showing different mandible shapes of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, right dentary PMO 229.916. **B**, left dentary PMO 229.917. **C**, right dentary PMO 229.918. **D**, left dentary PMO 229.920. **E**, left dentary PMO 229.919. A, B scale bar 2 cm; C, D, E scale bar 2 cm. Anterior is to the top for all photographs. **Abbreviations:** **ms**, mandibular symphysis; **os**, occlusal surface.

3.3 Dentition

The **premaxillary teeth** can be observed on the occlusal surface and in medial view of the premaxillae (Fig. 6). For PMO 229.922 (Fig. 12A, B) most of the teeth exposed in ventral view are worn down to the bone surface, so that only cross sections of the lower crowns are visible (Fig. 12A). The various stages of wear was suggested by Sander and Faber (2003) as a result of the irregular packing of the mature teeth in the bone. Two teeth have parts of the enamel cap preserved, showing an irregular surface structure. The cross section of the teeth show different shapes of the dome, which for PMO 229.922 appear as round, egg-shaped, elongated oval and irregular (Fig. 12A). In some of the cross sections of the crowns, structures resembling growth rings are visible. The maximum diameter of the lower tooth crowns in PMO 229.922 varies between 2 and 5 mm, where the larger teeth seems to be located anteriorly between the medial and lateral surface, as well as on the medial surface as seen in lateral view. The teeth are irregularly spaced, most densely packed anteriorly, spreading out along the medial and lateral margins posteriorly. The teeth of *Omphalosaurus* have previously been described as occurring in rows (Merriam 1906; Merriam & Bryant 1911; Wiman 1916; Mazin 1986), but distinct rows cannot be distinguished in any of the specimens earlier described (Wiman 1910; Motani 2000; Sander & Faber 2003) or in any of the tooth-bearing bones from Spitsbergen.

The dental lamina is visible in medial view of PMO 229.922 (Fig. 6B2). According to Sander and Faber (2003) the teeth forms along the dental laminae then spread out moving towards the occlusal surface, where the tooth-bearing field is much wider. The teeth located close to the dental laminae in PMO 229.922 have a rather dorsoventrally tall pulp cavity that gets entirely filled with dentine moving towards the occlusion surface (Fig. 12 B). The replacement teeth are all more or less globular in lateral view, where some are more pointed and drop shaped, than others that are more rounded and elongated. According to Sander and Faber (2003) the teeth of *Omphalosaurus* seems to both change in shape and orientation moving from the dental laminae towards the occlusion surface, due to resorption. The micro-unit enamel also differs between replacement teeth and functional teeth, indicating enamel maturation through the bone (Sander & Faber 2003), which could explain the different appearance of the replacement teeth from the dental laminae towards the occlusion surface.

The roots are not distinctly separated from the crown, which according to Sander and Faber (2003) is due to the continuous bulbous shape of the dentine core.

In PMO 229.921 (Fig. 12C) only a small part of the occlusion surface is preserved, showing teeth in various states of wear. In this specimen the teeth are more densely packed than in PMO 229.922 and the teeth seem to grow into each other, resulting in an irregular shape of the tooth crowns in cross section. Most of the enamel is gone on the teeth preserved on the occlusal surface, but the little preserved is along the margins of the crown, showing the typical “orange-peel structure” as described by Sander and Faber (2003) (Fig. 12B). The cross-section of the tooth crowns has a maximum diameter between 5 and 10 mm in PMO 229.921. In the Alpine specimen (MBG 1500) the crown diameter of the premaxillary teeth was measured 7-21 mm (Sander & Faber 2003). It is worth noting that the premaxillae of the Alpine specimen is almost twice as large as PMO 229.921, and that PMO 229.921 is only the posterior half of the premaxilla, so that larger teeth could have been present on the anterior part.

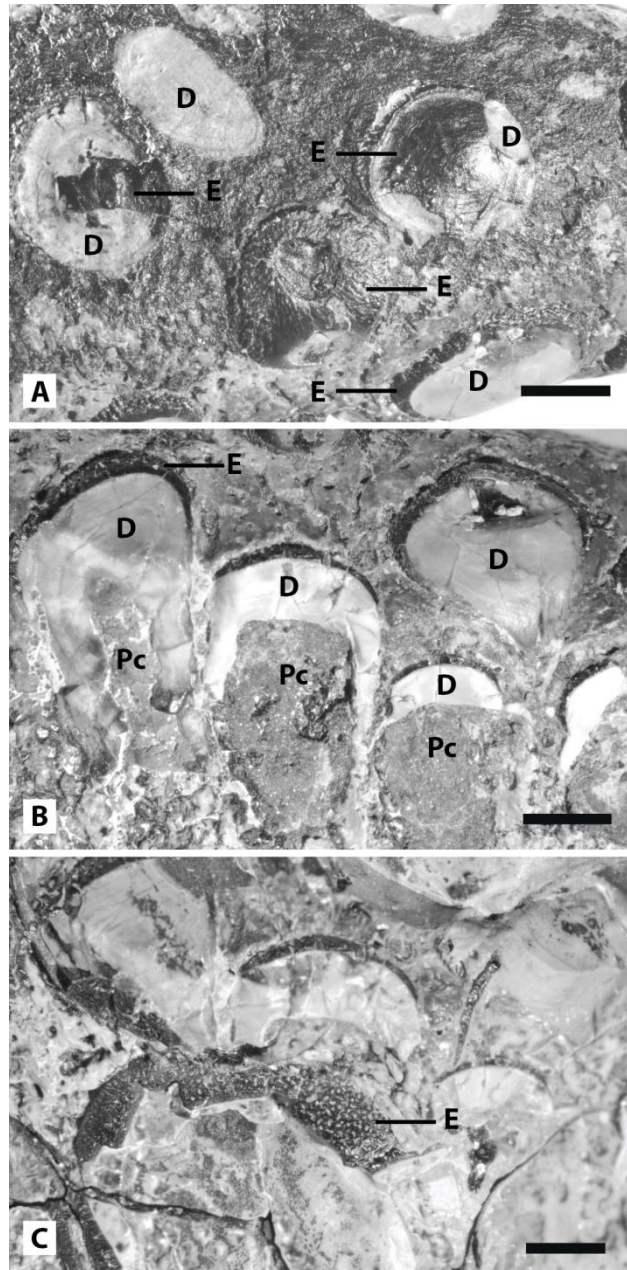


Figure 12. Premaxillary teeth of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, occlusal view PMO 229.922. **B**, medial view PMO 229.917. **C**, occlusal view PMO 229.921. Scale bar 2 mm.

Abbreviations: **D**, dentine; **E**, enamel; **Pc**, pulp cavity.

The **dentary teeth** in PMO 229.916 are not easily visible at the occlusion surface due to preservation and heavy wear. The same is observed in the holotype (UCMP 8281), which in addition to be incomplete contains little information of the morphology and arrangement of the teeth in the dentaries (Sander & Faber 2003). The tooth crowns are visible on a few of

the teeth, showing a rounded crown with the typical “orange-peel structure”, similar to the dentition described from the Alpine specimen (MBG 1500) (Sander & Faber 2003). The maximum diameter of the crowns in cross section of the Spitsbergen material varies between 6 and 11 mm, which are fairly similar to the size range in the Alpine specimen that was measured as 3.5 – 11 mm. By comparing the size of the tooth-bearing bones and the size of the teeth in the Spitsbergen material, it seems like the teeth are generally larger and more irregular in size for the premaxillae than the dentaries. This was also observed by Sander and Faber (2003) for the Alpine specimen (MBG 1500). One tooth is pointing anteriorly, as typical for the dentaries. This is the best preserved tooth in PMO 229.916 (Fig. 13A). The teeth are mainly located irregularly along the symphysis and medioposterior surface, and it seems like the teeth covered surface is wider in the premaxillae, which is peculiar since the convex surface of the premaxilla meets the concave occlusion surface of the dentaries. The replacement teeth are not very visible in medial view, possibly due to corrosion. PMO 229.918 has a few anteriorly located teeth where the tooth crowns are preserved with the “orange peel structure” (Fig. 13B). The bases of the crowns at the occlusal surface are irregular and densely packed. In this specimen some of the replacement teeth are visible in medial view, where the dentine replaces the pulp cavity towards the occlusion surface (Fig. 13C), as described for the premaxillary teeth in PMO 229.922. The teeth of PMO 229.918 have a diameter from 4-10 mm.

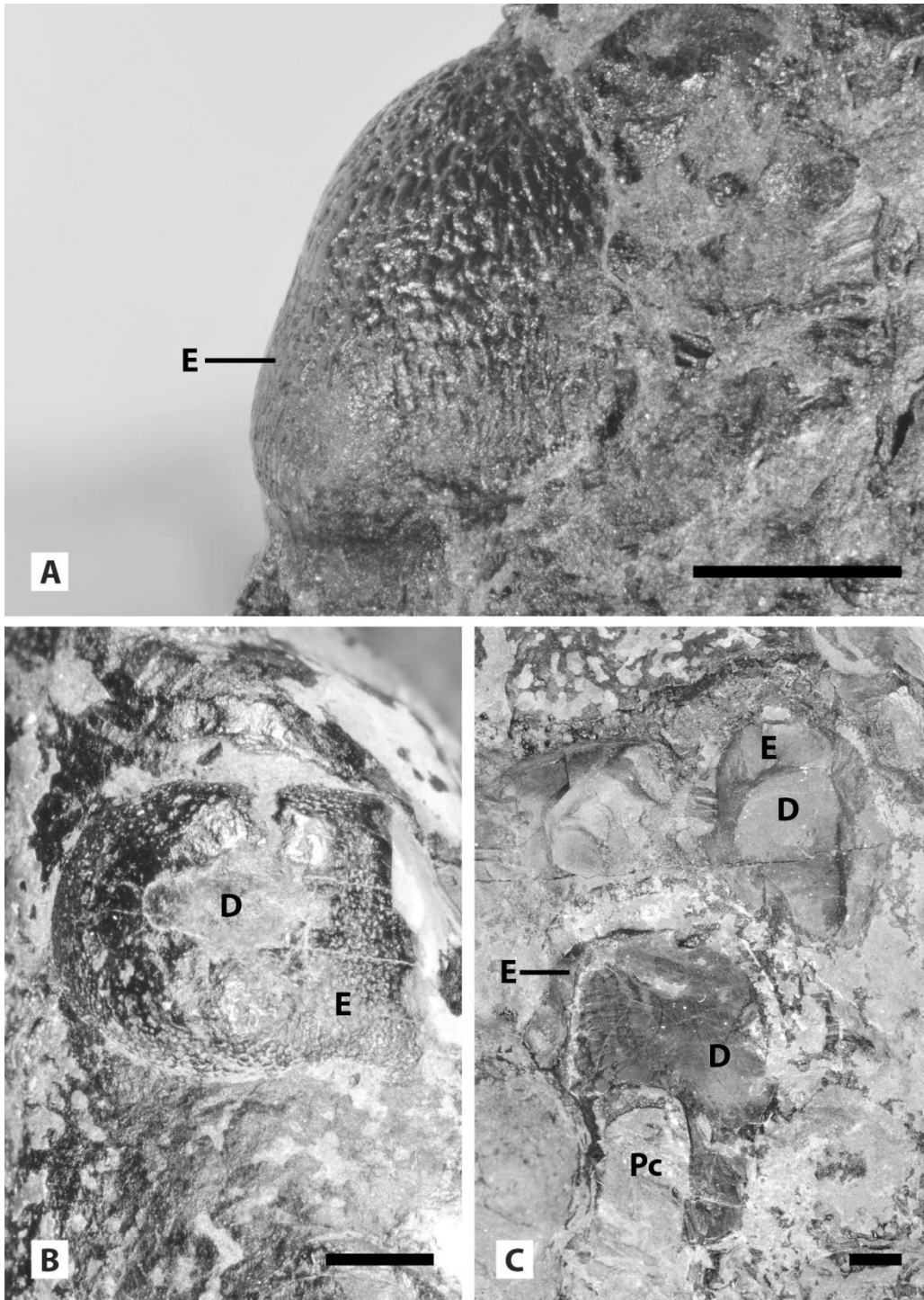


Figure 13. Dentary teeth of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, anteriormost tooth in lateral view of PMO 229.916. **B**, occlusal view PMO 229.918. **C**, medial view PMO 229.918. Scale bar 2 mm. **Abbreviations:** **D**, dentine; **E**, enamel; **Pc**, pulp cavity.

One of the more unique arrangements of teeth is observed in PMO 229.919 (Fig. 14). The teeth on the dorsal surface are located along the symphysis, the medioposterior margin (Fig. 14A) and the posterior half of the lateral margin (Fig. 14B). The teeth along the symphysis are rather large in contrast to the size of the bone compared to other specimens, and occur in one row (Fig. 10C1). This is different from all other dentaries described from *Omphalosaurus*, where the teeth normally are larger in number and irregularly packed along the symphysis (Sander & Faber 2003). On the posteriormost part in dorsal view of PMO 229.919 (Fig. 14A) the teeth are numerous, small and densely packed. The dentaries previously described show fewer teeth on the posteriormost part of the dorsal surface than PMO 229.919, and in PMO 229.916 there are almost none. The teeth on the posterior half of the lateral margin in dorsal view of PMO 229.919 (Fig. 14B) are even smaller than the more posterior teeth, and also irregularly and densely packed. No dentaries previously described of *Omphalosaurus* have teeth on the posterior half of the lateral surface in dorsal view. The teeth of PMO 229.919 are all visible as cross sections of the lower crown on the occlusal surface, as irregular elongated, egg-shaped and rounded. The diameter of the tooth crowns is measured as 1-5 mm, where the maximum represents the very elongated ones. In medial view densely packed and drop shaped replacement teeth are visible, where the larger part of the drop is ventrally directed (Fig. 14C). This is the opposite of the teeth previously described for *Omphalosaurus*, including the rest of the Spitsbergen material, where the crown is dome shaped, instead of the roots (Sander & Faber 2003). In PMO 229.922 no pulp cavity is visible in any of the teeth, only enamel and dentine. Another interesting feature of the medial surface of PMO 229.919 is that the replacement teeth are worn similar as the teeth observed on the occlusal surface. This is the same feature that was described of the medial surface of premaxilla PMO 229.922 (Fig. 6B2) as well as the dorsal part of the medial surface of dentary PMO 229.916 (Fig. 8B).

