

# A new species of *Pliosaurus* (Sauropterygia: Plesiosauria) from the Middle Volgian of central Spitsbergen, Norway

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Eight seasons of fieldwork in the Upper Jurassic black shales of the Slottsmøya Member of the Agardhfjellet Formation (Upper Jurassic; Middle Volgian) in the Arctic archipelago of Svalbard have yielded numerous skeletal remains of plesiosaurs and ichthyosaurs. Among the new discoveries from the Slottsmøya Member are two very large specimens of short-necked plesiosaurs. Dental and postcranial morphology suggest that they represent a new species of the genus *Pliosaurus*, a taxon known from several specimens of Kimmeridgian and Tithonian-aged strata in England, France and Russia. Skeletal dimensions of this new taxon suggest that it was one of the largest members of the Pliosauridae and that it possessed comparatively longer front limbs than other known pliosaurids. A morphometric analysis of pliosaurids indicates they had a wide range of interspecific variability in relative paddle lengths compared to body size.

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## Introduction

Pliosaurid plesiosaurs are a clade of cosmopolitan, short-necked and large-headed plesiosaurians that arose in the Jurassic and persisted into the Late Cretaceous (Bardet, 1993; Ketchum & Benson, 2011; Carpenter, 1996). Until now, most described Jurassic pliosaurid material has been from the Oxford Clay and Kimmeridge Clay formations of England and France, although a few Jurassic specimens have also been reported from Mexico and Argentina (Gasparini, 1997; Buchy 2003, 2007). One of the most iconic, yet poorly understood genera of the group is *Pliosaurus* (Owen, 1841a) Owen 1841b.

The sub-genus *Pleiosaurus* was erected by Owen (1841a). Later that same year he raised the taxon to genus level and renamed it *Pliosaurus* (Owen, 1841b). He diagnosed the genus based on the relative shortness of the cervical vertebral centra and the trihedral cross-sectional shape of the teeth that bear prominent longitudinal ridges on the lingual surface and a smooth labial surface (Owen, 1841a, 1841b, 1861, 1863, 1869). Tarlo (1960) reviewed Upper Jurassic pliosaurids and found four species of *Pliosaurus* to be taxonomically valid, one of which was the Callovian taxon *P. andrewsi*. Noè *et al.* (2004) described a fifth species, *P. portentificus*. Knutsen (2012) reviewed

the genus *Pliosaurus* and recognised four species based on mandibular tooth counts, number of premaxillary teeth, retroarticular morphology and relative humeral lengths to cervical vertebral sizes. *Pliosaurus rossicus* (Novozhilov, 1948) was provisionally retained as valid until more detailed descriptions of the material become available (Knutsen, 2012).

Recent fieldwork conducted by the Natural History Museum, University of Oslo, in the Upper Jurassic Slottsmøya Member of the Agardhfjellet Formation on the Spitsbergen island in the Svalbard archipelago, Norway, has yielded the skeletal remains of numerous specimens of both ichthyosaurians and plesiosaurians (Figure 1). Among the recovered specimens are two very large specimens, PMO 214.135 and PMO 214.136, of short-necked plesiosaurians referable to the genus *Pliosaurus*. The only other pliosaurid material previously found on Svalbard was an isolated caudal centrum described by Wiman (1914), which he found comparable to the Callovian taxon *Peloneustes* Lydekker, 1889. Incidentally, this was also the first plesiosaur material ever described from Svalbard. Here, we describe two new specimens from Svalbard, constituting a new species of *Pliosaurus*. As an integral part of this work, we conduct a comparative study on this new material and other pliosaurids based on skeletal morphology and morphometric analyses.

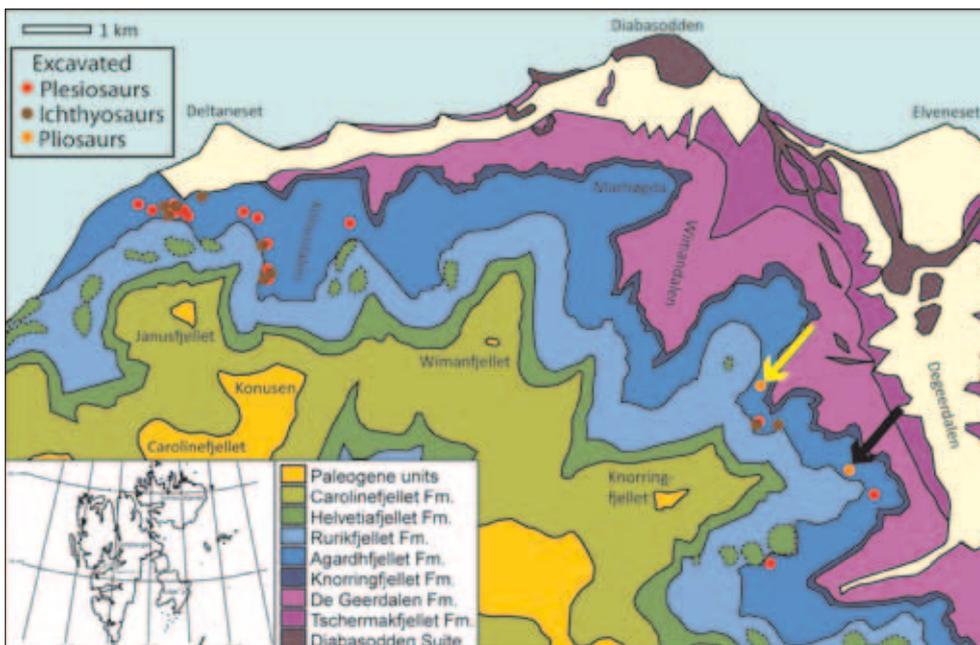


Figure 1. Map of the field area showing the sites of the two plesiosauroid specimens (yellow arrow: PMO 214.135; black arrow: PMO 214.136). Redrawn and adapted from Dallmann et al. (2001).

## Geological setting

The vast majority of marine reptile finds recorded and collected during the 2004–2012 field seasons occur in the Slottsmøya Member of the Agardhfjellet Formation. The Agardhfjellet Formation comprises part of the Adventdalen Group (Parker, 1976), a thick succession of Middle Jurassic to Lower Cretaceous sedimentary rocks that crops out extensively in central Spitsbergen. The Agardhfjellet Formation is underlain by shallow shelf to marginal marine sandstone and shale of the Wilhelmøya Formation (Kapp Toscana Group). The Rurikfjellet Formation overlies the Agardhfjellet Formation and together make up the Janusfjellet Subgroup (Parker, 1976), which consists of several hundred metres of organic-rich, clayey and silty sediment.

Four named members are recognised in the Agardhfjellet Formation, of which the Slottsmøya Member is the uppermost (Dypvik et al., 1991a). The Slottsmøya Member conformably overlies the Oppdalsåta Member and is overlain by the Myklegardfjellet Bed (i.e. base of the Rurikfjellet Formation; Birkemajer 1980). The Slottsmøya Member, which is 70–90 metres in thickness in the study area, consists of dark-grey to black silty mudstone, often weathering to paper shale, discontinuous silty beds, with local occurrences of red to yellowish sideritic concretions as well as siderite and dolomite interbeds (Dypvik et al., 1991a; Hammer et al., 2011; Collignon & Hammer, 2012). The Slottsmøya Member was deposited in an open marine environment under oxygen-deficient settings (Bjarke 1978; Nagy et al., 1988; Dypvik et al., 1991b). Paleogeographic reconstructions for Svalbard during the Kimmeridgian to Valanginian interval place paleoshorelines several hundred kilometres to the north and west (Dypvik et al., 2002).

The Agardhfjellet Formation ranges from the Middle Jurassic to the Lower Cretaceous based on macrofossils (mostly ammonites: Parker, 1976; Ershova, 1983; Wierzbowski et al., 2011), foraminifera (Nagy & Basov, 1998) and palynology (Løfaldli & Thusu, 1976; Bjarke, 1978). The Slottsmøya Member is largely Volgian in age, but recent work in the study area indicates that the unit becomes condensed up-section, with the top of the member lying at or close to the Volgian-Ryazanian boundary (Nagy & Basov, 1998; Hammer et al., 2011), or as young as the Boreal Valanginian (Collignon & Hammer, 2012). The specimens described here (PMO 214.135 and PMO 214.136) occur in either the *Dorsoplanites maximus* or *D. ilovaiskyi* zone, corresponding to the Middle Volgian. Precise age correlations between Upper Jurassic and Lower Cretaceous units of the Boreal and Tethyan regions remain controversial (Ogg, 2004; Hammer et al., 2011; Gradstein et al., in press). However, the Middle Volgian age assigned to these specimens correlates to an informally defined Mid Tithonian or Early Portlandian age of the Tethyan region (Gradstein et al., in press).

To further quantify the stratigraphic occurrence of the vertebrate remains, a laterally continuous, sideritic horizon rich in ammonites (especially *Dorsoplanites* sp.) and bivalves, and a yellow silt bed were used as upper and lower marker beds, respectively, against which the stratigraphic position of each skeleton was measured. The yellow silt bed was set as 0 m. The *Dorsoplanites* marker bed occurs 27 m above this yellow layer and 21 m below the top of the Slottsmøya Member (Myklegardfjellet Bed; see Hammer et al., 2012), and occurs in the Middle Volgian *D. maximus* or *D. ilovaiskyi* zone. The vertical position of each vertebrate specimen was recorded with a Leica TCR 110 total station with <1 cm error at 100 metre distance and later corrected with respect to dip. Both specimens described here

(PMO 214.135 and PMO 214.136) occur at almost exactly the same stratigraphic level within the member, at approximately 14 metres below the *Dorsoplanites* bed.

## Material and methods

### Preparation

Due to the Arctic climate found on Svalbard, the sediment in which the specimens were found has been subjected to repeated freeze-thaw cycles prior to collection. This process has led to extensive fracturing of the skeletal material down to one millimetre in size (for PMO 214.135), and has rendered the bones very unstable. Furthermore, *in situ* the material of PMO 214.135 was moist at the time of collection and degraded upon drying during the preparation process, requiring considerable stabilising by means of consolidants and hardeners.

### Morphometric Analysis

In order to objectively estimate and compare skeletal dimensions, measurements of cranial and postcranial dimensions were assembled for a taxonomically and temporally broad sample of pliosaurids (Table 1; for measurements see supplementary material). In an attempt to estimate skull length of the PMO specimens, the relationship between skull length and dimensions of the occipital condyle and cervical vertebral centra was tested using a linear regression. Skull length was measured from snout tip to the posterior margin of the occipital condyle, and skull width was measured at the widest point in the post-orbital area of the skull. Where the skull was incomplete, the width of the lower jaw at the mandibular glenoid was used as a proxy for skull width.

To estimate the total body length of the PMO specimens, vertebral centra dimensions were plotted with those of other pliosaurids. The results of this plot were then compared with the results of McHenry (2009) to give an approximate body length for both PMO specimens.

Whilst collecting morphometric data for this study, an apparent relationship between propodial length and vertebral dimensions was observed. In order to quantify this relationship and compare these data among different species of pliosaurids, a ratio of vertebral size (used as a proxy for body size) versus humeral length were calculated and visualised in box plots. Cervical and dorsal vertebrae are compared to humeral length separately to illustrate any differences in the values between the two. PMO 214.136 does not preserve limb material, and could not be included in this plot. Unfortunately, there are only two cervical centra available from PMO 214.135. However, in more complete cervical series it is observed that vertebral dimensions tend to increase caudad (Tarlo, 1959b; McHenry, 2009; pers. obs. by EMK and PSD).

Since both cervical centra preserved in PMO 214.135 are from the posterior neck region (see Description below), more anterior centra would most likely be smaller and thus increase the values for PMO 214.135 (Figure 21). For all other specimens included in this analysis, both anterior and posterior cervical vertebral centra were used, except for *P. rossicus*, in which only posterior cervical centra are available (giving *P. rossicus* inflated values compared to PMO 214.135).

The widths of the vertebral centra were measured as the horizontal diameter of the articular surface, excluding the rib facets. The width of vertebral centrum number two of PMO 214.135 (supplementary material) was estimated to be similar to that of the more complete centrum (number one in the same tables) based on length and relative rib facet location. The vertebral centra lengths were measured as the ventral distance between the anterior and the posterior articular surfaces. The humeral lengths were measured as the greatest distance between the proximal and the distal ends of the bone. It was necessary to exclude some specimens from some of the analyses due to incomplete data. For the humeral dimensions of *Pliosaurus rossicus* (Halstead, 1971; Storrs *et al.* 2000), the data in Halstead (1971), (PIN 304/1) was used in this analysis. The morphometric data set was constructed using Microsoft Excel 2007, then log transformed and analysed in PAST version 1.97 (Hammer *et al.*, 2001).

### Institutional abbreviations

BHN	Musée de Boulogne-sur-Mer, Boulogne, France. Museum now closed and collection moved to Museum of Lille.
BRSMG	Bristol City Museum and Art Gallery, Bristol, UK.
CAMSM	Sedgwick Museum, Cambridge, UK
LEICS	Leicester Museums, Arts and Records Service, UK
MCZ	Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts, USA
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MOZ	Museo Prof. Olsacher, Zapala, Neuquén, Argentina
NHMUK	Natural History Museum, London, UK
NMING	National Museum of Ireland, Natural History, Dublin, Ireland
OUMNH	Oxford University Museum of Natural History, UK
PIN	Paleontological Institute, Russian Academy of Sciences, Moscow, Russia
PMO	University of Oslo Natural History Museum, Norway
QM	Queensland Museum, Brisbane, Australia
USNM	National Museum of Natural History, Washington D.C., USA

For PMO specimens, individual elements are catalogued by specimen number followed by a slash and a number starting at one (e.g., PMO 214.135/1).

Table 1 List of skeletal material used for this study:

Taxon	Specimen no.	Data source	Comments
<i>Brachauchenius lucasi</i> Williston, 1903	USNM 4989	McHenry, 2009.	Holotype
<i>Brachauchenius</i> sp.	Unnumbered specimen	Hampe, 1992; McHenry, 2009.	Referred to <i>Brachauchenius</i> by Hampe, 2005.
<i>Kronosaurus boyacensis</i> Hampe, 1992	Unnumbered specimen	Hampe, 1992; McHenry, 2009.	Holotype, on display at the Villa de Leyva, Colombia.
<i>Kronosaurus queenslandicus</i> Longman, 1924	QM F10113	Personal observations (EMK); McHenry, 2009.	Specimen referred to species by McHenry, 2009.
<i>Kronosaurus queenslandicus</i> Longman, 1924	MCZ 1285	McHenry, 2009.	Referred specimen.
<i>Maresaurus coccai</i> Gasparini, 1997	MOZ 4386 V	Gasparini, 1997.	Holotype.
<i>Pliosaurus brachydeirus</i> (Owen, 1841a) Owen, 1841b	OUMNH J.9245	Personal observations (EMK), photographs provided by the Oxford University Natural History Museum; Phillips, 1871; Owen, 1841 a and b, 1861, 1863, 1869; Lydekker, 1889b; Tarlo, 1960.	Holotype and type species of genus.
<i>Pliosaurus brachydeirus</i> (Owen, 1841a) Owen, 1841b	OUMNH J.9192-9301	Personal observations (EMK); Phillips, 1871; Owen, 1841 a and b, 1861, 1863, 1869; Lydekker, 1889b; Tarlo, 1960.	Associated with the holotype.
<i>Pliosaurus brachydeirus</i> (Owen, 1841a) Owen, 1841b	OUMNH J.9285	Personal observations (EMK); Phillips, 1871; Owen, 1841 a and b, 1861, 1863, 1869; Lydekker, 1889b; Tarlo, 1960.	Associated with the holotype.
<i>Pliosaurus brachyspondylus</i> (Owen, 1839) Echwald, 1868	CAMSM J.35991	Personal observations (EMK); Tarlo, 1959a, 1960.	Referred to species by Tarlo, 1959a.
<i>Pliosaurus</i> sp.	BRSMG Cc332	Personal observations (EMK); Taylor and Cruickshank, 1993.	
<i>Pliosaurus tigrisensis</i> (Novozhilov, 1964) Tarlo, 1960	PIN 426	Novozhilov, 1948, 1964; Stors <i>et al.</i> , 2000.	
<i>Pliosaurus macromerus</i> (Phillips, 1871) Lydekker, 1889b	NHMUK 39362	Personal observations (EMK); Owen, 1869; Lydekker, 1889b; Tarlo, 1959b, 1960.	Referred to species by Tarlo, 1959b.
<i>Pliosaurus rossicus</i> Novozhilov, 1948	PIN 304	Novozhilov, 1948, 1964; Halstead, 1971; Stors <i>et al.</i> , 2000.	Holotype.
<i>Rhomaleosaurus cramptoni</i> (Carter and Bailey, 1863) Seeley, 1874	NMING F8785	Smith and Dyke, 2008.	Holotype.
<i>Rhomaleosaurus megacephalus</i> (Stutchbury, 1846) Andrews, 1922	LEICS G221.1851	Cruickshank, 1994.	Referred specimen.
<i>Simolestes vorax</i> Andrews, 1909	NHMUK R.3313	Personal observations (EMK); Noè, 2001.	Holotype.

