

Master Thesis, Department of Geosciences

A study of the propodial morphology on Late Jurassic plesiosaurs from Spitsbergen

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Abstract

It has been generally assumed amongst paleontologist studying the vast fossil record of marine reptiles, that Late Jurassic plesiosaurs have a specific characteristic morphology and that the humeri and femora can be easily distinguished, the latter being smaller of the two. A newly excavated locality yielding plesiosaurs in the Late Jurassic Slottsmøya Member of the Agardhfjellet Formation, Spitsbergen contradicts this observation and several new species shed new light on earlier theories of functional morphology. These results are supported by measurements, statistics and comparisons with contemporary species from the Oxford Clay Formation in England. The propodials of the Slottsmøya Member have the reverse proportional relationship than previously seen in the Late Jurassic plesiosaurs, with the femora being significantly larger in length and distal width than the humeri. This is presumably implied by a functional adaption to the ecology of the Boreal Sea.

1.1. Introduction

Plesiosaurs

Plesiosaurs (Sauropterygia: Plesiosauria) were successful inhabitants of the Mesozoic ocean, thriving from the Late Triassic up to the Late Cretaceous when they became extinct in the K-T event. During the Early Jurassic they became cosmopolitans, and were a morphologically diverse clade, with a temporal span of approximately 135 million years (Druckenmiller & Russell 2008; Ketchum & Benson 2010). Plesiosaurs were marine and carnivorous tetrapods, derived from basal sauropterygians, a group with a variety of semi-aquatic forms like nothosaurs, placodonts, pachypleurosaurs and pistosaurs inhabiting the oceans in the Triassic Period. Their exact origin is somewhat uncertain among this stem group (Caldwell 2002; Rieppel et al. 2002; Smith 2008; Carpenter et al. 2010). The phylogeny of the plesiosaurs is under constant revision, and the latest analysis by Ketchum and Benson (2010) presents 66 different taxa. With the exception of five taxa, they are divided into the two superfamilies Plesiosauroidea and Pliosauroidae. The former are characterized as very large reptiles, up to 15 meters in length (Chatterjee & Small 1989), and had a streamlined body, with long necks, a small skull and a rigid trunk. Pectoral and pelvic ventral plates were expanded and reinforced, together with a tightly packed gastralia to receive the insertions of the large muscles moving the limbs (Mazin 2001; Carpenter et al. 2010). They had four active, flipper-like limbs, and propelled solely by limb locomotion (Caldwell 2002). Pliosauroidae are characterized by large heads and short necks, and are larger than the plesiosaurs (Brown 1981). Pliosauroids have larger hind limbs than fore limbs, while the opposite is the common presumption in plesiosaurs (Tarlo 1957).

The description of the life of plesiosaurs has been varied and colorful, and compared with both crocodiles and snakes (Zarnik 1925). They preyed on cephalopods and fish attacking from below based on the position of their eyes (Carroll 1985; Everhart 2007). Their neck was much less flexible than previously suggested (Cruickshank & Fordyce 2002; Zammita et al. 2008). Since the plesiosaurs were cosmopolitans, it has been argued that they could be endothermic (Rich et al. 2002; Bernard et al. 2010).

Limb morphology and locomotion in plesiosaurs

Plesiosaurs are secondarily adapted to a fully-aquatic life, with limbs derived from a basal tetrapod limb (Caldwell 2002). This can be recognized in primitive sauropterygians which probably swam by an anguilliform movement, a lateral undulation of the body (Storrs 1993).

The plesiosaurs adaption to swimming is characterized by elaborated, hyperphalangic limbs with the extremities covered by a connective tissue, giving the external appearance of a flipper-like wing. No spacing between the epipodials and mesopodials stiffens the intralimb and nearly all flexibility is lost. An increased interlocking between the thoracic vertebrae stiffens the body as well. The neck is exposed to frequent lengthening in different genera. (Storrs 1993; Hall 2006). Plesiosaurs did not use undulation of the tail for propulsion, and shortening of the tail, used in steering the animal, is seen in all taxa (Chatterjee & Small 1989; Hall 2006). Thus, they favored limbs over the undulation of body or tail (Storrs 1993). The similar size of the humeri and femora suggests that both were used in locomotion, although the morphology of the humeral and femoral heads and of the glenoid articulations implies restricted movement above the horizontal axis (Tarsitsano & Riess 1982). Locomotion with four active limbs can only be found in pliosaurs and plesiosaurs amongst swimming vertebrates, and is an unusual functional response to a secondary invasion of the sea (Storrs 1993). Living aquatic tetrapods (e.g. otariid pinnipeds, sea turtles, penguins) use only the fore limbs for propulsion and have a distinctly different morphology between the fore limb and the hind limb. The latter are mainly used for steering and reduction of drag (Massare 1994).

Earlier works concerning limb morphology are various and extend back to the early 1800`s. In order to investigate the functional adaption the different morphology of the Slottsmøya Member plesiosaur limb, a review of theories on sub-aqueous locomotion in plesiosaurs are represented.

William Conybeare and Henry Thomas de La Beche were the first to be intrigued by the four limbs of the plesiosaurs, and wrote that their movement would resemble that of a wing in flight. This was based on disarticulated plesiosaurs (De la Beche & Conybeare 1821; Conybeare 1822). The first published description of a complete plesiosaur, was by Conybeare in 1824 based on a discovery made by Mary Anning that same year (Halstead 1969). Andrews (1913), based on the size of their limbs, concluded that Elasmosaurs used their fore limb as the main means of propulsion while the pliosaurs used their hind limb.

Brown (1981) diagnosed Plesiosauroidea with massive propodials, and humerus generally larger than femur. The reverse conclusion was made for the pliosaurs (Andrews 1913; Brown 1981; O'Keefe 2002).

The first functional analysis on the locomotion of plesiosaurs was made by Watson in 1924. He proposed a model illustrating the limbs functioning as oars, rowing through the water analogous to rowing a boat. This theory remained unchallenged for over 50 years (Watson 1924; Robinson 1975; Carpenter et al. 2010), due to the thorough work done on the muscular reconstructions of the pectoral girdle and the humerus. Tarlo (1957), studying pliosaurs, concluded that these relied on the hind limbs for propulsion, and used their forelimbs for both steering and stroke. This was based on the size of the larger hind limbs and smaller fore limbs in pliosaurs. The propulsive stroke of the two limbs would therefore differ. In 1975, Robinson used hydrodynamic principles in her argumentation that plesiosaurs had developed their limbs into hydrofoil-shaped wings, resembling other aquatic tetrapod groups, although these use solely their fore limb for "flying". Taristano and Riess (1982) proposed a model of flight in which the downstroke is the powerstroke, with a passive upstroke due to hydrodynamic force. Here the fore limb and hind limb would move in an alternating pattern to each other (Carpenter et al. 2010). In 1984, Godfrey compared the stroke cycle of plesiosaurs with that of otariid pinnipeds, employing a recovery stroke, feathering their limbs horizontally through the water, before beginning a powerstroke down and aft. He argued that morphological similarities in fore- and hind limb suggested they both functioned in a similar manner moving synchronously. The latest study done on plesiosaur locomotion was by Carpenter et al. (2010). They revised and combined previous theories in their experiment concluding that all four limbs would be active in a propulsive force, swimming semi-synchronized. The hind limb also helped steering and simultaneously participated in the propulsive force of the animal. They also concluded in their experiment that the reduction of the mesopodial length and the developed hyperphalangy, caused a significant improvement in swimming effectiveness and efficiency, being able to wrist-flick the tip of the limbs in both the upper and lower stage of the stroke.

Geological setting

The excavation sites of the studied propodials of the Plesiosauroidea are located on Spitsbergen, Norway, surrounded by the Barents Sea. This locality is in the Sassenfjorden area of central Spitsbergen (Hammer et al. 2011), (Fig.1). Stratigraphically, the material is from the Adventsdalen Group, Janusfjellet subgroup, Agardhfjellet Formation, the Slottsmøya Member (Parker 1967; Dypvik et al. 1991a), which is of mid-Volgian age (Hammer et al. 2011). During this period, Spitsbergen is thought to have been positioned at 70° North latitude compared with today's, 78° North (Ditchfield 1997; Vajda & Wigforss-Lange 2009).

The Jurassic Period was characterized as a warm and humid world, with high CO₂ concentrations and ice-free poles. The climatic zones were few and extended, with weak differentiations (Vajda & Wigforss-Lange 2009). The studied animals lived on an extensive marine shelf setting, covering the Barents and the Kara Sea, with a varying depositional environment. The dominant deposits in the Agardhfjellet Formation during this period were mudstone and shales. (Nagy et al. 1988; Smelror et al. 2009; Hammer et al. 2011). This was the result of a transgressive regime dominating the Late Jurassic and mostly linked to local tectonism, indirectly caused by extensive stresses initiated by the break-up of Pangea, which caused magmatic activity and plate movements that peaked during the Late Jurassic (Dorè 1991; Vajda & Wigforss-Lange 2009). Water depths are estimated at approximately 200 meters (Johnson & Baldwin 1996), suggestive of a shallow Boreal Sea, with a temperature range from 11 - 21° C (Price & Mutterlose 2004). The inclination of the Earth's rotational axis was much the same during Late Jurassic as of today. The seasonal cycles would therefore have remained more or less the same, including the amount of daylight (Rich et al. 2002). Bottom water conditions were generally low in oxygen levels, ranging from dysaerobic to anoxic (Smelror et al. 2009). The Volgian nectic fauna of the Slottsmøya Member consisted primarily of marine reptiles, here ichthyosaurs, pliosaurs and plesiosaurs, and macro-invertebrates such as ammonites and large coleoid cephalopods. In the field the Slottsmøya Member consists mostly of weathered, organic rich paper shales with discontinuous silt and sideritic beds with concretions of siderite and dolomite. (Dypvik et al. 1991a; Hammer et al. 2011).

This study

The adaption of plesiosaurs to the marine habitat is still unclear today and theories on locomotion and functional morphology change as new specimens are found prepared and described giving leading to new interpretations and phylogenies.

The first plesiosaurian remains in Spitsbergen were recorded as early as 1914 (Wiman 1914), and today the Volgian stratigraphic successions are one of the richest occurrences of marine reptile discoveries in recent times with over 60 specimens of marine reptiles mapped, and 13 plesiosaurs excavated (E.M. Knutsen pers. com.). It is also one of the few known occurrences from high paleolatitudes (Hurum et al. 2010; Hurum & Knutsen 2010).

The aim of this study is to shed light on the unique plesiosaurs from the Slottsmøya Member and to discuss their locomotary and functional adaption to the aquatic environment in the Boreal Sea during the Late Jurassic. The morphological and functional differences between the humeri and femora are examined and comparisons are made with contemporary specimens from the Oxford Clay and the Kimmeridgian Clay Formations in England. The present material studied from Spitsbergen represents four different species. Morphological details allow new questions on plesiosaurs never previously asked.

1.2. Material and Methods

Eight plesiosaurs (clade Sauropterygia, order Plesiosauria, superfamily Plesiosauroidea) have recently been excavated from the Slottsmøya Member on Spitsbergen and are used in this study. All are from the mid-Volgian (Hammer et al. 2011). The plesiosaurs occur mainly above the echinoderm bed, the majority 14 meters above this (Fig. 2). All specimens examined and described were prepared free of the matrix prior to this study, and have been catalogued with the prefix PMO and deposited in the collections of the Natural History Museum (Geology), in Oslo. The collection consists of seven femora, five humeri, three ulnae, two radii, two tibiae and four fibulae. In the field each specimen was found articulated or associated with other body parts allowing humeri and femora to be clearly recognizable. Before removal from the locality, all specimens, partly separated from the surrounding rock, were encased in a shell of plaster-of-Paris, the bones beneath being left unprepared and covered with matrix to prevent damage during transport.

In the laboratory the top side plaster casing was removed using an electrical handsaw before the work could begin to remove shale surrounding the fossil. This process was done with a brush and spoon close to the fossil, and with a specialized vacuum cleaner for faster cleansing in stabilized areas. Where necessary, matrix was left to some extent to help in stabilizing the fossil before turning the specimen over. When the skeletal bones are exposed they were first stabilized with mowelite and then a new plastering of the stabilized and prepared parts was done before the specimen turned and the reverse side plaster removed and preparation of skeletal bones carried out as before. In many cases where gypsum and shale covered the bones cleaning was done using a variety of tools including a *scalpel* together with *air abrasives* and *vibro hammer* on smaller and more delicate areas. Dental scalers (type *guenther*) were also used on various occasions during the cleaning of the bone before loose pieces were glued together using the cyanoacrylate *GEODUR* of three different thicknesses.

All propodials, with epipodials were photographed where present, using a Canon EOS 550D camera held perpendicular to the fossil and from directions dorsal and postaxial. These were the only views used herein although all bones were photographed in 6 different views. The photos are further processed in Adobe Photoshop CS4 and Adobe Illustrator CS4 for final finishing. All the figures carry a 5 cm scale to show the right proportions of the propodials

and epipodials. A note to this is the left femur in PMO 216.838. Since the bone is broken into two its size has been adjusted to being the same as the right femur.

Some of the illustrations are mirrored for the purpose of comparable orientation. The limbs are organized into morphotypes in a sequence of juvenile to adult based on the morphological characteristics of the bones.