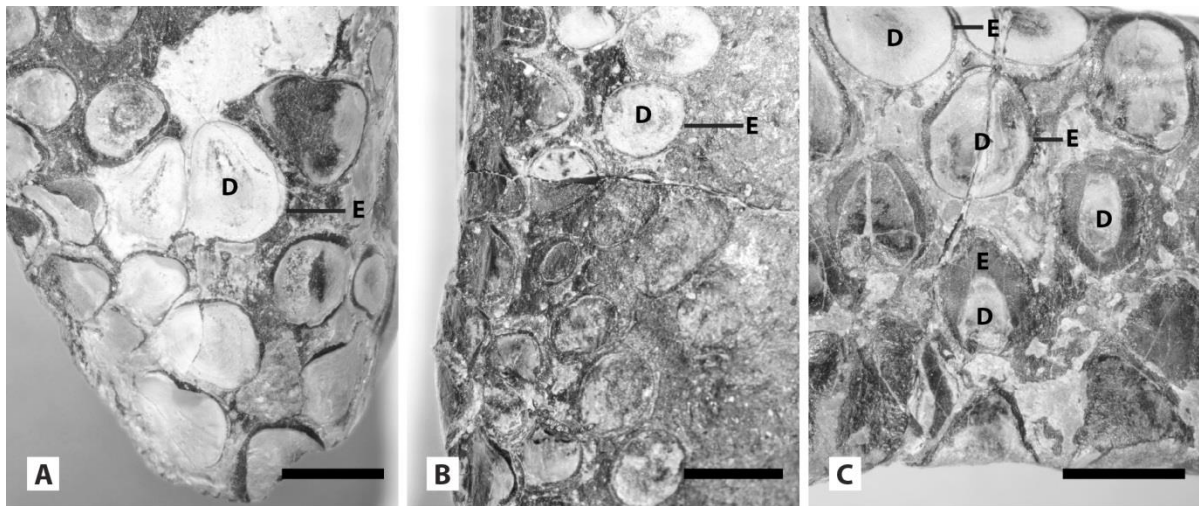


Figure 14. Teeth in dentary PMO 229.919 of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, occlusal view posteriormost. **B**, occlusal view posterolateral. **C**, medial view. Scale bar 2 mm.

Abbreviations: **D**, dentine; **E**, enamel; **Pc**, pulp cavity.

3.4 Vertebral column

The vertebrae centra described and pictured were found as isolated bones. An attempt to reconstruct the vertebral column of *Omphalosaurus* sp. from Spitsbergen is made. The pictured material shows the proposed morphological trend of the centra through the column.

Since the rib articulation facets of the centra, as well as the more posterior located vertebrae, is not known from any of the previously described specimens of *Omphalosaurus*, the reconstruction is based on the well-known vertebral column of *Cymbospondylus* (Merriam 1908). The vertebrae was identified as belonging to *Omphalosaurus* from being deeply amphicoelous and nearly notochordal at the centre, as described by Sander and Faber (2003). The centra shows a cancellous bone structure when observed with hand lens and the periosteum is “wrinkled”, a feature not previously described for *Omphalosaurus* (Fig. 15). With a few exceptions in the posterior caudals, all centra are discoidal, being dorsoventrally higher than anteroposteriorly long. The only other marine reptile found in great abundance in the bonebed is the ichthyopterygian *Grippia*, which is much smaller and show centra of a different morphology (Fig. 16). It is important to mention that the vertebral column of *Omphalosaurus* is composed from several individuals; therefore the size of the centra varies.

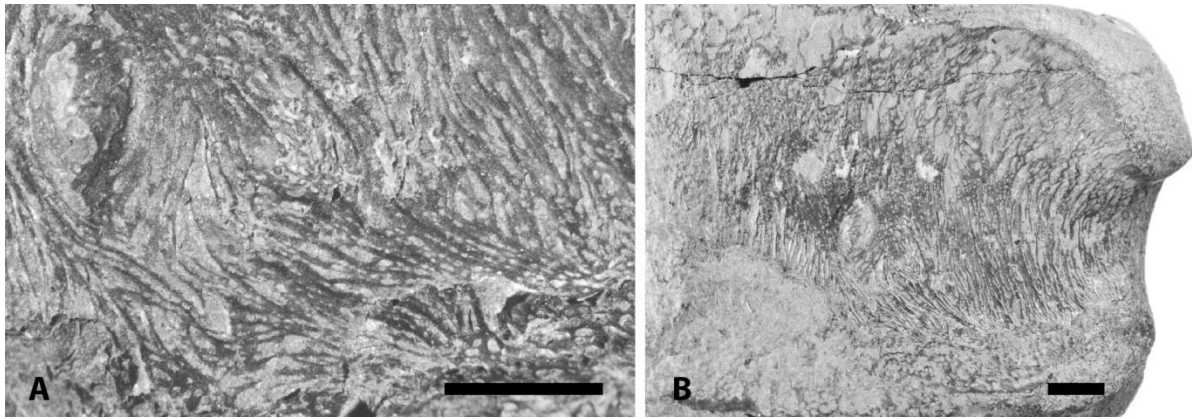


Figure 15. “Wrinkles” in the periosteum of centrum PMO 230.210 of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, Lateral surface, observed in microscope. **B**, Lateral surface, observed through macro lens. **C**, medial view. Scale bar 3 mm.

The centra of *Grippia* are of a much smaller size than *Omphalosaurus*, as well as being cylindrical where those of *Omphalosaurus* are discoidal. Similar for the two are parapophysis and diapophysis present in the cervicals. Both *Grippia* and *Omphalosaurus* show cervicals and dorsals with similar anterior outline of the centra, where the posterior face are shield shaped. The dorsal centra of *Grippia* have a patch of periosteal bone anterior to the apophysis in lateral view (Fig. 16B). This is not observed in *Omphalosaurus*. The caudals of *Grippia* is rounded or shield-shaped in anteroposterior view. A prominent ridge can be seen in the lateral view of the caudals located mid dorsoventrally, anteroposteriorly oriented (Fig. 16D). These features are not observed in the caudals of *Omphalosaurus*, where the caudals are elongated and laterally compressed in anterior and posterior view, with a lateral surface that is smooth.

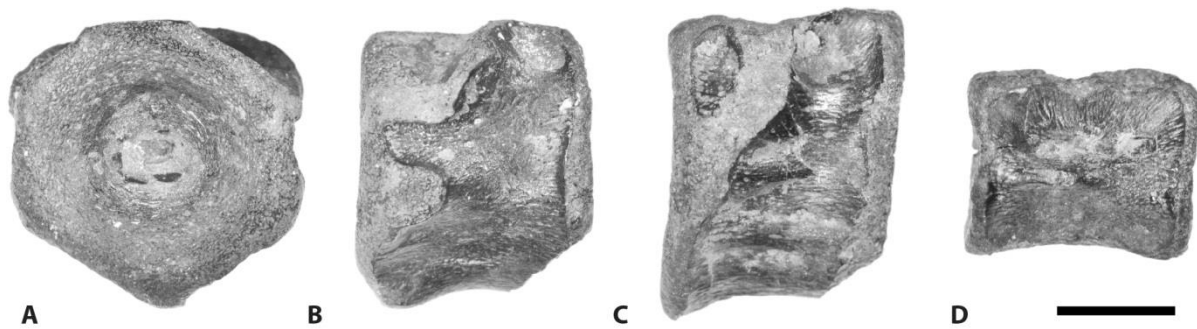


Figure 16. Vertebrae centra of *Grippia* from the Grippia bonebed, Marmierfjellet, Spitsbergen (Spathian). **A**, Cervical PMO 230.211 anterior view. **B**, Cervical PMO 230.211 lateral view. **C**, Dorsal PMO 230.212 lateral view. **D**, Caudal PMO 230.213 lateral view. Scale bar 5 mm.

Several criteria have been used for assigning the centra to the different regions of the vertebral column, and the most distinct are listed below. The **atlas** is identified by being anteriorly convex and posteriorly concave. **Cervicals** are identified by having both parapophysis and diapophysis present. The **anterior dorsals** have one apophysis present, with approximately a 45° angle from the anterior margin towards the posterior. The **posterior dorsals** have a dorsoventrally elongated facet (except the dorsal/caudal transition) and a heightened floor of the neural arch. In the **posterior caudals** the anteroposterior outline is hexagonal and higher than wide. Also the articulation facet is reduced to a circular process mid dorsoventrally. The **posterior caudals** are less wide and longer and have no rib articulation facet present.

The centra figured are listed with measurements and calculated ratios in Table 1. The trend of the ratios calculated is plotted in Fig. 17. In the Alpine specimen (MBG 1500), only a few of the vertebrae were measured by Sander and Faber (2003) due to the preservation of the specimen. It is important to notice that in the table given by Sander and Faber (2003) the calculated height/length ratio by mistake actually represent the height/width ratio. The correct height/length ratio is therefore calculated from the height and length measurements in the table.

It is not possible to suggest the number of vertebrae in each region through the column of *Omphalosaurus* from the Spitsbergen material, since all the centra were collected as isolated bones. From the pictured material, PMO 229.903 is the probable atlas, while PMO 229.904

and PMO 229.905 are interpreted as cervicals. PMO 229.906, PMO 229.907 and PMO 229.908 represent anterior dorsals, PMO 229.909 and PMO.229.910 posterior dorsals. 9 centra are pictured from the caudal region, where PMO 229.911, PMO 229.912, PMO 229.913, PMO 229.914 and PMO 229.915 are suggested anterior caudals. PMO 230.135, PMO 230.136, PMO 230.137 and PMO 230.138 are recognized as posterior caudals.

In addition to the pictured centra, 221 centra were identified and assigned to the different regions of the column. Of these centra 2 were atlases, 2 cervicals, 26 anterior dorsals, 35 posterior dorsals, 23 anterior caudals and 134 posterior caudals. Many of the centra are heavily compressed, especially the posterior dorsals. The centra were grouped based on similarity to the pictured specimens. The amount of centra in each group and the size range of the specimens are listed in Appendix 1.

The probable **atlas** of *Omphalosaurus*, PMO 229.903 (Figs. 18A), has a convex, nearly circular anterior face and deeply hollowed posterior face. This is compatible with the atlas in the Alpine specimen described by Sander and Faber (2003). For the holotype of *O. nevadanus* the atlas was described as concave both anterior and posterior, but this interpretation is probably due to poor preservation or loss of the atlas (Sander & Faber 2003). The anterior face of PMO 229.903 show a Y-mark located in the centre (Fig. 18A1), where the occipital condyle would have met the atlas. The surface of the atlas is very porous, and whether this is due to lack of finished bone or corrosion is uncertain. In lateral view there is no rib facets present, but dorsally the facet for the atlantar arch is visible. The height/length ratio of PMO 229.903 was calculated as 1.73, where for the Alpine specimen the measurements of Sander and Faber (2003) give a ratio of 2.07. In total three atlases was present in the collected material, for maximum and minimum measurements see Appendix 1.

In the **cervicals** (Figs. 18B, C) the anterior outline is pentagonal, slightly laterally wider than anteroposteriorly high and best preserved in PMO 229.904 (Fig. 18B1). PMO 229.905 (Fig. 18C1) is laterally compressed, so that shape and measurements are not accurate. In posterior view both PMO 229.904 (Fig. 18B2) and PMO 229.905 (Fig. 18C2) has a shield-shaped outline. In the holotype from Nevada (UCMP 8281) two vertebrae were found in articulation with the skull, and was interpreted as anterior cervicals by Merriam (1906). These vertebrae was deeply amphicoelous, nearly circular in cross section and according to Mazin (1986)

typical ichthyosaurian. It is worth noting that the centra of the holotype are poorly preserved, and have been interpreted variously by different authors (Mazin 1986; Motani 2000).

In the cervicals of the Spitsbergen material, the peripheral parts of the anterior and posterior face slopes steep towards the centre, being deeply amphicoelous. Both the parapophysis and diapophysis are present in lateral view. The two facets are confluent with the anterior rim of the vertebrae centrum, and the diapophysis is continuous with the facet for the neural arch as well as the posterior rim dorsally. From PMO 229.904 (Fig. 18B3) to PMO 229.905 (Fig. 18C3), the parapophysis is reduced and placed closer to the diapophysis along the anterior rim of the centrum. Whether the parapophysis is truly disappearing or merging with the diapophyses is uncertain, since the facets are never fully separated by periosteal bone, but continuously truncated by the anterior rim of the centrum.

The **anterior dorsals** (Figs. 19) are slightly more rounded in anterior view, but as the cervicals, also wider than high. The laterally widest part of the centrum in anterior view is located midway between the dorsal and ventral edges for PMO 229.906 (Fig. 19A1), but for PMO 229.907 (Fig. 19B1) and PMO 229.908 (Fig. 19C1) the widest part is more dorsally. The centra are still deeply amphicoelous, both in anterior and posterior view, and the posterior face has the same shield-shape as described for the cervicals. The feature with different peripheral shape of anterior and posterior face occurs only in the cervicals and anterior dorsals, making the anterior face wider than high, while the posterior face is always higher than wide. Since it is unknown if the parapophysis is disappeared or merged with the diapophyses, the term apophysis will be used for this single articulation facet. For PMO 229.906 (Fig. 19A3) the posterior rim of the apophysis is slightly curved, and the facet is fairly wide in the ventral part of the centrum. In PMO 229.907 the anterior rim of the apophysis in lateral view has moved dorsally, while the posterior rim has changed from curved to a straight line, having a 45 degree angle to the anterior face of the centrum. In PMO 229.908 (Fig. 19C3) the apophysis is even smaller, located on the dorsal half of the centrum. In all the dorsal centra the apophysis is still truncated by the anterior margin of the centrum, as well as by the posterior margin dorsalmost where the periosteal bone posterior to the apophysis ends. Dorsolaterally the apophyses are truncated by the posterior margin of the centrum. Only one of the dorsals (V10) in the Alpine specimen (MBG 1500) could give a height/length ratio, which was calculated as >1.29 (Sander & Faber 2003). The

height/length ratio of the anterior dorsals of the Spitsbergen material ranges between 1.57 and 1.65. For dorsal and ventral view, see below.