## Systematic paleontology

SAUROPTERYGIA Owen, 1860  
 PLESIOSAURIA de Blainville, 1835  
 PLIOSAUROIDEA Welles, 1943  
 PLIOSAURIDAE Seeley, 1874

*Pliosaurus* (Owen, 1841a) Owen, 1841b

LSID - urn:lsid:zoobank.org:act:F5506CE2-307F-4DD5-8C89-05A474814BD6

Type species - *Pliosaurus brachydeirus* (Owen, 1841a) Owen, 1841b

Holotype - OUMNH J.9245 and associated material OUMNH J.9247-J.9301.

Horizon - Lower Kimmeridge Clay Formation, *Rasenia cymodoce* ammonite zone (lower Kimmeridgian).

Diagnosis (modified from Owen, 1841a) - Pliosaurid plesiosaurian with teeth that have a flat, smooth labial surface, convex lingual surface with longitudinal ridges, and are trihedral in cross-section.

*Pliosaurus funkei* sp. nov.

Etymology - *funkei*; Latin (gender, masculine), in honour of Bjørn Funke, the discoverer of PMO 214.135, and his wife May-Liss Knudsen Funke who have dedicated several years of volunteer labour to the paleontological collections at the University of Oslo Natural History Museum.

Holotype - PMO 214.135: partial skeleton consisting of the anterior portions of the upper and lower jaws, including premaxillary and dentary teeth; one nearly complete cervical centrum and two partial cervical centra; three pectoral centra with neural arches; fifteen dorsal centra and eight neural arches; a complete right coracoid; the right forelimb including the humerus, epipodials, three mesopodials, and phalanges; numerous rib fragments and gastralia.

Type locality - South of Sassenfjorden, southeast side of Mount Knerten, Spitsbergen, Svalbard, Norway (UTM 33N 0526747 8693845).

Type horizon and age - Approximately 30 metres below the Myklegardfjellet Bed, Slottsmøya Member, Agardhfjellet Formation. *Dorsoplanites ilovaiskyi* to *Dorsoplanites*

*maximus* ammonite zones, Middle Volgian (Tithonian; Nagy & Basov, 1998; Collignon & Hammer, 2012; Gradstein *et al.* in press).

Differential diagnosis - Large pliosaurid (body length of 10-13 m) that possesses the following unique combination of characters; Type I retroarticular process (see discussion; differs from *P. brachydeirus* and *P. macromeris*: Type III, and *P. brachyspondylus*: Type II); cervical central bearing a rugose ventral surface lacking a rounded keel (differs from *Pliosaurus brachydeirus*, which has a smooth ventral surface and bears a rounded keel); humerus long, more than 7 times the average width of cervical vertebral centra (differs from *P. brachyspondylus* and *P. rossicus*, which have humeri less than 4.5 times the cervical width).

Referred specimen - PMO 214.136: partial skull including the occipital condyle, a complete left quadrate, and a partial left squamosal; an incomplete left(?) surangular and articular; left retroarticular process; five partial cervical centra; one partial dorsal centrum; several fragmentary and unidentified bones.

#### Ontogeny

In the vertebral column of PMO 214.135 and PMO 214.136, none of the neural arches are fused to their centra. It is noteworthy that the fusion of neural arches with vertebral centra has not been observed in any of the *Pliosaurus* specimens examined in this study, nor has this been previously reported for any other of the large pliosaurids (e.g., Philips, 1871; Tarlo, 1959 a and b; 1960; Halstead, 1971; Buchy, 2007), and it is therefore difficult to determine whether this is truly a reliable indicator of a juvenile or whether it is possibly a pedomorphic feature in pliosaurids. The humerus of PMO 214.135 has a distinct tuberosity that is partially separated

from the capitulum, suggesting it is a mature individual (Brown, 1981). The coracoid bears a well developed anterior process, normally seen in adult specimens, when present (pers. obs., EMK). Wiffen *et al.* (1995) discussed potential histological indicators of ontogeny in a Late Cretaceous elasmosaurid and a pliosaurid. They noted that adult specimens had an osteosclerotic pattern of growth compared to the pachyosteosclerotic bones of juveniles (but see discussion in Liebe & Hurum, 2012). The cervical vertebral centra of PMO 214.135 and PMO 214.136 display a clear osteosclerotic state with a very spongy internal structure. Thus, morphological and histological characters indicate that both Svalbard specimens were adult individuals.

## Description of the holotype (PMO 214.135)

### Taphonomy

The specimen appears to have settled on its dorsal side on the sea-bed, and was disarticulated prior to burial (Figure 2). The axial remains are roughly arranged in anatomical order (anterior to posterior), though broken into sections. Parts of the anterior portion of the vertebral column were found weathering out on the surface and erosion had removed much of the skull, distributing fragments into a narrow ravine. Two minor, right-lateral, strike-slip fault lines run through the excavation site, offsetting parts of both the coracoid and the humerus. Most of the paddle is articulated, including the propodial and epipodials as one unit, and a large number of phalanges as another. No portion of the specimen was preserved in a concretion, unlike other specimens from the same

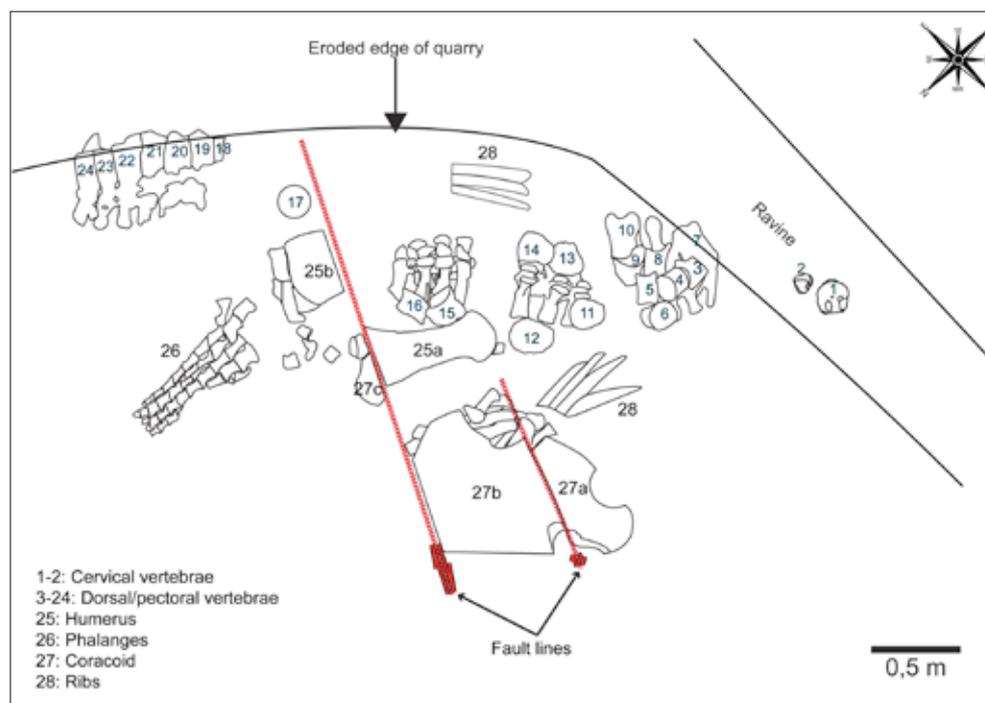


Figure 2. Quarry map of PMO 214.135 at the time of excavation. The cranial fragments were recovered from a narrow ravine adjacent to the quarry and two parallel faults within the excavation area resulted in displacement of parts of the coracoid and humerus.

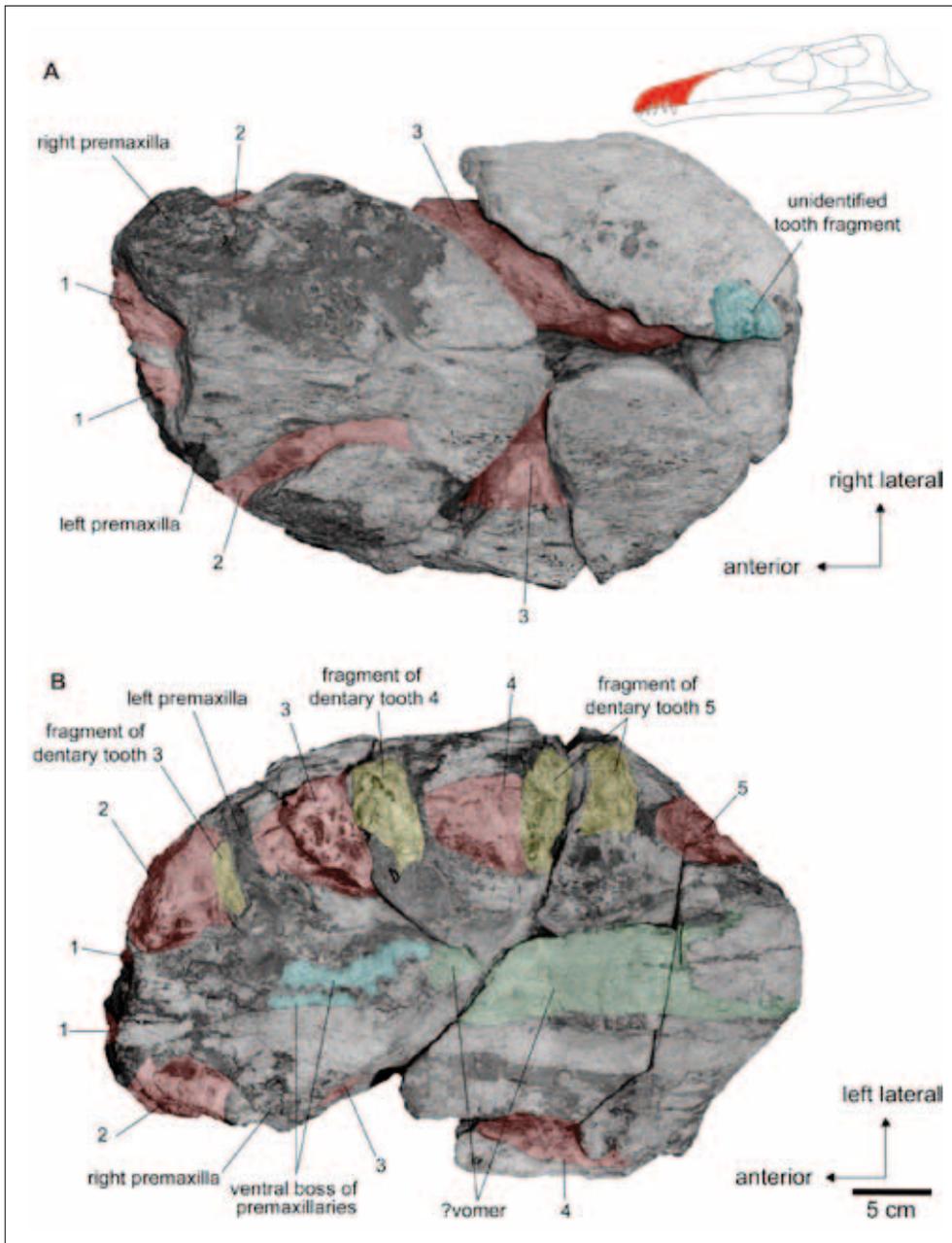


Figure 3. Premaxillary fragment of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in dorsal (A) and ventral (B) view. Dentary tooth fragments are located between the premaxillary teeth, showing the interlocking arrangement between the teeth from the upper and lower jaw. Numbers indicate tooth number. Yellow shading indicates dentary teeth, red shading indicates premaxillary teeth. Note the trihedral outline of tooth number four in the left premaxilla (the posterior surface of this has been somewhat deformed).

stratigraphic member. Fragmented ophiuroid remains were found in the surrounding matrix, but their relative age and association with the skeleton is uncertain.

#### Cranial skeleton

The preserved portion of the skull was reassembled largely from fragments weathered out of the outcrop. The two large fragments are identified as the anterior portion of the left and right premaxilla (Figure 3), and the middle or posterior part of the mandibular symphysis (Figure 4). It is apparent that the right premaxilla had been resting, and was compressed onto, the left dentary of the mandibular symphysis during preservation, resulting in deformation of the bones where they overlapped. The

largest bone fragments have been slightly compressed dorsoventrally, causing the teeth and alveoli to protrude laterally.

#### Premaxilla and vomer

The two premaxillae (Figure 3) are preserved from alveolus one to five. In ventral view, the posterior margin of the preserved fragment resembles the maxillary suture in other pliosaurids, suggesting that the premaxilla broke off of the rostrum in this area. Under this assumption, PMO 214.135 has a premaxillary tooth-count of five. The diastema separating alveolus four from five is almost twice the length of other teeth in the tooth-row. The rostrum is broken anterior to the maxilla-premaxilla

suture, which is therefore not visible. The right premaxilla has been compressed dorsoventrally, while the left premaxilla appears undistorted. The very tip of the rostrum has broken off, exposing the roots of the two anterior-most teeth. The left and right premaxillary suture is not visible on the dorsal surface; however, ventrally, an interdigitating suture referred to as the ventral boss of the premaxillae by Taylor & Cruickshank (1993) can be seen beginning in line with the third tooth pair and extending anteriorly to the first tooth pair. The anterior-most extension of the vomer can be seen extending to the posterior portion of the premaxillary boss. The lateral and dorsal surfaces of the premaxillae are smooth and slightly sculptured.

*Mandible*

Only the posterior portion of the mandibular symphysis (Figure 4) has been preserved. The left dentary preserves three teeth and one small tooth fragment, while the right dentary preserves three teeth and one replacement tooth. Ventrally the anterior-most projections of the splenials can be seen to participate in the symphysis, and terminate anteriorly at a point in line with the anterior margin of the third preserved tooth pair. The diastema separating the posterior-most two alveoli on the right side is half the length of that separating tooth one from tooth two.