Following Hammer et al. (2011), the stratigraphical occurrence of the fossil is referred to as below, at or above the echinoderm bed, and below, at or above the dorsoplanites bed (Fig. 2).

In the appendix, each propodial is measured in mm from anterior–posterior in length, diaphysis in mm, distal epiphysis, both anterior-posterior and dorsal-ventral, and the head of the femur/humerus both anterior-posterior and dorsal-ventral (Bardet et al. 1999) (Tab. 1).

The measurements made on the PMO 216.838, left femur, and PMO 218.377 and the epipodials in the description are measured in cm for the simplicity in the text. In the discussion centimeters are also used. Where possible, most of the lengths were measured with a digital caliper.

The angles on the epipodials are only shown in the adult specimens. This is because of the rounded margins dorso-ventrally in the juvenile epipodials. This makes the measurements uncertain for conclusions. On the adult specimens of PMO 216.863, PMO 212.662, PMO A 27745 and PMO 218.377, the facets are fully developed with correct angles. The angles of the epipodials were measured using a protractor.

The comparisons have been made with contemporary Upper Jurassic species previously described from the Callovian of England. Two species from the Tithonian in England are known but these are disarticulated and difficult to compare with. The former are well described but uncertainty remains about the grade of articulation/association of the animals, together with uncertainties around the excavation sites (Tab. 3). Without this knowledge the comparisons are made assuming that the differentiation of the humeri and femora are correct. All the described comparisons made from contemporary species are described and/or figured in Andrews (1910), Brown (1981), Brown and Cruickshank (1994).

The mean measurements of the length and distal width are taken of the *Cryptocleidus eurymerus* (Phillips 1871), *Muraenosaurus leedsi* (Seeley 1874), *Tricleidus seeleyi* (Andrews 1909) and *Muraenosaurus beloclis* (Seeley 1892) and compared with the Slottsmøya Member

plesiosaurs. These measures are taken from the adult individuals. *C. eurymerus* NMH R. 2860 is described as a nearly adult. *C. eurymerus* include 4 humeri and 5 femora, *M. leedsi* include 8 humeri and 8 femora, *T. seeleyi* include 1 humerus and 1 femur, *M. beloclis* include 2 humeri and 1 femur. All the measurements are taken from Andrews (1910). The specimens from the Slottsmøya Member are however, of several species, and are therefore compared with the Oxford Clay plesiosaurs with the two juvenile humeri of SVB 1450 and left humerus of PMO 216.839. The femora used for comparisons are the adult right femur of PMO 216.838, and the juvenile femur of PMO 216.839. These are used instead of mean measurements to give a best possible impression of the general size in the Slottsmøya Member plesiosaurs. Single measurements instead of mean measurements are also carried out on the specimens of *M. beloclis* NMH R. 3698 and *T. seeleyi* NMH R. 3539, because the data only included one femur and/or humerus.

The measurements of the ratio to the propodials of the Slottsmøya Member plesiosaurs, compared with *M. leedsi*, *C. eurymerus*, *M. beloclis* and *T. seeleyi* (Andrews 1910) are obtained by calculating the ratio of the anterior-posterior width of the proximal head divided with the length of the propodial. The anterior-posterior width of the diaphysis and the anterior-posterior width of the epiphysis are also divided by the length of the propodial (Tab. 2). The PMO 216.838, left femur and PMO 218.377, humerus and femur are both unsuitable for measurements. It should also take into consideration that the PMO A 27745 are preserved without its proximal end.

Further statistics on the values calculated in Table 2 were carried out using Past, version 2.08 (Hammer et al. 2001). The values were plotted in PCA (Principle Components Analysis), a multivariate analysis tool. In PCA, the 6 different variables are plotted in a two-dimensional plane, where the 6 dimensions (variables) are reduced to 2. Component 1 and 2 shows the axes of maximal variance (Hammer & Harper 2006). The x-axis represents 48% of the variance in the 6 variables, while the y-axis represents 23% of the variance in the 6 variables.

With the exception of the specimen SVB 1450, all material in the thesis is in the collections of the Natural History Museum in Oslo, Norway. Comparisons made with material from England for additional support, are from Andrews (1910) and listed accordingly in the text.

Abbreviations:

SVB: Svalbard Museum, Longyearbyen.

PMO: Paleontological Museum Oslo (now a part of Natural History Museum, University of Oslo).

PETMG: Geological Collections, Peterborough City Museum and Art Gallery, Priestgate, Peterborough PE1 1LF.

NMH: Natural History Museum, London.

HMG: Hunterian Museum, Glasgow.

C.M.N: The Castle Museum, Norwich.

M.M: Manchester Museum, University of Manchester.

1.3. Description

PMO 216.839

Juvenile associated specimen consisting of incomplete cranial remains, a nearly complete cervical vertebral series, a partial shoulder girdle, two dorsal vertebrate series, and a partial pelvic girdle. Excavation site was located 7 meters above the echinoderm bed (Fig.2). All three propodials exhibit a distal pre-postaxial expansion, and taper in dorso-ventral height in proximal-distal direction. This can be seen in all the propodials described. The juvenile status of the specimen is supported by the rounded distal margins without facets of the propodials, the space, presumably filled with cartilage due to lack of fusion between the propodials and the epipodials as seen on the articulated hind flipper, and the unfused neural arches and vertebral centra. The capitulum on all three propodials, the trochanter on the femur, and the tuberosities on the two humeri are juvenile and assumed consisting of cartilage. No separation can be seen between the capitulum and the tuberosity/trochanter. Left humerus and right femur, have collapsed cones, and are compressed dorso-ventrally. All three propodials exhibit a wider pre-postaxial expansion than seen on the other propodials from the Slottsmøya Member. The femur is articulated with the epipodials. One of the humeri has intact epipodials, mesopodials and tarsals, although not articulated. The hind paddle is almost complete and articulated.

Humerus (Fig. 3F, 5B, 7B). Left. In dorsal view the distal-postaxial margin has a slightly sharper curve, than on preaxial side, marking the development of the expanded, distal flange seen postaxially in all the specimens (except right humerus in PMO 216.863 where its placed preaxially). The tuberosity is placed in preaxial direction of the head, whereas on the postaxial side, an indication of a muscle insertion is observed, and a small expanded piece of the capitulum. Normally, the tuberosity should be tilted on the postaxial side, as seen in the other described humeri. The length of preaxial and postaxial side of the humerus is approximately the same. In ventral view, the humerus has two collapsed cones (placed mirrored to each other, expanding in proximal/distal direction), making the whole side concave in the shape of the two cones originating from the diaphysis (for a further description of a cone and its inner structure see Liebe (2011). This collapse covers the full length of the bone both distally and proximally, and hides the bones original ventral margins. The collapse decreases in a 35 degree straight angle from beginning to the proximal end of the presumed capitulum.

The ventral side appears more flattened from the distal end of capitulum towards the epiphysis than the dorsal side. In preaxial/postaxial view, the dorso-ventral height is highest a little proximal of the diaphysis, and decreases in both distal and proximal direction. From the highest point of the dorso-ventral height to the humeral head, the distance is 1/3 down the shaft towards the distal end. The tuberosity extends dorsally in producing a smooth depression between the highest point on the dorsal side and to the proximal end of tuberosity. In distal view, the epiphysis is rough, rounded and symmetrical, with a slightly longer postaxial flange. No signs of distinct facets can be seen. The thickness of the epiphysis is greatest at its centre, as seen in all of the described propodials. In proximal view, the tuberosity is flattened and preserved. The capitulum is collapsed. The tuberosity has a smooth expanding slope towards the assumed start of the presumed capitulum.

Humerus (Fig. 3E, 5C, 7C). Right. Approximately the same size as left humerus, with only small dimensional differences (Tab. 1). In dorsal view, the shape is nearly equal to the left humerus. A fracture in the proximal part of the bone has altered the overall shape when glued together. The tuberosity is angled postaxially, relative to the capitulum. A muscle insertion and expansion of the capitulum placed dorsal-preaxially as described on the left humerus. In ventral view, no collapsed cones have occurred like seen in the left humerus and the right femur of this specimen. The capitulum lies in preaxial direction, relative to the tuberosity. Some rugosities can be seen below the capitulum, indicating a muscle attachment. In preaxial/postaxial view, the postaxial side is a longer smooth curve than the preaxial where its curve has been interrupted by the fractures glued together. The highest dorso-ventral height is located on diaphysis, decreasing distally and proximally. In distal view, the epiphysis curves higher from the ground on the preaxial side. In proximal view, the head has a small amount of rugosities. The tuberosity is small with rounded margins. The collapsed capitulum forms a steep slope under the tuberosity.

Femur (Fig. 4G, 5D, 7D). Right. The femur is larger than the two humeri (Tab. 1). In dorsal view, the proximal end tilts postaxially, and the capitulum is slightly visible. Distal-postaxial to the capitulum the shaft has a large fossa, indicating muscle insertions as seen on the two humeri of the same specimen. The trochanter lies preaxially on the capitulum. In ventral view, the bone has collapsed like the left humerus, but to a lesser degree, affecting only one cone, from the diaphysis to the femoral head. The capitulum is placed preaxially, like the trochanter and has better developed rugosities than on the humeri. Muscle scars can be seen distal from

the capitulum. In preaxial/postaxial view, the postaxial side is longer, and convexes more distally than the shorter, preaxial side. The ventral side has a small, concave curve at diaphysis and below capitulum. Epiphysis and capitulum is aligned with the diaphysis ventrally. In distal view, the epiphysis is similar to the other propodials. The postaxial-distal flange is more expanded with a sharper curve than preaxially. Small amounts of rugosity can be seen dorsal/ventral. In proximal view, the trochanter and capitulum is tilted on the same lateral side, otherwise equal to the right humerus.

Epipodials (Fig. 4G, 9B1, 9B2). Both tibia and fibula have rounded margins in dorsal/ventral view and have less developed facets than the adult specimen.

Tibia. The tibia got four juvenile facets, but only three can clearly be observed. Is broken in two equally large parts and glued together. The measurements of the tibia are 5 cm anterior-posterior, 3,8 cm proximal-distal.

Fibula. The fibula also has three facets. The bone has been compressed dorso-ventrally and was found misplaced dorsally, leaving the proximal side to lie in the same position and shape as its dorsal side would. The measurements of the fibula are: anterior-posterior: 2,5 cm, proximal-distal: 4,8 cm.

SVB 1450

Juvenile associated specimen consisting of an incomplete skeleton, with a series of articulated cervical vertebrae, skull fragments, lower jaw and one fore limb. The excavation site was located 17,8 meters above the echinoderm bed (Fig. 2). Epiphysis is rounded, with a rough appearance. Capitulum and tuberosity is juvenile and presumed consisting of cartilage. No facets occurs on the propodial, solely the epipodials have developed facet traits.

Humerus (Fig. 3D, 5A, 7A) Left. In dorsal view, the propodial is symmetrical and rounded, viewing only a slight increase in the postaxial-distal expansion. The preaxial-distal margin is slightly more rounded. Muscle scars can be seen proximal-preaxial on the expansion of the capitulum that originates ventrally. In ventral view, muscle insertions are found postaxial-distal of the capitulum. Proximal-postaxially, a small, partly broken off expansion of the capitulum is observed. In preaxial/postaxial view, a small concave curve towards the distal end is seen on dorsal/ventral side. The tuberosity is small and expands slightly in proximal-ventral direction. In distal view, the epiphysis tapers postaxially. In proximal view, the

tuberosity is small, decreasing ventrally. The capitulum has a sharp transition ventral-proximal, decreasing dorsally. The capitulum is bigger than the tuberosity (and trochanter), as seen on all the propodials described below.

Epipodials (Fig. 3D, 9A1, 9A2). Articulated with the propodial. The epipodials exhibit rounded corners in dorsal/ventral view. Presumed cartilage fills the space between the radius, ulna, and the propodial. The ulna is smaller than the radius, a characteristic on all the humeri with epipodials described. The fifth metatarsal confirms the orientation of the postaxial-distal flange.

Radius. Three juvenile facets anterior-proximal, posterior-proximal and distal. The fourth are underdeveloped anterior-distally. The measurements of the radius: anterior-posterior: 6,7 cm, proximal-distal: 4,3 cm.

Ulna. Three partly developed facets located similar as radius. The measurements of the ulna: anterior-posterior: 4,9 cm, proximal-distal: 3,2 cm.

PMO 216.863

Adult articulated specimen consisting of an incomplete post-cranial skeleton. One humerus and one femur preserved. The excavation site was located 5 meter above the echinoderm bed (Fig. 2). Both propodials are twisted on the shaft from diaphysis till proximal end, making the positions of tuberosity/trochanter, capitulum is compressed. A small separation between tuberosity/trochanter confirms the adult stage. The humerus differs from the other humeri in the plesiosaurs of the Slottsmøya Member as the distal flange faces preaxial, not postaxial. Distinctive facets on epiphysis are adult on the humerus and femur. An articulated ulna is found, radius, tibia and fibula are missing.