In the **posterior dorsals**, PMO 229.909 (Figs. 20A) is more rounded in anterior view than the anterior dorsals. The posterior face of the centrum has lost the shield-shape described for the cervicals and anterior dorsals, showing a fairly similar shape of the anterior and posterior face. PMO 229.909 is more discoidal than the more anterior located centra, and the data from Table 1 indicate a trend in the column of increasing H/L ratio from anterior to posterior in the first two vertebral regions. In lateral view of PMO 229.909 the apophysis has changed to a long dorsoventral facet, covering the entire anterior rim of the centra, indicating unicipital ribs with a very broad head. The heavily weathered PMO 229.910 (Fig. 20B) is thought to mark the dorsal-caudal transition, where the shape in anterior and posterior view has changed from rounded to being higher than wide. The apophysis has also changed from being long and broad, to a small half circle located on the anterior rim on the ventral half of the centra, as seen in lateral view (Fig. 20B3). For dorsal and ventral view, see below.

The centra identified as **anterior caudals** (Figs. 21) are recognized by being higher than wide, with a single articulation facet that decreases posterior in the column until it disappears. The anterior dorsals are also notochordal at the centre, as observed in Fig. 21, as well as for PMO 229.912 (Fig. 21B) where the notochordal foramen is clearly visible in anteroposterior view. PMO 229.911 (Figs. 21) is fairly rounded in anteroposterior view, and the apophysis is located on the anterior rim, slightly ventral to the middle of the centra in lateral view. The apophysis of this centrum is dipping ventrally, but moving posterior to PMO 229.912 (Figs. 21B) the apophysis is more prominent, pointing posteriorly. PMO 229.912 (Figs. 21B) is hexagonal in shape, with higher H/L and W/L ratios than the centra interpreted to be anterior and posterior to it. This centrum is less corroded than the one anterior and posterior to it, which could have affected the measurements. In PMO 229.913 (Figs. 21C) the articulation facet is much reduced, while in PMO 229.914 (Figs. 21D) it is almost gone and barely visible. PMO 229.914 (Fig. 21D3) differs from the other centra by being wider dorsal than ventral in lateral view. Since no caudal centra has been described for *Omphalosaurus* from other specimens, it has not been discussed whether it possessed a downward flexure in the caudals or not. This centrum could represent a member of the apical series and by that indicate a caudal peak in *Omphalosaurus*. By using the dorsal width,

ventral width and height of the centra in lateral view, the angle contribution to the column from this centrum can be calculated using geometry, as showed by McGowan and Motani (2003). With a dorsal width of 21.09 mm, ventral width of 18.91 mm and dorsoventral height of 32.6 mm, the angle, α , can be calculated from the equation $\tan a = \frac{DW-VW}{H} = \frac{21,09-18,91}{32,6}$. This gives an angular contribution of proximately 5.24°. This is not much compared to the tail bend observed in Early Jurassic species. For example the better preserved specimens of *Stenopterygius* from Holzmaden shows angles between 18-39 ° (McGowan 1992). It is worth considering that other caudal centra could have a higher attribution to the caudal peak, and that a caudal series in articulation is needed to confirm the angle of the caudal peak of *Omphalosaurus*.

The **posterior caudals** (Figs. 22) have no apophysis. The height/width ratio is increasing posterior in the column, while height/length ratio is decreasing. Including the anterior caudals, the height/length ratio decreases after PMO 229.914, the possible apical centra (Fig. 22). PMO 230.135 (Figs. 22A) has an elongated rounded hexagonal shape in anteroposterior view, but moving posterior in the column, the centra turns more oval, as seen in PMO 230.137 (Figs. 22C) until in PMO 230.138 (Figs. 22D) where the centra is fairly anteroposteriorly thin in lateral view. In lateral view the anterior and posterior rim of the centra are prominent, and a ridge runs lateral, mid dorsoventrally, where the more anterior centra would possess an articulation surface. For dorsal and ventral view, see below.

Dorsal and ventral faces

The changes through the column of the dorsal and ventral faces are pictured in Fig. 23. In dorsal view of the cervicals (Fig. 23A1) the floor of the neural canal is shaped as a slender hourglass, with the articular surfaces for the neural arch being located lateral to it, as small narrow pits. The ventral surface (Fig. 23A2) shows a pronounced keel. In dorsal view of the anterior caudals (Fig. 23B1) the floor of the neural canal is not flat as for the cervicals, but appears as a deep elongated embayment, with heightened ridges on the lateral borders. The facets of the neural arch are not as distinct as for the cervicals, where the surface lateral to the floor of the neural canal is rather flat. This could indicate a broader articulation surface

of the neural arches in the dorsal centra. In ventral view (Fig. 23B2) the caudals lack the keel, being more rounded and nearly flat ventralmost. In dorsal view of the posterior dorsals (Fig. 23C1) the floor of the neural canal is heightened, which also can be observed in anterior and posterior view of the centra (Fig. 23A). Lateral to the floor of the neural canal, the centrum slopes with almost a 45 degree angle. Whether this is due to a broad and tilted articulation surface of the neural arch, or the dorsal part of the centra being covered by much cartilage, is uncertain due to the poor preservation of the bone surface. The dorsal surface of the posterior caudals (Fig. 23C2) is more rounded than the more anterior located dorsals. In dorsal view of the anterior caudals (Fig. 23D1) the floor of the neural canal is visible as a prominent elongated embayment, and the facets for the neural arch is located lateral to it, as flat surfaces lateral to the embayment. The ventral surface (Fig. 23D2) is flat. For the posterior caudals, there is no sign of facets for the neural arch in dorsal view (Fig. 23E1), but the floor of the neural canal is prominent. The ventral surface (Fig. 23E2) is highest at the anterior and posterior edges of the centra, with a depression mid anteroposterior.

		Length	Width	Height	W/L	H/W	H/L
PMO 229.903	Atlas	14.11	25.24	24.37	1.79	0.97	1.73
PMO 229.904	Cervical	17.09	25.6	23.48	1.5	0.92	1.37
PMO 229.905	Cervical	20.26	27.31	27.54	1.35	1.01	1.36
PMO 229.906	Anterior Dorsal	21.6	38.54	35.63	1.78	0.92	1.65
PMO 229.907	Anterior Dorsal	22.33	38.53	34.99	1.73	0.91	1.57
PMO 229.908	Anterior Dorsal	17.38	29.84	27.76	1.72	0.93	1.6
PMO 229.909	Posterior Dorsal	25.34	44.15	43.63	1.74	0.99	1.72
PMO 229.910	Dorsal/Caudal	20.75	33.31	46.94	1.61	1.41	2.26
PMO 229.911	Anterior Caudal	13.05	18.35	21.15	1.41	1.15	1.62
PMO 229.912	Anterior Caudal	20.68	35.73	41.84	1.73	1.17	2.02
PMO 229.913	Anterior Caudal	15.77	18.79	24.55	1.19	1.31	1.56
PMO 229.914	Anterior Caudal	19.8	21.47	32.66	1.08	1.52	1.65
PMO 229.915	Anterior Caudal	14.39	15.22	22.82	1.06	1.5	1.59
PMO 230.135	Posterior Caudal	16.14	11.26	21.25	0.7	1.89	1.32
PMO 230.136	Posterior Caudal	18.72	10.43	19.01	0.56	1.82	1.02
PMO 230.137	Posterior Caudal	14.73	7.53	14.55	0.51	1.93	0.99
PMO 230.138	Posterior Caudal	10.87	5.37	13.06	0.49	2.43	1.2

Table 1. Vertebral dimensions in mm. W/L = width/length ratio, H/W = height/width ratio (resembling H/L in Table 1, Sander and Faber (2003)), H/L = height/length ratio.

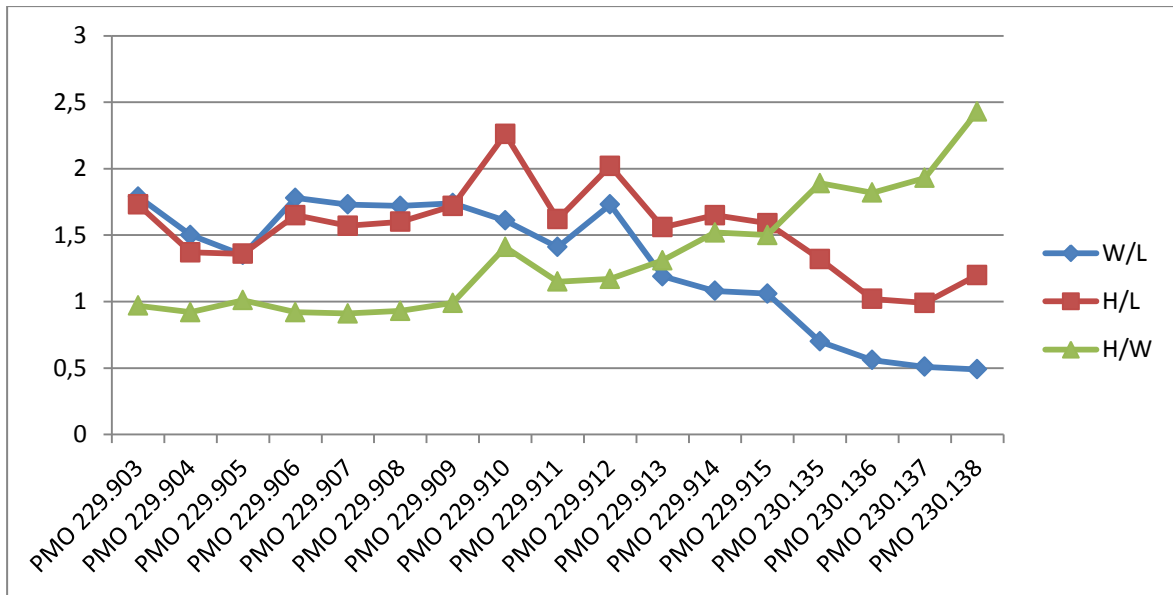


Figure 17. Plot of W/L, H/L and H/W from table 1. W/L = width/length ratio, H/W = height/width ratio (resembling H/L in Table 1, Sander and Faber (2003)), H/L = height/length ratio.

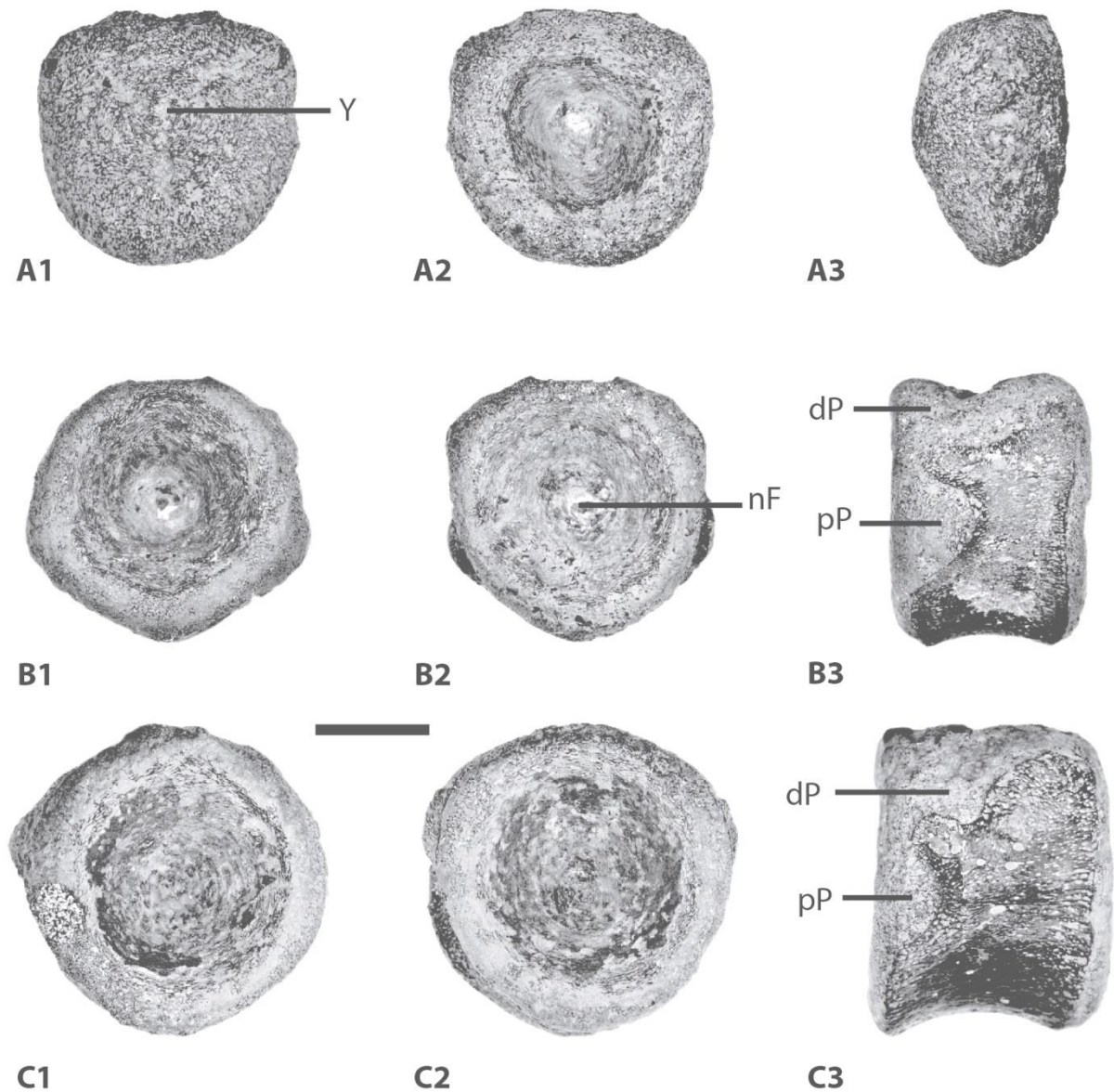


Figure 18. Cervical vertebrae of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, PMO 229.903, atlas. A1. Anterior view, A2. Posterior view, A3. Lateral view. **B**, PMO 229.904. B1. Anterior view, B2. Posterior view, B3. Lateral view. **C**, PMO 229.905. C1. Anterior view, C2. Posterior view, C3. Lateral view. Scale bar 1 cm, anterior is to the left for the lateral view of the centra (3). **Abbreviations:** **dP**, diapophysis; **nF**, notochordal foramen; **pP**, parapophysis; **Y**, Y-mark.