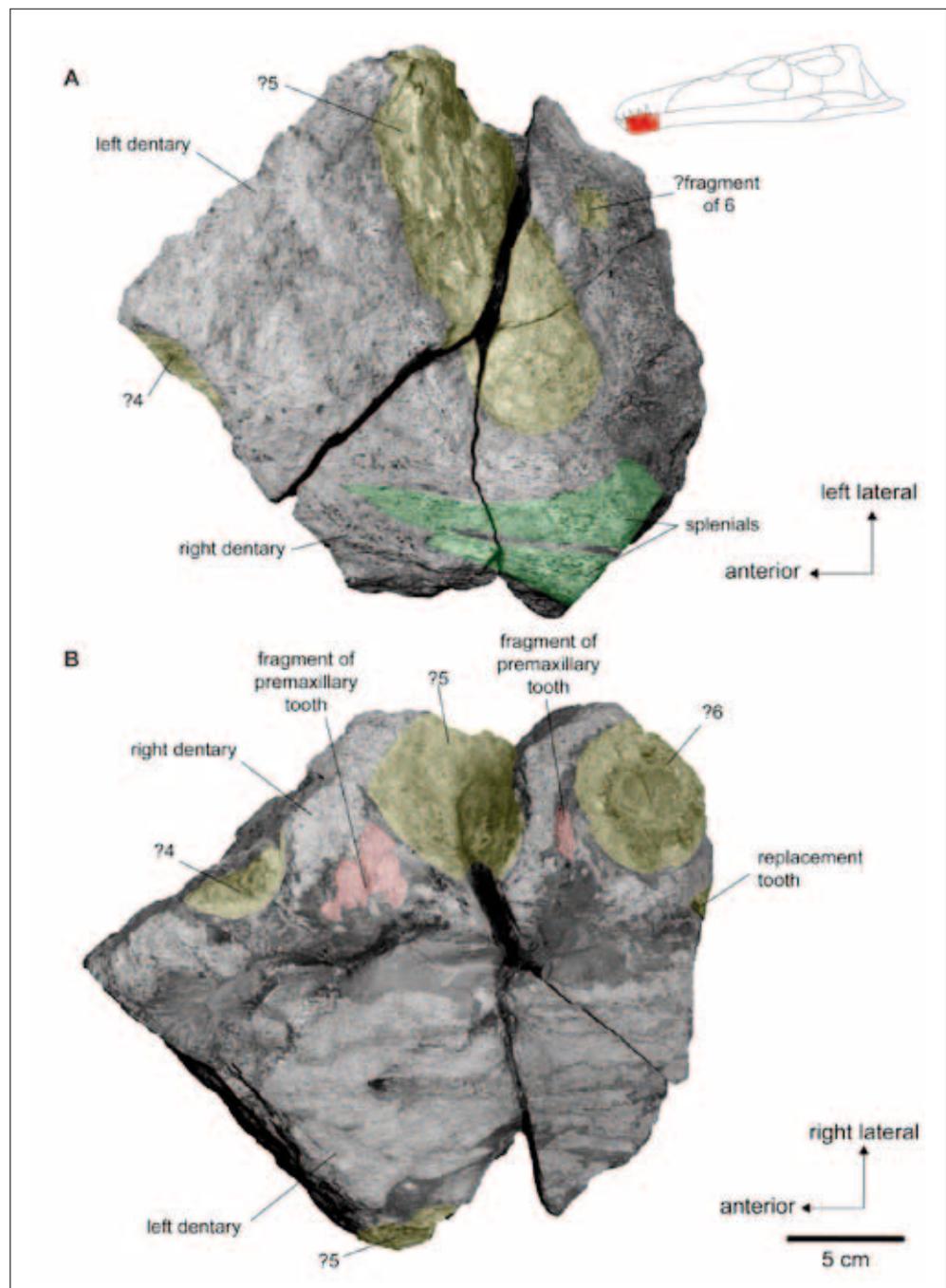


Figure 4. Anterior dentary fragment of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in ventral (A) and dorsal (B) view. Numbers indicate tooth number. Yellow indicates dentary teeth, orange indicates premaxillary teeth.

### Dentition

With the exception of a single replacement tooth on the right dentary, the crowns of the teeth are broken off, leaving only cross-sections of the teeth visible. The fourth tooth of the left premaxilla (Figure 3B) clearly shows a trihedral outline, but this part of the crown is missing in the other teeth. The trihedral crown exhibits enamelled ridges on the lingual surface and a smooth labial surface. Due to dorsoventral compression, several teeth in the dentary and premaxillae have been forced laterally, leaving a partial imprint and/or tooth remains on the ventrolateral surface of the left premaxilla and the dorsolateral surface of the right dentary. Impressions or partial remains of the coarsely enamelled ridges from the lingual part of the crowns of these teeth can be seen in the matrix.

### Axial skeleton

There are a total of 24 vertebral centra, of which three are cervical, at least three are pectoral, and the remainder are dorsal. Eight dorsal neural arches are also preserved but have separated from their attendant vertebra along the neurocentral suture.

### Cervical vertebrae

All three of the cervical vertebrae were found exposed and fragmented on the outcrop. Only the centra of the cervical vertebrae are preserved, and these are incomplete. However, by combining information from all three, it is possible to accurately reconstruct their complete morphology. Cervical centra are distinguished from pectoral and dorsal centra by bearing their rib facets on the centrum only. In articular view, the centra are circular in outline, and exhibit slightly concave articular surfaces with a central elevated notochordal pit (Figure 5). Centrum length is approximately half that of width or height. Laterally, the surface is rugose ventral to the rib facets. The rugosity continues around the rib facets and

diminishes dorsally. Ventrally, the rugosity is more prominent on the posterior and anterior border. However, the ventral-most part is missing in all three preserved centra, so the ventral extent of this rugosity pattern is unknown. The centra bear two rib facets (diapophysis and parapophysis) for each rib, the parapophysis being round and the diapophysis triangular with the apex pointing dorsally. The facets are subequal in size. The presence of a ventral foramen and keel is equivocal as the ventral surface is either too damaged or missing.

### Pectoral vertebrae

As typically defined, the pectoral vertebrae (Figure 6) can be distinguished from the cervical and dorsal vertebrae on the basis of ribs that are borne partly on the centrum and partly on the transverse process of the neural arch. The centrum outline is round in articular view, with a dorsolaterally flaring lip resulting from the position of the rib facets. In cross-section the transverse process is triangular, with the apex pointing ventrally, compared to those in the dorsal vertebrae which are dorsoventrally flattened.

### Dorsal vertebrae

The dorsal vertebrae (Figures 7 and 8) are distinguished from the cervical and pectoral vertebrae in having the ribs borne only on the transverse process of the neural arch. The centrum outline is pear shaped, being widest ventrally. Dorsal centra are approximately equally long as wide, in contrast to the cervical vertebral centra. The ribs and their respective facets are dorsoventrally flattened. The lateral surfaces of the centra are concave, circumscribing the centrum with a pronounced constriction.

The dorsal neural arches have long transverse processes (Figure 8) that terminate in cross-sectionally oblong facets. The width of this transverse process is more than 1.5 times the width of the centrum. The thin neural spine is posteriorly curved in lateral view, and approximately the

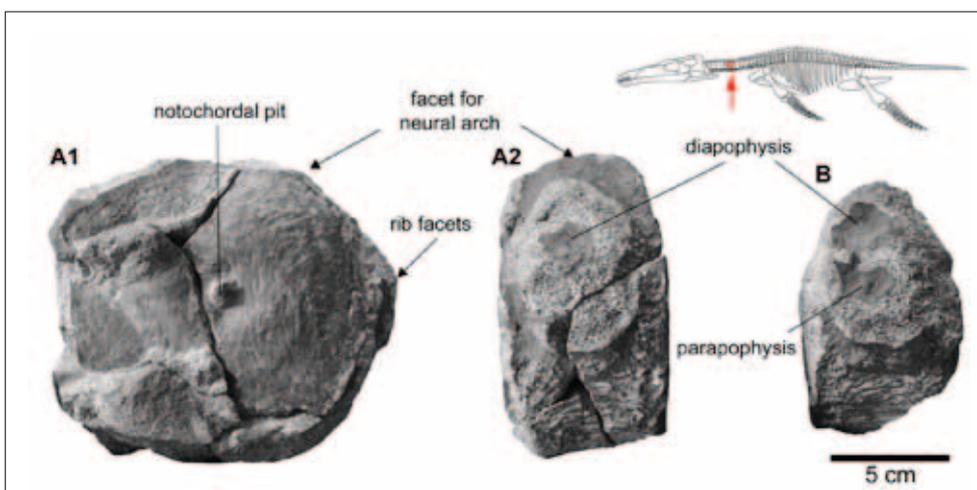
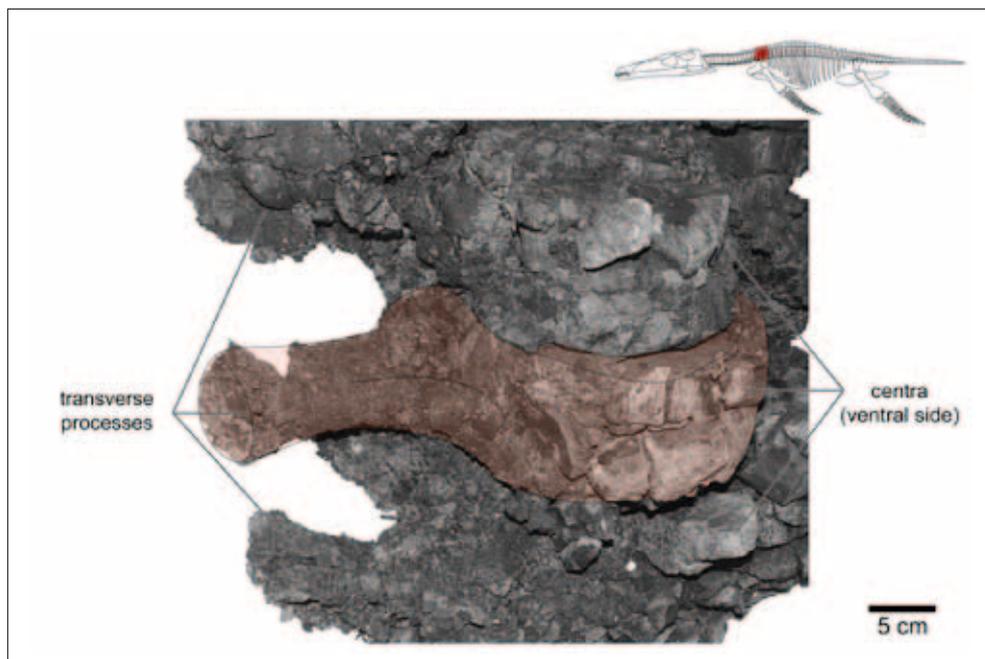


Figure 5. Cervical centrum of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in articular (A1) and left(?) lateral (A2) view, and a second cervical centrum from the same specimen in left(?) lateral view (B) showing the triangular diapophysis and circular parapophysis. The notochordal pit is inverted as it is a negative mould of the articular surface of a third centrum that was mechanically removed. The ventral surface of both centra is eroded away.

Figure 6. Pectoral vertebrae from the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in right(?) ventrolateral view. The transverse processes originate from both the vertebral centra and the neural arches.



same height as the associated centrum. A groove is present along the anterior margin of all the neural spines.

*Dorsal ribs and gastralia*

Fragmentary dorsal ribs were preserved on, and adjacent to, the coracoid (Figure 9) and have an oval cross-section. No rib heads are preserved. Eight gastralia are preserved ventrally on the coracoid (Figure 9). They are gently curved and taper to a point both laterally and medially. A longitudinal groove is present on all gastralia.

*Appendicular skeleton*

The appendicular skeleton preserves one complete coracoid and a nearly complete right front limb. No portions of the scapulae were preserved. The poorly preserved coracoid is interpreted as being from the right side based on its close association with the right front limb. The presence of dorsal ribs beneath the coracoid (*in situ*) suggests that it was preserved ventral side up. The limb is interpreted as a right based on the postaxial shift of the tuberosity in relation to the capitulum in proximal view, as is typical in the humeri of other plesiosaurians (Brown, 1981).

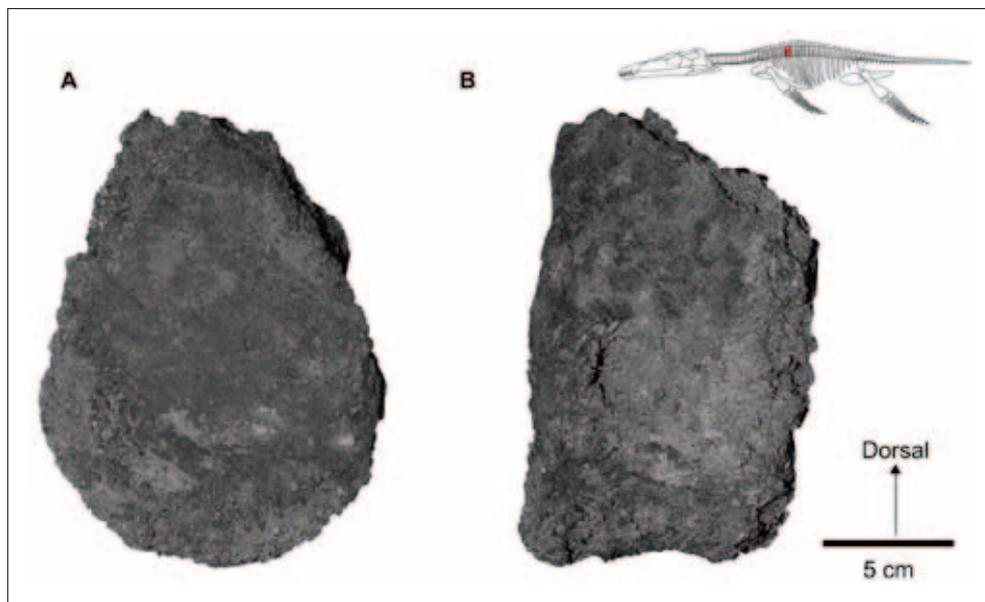


Figure 7. Dorsal centrum of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in articular (A) and lateral (B) view. The anteroposterior orientation is unknown.

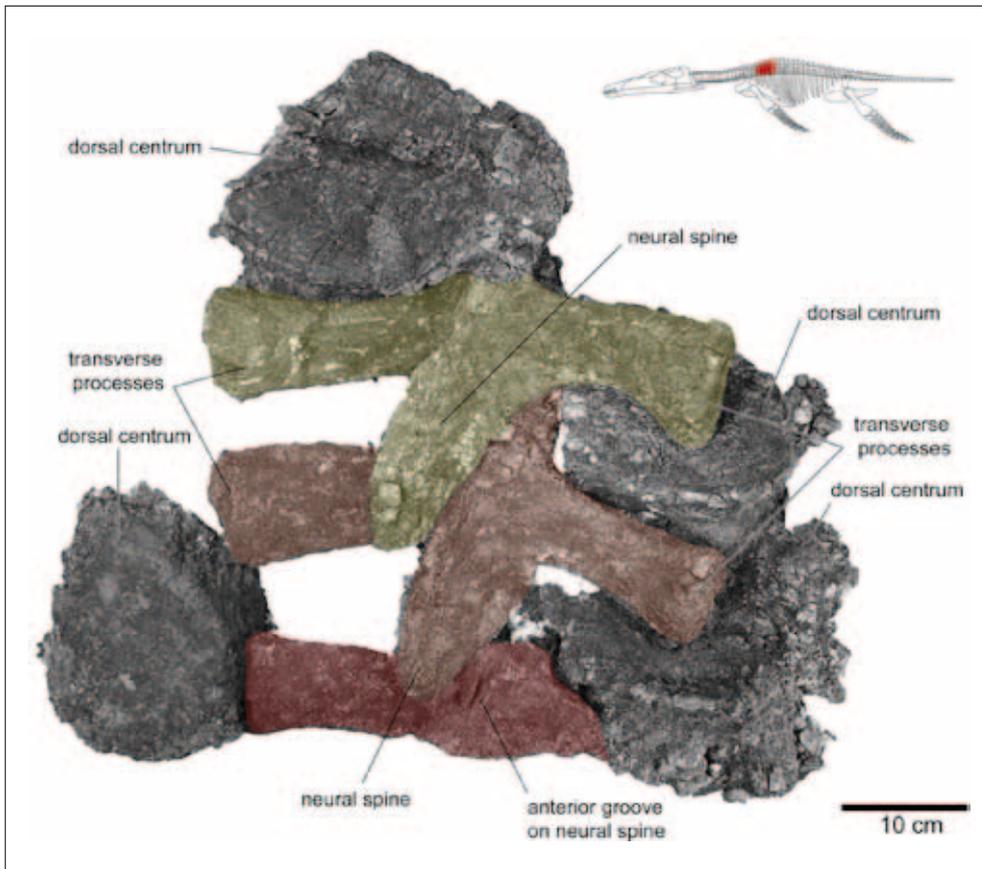


Figure 8. Four dorsal vertebral centra and three associated neural arches (shaded yellow, orange, and red) of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135).