Humerus (Fig. 3C, 6H, 8H). Right. In dorsal view, a piece of the humerus in the distal end, a piece of the shaft a little proximal-preaxial above the diaphysis, and a piece postaxial to the proximal end is lost. Postaxially, the shaft is concave, with a sharp margin on the transition to the epiphysis. Preaxially, the shaft is convex. A slight expansion with a fossa is seen postaxially above the diaphysis, also located at the same place in the left femur described below. No muscle scars above the fossa. The pre-postaxial expansion of capitulum are seen from dorsal view, as in the left femur. The preaxial side of the expansion of capitulum has muscle scars, and rugosities preaxial/postaxial. In ventral view, muscle scars are clearly seen

on a large area distal to the capitulum. In preaxial/postaxial view, the capitulum expands ventral-proximally. The tuberosity expands dorsally in a gradual curve from the humeral shaft, and located higher than on the other humeri from the Slottsmøya Member. This feature is also seen in the left femur. The tuberosity decreases ventrally. In distal view, the facet for radius is thicker dorso-ventrally, than the partly broken-off facet for ulna, decreasing preaxially in thickness. Rugosities are seen dorso-ventral. In proximal view, the capitulum has an adult, globular shape. Rugosities seen between fractures and missing pieces on the capitulum. The trochanter is half the size, and decreases towards capitulum. A small piece is missing of the trochanter.

Epipodial (Fig. 3C, 10E). Part of the epipodial is found in articulation with the humerus. The radius is missing; only ulna and what is presumably the pisiform are preserved.

Ulna. Large. The ulna has five adult facets exhibiting rounded corners. Two facets are dividing the postaxial side in two. Ventral-proximal, a piece of the bone is missing. The measurements are: anterior-posterior 7,7 cm, and proximal-distal 5 cm. The five angles measured on the ulna: anterior-proximal: 90 degrees, anterior-distal: 135 degrees, posterior-proximal: 70 degrees, posterior: 135 degrees, posterior-distal: 120 degrees.

Femur (Fig. 4F, 6G, 8G). Left. In dorsal view, the femur is larger than the right humerus. Preaxially, a concave, gradual curve spans distally towards the twisted area of the shaft. On the diaphysis and towards the femoral head, the shaft is slimmer than the other femora of the Slottsmøya Member. The postaxial flange convexes indistinct with a sharp transition to the postaxial shaft. Preaxially, the side has a smooth, short transition to the shaft. The twisted area is larger preaxially. A slight expansion and a fossa on the shaft are located the same place as on the right humerus. A muscle scar is seen proximal of the expansion. The capitulum expands pre-postaxially like the right humerus. In ventral view, the twisted area obtains equal thickness transversally. In preaxial/postaxial view, the whole bone concaves from diaphysis to the capitulum ventrally. The postaxial side decreases in thickness distally. The expansion of the capitulum and the trochanter is similar to the capitulum and tuberosity in the right humerus. The thickness of the epiphysis decreases postaxially. In distal view, rugosities are placed dorso-ventrally. The facet for tibia is slight concave. In proximal view, the capitulum is similar to the right humerus, apart from more rugosities. The trochanter has the same shape as described with the humerus. A small part has been broken off.

PMO 214.452

Sub-adult specimen consisting of an articulated pelvic girdle and caudal vertebrae, and one associated femur. The excavation site was located approximately 5 meter below the echinoderm bed (Fig. 2). The propodial is large and obtain a clearly viewed facet to the fibula on the epiphysis.

Femur (Fig. 4A, 6E, 8E). Right. In dorsal view, you can see a slight expansion of the propodial dorsal-postaxially as described in PMO 216.863. The distal-postaxial flange expands less compared to the adult specimen in posterior-distal direction. A concave margin marks the expansion with a short, gradual transition towards the shaft proximally. Distal-preaxially, it forms a long convex curve, meeting the shaft higher distal-proximally than the distal-postaxial flange. Distally, the epiphysis is thinner on the preaxial side, than on the postaxial flange. Small rugosities are indicated on distal end. In ventral view, the rugosities indicating muscle insertions are much clearer, and are located ventral-distally of the capitulum. In preaxial/postaxial view, a dorsal-proximal straight line decreases some in thickness from diaphysis to the distal end, thickening dorso-ventrally into a slight concave curve distally. On ventral side, the proximal-distal shaft is straighter towards the epiphysis. The shaft expands slightly in proximal direction to the capitulum. In proximal view, the capitulum has less dominating shape here than on the other adult femora. It expands slightly proximal-ventral, with a sharp transition proximally, increasing ventral-dorsally. The trochanter is small and compressed dorsally in preaxial/postaxial direction. Rugosities are located dorso-ventrally on the femoral head. The proximal head exhibit juvenile traits, with underdeveloped characters and presumably consisting of cartilage. Unossified aral bows (E.M. Knutsen pers.com.) indicate a sub-adult specimen. A piece of the trochanter is positioned preaxially.

PMO 212.662

Adult specimen consisting of an articulated braincase, cervical and thoracic vertebrae and one associated humerus. The excavation site was located 27 meters above the echinoderm bed, on the dorsoplanites bed (Fig. 2). The left humerus is very fragmented, and determined by the epipodials. Two pieces of the propodial positively identified as distal. The epipodials, mesopodials and some tarsals was articulated and intact.

Epipodials (Fig. 3B, 10B1, 10B2). The radius is large compared to the ulna. The developed facets on the epipodials indicate an adult stage.

Radius. The adult radius exhibits four facets. The distal margin is slightly concave, and preaxial/postaxial and proximal margin is approximately angular. The radius is partly fractured. The measurements on the radius: anterior-posterior: 10 cm, proximal-distal: 6,3 cm. The angles: anterior-proximal: 75 degrees, anterior-distal: 80 degrees, posterior-proximal: 95 degrees, posterior-distal: 80 degrees.

Ulna. The adult ulna exhibits five facets with angular corners. The shape is indistinct compared to the other epipodials described of the Slottsmøya Member. Dorso-ventrally flattened. The measurements of the ulna: anterior-posterior: 6,2 cm, Proximal-distal: 5 cm. The angles: anterior-proximal: 125 degrees, anterior: 125 degrees, anterior-distal: 115 degrees, posterior-proximal: 65 degrees, posterior-distal 75 degrees.

PMO A 27745

Adult articulated specimen, consisting of an incomplete postcranial skeleton with articulated pelvic girdle and right femur. Associated with the lumbar and caudal vertebrae. The excavation site was located 14 meters above the echinoderm bed (Fig. 2). The femoral head is partly lost, missing parts of the trochanter and the capitulum. The epipodials found articulated with the propodial. Clear facet to the fibula, the facet to the tibia is partly broken off. Propodial and epipodials are dorso-ventrally compressed.

Femur (Fig. 4B, 6F, 8F). Right. In dorsal view, pieces of the shaft are missing on the propodial surface. Preaxially, the shaft exhibits a gradual concave line proximal-distally extending slightly preaxial-distal. The developed distal-postaxial flange concaves gradually from the shaft. The proximal head expands slightly preaxially of the presumed capitulum. The trochanter tilts dorsal-postaxially. Rugosities are seen on all of the preserved surfaces of the limb, indicating an “old” adult (Brown 1981). In ventral view, the capitulum is missing, including small parts preaxially/postaxially of the diaphysis, located postaxial-ventral, decreasing the appearance of the shaft. Scattered pieces occur on the surface. Parts absent, proximal-distally. In preaxial/postaxial view, the diaphysis is also decreased by fracturing postaxially. Proximal-postaxial of the diaphysis, the rugosities are greater than on other parts of the propodial, indicating muscle attachments. The femoral head is greatest in dorso-ventral height postaxial-proximally of the trochanter. The compression decreases the dorso-ventral

thickness in the distal-postaxial flange, resembling a wing. In distal view, the femur exhibits characteristic features described above.

Epipodials (Fig. 4B, 10D1, 10D2). The epipodials are somewhat fractured and compressed. The fibula is somewhat larger than tibia.

Tibia. The adult tibia exhibits four facets, partly fractured in distal-postaxial margins. The margin preaxial-distally is rounded, presumably lacks a part. The measurements of the tibia: anterior-posterior: 8,3 cm, proximal-distal: 6,2 cm. The angles: anterior-proximal: 85 degrees, anterior-distal: 80 degrees, posterior-proximal: 85 degrees, posterior-distal: 95 degrees.

Fibula. The adult fibula exhibits three facets, rounded edges preaxially, and one postaxially due to fracturing. The measurements of the fibula: anterior-posterior: 9,2 cm, proximal-distal: 6,6 cm. The angles: anterior-proximal: 90 degrees, anterior-distal: 110 degrees, distal: 110 degrees, posterior-proximal: 90 degrees, posterior-distal: 110 degrees.

PMO 216.838.

“Old” adult associated specimen consisting of two caudal vertebrae, unidentified fragments in siderite concretion, and two femora. The excavation site was located approximately 14 meters above the echinoderm bed (Fig 2). Left femur fractured into a distal part including half the shaft and epiphysis with facets. A proximal part includes half the shaft and the proximal head. The right femur lacks a small, slender segment preaxially, expanding in a proximal-ventral direction of the capitulum to the diaphysis on the shaft. The two femoral heads is separated between the capitulum and trochanter. The fibula and the postaxial ossicle are intact and articulated. The tibia is missing.

Femur (Fig. 4D, 6C, 8C). Left. In dorsal view, the proximal head is pre-postaxially slimmer than previously described propodials. The pre-postaxial thickness is equal the whole shaft. Dorsal-preaxial depression described further down. The capitulum expands postaxially from the ventral side exhibiting muscle scars dorsal-proximal of the postaxial expansion of the capitulum. The dorsal surface is rugose. The trochanter is tilted preaxially. The distal postaxial flange has a distinctive shape, expanding into a triangle, not a convex curve as described previously in the other specimens. Preaxially the curve is slightly convex, without expansion. In ventral view, the capitulum tilts postaxially exhibiting developed rugosities. Ventral-distal of the capitulum, a large fossa with rugosities around is seen.

In preaxial/postaxial view, the distal-postaxial flange is fractured dorsally. The distal fracture zone spans preaxial/postaxially from diaphysis, and 9,5 cm cut towards the distal end. The proximal part has the opposite cut fitting the distal fracture zone. In distal view, the postaxial-distal flange is thinner dorso-ventrally, than the distal-preaxial side. Rugosities seen dorso-ventral on the epiphysis. In proximal view, the trochanter expands slightly dorso-ventrally and is located dorso-ventrally higher like right humerus and left femur in PMO 216.863. Compression of the proximal-preaxial end makes it a slightly flattened. The capitulum appears small, expanding ventral-proximally as seen in the other adult propodials.

Femur (Fig. 4C, 6D, 8D). Right. In dorsal view, approximately, the same length as PMO 214.452 (Tab. 1). Dorso-ventrally the propodial, particularly from diaphysis to the proximal end are fractured. The distal-postaxial flange is greatly expanded, resembling a rounded triangle; distal-preaxial side is similar to the left femur. The shaft is straight pre-postaxially in proximal-distal direction. The capitulum expands significantly preaxially, making the appearance of the femoral head extensive. The trochanter is tilted postaxially. Strong rugosities proximal-preaxially of the trochanter, indicates muscle attachments. In ventral view, a small postaxial expansion is located on the diaphysis. Ventral-distal of the capitulum, muscle scars are located and rugosities ventral-proximal of the postaxial-distal flange. A small, distinct dorso-ventral increase in height marks a transition proximally of the shaft to the capitulum. In a preaxial/postaxial view, the preaxial side on diaphysis exhibits a rugose area indicating muscle attachments. In distal view, the epiphysis has three adult facets. The postaxial-distal margin decreases more in dorso-ventral thickness than seen distal-preaxially. In proximal view, the trochanter expands dorso-ventrally as seen in the left femur and PMO 216.863. The slope towards the capitulum is less distinct on this specimen. Ventral-proximally, the capitulum expands little compared to the left femur.

Epipodial (Fig. 4C, 10C). Only fibula of the epipodials intact.

Fibula. The adult fibula exhibit three angular facets with the preaxial/postaxial margin broken off. The measurements of the fibula: anterior-posterior: 7,9 cm, proximal-distal: 4,8 cm. The angles: anterior-proximal: 90 degrees, anterior-distal: 120 degrees, distal: 120 degrees, posterior-proximal: 90 degrees, posterior-distal: 120 degrees.

PMO 218.377.

Adult specimen with an associated almost complete hind limb and humerus. The excavation site is located 14 meters above the echinoderm bed (Fig. 2). Differences in size including the placement of the trochanter dorso-ventrally of the capitulum, positively confirms the distinction of the limbs, although not the distinction between right and left propodial. The femur also resembles the shape to the femora PMO 216.838 and the femur in PMO A 27745. Both limbs have broken off shafts, and are partly preserved as fragments of distal and proximal propodials. The humerus has a larger preserved proximal end. The femur has a larger preserved distal end. Separation is determined between the capitulum and trochanter on the femoral head. The capitulum and tuberosity of the humeral head have no separation, exhibiting juvenile characters. The humerus has no intact epipodials distally. On the femur tibia is lost. The fibula and postaxial ossicle are intact. Both propodials have strong concave facets.

Humerus (Fig. 3A, 6A, 8A). In dorsal view, the distal-postaxial flange is partly broken off. The preaxial/postaxial direction of strong rugosities dorso-ventrally on the distal surface confirms the locality of the distal-postaxial flange. The distal-preaxial side is almost intact, with rugosities developed in a distal-proximal direction. On the proximal part of the humerus, the tuberosity is tilted postaxially. Dorsal-distal of the tuberosity exhibits small rugosities, postaxial-distal of the tuberosity, a muscle scar is located. Proximal-preaxial, a fracture is missing from the shaft. In ventral view, the capitulum is tilted preaxially and exhibits rugosities. A muscle attachment is located ventral-distally of the capitulum. The proximal head expands pre-postaxially. In preaxial/postaxial view, a piece is missing distal-preaxially. The fracture zone of the distal part is 16 cm transversally. The preaxial fracture measures 8,5 cm distal-proximally. The postaxial fracture measures 7, 3 cm. In proximal view, the tuberosity decreases dorso-ventrally. The capitulum decreases ventral-dorsally.