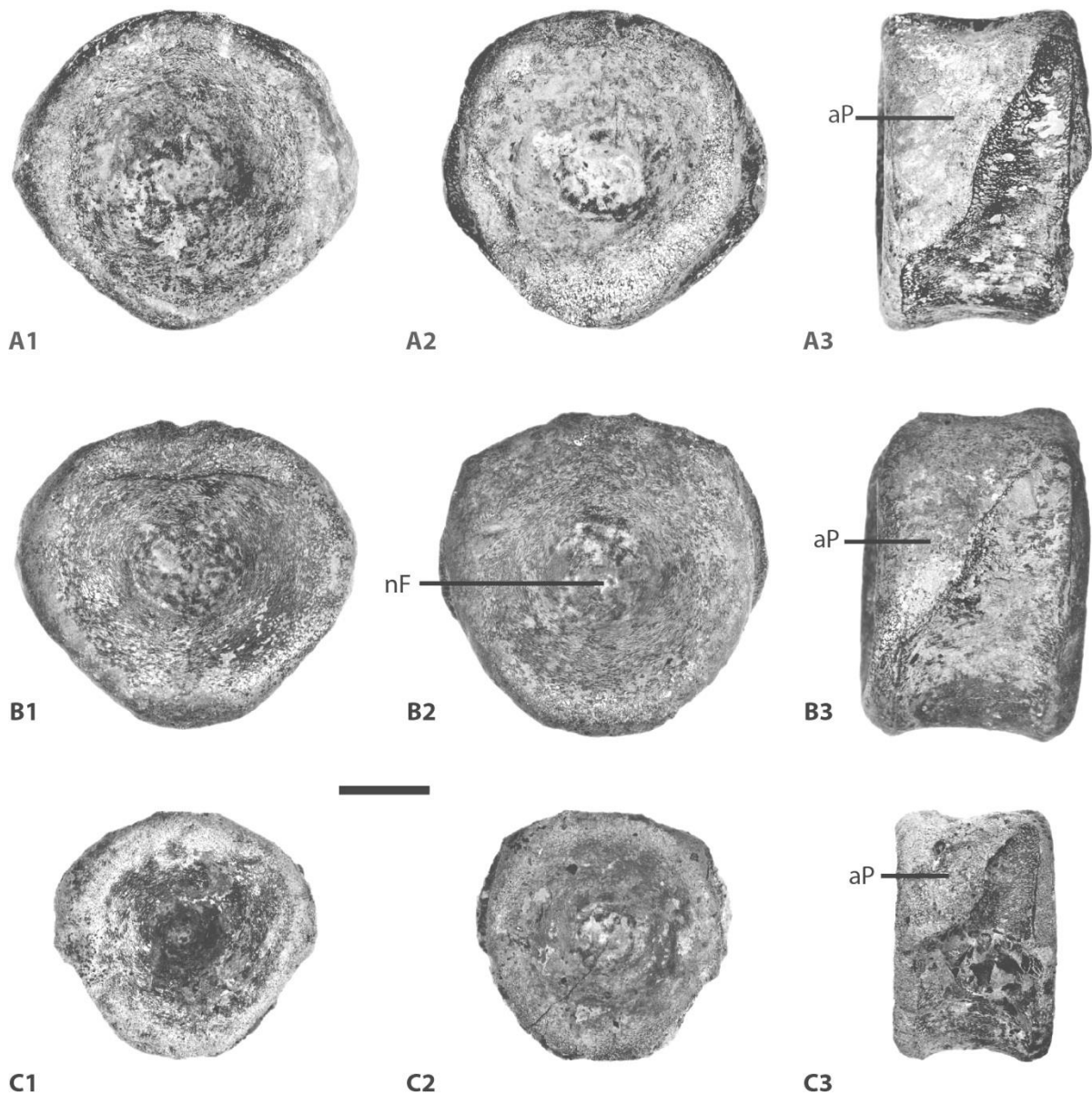


Figure 19. Anterior dorsal vertebrae of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, PMO 229.906. A1. Anterior view, A2. Posterior view, A3. Lateral view. **B**, PMO 229.907. B1. Anterior view, B2. Posterior view, B3. Lateral view. **C**, PMO 229.908. C1. Anterior view, C2. Posterior view, C3. Lateral view. Scale bar 1 cm, anterior is to the left for the lateral view of the centra (3). **Abbreviations:** **aP**, apophysis, **nF**, notochordal foramen.

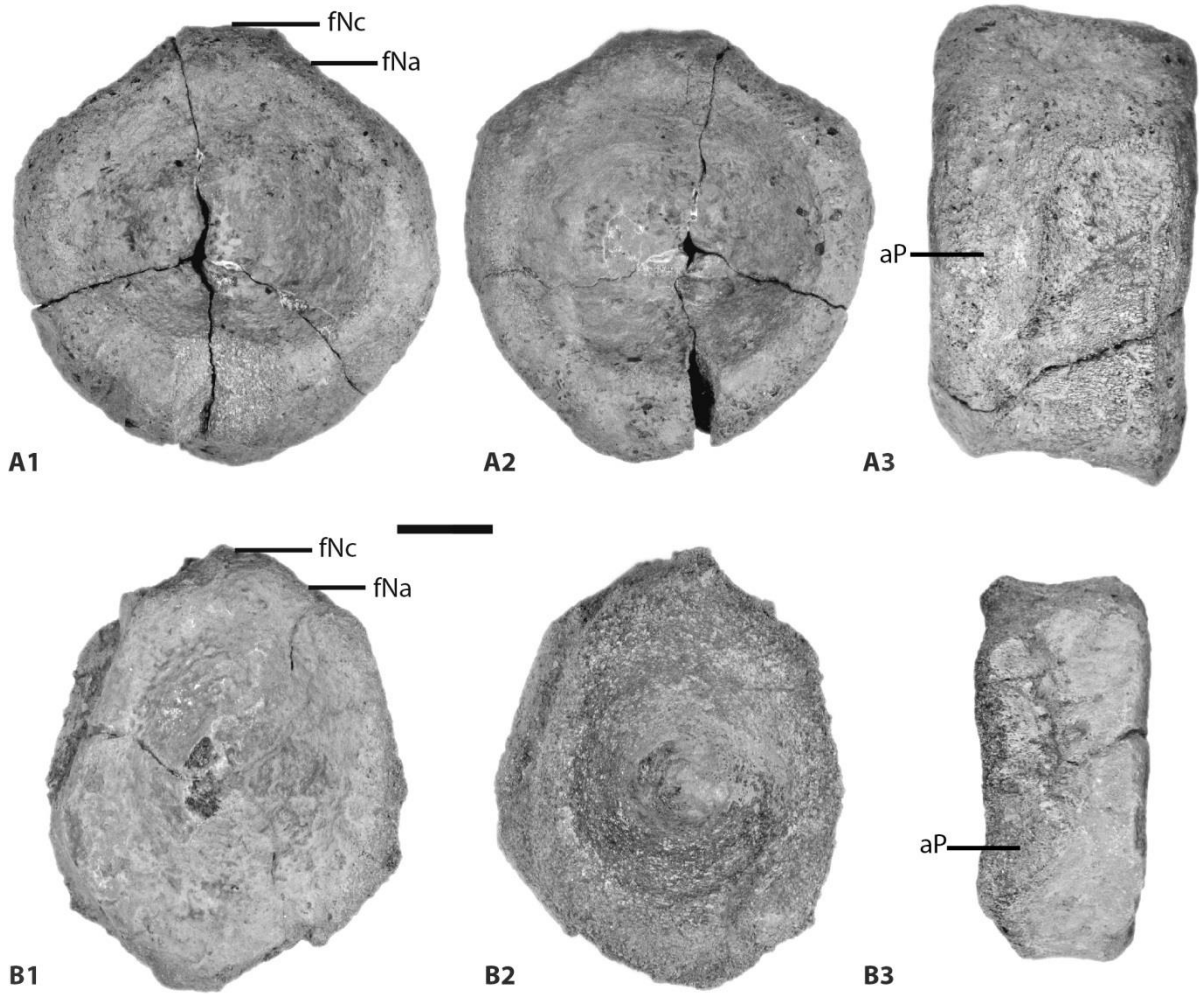


Figure 20. Posterior dorsal vertebrae of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, PMO 229.909. A1. Anterior view, A2. Posterior view, A3. Lateral view. **B**, PMO 229.910. B1. Anterior view, B2. Posterior view, B3. Lateral view. Scale bar 1 cm, anterior is to the left for the lateral view of the centra (3). **Abbreviations:** aP, apophysis; fNa, facet for neural arch; fNc, floor of neural canal.

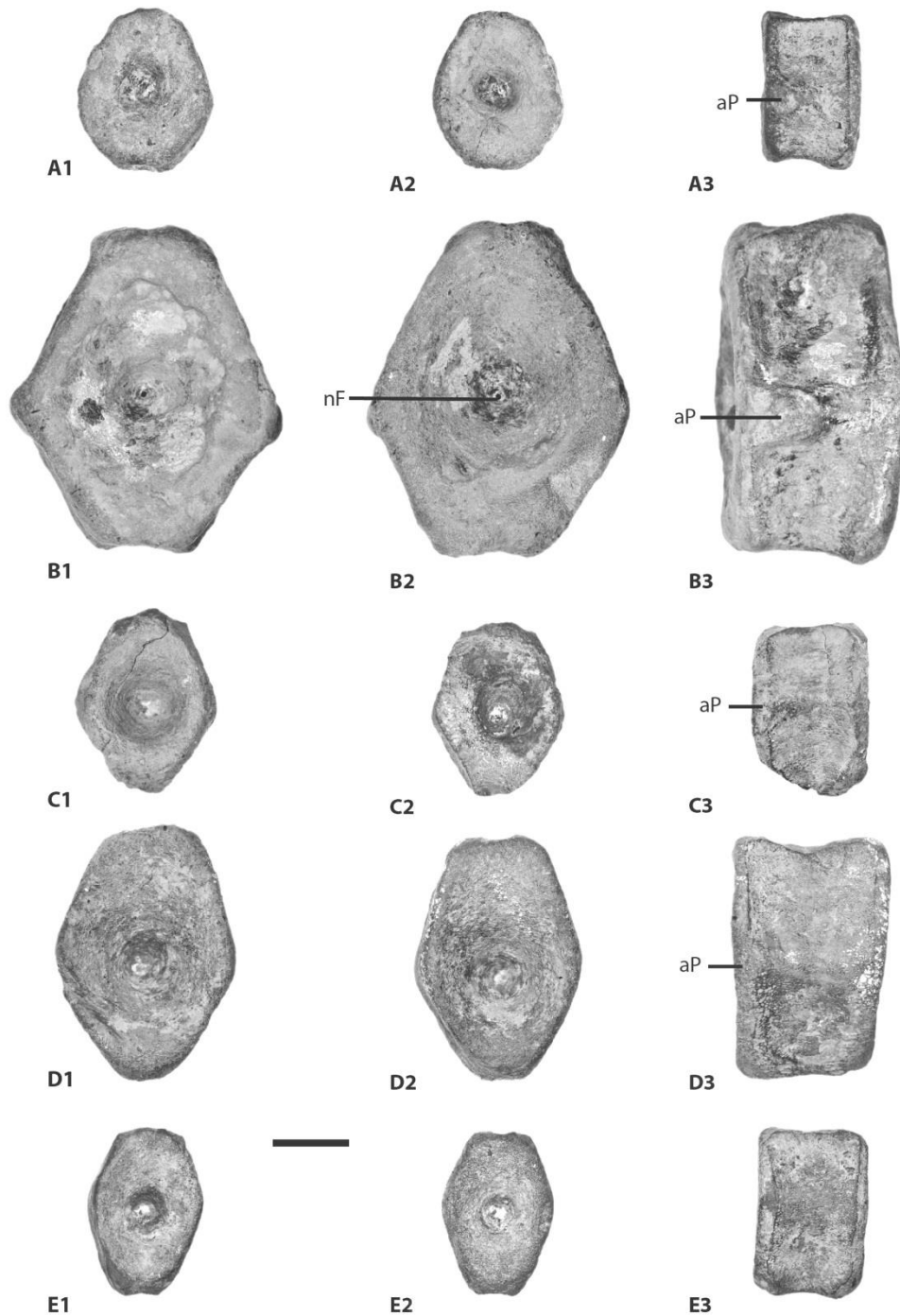


Figure 21. Anterior caudal vertebrae of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, PMO 229.911. A1. Anterior view, A2. Posterior view, A3. Lateral view. **B**, PMO 229.912. B1. Anterior view, B2. Posterior view, B3. Lateral view. **C**, PMO 229.913. C1. Anterior view, C2. Posterior view, C3. Lateral view. **D**, PMO 229.914. D1. Anterior view, D2. Posterior view, D3. Lateral view. **E**, PMO 229.915. E1. Anterior view, E2. Posterior view, E3. Lateral view. Scale bar 1 cm, anterior is to the left for the lateral view of the centra (3). **Abbreviations:** **aP**, apophysis, **nF**, notochordal foramen.