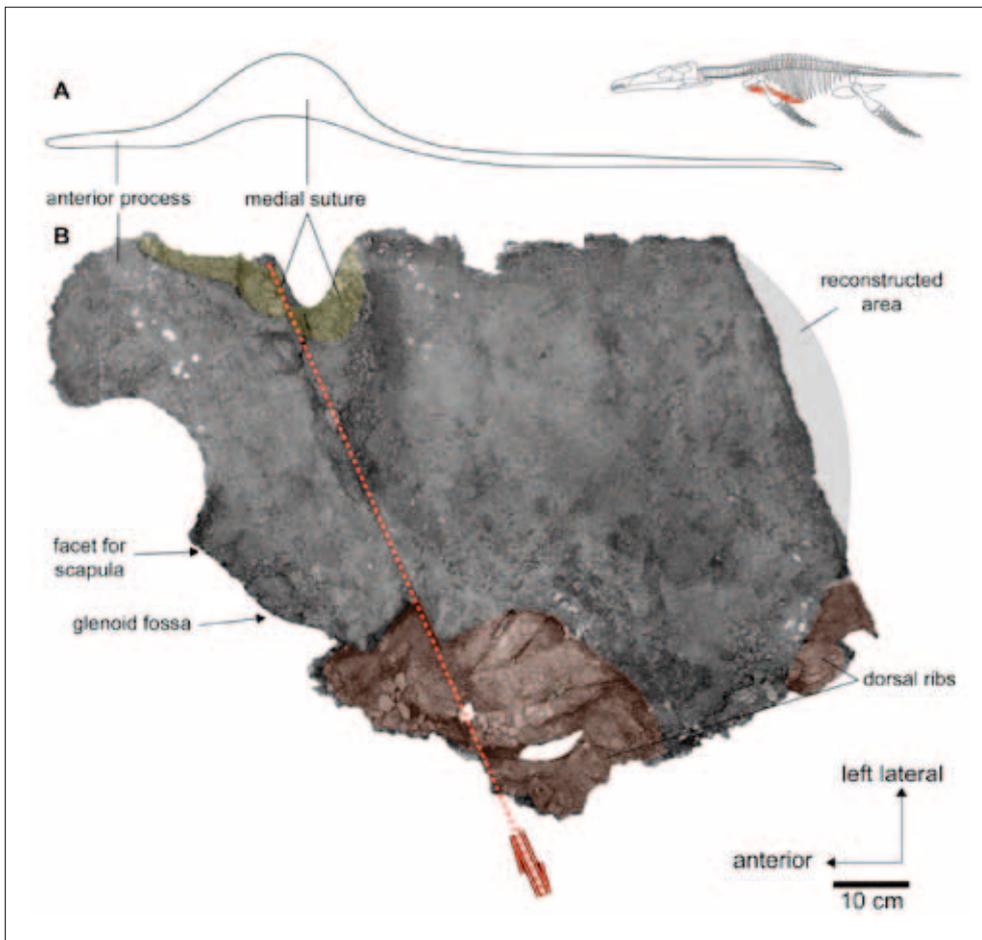
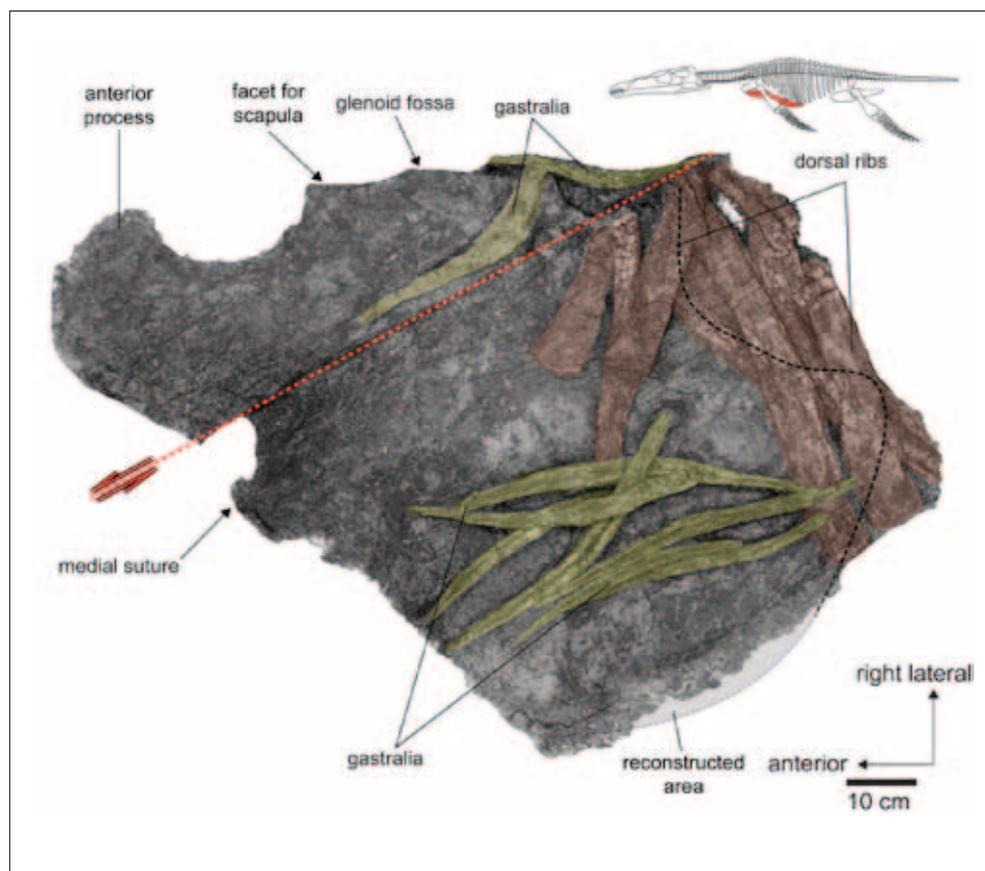


Figure 9. Right coracoid of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in ventral view. A fault (red dashed line) runs obliquely across the coracoid. Several dorsal ribs (shaded orange) lie dorsally to the coracoid. The posterior part was reconstructed based on a preserved element, which was displaced along a fault.

Figure 10. Right coracoid of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in dorsal view. A fault (red dashed line) runs obliquely across the coracoid. Several gastralia (shaded yellow) lie on the dorsal side of the coracoid. The posterior part was reconstructed based on a preserved element, which was displaced along a fault.



### Coracoid

The right coracoid (Figures 9 and 10) is preserved almost in its entirety, but a small portion of the posterior margin has been displaced along a fault. A second right-lateral fault crosses the mid-portion of the coracoid in the transverse plane. In dorsal view, the coracoid is longer than it is wide (Table 2) and tapers in width anteriorly. It has a maximum length-to-width ratio of approximately 1.54. The anterior process of the coracoid is approximately as wide as it is long, and is slightly expanded in mediolateral width anteriorly. A dorsoventrally thickened transverse buttress extends between the medial suture and the posterior margin of the glenoid fossa, and thins laterally. In medial view, the buttress forms a fold in the coracoid. The median symphysis between the left and right coracoid is obliquely angled, but this could be a result of dorsoventral compression. The posterolateral margin of the coracoid is laterally expanded producing a weakly developed cornu that does not extend laterally beyond a line drawn in the parasagittal plane through the glenoid.

### Humerus

The identification of the propodial as a humerus is based on its close association with the coracoid, its proximity to the pectoral and cervical vertebrae (Figure 2), and the postaxially shifted tuberosity in relation to the capitulum. The proximal end of the humerus is strongly offset from the shaft by a prominent constriction immediately distal

to the humeral head and then gradually expands in pre-axial-postaxial width distally (Figure 11 A). The capitulum is oval in shape, being wider than tall (Figure 11 B), although this may be a result of crushing. The tuberosity appears to be somewhat dorsoventrally crushed, and lies posterodorsal to the capitulum in proximal view. The tuberosity also demarcates the terminal end of a weak dorsal ridge that runs approximately half of the length of the humerus in the proximodistal direction. The capitulum-tuberosity contact is broadly confluent.

Distally, the pre- and postaxial margins of the shaft are symmetrical and there is no prominent postaxial expansion at the distal end. A well developed rugosity on the posteroventral surface of the shaft, approximately 30 cm from the proximal end, probably represents the insertion of the pectoral musculature. Distally, the humerus bears two distinct facets for the epipodials. In dorsal view, the articular end is nearly straight in outline. The width of the humeral proximal end is approximately 60% of that of the distal end.

### Epipodials and mesopodials

The epipodials (Figure 11 A) are dorsoventrally compressed, slightly distorting their original shape, but their general dimensions can be confidently ascertained. The radius and ulna are nearly equidimensional in length and width. Most significantly, both epipodials

Table 2: Table of measurements for PMO 214.135 and PMO 214.136.	
<b>Measurements (in mm)</b>	
<b>PMO 214.135</b>	
<b>Cranial</b>	
Width of premaxillary fragment	200
Length of premaxillary fragment	300
Width of mandibular fragment	220
Length of mandibular fragment	240
Diameter of largest tooth	60
<b>Appendicular</b>	
Maximum length of humerus	1000
Maximum distal width of humerus	400
Maximum width of humeral capitulum	245
Width of shaft mid-way	275
Width of radius	190
Length of radius	120
Width of ulna	245
Length of ulna	110
Length of complete paddle	~3000
Anteroposteior length of coracoid	1200
Medial symphyseal-to-glenoidal length on coracoid	435
Maximum posterior width of coracoid	780
Length of medial symphysis of coracoid	340
Length of glenoid of coracoid	300
<b>PMO 214.136</b>	
<b>Cranial</b>	
Width of basioccipital condyle	150
Height of basioccipital condyle	105
Length of surangular fragment	570
Maximum height of surangular fragment	180
Posterior width of surangular fragment	85
Anterior width of surangular fragment	40
Width of mandibular glenoid	250
Length of mandibular glenoid	~110
Width of retroarticular process	140
Length of retroarticular process	130

are approximately twice as wide as they are long (Table 2). The intermedium (Figure 11 A) appears to have been displaced proximally, and now covers the ventromedial portion of the ulna. Two bones lying between

the epipodials and the phalanges are interpreted to be proximal mesopodials based on their size, although their distorted shape makes identification equivocal.

Figure 11. Right front paddle of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135). Humerus and epipodials in dorsal view (A), and the humerus in proximal view (B).

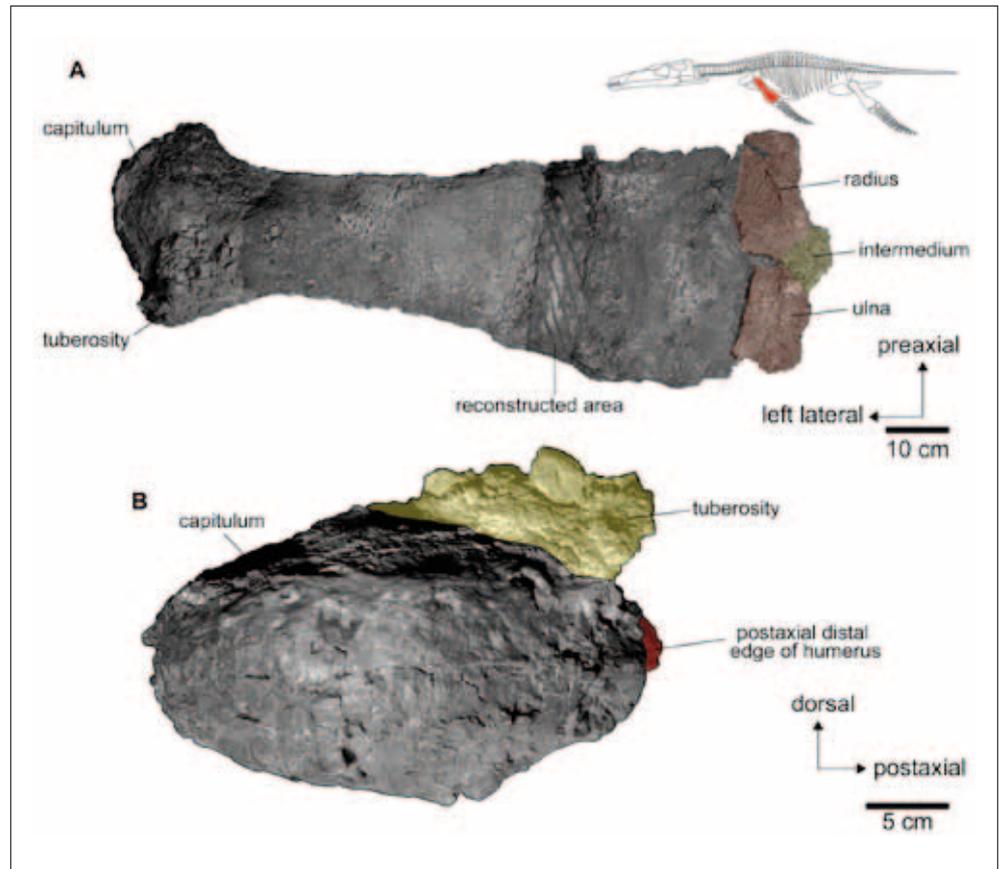
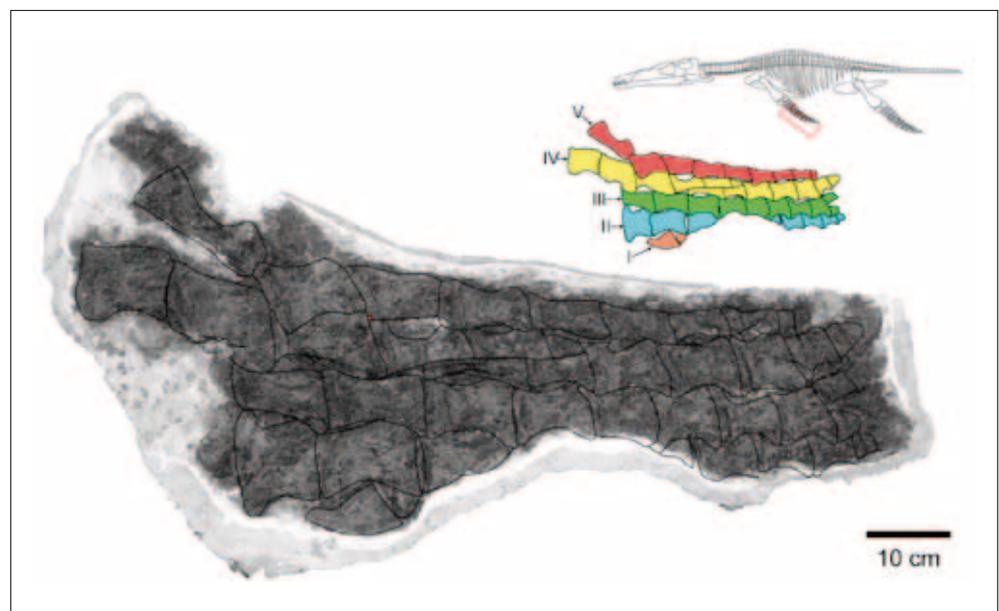


Figure 12. The phalanges of the right front paddle of the holotype of *Pliosaurus funkei* sp. nov. (PMO 214.135) in ventral view.