Femur (Fig. 4E, 6B, 8B). In dorsal view, the distal-postaxial flange is broken off. Distal-preaxially, the flange lacks a fragment, and three fragments located distal-proximally are lost. Great rugosities are located on the preserved surface dorsal/ventral. In the center of the distal end, a large crevasse dominates distal-proximally. In preaxial/postaxial view the fracture zone preaxially is 21 cm above the distal margin. Postaxially, the fracture zone is located 12,5 cm above distal end. The fracture is measured 13 cm transversally. In proximal view, the femoral

head exhibits a partly trochanter and a capitulum, placed dorso-ventrally to each other. The dorso-ventral width of the broken femoral head is measured to 4,3 cm

Epipodial (Fig. 4E, 10A). Only fibula of the epipodials intact. The fibula is large and thick dorso-ventrally.

Fibula. The adult fibula exhibits three angular facets, triangular shaped. The measurements of the fibula: anterior-posterior: 8,3 cm, proximal-distal: 5,5 cm. The angles: anterior-proximal: 85 degrees, anterior-distal: 110 degrees, posterior-proximal: 85 degrees, posterior-distal: 110 degrees, distal 70 degrees.

1.4. Discussion

Morphotypes on the propodials from the Slottsmøya Member

The morphology is based on the stratigraphic occurrence of the specimen and the phylogeny.

Morphotype 1: Specimen PMO 216.863. Characterized by the morphological features of the humerus. The humerus exhibits a preaxial-distal flange. The distal flange expands in all other specimen from the Slottsmøya Member, including the femur on this individual in postaxial direction, meaning that the flange is facing towards the tail of the animal. On the humerus of PMO 216.863, the distal flange is placed preaxially, facing towards the head. This has never been seen before on a described propodial of a plesiosaur. On the humerus a small expansion occurs on diaphysis facing dorsal-preaxial on the limb. On this expansion, a fossa is also present. This indicates large muscle attachment, which on the humerus would be facing the opposite direction than common (Watson 1924), and suggests a different locomotion pattern in the fore limb than in the hind limb of the animal. On the femur, the distal flange is concluded facing postaxially, similar to that of the other specimen from the Slottsmøya Member. Like the humerus it also has an expansion and fossa located dorsal-preaxially. The trochanter and the tuberosity have expanded more in dorso-ventral height, than seen in the others, with the exception of the femora in PMO 216.838 (see Morphotype 3). These are also much smaller than the other adult individuals (PMO 216.838, PMO 218.377, PMO 214.452 and PMO A 27745). The stratigraphic position of this specimen is 5 meter above the echinoderm bed, unique stratigraphically compared to all the other studied specimens. Both propodials are twisted dorsal-ventrally in a proximal direction.

Morphotype 2: Specimen PMO 216.839. Characterized by the pre-postaxial width of the diaphysis in the two humeri and femur. Comparing the measured ratio of antero-posterior diaphysis/length (Tab. 2, humeri, femora), the propodials of PMO 216.839 is significantly wider in their shafts than the other specimens from the Slottsmøya Member. The specimen was located stratigraphically 7 meter above the echinoderm bed, and thus an older specimen than the others (except PMO 214.452).

Morphotype 3: Specimen PMO 216.838, PMO A 27745 and PMO 218.377. All three have an apparently similar shape and size (Tab. 1, Tab. 2, femora, ratio: a-p epiphysis/length) in

their propodial and epipodials. By a conservative distinction this places them together under the same morphotype. They have all slender shafts (Tab. 2, femora, ratio: a-p diaphysis/length), and presumably the same shape on the distal flange. Because of lost parts of the propodials; the capitulum and trochanter in PMO A 27745, and parts of the femoral head in PMO 218.377, one can only presume that they have the same characters, based on their other similarities. Parts of the shaft in PMO A 27745 and most of the shafts in PMO 218.377 are also missing and can explain why neither the fossa dorsal-postaxially, nor an elevation in the trochanter like seen in PMO 216.838 can be seen. All three specimens was stratigraphically placed 14 meters above the echinoderm bed, placing them in the same stratigraphic age and in the main cluster of the plesiosaurs excavated in the Slottsmøya Member (Fig. 2).

Morphotype 4: Specimen PMO 214.452. Characterized by an expansion above the diaphysis on the postaxial side of the propodial. This expansion are only seen in this and the PMO 216.863, and indicates larger muscle attachments for *M. pectoralis* then what appears normal. Considering this, and that the animals position in the stratigraphic layers was located 8 meters below the echinoderm bed, gives the PMO 214.452 a distinct phylogenetic character.

SVB 1450: Difficulties in placing this propodial in a specific morphotype due to its juvenile characters. Although the shaft is slender as described as a feature in Morphotype 3, there is no overlapping material to confirm the ontogenetic patterns towards a similar shape. The epipodials are however triangular as also seen in Morphotype 3.

Comparisons of the different individuals from the Slottsmøya Member

Propodials

PMO 212.662 is not compared with the other specimen here because most of the propodial are missing.

In PMO 216.839, the trochanter in the right femur is located preaxially of the capitulum. The trochanter should normally be placed dorsally of the capitulum, not on either side like seen in this propodial. The femur is dorso-ventrally compressed, so the preaxial tilt of the trochanter can be explained by this. In the left humerus, the tuberosity is located in preaxial direction of

the proximal head, whereas postaxially, you can see muscle scars and a small expansion of the capitulum. Normally, the tuberosity should be tilted on the postaxial side, like seen in the other described humeri. This exception could be also because of the dorso-ventral compression of the propodial, pressing the tuberosity out of its original position.

In PMO 216.863, on the left femur, a slight expansion and a fossa on the shaft are located the same place as the right humerus on the same specimen. This locality for muscle attachments, is a general trend also seen in other propodials on postaxial side, and is why the distal flange is assumed positioned on postaxial side as normal, instead of preaxial side as seen in humerus. A fossa shown on the broken hind limb PMO 216.838 lies ventral-distal of the capitulum; the same fossa lies dorsal-preaxial on PMO 216.863 humerus and dorsal-postaxial on femur. This indicates an attachment for a large muscle/tendon. This type of fossa is not seen in the comparable material (Andrews 1910; Watson 1924; Brown 1981), or in the other specimens from the Slottsmøya Member.

A pre/postaxial expansion dorsally at same location as the fossa is also found on both the right humerus and left femur in PMO 216.863, and the same in femur PMO 214.452, and not seen on the other propodials. In Watson (1924), the *M. pectoralis* is described as a muscle attachment at the same location on the humerus in *Plesiosaurus dolichodeirus* and in *Colymbosaurus sp.*, but without the expansion found in the propodials PMO 216.863 and PMO 214.452 from the Slottsmøya Member. On PMO 216.863 it is placed preaxially, normally the expansion for the *M. pectoralis* would be found postaxially, as seen in the left femur of the same specimen. The expansions seen on PMO 214.452 and PMO 216.863 and the fossa seen on PMO 216.863 in the location for the *M. pectoralis* on the propodial leads to the conclusion that a greater muscle attachment of the *M. pectoralis* was in place, thus generating greater force from this muscle in life. This can be caused by need for greater force due to a different locomotion behavior in the humerus, which could again lead to a need for greater force in the femora. The left humerus of PMO 216.863 remains to be preperated, therefore a full description on the animals propodials are still awaiting, together with a full discussion. Considering the expansion located dorsal-postaxial on PMO 214.452, a parallel explanation to the PMO 216.863 can be presumed. The lack of comparable material, to the fossa located ventral-distal of the capitulum in PMO 216.838, makes it difficult to lead a discussion, and thus leaves it out in the open.

The measurements of the propodials shows that the main differences between the humeri and femora reveals itself in the anterior-posterior length, and in the width of the epiphysis (Tab. 1). The only exception is in the measurement of the dorso-ventral diameter of the proximal head in the femur to PMO 216.838. In the other propodials, these measurements are approximately the same between the propodials within each individual. The PMO 216.863 shows no differences in the width of epiphysis. The PMO 216.863 is also significant shorter than the other adult specimen in the collection, about 10 cm shorter in length and 5 cm in distal width compared with the other femora.

The measurements reveal a trend of greater values in the femora, and lower values in the humeri. Between the femur and the humeri in PMO 216.839 the femur is larger in all measurements except from antero-posterior and dorso-ventral mm of the head. This is explained by the compression of the ventral-proximal part of the femora, altering its shape. In PMO 216.863 the differences between the humerus and femur are altered due to compression on especially the femur (see description), but the femur is clearly larger according to its length and the antero-posterior width of the epiphysis. The femora in PMO 214.452, PMO A 27745 and right femur in PMO 216.838 are all measured over 40 cm in length. Between the humerus and femora in PMO 218.377, larger parts of both propodials are missing except well preserved parts distally on both propodials. Even though the humeri distally have greater parts preserved; the antero-posterior width is higher in the femur. The dorso-ventral width is also wider in the femur, thus reasoning that the rest of the propodials are aligned with these proportions.

The development towards a characteristic distal-postaxial/preaxial flange appears to follow the ontogenetic stages of the animal. In juveniles, these features appear small and less progressed. Another development linked to ontogenic stages are seen distal-ventral of the capitulum where there is in general a muscle attachment for the pectoral muscle, marked by rugosities. These rugosities increase with the age of the animals according to the complete ten preserved propodials seen from the Slottsmøya Member.

Epipodials.

A trend shows that the juvenile epipodials exhibit rounded corners, while the adult individuals exhibit corners that are angular. The development of the epipodials towards distinct facets

appear thus to follow ontogenetic stages. Due to this they can not be used as comparison in measured size and angles, but as an additional evidence for the difference between juvenile and adult individuals.

The number of facets and morphology are different on the tibia and fibula, and on the radius and ulna. In the Slottsmøya Member specimens, four hind limbs and three fore limbs has intact, articulated epipodials. The adult/juvenile epipodials in the fore limbs exhibit four facets, consisting of four angles on the radius, and three facets, consisting of five angles on the ulna. The epipodials of the hind limb exhibits four facets, consisting of four angles on the tibia, and three facets, consisting of five angles on the fibula. On the radius in the juvenile specimen SVB 1450, there are four facets, with evolving traits towards a rectangular, four angled facet. The ulna, exhibits three facets, with evolving traits towards a triangular, three angled facet (Fig. 9A1, 9A2).

The angular measurements done on the adult epipodials in this study can provide information on how the epipodials connects with the mesopodials, affecting the orientation of the bones in the distal end of the limb. This is however beyond the scope of this study.

The importance of articulated and associated specimen.

The articulated/associated nature of the bones in a specimen is important factors for our understanding of the skeletal construction, movement and ecology of the animal examined. In the following discussion on the functions and morphology of the plesiosaur fore limb and hind limb, it is necessary to understand, and be certain of, the differences between humeri and femora. A lot of work considering collections of specimen from the Oxfordian to Tithonian time periods of the Upper Jurassic (Oxfordian to Kimmeridgian) of Laurasia (Andrews 1910; Brown 1981), detailed descriptions of articulation are often lacking and increases the possibility of making an observation based on misplaced material (Tab. 3).

Comparisons of the individuals from the Slottsmøya Member and the Oxford Clay plesiosaurs.

It is generally assumed that plesiosaurs, including those from the Late Jurassic, have large humeri and smaller femora (Brown 1981; O'Keefe 2002). Unfortunately, the material supporting this theory lacks information whether or not particular specimens were found in an articulated/associated state or not (Tab. 3). Comparisons made here are with well described specimens from Oxfordian but these too lack information on taphonomy and articulation (P. Druckenmiller and R. Forrest pers.com.). Two additional specimens from the Tithonian include *Colymbosaurus trochanterius* which has only the non articulated body preserved and the crania of *Kimmerosaurus langhami* (Brown 1981).

The humerus in *Muraenosaurus leedsi* as described by Andrews (1910), is considerably larger than the femur, with the distal end of the humerus more expanded than on the femur. This is the reverse of what is observed of humeri and femora from the Slottsmøya Member. In *M. leedsi* the humerus becomes increasingly massive with age. Preaxially, both the humerus and the femur have a tilted, straight posterior line, while on the postaxial side of the shaft the humerus and the femur have a concave curve distal-proximally, making the appearance of the whole propodials tilted posteriorly. In the propodials of the Slottsmøya Member, the shafts preaxial/postaxial is approximately straight in proximal-distal direction. Both propodials in *M. leedsi* have large proximal heads compared to their distal length (a-p proximal head/length, Tab. 2, humeri, femora). The epipodials in *M. leedsi* have a rounded posterior margin on the fibula and ulna, and a rounded anterior margin of the tibia. The radius has a proximal-distal dumb-bell shape, with a shorter posterior side than the anterior. On the articulated side of the epipodials, were they connect with each other, they all have a compressed proximal-distal dumb-bell shape.