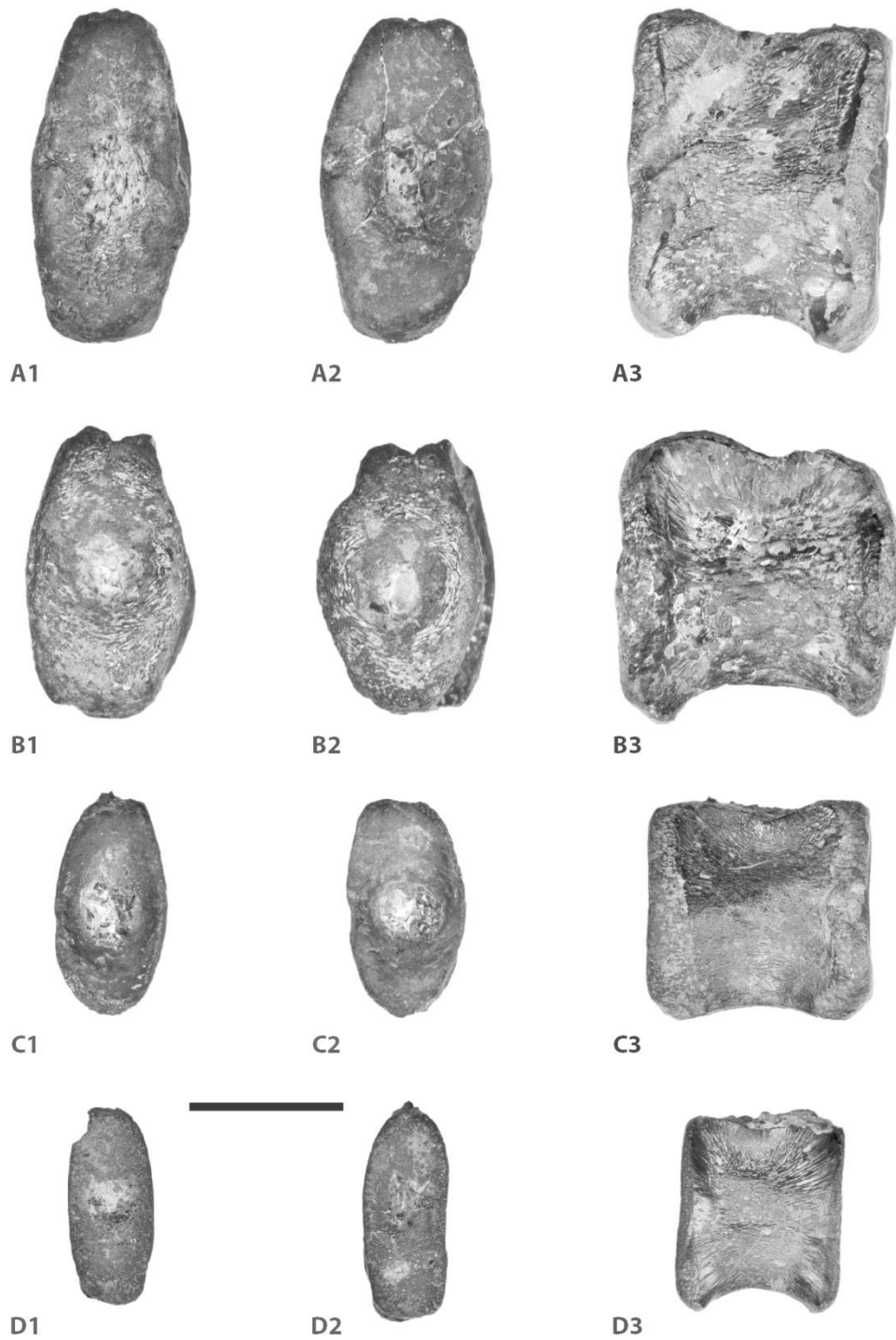


Figure 22. Posterior caudal vertebrae of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). **A**, PMO 230.135. A1. Anterior view, A2. Posterior view, A3. Lateral view. **B**, PMO 230.136. B1. Anterior view, B2. Posterior view, B3. Lateral view. **C**, PMO 230.137. C1. Anterior view, C2. Posterior view, C3. Lateral view. **D**, PMO 230.138. D1. Anterior view, D2. Posterior view, D3. Lateral view. Scale bar 1 cm, anterior is to the left for the lateral view of the centra (3).

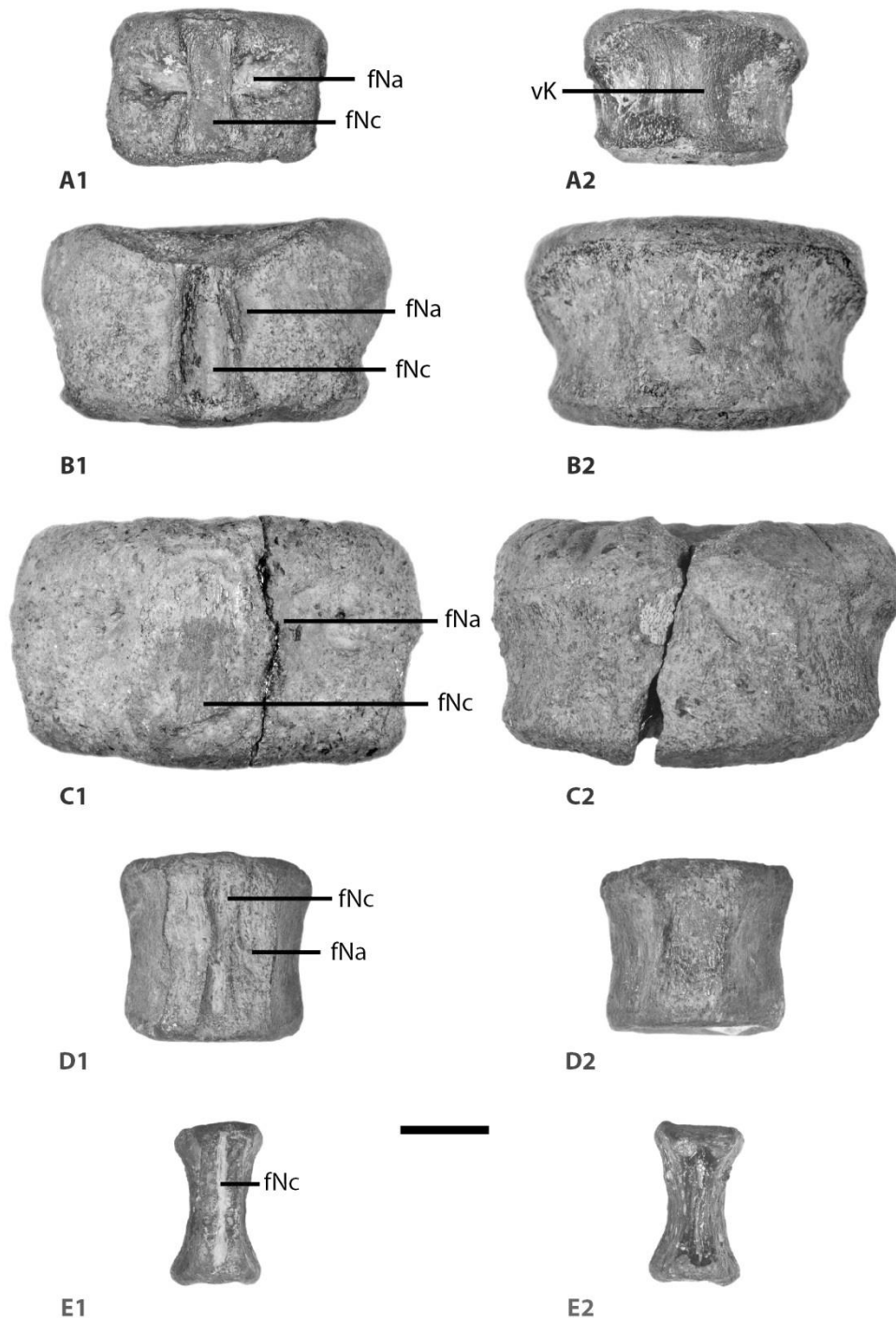


Figure 23. Centra of *Omphalosaurus* sp. from Spitsbergen in dorsal and ventral view. **A**, cervical, PMO 229.904. A1. Dorsal view, A2. Ventral view. **B**, anterior dorsal, PMO 229.907. B1. Dorsal view, B2. Ventral view. **C**, posterior dorsal, PMO 229.909. C1. Dorsal view, C2. Ventral view. **D**, anterior caudal, PMO 229.914. D1. Dorsal view, D2. Ventral view. **E**, posterior caudal, PMO 230.904136. E1. Dorsal view, E2. Ventral view. Scale bar 1 cm, anterior is up for all the photographs. **Abbreviations:** **fNa**, facet for neural arch; **fNc**, floor of neural canal; **vK**, ventral keel.

4. Discussion

4.1 Jaw function

Identification of the tooth-bearing bones

The similarity between the suggested dentaries in the Spitsbergen material and the dentaries in the Alpine specimen and the holotype of *Omphalosaurus*, highly suggests that the dentaries described in this study are true dentaries of *Omphalosaurus*.

The groove described on the ventral surface of dentary PMO 229.916 is most likely a suture for the more ventrally placed bones in the lower jaw. In the holotype from Nevada, the assumed splenials are located ventral to the dentaries where they contribute to a large part of the symphysis (Sander & Faber 2003).

Several tooth-bearing bones can be present in the upper jaw of marine reptiles. The tooth-bearing bones of the upper jaw of *Omphalosaurus* were suggested to be premaxillae by Sander and Faber (2003), which has been followed in this study. From premaxilla PMO 229.922 in the Spitsbergen material, it seems unlikely that another bone was located anterior to it. The convex occlusion surface fits perfectly with the concave occlusion surface of the dentaries. No other tooth-bearing bones than the dentaries and premaxillae have been described for *Omphalosaurus* (Sander & Faber 2003). From the Spitsbergen material this seems reasonable, since when mirroring the premaxilla PMO 229.922 (Fig. 7) the result is a wide occlusion surface, similar to that of the dentaries.

If the suggested premaxilla truly is a premaxilla, the embayment visible posterior to the dorsal process (Fig. 6A2, B2) could have contributed to the external naris. The anterior part of the premaxillae would most likely have been covered by an elongation of the nasals ventrally. A dorsal process on the premaxillae was mentioned by Sander (2000) as common in Triassic ichthyopterygians, where the process would separate the nasals from the external nares. On the other hand, if the assumed premaxilla is a maxilla, the anterior embayment of the dorsal process possibly contributed to the external naris, and the posterior embayment to the orbit. This would imply that the premaxillae were located anteriormost dorsal to the

maxillae, contributing to the external naris together with the nasals. The nasal openings would then have been located very near the tip of the snout.

Palatines and vomers could be a possibility if the bones are not premaxillae or maxillae, as discussed by Sander and Faber (2003). If the assumed premaxillae were paired vomers this would explain the unfinished lateral surfaces of the bones, since those surfaces would have been covered by the premaxillae. This would imply a toothless premaxilla. Suggested vomers are preserved in the holotype from Nevada, and appear flat and toothless (Sander & Faber 2003). Due to the wideness of the occlusion surface of the supposed premaxillae compared with the occlusion surface of the dentaries, it seems unlikely that the suggested premaxillae represent vomers. Palatines seem rather unlikely as well, since the supposed premaxillae appear deep dorsoventrally. The suggested palatines in the holotype from Nevada appear toothless (Sander & Faber 2003).

From what is discussed above, the assumed premaxillae could be either maxillae or premaxillae. Vomers and palatines seem unlikely. A complete skull of *Omphalosaurus* in articulation is needed to further understand the cranial morphology of this animal.

Jaw symphysis

There are several peculiar features observed in the assumed symphysis of *Omphalosaurus*. Sander and Faber (1998) suggested that the medial surface of the premaxillae was an active grinding surface, while later Sander and Faber (2003) thought the medial sides met in a symphysis of the upper jaw. From premaxilla PMO 229.922 it seems that at least a part of the medial surface was an active grinding surface, due to the wear of the teeth. This is also observed in dentary PMO 229.919, where all the teeth exposed in medial view are worn. For both the dentaries and premaxillae, tooth arrangement and morphology suggests that the medial surfaces met in the sagittal plane of the skull. At the same time the wear of the teeth in medial view imply that this was an active grinding surface, as the occlusion surface.

A fused, strong symphysis would have been expected for a durophagous animal. Still, an unossified symphysis does not necessarily imply less force in the jaw, but could rather explain how the forces acted in the jaw. Lieberman and Crompton (2000) studied the

mandible in mammals, concluding that the fusion of the mandible symphysis is a function of how the teeth move in occlusion. Mammals with a mainly vertical occlusion commonly show unfused symphysis, while mammals with the lateral occlusion often have a fused symphysis (Lieberman & Crompton 2000).

If this can be implied to *Omphalosaurus*, it suggests a vertically oriented crushing movement of the jaws. A loose jaw symphysis will allow the different dentaries to be somewhat mobile independently of each other. The hypothesis of a loose symphysis could explain the wear of the teeth on the medial surface, caused by the dentaries grinding in the symphysis. At the same time this is highly unlikely since some sort of soft tissue would be expected between the bones, even if the symphysis was unossified.