*Phalanges*

There are a total of 36 phalanges preserved, of which 30 are complete (Figure 12). The proximal phalanges have been compressed and their outline distorted. The rest

exhibit an hour-glass shape and become shorter and narrower distally.

## Description of the referred specimen (PMO 214.136)

### Taphonomy

The specimen was collected from a large slumped block of shale that probably became displaced due to melting of permafrost. During the slumping process, the internal bedding of the block was distorted and the skeletal material closer to the surface became more displaced than that found lower down in the block. As a result, the recovered parts of the specimen had slid out over an area roughly 6 by 12 metres. Based on the distribution of bones found during the excavation it is likely that the *in situ* cranial remains were nearly articulated prior to burial. Some of the bones were covered in an iron-rich

concretionary matrix that contained sporadic ophiuroid remains.

### Cranial skeleton

The occipital condyle (Figure 13) was found as an isolated and fragmented element. It is slightly dorsoventrally compressed, giving the occipital condyle an oblong outline in posterior view. Its surface has an uneven, broadly pitted texture, but a distinct notochordal pit is not visible. The anterior margins of the condyle are incomplete. The right exoccipital facet is preserved on the dorsal surface of the basioccipital, but it is incomplete.

The largest cranial fragment (Figure 14) is a large portion of the suspensorium complex including the left quadrate

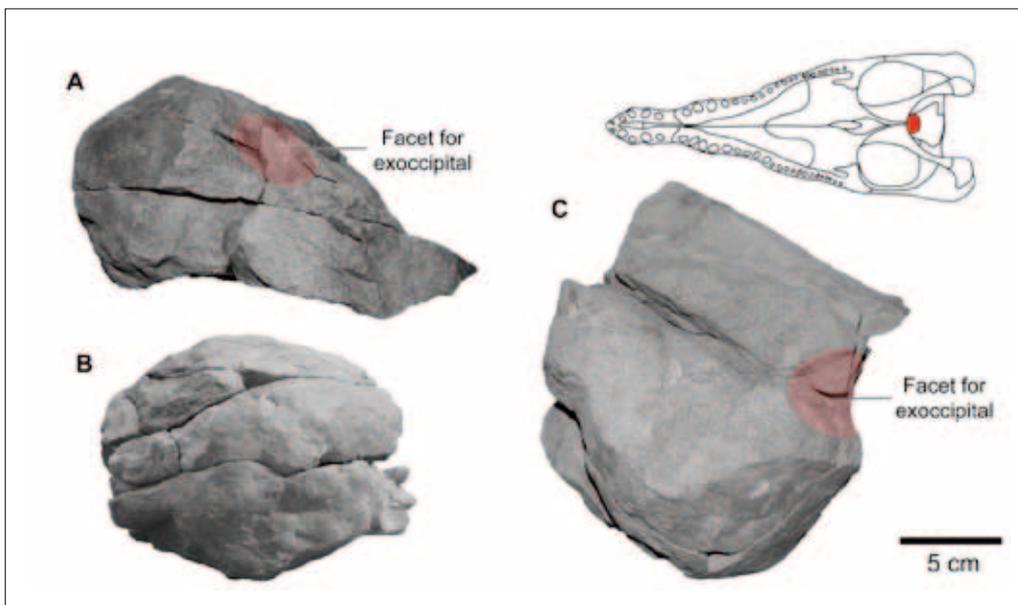


Figure 13. Partial basioccipital including the occipital condyle of the referred specimen of *Pliosaurus funkei* sp. nov. (PMO 214.136) in right lateral (A), posterior (B) and dorsal (C) views.

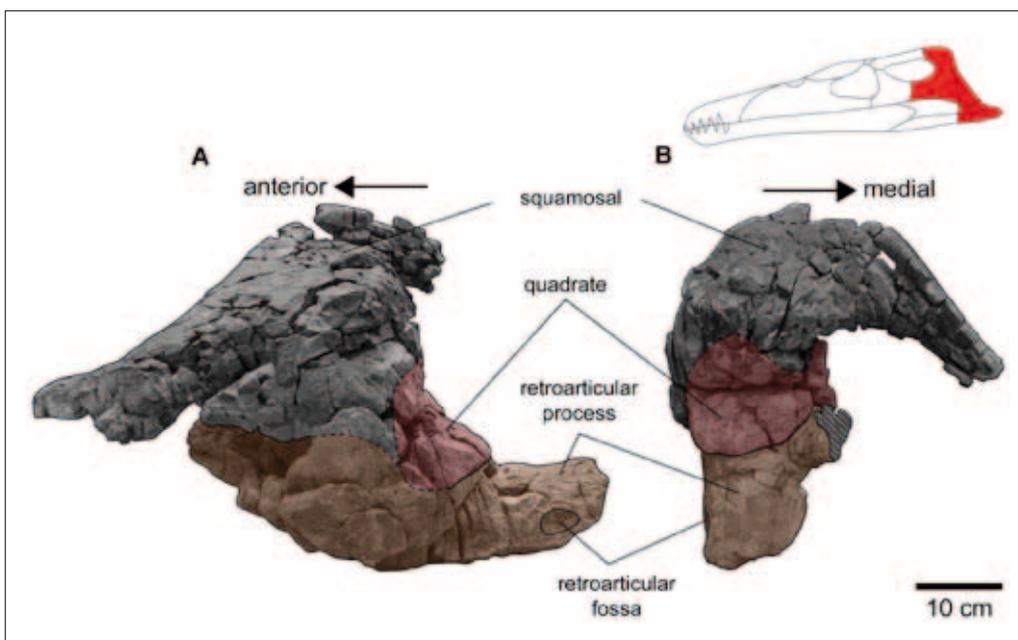
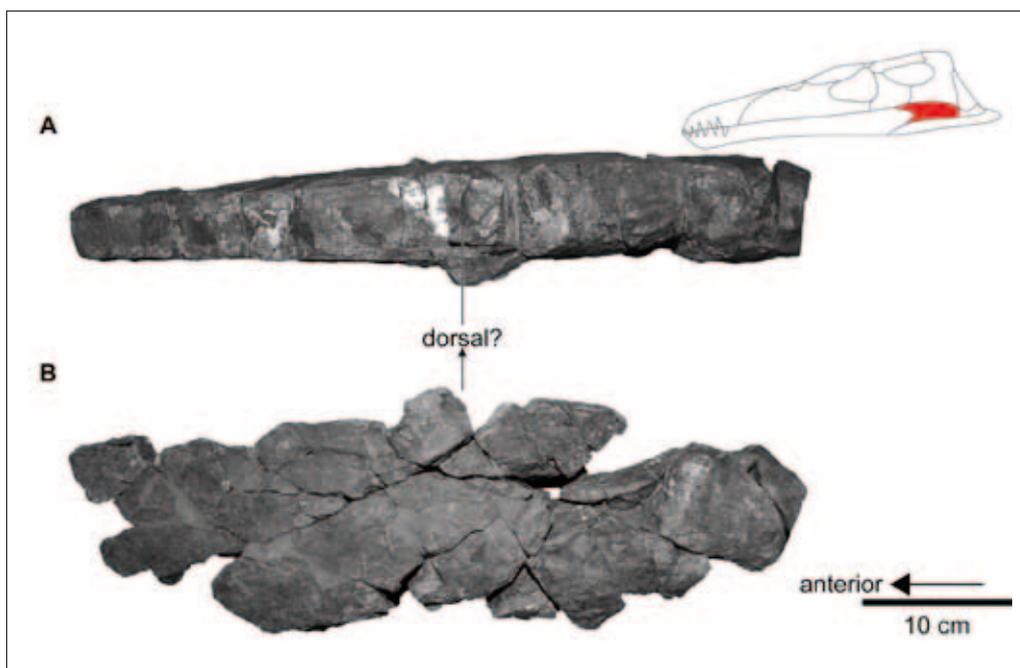


Figure 14. Left posterior jaw fragment of the referred specimen of *Pliosaurus funkei* sp. nov. (PMO 214.136) in lateral (A) and oblique posterior (B) view. Dashed lines indicate approximate interpreted positions of sutures. Red shading indicates the quadrate, and yellow shading indicates the mandibular ramus.

Figure 15. Left(?) surangular of the referred specimen of *Pliosaurus funkei* sp. nov. (PMO 214.136) in dorsal(?) (A) and lateral(?) (B) views.



and the lateral portion of the left squamosal. The ventral-most portion of the quadrate is cemented to the mandible at the quadrate-glenoid joint. The quadratosquamosal suture is not visible, and was likely fused in life. The posterior and lateral margins of the quadrate are vertical, and its posteroventral edge curves slightly posteriorly. A cross-section just above the ventral surface of the quadrate is crescent-shaped, the curve's apex facing posteriorly. The squamosal forms the posterior and lateral borders of the temporal fenestra and bears a medial, a posterior, and an anterolateral projection. The posterior portion of the bone forms a horizontal platform dorsal to the quadrate, producing a corner where it meets the vertical posterior and lateral walls in the area of the contact with the quadrate. The squamosal's medial projection ascends dorsomedially from the horizontal platform towards the dorsal midline of the skull. Its lateral process does not preserve the contact with the jugal.

#### Mandible

A posterior portion of the left mandibular ramus is preserved, beginning just anterior to the mandibular glenoid and including the complete retroarticular process (Figure 14). The medial part of the glenoid fossa is missing. There are no clear sutures separating the different elements making up the preserved fragment. The retroarticular process is very massive, and possesses a large fossa, approximately 4 cm long and 2 cm high, that may have functioned as a muscle or tendon attachment. In lateral view, its ventral margin curves abruptly dorsally near its posterior end to intersect the almost horizontally-oriented dorsal margin, where they form a convexly rounded posterior end. In dorsal view the process is mediolaterally widest near its midpoint and has a

nearly straight lateral margin and a convex medial margin. In dorsal view, the lateral and medial margins meet at a rounded edge posteriorly. In cross-section (as viewed posteriorly), the posterior half of the process is triangular in shape (apex pointing dorsally), with a nearly flat ventral margin. In the area of the mandibular glenoid the jaw expands laterally and medially to accommodate the quadrate condyle, and then narrows anteriorly to this.

A large, mediolaterally flattened, incomplete bone fragment that tapers dorsally, ventrally and anteriorly is interpreted as the surangular (Figure 15). Most of its dorsal and ventral surfaces are missing, but in the areas where it is present it terminates in a rounded edge. Its lateral and medial surfaces are smooth except in its posteriormost portion where it is coarsely rugose. In dorsal view, the element tapers in thickness anteriorly.

#### Axial skeleton

There are a total of six vertebral centra preserved in PMO 214.136, of which five are cervical, and one is dorsal. Where discernible, the cervical centra are more than twice as wide as they are long. Due to its preservation and lack of a neural arch, determining the anterior and posterior directions is difficult. Based on size differences and relative position of rib facets, it is possible to determine the relative position along the neck following Tarlo's (1959a) description of relative rib facet position in *Pliosaurus brachyspondylus*. All preserved centra are biconcave, the more anterior with the deepest concavities. What Tarlo (1959a) refers to as a "peripheral groove" runs just medial to the outer rim of the articular surfaces of centra PMO 214.136/1, 3 and 5. Rib facets are best preserved in the anterior centra of PMO 214.136/1

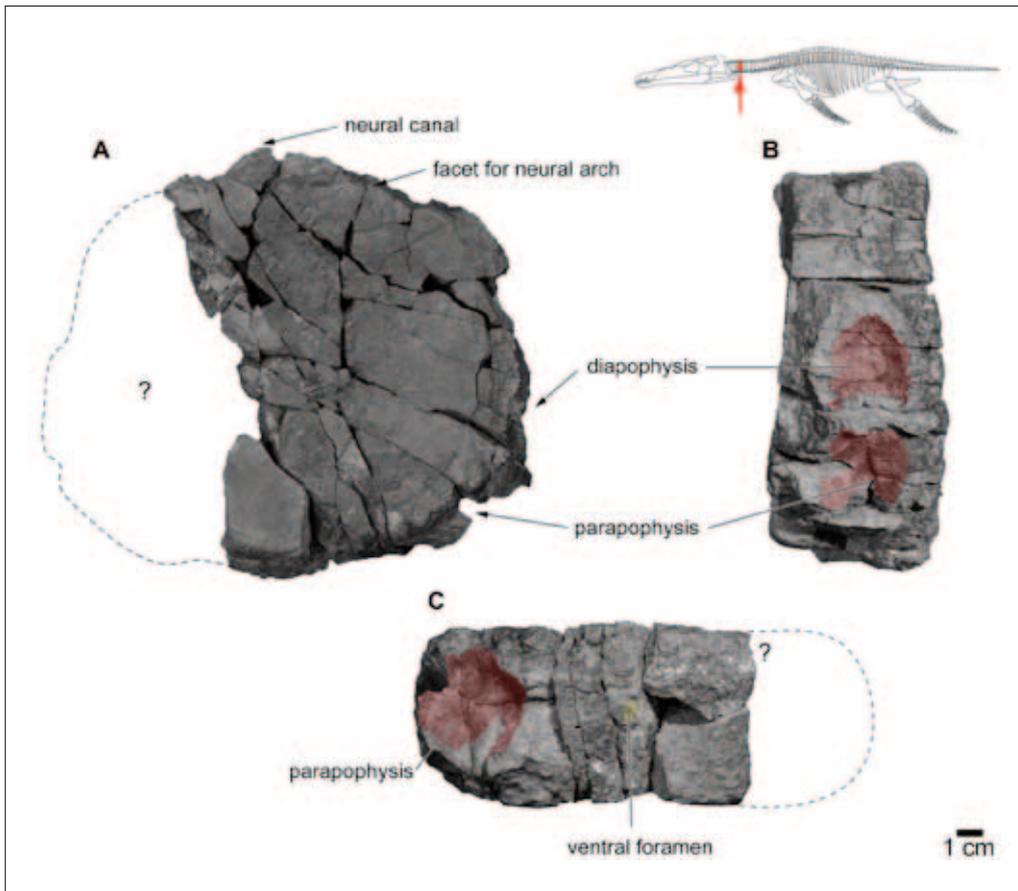


Figure 16. Anterior cervical vertebral centrum of the referred specimen of *Pliosaurus funkei* sp. nov. (PMO 214.136) in anterior(?) articular (A), left(?) lateral (B) and ventral (C) view.

and 2. In the latter (Figure 16), the triangular diapophysis and the circular parapophysis are separated by a bony septum. The anterior-most centrum, PMO 214.136/1, exhibits an anteroventrally extended margin, referred to by Tarlo (1959a) as the ventral lip. This is also present, but less prominent, in PMO 214.136/2. Ornamentation/rugosities are present on the ventral surfaces of all cervical centra but vary in their pattern, having strong marginal rugosities with finer inter-marginal structures in anterior cervicals, and coarse marginal rugosities with a smooth inter-marginal area in posterior cervicals. In PMO 214.136/2 there is a weakly developed ridge stretching 2 cm dorsally from the parapophysis. A small number of fragmented remains of neural arches and cervical ribs are also preserved, but are unremarkable.