The humerus of *Cryptocleidus eurymerus* is characterized by its great expansion at the distal end, a unique feature for this species (Andrews 1910), and is considerably more massive than the humeri from the Slottsmøya Member. This is an ontogenetic feature as it is lacking in juvenile specimens. The distal-preaxial side has a higher, rounded expansion than on the distal-postaxial side. The proximal head do not seem to reach full ossification. The tuberosity exhibit a considerable expansion postaxially of the proximal head, in a greater extent than the plesiosaurs from the Slottsmøya Member. The distal end of the humerus articulates with a

massive angular radius exhibiting rounded proximal margins, and a large triangular ulna, with similar rounded proximal margins. In juveniles, the radius is still very large with an indistinct morphology; the ulna is small and underdeveloped. In the hind limb, the femora are similar to the structure of the humeri but are smaller. The shaft is more slender, and the postaxial-distal flange is less extended, and similar with the preaxial-distal expansion. The trochanter is large and prominent, with muscle attachments on its proximal margins. They both have strong muscle scars distal-ventrally of the capitulum. On the femur, these attachments are located more posteriorly. The proximal head is strongly convex in the adult individuals. The femur articulates only with the tibia and fibula. With the facets for tibia angular and slightly concave, while the facet for fibula is triangular and straight.

The humerus in *Muraenosaurus beloclis*, is short and stout, with a strongly convex proximal head. The distal-postaxial expansion is well developed, while distal-preaxially there is no expansion. Preaxially the shaft is straight proximal-distally, with a concave, gradual curve postaxially towards the postaxial-distal flange (Andrews 1910). A similar appearance is observed in the Slottsmøya Member plesiosaurs. The tuberosity and the capitulum are located dorso-ventrally of each other on the proximal head. In distal view, the humerus exhibits clear facets for the radius and ulna, and a small facet for a presumed pisiform, supporting the postaxial ossicle. The radius exhibits a weak dumb-bell shape and is compressed proximal-distally on posterior side. The ulna is compressed into a dumb-bell shape on anterior side, and has five straight facets on the other sides. The femur, has a large trochanter, forming a considerable visual part of the proximal-dorsal end. The ventral side is much roughened by muscle scars, including a dorso-ventral increase in height distal-posteriorly of the capitulum. The distal-postaxial expansion is poorer developed than in the humerus, a trait that appear to be common in all four compared species, and with a more equal expansion in both pre-and postaxial direction.

The humerus in *Tricleidus seeleyi* differs from *Muraenosaurus leedsi*, *Muraenosaurus beloclis*, *Cryptocleidus eurymerus* and the plesiosaurs of the Slottsmøya Member. The outline is short and stout, with a straight preaxial shaft proximal-distally, and a concave curve postaxially, making the propodial tilt in a postaxial direction. Muscle scars are located distal-posteriorly of the capitulum. The distal end articulates to four bones; radius, ulna, pisiform and a small postaxial ossicle. The facet for the radius is greatest and all of the epipodials have the same internal dumb-bell shape as in *M. leedsi*. The proximal, anterior/posterior and distal

facets on the epipodials are sharper, with more angular margins. On the femur, the shaft is more slender and straighter proximal-distal, although of the same length as the humerus. The proximal head is convex, and the trochanter is strongly developed. The femur expands less postaxial-distally than the humerus. In ventral view, on the proximal and proximal-posterior end towards the diaphysis, muscle scars are located. In distal view the femur articulates solely with the tibia and fibula.

Mean measurements taken of the species *M. leedsi*, *C. eurymerus*, *M. beloclis*, and measurements of *T. seeleyi* and the Slottsmøya Member plesiosaurs shows characteristic differences in size and length.

Length humeri: *M. leedsi*: 31,7 cm, *C. eurymerus*: 33 cm, *M. beloclis*: 20, 4 cm, *T. seeleyi*: 20,7 cm, the Slottsmøya Member SVB 1450. Juvenile: 32,7 cm, and PMO 216.839. Left, juvenile: 30,5 cm.

Length femora: *M. leedsi*: 30,4 cm, *C. eurymerus*: 30,5 cm, *M. beloclis*: 16 cm, *T. seeleyi*: 21,6 cm, the Slottsmøya Member PMO 216.838. Right, adult: 44,0 cm, and PMO 216.839. Juvenile: 36,4 cm.

Distal width humeri: *M. leedsi*: 19 cm, *C. eurymerus*: 24, 5 cm, *M. beloclis*: 11, 2 cm, *T. seeleyi*: 11,8 cm, the Slottsmøya Member SVB 1450. Juvenile: 14,7 cm, and PMO 216.839. Left, juvenile: 14,5 cm.

Distal width femora: *M. leedsi*: 16 cm, *C. eurymerus*: 18,4 cm, *M. beloclis*: 8, 6 cm, *T. seeleyi*: 11,3 cm, the Slottsmøya Member PMO 216.838. Right, adult: 22,0 cm, and PMO 216.839. Juvenile: 18,4 cm.

The measurements show that although the length of the humeri are similar, except from *M. beloclis* and *T. seeleyi*, the width is largest in the humeri from *C. eurymerus*, but there is quite large differences between the four species and the Slottsmøya Member plesiosaurs in distal width, except from *M. beloclis* and *T. seeleyi*. The two femora from the Slottsmøya Member are both longer and wider. The lengths of the humeri and femora in *C. eurymerus* and *M. leedsi* are almost equal. The two humeri in the Slottsmøya Member have nearly the same length as *C. eurymerus* and *M. leedsi*, but the femora are larger and differ from all the four compared species in length. The distal width is wider in *C. eurymerus* than in both the Slottsmøya Member humeri, and the other species.

The multivariate statistics performed on the measurements of the ratios supports the differences described above and their differences to the Slottsmøya Member plesiosaurs (Fig.11).

In PCA (Fig.11), the x-axis is the most valuable, and gives the best information (48%) on the 6 dimensions. The HUM-phl (the antero-posterior proximal head/length in humerus), FEM-el (the antero-posterior epiphysis/length in femur), and HUM-phl (the antero-posterior proximal head/length in humerus) gives the most significant information of the differences between the two groups, meaning that either the length of both propodials, or the antero-posterior proximal head width is the main difference between the Oxford Clay plesiosaurs and the Slottsmøya Member plesiosaurs. The antero-posterior width of the epiphysis or the length of the femora is the other most significant differentiation between the two groups. The y-axis (23%) shows less of the variance in the 6 dimensions.

Functional morphology in Upper Jurassic plesiosaurs from the Slottsmøya Member.

Maneuverability vs. thrust.

Using the results of the measurements above, the question is why this difference occurs in the plesiosaurs from the Slottsmøya Member? A wider limb might indicate a higher need for energy saving locomotion over large distances at the cost of lower maneuverability as in pliosaurus (O'Keefe 2001) or perhaps a more delicate maneuverability in the hunt for prey. Perhaps they had both? Assuming that the plesiosaurs in Spitsbergen were permanent inhabitants of the Boreal Sea, the need for saving energy over long distances seems less likely than a need for higher maneuverability. A different version would appear if the plesiosaurs in Spitsbergen did travel over long distances, like extant migrating whales (Corkeron & Connor 1999).

Plesiosaurs are designed for aquatic locomotion. The use of both fore and hind limbs, as seen in pliosaurus and plesiosaurs, give increased maneuverability, although not necessarily higher velocity, but a more balanced gliding and energy efficient locomotion (Carpenter et al. 2010). They have a proximal-distal tapering of the phalanges, making the flippers more flexible distally. This allows chord-wise (following the straight line in the centre of the hydrofoil limb) flexing with a wave moving distally along the plesiosaur limb (Carpenter et al. 2010).

A different use of the fore limb and hind limb can be explained by the limited anterior-posterior movement due to the limitations enforced by the scapulae and coracoids as well as the shallow round-off of the humeral head. Hind limbs have nearly the same stroke curve due to the overhanging ileum, forming the dorso-posterior margin of the acetabulum. As a result, the morphology suggests restricted movement above the horizontal axis. (Tarsitsano & Riess 1982; Carpenter et al. 2010). Table 2 in Carpenter et al. (2010) shows a larger antero-posterior arc of motion for the hind limb, which may indicate that the hind limbs were important in maneuvering. There is no reason to assume that these restraints in limb movement are any different in the Slottsmøya Member plesiosaurs. The pectoral and pelvic girdle shows in this stage of analysis (E.M. Knutsen pers. com.), that they are similar with contemporary species. This agrees with Carpenter et al. (2010) that although all four limbs provided propulsive force, the hind limbs would in addition be used for steering. The movement were presumable semi-synchronous. This theory is supported by O'Keefe (2001) who presented a generalized study on the aspect ratio on plesiosaur limbs. The results indicated a high aspect ratio similar to those of migrating birds. Translated to limb morphology in plesiosaurs, this suggests adoptions to efficient locomotion, although at low speed, travelling long distances and hunting with low maneuverability. In general plesiosaurs have a fore limb that exhibits a higher aspect ratio than the hind limb (Robinson 1975). Lower aspect ratio would increase maneuverability, resulting in refined steering mechanism in the hind limb of the animal.

This can explain the difference seen in humeri and femora in the Slottsmøya Member plesiosaurs. If a higher need for maneuverability were present, larger femora would aid steering. The femora could also be an indication for animals in need of a larger propulsive thrust, travelling over larger distances with efficient, balanced speed.

Thrust produced by any propulsive stroke is equal to the amount of water accelerated backward by the motion. Due to this, large limbs moving slowly would produce a more efficient thrust than smaller, slender limbs moving rapidly. According to this, pliosaurs were probably more efficient in producing thrust than plesiosaurs (Massare 1988). This is however not true for the Slottsmøya Member plesiosaurs. Although the plesiosaur were smaller in size compared to the much larger pliosaurs, the proportions between the body and limbs should remain the same (Carpenter et al. 2010). In the Slottsmøya Member, the plesiosaurs are like the pliosaurs in having larger femora than humeri. They would then need fewer and slower limb strokes to keep themselves at a given speed, and thus be faster and more sustained

swimmers pursuing prey instead of an ambush predator strategy as suggested by Bakker (1993).

The question is could the limbs provide more thrust and maneuverability? The hind limbs are best situated for control because they are far from the centre of gravity and can generate large directional moments because of the long lever arm (Carpenter et al. 2010). The ability to maneuver in rapid turns is critical for predators to catch prey. Plesiosaurs have anhedral (downward angle) limbs similar to those of cetaceans (Fish 2004), which allowed controlled yaw and roll in maneuvering. This maneuvering was most likely lift based as in cetaceans and fishes. To uphold a constant propulsion is energetically expensive, and the propulsive phase could have alternated with a glide phase as seen in extant underwater fliers (Carpenter et al. 2010). With great limbs and great muscles (see below), the linking of this two physical qualities could possibly create plesiosaurs that are faster and more maneuverable.

The greater muscle attachments for the *M. pectoralis* seen also in some of the plesiosaurs from the Slottsmøya Member, marked by an expansion and/or fossa, (PMO 216.863, PMO 21.838, left, and PMO A 27745) gives the impression of need for more powerful propulsive force in the fore limbs, and for more accurate steering in the hind limbs (Carpenter et al. 2010).

The *M. pectoralis*, in contrast to earlier proposals (Robinson 1975), is noted as the most important adductor muscle involved in the power flight stroke and is consistent with that of other vertebrate fliers. This muscle is greatest on the animals larger limb (Lingham-Soliar 2000).

Turning the whole discussion around, Carpenter et.al (2010) concluded that the hind limbs were used for steering in plesiosaurs. This conclusion is however taken from the assumed fact that hind limbs are smaller than fore limbs. Would the conclusion be different if the opposite were true, and what function would the forelimbs have in this scenario? Why are the humeri in other species large and what would it mean if the humeri is suddenly small? Plesiosaurs from the Slottsmøya Member on Spitsbergen could be more derived than its contemporate relatives in the Tethys Ocean with smaller humeri driven by greater muscles and larger femora, also provided with great muscles; these would have been a special adaptation for the conditions in the Boreal Sea.

Ecology.

The climate and environment in Spitsbergen is an important factor to consider when trying to puzzle together a plesiosaurs way of life. As mentioned in the introduction, in the mid- to late Mesozoic the paleolatitudes on Spitsbergen has been estimated to be on 70° North (Ditchfield 1997). With a sea temperature ranging from 11 - 21° C (Price & Mutterlose 2004), the nectic fauna of the Boreal basin where under the same extreme seasonal cycles and daylight conditions as of today (Lüning 1990; Rich et al. 2002).

Functional adaption is an important factor to considerate in the hunt for reasons for the limb morphology in the Slottsmøya Member plesiosaurs. An interesting question is why are fossils of other vertebrates than marine reptiles lacking? In the Boreal sea, animals such as fish, sea crocodiles or sharks were apparently absent in the Late Jurassic. Only fossils of invertebrates are to be found between the reptile skeletons and cephalopods especially were extremely abundant. Studies by Vaquer-Sunyer and Duarte (2008) and Dahl et al. (2010) indicate that cephalopods can live on a lower oxygen threshold than fish. There were low oxygenic to anoxic levels in the Boreal Sea during the Late Jurassic (Nagy et al. 1988; Smelror et al. 2009; Vajda & Wigforss-Lange 2009). If the plesiosaurs in Spitsbergen did not hunt fish, simply because they were not there, could this have a functional impact on the morphology of the limbs? Plesiosaurs are characterized as generalists, living of different species of cephalopods and fish. But in a semi-closed basin like the Boreal Sea, with solely cephalopods to prey on, the plesiosaur could be determined as a specialist. This transformation can have caused a change in movement in the plesiosaurs from Spitsbergen. With this specialized predator-prey relation an evolutionary arms race can easily be imagined happening in the shallow basin of the Boreal Sea.