Bone surface

The only finished surfaces of the tooth-bearing bones are the occlusion surface and parts of the medial surface. The lack of periosteal bone could imply that these surfaces were covered by other bones. This would be very unusual, and no other animal known has been described to have all surfaces (except the occlusal surface) of dentaries and premaxillae covered by other bones. Another possibility is that some sort of tissue could have covered the bone surface. The Late Triassic archosauromorph *Teraterpeton hrynewichorum* was described by Sues (2003) with a possible keratinous beak covering the premaxillary rostrum, the anterior portion of the maxilla and the dorsal margin of the anterior portion of the dentary. This suggestion was based on structures in the bone surface. In marine reptiles some placodonts evolved beaks together with the transition to more toothless forms, as seen in *Placochelys*, which possessed a sharp beak on the end of its slim snout (Romer 1966).

Another possibility is some sort of soft tissue covering the bones, like lips or cheeks. This is known from the modern beaked whale, and was suggested as possible in the edentulous ichthyopterygian *Shastasaurus* by (Sander et al. 2011). Three large foramina on the lateral surface of the maxilla were used to support this hypothesis, which is similar to the three foramina observed on the suggested premaxillae of *Omphalosaurus* from Spitsbergen (Fig. 6B4).

An interesting feature of the dentition of *Omphalosaurus* is that the teeth are located mainly along the symphysis in the dentaries, but more widespread in the premaxillae. The toothless smooth surface of the dentaries would meet the teeth of the premaxilla, an unusual feature in a supposed durophagous animal.

A possibility is that *Omphalosaurus* was evolving an edentulous jaw. An edentulous jaw is not uncommon in marine reptiles, and can be observed in the placodont *Placochelys* which evolved a toothless snout, and *Henodus* which became nearly toothless (Romer 1966). Several edentulous ichthyopterygians are also known, like the basal *Cartorhynchus*, hupehsuchians and some species of *Shastasaurus* (Sander et al. 2011; Motani et al. 2015b). The edentulous *Shastasaurus liangae* was described with a smooth surface of the dentaries, as in *Omphalosaurus* (Sander et al. 2011). This has not been observed in any Jurassic ichthyopterygians.

The dentaries of *Omphalosaurus* observed in the Spitsbergen material show the peculiar anteriormost single tooth (Fig. 13A), which speaks against any bone or tissue covering this part of the bone. Since this feature is present in all the dentaries with the anterior tip preserved, it is more likely a morphological feature than a result of corrosion of the bone. The function of these teeth are hard to interpret, since they are rounded and dorsoventrally oriented, so that they would serve poorly as grasping teeth. If this is a feature of the suggested premaxilla as well is not possible to tell, since the most complete premaxilla, PMO 229.922, lacks the anteriormost portion of the bone.

4.2 Axial skeleton

Both of the cervicals described from the Spitsbergen material are wider than high, possessing a ventral keel. The diapophysis is located high on the lateral surface of the centrum, confluent with the neural arch. The cervicals have a higher height/length ratio than the caudals, which is opposite to the later occurring ichthyopterygians (Buchholtz 2001).

Mean width and height of the centra identified (Appendix 1) increase from the cervicals until the posterior dorsals. The dorsals are rounded in anterior and posterior face

and relatively anteroposteriorly short. A wide area of contact between two centra is found in centra that are high and wide, and a short length of the centra will minimize intervertebral movement (Buchholtz 2001). This suggests that the dorsal series of *Omphalosaurus* could have been relatively rigid.

The wedge shape observed in PMO 229.914 indicates a caudal peak in *Omphalosaurus*, which is uncommon among Triassic ichthyopterygians (Sander 2000).

4.3 Mode of life

Bone histology

The bone histology of *Omphalosaurus* has been studied by several authors (de Buffrenil & Mazin 1990; Sander & Faber 2003; Houssaye et al. 2014). It is important to notice that the bones studied by de Buffrenil and Mazin (1990), which the study of Houssaye et al. (2014) is based on, is not confirmed as belonging to *Omphalosaurus*. The bones studied by de Buffrenil and Mazin (1990) are limb bones described as *Omphalosaurus* by Mazin (1983), originally described as *Pessopteryx* by Wiman (1910). Still, the bones studied by de Buffrenil and Mazin (1990) show the same unique primary cancellous bone structure as described by Sander and Faber (2003) from ribs and vertebrae of the Alpine specimen (MBG 1500). Whether the limb elements of *Pessopteryx* truly belong to *Omphalosaurus* or not are beyond the scope of this paper, but are worth considering due to the similar bone structure.

According to de Buffrenil and Mazin (1990) the cancellous bone of *Omphalosaurus* implies a rapid growing marine reptile with an active metabolism. The surfaces of the periosteal bone of *Omphalosaurus* in the Spitsbergen material also show a wrinkled surface (Fig. 15), assumed to be vascular canals. The high amount of vascular canals could be another factor suggesting rapid growth, increasing the blood supply to the individual bones. This is also observed in the dentary PMO 229.916 (Fig. 8), where the vascular canals probably contributed to the rapid replacement of teeth occurring in the jaws of *Omphalosaurus*.

A reduction of bone mass is assumed to improve locomotion, especially the ability to accelerate and maneuver. This is an advantage for more rapid swimmers and animals cruising for a longer time in open water (de Ricqlès & de Buffrenil 2001). The cancellous nature of *Omphalosaurus* therefore suggests an animal well adapted to an open water environment.

Mode of Swimming

The anterior caudals in *Omphalosaurus* show an increase in centrum length after the dorsal-caudal transition. The centra are hexagonal and higher than wide. In Jurassic ichthyopterygians the anterior caudals were nearly round in cross section, which suggest a rounded body that prevented both lateral and vertical movement (Buchholtz 2001). The Jurassic ichthyopterygians also had anterior caudals of short anteroposterior length, indicating that the anterior part of the tail was rather stiff. By comparing this to the centra of *Omphalosaurus*, it seems plausible to suggest a laterally slim body shape in the caudal region, specialized for lateral movement, where the increased length of the centra caused a higher range of movement between the centra. Further posterior in the anterior caudals, the centra get more laterally compressed while the relative length is increasing, suggesting higher column flexion and further lateral slimming of the tail.

The posterior caudals observed in *Omphalosaurus* are even more laterally compressed than the anterior, with an increased relative length of the centra. Centra that are more cylindrical and have smaller anteroposterior faces will have greater intervertebral movement than centra that are higher, wider and shorter (Buchholtz 2001). It is therefore likely that the maximum flexibility was located in the posterior part of the column, but that the entire caudal series served as the propulsive surface in this animal. The heightened floor of the neural canal observed in the dorsals of *Omphalosaurus* is an unusual feature, with an unknown function. One suggestion is that the neural arches were wide and deep in this region of the vertebral column. Another possibility is that the amount of cartilage between the centrum and neural arch were greater in this region, so that the neural arches were more mobile than in other parts of the vertebral column.

From the reconstructed vertebral column, *Omphalosaurus* is suggested to be an axial swimmer (Motani et al. 1996). The more primitive ichthyopterygians are assumed to have an anguilliform swimming mode, much like eels, where later forms were thunniform swimmers (Motani et al. 1996). From the centra in the Spitsbergen material, *Omphalosaurus* are assumed to have a high presacral count (Appendix 1). In early ichthyopterygian evolution, a high presacral count was suggested as an adaption to anguilliform swimming by Motani et al. (1996). An interesting feature of the centra in *Omphalosaurus* is that all centra, except the very posteriormost caudals, are discoidal. Motani et al. (1996) suggested that the deep fusiform body common in the more derived ichthyopterygians, began evolving with the evolution of discoidal centra. This implies that *Omphalosaurus* probably shared characters common in the more derived Ichthyopterygians. The size and shortness of the dorsal centra suggests that the trunk did not largely participate in locomotion, so that undulations were confined to the caudal series. It is therefore possible that *Omphalosaurus* was in the transition between two body-forms, the anguilliform and thunniform. To confirm this hypothesis an articulated vertebral column of *Omphalosaurus* is needed.

Feeding

The enamel of *Omphalosaurus* show a smooth enamel-dentine-junction, together with a bulbous shape and uneven surface of the enamel, characteristic for durophagous ichthyopterygians (Sander 1999).

Motani et al. (2015a) found durophagy unlikely for *Omphalosaurus* due to arrangement of the teeth and the assumable weak forces present at the front of the jaws. A pelagic ram feeder was suggested, grasping its food with an extended jaw symphysis, similar to the spoon of spoon bills. A spatula shaped snout was described for the Nevada specimen *O. nettarhynchus* (Mazin & Bucher 1987), but has not been described for any other specimens of *Omphalosaurus*. The specimen used to erect *O. nettarhynchus* consists of the posterior part of the suggested mandible (Mazin & Bucher 1987), and it is necessary to consider that this specimen could be compressed or misinterpreted.

Even though durophagy is suggested as the mode of feeding in *Omphalosaurus*, the arrangement of teeth in the jaw differs from typical durophagous marine reptiles like the placodonts. Animals with crushing dentition often have short snouts with the dentition placed far back to maximize the bite force (Sander & Faber 2003). In premaxilla PMO 229.922 the teeth are placed on the anterior half of the occlusion surface, while in the dentaries studied the teeth are mainly concentrated along the symphysis, as seen in PMO 229.919. This seems like an unusual arrangement of teeth in a suggested durophagous marine reptile. The snout of *Omphalosaurus* is relatively long compared with other durophagous marine reptiles (Sander & Faber 2003).

Sander and Faber (2003) suggested that *Omphalosaurus* fed in the water column, on thin shelled invertebrates such as ammonites and pelagic bivalves. The lack of grasping teeth and strange arrangement of teeth in the lower jaw in the Spitsbergen material, as seen in dentary PMO 229.916 and PMO 229.919, supports this hypothesis. Perhaps *Omphalosaurus* used some sort of suction feeding, where the dentition was mainly for crushing thin shelled invertebrates. According to Sander and Faber (2003) even thin shelled invertebrates could cause the heavy wear of the teeth as observed in *Omphalosaurus*. The extreme wear of teeth in *Omphalosaurus* is well exemplified by premaxilla PMO 229.922 and dentary PMO 229.919.

Sander et al. (2011) suggested a Late Triassic diversification of suction feeders based on similarities between toothless species of *Shastasaurus* and modern suction feeding odontocete whales. Specialized soft tissue on the snout, such as lips or cheeks were suggested as possible for *Shastasaurus* to increase the efficiency of suction, as observed in the beaked whales (Sander et al. 2011). The unfinished bone surfaces, as observed well in lateral view of dentary PMO 229.918 and premaxilla PMO 229.921, could have been covered by a similar tissue. Suction feeding was suggested for the basal ichthyopterygian *Cartorhynchus* from the Lower Triassic of China (Motani et al. 2015b).

Motani et al. (2013) studied the hyobranchial apparatus of several ichthyopterygians and compared it to both ram-feeding and suction-feeding modern odontocete whales and sharks. The slenderness of the hyobranchial apparatus and mandibular morphology of ichthyopterygians were more similar to ram feeding sharks than suction feeding odontocete

whales. Ram feeding was therefore suggested as the common mode of feeding for both Triassic and Jurassic ichthyopterygians. The hyobranchial apparatus of *Omphalosaurus* is unknown, so that a comparison to suction-feeding animals is not possible at the moment.

Omphalosaurus has been described as a rather plump marine reptile (Motani 2000) due to the massive bones, as seen in dentary PMO 229.916. This description does not fit well with a possible ammonite feeder. Tichy (1995) suggested a swimming speed of 5 km/h for *Omphalosaurus*, to follow ammonites which are assumed to have had a swimming speed of equivalent 5.04 m/s. This speed is based on the living mollusk *Nautilus* (Tichy 1995). The bone structure and vertebrae morphology suggests that *Omphalosaurus* might have been capable of higher swimming speeds than earlier expected. This supports the hypothesis of a pelagic ram feeder or suction feeder. If *Omphalosaurus* possessed a beak in real life, this would suggest a benthic feeder, which seems unlikely due to the high specialization to an open marine environment.

Different species, morphological variation or stages of growth?

The different assumed premaxillae of *Omphalosaurus* in the Spitsbergen material (Fig. 6) are difficult to compare morphologically due to lack of complete specimens. The most complete specimen, PMO 229.922, is collected from the Lower Saurian Niveau and shows fewer and more widely spaced teeth than the other premaxillae, which are collected from the Grippia Niveau. PMO 229.922 also has very few teeth on the posterior part of the occlusion surface, which differ from PMO 229.921 that mainly have teeth on the posterior part of the occlusion surface. These two premaxillae could represent different taxa, although PMO 229.922 is much smaller than PMO 229.921, so that different ontogenetic stages are possible.

For the dentaries, PMO 229.916, PMO 229.918 and PMO 229.920 show a fairly similar morphology, except the latter two being somewhat slimmer anteriorly in dorsal view than PMO 229.916. PMO 229.918 and PMO 229.920 are from the Grippia Niveau, while PMO 229.916 was collected from the Grippia bonebed. These dentaries probably belong to the same species of *Omphalosaurus*, where the anteriorly slimmer PMO 229.918 and PMO

229.920 might represent ontogenetically younger individuals than PMO 229.916. Still, the teeth and anteriormost dorsoventrally height is somewhat larger in PMO 229.918 and PMO 229.920, which could be due to individual differences.

PMO 229.917 and PMO 229.919 from the Lower Saurian Niveau show morphological features that differ from the dentaries from the Grippia Niveau and Grippia bonebed. PMO 229.917 is anteroposterior short and laterally wide in dorsal view, clearly different from PMO 229.916. The ratio of the length of symphysis compared to the anteroposterior length of the dentary is also greater than for PMO 229.916. PMO 229.919 also differs greatly from the other dentaries by having tooth replacement visible on the entire medial surface and teeth located posteriormost and on the posterior part of the lateral surface in dorsal view.