## Results

### Morphometric analysis

There is a positive relationship between the size of the occipital condyle and the total length of the skull among selected pliosaurid taxa (i.e., longer skulls have a larger occipital condyle; Figure 17). The same relationship exists between average cervical centrum width and total skull length (i.e., long skulls belong to animals with wide cervical centra; Figure 18).

Among selected pliosaurid taxa, the widest cervical vertebral centra correlate with those that are the longest (Figure 19). Of the specimens included in the analyses of McHenry (2009), those to which he attributed the longest snout-to-hip length are located on the right side of the plot and the smallest to the left (Figure 19). The same relationship is seen for dorsal vertebral centra (Figure 20) with the largest individuals again having the largest centra. The PMO specimens (red crosses and blue squares) are positioned to the right in these plots.

There is great variability in the length of humeri compared to both vertebral centrum width and height (Figures 21 and 22), suggesting that there exist several body types within Pliosauridae. The cervical centra of PMO 214.135, OUMNH J9245 and CAMSM J.35990 (all referred to *Pliosaurus* spp.) are less wide than dorsal centra (Figure 21), whilst the reverse condition is found in QM F10113 (referred to *Kronosaurus*). Cervical centrum length is consistently shorter than dorsal centrum length in all specimens analysed (Figure 22). There is also a wide range of centrum lengths present in dorsal vertebrae (Figure 22) for at least MCZ 1285 (*K. queenslandicus*) and CAMSM J.35991 (*P. brachyspondylus*). PMO 214.135 displays high values for both cervical and dorsal vertebrae, and has comparatively higher values than other *Pliosaurus* spp. *Brachauchenius* sp., a much smaller specimen of a genus closer related to *Kronosaurus* than to *Pliosaurus*, has similar values to PMO 214.135.

Figure 17. Linear regression plot showing the relationship ( $r=0,91$ ,  $R^2 = 0,91$ ,  $n=7$ ) between skull length and width of the occipital condyle. The estimated skull length based on the width of occipital condyle for PMO 214.136 is shown in blue. The data points are few and the results are indicative, not conclusive.

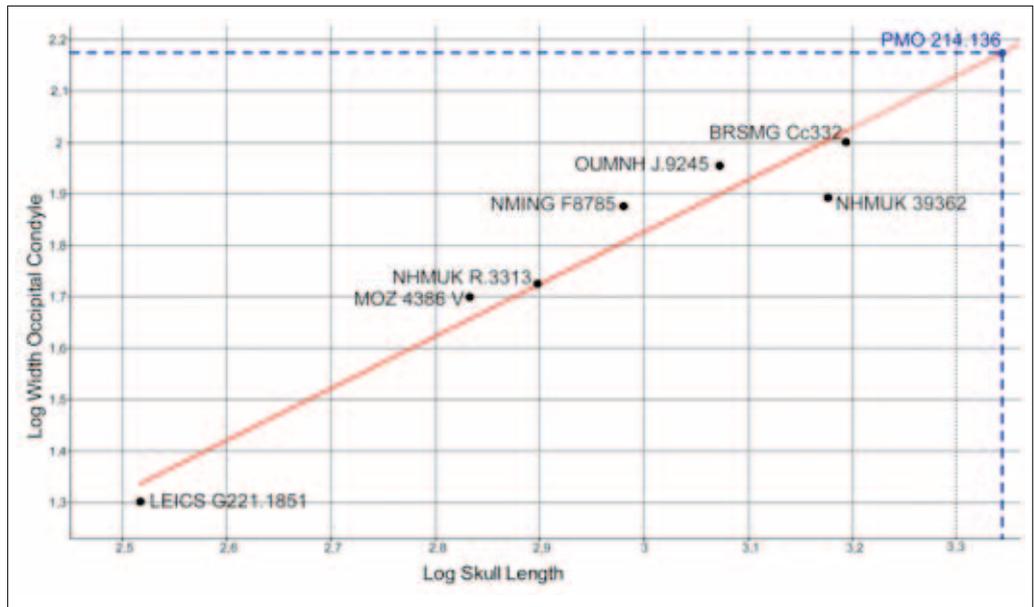


Figure 18. Linear regression plot showing the relationship ( $r=0,99$ ,  $R^2 = 0,97$ ,  $n=10$ ) between skull length and average width of cervical vertebral centra. The estimated skull length based on average width of cervical centra of PMO 214.135 and PMO 214.136 is shown in blue. Although the data points are few, the results demonstrate a general trend in pliosaurid cranial-to-neck proportions (increasing skull length correlates with increasing vertebral centrum width).

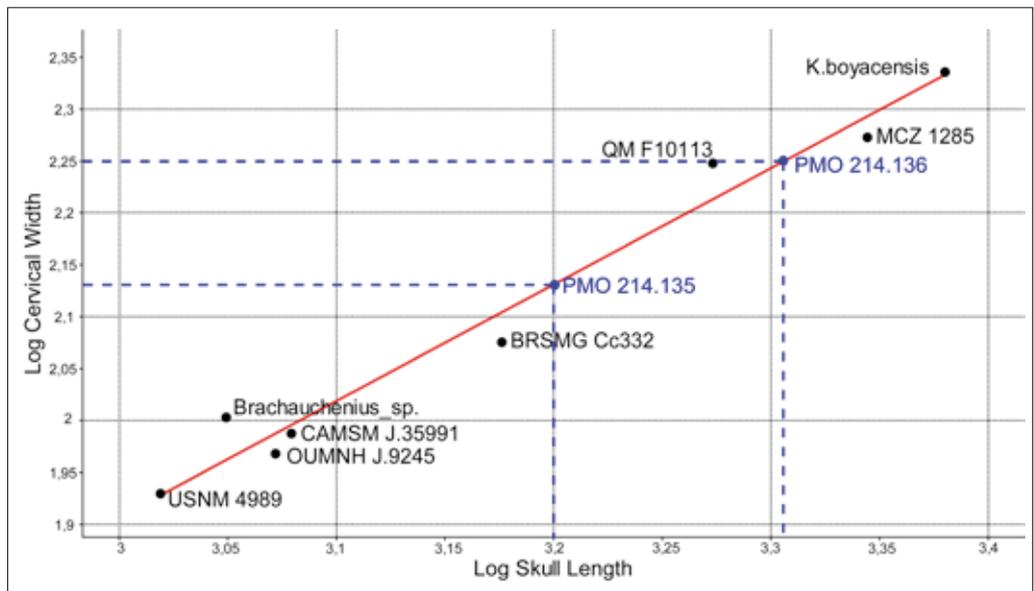
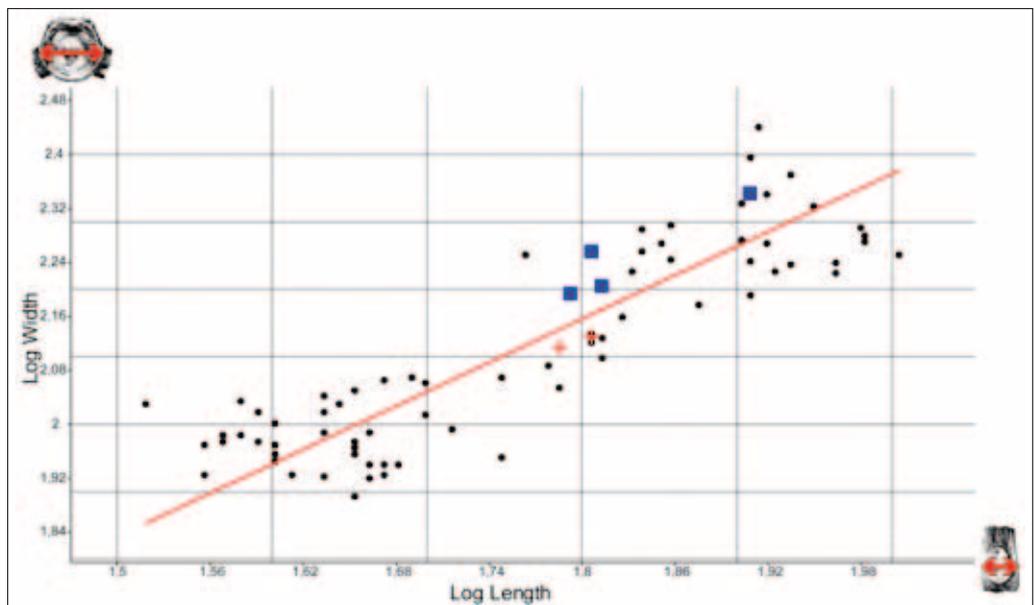


Figure 19. Linear regression plot showing the relationship ( $r=0,88$ ,  $R^2 = 0,77$ ,  $n=76$ ) between the length and width of cervical vertebral centra in PMO 214.135 (red crosses), PMO 214.136 (blue squares), and the pliosaurids CAMSM J.35991, OUMNH J.9245, BRSMG Cc332, PIN 304/1, CAMSM J.35990, Kronosaurus boyacensis, QM F10113, Brachauchenius sp., USNM 4989, and MCZ 1285 (black circles).



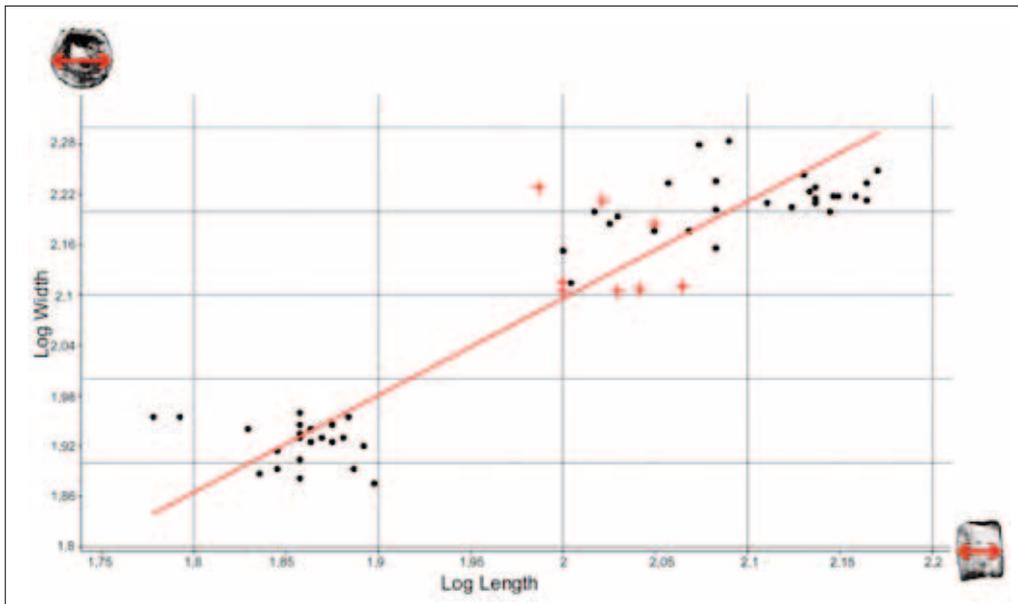


Figure 20. Linear regression plot showing the relationship ( $r=0,93$ ,  $R^2 = 0,86$ ,  $n=57$ ) between length and width between dorsal vertebral centra in PMO 214.135 (red crosses), and the pliosaurids CAMSM J.35990, QM F10113, USNM 4989, and MCZ 1285 (black circles). The gap in the middle of the plot is due to a lack of intermediate-sized samples, and not the result of grouping.

## Discussion

The remains of both pliosaurid skeletons, PMO 214.135 and PMO 214.316, are referred to the same new taxon, *Pliosaurus funkei*, on morphological, stratigraphic and ecological grounds. Although both specimens largely preserve different regions of the skeleton, they do share overlapping material in the cervical vertebrae, which are morphologically indistinguishable. Stratigraphically, both skeletons were not only recovered in the same Member of the Agardhfjellet Formation, but were also found at exactly the same stratigraphic horizon within the Slottsmøya member (see above; estimated margin of error, approximately 1 m). Given that both individuals were discovered within 2 km of one another (Figure 1), we argue that it is unlikely that two different species of large-bodied macropredators would have co-existed in the same ecosystem at exactly the same time. Pending discovery of new material that may alter our interpretation, we consider both specimens to be conspecific and use complementary data from both specimens for our comparative analysis below.

### Skeletal comparisons

The described material was compared to other species and specimens referable to *Pliosaurus* (*sensu* Knutsen, 2012). These consist of slightly older and coeval taxa from the Kimmeridge Clay Formation of England and France, and Volgian taxa from the Buinsk oil shales of the right bank of the Volga River in Russia. The body proportions were also compared to other older and younger pliosaurid taxa (see Table 1).

### Cranial skeleton

The upper jaw remains of PMO 214.136 are very fragmented and, apart from their large size, do not distinguish

themselves noticeably from other species of *Pliosaurus*. The mandibular remains of PMO 214.135 (Figure 4) have broken off anterior to the end of the mandibular symphysis, and the total number of functional alveoli in the mandibular symphysis cannot be determined directly. The interlocking of dentary and premaxillary teeth of *P. rossicus* (PIN 304/1) indicate that the anterior dentary teeth lay anterior to premaxillary teeth in lateral view (i.e., premaxillary tooth three lies between dentary tooth three and four). This interlocking configuration is visible in PMO 214.135 where the crowns from the opposite jaw lie between the alveoli (Figures 3 and 4). If the teeth of PMO 214.135 interlock in the same pattern as in *P. rossicus*, then the dentary preserves teeth three to six. The mandibles of *P. brachyspondylus* (CAMSM J.35991, BHN2R.370 and MNHN cat.24.1 (for the latter two see Bardet, 1993, fig. 2 a and b; Bardet *et al.* 1993), *P. macromerus* (NHMUK 39362) and *P. brachydeirus* (OUMNH J.10454) display a consistent pattern in alveolar sizes from the first to the seventh tooth; the first tooth is smaller than the following five teeth; the second tooth is slightly smaller than the following four; teeth three, four, five and six are the largest and the seventh tooth is noticeably smaller than the previous four. All mandibular teeth preserved in PMO 214.135 are nearly equal in size, also suggesting they are from the interval between tooth three and six.

In the lower jaw of *P. macromerus* (NHMUK 39362), the gap between the fifth and sixth tooth sockets is about half the length of those separating alveolus four from five, and three from four. It is possible that this reduction in the spacing is to accommodate the two large mandibular teeth within the rostral constriction of the upper jaw. This feature is also visible in between the last two teeth in the right dentary of PMO 214.135, further supporting the interpretation that the posterior-most tooth is number six in the lower jaw. The same variability in

Figure 21. Boxplot of humeral length (HL) divided by the width of the cervical (open boxes) and dorsal (cross-hatched boxes) vertebral centra. The two outliers in OUNHM J.9245 include one pectoral and one dorsal centrum that are larger than the remaining centra of the same specimen. Only one cervical centrum was available for this analysis in CAMSM J. 35991. The humerus of CAMSM J.35990 is incomplete, and its length is therefore an estimate (Tarlo, 1959b).