1.5. Conclusion

The statistical (Fig. 11) and measured (Tab. 1, Tab. 2, humeri, femora) analysis of this study leads to the conclusion that the articulated/associated propodials in the eight plesiosaurian individuals from the Late Jurassic of the Slottsmøya Member, has different morphology to its contemporate species from the Oxford Clay Formation in England. The propodials in the Slottsmøya Member plesiosaurs have the reverse proportional relationship compared to contemporary plesiosaurs discovered elsewhere in the world, with the femora being larger than the humeri – a state commonly associated with short-necked forms. The femora have a significantly larger length and distal width than the much smaller humeri. A trait seen in both the juvenile and adult individuals. Some of the plesiosaurs of the Slottsmøya Member were also provided with large muscle attachments, also different from described contemporary species.

The difference is presumably implied by a functional adaption to the specific locality of the shallow Boreal Sea in the high latitudes of the northern hemisphere and to an apparent adaption to a limited food source in the form of cephalopods.

There is a great need for more material from the Slottsmøya Member plesiosaurs to enable a more detailed taxonomy of the group.

1.6. Literature

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Figure 1. Geological map over the Sassenfjorden area (Hammer et al. 2011).

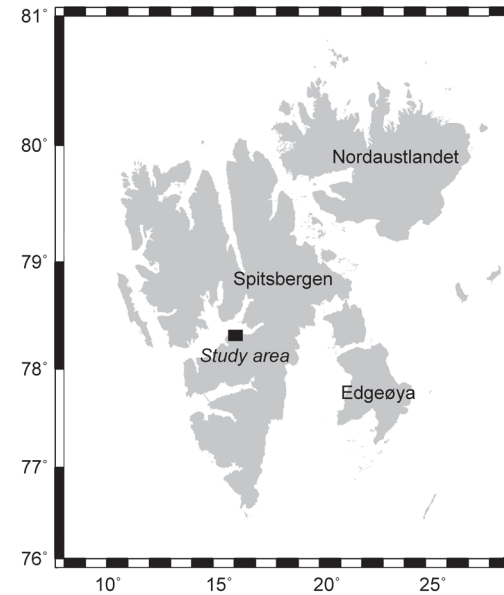
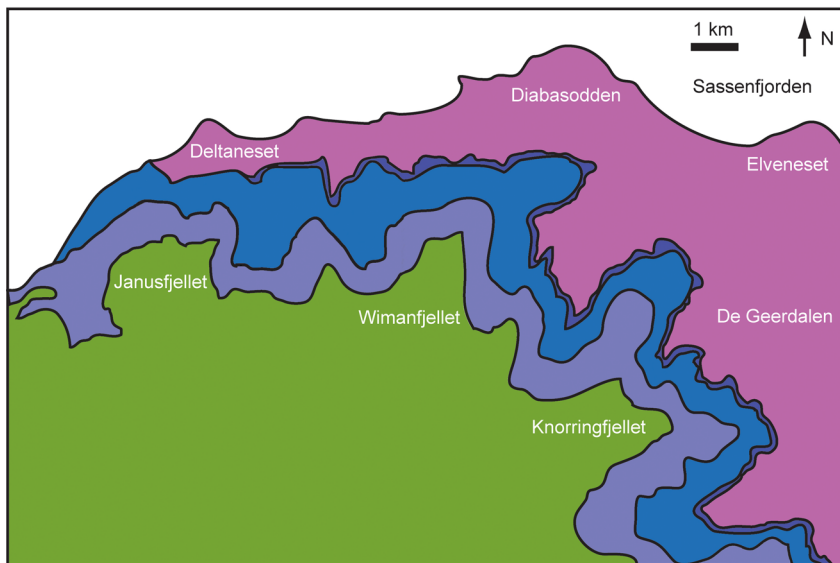


Figure 2. Stratigraphical Column of the Slottsmøya Member showing the stratigraphical localities of the excavated plesiosaurs in this study (Hammer et al. 2011).

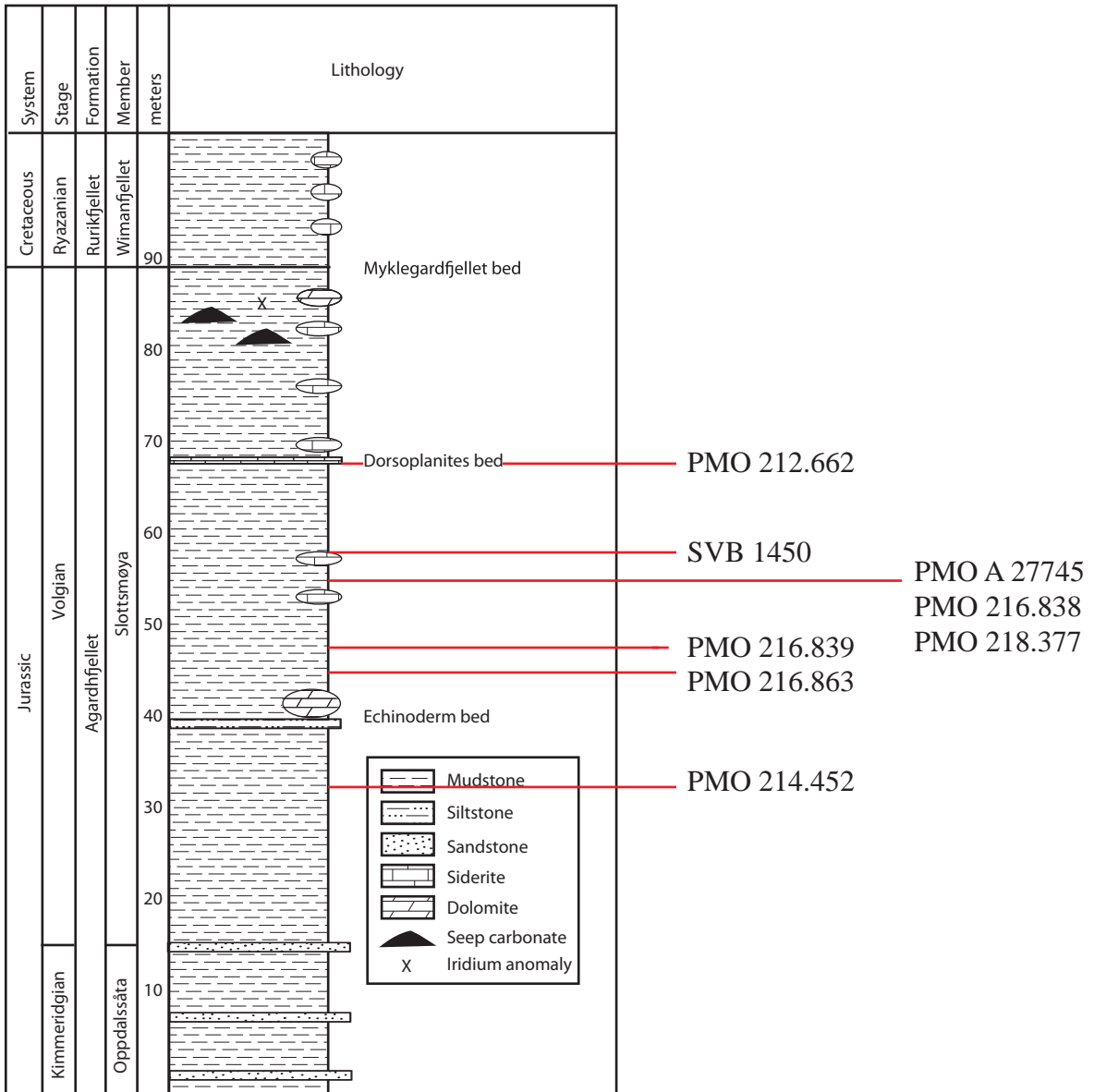


Figure 3. Fore limbs of the Slottsmøya Member plesiosaurs. **A:** PMO. 218.377. Humerus with proximal and distal end, dorsal view. **B:** PMO 212. 662. Humerus with small distal end epipodials, mesopodials and tarsals, presumably dorsal. **C:** PMO 216.863. Right humerus with ulna, dorsal view. **D:** SVB 1450. Left humerus with epipodials, mesopodials and tarsals, ventral view (mirrored). **E:** PMO 216.839. Right humerus, dorsal view. **F:** PMO 216.839. Left humerus, dorsal view.

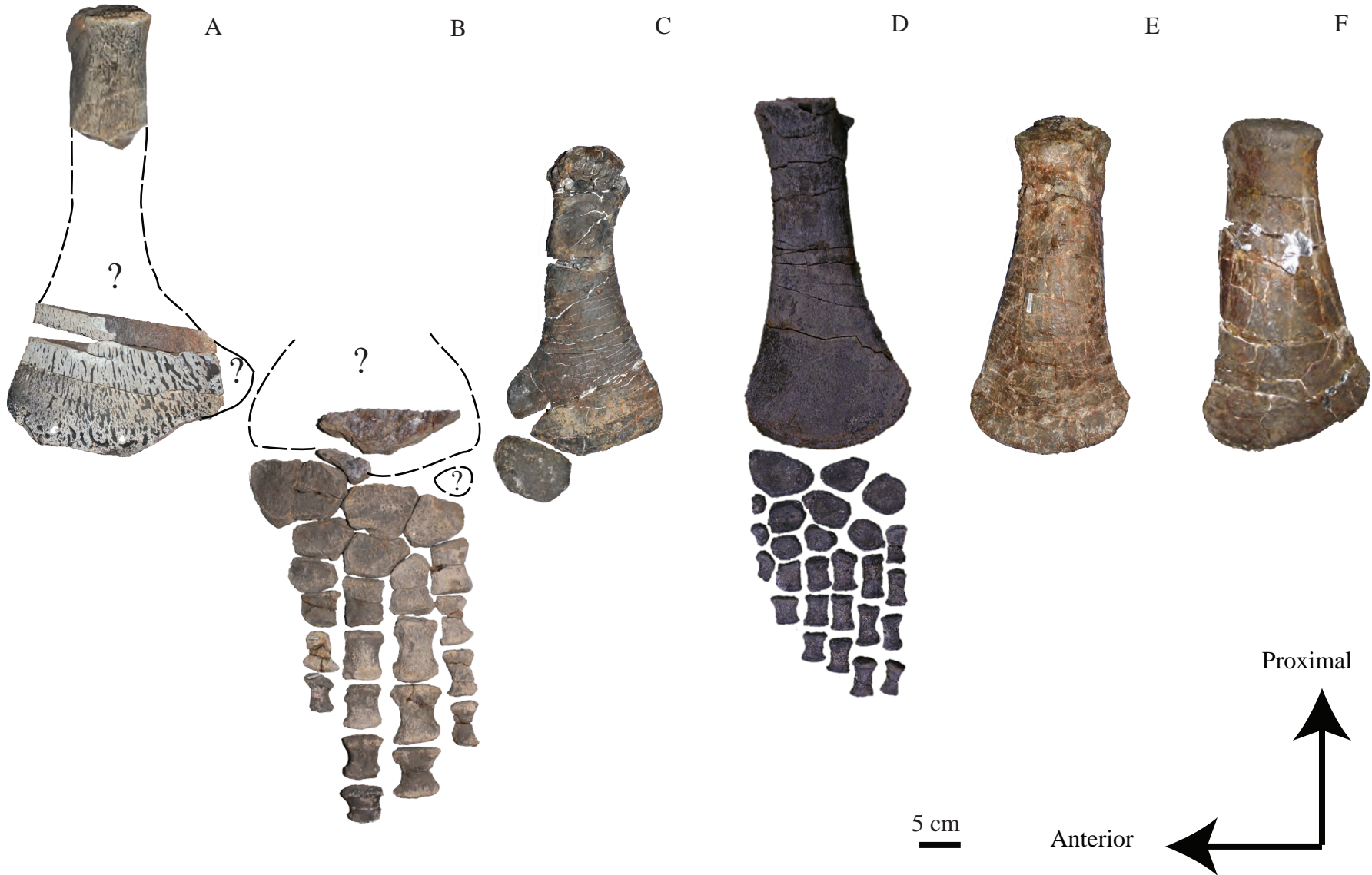
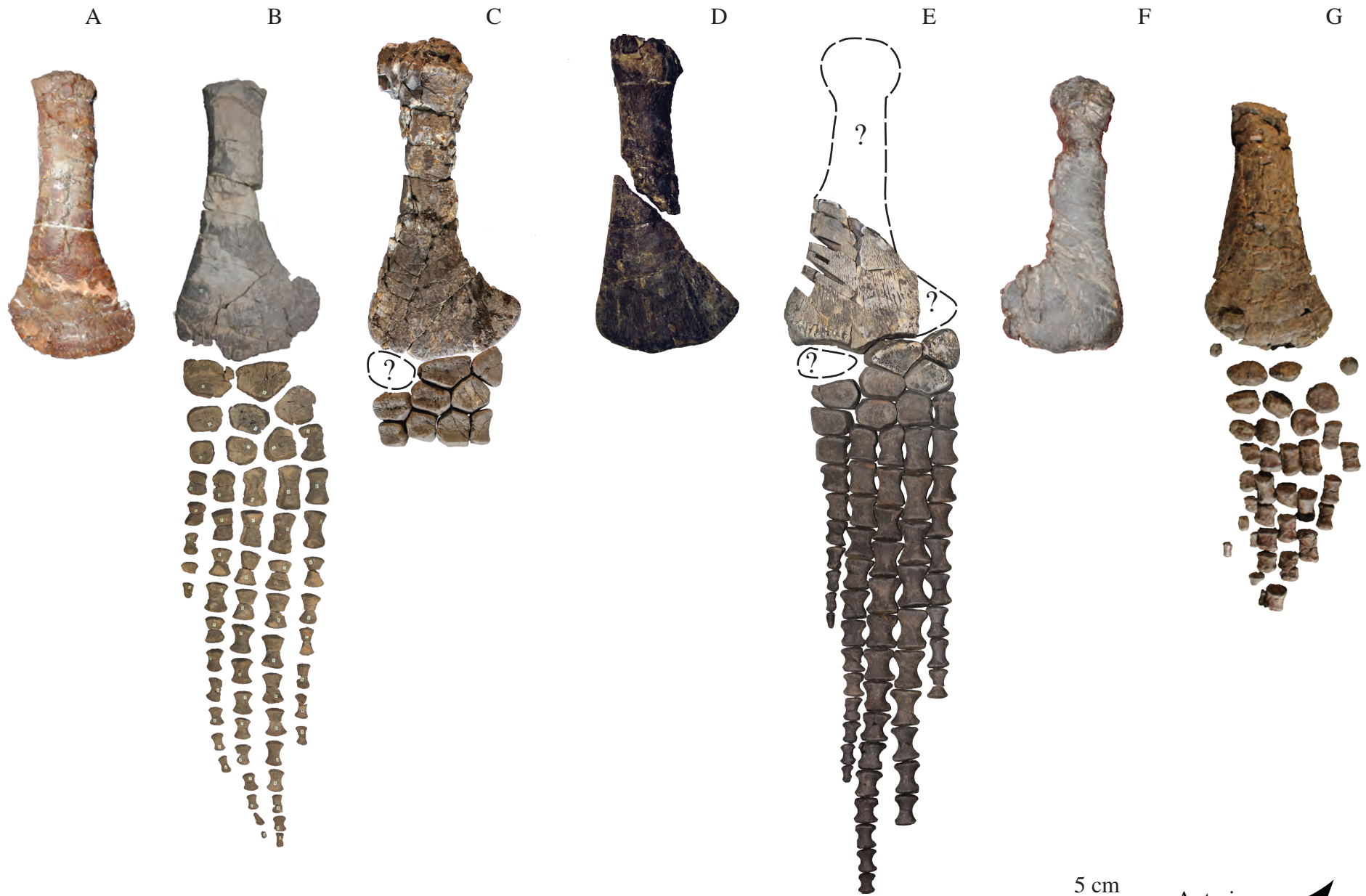