From the studied dentaries three different morphologies can be distinguished, one from the Grippia Niveau and two from the Lower Saurian Niveau. The morphological differences could be due to different taxa, ontogenetic age or individual differences. Whether the specimens studied represent ontogenetically young or adult animals could be resolved by looking at the enamel in SEM or thin sections of the histology, which is beyond the scope of this paper.

All the vertebrae centra were collected from the Grippia bonebed and Grippia Niveau, showing a wide size range. Three different atlas were collected (suggesting at least three different animals present in this bonebed) with an atlas size range of 8.82-24.37 mm. The largest centrum is observed from the anterior caudal region, being 80.19 mm high. These centra vary little in morphology, and are assumed to represent same species but different ontogenetic stages of *Omphalosaurus*.

4.4 Systematic affinities

Ichthyopterygian affinities of *Omphalosaurus* have been discussed for more than a century and still the phylogenetic position of the taxon is uncertain. Clearly there are several characters in *Omphalosaurus* common among ichthyopterygians. *Omphalosaurus* possesses

a relatively short and massive lower jaw, common in durophagous ichthyopterygians (Sander 2000). Rounded, blunt teeth is also common in ichthyopterygians, but here *Omphalosaurus* differs by lacking plicidentine, a synapomorphy of the ichthyopterygians (Sander 2000). Another suggested synapomorphy of the ichthyopterygians are the presence of microunit enamel, which is present in *Omphalosaurus* (Sander 1999).

The centra of *Omphalosaurus* described in this study are typical ichthyopterygian by being deeply amphicoelous and discoidal. Discoidal centra are common in more derived Ichthyopterygians, where more basal forms possess centra that are longer than high (Sander 2000). *Omphalosaurus* is assumed to have a short neck and long caudal region, due to the identified centra described in this thesis (in total 7 cervicals (3 atlases), and 167 caudals). An articulated specimen of *Omphalosaurus* is needed to support this hypothesis.

Ichthyopterygian affinities are also supported from the rib articulation facets, which are described for the very first time in this study. The cervicals have double articulation facets, where the diapophysis is confluent with the facet for the neural arch. The dorsals show a single elongated articulation facet, transitioning to a single round facet in the caudals. These trends are common among ichthyopterygians, especially in the Triassic forms (Sander 2000). Posterior towards the caudals the articulation facets moves down on the centra, losing the contact to the facet for the neural arch. This normally happens in anterior or middle region for ichthyopterygians, where in *Omphalosaurus*, as in primitive diapsids (Sander 2000), this transition takes place entering the caudals, as observed in the Spitsbergen material.

In the latest phylogeny by Ji et al. (2015), 14 characters are used to diagnose the Ichthyopterygia. Only 4 of them can be discussed for *Omphalosaurus*, since the bones considering the other 10 is not found in the Spitsbergen material attributed to *Omphalosaurus*;

- Character 10: Nasal anteriorly extending beyond external naris (1).
- Character 153: Neural spine articulation in tail present (1).
- Character 155: Caudal peak present (1).
- Character 160: Tail stem count $\frac{1}{2}$ or more that of the presacral count (1).

The position of the nasal depends if the suggested premaxilla truly is the premaxilla. If it is, the dorsal anterior part of the premaxilla may have been covered by the nasal. This indicates nasals extending beyond the external naris. From the caudals observed in the Spitsbergen material of *Omphalosaurus*, it is clear that neural spine articulation in the tail is present. *Omphalosaurus* is suggested by the discovery of centrum PMO 229.914 to have a caudal peak, which is common in post-Triassic ichthyopterygians (Sander 2000). 167 caudal centra were collected from the Grippia bonebed, where the total amount of dorsals and cervicals are 70. It therefore seems likely that the number of centra in the caudals were $\frac{1}{2}$ or more than the number of centra in the presacral region.

Only two of the characters, the caudal spine articulation and caudal peak, can be observed clearly. The character considering the nasal needs more material of *Omphalosaurus* to be confirmed, but does not seem unlikely from the material present in the Spitsbergen collection. The same is for the tail stem count. Since no character clearly is absent in *Omphalosaurus*, an ichthyopterygian affinity of *Omphalosaurus* is likely.

Early Triassic ichthyopterygians

Mazin (1986) suggested that *Omphalosaurus* and *Grippia* were closely related, because both possessed large shield shaped frontals and several rows of teeth in the posterior part of the jaw. The *Grippia* material observed from the Grippia bonebed show vertebral centra with similar morphology as observed in the centra of *Omphalosaurus* (Fig. 16). For *Grippia*, as in *Omphalosaurus*, the rib facets are confluent with the anterior rim of the centra. This is easily observed in the *Grippia* cervical PMO 230.211 (Fig. 16B) and *Omphalosaurus* cervical PMO 229.905 (Fig. 18C3). The typical shield-shape of the cervicals and dorsals in posterior view described for *Omphalosaurus*, as seen in the dorsal centra PMO 229.907 (Fig. 19B2) is also present in *Grippia*. A keel on the ventral surface of the centra is present in both genera, which is well preserved in cervical PMO 229.904 of *Omphalosaurus* (Fig. 23A2). What differs between the two is the size, centra being longer than high in *Grippia*, and a patch of periosteal bone between the apophysis and anterior rim of the centra in the presumable anterior dorsals of *Grippia*. The patch of periosteal bone is clearly visible in PMO 230.212 (Fig. 16C). The caudals are more rounded in anteroposterior face for *Grippia*, with a

prominent ridge in lateral view, mid-dorsoventrally, that is anteroposteriorly oriented, as observed in PMO 230.213 (Fig. 16D). These features are not observed in any of the centra of *Omphalosaurus*.

Ji et al. (2015) placed *Grippia* in the clade Grippioidea with *Gulosaurus* and *Utatusaurus*. *Gulosaurus* was first described as *Grippia* but different from *Grippia longirostris* by Brinkman et al. (1992). Three autapomorphies were noticed by Cuthbertson et al. (2013) who erected the genus *Gulosaurus*. *Gulosaurus* have rounded tooth crowns anteriorly, similar to *Omphalosaurus* as observed in premaxilla PMO 229.922 (Fig. 6 B2). This differs from other Early Triassic species as *Grippia*, *Utatusaurus*, *Chaohusaurus*, *Thaisaurus* and *Parvinator*, which have cone shaped crowns. Centra of *Gulosaurus* are deeply amphicoelous, with double rib articulation in the cervicals and single in the dorsals. This is similar to *Omphalosaurus* and *Grippia*, as observed in the centra pictured in figs. 16 (*Grippia*), 18 and 19 (*Omphalosaurus*). The cervicals and dorsals of *Gulosaurus* are discoidal (Brinkman et al. 1992), similar to *Omphalosaurus* (Table 1, Fig. 17). This differs from *Grippia*, *Utatusaurus* and *Chaohusaurus* where the centra are longer than high (Wiman 1928; Mazin 1981; Maisch & Matzke 2000). This suggests that *Omphalosaurus* and *Gulosaurus* had more derived characters than *Grippia*, *Utatusaurus* and *Chaohusaurus*.

Brinkman et al. (1992) stated that *Utatusaurus* (Shikama et al. 1978) showed teeth without folding of the dentine, so-called plicidentine. Motani (1999) suggested plicidentine as a possible basal synapomorphy for the Ichthyopterygia, but plicidentine is not confirmed in *Utatusaurus* and *Parvinator* (Motani 1999). Plicidentine was suggested present in *Omphalosaurus* by Wiman (1910) but was only observed in a few specimens and was later suggested as irregularities in the dentine from the attachment to the bone (Motani 2000). No plicidentine are observed in any of the dental fragments in the collection described in this thesis.

Brinkman et al. (1992) described striations on the bone surface of *Utatusaurus*, but unfortunately no picture was present in the paper. This may be comparable to the suggested vascular canals observed on the periosteum of *Omphalosaurus*, as seen on the surface of centrum PMO 230.210 (Fig. 15). The cancellous organization of the bone structure observed in *Omphalosaurus* is according to Nakajima et al. (2014) also observed in *Utatusaurus*

hataii. These two species are then the first known marine reptiles to have possessed this specialization, which are assumed to be an adaptation to open marine environment (Nakajima et al. 2014).

Tholodus and *Xinminosaurus* also possess rounded tooth crowns, but these greatly differ from *Omphalosaurus*, especially in the enamel microstructure (Sander 1999; Arkhangelsky et al. 2016). *Xinminosaurus* is thought to have an edentulous snout, with rounded crushing teeth on the maxilla and posterior part of dentary (Jiang et al. 2008). Crushing teeth on the posterior part of the dentary is observed from the Spitsbergen material in dentary PMO 229.919 (Fig. 14A). *Xinminosaurus* was identified as an ichthyopterygian by Jiang et al. (2008) by the presence of a caudal peak, which is here also suggested for *Omphalosaurus* based on caudal centra PMO 229.914 (Fig. 21D).

The humeri of *Xinminosaurus* show a flange on the anterior edge. This feature is common in primitive ichthyopterygians (Brinkman et al. 1992), and was described for *Omphalosaurus* by Sander and Faber (1998) and Mazin (1983). It is worth noticing that the humerus assumed belonging to *Omphalosaurus* was based on comparison to the postcranial material assigned to *Pessopteryx nisseri* by Wiman (1910). As already mentioned, these humeri were also used in the study of bone histology by de Buffrenil and Mazin (1990). Preserved articulated limb elements of *Omphalosaurus* is needed to determine whether the postcranial bones of Wiman (1910) belongs to *Omphalosaurus* or not.

5. Conclusion

The *Omphalosaurus* material described from Spitsbergen is unique in the amount of material, size range and relatively good preservation, despite all material collected as isolated bones. Three different morphologies of *Omphalosaurus* are suggested present in the Spitsbergen material based on the dentaries. The jaw fragments show unusual features such as tooth wear in the assumed symphysis, a loose unossified symphysis and unfinished bone surfaces in lateral view of the tooth-bearing bones. The assumed premaxilla consists of larger and more irregularly placed teeth, where in the dentary the teeth were mainly located along the symphysis. A possibility is that *Omphalosaurus* was at the transition between fully toothed and edentulous jaw, where the unfinished surfaces of the bone were covered by some sort of tissue in life.

Even though much of the morphology considering the skull and appendicular skeleton is unknown in *Omphalosaurus*, an ichthyopterygian affinity seems possible based on the vertebral column described for the first time in this study. The vertebrae centra were identified as *Omphalosaurus* from the very porous bone structure and by being deeply amphicoelous. Of the 14 characters by Ji et al. (2015) used to diagnose the ichthyopterygia, 4 is suggested as likely present in *Omphalosaurus*; nasal anteriorly extending beyond external naris, neural spine articulation in tail present, caudal peak present and tail stem count $\frac{1}{2}$ or more than that of the presacral count.

Omphalosaurus is probably more specialized than many of the basal Ichthyopterygians due to the presence of discoidal vertebrae centra and a caudal peak, which are thought to be a derived feature of the ichthyopterygia (Motani et al. 1996; Sander 2000). Based on the vertebral column it is suggested that *Omphalosaurus* was at the transition between anguilliform and thunniform swimming mode. Together with the unique cancellous bone histology, this supports an animal living in an open water environment (de Ricqlès & de Buffrenil 2001).

Of the Early Triassic ichthyopterygians, centra of *Omphalosaurus* show morphological features similar to centra of *Grippia*, except that the centra of *Grippia* are cylindrical while those of *Omphalosaurus* are discoidal. Centra of *Omphalosaurus* are much larger than those of *Grippia*. A relationship between the two is suggested, where *Omphalosaurus* is more specialized than *Grippia* due to lack of periosteal bone surfaces and centra being discoidal. *Gulosaurus* has discoidal centra and cylindrical teeth, more similar to *Omphalosaurus* than other Early Triassic ichthyopterygians. *Utatusaurus* is the only ichthyopterygian sharing the unique cancellous bone structure observed in *Omphalosaurus*. Centra of *Utatusaurus* are cylindrical, and *Utatusaurus* might be a related, less derived, ichthyopterygian.