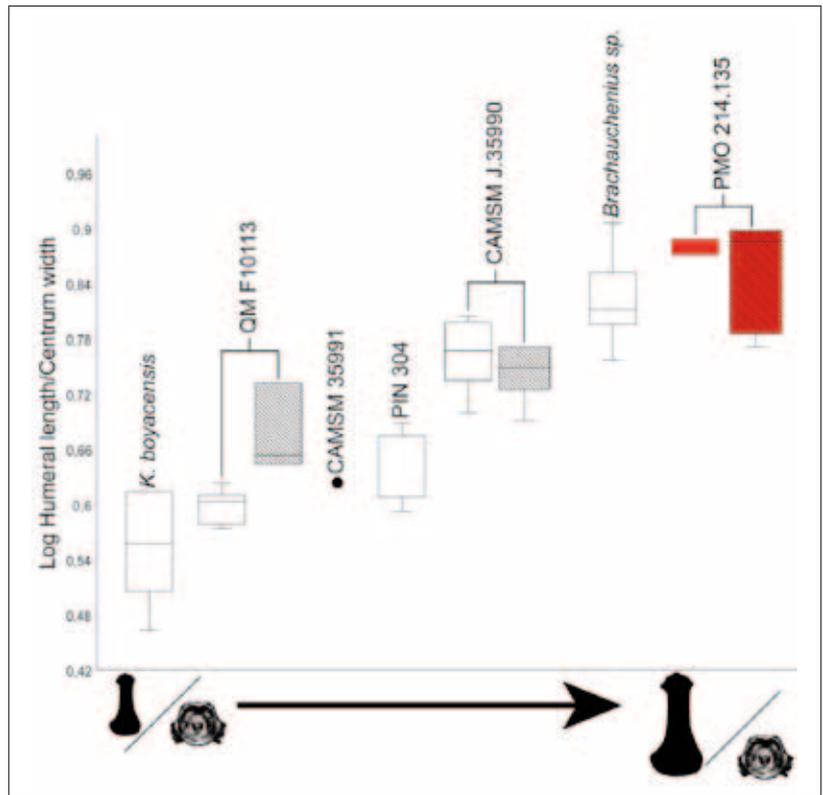
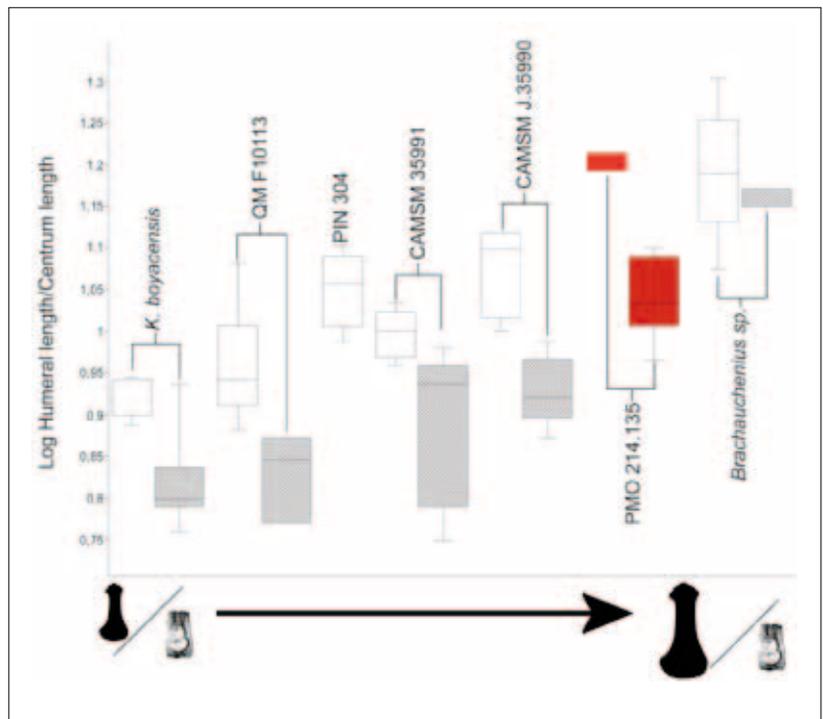


Figure 22. Boxplot of humeral length (HL) divided by length of cervical (open boxes) and dorsal (cross-hatched boxes) vertebral centra. The humerus of CAMSM J.35990 is incomplete, and its length is therefore an estimate (Tarlo, 1959b).



inter-alveolar space can also be observed in right lateral view of the skull of *P. rossicus* (PIN 304/1) where the space between the fifth and sixth mandibular teeth fits a relatively smaller premaxillary tooth than that between the more anterior teeth. Thus, the mandibular symphysis of PMO 214.135 must have contained at least six pairs of teeth. Six teeth are present in the mandibular symphyses of *P. rossicus* and *P. macromerus*. However, we cannot

discount the possibility that *P. funkei* (PMO 214.135) possessed more symphyseal teeth and were more equal to *P. brachydeirus* (8-9 or more teeth) or *P. brachyspondylus* (8-9 teeth) in this respect.

In ventral aspect, the mandibular symphysis of PMO 214.135 (Figure 4A) is similar to that of *P. macromerus* (NHMUK 39362) in that the splenial contributes to the

symphysis and extends anteriorly to between the fourth and fifth alveolus. It is not possible to determine the condition in *P. brachydeirus* (OUMNH J.9245), BRSMG Cc332, or in *P. brachyspondylus* (CAMSM J.35991) due to incompleteness and access (CAMSM J. 35991 is attached to a mould covering its ventral side). The anterior extent of the splenial can be seen in CAMSM J.46380 (*Pliosaurus* sp.), where it extends to the fifth tooth.

Material from *P. rossicus* (PIN 304/1) and *P. macromerus* (NHMUK 39362) show that the largest (in diameter) of the posterior teeth in the mandibular symphysis in these species is aligned with the lateral pinching of the upper jaw (in dorsal view), and to the diastema at the maxilla-premaxilla suture. The sixth mandibular tooth of *P. funkei* (PMO 214.135) lies just posterior to the fifth tooth in the premaxilla, suggesting that the pinching of the upper jaw lies just posterior to this point. Based on the shape of the break in the preserved upper jaw fragment of PMO 214.135 (Figure 3) it is likely that its premaxilla contained five teeth. This is the same number as in *P. macromerus* (NHMUK 39362) and *P. rossicus* (PIN 304/1). In *P. brachydeirus* (OUMNH J.9245) four premaxillary alveolar pairs are preserved, but the missing anterior part is assumed to have accommodated one or two more pairs (Knutsen, 2012). Five pairs of alveoli are preserved in the premaxillae of BRSMG Cc332, but here too the anterior-most part is missing and likely accommodated one more pair of teeth, giving BRSMG Cc332 a premaxillary tooth-count of six or more (Knutsen, 2012). There is an anteroposteriorly extended diastema (compared to the other premaxillary teeth) between the fourth and fifth tooth in the premaxilla of PMO 214.135. A similar situation is present in *P. macromerus* (NHMUK 39362), albeit less prominent, as described by Owen (1869). The diastema of *P. macromerus*, however, is smaller than the one separating the premaxillary and maxillary tooth rows (between teeth five and six).

Knutsen (2012) describes four distinct types of retroarticular process morphologies for *Pliosaurus*. In this regard, PMO 214.136 differs from those seen in *P. brachyspondylus* (CAMSM J. 35991: Type II, evenly tall in lateral view, and squared off posteriorly), *P. brachydeirus* (OUMNH J.9245: Type III, tapering to a point in lateral view; less than half the width of the glenoid fossa in dorsal view), and *Pliosaurus* sp. (BRSMG Cc332: Type IV, dorsoventrally flat posteriorly; less than half the width of the glenoid fossa) in both morphology and size. The only *Pliosaurus* material studied that is similar to PMO 214.136 in absolute size are those of OUMNH J.50376 and J.50377, which are referable to *P. macromerus* (Knutsen, 2012). However, these are referable to the Type III retroarticular.

#### Dentition

Only one tooth in PMO 214.135 clearly exhibits the trihedral shape characteristic of *Pliosaurus*. The remaining tooth crowns have either been broken off or are too

deformed. The tooth displaying the trihedral shape also shows the characteristically ridged lingual surface and smooth labial surface described for other species of *Pliosaurus* (e.g., Owen, 1861; Tarlo, 1959a, 1959b, 1960).

#### Postcranial skeleton

The cervical vertebral centra of both PMO specimens exhibit the relative anteroposterior shortness and the double-headed rib facets seen in other Middle to Upper Jurassic pliosaurids. The ventral rugosity and lack of a ventral keel in the cervical centra of both Svalbard specimens is similar to that of *P. brachyspondylus* and *P. rossicus*, but differ from the smooth, keeled ventral surface seen in *P. brachydeirus*. Dorsal and pectoral vertebral centra have the same general morphology seen in other pliosaurs.

The coracoid, along with being the largest one described from any specimen of *Pliosaurus*, has a relatively longer anteromedial process than that described for *P. brachyspondylus* (Tarlo, 1957) and *P. rossicus* (Novozhilov, 1964). However, this variation might be related to ontogeny, especially for *P. rossicus* (PIN 304/1), which was described as being an immature individual by Storrs *et al.* (2000).

The humerus of PMO 214.135 is, like the coracoid, among the largest known from any pliosaur. The humerus of PMO 214.135 can be distinguished from that of *P. brachyspondylus* (CAMSM J.35991) in having a wide, anteroposteriorly elongate capitulum that is strongly offset from the humeral shaft by a marked constriction, compared to that of the latter, whose width is equal to the width of the humeral shaft. *P. brachyspondylus* also exhibits an asymmetrically-shaped outline of the humerus, with the postaxial margin being more strongly curved posteriorly than the preaxial margin. In contrast, the humeral shaft of PMO 214.135 has nearly symmetrically-shaped pre- and postaxial margins. The humerus of PMO 214.135 is similar in shape to that of CAMSM J.35990 (*Pliosaurus* sp.), although the tuberosity in the latter lies directly dorsal to the capitulum compared to the posteriorly shifted tuberosity in PMO 214.135. The epipodials of PMO 214.135 are proximodistally shorter than anteroposteriorly wide, as in *P. brachyspondylus* (CAMSM J.35991), *P. brachydeirus* (OUMNH J.9245) and CAMSM J.35990 (*Pliosaurus* sp.), but there is no sign of an interosseal gap (epipodial foramen) as in the latter two.

#### Body proportions and size

Based on the preserved parts of both PMO specimens, we attempt to estimate the overall body length, the skull length and relative paddle lengths of the Svalbard specimens and compare these data with those of other pliosaurid taxa. These three points are discussed separately below. However, body proportions of an animal may vary through ontogeny, and/or due to differences in ecology

and ancestry, which makes it difficult to use isolated or fragmented skeletal material to estimate size and compare body proportions. The values provided here are therefore considered first approximations, given the available data.

#### Skull size

A relationship between the diameter of the occipital condyle and the skull length exists in pliosaurids (Figure 17). Thus, a size relationship between skull length and width of the cervical vertebral centra (Figure 18) is predicted as the skull connects to the vertebral column via the occipital condyle. Using the relationships between cervical vertebral centra and occipital condyle dimensions (Figures 17 and 18), we estimate a skull length of 2.0 – 2.5 m for PMO 214.136, similar to that of *Kronosaurus queenslandicus* (QM F10113, MCZ1285) and *K. boyacensis*. This is corroborated by the similarity in size between the preserved portion of the posterior portion of the mandible of PMO 214.136 and the equivalent portion in *K. boyacensis* (data derived from Hampe, 1992, fig. 3). The cervical centra dimensions of PMO 214.135 predict a skull approximately 1.6 – 2.0 m in length, similar in size to the skull of NHMUK 39362 (*Pliosaurus macromerus*, but not plotted in Figure 18 as this specimen preserves only the cranium). These size estimates are also consistent with comparisons of the anterior parts of the rostrum preserved in both PMO 214.135 and NHMUK 39362. However, we emphasize that these approximations of skull length are based on the assumption that the overall skull shape and proportions are reasonably consistent among different species of *Pliosaurus*, and we urge caution in drawing far-reaching conclusions of pliosaur ecology and behaviour using estimates derived from postcranial remains.

In *Kronosaurus boyacensis*, the complete front limb is slightly shorter than the skull and the propodial represents approximately one half the total limb length (Hampe, 1992, fig.4). The nearly complete forelimb of PMO 214.135 is approximately 3.0 m long. Following the same relationship as that in *K. boyacensis*, this results in a skull length much greater than 1.6 – 2.0 m estimated above, which suggests that there is no consistent relationship between absolute skull length and humeral length that can be used across pliosaurid taxa. Additionally, the propodial of PMO 214.135 comprises only one third of the total length of the limb, in contrast to half in *K. boyacensis*, a character previously used in systematic studies (e.g., O'Keefe, 2001; Druckenmiller & Russell, 2008; Ketchum & Benson, 2010).

#### Limb-to-body-length proportions

McHenry (2009) estimated total body length and relative lengths of body segments for several pliosaurid taxa, based on cranial, axial and limb dimensions. Snout-to-hip length (used by McHenry, 2009) will inevitably be dependent on skull length and on the number and length of the presacral vertebrae. Even a small change

in average length of the individual vertebrae will potentially have a large consequence on the overall length of the animal. Among pliosaurids, a clear correlation exists between centrum width and length (Figures 19 and 20), indicating that the vertebral centra that are longest in anteroposterior length are also the widest mediolaterally. The largest centra also correspond to those specimens that McHenry (2009) estimated as having the longest snout-to-hip length. There is some unresolved variation in the plots (Figures 19 and 20). A lot of this variation likely comes from interspecific differences in relative centrum length to width and height, a feature for cryptoclidian plesiosaurs defined by Brown (1981) as the vertebral length index (VLI) which is often used in plesiosaur taxonomy (Brown, 1981; O'Keefe, 2001; Druckenmiller & Russell, 2008; Ketchum & Benson, 2010, but see Knutsen *et al.* 2012). McHenry (2009) also observed a positive relationship between snout-to-hip length and propodial length in brachaucheniid pliosaurs (*Brachauchenius* and *Kronosaurus*), although his data was only derived from three specimens. Therefore, it is reasoned that a positive correlation exists between propodial length and vertebral centrum dimensions, as body length is dependent on the latter.

The proportional humeral lengths vs. centrum width and length (seen in Figures 21 and 22) indicate the presence of a wide range of relative paddle sizes within pliosaurids. Some of this variation may be due to ontogeny, while parts reflect interspecific differences. In either case, the proportional differences in humeral lengths are likely indicative of a variety of swimming modes and lifestyles among different taxa and possibly reflect ontogenetic changes. This suggests that a strict relationship between total body length and propodial size does not exist between species, and probably varies intraspecifically as well. Therefore, propodial size is not a reliable means by which to estimate overall body size.

Another interesting outcome of this analysis (Figure 21) is that the specimen of *Kronosaurus queenslandicus* (QMF 10113) has cervical vertebral centra that are larger in mediolateral width than the dorsal centra. This is the reverse of what is observed in all referred specimens of *Pliosaurus* in the present analysis. The functional significance of this relationship is unclear and beyond the scope of this study.

The presence of a large range of dorsal centrum lengths is also noteworthy as this indicates a change in relative vertebral dimensions within the dorsal series (Figure 22). This has been studied in some plesiosauroid groups (e.g., Brown, 1981; Knutsen *et al.*, 2012), in which the dorsal centra increase slowly in relative length posteriorly to the sacrum, compared to the changes in relative sizes observed within the cervical series. The large range of sizes observable in the dorsal centra of pliosaurids indicates a greater degree of variability in relative sizes than in plesiosauroids, although this needs to be studied further.

The specimen of *Pliosaurus* most similar to PMO 214.135 (in Figures 21 and 22) is CAMSM J. 35990 (*Pliosaurus* sp.). CAMSM J.35990, which is subequal in overall size to PMO 214.135, exhibits a much smaller humerus than PMO 214.135 (approximately 25 cm shorter), despite their both being adult individuals (Tarlo, 1959b; pers. obs. by EMK). The contemporary Russian specimen (PIN 304/1) has a proportionally shorter propodial than the Svalbard specimen. PIN 426 has a slightly longer propodial than *P. rossicus*. However, this can be attributed to using dimensions of the femur for the former, rather than the humerus.