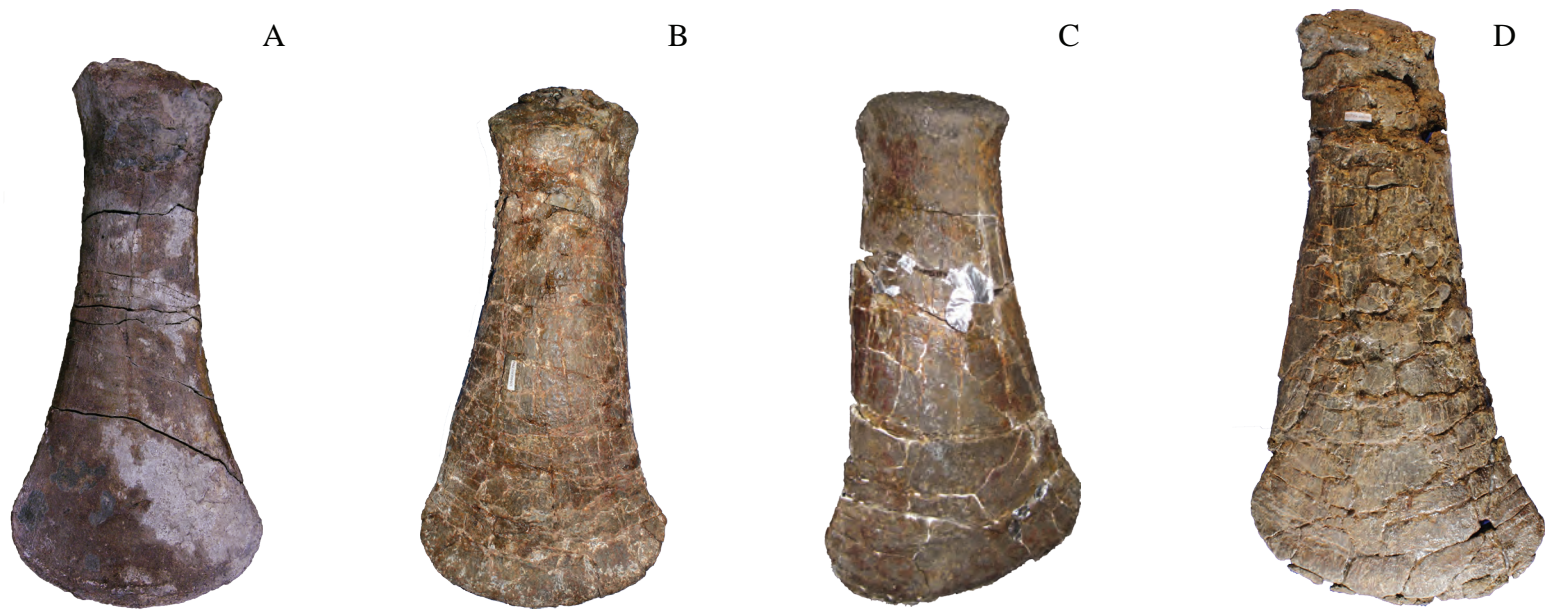
Figure 4: Hind limbs of the Slottsmøya Member plesiosaurs. **A:** PMO 214.452. Right femur, dorsal view (mirrored). **B:** PMO A 27745. Right femur with epipodials, mesopodials and tarsals, lost trochanter/capitulum, dorsal view. **C:** PMO 216.838. Right femur with fibula and mesopodials, dorsal view. **D:** PMO 216.838. Left femur, fractured, dorsal view. **E:** PMO 218.377. Femur with distal end, fibula, mesopodials and tarsals, dorsal view (mirrored). **F:** PMO 216.863. Left femur, dorsal view (mirrored). **G:** PMO 216.839. Right femur with epipodials, mesopodials and tarsals, dorsal view.



5 cm

Anterior ← ↑ Proximal

Figure 5: Juvenile propodials, dorsal view. **A:** SVB 1450. Left humerus. **B:** PMO 216.839. Right humerus. **C:** PMO 216.839. Left humerus. **D:** PMO 216.839. Right femur.



A

B

C

D

5 cm

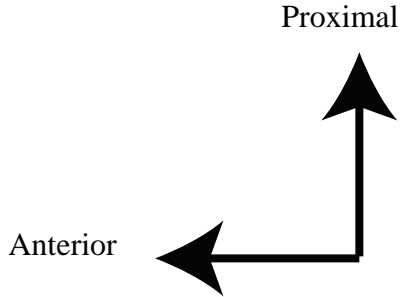
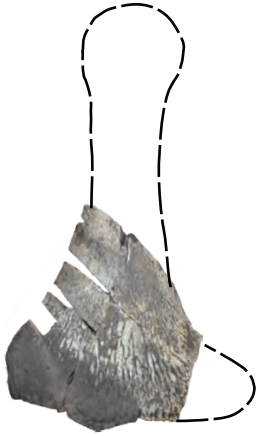


Figure 6. Adult propodials, dorsal view. **A:** PMO 218.377. Humerus with proximal and distal end. **B:** PMO 218.377. Femur with distal end. **C:** PMO 216.838. Left femur, fractured. **D:** PMO 216.838. Right femur. **E:** PMO 214.452. Right femur (mirrored), sub-adult. **F:** PMO A 27745. Right femur, lost trochanter/capitulum. **G:** PMO 216.863. Left femur (mirrored). **H:** PMO 216.863. Right humerus.

A



B



C



D



E



F



G



H



5 cm

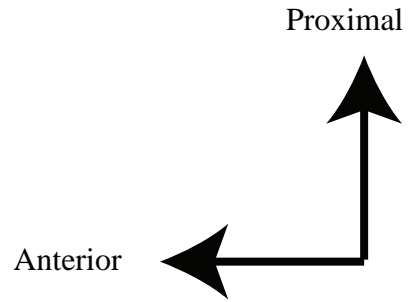


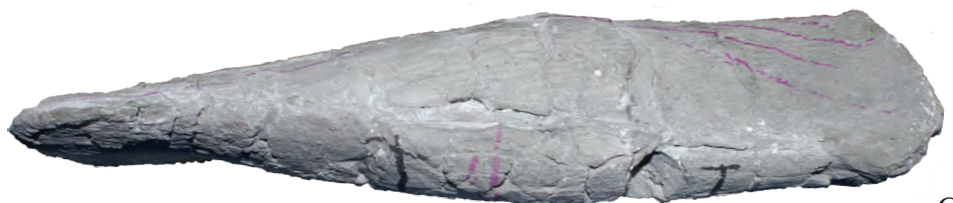
Figure 7. Juvenile propodials, postaxial view. **A:** PMO SVB 1450. Left humerus. **B:** PMO 216.839. Right humerus. **C:** Cast of PMO 216.839. Left humerus. **D:** PMO 216.839. Right femur.



A



B



C



D

5 cm
—

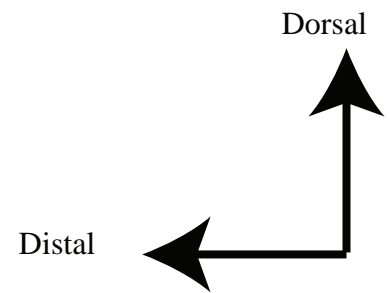


Figure 8. Adult propodials, postaxial view. **A:** PMO 218.377. Humerus, with proximal and distal end. **B:** PMO 218.377. Femur, with distal end. **C:** Cast of PMO 216.838. Left femur, fractured. **D:** PMO 216.838. Right femur. **E:** PMO 214.452. Right femur (mirrored), sub-adult. **F:** PMO A 27745. Right femur, lost trochanter/capitulum (mirrored). **G:** PMO 216.863. Left femur. **H:** PMO 216.863. Right humerus (mirrored).



5 cm

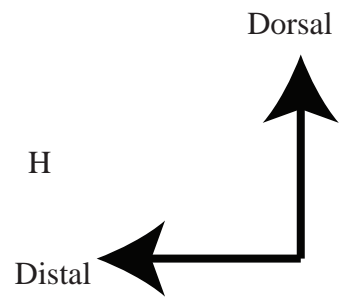


Figure 9. Juvenile epipodials, dorsal view. **A1:** SVB 1450 (mirrored). Radius. **A2:** SVB 1450. Ulna. **B1:** PMO 216.839. Tibia (compressed). **B2:** PMO 216.839. Fibula (compressed).



A1

A2



B1

B2

5 cm

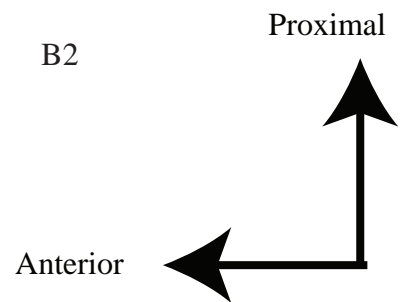


Figure 10. Adult epipodials, dorsal view. **A:** PMO 218.377. Fibula (mirrored). **B1:** PMO 212.662. Radius. **B2:** PMO 212.662. Ulna. **C:** PMO 216.838. Fibula. **D1:** PMO A 27745. Tibia. **D2:** PMO A 27745. Fibula. **E:** PMO 216.863. Ulna.



A

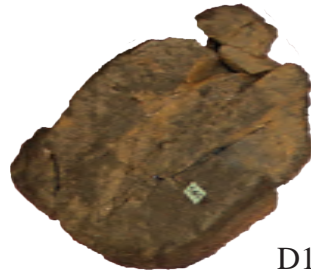


B1

B2



C



D1



D2



E

5 cm

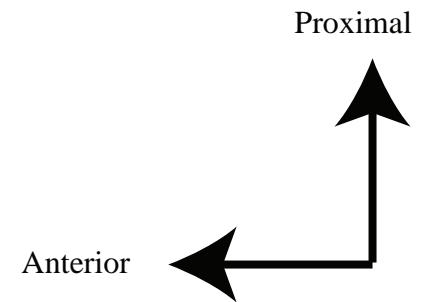


Figure 11: PCA scatter diagram of the Slottsmøya Member plesiosaurs and the Oxford Clay plesiosaurs *Muraenosaurus leedsi*, *Cryptocleidus eurymerus* and *Muraenosaurus beloclis*. PCA scatter diagram based on the values of the ratios measured in Table 3. Note that this places the Slottsmøya Member plesiosaurs in a separate group from the Oxford Clay plesiosaurs. *M. beloclis* give little information due to few values. FEM-phl, HUM-el and HUM-phl show the greatest differences in the plotted values between the Slottsmøya Member plesiosaurs and the compared Oxford Clay plesiosaurs. FEM-dl: a-p diaphysis/length in femora, FEM-el: a-p epiphysis/length in femora, FEM-phl: a-p proximal head/length in femora, HUM-dl: a-p diaphysis/length in humerus, HUM-el: a-p epiphysis/length in humerus, HUM-phl: a-p proximal head/length in humerus. Component 1 and 2: axes of maximal variance.