6. References

- Arkhangelsky, M.S., Zverkov, N.G., Zakharov, Y.D. & Borisov, I.V. 2016: On the first reliable find of the genus *Tholodus* (Reptilia: Ichthyopterygia) in the Asian Peripheral Area of the Panthalassic Ocean. *Paleontological Journal*, 50, 78-86.
- Brinkman, D.B., Zhao, X. & Nicholls, E.L. 1992: A primitive ichthyosaur from the Lower Triassic of British Columbia, Canada *Palaeontology*, 35, 465-474.
- Buchan, S.H., Challinor, A., Harland, W.B. & Parker, J.R. 1965: The Triassic stratigraphy of Svalbard. *Norsk Polarinstitutt Skrifter*, 135, 1-94.
- Buchholtz, E.A. 2001: Swimming styles in Jurassic ichthyosaurs. *Journal of Vertebrate Paleontology*, 21, 61-73.
- Cox, C.B. & Smith, D.G. 1973: A review of the Triassic vertebrate faunas of Svalbard. *Geological Magazine*, 110, 405-418.
- Cuthbertson, R.S., Russell, A.P. & Anderson, J.S. 2013: Cranial morphology and relationships of a new grippidian (Ichthyopterygia) from the Vega-Phroso Siltstone Member (Lower Triassic) of British Columbia, Canada. *Journal of Vertebrate Paleontology*, 33, 831-847.
- Dalla Vecchia, F.M. 2004: First record of the rare marine reptile *Tholodus schmidi* from the Middle Triassic of the Southern Alps. *Rivista italiana di Paleontologia e Stratigrafia*, 110, 479-492.
- Dallmann, W.K. 2015: *Geoscience Atlas of Svalbard*. Edited by Dallmann, W.K. Norwegian Polar Institute Report Series 148, Norwegian Polar Institute, Tromsø, Norway, 292 pp.
- de Buffrenil, V. & Mazin, J.-M. 1990: Bone Histology of the Ichtyosaurs: Comparative Data and Functional Interpretation. *Paleobiology*, 16, 435-447.
- de Ricqlès, A. & de Buffrenil, V. 2001: Bone histology, heterochronies and the return of Tetrapods to life in water: where are we? In Mazin, J.-M. & de Buffrenil, V. (eds.):

- Secondary adaptation of tetrapods to life in water*, 289–310, Verlag Dr. Friedrich Pfeil, Munich.
- Houssaye, A., Scheyer, T.M., Kolb, C., Fischer, V. & Sander, P.M. 2014: A new look at ichthyosaur long bone microanatomy and histology: implications for their adaptation to an aquatic life. *PLOS ONE*, 9, 1-10.
- Huene, F.v. 1951: Eine neue Ichthyosaurier-Gattung der mittleren Trias. *Neues Jahrbuch für Geologie und Paläontologie*, 94, 80-92.
- Huene, F.v. 1956: *Paläontologie und Phylogenie der Niederen Tetrapoden*, Gustav Fischer Verlag, Jena, XII + 716 pp.
- Hulke, J.W. 1873: Memorandum on some fossil vertebrates collected by Swedish expeditions to Spitzbergen in 1864 and 1868. *Bihang till Kungliga Svenska Vetenskaps Akademiens Handlingar*, 1, Afdeling IV, 9, 1-11.
- Ji, C., Jiang, D.-Y., Motani, R., Rieppel, O., Hao, W.-C. & Sun, Z.-Y. 2015: Phylogeny of the Ichthyopterygia incorporating recent discoveries from South China. *Journal of Vertebrate Paleontology*, 36, DOI:10.1080/02724634.02722015.01025956.
- Jiang, D., Motani, R., Hao, W., Schmitz, L., Rieppel, O., Sun, Y. & Sun, Z. 2008: New primitive ichthyosaurian (Reptilia, Diapsida) from the Middle Triassic of Panxian, Guizhou, southwestern China and its position in the Triassic biotic recovery. *Progress in Natural Science*, 18, 1315-1319.
- Korneisel, D., Gallois, R.W., Duffin, C.J. & Benton, M.J. 2015: Latest Triassic marine sharks and bony fishes from a bone bed preserved in a burrow system, from Devon, UK. *Proceedings of the Geologists' Association*, 126, 130-142.
- Kuhn, O. 1934: Pars 63: Ichthyosauria. In Quenstedt, W. (ed.): *Fossilium Catalogus 1: Animalia* 1-75, W. Junk, Berlin.
- Lieberman, D.E. & Crompton, A.W. 2000: Why fuse the mandibular symphysis? A comparative analysis. *American journal of physical anthropology*, 112, 517-540.
- Lundschieen, B.A., Høy, T. & Mørk, A. 2014: Triassic hydrocarbon potential in the Northern Barents Sea; integrating Svalbard and stratigraphic core data. *Norwegian Petroleum Directorate Bulletin*, 11, 3-20.

- Maisch, M.W. 2010: Phylogeny, systematics, and origin of the Ichthyosauria - the state of the art. *Palaeodiversity*, 3, 151-214.
- Maisch, M.W. & Lehmann, J. 2002: A new basal omphalosaurid from the Middle Triassic of Germany. *Neues Jahrbuch für Geologie und Palaontologie-Monatshefte*, 513-525.
- Maisch, M.W. & Matzke, A.T. 2000: *The Ichthyosauria*. Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie), 298, 159 pp.
- Maxwell, E.E. & Kear, B.P. 2013: Triassic ichthyopterygian assemblages of the Svalbard archipelago: a reassessment of taxonomy and distribution. *GFF*, 135, 85-94.
- Mazin, J.-M. 1981: *Grippia longirostris* Wiman, 1929, un Ichthyopterygia primitif du Trias inférieur du Spitsberg. *Bulletin du Muséum National d'Histoire Naturelle, Paris, C, Série IV*, 3, 317-340.
- Mazin, J.-M. 1983: *Omphalosaurus nisseri* (Wiman, 1910), un ichthyoptérygien à denture broyeuse du Trias moyen du Spitsberg. *Bulletin du Muséum national d'histoire naturelle, Paris, C, Série IV*, 5, 243-263.
- Mazin, J.-M. 1986: A new interpretation of the type specimen of *Omphalosaurus nevadanus* Merriam 1906. *Palaeontographica Abteilung A*, 195, 19-27.
- Mazin, J.-M. & Bucher, H. 1987: *Omphalosaurus nettarhynchus*, une nouvelle espèce d'Omphalosauridé (Reptilia, Ichthyopterygia) du Spathien de la Humboldt Range (Nevada, USA). *Comptes rendus de l'Académie des Sciences, Paris, Série II*, 305, 823-828.
- McGowan, C. 1992: The ichthyosaurian tail: sharks do not provide an appropriate analogue. *Palaeontology*, 35, 555-570.
- McGowan, C. & Motani, R. 2003: *Ichthyopterygia*. Edited by Sues, H.-D. Handbook of Paleoherpétology, Verlag Dr. Friedrich Pfeil, München, 175 pp.
- Merriam, J.C. 1906: Preliminary note on a new marine reptile from the Middle Triassic of Nevada. *University of California Publications, Bulletin of the Department of Geology*, 5, 71-79.
- Merriam, J.C. 1908: *Triassic Ichthyosauria, with special reference to the American forms*. Memoirs of the University of California, 1, The University Press, Berkeley, 155 pp.

- Merriam, J.C. 1911: Notes on the relationships of the marine saurian fauna described from the Triassic of Spitzbergen by Wiman. *University of California Publications, Bulletin of the Department of Geology*, 6, 317-327.
- Merriam, J.C. & Bryant, H.C. 1911: Notes on the dentition of *Omphalosaurus*. *University of California Publications, Bulletin of the Department of Geology*, 6, 329-332.
- Motani, R. 1999: Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology*, 19, 473-496.
- Motani, R. 2000: Is *Omphalosaurus* ichthyopterygian?—A phylogenetic perspective. *Journal of Vertebrate Paleontology*, 20, 295-301.
- Motani, R., Chen, X.-h., Jiang, D.-y., Cheng, L., Tintori, A. & Rieppel, O. 2015a: Lunge feeding in early marine reptiles and fast evolution of marine tetrapod feeding guilds. *Scientific reports*, 5, 1-8.
- Motani, R., Ji, C., Tomita, T., Kelley, N., Maxwell, E., Jiang, D.-y. & Sander, P.M. 2013: Absence of suction feeding ichthyosaurs and its implications for Triassic mesopelagic paleoecology. *PLOS ONE*, 8, 1-11.
- Motani, R., Jiang, D.-Y., Chen, G.-B., Tintori, A., Rieppel, O., Ji, C. & Huang, J.-D. 2015b: A basal ichthyosauriform with a short snout from the Lower Triassic of China. *Nature*, 517, 485-488.
- Motani, R., You, H. & McGowan, C. 1996: Eel-like swimming in the earliest ichthyosaurs. *Nature*, 382, 347-348.
- Mørk, A., Elvebakk, G., Forsberg, A.W., Hounslow, M.W., Nakrem, H.A., Vigran, J.O. & Weitschat, W. 1999: The type section of the Vikinghøgda Formation: a new Lower Triassic unit in central and eastern Svalbard. *Polar Research*, 18, 51-82.
- Nakajima, Y., Houssaye, A. & Endo, H. 2014: Osteohistology of the Early Triassic ichthyopterygian reptile *Utatsusaurus hataii*: Implications for early ichthyosaur biology. *Acta Palaeontologica Polonica*, 59, 343-352.
- Peyer, B. 1939: Über *Tholodus schmidi* H. V. Meyer. *Palaeontographica*, 90, 1-47.

- Richter, M. & Toledo, C.E.V. 2008: The first Triassic lungfish from South America (Santa Maria Formation, Paraná Basin) and its bearing on geological correlations within Pangaea. *Geological Society, London, Special Publications*, 295, 43-54.
- Romer, A.S. 1956: *Osteology of the Reptiles*, The University of Chicago Press, Chicago, 772 pp.
- Romer, A.S. 1966: *Vertebrate paleontology*. 3 ed, The University of Chicago Press, Chicago, 468 pp.
- Sander, P.M. 1999: *The microstructure of reptilian tooth enamel: terminology, function, and phylogeny*, 38, Münchner geowissenschaftliche Abhandlungen, 102 pp.
- Sander, P.M. 2000: Ichthyosauria: their diversity, distribution, and phylogeny. *Paläontologische Zeitschrift*, 74, 1-35.
- Sander, P.M., Chen, X., Cheng, L. & Wang, X. 2011: Short-snouted toothless ichthyosaur from China suggests Late Triassic diversification of suction feeding ichthyosaurs. *PLOS ONE*, 6, 1-10.
- Sander, P.M. & Faber, C. 1998: New finds of *Omphalosaurus* and a review of Triassic ichthyosaur paleobiogeography. *Paläontologische Zeitschrift*, 72, 149-162.
- Sander, P.M. & Faber, C. 2003: The Triassic marine reptile *Omphalosaurus*: osteology, jaw anatomy, and evidence for ichthyosaurian affinities. *Journal of Vertebrate Paleontology*, 23, 799-816.
- Sander, P.M. & Mazin, J.-M. 1993: The paleobiogeography of Middle Triassic ichthyosaurs: the five major faunas. *Paleontologia Lombarda, Nuova Serie*, 2, 145-152.
- Shikama, T., Kamei, T. & Murata, M. 1978: Early Triassic ichthyosaur, *Utatsusaurus hataii* gen. et sp. nov., from the Kitakami Massif, Northeast Japan. *東北大學理科報告地質學 [Tohoku University, Science Report, 2nd Series (Geology)]*, 48, 77-92.
- Stensiö, E.A. 1921: *Triassic fishes from Spitzbergen*, Part I, A. Holzhausen, Vienna, 307 pp.
- Suan, G., Föllmi, K.B., Adatte, T., Bomou, B., Spangenberg, J.E. & Van De Schootbrugge, B. 2012: Major environmental change and bonebed genesis prior to the Triassic–Jurassic mass extinction. *Journal of the Geological Society*, 169, 191-200.

- Sues, H.-D. 2003: An unusual new archosauromorph reptile from the Upper Triassic Wolfville Formation of Nova Scotia. *Canadian Journal of Earth Sciences*, 40, 635-649.
- Tichy, G. 1995: Ein früher, durophager Ichthyosaurier (Omphalosauridae) aus der Mitteltrias der Alpen. *Geologisch-paläontologische Mitteilungen Innsbruck*, 20, 349-369.
- Vigran, J.O., Mangerud, G., Mørk, A., Worsley, D. & Hochuli, P.A. 2014: *Palynology and geology of the Triassic succession of Svalbard and the Barents Sea*. Special Publication, 14, Geological Survey of Norway 270 pp.
- Wiman, C. 1910: Ichthyosaurier aus der Trias Spitzbergens. *Bulletin of the Geological Institution of the University of Upsala*, 10, 124-148.
- Wiman, C. 1916: Notes on the marine Triassic reptile fauna of Spitzbergen. *University of California Publications, Bulletin of the Department of Geology*, 10, 63-73.
- Wiman, C. 1928: Eine neue marine Reptilien-Ordnung aus der Trias Spitzbergens. *Bulletin of the Geological Institute of the University of Uppsala*, 22, 183-196.
- Wintrich, T. 2014: The first record of the enigmatic marine reptile *Omphalosaurus* from Poland (Middle Triassic) of the Germanic Basin, Rheinische Friedrich-Wilhelms-Universität Bonn, 33 pp.
- Woodward, A.S. 1932: *Textbook of Paleontology by K.V. Zittel*, 2, Macmillan & Co, London, 464 pp.

7. Appendix

Group	Position in column	Centra in total	Lenght (mm)	Width (mm)	Height (mm)
Atlas	Atlas	3	5.47 – 14.11	10.7 – 25.24	8.82 – 24.37
Cervicals	Cervicals	4	9.1 – 21.27	17.07 – 34.87	16.65 – 29.51
PMO 229.906	Anterior dorsal	8	12.27 – 23.71	19.21 – 38.14	18.39 – 35.75
PMO 229.907	Anterior dorsal	13	10.35 – 22.33	15.06 – 38.53	14.02 – 34.99
PMO 229.908	Anterior dorsal	8	8.75 – 17.8	15.1 – 31.84	14.62 – 29.27
PMO 229.909	Posterior dorsal	36	12.13 – 25.34	20.9 – 44.15	22.4 – 43.63
PMO 229.910	Posterior dorsal	1	20.75	33.31	46.94
PMO 229.911	Anterior caudal	6	13.05 – 19.67	18.35 – 33.6	21.15 – 39.04
PMO 229.912	Anterior caudal	8	9.19 – 28.67	13.95 – 52.27	19.63 – 58.61
PMO 229.913	Anterior caudal	8	6.8 – 13.7	8.55 – 21.62	11.31 – 31.25
PMO 229.914	Anterior caudal	3	8.52 – 19.8	5.35 – 21.47	10.31 – 32.66
PMO 229.915	Anterior caudal	4	14.39 – 35.2	15.22 – 54.62	22.82 – 80.19
PMO 230.135	Posterior caudal	29	6.51 – 20.33	3.41 – 25.28	7.31 – 40.63
PMO 230.136	Posterior caudal	18	5.82 – 18.72	2.62 – 10.43	4.39 – 19.01
PMO 230.137	Posterior caudal	50	4.99 – 15.1	1.91 – 9.4	4.32 – 16.82
PMO 230.138	Posterior caudal	41	4.21 – 13.8	2.3 – 7.3	3.64 – 17.19

Appendix 1: Count and size range of the identifiable centra of *Omphalosaurus* sp. from Marmierfjellet, Spitsbergen (Spathian). The groups are based on the pictured and described centra (Figs. 18, 19, 20, 21, 22, 23).