In describing a juvenile specimen of *Leptocleidus*, Kear (2007) noted that the individual had proportionally larger paddles compared to body length than adult members of the same taxon. This has also been shown to be common in other plesiosaurs (O'Keefe & Carrano, 2005). PMO 214.135 and PMO 214.136 are both interpreted as adult specimens (see above), whereas *Pliosaurus rossicus* (PIN 304/1) has been considered to be a juvenile by Halstead (1971) and Storrs *et al.* (2000). Based on available material, it cannot be conclusively ruled out that *P. funkei* and *P. rossicus* represent different ontogenetic stages of the same species. However, both species have very different relative humeral lengths (Figures 21 and 22) indicating an allometric relationship opposite to that described for other plesiosaurians. Until more material becomes available for both species, we propose using the new taxon *P. funkei* for reception of the new Svalbard material.

### Body length

In the plots in Figures 19 and 20, it can be seen that both PMO specimens have vertebral centra in the same size range as the largest specimens in the analyses of McHenry (2009). Based on this, PMO 214.135 and PMO 214.136 probably had a total body length of approximately 10 - 13 m, similar to what McHenry (2009) calculated for the largest pliosaurids. It should be noted that a complete vertebral count is unknown for either animal, which could greatly affect this estimate. However, dimensions of other elements (cranium, coracoid) are consistent with that expected for an individual with this range of body length.

## Conclusions

Two new specimens of a large pliosaurid are documented to co-occur within a narrow stratigraphic interval of the Slottsmøya Member of the Agardhfjellet Formation in the Arctic archipelago of Svalbard. Both specimens are morphologically indistinguishable and referable to the Late Jurassic taxon *Pliosaurus* on the basis of tooth and cervical vertebral morphology. A unique combination of characters indicates that the material represents a new taxon, *P. funkei* sp. nov. *P. funkei* has six or more pairs of teeth in the mandibular symphysis, five or more premaxillary tooth pairs, and cervical centra with a rugose ventral surface lacking a keel. *P. funkei* is more similar to

*P. macromerus* (NHMUK 39362) and *Pliosaurus rossicus* (PIN 304/1 and PIN 2440/1) than to any other member of the genus in anterior cranial morphology. Morphometric analyses indicate that *P. funkei* had a very different limb proportions compared to most other large pliosaurids (*Kronosaurus queenslandicus*, *K. boyacensis*, *P. brachyspondylus*, CAMSM. 35990, *P. rossicus*). Retroarticular morphology and differences in stratigraphic distribution also suggest that *P. funkei* is not conspecific with either *P. brachyspondylus* or *P. macromerus*. Relative humeral lengths indicate that the new Svalbard taxon is different than the poorly characterised *P. rossicus*.

Estimates of skull length are approximately 1.6 - 2.0 m long in PMO 214.135 and 2.0 - 2.5 m in PMO 214.136. Based on comparisons of vertebral dimensions of the PMO specimens with those in the data set of McHenry (2009), a total body length of 10 - 13 m is estimated for both animals, although PMO 214.136 is notably larger than PMO 214.135, making *P. funkei* one of the largest pliosaurs described so far.

Analyses of the body proportions of pliosaurids suggest that there is no relationship between limb size and skull or body length at the interspecific level. There is also previously unexplored interspecific variability in the size relationship between cervical and dorsal vertebral centra, which probably had functional implications.

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### Supplementary material:

The following supplementary material can be found with the online version of this at <http://www.geologi.no/njg/>  
 Supplementary material 1 – Centrum lengths for selected pliosaurid taxa (in mm).  
 Supplementary material 2 - Centrum widths for selected pliosaurid taxa (in mm).  
 Supplementary material 3 – Ratio of humeral length vs. centrum width in selected pliosaurid taxa.  
 Supplementary material 4 - Ratio of humeral length vs. centrum length in selected pliosaurid taxa.

## References

- Bardet, N. 1993: Pliosaurus and plesiosaurs from the Middle Jurassic (Callovian) of Normandy. *Revue de Paléobiologie* 7, 1-7.
- Bardet, N., Mazin, J.M. & Martin, M. 1993: Une mandibule de *Pliosaurus brachyspondylus* (Reptilia, Sauropterygia) dans le Kimméridgien du Boulonnais (France). *Neues Jahrbuch Für Geologie und Paläontologie Monatshefte* 1993, 385-392.
- Birkemajer, K. 1980: Jurassic-Lower Cretaceous succession at Agardhbukta, east Spitsbergen. *Studia Geologica Polonica* 66, 35-52.
- Bjærke, T. 1978: Mesozoic palynology of Svalbard III. Dinoflagellates from the Rurikfjellet Member, Janusfjellet Formation (Lower Cretaceous) of Spitsbergen. *Palynologia num extraordin 1*, 69-93.
- Blainville, H.D.De. 1835: Description de quelques espèces de reptiles de la Californie, précédé de l'analyse d'un système general d'Erpetologie et d'Amphibiologie. *Nouvelles Annales du Museum National d'Histoire Naturelle, Paris* 4, 233-296.
- Brown, D.S. 1981: The English Upper Jurassic Plesiosauroida (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum (Natural History), Geology* 35, 253-347.
- Buchy, M.C. 2003: First occurrence of a gigantic pliosaurid plesiosaur in the Late Jurassic of Mexico. *Bulletin de la Société Géologique de France* 174, 271-278.
- Buchy, M.C. 2007: Mesozoic marine reptiles from north-east Mexico: description, systematics, assemblages, and palaeobiogeography. Ph.D. Thesis, Universität Karlsruhe, 98 pp.
- Carpenter, K. 1996: A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 201, 259-287.
- Collignon, M. & Hammer, Ø. 2012: Lithostratigraphy and sedimentology of the Slottsmøya Member at Janusfjellet, Spitsbergen: evidence for a condensed section. *Norwegian Journal of Geology* 92, 89-101.
- Dallmann, W.K., Major, H., Haremo, P., Andresen, A., Kjærnet, T. & Nøttvedt, A. 2001: Geological map of Svalbard 1:100,000, sheet C9G Adventdalen. With explanatory text. *Norsk Polarinstitutt Temakart* 31/32, 4-55.
- Druckenmiller, P.S. & Russell, A. P. 2008: A phylogeny of Plesiosauria (Sauropterygia) and its bearing on the systematic status of *Leptocleidus* Andrews, 1922. *Zootaxa* 1863, 1-120.
- Dypvik, H., Eikeland, T.A., Backer-Owe, K., Andersen, A., Haremo, P., Bjærke, T., Johansen, H. & Elverhøi, A. 1991a: The Janusfjellet Subgroup (Bathonian to Hauterivian) on central Spitsbergen: a revised lithostratigraphy. *Polar Research* 9, 21-43.
- Dypvik, H., Nagy, J., Eikeland, T.A., Backer-Owe, K. and Johansen, H. 1991b: Depositional conditions of the Bathonian to Hauterivian Janusfjellet Subgroup, Spitsbergen. *Sedimentary Geology* 72, 55-78.
- Dypvik, H., Håkansson, E. and Heinberg, C. 2002: Jurassic and Cretaceous palaeogeography and stratigraphic comparisons in the North Greenland-Svalbard region. *Polar Research* 21, 91-108.
- Ershova, E.S. 1983: Explanatory notes for the biostratigraphical scheme of the Jurassic and Lower Cretaceous deposits of Spitsbergen archipelago. *Leningrad PGO Sevmorgeologia*.
- Gasparini, Z. 1997: A new pliosaur from the Bajocian of the Neuquen basin, Argentina. *Palaeontology* 40, 135-147.
- Gradstein, F.M., Ogg, J., Schmitz, M.A. & Ogg, G. In press: *A Geologic Time Scale 2012*. Elsevier Publishing Company.
- Halstead, L.B. 1971: *Liopleurodon rossicus* (Novozhilov) - a pliosaur from the Lower Volgian of the Moscow basin. *Palaeontology* 14, 566-570.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. 2001: PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4, 9.
- Hammer, Ø., Nakrem, H.A., Little, C.T.S., Hryniewicz, K., Sandy, M.R., Hurum, J.H., Druckenmiller, P., Knutsen, E.M. & Høyberget, M. 2011: Hydrocarbon seeps from close to the Jurassic-Cretaceous boundary, Svalbard. *Palaeogeography, Palaeoclimatology, Palaeoecology* 306, 15-26.
- Hampe, O. 1992: Ein großwüchsiger Pliosauride (Reptilia: Plesiosauria) aus der Unterkreide (obers Aptium) von Kolumbien. *Courier Forschungs-Institut Senckenberg* 145, 1-32.
- Kear, B.P. 2007: A juvenile pliosauroid plesiosaur (Reptilia - Sauropterygia) from the Lower Cretaceous of South Australia. *Journal of Paleontology* 81, 154-162.
- Ketchum, H.F. & Benson, R.B.J. 2010: Global interrelationships of Plesiosauria (Reptilia, Sauropterygia) and the pivotal role of taxon sampling in determining the outcome of phylogenetic analyses. *Biological Reviews* 2009, 1-32.
- Ketchum, H.F. & Benson, R.B.J. 2011: The cranial anatomy and taxonomy of *Peloneustes philarchus* (Sauropterygia, Pliosauridae) from the Peterborough Member (Callovian, Middle Jurassic) of the United Kingdom. *Palaeontology* 54, 639-665.
- Knutsen, E.M. 2012: A taxonomic revision of the genus *Pliosaurus* (Owen, 1841a) Owen, 1841b. *Norwegian Journal of Geology* 92, 259-276.
- Knutsen, E.M., Druckenmiller, P.S. & Hurum, J.H. 2012: A new plesiosaurian taxon (Reptilia - Sauropterygia) from the Agardhfjellet Formation (Middle Volgian) of central Spitsbergen, Norway. *Norwegian Journal of Geology* 92, 213-234.
- Liebe, L. & Hurum, J.H. 2012: Gross internal structure and microstructure of plesiosaur limb bones from the Late Jurassic, central Spitsbergen. *Norwegian Journal of Geology* 92, 285-309.
- Lydekker, R. 1889: On the remains and affinities of five genera of Mesozoic reptiles. *Quarterly Journal of the Geological Society* 45, 41-59.
- Løfaldli, M. & Thusu, B. 1976: Microfossils from the Janusfjellet Subgroup (Jurassic-Lower Cretaceous) at Agardhfjellet and Keilhausfjellet, Spitsbergen. A preliminary report. *Norsk Polarinstitutt Årbok*, 125-136.
- McHenry, C.R. 2009: Devourer of Gods: the palaeoecology of the Cretaceous pliosaur *Kronosaurus queenslandicus*, Unpublished Ph.D. thesis. University of Newcastle, Australia, 642 pp.
- Nagy, J. & Basov, V.A. 1998: Revised foraminiferal taxa and biostratigraphy of Bathonian to Ryazanian deposits in Spitsbergen. *Micro-paleontology* 44, 217-255.
- Nagy, J., Løfaldli, M. & Bäckström, S.A. 1988: Aspects of foraminiferal distribution and depositional conditions in Middle Jurassic to Early Cretaceous shales in eastern Spitsbergen. In Rogl, F. and Gradstein, F.M. (eds.): *Second Workshop on Agglutinated Foraminifera*, 30, 287-300. *Abhandlungen der Geologischen Bundesanstalt, Vienna*.
- Noè, L.F., Smith, D.T.J. & Walton, D.I. 2004: A new species of Kimmeridgian pliosaur (Reptilia; Sauropterygia) and its bearings on the nomenclature of *Liopleurodon macromeris*. *Proceedings of the Geologists' Association* 115, 13-24.
- Novozhilov, N. 1948: Two new pliosaurs from the Lower Volga beds Povolzhe (right bank of Volga) [In Russian]. *Doklady Akademii Nauk SSSR* 60, 115-118.
- Novozhilov, N. 1964: Order of Sauropterygia. *Osnovy Paleontologii* 12, 309-332.
- Ogg, J. 2004: The Jurassic Period. In Gradstein, F.M., Ogg, J. and Smith, A. (eds.): *A geologic time scale 2004*, 307-343. Oxford University Press.
- O'Keefe, F.R. 2001: A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). *Acta Zoologica Fennica* 213, 1-63.
- O'Keefe, F.R. & Carrano, M. T. 2005: Correlated trends in the evolution of the plesiosaur locomotor system. *Paleobiology* 31, 656-675.
- Owen, R. 1841a: *Odontography*. Edited by Owen, R. Part 2. Hippolyte Bailliere, foreign booksellers to the Royal College of Surgeons, London, UK, 282-284 pp.
- Owen, R. 1841b: Report on British fossil reptiles Part 2. *Report of the Eleventh Meeting for the British Association for the Advancement of Science*, 60-204.

- Owen, R. 1860: On the orders of fossil and recent Reptilia, and their distribution through time. *Report of the British Association for the Advancement of Science* 29, 153-166.
- Owen, R. 1861: Monograph on the British fossil reptilia from the Kimmeridge Clay. *The Palaeontographical Society, London Part 1*, 1-16.
- Owen, R. 1863: Monograph on the British fossil reptilia from the Kimmeridge Clay. *The Palaeontographical Society, London Part 2*, 1-28.
- Owen, R. 1869: Monograph on the British fossil reptilia from the Kimmeridge Clay. *The Palaeontographical Society, London Part 3*, 1-20.
- Parker, J.R. 1976: The Jurassic and Cretaceous sequence in Spitsbergen. *Geological Magazine* 104, 487-505.
- Phillips, J. 1871: *Geology of Oxford and the Valley of the Thames*. The Clarendon Press, Oxford, UK, 523 pp.
- Seeley, H.G. 1874: Note on some of the generic modifications of the plesiosaurian pectoral arch. *Quarterly Journal of the Geological Society* 30, 436-449.
- Storrs, G. W., Arkhangel'skii, M.S. & Efimov, V. 2000: Mesozoic marine reptiles of Russia and other former Soviet republics; pp. 187-210 in Benton, M. J., Shishkin, M.A., Unwin, D.M., Kurochkin, E.N. (ed.), *The age of dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, UK.
- Tarlo, L.B. 1957: The scapula of *Pliosaurus macromerus* Philips. *Palaeontology* 1, 193-199.
- Tarlo, L.B. 1959a: *Pliosaurus brachyspondylus* (Owen) from the Kimmeridge Clay. *Palaeontology* 1, 283-291.
- Tarlo, L.B. 1959b: *Stretosaurus* gen. nov., a giant pliosaur from the Kimmeridge Clay. *Palaeontology* 2, 39-55.
- Tarlo, L.B. 1960: A review of Upper Jurassic Pliosaurus. *Bulletin of the British Museum (Natural History), Geology* 4, 145-189.
- Taylor, M.A. & Cruickshank, A.R.I. 1993: Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 341, 399-418.
- Welles, S.P. 1943: Elasmosaurid plesiosaurs, with description of new material from California and Colorado. *University of California, Memoirs* 13, 125-254.
- Wierzbowski, A., Hryniewicz, K., Hammer, Ø., Nakrem, H.A. & Crispin, T.S.L. 2011: Ammonites from hydrocarbon seep carbonate bodies from the uppermost Jurassic–lowermost Cretaceous of Spitsbergen, Svalbard, and their biostratigraphic importance. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 262/3, 267-288.
- Wiffen, J., Buffrenil, V., Ricques, A.D. & Mazin, J. 1995: Ontogenetic evolution of bone structure in late Cretaceous Plesiosauria from New Zealand. *Geobios* 7, 625-636.
- Wiman, C. 1914: Ein Plesiosaurierwirbel aus dem jüngeren Mesozoicum Spitzbergens. A *Pliosaurus* vertebra from the Upper Mesozoic of Spitsbergen. *Bulletin - Uppsala Universiteter, Mineralogisk-geologiska Institut* 12, 201-204.