PCA, Axes 1+2

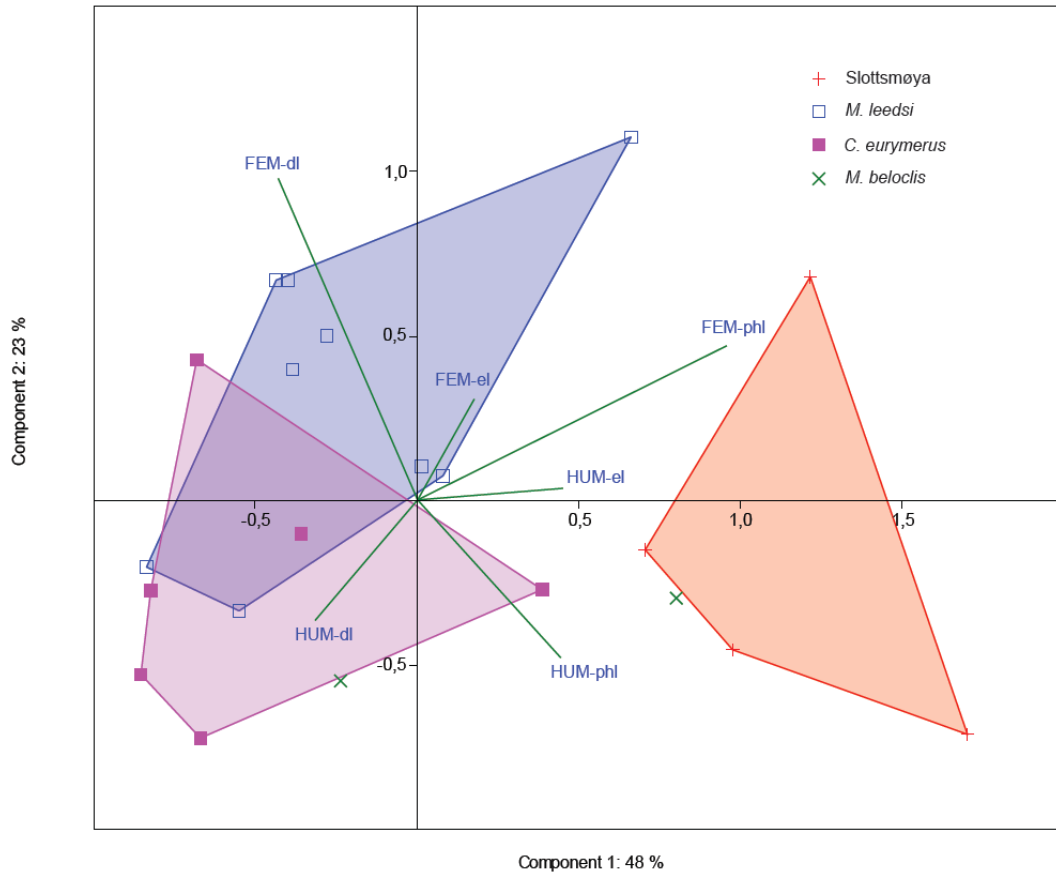


Table 1. Measurements of the propodials in 7 directions, shown in millimeters. PMO 218.377 is missing measurements in humerus and femur as parts of the propodial is missing. a-p: anterior-posterior, d-v: dorso-ventral, F: Femur, H: Humerus. Diaphysis is on the middle of the shaft and distal epiphysis is the margin to the epipodials. For detailed explanation, see Material and methods.

Measurements	PMO 216.839			PMO 216.863		PMO 214.452	SVB 1450	PMO A 27745	PMO 216.838		PMO 218.377	
	Left H:	Rigth H:	F:	H:	F:	F:	H:	F:	Left F:	Rigth F:	F:	H:
length of humerus/femur:	305,0	293,0	364,0	277,0	319,0	435,0	327,0	415,0	244,0	440,0	205,0	110,0
a-p-dm of h./f.head:	84,5	83,0	79,0	71,0	69,0	109,0	90,5	96,0	120,0	125,0	x	78,0
d-v dm of h./f.head:	38,0	52,0	51,5	82,0	75,5	90,0	58,5	85,0	92,0	123,5	x	62,0
a-p dm of diaphysis:	88,5	96,0	105,0	68,0	63,5	91,0	74,0	96,0	x	78,0	x	x
d-v dm of diaphysis:	49,0	52,0	55,0	38,0	35,0	57,0	49,0	55,0	x	54,5	x	x
a-p dm of distal epiphysis:	145,0	152,0	184,0	146,0	149,0	197,0	147,5	225,0	200,0	220,0	190,0	175,0
d-v dm of distal epiphysis:	17,5	18,0	22,5	32,5	31,0	24,5	21,5	45,5	53,5	60,0	59,0	45,0

Table 2. Ratio of the humeri in the plesiosaurs of the Slottsmøya Member propodials and *M. leedsi*, *C. eurymerus*, *M. beloclis* and *T. seeleyi*. a-p: antero-posterior. The a-p proximal head/length on the specimen numbers marked with an * has either a different measurement than the other specimens or a compressed head.

Humerus

Taxon	Specimen number	a-p proximal head/length	a-p diaphysis/length	a-p epiphysis/length
The Slottsmøya Member plesiosaurs	PMO. 216.839 (L)	3,63	3,46	2,10
	PMO. 216.839 (R)	3,53	3,05	1,92
	PMO. 216.863	3,90	4,07	1,89
	SVB. 1450	3,61	4,42	2,21
<i>M.leedsii</i>	NMH R.2421	4,49	4,04	1,66
	NMH R.2422	x	4,00	1,74
	NMH R.2424	4,04	3,76	1,70
	NMH R.2864	2,76	4,00	1,78
	NMH R.2428	2,97*	4,03	0,16
	NMH R.2863	3,69	3,73	1,62
	NMH R.2678	2,65*	3,70	1,65
	NMH R.2425	3,36	3,78	1,55
NMH R.2456	3,05*	4,00	1,70	
<i>C.eurymerus</i>	NMH R.2860	3,80	4,07	1,33
	NMH R.2862	3,60*	4,48	1,37
	NMH R.2412	4,02	4,64	1,34
	NMH R.2417	2,96*	3,57	1,57
	NMH R.2416	2,84*	3,75	1,60
	NMH R.2420	3,81	4,20	1,35
<i>M.beloclis</i>	NMH R.1965	3,73	4,16	1,85
	NMH R.2429	3,81	4,10	1,78
<i>T. seeleyi</i>	NMH R.3539	3,28	3,90	1,75

Table 2. Ratio of the femora in the plesiosaurs of the Slottsmøya Member propodials and *M. leedsi*, *C. eurymerus*, *M. beloclis* and *T. seeleyi*. a-p: antero-posterior. The a-p proximal head/length on the specimen numbers marked with an * has either a different measurement than the other specimens or a compressed head.

Femora

Taxon	Specimen number	a-p proximal head/length	a-p diaphysis/length	a-p epiphysis/length
The Slottsmøya Member plesiosaurs	PMO. 216.839	4,60	3,46	1,98
	PMO. 216.863	4,62	5,02	2,14
	PMO. 214.452	4,00	4,78	2,20
	PMO. A 27745	4,32	4,32	1,84
	PMO. 216.838	3,52	5,64	2,00
<i>M.leedsii</i>	NMH R.2421	3,75	5,48	1,97
	NMH R.2422	x	4,82	1,92
	NMH R.2424	3,97	5,60	2,00
	NMH R.2864	3,21*	4,76	1,95
	NMH R.2428	3,55	5,26	1,80
	NMH R.2861	4,76	5,32	2,17
	NMH R.2678	3,78	4,62	1,70
	NMH R.2425	3,56	4,78	1,78
	NMH R.2456	3,30*	5,33	1,97
<i>C.eurymerus</i>	NMH R.2860	3,42	4,65	1,68
	NMH R.2862	3,30*	4,96	1,68
	NMH R.2412	3,47	4,81	1,62
	NMH R.2417	3,91	4,18	1,74
	NMH R.2420	3,39	4,5	1,35
	NMH R.3703	3,43	4,87	1,6
<i>M.beloclis</i>	NMH R.3698	4,20	4,57	1,86
<i>T. seeleyi</i>	NMH R.3539	3,13	5,02	1,91

Table 3: Synopsis of articulated/associated specimens from *Colymbosaurus trochanterius*, *Cryptocleidus eurymerus*, *Muraenosaurus leedsi*, *Muraenosaurus beloclis*, *Tricleidus seeleyi*.
PETMG.R.283.412: No description of the postcranial skeleton (Martill 1988).

Taxon	Stratigraphy	Sp. no.	Data source	Comment
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	NMH 31787	Brown 1981	Holotype. Isolated right humerus.
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	NMH 31785	Brown 1981	Referred specimen. Isolated left femur
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	NMH 31795	Brown 1981	Referred specimen. Isolated left humerus.
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	NMH 40106	Brown 1981	Referred specimen. Articulation uncertain.
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	NMH 40640	Brown 1981	Referred specimen. Isolated associated right femur.
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	NMH 46479	Brown 1981	Referred specimen. Isolated right humerus.
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	C.M.N 15.72(2)	Brown 1981	Referred specimen. Isolated incomplete left hind limb and right femur.
<i>Colymbosaurus trochanterius</i> , Owen 1840	Kimmeridge Clay (Tithonian)	M.M. LL.5513-8	Brown 1981	Referred specimen. Articulation uncertain.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Ca/Ox)	NMH R.2860	Andrews 1910; Brown, 1981; Brown and Cruickshank 1994	Neotype. Articulated partial skull.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	HMG V.1104	Brown, 1981	Referred specimen. Articulation uncertain
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.2862	Andrews 1910; Brown, 1981	Referred specimen. Uncertain of authors description.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.3730	Andrews 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.2412	Andrews 1910; Brown, 1981	Referred specimen. Referred specimen. Associated fore limb of partial skeleton.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.2616	Andrews 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.2417	Andrews 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.2416	Andrews 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.2431	Andrews, 1910	Referred specimen. Disarticulated propodials.

<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	NMH R.2420	Andrews, 1910	Referred specimen. Articulation uncertain.
<i>Cryptocleidus eurymerus</i> , Phillips 1871	Oxford Clay (Callovian)	PETMG R.283.412	Brown and Cruickshank 1994; Martill 1988	Type species. Articulated/associated specimen.
<i>Cryptocleidus richardsoni</i> , Lydekker 1889	Oxford Clay (Ca/Ox)	NMH R.6696	Brown, 1981	Holotype. Articulation uncertain.
<i>Muraenosaurus leedsii</i> , Seeley, 1874	Oxford Clay (Callovian)	NMH R.2421	Andrews, 1910; Brown, 1981	Holotype. Articulation uncertain.
<i>Muraenosaurus leedsii</i> , Seeley, 1874	Oxford Clay (Callovian)	NMH R.2422	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain
<i>Muraenosaurus leedsii</i> , Seeley, 1874	Oxford Clay (Callovian)	NMH R.2424	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain
<i>Muraenosaurus leedsii</i> , Seeley, 1874	Oxford Clay (Callovian)	NMH R.2864	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Muraenosaurus leedsii</i> , Seeley, 1874 (<i>M. durobrivensis</i> , Lydekker, sp.)	Oxford Clay (Callovian)	NMH R.2863	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Muraenosaurus leedsii</i> , Seeley, 1874 (<i>M. durobrivensis</i> , Lydekker, sp.)	Oxford Clay (Callovian)	NMH R.2861	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Muraenosaurus leedsii</i> , Seeley 1874 (<i>M. platyclis</i> , Seeley. Holotype)	Oxford Clay (Callovian)	NMH R.2678	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Muraenosaurus leedsii</i> , Seeley 1874 (<i>M. platyclis</i> , Seeley)	Oxford Clay (Callovian)	NMH R.2425	Andrews, 1910	Referred specimen. Articulation uncertain.
<i>Muraenosaurus leedsii</i> , Seeley 1874 (<i>M. platyclis</i> , Seeley)	Oxford Clay (Callovian)	NMH R.2456	Andrews, 1910	Referred specimen. Articulation uncertain.
<i>Muraenosaurus beloclis</i> (Seeley, 1892)	Oxford Clay (Callovian)	NMH R.1965	Andrews, 1910; Brown, 1981	Holotype. Articulation uncertain.
<i>Muraenosaurus beloclis</i> (Seeley, 1892)	Oxford Clay (Callovian)	NMH R. 3698	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Muraenosaurus beloclis</i> (Seeley, 1892)	Oxford Clay (Callovian)	NMH R.2429.	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Muraenosaurus beloclis</i> (Seeley, 1892)	Oxford Clay (Callovian)	NMH R.2739.	Andrews, 1910; Brown, 1981	Referred specimen. Articulation uncertain.
<i>Tricleidus seeleyi</i> , Andrews 1909	Oxford Clay (Callovian)	NMH R. 3539	Andrews, 1910; Brown, 1981	Holotype. Disarticulated, scattered over large area.